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Laboratory of Functional Morphology

When does being smart pay off?

Ecology and evolution of cognition in lacertid lizards

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Gilles De Meester

Promotors:

Prof. dr. Raoul Van Damme

Prof. dr. Panayiotis Pafilis

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SUMMARY

Cognition, i.e. the neural processes involved in the acquisition, processing, retention and use of environmental information, is essential within the life of every individual animal. Yet, across the animal kingdom, biologists observe great variation in cognitive abilities, both among species, among populations and even among individuals within the same population. Such variation likely arises due to ecological conditions shifting the balance between the costs and benefits of cognition. However, which exact (socio-)ecological forces favour, or hamper, the evolution towards higher cognitive abilities remains speculative.

Both the spatial complexity and the temporal variability of the environment have been advanced as important selective pressures driving the evolution of cognition. While past research has often reported (relatively) larger brains in animals living in more complex or more dynamic environments, this trend is not universal. In addition, data on how environmental complexity and variability favour actual cognitive performance is currently lacking.

In this thesis, I have studied how habitat complexity and variability shape cognitive variation both among and within lacertid lizard species. The Lacertidae are a speciose family of lizards, whose members can be found along a broad gradient of ecological conditions across Eurasia and Africa. This ecological diversity, both among and within species, makes them ideal to answer broader questions regarding the role of ecology in cognitive evolution.

The first part of my thesis investigated cognitive variation at the intraspecific level, by looking at the evolution of relative brain size across Squamata (lizards + snakes), and by comparing the performance of thirteen species of Lacertidae on five cognitive tasks. In contrast to expectations based on the prevailing literature, relative brain size was not associated with habitat complexity in Squamata, and social species had relatively smaller brains than solitary ones. Lacertid species differed considerably in their performance in all cognitive tests, but this variation was unrelated to differences in species' ecology and life-history. However, I did observe some trends implying that species from more seasonal habitats displayed lower behavioural flexibility.

The second part of my PhD looked at the link between environment and cognitive variation among populations of the Aegean wall lizard (*Podarcis erhardii*). Wall lizards from the island of Naxos experience stronger seasonal fluctuations in resource availability compared to mainland conspecifics. Insular lizards concomitantly performed better during a spatial learning assay than mainland lizards, but demonstrated lower cognitive flexibility during a reversal learning task. Secondly, lizards from structurally complex habitats were superior spatial learners compared to conspecifics from more simple environments, but no other differences in cognition or personality were observed. Interestingly, several aspects of lizard personality and cognition were associated with each other, but such behavioural covariance was often year – and habitat-dependent.

Finally, I investigated variation at the individual level. First, I tested the long-term repeatability and heritability of cognition and personality in Aegean wall lizards kept in semi-natural enclosures for one year. Spatial learning and exploration showed moderate long-term repeatability, but reversal learning less so and problem-solving not at all. My data did not provide convincing evidence that cognition or personality were heritable.

Next, I followed up the survival and reproductive success of individual lizards with known cognitive abilities and personality traits in large outdoor enclosures characterized by either complex or simple vegetation. This allowed me to specifically test whether cognition would be more advantageous in complex environments. I found that cognition was indeed associated with survival, albeit in unexpected ways. Spatial learning performance was negatively associated with female survival, but was unrelated to male mortality. Problem-solving ability was linked to survival in a non-linear way, with moderate solvers suffering higher mortality than non-solvers or consistent solvers. Lastly, cognition was unrelated to reproductive success. In contrast to my expectations, the link between any cognitive trait and fitness was independent of habitat complexity.

Overall, my thesis shows that the role of ecology on cognitive evolution is not straightforward, and the same ecological factor can have different effects depending on which cognitive trait is investigated and at which taxonomic level. One seemingly common trend, however, was the negative association between environmental variability and behavioural flexibility. My results also show that at least part of the observed cognitive variation across populations of *P. erhardii* is shaped by environmental rather than genetic effects. This thesis thus illustrates how an integrative approach, looking at both macro-evolutionary patterns and selection within species, can provide valuable new insights in the evolution of cognition

SAMENVATTING

Cognitie, d.i. de verwerving, de verwerking, de opslag en het gebruik van informatie uit de omgeving, speelt een essentiële rol binnen het leven van elk individueel dier. Desondanks zien biologen grote verschillen in cognitieve vaardigheden doorheen het dierenrijk, zowel tussen soorten, tussen populaties, als tussen individuen binnen dezelfde populatie. Dergelijke variatie ontstaat waarschijnlijk omdat lokale ecologische factoren de balans tussen de voor - en nadelen van cognitie veranderen. Maar exact wélke ecologische condities de evolutie naar hogere cognitieve vaardigheden bevoordelen, of juist afremmen, blijft alsnog een open vraag.

Twee factoren die vaak naar voren worden geschoven als mogelijke drijfveren achter cognitieve evolutie zijn de ruimtelijke complexiteit en temporele variatie in de omgeving. Vergelijkend onderzoek in het verleden heeft inderdaad aangetoond dat dieren uit meer complexe of dynamische omgevingen vaak relatief grotere hersenen hebben, zij het niet altijd. Data over hoe deze omgevingsfactoren effectief de cognitieve vaardigheden van een dier beïnvloeden is echter schaars.

Het doel van deze thesis was om te testen hoe habitat complexiteit en stabiliteit leiden tot cognitieve variatie tussen en binnen soorten lacertide hagedissen. De Lacertidae (Echte Hagedissen) zijn een soortenrijke groep, waarvan de leden verspreid voorkomen over een groot deel van Eurazië en Afrika, en in een breed scala van ecologische omstandigheden. Dit maakt hen een interessante groep om algemene vragen over de rol van ecologie in cognitieve evolutie te beantwoorden.

Het eerste deel van mijn thesis onderzocht cognitieve variatie tussen soorten. Eerst analyseerde ik de evolutie van relatieve hersengrootte binnen de Squamata (hagedissen + reptielen) en daarnaast vergeleek ik de prestatie van dertien soorten lacertide hagedissen op vijf cognitieve taken. In tegenstelling tot wat ik verwachtte o.b.v. de literatuur, bleek dat habitat complexiteit niet geassocieerd was met hersengrootte binnen de Squamata, en dat sociale soorten kleinere hersenen hadden dan solitaire soorten. Binnen de Lacertidae documenteerde ik aanzienlijke soort-verschillen in cognitieve vaardigheden, doch deze verschillen konden in het algemeen niet worden gelinkt aan de ecologie en levensgeschiedenis van de bestudeerde soorten. Eén uitzondering was echter dat soorten uit meer seizoenale omgevingen lagere gedragsflexibiliteit leken te vertonen.

In deel twee bestudeerde ik de link tussen omgeving en cognitie overheen verschillende populaties van de Egeïsche muurhagedis (*Podarcis erhardii*). Muurhagedissen afkomstig van Naxos, een eiland, leefden in een omgeving met meer seizoensgebonden variatie in de beschikbaarheid van hulpbronnen dan hun soortgenoten op het vasteland. Eiland-hagedissen scoorden inderdaad beter op een ruimtelijke leertaak, maar vertoonden lichtjes lagere flexibiliteit gedurende een ‘reversal learning’ taak. Daarnaast hadden hagedissen uit meer complexe omgevingen betere ruimtelijke leervermogens dan soortgenoten uit meer simpele, open gebieden, hoewel er geen verschil werd gevonden in andere cognitieve vaardigheden. Verschillende aspecten van cognitie en persoonlijkheid waren met elkaar gecorreleerd in deze soort, doch deze co-variatie was sterk afhankelijk van jaar en habitat.

Tot slot onderzocht ik cognitieve variatie op het individuele niveau. Eerst testte ik de lange-termijn herhaalbaarheid en heritabiliteit van cognitie en persoonlijkheid in

Egeïsche muurhagedissen die in grote openlucht terraria werden gehuisvest voor een jaar. Ruimtelijk leren en exploratie waren matig herhaalbaar, maar ‘reversal learning’ minder, en probleemoplossend vermogen helemaal niet. Mijn data leverde ook geen overtuigend bewijs voor heritabiliteit in de gemeten aspecten van cognitie en persoonlijkheid.

Vervolgens werden hagedissen met gekende cognitieve vaardigheden en persoonlijkheidskenmerken losgelaten in grote openlucht terraria en hun overleving en reproductief succes werden opgevolgd. De terraria bevatten simpele of complexe vegetatie, zodat ik expliciet kon testen of hogere cognitieve vaardigheden voornamelijk voordelig zouden zijn in meer complexe omgevingen. Cognitie was inderdaad geassocieerd met de overlevingskans van individuele hagedissen, doch niet in de verwachte richting. Vrouwelijke hagedissen met betere ruimtelijke leervermogens hadden een lagere overlevingskans, maar voor mannetjes was er geen verband tussen ruimtelijk leren en overleving. Probleem-oplossend vermogen had een niet-lineair effect op overleving, waarbij matige oplossers de hoogste mortaliteit kenden. Cognitieve prestaties waren niet gerelateerd aan voortplantingssucces. In tegenstelling tot de verwachtingen verschilde de link tussen cognitie en fitness niet tussen habitattypes.

Mijn thesis toont dus aan dat dezelfde ecologische krachten een verschillend effect kunnen hebben op cognitieve variatie, al naargelang het exacte cognitieve kenmerk en het taxonomisch niveau dat wordt bestudeerd. Een algemene trend leek echter de negatieve associatie tussen temporele variatie en gedragsflexibiliteit te zijn. Mijn resultaten suggereren ook dat de verschillen in cognitie tussen populaties van *P. erhardii* eerder te wijten zijn aan plasticiteit dan aan genetische verschillen. Met deze thesis hoop ik dus te illustreren hoe een geïntegreerde aanpak, waar bij zowel vergelijkend als op individueel niveau wordt gewerkt, kan leiden tot interessante nieuwe inzichten in de evolutie van cognitie.

CHAPTER 1

GENERAL INTRODUCTION

"There is no intelligence where there is no change and no need of change. Only those animals partake of intelligence that have to meet a huge variety of needs and dangers"

- H. G. Wells (The Time Machine)

All animals are capable of and need to learn to some degree. A lizard has to learn where it can safely hide within its territory to quickly escape when danger arises. A chickadee needs to memorize the location of its food caches or else it will fail to recover these during the upcoming winter. And a PhD student should remember its deadlines to obtain his degree. The ability to learn is highly conserved across the animal kingdom; even nematodes are capable of learning simple associations between a cue and a reward (Ginsburg & Jablonka, 2010; Morand-Ferron, 2017). Nevertheless, learning, and other cognitive abilities, have diverged immensely throughout the animal kingdom. Species, populations and even individuals within the same population can differ drastically in the extent of their cognitive capacities (Boogert et al., 2018; Henke-von der Malsburg et al., 2020). This variation has intrigued biologists for ages, especially since it may be the key to understanding how the human intellect arose (MacLean et al., 2012). Unfortunately, the evolution of cognition within the animal kingdom remains one of the most poorly understood topics within biology (Thornton et al., 2014).

The main goal of this thesis is to gain new insights regarding the role of ecology in cognitive evolution. Specifically, I will look at cognitive variation in lacertid lizards, both among and within species, and test which ecological forces may shape this variation and under which environmental conditions higher cognitive abilities are favoured.

WHAT IS COGNITION?

Cognition is defined as the mechanisms by which animals acquire, process, store and use environmental information (Dukas, 2004). These include perception, learning, memory, attention and decision-making (Dukas, 2004; Shettleworth, 2010; Cauchoix & Chaine, 2016). Perception is the conversion of external stimuli into mental representations. Learning is the ability to acquire new information, in the form of new associations or novel motor patterns. Memory involves storing these mental representations, either for a short time (short-term memory), a long time (long-term memory) or in relation to an ongoing task (working memory). Attention is the ability to focus on a particular subset of mental representations. Finally, decision-making is the process of determining an action by taking into account both the current environmental context and previously acquired mental representations (Dukas, 2004; Cauchoix & Chaine, 2016; Roth et al., 2021). Researchers have designed a wide variety of protocols to test aspects of animal cognition, more in particular the animals capacity to learn and to remember things (see Box 1).

BOX 1. MEASURING COGNITION

Measuring the cognitive abilities of an animal is challenging, both on a conceptual and methodological level, as discussed in great detail in Rowe and Healy (2014) and Thornton et al. (2014). As cognition cannot be directly observed, it has to be inferred from cautious behavioural experiments (Boogert et al., 2018). When designing such experiments, researchers should consider a) which exact cognitive processes they aim to measure, as this is not always evident (Rowe & Healy, 2014; Thornton et al., 2014) and b) which non-cognitive influences, such as the experience or motivation of animals, could affect task performance, and how to account for them (Rowe & Healy, 2014).

Inhibitory control is the ability to supress a predominant, but no longer relevant, behaviour in favour of a new action (Diamond, 2013). Inhibitory control, also referred to as response inhibition or self-control, is considered a key aspect of behavioural flexibility, i.e. the ability of an individual to adjust its behaviour to changing environmental conditions (Jones, 2005; Daniels et al., 2019; Szabo et al., 2020b). It is commonly measured using detour tasks, in which an animal needs to move over or around a (semi-)transparent barrier to reach a reward instead of directly going for it (MacLean et al., 2014; Kabadayi et al., 2018; Johnson-Ulrich & Holekamp, 2020; Szabo et al., 2020b; Figure 1a). Inhibitory control is sometimes also measured using a reversal learning task (see below) (Szabo & Whiting, 2020).

BOX 1. (continued)

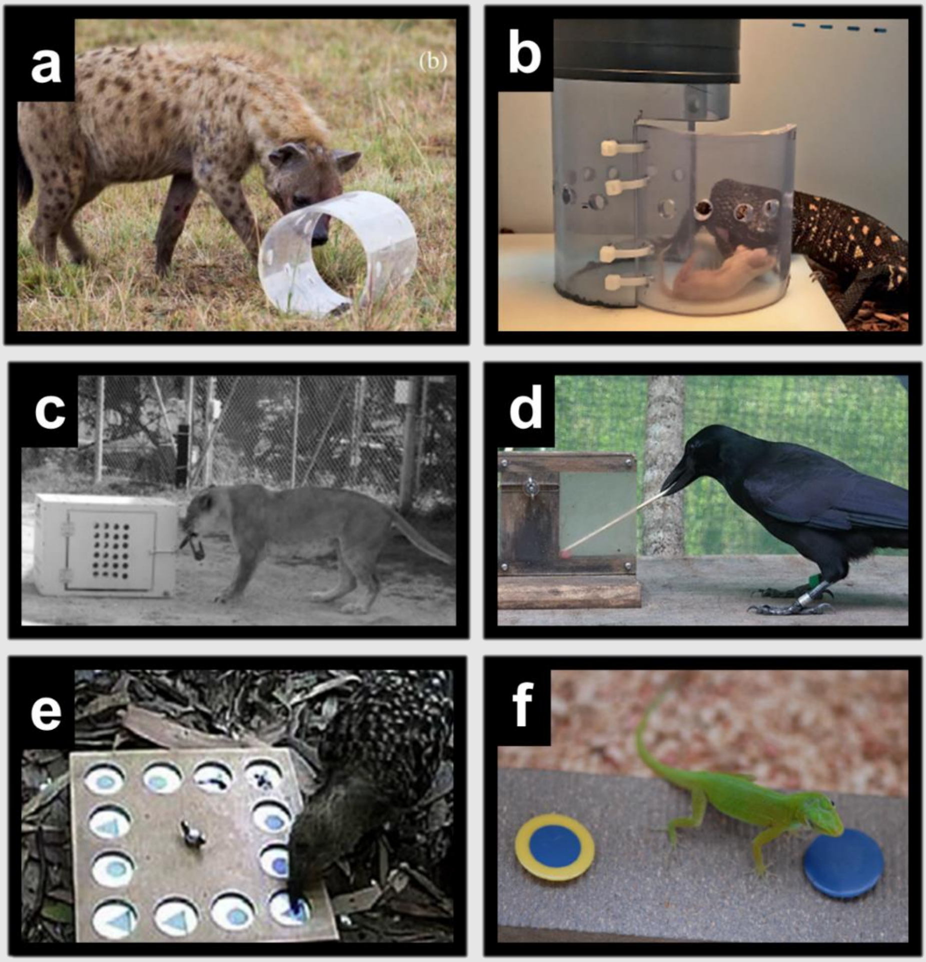

Figure 1. Measuring a) inhibitory control in spotted hyenas (*Crocuta crocuta*) using the transparent cylinder (detour) task (Johnson-Ulrich & Holekamp, 2020), b-d) problem-solving with a variety of puzzles boxes and extractive foraging tasks in a Guatemalan beaded lizard (*Heloderma charlesbogerti* - b) (Cooper et al., 2019), a lion (*Panthera leo* - c) (Borrego & Gaines, 2016) and a New Caledonian crow (*Corvus moneduloides* - d) (McCoy et al., 2019). e) a spotted bowerbird (*Ptilonorhynchus maculatus*) during a shape discrimination task, where the wells with triangles hide food (Isden et al., 2013), f) an emerald anole (*Anolis evermanni*) in a colour/pattern discrimination task (Leal & Powell, 2012).

BOX 1. (continued)

Problem-solving is the capacity to solve a novel problem, either by inventing a new behaviour or applying a familiar one in a new context, and is thus believed to reflect an animal's innovative potential (Griffin & Guez, 2014; Tebbich & Teschke, 2014). Typical problem-solving assays require the animal to remove an obstacle, or manipulate a tool, in order to reach a reward (Overington et al., 2011; Benson-Amram et al., 2016; Borrego & Gaines, 2016; Cooper et al., 2019; Figure 1b-d). Nonetheless, problem-solving tasks are criticized because it is often unclear which exact cognitive processes underly an animal's performance and to what extent it is influenced by non-cognitive factors (Thornton et al., 2014; Audet & Lefebvre, 2017).

Associative learning requires animals to learn the association between a cue and the presence/absence of a reward/punishment (Griffin et al., 2015). An extension of this is **discrimination learning**, where animals need to distinguish between multiple stimuli predicting different outcomes (Griffin et al., 2015; Griffin et al., 2016). Many animals can be successfully trained to discriminate between e.g. colours (Leal & Powell, 2012; Buechel et al., 2018), shapes (Szabo et al., 2019a), visual patterns (Paulissen, 2014), odours (Namekawa et al., 2018) and sounds (Guillette et al., 2009) (Figure 1e - f).

Spatial cognition refers to the capacity of an animal to learn and remember the location of resources in its environment. Animals can use different strategies for spatial learning: they can use egocentric cues (e.g. turn left in maze, Sheenaja &

BOX 1. (continued)

Thomas, 2011), use a local cue associated with the goal as guidance (López et al., 2000; López et al., 2001), form a mental representation of the environment, i.e. a cognitive map (Toledo et al., 2020), or a mix of those (Stone et al., 2000). Spatial learning is usually tested in a broad assortment of mazes and arenas (Figure 2a-b, López et al., 2001; Liu et al., 2016; Matzel et al., 2020; Vardi et al., 2020) or by using spatial feeding arrays (Figure 2c, Shaw et al., 2019). Outdoor enclosures (Noble et al., 2012) or tracking devices (Figure 2d, Roth & Krochmal, 2015; Toledo et al., 2020) allow to test spatial cognition under more natural conditions. Probe tests, in which cues in and around the maze/arena are manipulated, can provide more information on the strategies employed by animals to learn (López et al., 2001).

To test **reversal learning**, individuals are initially trained on a discrimination (Leal & Powell, 2012) or spatial learning task (Noble et al., 2012). After either reaching a certain level of success (e.g. Leal & Powell, 2012; Tebbich & Teschke, 2014; Mazza et al., 2018) or completing a fixed number of trials (e.g. Bebus et al., 2016; Moldoff et al., 2017; van Horik et al., 2018; Madden et al., 2018; Mason et al., 2021), the meaning of the cues/locations is reversed and animals need to inhibit the previously learnt behaviour in favour of switching to the former unrewarded cue or location. Reversing an association is generally considered to be more cognitively demanding than learning a task *de novo*, and is thus seen as an indicator of behavioural and cognitive flexibility (Tebbich & Teschke, 2014; Buechel et al., 2018).

BOX 1. (continued)

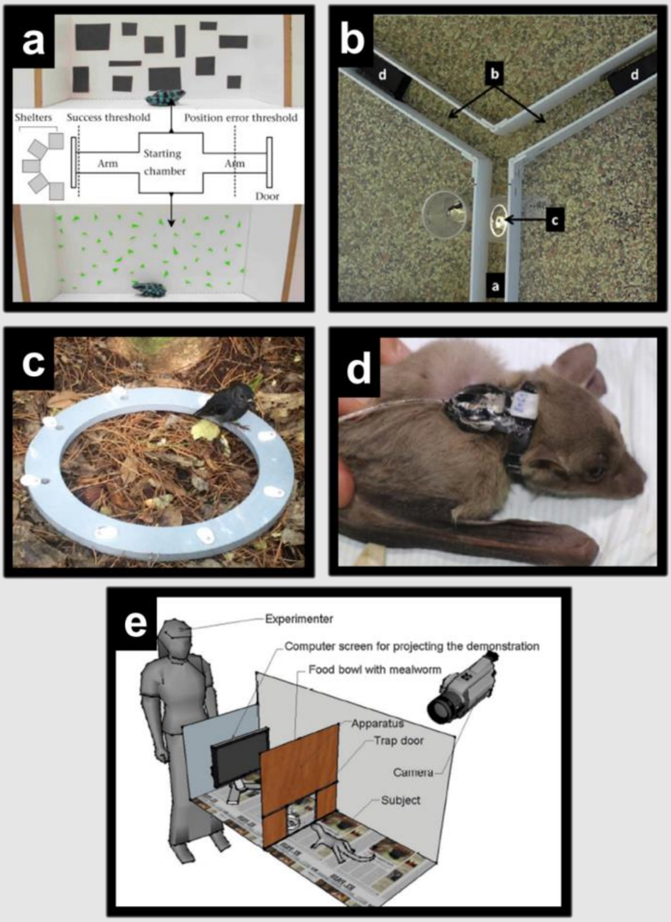

Figure 2. a) a poison frog (*Dendrobatus auratus*) within a two-arm maze. Each wall of the starting chamber has a different lay-out to allow orientation (Liu et al., 2016), b) Y-maze used to test spatial learning in delicate skinks (*Lampropholis delicata*) by Vardi et al. (2020). Only one of both arms contains an accessible shelter. c) Feeding array utilized to test spatial memory in wild New Zealand robins (*Petroica longipes*) by Shaw et al. (2019). Birds had to remember under which lids food was hidden based on spatial cues from their territory d) the use of cognitive maps by free-ranging Egyptian fruit bats (*Rousettus aegyptiacus*) has been inferred with the use of ATLAS tracking device (Toledo et al., 2020). e) social learning test in bearded dragons (*Pogona vitticeps*) from (Kis et al., 2015). Lizards first saw a video of a conspecific sliding open a door to obtain a food reward, and were then given the same task.

BOX 1. (continued)

Social learning is the process by which individuals acquire information either by observing or interacting with other individuals (Heyes, 1994). This can range from simply interfering information about e.g. the presence or absence of resources (Damas-Moreira et al., 2018), to copying novel motor actions and behavioural patterns (Kis et al., 2015). Social learning is usually measured by exposing individuals to a demonstrator (either live or video, Figure 2e) performing a novel task, and testing whether they copy this behaviour or not (Noble et al., 2014; Guillette & Healy, 2017).

Albeit the aforementioned protocols are often referred to as 'learning' tasks, they can also be highly informative regarding other cognitive mechanisms. Discrimination learning assays help us to understand the **perceptive** abilities of animals, e.g. Pérez i de Lanuza et al. (2018) trained common wall lizards (*Podarcis muralis)* to find food in one of four coloured wells, three of which corresponded to natural occurring ventral colours in adult wall lizards (white, yellow, orange). The fact that lizards were capable of learning this task, also provided evidence that they should be able to perceive and assess the colour morphs of conspecifics. Once an animal has learnt a task, it can then be retested days, weeks, months or even years later to probe the strength and accuracy of its **memory** (du Toit et al., 2012; Cooper et al., 2020; Ko et al., 2020). **Decision-making** processes can be studied by observing how animals use acquired knowledge in new contexts. For instance, eastern painted turtles (*Chrysemys picta*), previously trained to associate a particular arm of a Y-maze with food, were able to ignore an innate bias for blue light in favour of going to this rewarded arm, but still avoided

BOX 1. (continued)

yellow light even if they knew food was present underneath it (Roth et al., 2021). Italian wall lizards (*Podarcis siculus*) would forsake their personal knowledge about the location of a food reward if they observed a conspecific foraging in another location (Gavriilidi et al., 2022).

THE GAINS AND PAINS OF BEING SMART

Some animals have evolved remarkable cognitive skills to solve ecological problems. For instance, spatial memory enables many corvids and parids, such as Clark's nutcrackers (*Nucifraga columbiana*), to hide and recover numerous food items (up to more than 100 000) with great accuracy (Brodin, 2005; Healy et al., 2009; Pravosudov & Roth II, 2013), which is crucial to survive during harsh winter conditions (Sonnenberg et al., 2019). Other birds (e.g. crows and woodpecker finches) use tools to extract hidden prey (Tebbich et al., 2002; McCoy et al., 2019). Individual painted turtles (*C. picta*) follow the same migration routes between temporary ponds each year with great precision, unless being treated with memory-blocking drugs (Roth & Krochmal, 2015; Roth & Krochmal, 2018). Likewise, African elephants (*Loxodonta africana*) and Egyptian fruit bats (*Rousettus aegyptiacus*) make use of extensive cognitive maps to navigate between familiar resources (Presotto et al., 2019; Toledo et al., 2020).

Cognition helps animals to deal with these, and many other, environmental challenges, because learning and problem-solving allow cognitive/behavioural flexibility (Godfrey-Smith, 2002; Sol, 2009). Behavioural flexibility is a general term referring to the ability of an animal to adjust its behaviour in response to changing environmental stimuli (Jones, 2005; Daniels et al., 2019), which can be facilitated by multiple cognitive processes (e.g. inhibitory control, problem-solving and reversal learning, Griffin & Guez, 2014; Audet & Lefebvre, 2017; Szabo et al., 2020b; see also Box 1). Albeit often used interchangeably, cognitive flexibility refers more specifically to the capacity to learn new information which requires the reversal of previously acquired contingencies, i.e. reversal learning (Croston et al., 2017; Tello-Ramos et al., 2019).

Several studies across species have provided evidence for the advantages of higher cognitive abilities and behavioural/cognitive flexibility. Species with larger brains (relative to their body size) have higher rates of innovation and social learning (primates: Reader & Laland, 2002; birds: Sol et al., 2005a), are more successful in colonizing new habitats (in birds: Sol et al., 2005a; in mammals: Sol et al., 2008; in amphibians and reptiles: Amiel et al., 2011; but not in fish: Drake, 2007), and suffer from lower mortality in the wild (Sol et al., 2007). Higher behavioural flexibility (in terms of feeding innovations) also lowers extinction risk in birds (Ducatez et al., 2020). Within species, individual brain size and cognitive performance have been linked to fitness in a small number of studies (see paragraph ‘Cognition and fitness’ below).

Nevertheless, behavioural flexibility comes with a price. Cognition is costly, as it requires energetically expensive neural tissue (Expensive Brain/Tissue Hypothesis - EBH - Aiello & Wheeler, 1995; Isler & van Schaik, 2006b; Isler & van Schaik, 2009). Larger brains and higher cognition thus often mean reduced investment in other traits and processes, such as fecundity (Isler & van Schaik, 2009; Kotrschal et al., 2013; Ebneter et al., 2016), somatic maintenance (Kotrschal et al., 2019; van der Woude et al., 2019), immunity (Kotrschal et al., 2016), growth (Kotrschal et al., 2013), competitive ability (Mery & Kawecki, 2003), antipredator defences (Stankowich & Romero, 2017) and digestive systems (Kotrschal et al., 2013; Liao et al., 2016).

It is proposed that cognitive variation arises due to environmental forces shifting the balance between these costs and benefits of cognition. However, which exact socio-ecological factors favour or constrain the evolution towards higher cognitive abilities in which taxa remains heavily disputed (MacLean et al., 2012; Mettke-Hofmann, 2014; Morand-Ferron, 2017; Henke-von der Malsburg et al., 2020). Identifying how environmental pressures shape cognitive abilities has thus become a major goal within the field of cognitive ecology (Mettke-Hofmann, 2014).

THE DRIVERS OF COGNITIVE EVOLUTION

Two school of thoughts have tried to explain the evolution of cognition (Henke-von der Malsburg et al., 2020). Both camps seemingly agree that cognition is favoured by environmental complexity (Godfrey-Smith, 2002), but the first one regards complexity in the social environment as the driver of cognitive evolution, while the second one emphasises the role of ecological challenges posed by the physical environment.

Social challenges

The Social Intelligence Hypothesis (SIH – a.k.a. the Machiavellian Intelligence Hypothesis or Social Complexity Hypothesis) states that higher cognitive abilities, especially in the social cognition domain, evolved to help animals, specifically primates, with the challenges of group-living: e.g. maintaining and remembering social relationships, predicting and manipulating the behaviour of conspecifics etc.

(Humphrey, 1976; Byrne & Whiten, 1988; Holekamp & Benson-Amram, 2017). Later research gradually shifted toward linking social complexity with (relative) brain size, hence rebranding the SIH as the Social Brain Hypothesis (SBH, Dunbar, 1998; Dunbar, 2009). Although initially proposed specifically to explain primate intelligence, and well supported within this group (e.g. Sawaguchi, 1990; Dunbar, 1992; Dunbar, 1998; Street et al., 2017), the SBH was extended and supported in other mammalian taxa as well (e.g. in cetaceans: Marino, 1996; in ungulates: Shultz & Dunbar, 2006; in Carnivora, Artiodactyla and bats: Dunbar & Shultz, 2007; in ungulates and Carnivora: Perez-Barberia et al., 2007). However, recently, several studies have failed to support the SBH in e.g. birds (Fedorova et al., 2017; Wagnon & Brown, 2020), mole-rats (Kverková et al., 2018), fish (Reddon et al., 2016) and even primates (DeCasien et al., 2017; Powell et al., 2017; ManyPrimates et al., 2021). In fact, it has been proposed that brain size and sociality co-evolve in primates as both are being selected in response to the same ecological challenges (van der Bijl & Kolm, 2016).

Unfortunately, and in spite of the original proposed SIH, very little research has tested the relation between social complexity and actual cognitive performance. The handful of studies doing so have found mixed support for the SIH. Both social learning and relative brain size were related to social group size across primates (Street et al., 2017). Australian magpies (*Cracticus tibicen dorsalis*) from larger groups perform better on a variety of cognitive tasks (Ashton et al., 2018) and spotted hyenas (*Crocuta crocuta*) from larger groups show stronger inhibitory control (Johnson-Ulrich & Holekamp, 2020). Conversely, problem-solving success across 39 carnivore species was predicted by their relative brain size, but not by social complexity (Benson-Amram et al., 2016).

Across primate species, neither general intelligence (compiled from natural observations, 62 species, Reader et al., 2011) nor self-control (23 species, MacLean et al., 2014) was related to group size.

Ecological challenges

A second line of research has proposed that non-social ecological challenges, especially those regarding food acquisition, are the main driver of cognitive evolution (Ecological Intelligence Hypothesis - EIH - Parker & Gibson, 1977; Milton, 1981; Henke-von der Malsburg et al., 2020). For instance, object manipulation and tool use in primates may have evolved to allow more efficient foraging on seasonally limited food sources (Parker & Gibson, 1977). Several aspects of a species' foraging niche have indeed been linked to relative brain size and cognition, such as diet (Clutton-Brock & Harvey, 1980; Harvey et al., 1980; MacLean et al., 2014; DeCasien et al., 2017), foraging strategy (Day et al., 1999a; Day et al., 1999b; Clarin et al., 2013), home range size (Powell et al., 2017) and food hoarding (Garamszegi & Eens, 2004; Healy, 2021). Another often suggested factor is structural habitat complexity.

Navigating through, finding resources and avoiding dangers in complex habitats is supposed to be cognitively demanding. Animals will need to process and store vast amounts of information fast and efficiently, while filtering out large quantities of irrelevant background noise (Safi & Dechmann, 2005; Shumway, 2008; Mettke-Hofmann, 2014; Powell & Leal, 2014; Pamela Delarue et al., 2015; Calisi et al., 2017; Steck & Snell-Rood, 2018). For instance, an animal wishing to return to a previously visited location (e.g. shelter) in a densely vegetated, and thus visually restricted, habitat likely needs to memorize more cues along the way compared to a conspecific living in a more open environment. Comparative studies have indeed revealed that species or populations living in more complex environments often possess relatively larger brains, or regions thereof (e.g. in chipmunks: Budeau & Verts, 1986; anurans: Taylor et al., 1995; storm-petrels: Abbott et al., 1999; bats: Safi & Dechmann, 2005; fish: Pollen et al., 2007; Shumway, 2008; Axelrod et al., 2018; lesser earless lizards: Calisi et al., 2017; chondrichthyans: Mull et al., 2020; squirrels: Bertrand et al., 2021), although this pattern does not seem to be universal (e.g. primates: Clutton-Brock & Harvey, 1980; Powell et al., 2017; *Anolis* lizards: Powell & Leal, 2014; Storks et al., 2020; anurans: Liao et al., 2015; three-spined sticklebacks: Ahmed et al., 2017; mammals: Heldstab et al., 2018).

On the other hand, how habitat complexity affects actual cognitive performance has only been tested in a select number of species, and their results are inconclusive. For instance, habitat complexity has a positive effect on spatial learning in fish (Odling-Smee et al., 2008; Shumway, 2008; White & Brown, 2014; White & Brown, 2015), in bats (*Myotis* sp., Clarin et al., 2013, but only during the most complex tasks) and in mole-rats (Costanzo et al., 2009), but not in African striped mice (*Rhabdomys* sp., Mackay & Pillay, 2017). In contrast, memory retention seems to be unaffected by habitat structure in these species (Costanzo et al., 2009; Mackay & Pillay, 2017). Whether and how habitat complexity affects performance in other cognitive domains is also underexplored, save for a single study showing that anoles (*Anolis evermanni*) occupying a dense canopy-trunk microhabitat learnt a novel motor task faster than a related trunk-ground ecomorph (*A. cristatellus*) (Storks et al., 2020). The role of habitat complexity in cognitive evolution is thus inconclusive.

Another challenging aspect of the environment is temporal variability. The Cognitive Buffer Hypothesis (CBH) states that larger brains and higher cognitive abilities mainly evolved to buffer animals from the negative impact of changes in the socio-ecological environment (Allman et al., 1993; Deaner et al., 2003; Sol, 2009). In a sense, the CBH represents a reconciliation between the EIH and SIH (Cauchoix & Chaine, 2016). In temporally variable (e.g. highly seasonal) habitats, fast and flexible learning may be necessary to always have the most up-to-date information regarding the availability and distribution of resources, while problem-solving helps to acquire novel resources when the traditional ones become scarce (Parker & Gibson, 1977; Tebbich et al., 2002; Greenberg, 2003; Sol, 2009; Tebbich & Teschke, 2014; Griffin et al., 2016; Morand-Ferron et al., 2019). Some research has supported the idea that environmental variability is associated with greater learning abilities (e.g. climbing perch: Sheenaja & Thomas, 2011; woodpecker finches: Tebbich & Teschke, 2014; blue-tongued skinks: Szabo & Whiting, 2020), higher behavioural diversity e.g. tool use (woodpecker finches: Tebbich et al., 2002; chimpanzees: Kalan et al., 2020), enhanced problem-solving skills (black-capped chickadees: Roth et al., 2010b) and larger brains (birds: Schuck-Paim et al., 2008; Fristoe et al., 2017; Sayol et al., 2018). Further evidence for the CBH comes from the observation that species feeding on more unpredictable food sources often have better spatial cognition (Henke-von der Malsburg et al., 2020) and resident birds species, who have to deal with seasonal changes, often have larger brains than migratory ones (Sol et al., 2005b; Vincze, 2016).

However, one might just as well maintain that environmental variability is likely to constrain (rather than promote) the evolution of high cognition. Firstly, if the environment is too unpredictable, animals will be incapable of learning fast enough to keep up with the pace of change (Niemela et al., 2013; Mettke-Hofmann, 2014). Secondly, animals living in fluctuating environments will regularly experience periods of low resource availability and food intake, and hence, may be unable to sustain energetically expensive cognitive processes (Aiello & Wheeler, 1995; van Woerden et al., 2010; Luo et al., 2017). Several studies have supported the idea of reduced learning performance (gobies: White & Brown, 2014; mountain chickadees: Croston et al., 2017; great tits: Hermer et al., 2018) and brain size (strepsirrhine primates: van Woerden et al., 2010; marsupials: Weisbecker et al., 2015; anurans: Luo et al., 2017) in animals inhabiting environments more variable in time. Interestingly, a recent study by Fristoe and Botero (2019) showed that bird species from the most northern and temporally most variable regions of our planet either have very large or very small brains (relative to their body size). Environmental variability can thus simultaneously favour and constrain the evolution of higher cognitive abilities.

It should be noted that cognitive variation may not be due to selection (alone). The structural complexity and predictability of the environment experienced during (early) life can also induce non-genetic changes in brain and cognitive development (Kotrschal & Taborsky, 2010; Spence et al., 2011; du Toit et al., 2012; LaDage et al., 2013; LaDage et al., 2016; Roy et al., 2016; Carbia & Brown, 2019; van Horik et al., 2019a; Vardi et al., 2020).

STUDYING THE EVOLUTION OF COGNITION: THE COMPARATIVE METHOD

"Nevertheless the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind. We have seen that the senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason, etc., of which man boasts, may be found in an incipient, or even sometimes in a well-developed condition, in the lower animals."

- Charles Darwin (1871)

The interest in the evolution of animal cognition started with Darwin himself. His proposition that humans and animals share similarities in mental abilities was a drastic departure from the Cartesian view on animals as "soulless automata" (Darwin, 1871; Lamontagne et al., 2020). The idea that the minds of animals, like their bodies, undergo evolution through natural or sexual selection eventually provided the stage for comparative studies on animal cognition. One of the first attempts to do so was by George Romanes, who intensively collected anecdotes regarding the intellectual performance of animals in order to compare and reconstruct the evolution of cognition throughout the animal kingdom (Romanes, 1883; Wasserman, 1993). Although anecdotical natural observations can be useful for cognitive research (see e.g. Reader & Laland, 2002; Sol et al., 2005a; Ducatez et al., 2020), Romanes was nonetheless criticized by contemporaries and successors. Pioneers such as C. Llyod Morgan, Edward Thorndike, John Watson and Ivan Pavlov shifted towards an experimental approach, studying animal learning in a standardized, controlled and replicable way (Wasserman, 1993; Olmstead & Kuhlmeier, 2015; Lamontagne et al., 2020). Unfortunately, at the same time, the number and diversity of species in cognitive research rapidly declined, as Watson and successors focused on uncovering general cognitive processes in a limited set of model-species (Bitterman, 1965; Krasheninnikova et al., 2020).

The development of phylogenetic statistical methods in the 20th century allowed biologists to more explicitly test evolutionary hypotheses regarding cognition (MacLean et al., 2012; Cauchoix & Chaine, 2016). Comparing the performance across a large number of related species, chosen over a broad socio-ecological gradient, and preferably over a diversity of cognitive tasks, could be a powerful approach to uncover the environmental forces driving cognitive evolution (MacLean et al., 2012; Mettke-Hofmann, 2014; Cauchoix & Chaine, 2016; Shaw, 2017; Krasheninnikova et al., 2020). Despite a first step in the right direction by Morton E. Bitterman in the 1960s (Bitterman, 1960; Bitterman, 1965; Bitterman, 1975), the majority of comparative studies have mostly been limited to two, and rarely more than five, species (Henke-von der Malsburg et al., 2020). Albeit such comparisons can be interesting, using only a few species is obviously insufficient to establish whether robust evolutionary relationships between cognition and ecology exist (Krasheninnikova et al., 2020).

It also quickly became popular to use (relative) brain size as a proxy for cognitive capacity, due to the ease of collecting such data. The general assumption here is that animals with larger brains, after correcting for body size (either by calculating an encephalization quotient ‘EQ’, using residuals from a log-log brain size on body size regression, or by including body size as controlling covariable in the analyses) will have overall greater cognitive capacities (Deaner et al., 2007; Fox et al., 2017; Iwaniuk, 2017).

Comparative brain size studies have taught us a lot (see above), but despite their ubiquity they are not without issue (Roth & Dicke, 2005; Healy & Rowe, 2007; Logan et al., 2018; Smaers et al., 2021). Brain size may simply be too crude of a measure of (specific) cognitive abilities. True, it has been linked to e.g. innovation rates, learning abilities, general intelligence and problem-solving both across (primates: Reader & Laland, 2002; Reader et al., 2011; birds: Sol et al., 2005a; Carnivora: Benson-Amram et al., 2016) and within species (guppies: Kotrschal et al., 2013; Kotrschal et al., 2015b; Buechel et al., 2018), but not all studies show a straightforward relationship. Bees with relative larger brains are more likely, but not faster, to learn a new association (Collado et al., 2021). Absolute brain size predicted performance on some, but not all cognitive tasks across dog breeds (Horschler et al., 2019). Within guppies (*Poecilia reticulata*), the effect of brain size on cognition was both sex- and task-dependent (Kotrschal et al., 2013; Kotrschal et al., 2015b; Buechel et al., 2018), and relative brain size did not predict olfactory memory at all in parasitic wasps (*Nasonia vitripennis*, van der Woude et al., 2019). Studies using brain size as proxy for cognition also often assume that all parts of the brain evolve together, but it is perhaps more likely that different areas evolve independently from each other in response to differential selective pressures (Mosaic Brain Evolution, or Adaptive Specialization Hypothesis: Mettke-Hofmann, 2014). Yet, even looking at size variation in very specific brain areas may not be informative enough (Healy & Rowe, 2007). For instance, food-storing bird species have relatively larger hippocampi, the brain region involved in spatial cognition, than non-storing birds (Garamszegi & Eens, 2004). Although it could thus be concluded that food-hoarding selects for spatial cognition, such conclusion would be an oversimplification at best. Several more detailed experiments showed that hoarders do not show superiority in every single aspect of their spatial cognition compared to non-hoarders (reviewed in Healy et al., 2009; Healy, 2021). For instance, food-hoarding coal tits (*Poecile palustris*) excelled in spatial memory duration, but not capacity (i.e. number of items) or accuracy, compared to non-hoarding great tits (*Parus major*) (Biegler et al., 2001). Actual cognitive comparisons across species were necessary to understand which exact cognitive traits were selected for in relation to food-hoarding, and how birds exactly manage such a difficult task. This is not to say that comparative brain size studies are a pointless pursuit. They can provide interesting starting points for future comparative work on cognition, but they have too often become an endpoint (Healy & Rowe, 2007).

Notwithstanding a few remarkable exceptions (general intelligence in 62 primates: Reader et al., 2011; inhibitory control in 36 species of birds and mammals: MacLean et al., 2014; problem-solving in 39 Carnivora: Benson-Amram et al., 2016; habituation in 13 species of pit vipers: Krochmal et al., 2018; associative learning in 16 bee species: Collado et al., 2021; short-term memory in 41 primate species: ManyPrimates et al., 2021), large-scale cross-species comparisons in cognitive performance are extremely rare, for a number of reasons. First of all, measuring cognition is notoriously time-consuming. Researchers will often face the difficult choice between restricting the number of species, or the number of cognitive tasks (Krasheninnikova et al., 2020). Secondly, these studies will also struggle with the issue of standardizing cognitive assays across species (Chittka et al., 2012; MacLean et al., 2012; Krasheninnikova et al., 2020), which becomes even more troublesome the greater the phylogenetic distance between them. Non-cognitive differences between species (e.g. body size, colour vision, motivation, the presence of appendages which allow object manipulation, etc.) may bias the results of such cross-species comparisons, and should thus be accounted for (MacLean et al., 2012; Krasheninnikova et al., 2020). Lastly, there are the plenty of obvious logistical challenges involved with collecting, housing and testing a large number of species within a reasonable timeframe. Albeit these challenges may seem difficult to overcome (but see e.g. MacLean et al., 2012; Krasheninnikova et al., 2020 for suggestions), the lack of a truly comparative perspective is severely limiting our understanding of cognitive evolution (Shettleworth, 2009; Krasheninnikova et al., 2020).

Intraspecific comparisons - populations

One possible solution to at least the problem of standardization, would be to compare cognition across populations of the same species along an ecological gradient. In fact, some authors have claimed that looking at intraspecific variation may even be more informative than studying interspecific differences, as we can tell with greater certainty to which ecological conditions these populations are currently or were recently exposed (Roth et al., 2010b). Contrariwise, variation across species is shaped by a long series of (often unknown) selective pressures throughout their evolutionary history (Roth et al., 2010b). Various hypotheses regarding the environmental drivers of cognitive evolution can be answered by carefully picking study species with populations exposed to various levels of e.g. environmental variability (Roth et al., 2010b; Croston et al., 2017; Hermer et al., 2018; Kalan et al., 2020), predation pressure (Brown & Braithwaite, 2005), habitat complexity (Sheenaja & Thomas, 2011), urbanization (Audet et al., 2015), etc. These comparisons can be supplemented with common garden experiments to determine to what extent the link between an environmental variable and cognition is shaped by selection or phenotypic plasticity (Roth et al., 2010b).

Artificial selection experiments are another promising approach. In the past, very valuable insights regarding the costs and benefits of cognition have been revealed by comparing lines of animals artificially selected for relative brain size (guppies: Kotrschal et al., 2013; Kotrschal et al., 2015a; Kotrschal et al., 2015b; Kotrschal et al., 2016; Kotrschal et al., 2019; *Nasonia* wasps: van der Woude et al., 2019) or learning/memory performance (homing pigeons: Sherry et al., 1992; fruit flies: Mery & Kawecki, 2003; Lagasse et al., 2012; parasitic wasps: van den Berg et al., 2011; Liefting et al., 2018). Artificial selection studies on other traits, such as maternal investment (Japanese quails: Ebneter et al., 2016), personality (great tits: Groothuis & Carere, 2005; Amy et al., 2012), schooling behaviour (guppies: Vega-Trejo et al., 2020), friendly behaviour towards humans (a.k.a. domestication, dog breeds: Hare, 2017), etc., have also revealed parallel changes in cognition and/or brain size, thus further advancing our understanding of cognitive evolution. Animals from different lines can then be tested in their response to different ecological challenges (e.g. predation: Kotrschal et al., 2015a). Alternatively, it should be possible to expose animals for several generations to different ecological conditions (e.g. structural complexity, food availability, temporal variation), and measure whether this would induce changes in cognitive ability over time. E.g. Samuk et al. (2018) compared the brain size of sticklebacks after two generations in experimental ponds with or without predation.

Comparative studies may be a powerful approach to advance our understanding of cognitive evolution, but possibly even more exciting insights can be gained by zooming in at the individual level.

INDIVIDUAL VARIATION IN COGNITION

Individual differences in cognition have been ignored in non-human research up until very recently (Boogert et al., 2018). Remarkably, there has been some ground-breaking work on individual variation in the early days of cognitive research. Charles H. Turner, a contemporary of Thorndike and Watson, conducted rigorous experiments in which he documented differences in learning ability and speed-accuracy trade-offs among individual ants and cockroaches (Turner, 1907; Turner, 1913), almost a century before Sih and Del Giudice (2012) coined the Cognitive Style Hypothesis. Unfortunately, as an African American in the early 1900s, Turner would face many difficulties in advancing his academic career, and in the end, this pioneer left very little impact on the field of animal cognition (Dona & Chittka, 2020; Lee, 2020). Hence, biologists in the decades to come would treat individual variation in cognition (or any behaviour for that matter) as random noise around a golden mean (Roche et al., 2016). Only recently, the field of cognitive ecology has shifted its attention to understanding the causes and consequences of individual differences in cognition (Boogert et al., 2018), perhaps inspired by the contemporary emerging field of animal personality (see Box 2).

Nowadays, it is clear that animals not only differ in their cognitive abilities, but also in their cognitive styles, i.e. the specific strategy used to acquire, process and use environmental information. Specifically, individuals face a trade-off between fast-but-inaccurate or slow-but-attenuative learning and decision making (Cognitive Style Hypothesis: Sih & Del Giudice, 2012; Bensky et al., 2017; Dougherty & Guillette, 2018; Mazza et al., 2018). Animals with a 'fast' cognitive style sample their environment fast yet superficially, enabling quick learning and problem-solving. This comes at the expense of lower accuracy and flexibility; the superficial knowledge of faster learners renders them less capable of responding to environmental changes. Contrary, slow learners acquire new information with more precision, allowing for higher accuracy and behavioural flexibility (Sih & Del Giudice, 2012). Indeed, animals making faster decisions often make more mistakes in a cognitive task (e.g. in guppies: Burns & Rodd, 2008; in zebrafish: Wang et al., 2015; in bank voles: Mazza et al., 2018; in archerfish: Jones et al., 2020; but not in e.g. African striped mice: Rochais et al., 2021). Studies also frequently report a trade-off between an individual's ability/speed to learn a new association, and his/her ability/speed to reverse it (e.g. in Indian mynas: Griffin et al., 2013; in Florida scrub-jays: Bebus et al., 2016; in bank voles: Mazza et al., 2018; in red junglefowl: Sorato et al., 2018) although this is not always the case (e.g. in bumblebees: Raine & Chittka, 2012; in Chimango Caracaras: Guido et al., 2017; in guppies: Vila Pouca et al., 2021). An individual's cognitive style has also been proposed to be closely intertwined with his/her personality type (see Box 2), specifically with his/her boldness, explorative behaviour, aggressiveness, activity and sociability (the five broad behavioural categories in which personality variation is typically measured cfr. Smith & Blumstein, 2008; McEvoy et al., 2015; Dougherty & Guillette, 2018).

Albeit biologists are now acknowledging the existence of individual variation in cognitive abilities and styles, still very little is known regarding the repeatability or heritability of such variation (Croston et al., 2015; Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016; Boogert et al., 2018; Cauchoix et al., 2018). While estimating the consistency of among-individual variance in personality traits has become an almost standard procedure within behavioural ecology, few attempts have been made to do the same for cognition (Cauchoix et al., 2018). Likewise, although common garden experiments (Roth et al., 2010b), artificial selection programs (e.g. Buechel et al., 2018) and genome-wide association studies (Gnanadesikan et al., 2020) did provide evidence for a genetic basis of cognition, actual estimations of heritability are rare, leaving us in the dark regarding how much of the cognitive variation in a population can be attributed to genetic differences among individuals, or is shaped by environmental effects, i.e. developmental or activational plasticity (Croston et al., 2015). Both assumptions are nonetheless critical to understand whether and how fast a cognitive trait my respond to selection. Measuring cognitive performance multiple times across the lifetime of individuals will also inform us about the within-individual consistency. It has become increasingly clear that cognition is plastic, and specific environmental characteristics may promote or enhance cognitive development, even in adults (e.g. Kotrschal & Taborsky, 2010; Spence et al., 2011; du Toit et al., 2012; Carbia & Brown, 2019; Fong et al., 2019). From an evolutionary perspective, it is important to take this into account, as such context-dependent plasticity may counter selection and slow down evolutionary changes (Croston et al., 2015).

BOX 2. COGNITION AND PERSONALITY

Animal personality refers to the existence of consistent interindividual variation in behaviour across time and context (Réale et al., 2007). Personality variation in animals is generally measured in five broad categories (McEvoy et al., 2015): aggression towards conspecifics, explorative behaviour (reacting to novelty), boldness (risk-taking), activity and sociability. Multiple personality traits correlated with each other are referred to as a behavioural syndrome (Sih et al., 2004). Consistent interindividual behavioural variation has now been demonstrated for a broad diversity of species (Bell et al., 2009; Dougherty & Guillette, 2018) and it has become increasingly clear that such personality variation plays an important role in ecological and evolutionary processes (Réale et al., 2007; Reale et al., 2010a; Reale et al., 2010b; Moiron et al., 2020). A central question within personality research is how such consistent individual behavioural variation is maintained within populations. An often proposed explanation is that different personality types correspond to different risk – reward trade-offs (Wolf et al., 2007). ‘Faster’ personality types try to maximize their current reproductive success, and have to behave aggressive, active, explorative and bold to acquire and monopolize resources. Such behaviours, however, are risky, and thus faster personalities will face a penalty in the form of higher mortality (e.g. being very active and explorative may increase the chance of encountering predators). Slower personality types, on the other hand, value survival over current reproduction, and thus behave more cautious (Wolf et al., 2007; Smith & Blumstein, 2008; Reale et al., 2010b).

BOX 2. (continued)

Similar risk-reward trade-offs are hypothesized to underly variation in cognitive styles among individuals (Sih & Del Giudice, 2012; Liedtke & Fromhage, 2019a; Mazza et al., 2019), and hence cognitive styles and personality should be closely linked to each other (Figure 3). In particular, it is predicted that faster personality types should adopt a fast-but-inaccurate learning strategy because 1) this will allow them to maximize resource acquisition, 2) high mortality associated with risk-taking behaviours may select for the need to learn fast and 3) high mortality in fast personalities could theoretically make cognitive flexibility useless, as the animals will not live long enough to experience changes in the environment (Reale et al., 2010b; Sih & Del Giudice, 2012; Mazza et al., 2019). Slow personality types should exhibit a slow-but-flexible learning style, as they prioritize survival and are thus more likely to reap the (long-term) benefits of behavioural flexibility (Sih & Del Giudice, 2012; Mazza et al., 2019).

Nonetheless, literature has reported mixed results regarding the link between cognition and personality (see e.g. meta-analysis by Dougherty & Guillette, 2018). Some studies have indeed found evidence that fast personalities align with fast learning and problem-solving (e.g. in black-capped chickadees: Guillette et al., 2009; Carib grackles: Overington et al., 2011; tree-spined sticklebacks: Bensky et al., 2017; bank voles: Mazza et al., 2018) but lower flexibility (e.g. in black-capped chickadees: Guillette et al., 2011; woodpecker finches: Tebbich et al., 2012; bank voles: Mazza et

BOX 2. (continued)

al., 2018). Others, however, failed to (fully) support these proposed relationships (e.g. in delicate skinks: Chung et al., 2017; Chimango Caracaras: Guido et al., 2017; pheasants: Madden et al., 2018; three-spined sticklebacks: Bensky & Bell, 2020; common waxbills: Gomes et al., 2020). Cognition – personality covariance can also vary across ages (Zidar et al., 2018), sexes (Titulaer et al., 2012) and habitats (Dalesman, 2018). It is thus possible that ecological forces not only shape cognition and personality, but also their correlation. Most authors agree that, due to their close connection, personality and cognition should be studied together (Griffin et al., 2015).

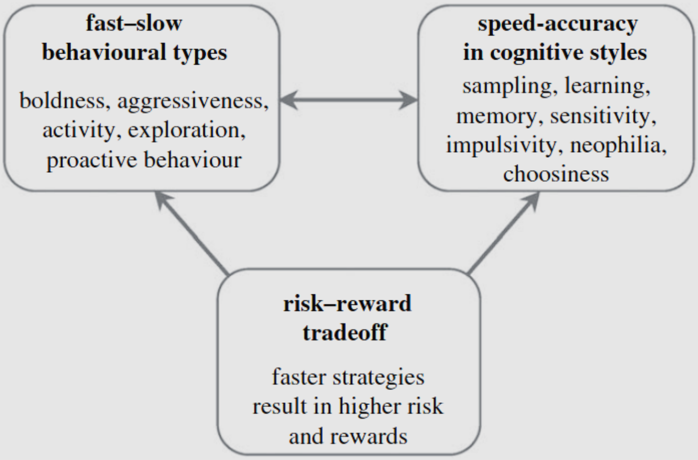

Figure 3. The hypothesized connection between personality types and cognitive styles, and how both are driven by risk-reward trade-offs. Figure from Sih and Del Giudice (2012).

Cognition and fitness

Comparative studies can detect macro-evolutionary relationships between cognition/brain size and ecology, but their results remain purely correlational (Healy et al., 2009; Cauchoix & Chaine, 2016). Individual differences in cognition represent the raw material upon which natural and sexual selection can act and thus, studying this variation will learn us more about the costs and benefits of specific cognitive traits, and how these depend on socio-ecological context (Chittka et al., 2012; Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016; Boogert et al., 2018; Branch et al., 2019). By zooming in onto the individual level, we may be able to identify the socio-ecological selective pressures on cognition in real-time (Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016; Preiszner et al., 2017). Regrettably, however, very few attempts have been made so far to relate individual cognitive variation to fitness.

Studying selection on cognition in the wild is laborious. Quantifying cognitive variation in a sufficient large number of individuals will be time-consuming, and following up their survival and (lifetime) reproductive success in the wild can be difficult. Survival estimates may be biased if animals disperse or behave very secretively (Rochais et al., 2022a). For most species, genetic pedigree analyses will be necessary to accurately estimate individual reproductive success (Szabo et al., 2022). Nonetheless, some studies have been able to overcome these limitations. Cognition can be measured using a problem-solving assay with only a single or a few trials (e.g. Keagy et al., 2009; Cole et al., 2012; Preiszner et al., 2017; but see Box 1) or be represented by relative brain size (Kotrschal et al., 2015a; Jaatinen et al., 2019; Wagnon & Brown, 2020; Colby et al., 2021; but see earlier discussion). Various strategies have also been used to ensure unbiased survival-estimates, such as focusing on animals in a stage of their life when dispersal is limited (Maille & Schradin, 2016; Dayananda & Webb, 2017; Sonnenberg et al., 2019), using tracking-devices (Madden et al., 2018) or studying animals in more or less enclosed areas (wildlife release pens: Madden et al., 2018; islands: Colby et al., 2021). Several studies were conducted in nest box populations of birds, where reproductive success can more easily be monitored by regular nest box checking (e.g. Cole et al., 2012; Cauchard et al., 2017; Preiszner et al., 2017; Wetzel & Koenig, 2017).

Results from the few studies on the link between individual cognitive performance and survival have been quite divergent. Some supported the popular notion that cognition is advantageous. Velvet geckoes (*Amalosia lesueurii*) and mountain chickadees (*Poecile gambeli*) demonstrating superior spatial learning had a higher chance of survival in the wild, presumably due to being more efficient in remembering the location of respectively safe shelter and food caches in their environment (Dayananda & Webb, 2017; Sonnenberg et al., 2019). Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) using tools were more likely to survive an extreme heat wave, as they may have exploited an alternative – less severely affected – foraging niche (Wild et al., 2019). But not all studies corroborated these positive results. Grey house lemurs (*Microcebus murinus*) profited from neither problem-solving nor spatial learning in terms of survival, although problem-solving efficiency did have a positive impact on their body condition (Huebner et al., 2018). Similarly, problem-solving ability was unrelated to adult survival in great tits (*Parus major,* Cole et al., 2012). Cognition might even be selected against in some cases. Fast-learning bumblebees (*Bombus terrestris*) had a reduced lifespan (Evans et al., 2017). Pheasant chicks (*Phasianus colchicus*) scoring better in a reversal learning task suffered from higher mortality (Madden et al., 2018).

Other research revealed that the effect of cognition on survival can be context-dependent. Relatively larger brains increase survival of female guppies (*P. reticulata*) and eider ducks (*Somateria mollissima*) under high predation risk, but reduce it under safer conditions (Kotrschal et al., 2015a; Jaatinen et al., 2019; Kotrschal et al., 2019). Associative learning speed had opposite effects on survival of small versus heavy pheasant chicks (Madden et al., 2018) and another study on the same species showed that learning was beneficial only when living in groups of fewer than five individuals (Langley et al., 2020b). The cognition-fitness link may also be sex-dependent: spatial cognition had a positive impact on the survival of male African striped mice (*R. pumilio*) but the opposite was observed in females (Maille & Schradin, 2016). Relative brain size predicted survival in female, but not male guppies in the presence of a predator (Kotrschal et al., 2015a). Finally, a long-term study on cliff swallows (*Petrochelidon pyrrhonota*) showed that individuals with relative smaller brains were more likely to die due to extreme cold weather conditions, but not due to other causes (Wagnon & Brown, 2020).

From an evolutionary perspective, survival is still pointless if animals do not reproduce. Another line of research has thus looked at how cognition relates to an individual's reproductive success. In some species, females were found to prefer males with higher cognitive performance (male satin bowerbirds: Keagy et al., 2009; guppies: Shohet & Watt, 2009; three-spined sticklebacks: Minter et al., 2017; budgerigars: Chen et al., 2019; but not in spotted bowerbirds: Isden et al., 2013), and one study found that males prefer females with better spatial memory (brown-headed cowbirds: White et al., 2021). How exactly individuals recognize 'smarter' partners is unclear. Only one of these studies (Chen et al., 2019), allowed females to directly observe male performance on a cognitive (problem-solving) task. One hypothesis has been that secondary sexual traits may act as honest signals for cognitive ability. Indeed, in birds, learning abilities have been positively associated with song complexity and attractiveness (Boogert et al., 2008; White et al., 2021). Yet, although sexual signals were unrelated to either spatial learning in male guppies (Shohet & Watt, 2009) or inhibitory control in male three-spined sticklebacks (*Gasterosteus aculeatus*, Minter et al., 2017), females of both species were still able to pick out the males with better cognitive performance.

There are two reasons why females may prefer a cognitively superior male: either because of its “good genes”, or because such males provide better parental care (Keagy et al., 2009; Isden et al., 2013; Minter et al., 2017; Branch et al., 2019). Some studies support the former hypothesis. Female chickadees lay larger clutches if paired with a better spatial learner. However, male cognitive performance was unrelated to fledgling mass, implying that females prefer better learners for indirect genetic rather that direct parental care benefits (Branch et al., 2019). More studies have reported a positive relationship between reproductive success and either problem-solving skills (great tits: Cauchard et al., 2013; Cauchard et al., 2017; Preiszner et al., 2017; house sparrows: Wetzel & Koenig, 2017), spatial cognition (mountain chickadees: Branch et al., 2019; male New Zealand robins: Shaw et al., 2019; female brown-headed cowbirds: White et al., 2021) or general cognitive ability (female Australian magpies: Ashton et al., 2018), and a few of these indeed confirmed that parents with better cognitive performance provide their offspring with more and/or higher quality food (Cauchard et al., 2017; Wetzel & Koenig, 2017; Shaw et al., 2019). On the other hand, problem-solving spotted hyenas did produce more offspring, but fewer of them survived (Johnson-Ulrich et al., 2019), and similarly, problem-solving great tits did produce larger clutches but also deserted their nests more often (Cole et al., 2012), resulting in no net impact of cognition on reproductive success in either study. As was the case with survival, the link between cognition and reproductive success seems to be context-dependent, varying across years (Cauchard et al., 2017; Branch et al., 2019) or depending on the mating strategy adopted by the individuals (rose bitterlings: Smith et al., 2015).

To summarize, the fitness consequences of individual variation in cognition are not straightforward, and vary greatly depending on the species (or even population), specific cognitive traits and socio-ecological context. Disheartening as this may seem at first, several researchers have proclaimed that comparing selection on cognitive traits under different socio-ecological conditions could become a very powerful approach to identify the ecological forces driving cognitive evolution. Such selection studies could also be a first step in examining to what extent cognitive variation among populations or species across an ecological gradient is due to differential selection pressures or caused by phenotypic plasticity, especially if survivors are retested on their cognitive performance (e.g. as in Bell & Sih, 2007). Unfortunately, while studies on the link between cognition and fitness are rare, those that study this link under different environmental conditions are even rarer (but see e.g. Kotrschal et al., 2015a; Kotrschal et al., 2019; Jaatinen et al., 2019 for various levels of predation risk; Pasquier & Grüter, 2016 for simple versus complex habitats; Preiszner et al., 2017 for urban versus forest habitats; Wagnon & Brown, 2020 for different causes of mortality). This thesis will try to fill in that gap, by explicitly testing whether selection on cognition depends on the structural complexity of the environment. In addition, I will combine this approach with the more traditional comparative method, in order to gain more insights into the role of ecology in shaping cognitive variation. My research will focus on an underrepresented taxon within cognitive research: squamate reptiles, and in particular the family of true lizards (Lacertidae).

STUDY SYSTEM: LACERTID LIZARDS

A short history of reptile cognition

As explained above, ever since the start of the 20th century, cognitive research has suffered from a severe taxonomic bias, with most focus being placed on mammals and birds (Bitterman, 1975; Shettleworth, 2009; Beran et al., 2014; Agrillo & Bisazza, 2017; Lamontagne et al., 2020). The lack of diversity in study species was especially concerning for the field of comparative cognition, and several authors have pointed out that this is constraining our understanding of the evolution of cognition (Shettleworth, 2009).

One particular group of animals that received very little attention in cognitive research up until recently, are non-avian reptiles (turtles, squamates, tuatara, and crocodiles) (Agrillo & Bisazza, 2017; Szabo et al., 2021b). Likely, this neglect was due to the long-held belief that reptiles were slow, inflexible and 'dumb' creatures (Turner, 1892; Robin, 1973), and were nothing but simple 'reflex machines' incapable of learning (Jerison, 1973). The stereotype of the 'dumb reptile' largely rested on anecdotical evidence, the relative small size and simplicity of the reptile brain, and early experimental work seemingly confirming these animal's cognitive faintness. However, later authors would point out that the underperformance of reptiles could often be explained by the poor experimental design of such studies, which failed to take into account the natural behaviour[1] and ecology of reptiles (e.g. suboptimal room temperature) or struggled with motivating reptiles to learn (Burghardt, 1977; Font, 2020). While food rewards can be strong motivators for rodents and birds to participate in many trials per day (e.g. up to 50 trials/day in Ashton et al., 2018), it is far less effective for reptiles with their lower metabolic rate and infrequent feeding regimes (Burghardt, 1977; Szabo & Whiting, 2022), e.g. some snake species only consume one large prey every few months (Emer et al., 2015).

Recently, however, the tide has turned. The last two decades have experienced a drastic increase in the number of cognitive studies on reptiles, and in particular lizards (Burghardt, 2021; Szabo et al., 2021b). More appropriate methods have been designed and applied to measure learning and problem-solving within this taxon (reviewed in Whiting & Noble, 2018), including, but not limited to, strictly controlling hunger motivation (Amiel et al., 2014; Emer et al., 2015), using alternative rewards (e.g. access to heat: Day et al., 2001; safe shelter: Paulissen, 2008), testing animals in their home enclosures to avoid stress of a non-familiar environment (Paulissen, 2008; Szabo et al., 2018) studying cognition in more natural conditions (Noble et al., 2012; Storks & Leal, 2020; Pettit et al., 2021) and designing experiments which better align with the behavioural repertoire and ecology of the studied species (Font, 2020).

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[1] One striking example comes from Powell (1967). Powell tested green anoles (*Anolis carolinensis*) in a classical two-way shuttle box, where the animals needed to escape towards another part of the box after a cue (light) was shown to avoid being electrocuted. Rodents generally learn to avoid the unsafe part of the box as soon as the cue is given, anoles did not show such avoidance learning. Nonetheless, as pointed out by Burghardt (1977), this is an unfair task, as anoles are arboreal, and thus more inclined to escape in a vertical direction. In fact, Powell did report anoles crawling the walls of the unsafe room, albeit he did not note how often and when exactly they showed this behaviour, making it very difficult to deduce whether the animals did or did not in fact learn an association between the light cue and danger.

This new wave of experiments has revealed that lizards possess a quite impressive set of cognitive skills, even on par with some mammals and birds (Leal & Powell, 2012; Szabo et al., 2019b). Lizards have been shown to quickly learn to discriminate between two or multiple visual stimuli (colours, patterns or shapes, Day et al., 1999b; Leal & Powell, 2012; Clark et al., 2013; Szabo et al., 2018; Pérez i de Lanuza et al., 2018 ; Rodrigues & Kohlsdorf, 2019) and are also capable of fast spatial learning (Noble et al., 2012; Carazo et al., 2014; Dayananda & Webb, 2017; Batabyal & Thaker, 2019; Font, 2019). Considerable cognitive flexibility was also demonstrated in multiple species, by showing response inhibition during detour (Szabo et al., 2019b; Storks & Leal, 2020; Szabo et al., 2020b) and reversal learning tasks (Leal & Powell, 2012; Noble et al., 2012; Batabyal & Thaker, 2019; Szabo et al., 2019a; Szabo & Whiting, 2020). They also rapidly acquire novel motor actions to solve new problems (e.g. Leal & Powell, 2012; Storks et al., 2020), which seems to be especially well-developed in monitor lizards (Manrod et al., 2008; Cooper et al., 2019; Cooper et al., 2020). Several lizard species can learn to avoid noxious or toxic prey, or a novel invasive predator, even after a single encounter with them, and will continue to exhibit this avoidance up to several weeks (Shanbhag et al., 2010; Ward-Fear et al., 2016; Ward-Fear et al., 2017; Ko et al., 2020; Robbins & Langkilde, 2021). Numerical cognition, i.e. being able to judge the relative size difference between two groups of items, is less well-investigated in lizards, and studies have reported mixed findings on how well lizards perform in this area (Miletto Petrazzini et al., 2018; Recio et al., 2021; Szabo et al., 2021a). Finally, in spite of their often solitary nature, social learning has been documented in lizards (e.g. Noble et al., 2014; Kis et al., 2015; Gavriilidi et al., 2022), even across species (Damas-Moreira et al., 2018). The stereotype of reptiles as dumb, clueless instinct machines is thus clearly ready to be abandoned.

What can lizards tell us about the evolution of cognition?

The Squamata, the reptilian order consisting of snakes and lizards, is a highly diverse group, both in number of species (> 11 000 sp., Uetz et al., 2021) and in their ecology and sociality. Throughout their evolutionary history, squamate reptiles have colonized and adapted to a broad variety of ecosystems and habitat types, ranging from arid deserts to tropical jungles, and from being cryptic fossorials to having completely arboreal lifestyles (Pianka & Vitt, 2003; Allemand et al., 2017; Whiting & Noble, 2018). Squamate reptiles differ greatly in foraging ecology (Reilly et al., 2009) and mating system (Whiting & While, 2017).

In addition, they also show great variation in their sociality. While many species are solitary, others do form social groups, which can either be temporary aggregations (e.g. gravid female pit vipers in rookeries) or stable associations across seasons or even years with consistent membership (e.g. long-term monogamy in *Tiliqua rugosa*, family-living in *Egernia* sp.) (Gardner et al., 2016; Halliwell et al., 2017; Whiting & While, 2017). This ecological and social diversity, both among and within species, provides great potential to test some of aforementioned hypotheses regarding the environmental drivers of cognitive evolution. From an evolutionary perspective, the phylogenetic position of lizards (and reptiles in general) relative to mammals and birds (Irisarri et al., 2017) could also inform us about whether shared cognitive characteristics among these taxa are due to a shared ancestry or convergent evolution. Studying their cognitive abilities can also provide further insights in the hypothesis that endothermy facilitated the evolution of larger brains and higher cognition (Gillooly & McCoy, 2014).

This thesis will mainly focus on the family of Lacertidae, a speciose group of lizards (362 species, Uetz et al., 2021) widespread across Eurasia and Africa. As all lizards, they exhibit great ecological diversity both within and among species (Arnold, 1989; Arnold et al., 2007). For instance, one of its members, the common lizard (*Zootoca vivipara*) is the reptile with the largest geographic distribution, and across its range it can be found in temperate, boreal, Atlantic, continental and alpine climates (Horreo et al., 2021). What makes this family ideal for comparative cognitive research is that despite their great ecological diversity, they are rather conservative in other aspects of their biology, such as foraging style (majority are active foragers), diet, body plan, thermoregulatory behaviour, etc. (Arnold, 1989; Arnold et al., 2007), making standardization of tasks across species feasible.

The ecological diversity of lizards has already been used in the past to address questions regarding the effect of e.g. habitat variability (Szabo & Whiting, 2020), habitat complexity (Storks et al., 2020), territory harshness (Rodrigues & Kohlsdorf, 2019), foraging style (Day et al., 1999b), invasiveness (Bezzina et al., 2014) and urbanization (Kang et al., 2018; Batabyal & Thaker, 2019) on cognitive performance (both within and across species). Recently, four studies have compared cognition across more than two species: taste aversion learning in two basilisk species (*Basiliscus* sp.) and two skink species (Paradis & Cabanac, 2004), inhibitory control in five species of skinks (Szabo et al., 2020b), problem-solving in three varanid and one helodermatid species (Cooper et al., 2019) and habituation in 13 species of pit vipers (Krochmal et al., 2018). However, these either lacked the sample size or the phylogenetic informed statistical analyses to draw firm conclusions regarding the link between cognitive performance and ecology.

THIS THESIS

The overall goal of this thesis is to study how ecology shapes cognitive variation, both across species, populations and individuals, using lacertid lizards as a model system. The first part of my thesis will adopt a traditional comparative method. I will compare both relative brain size and cognitive performance across species and populations sampled across an ecological gradient. In the second part, I switch to an individual-based approach, and test whether the fitness consequences of cognition depend on the structural complexity of the environment. By combining both approaches, I hope that my thesis will help to unravel the ecological forces driving the evolution of animal cognition. Box 3 gives a more detailed overview of the specific cognitive abilities which will be investigated throughout this thesis, why they are ecological relevant to (lacertid) lizards, and in which direction and why exactly a link with habitat complexity and/or environmental variability is to be expected.

In **Chapter 2,** I test how relative brain size evolved within Squamata in respect to habitat and social complexity, using a dataset on relative brain sizes of 171 species of squamates compiled from literature.

Chapter 3 zooms in on the Lacertidae. Performance on five cognitive tasks (inhibitory control, two problem-solving assays, spatial and reversal learning) is measured in thirteen species of lacertid lizards, and related to the quality, complexity and variability of their habitat, as well as to their life-history traits.

Next, I move to the intraspecific level. In **Chapter 4,** I test whether environmental variability stimulates (Cognitive Buffer Hypothesis) or constrains (Expensive Brain Hypothesis) the evolution towards higher cognitive abilities and behavioural flexibility, by comparing neophobia, problem-solving, spatial and reversal learning between an island (variable, resource scarce) and mainland (stable, more resources) population of the Aegean wall lizard (*Podarcis erhardii*).

Chapter 5 deals with the effect of structural habitat complexity on cognitive performance (problem-solving, spatial learning, reversal learning) and personality (aggression, neophobia and exploration), and their covariance, across populations of Aegean wall lizards on Naxos island.

Finally, I look at individual variation in cognition. In **Chapter 6** I measure the long-term repeatability and heritability of exploration and spatial cognition within Aegean wall lizards, two implicit assumptions often made but rarely verified in selection studies on cognition. In addition, I examine how habitat complexity is associated with plastic changes in cognitive performance over time.

In the penultimate **Chapter 7**, I test how lizards with known cognitive performance and personality scores survive and reproduce in either structural simple or structural complex habitats. This allows me to directly test the hypothesis that structural complex environments select for higher cognitive abilities.

Chapter 8 is the synthesis and general discussion of this thesis.

BOX 3. LIZARD COGNITION AND ECOLOGY: PREDICTIONS

Many studies investigating the evolution of cognition use either relative brain size or performance on a single cognitive task as indicators for overall cognitive ability. The implicit assumption here is that most, or all, cognitive abilities evolve together in the same direction and animals will thus perform consistently well or poorly across multiple cognitive tasks (domain general learning/the General Purpose Problem Solving Brain Hypothesis, Magphail & Bolhuis, 2001; Mettke-Hofmann, 2014; Holekamp & Benson-Amram, 2017; Qi et al., 2018). However, support for the existence of a general intelligence/cognition (‘*g*’) factor appears to be weak in non-human animals (Poirier et al., 2020; Aellen et al., 2022), suggesting that different cognitive traits evolve independently. Specific ecological conditions may favour one aspect of cognition, while having no impact on or selecting against other cognitive skills. Performance on one cognitive task will then not necessarily predict performance on another. Rather than having a general ‘all purpose’ intelligence, different animal species and populations will possess a unique set of cognitive abilities shaped by the particular set of ecological problems they face (domain-specific learning or the Adaptive Specialization Hypothesis; Magphail & Bolhuis, 2001; Mettke-Hofmann, 2014; Qi et al., 2018). For this reason, I have chosen to include a broad range of cognitive tasks within my thesis (for their definitions, see Box 1), aimed to sample different cognitive domains which are supposedly ecological relevant for lacertid lizards.

BOX 3. (continued)

Inhibitory control is considered to be an important ability within a foraging context. For instance, lizards may increase their foraging success by waiting until the right moment to attack a visible prey (Szabo et al., 2020b). Most lacertid lizards are active foragers (Arnold, 1989; Arnold et al., 2007) and therefore expected to perform better on detour tasks (a common method to measure inhibitory control) due to a high need to move around/over obstacles when pursuing prey, especially in more structurally complex habitats (Kabadayi et al., 2017). Inhibitory control is also expected to be particularly beneficial in changing environments, as animals will need to refrain from responding to environmental cues that are no longer relevant (e.g. returning to locations where food is no longer available) or may profit from ignoring familiar resources in favour of more valuable alternatives (van Horik et al., 2019a; Szabo et al., 2020b; Coomes et al., 2021). Thus, we expect lizards to show higher inhibitory control (i.e. be faster and more likely to inhibit an ineffective behaviour) in more complex and more variable environments.

High **problem-solving abilities** (i.e. being more likely and faster to solve a novel problem) are likely to increase foraging success and efficiency because they will expedite the discovery of new resources or resource acquisition strategies (Greenberg, 2003; Griffin et al., 2016). Most lacertid lizards are active foragers, and the ability to ‘invent’ and learn novel motor patterns could certainly be advantageous to e.g. extract otherwise inaccessible prey (e.g. invertebrates hidden underneath tree bark, inside

BOX 3. (continued)

rock crevices, burrows, … Mendyk & Horn, 2011; Cooper et al., 2019; Henke-von der Malsburg et al., 2020) or manipulating dangerous or difficult food items (e.g. venomous arthropods; Castilla et al., 2008; Herr et al., 2016). In more complex habitats, lizards are more likely to encounter such cryptic or hidden prey, and may be required more often to remove obstacles in order to obtain certain resources (Mendyk & Horn, 2011; Mettke-Hoffman, 2014). In addition, complex habitats might select for better and more diverse motor skills, which may be a prerequisite for problem-solving ability (Griffin et al., 2016; Stork et al., 2020). As problem-solving is predicted to increase foraging success, it should be particularly useful during periods of food scarcity in fluctuating environments (Tebbich & Teschke, 2014; Kalan et al., 2020). For instance, tool use in woodpecker finches (*Cactospiza pallida*) is mostly observed during the dry season (Tebbich et al., 2002). Hence, I predict that lizards will show higher problem-solving skills in more complex and more variable environments, and that lizards will benefit from problem-solving upon arrival in a new environment (Griffin et al., 2016).

Small (lacertid) lizards are also expected to benefit from strong **spatial learning** abilities due to their natural antipredator behaviour. Lacertids approached by predators flee towards safe hiding spots (e.g. rock crevices, underneath logs and stones, burrows) and remembering the location of and the path towards these hiding spots is expected to increase the probability of an successful escape (Martín & López, 2003;

BOX 3. (continued)

Paulissen, 2008; Noble et al., 2012; Font 2019). Spatial learning should also allow individual lizards to memorize the location of other resources (e.g. food, mates, basking spots) in their environment (Dukas, 2004). Navigating between resources in spatially complex environments is typically expected to require stronger spatial cognition, as animals will need to learn and remember a surplus of environmental information, while also sifting out meaningful cues from irrelevant background noise (Safi & Dechmann, 2005; Shumway, 2008; Mettke-Hofmann, 2014; Powell & Leal, 2014; Pamela Delarue et al., 2015; Calisi et al., 2017; Steck & Snell-Rood, 2018). Spatial learning is also believed to increase foraging efficiency (e.g. due to being able to remember where food can be found, which patches have already been depleted etc.) and would thus be valuable to survive periods of food scarcity in variable environments (Croston et al., 2017; Hermer et al., 2018; Tello-Ramos et al., 2018). Fast (spatial) learning should also allow individuals to quickly become familiar with a new environment (Szabo et al., 2020a). Thus, I expect lizards from more complex and more variable environments to be faster and more successful in spatial learning.

As environmental conditions change (e.g. food patches get depleted), lizards will need to update information about their environment regularly and adjust their behaviour accordingly. The ability to do so is typically measured by using **reversal learning** tasks (Noble et al., 2012), and individuals adept at reversal learning (i.e. more likely to relearn, faster in relearning, making fewer errors) are considered to be

BOX 3. (continued)

behaviourally more flexible (Audet & Lefebvre, 2017). Reversal learning is expected to be especially beneficial in temporally variable habitats, such as environments with strong seasonality (Tebbich & Teschke, 2014; Tello-Ramos et al., 2019; Szabo & Whiting, 2020). Structurally complex habitats are also often assumed to be more variable in time as well. Animals living in such habitats may encounter new situations and/or resources more often (e.g. due to a higher diversity of microhabitats and prey items) (Mettke-Hofmann et al., 2002) and could thus also require stronger reversal learning skills. For instance, (lacertid) lizards on Mediterranean islands often switch to alternative food sources during dry and hot summers, which may indicate a certain degree of cognitive flexibility (Pérez-Mellado & Corti, 1993; Adamopoulou et al., 1999; Lo Cascio et al., 2001; Rodríguez et al., 2008; Sagonas et al., 2015).

Note however, that environmental variability may also have an opposite effect on these cognitive abilities. Inhibitory control, problem-solving and learning may be too costly to maintain when lizards are unable to uphold a continuously high energy intake in habitats with fluctuating levels of food availability (van Woerden et al., 2010).

Neophobia (the fear of novelty cfr. Tebbich & Teschke, 2014) influences how likely an individual is to come into contact with new information, and thereby determines its propensity to learn and innovate (Tebbich et al., 2010; Tebbich & Teschke, 2014). Lower levels of neophobia may facilitate the discovery and exploitation of new resources by lizards (Greenberg, 1983; Greenberg, 2003) and permit them to develop

BOX 3. (continued)

innovative feeding techniques (Daniels et al., 2019), but could be a disadvantage when foraging becomes dangerous, e.g. due to toxic prey, predation or competition (Mettke-Hofmann et al., 2002; Mettke-Hofmann, 2014; Ward-Fear et al., 2020). Neophobia is therefore predicted to be more advantageous in environments with low predation risk but high potential rewards (Mettke-Hofmann et al., 2002). Lizards are expected to show lower levels of neophobia (i.e. faster to approach novelty) in temporally more variable habitats due to the frequent scarcity of resources (Mettke-Hofmann et al., 2002; Tebbich & Teschke, 2014). Lizards should also demonstrate lower levels of neophobia in structural more complex habitats, as animals in habitats with more vegetation cover likely experience a greater safety from predation (Crane et al., 2019). Lastly, reduced neophobia should be beneficial for individuals introduced in a novel environment (Candler & Bernal, 2014). For similar reasons, I expect higher levels of **exploration** (the tendency to sample new environmental information cfr. Verbeek et al., 1994) in more complex and more variable environments. Due to their strong impact on information gathering, neophobia and exploration are sometimes considered cognitive adaptations as well (Mettke-Hofmann, 2014). In accordance with the prevailing framework of personality variation across the five behavioural axes (exploration, risk-taking, aggression, sociability and activity, see Box 2) in literature, I will nonetheless refer to them as personality traits throughout this thesis (with neophobia being an aspect of risk-taking).

BOX 3. (continued)

Table 1. Overview of the predicted effects of structural habitat complexity and environmental variability (in time) on different cognitive abilities and neophobia and exploration. Upward arrows (↑) indicate that lizards are expected to perform better (i.e. being more successful or faster, making fewer errors) in this cognitive task. Grey colours indicate that based on literature I expect this cognitive ability to be especially useful to deal with that ecological challenge, and thus predict a particular strong effect of the ecological variable on performance in this cognitive task.

	Complexity	Variability
Neophobia	↓	↓
Exploration	↑	↑
Inhibitory control	↑	↑
Problem-solving	↑	↑
Spatial learning	↑	↑
Reversal learning	↑	↑

Overall, I thus predict that the effect of habitat complexity and environmental variability will be in the same direction for most of these cognitive abilities, albeit this does not necessary exclude the possibility that particular cognitive skills would be more strongly selected for in response to particular ecological challenges (see Table 1 for an overview). For the sake of simplicity, I will thus often simply speak about “higher or lower (or better or stronger) cognitive abilities” while stating hypotheses in the following chapters, e.g. because I expected that habitat complexity would have a positive effect on performance in all cognitive tasks used in that chapter.

CHAPTER 2

BRAIN SIZE, ECOLOGY AND SOCIALITY: A REPTILIAN PERSPECTIVE

Adapted from:

De Meester, G., Huyghe, K. & Van Damme, R. (2019). Brain size, ecology and sociality: a reptilian perspective. — Biological Journal of the Linnean Society 126, 381-391.

ABSTRACT

It is often hypothesized that larger brains evolved to deal with environmental complexity, by means of enhanced cognition and behavioural flexibility. Decades of research have tried to relate relative brain size to either habitat or social complexity, however, often with conflicting results. Which selective pressures favour larger brains and whether they act in the same way in different taxa is unclear, especially as the majority of studies focused on either mammals or birds. We present the first large-scale comparative study investigating the effect of habitat and social complexity on brain size evolution in Squamata (lizards and snakes), using a dataset of 171 species. Our analyses confirmed earlier findings that both the degree of limb reduction and the biogeographical origin of a species affected relative brain size, and should be controlled for. Habitat complexity had no effect on brain size, and solitary species had larger brains than social species. These results suggest that different selective forces may drive brain size evolution in Squamata compared to other taxa. Future comparative studies should also consider using other, non-traditional, taxa. This will contribute to a more comprehensive understanding of how the vertebrate brain evolved.

INTRODUCTION

Biologists have long been fascinated by the question of why some species have relatively larger brains than others (Jerison, 1973). It is often postulated that enhanced cognition, and therefore higher behavioural flexibility, is the major advantage of possessing a large brain (Iwaniuk, 2017). Indeed, relative brain size has been positively associated with several cognitive aspects in different taxa (Reader & Laland, 2002; Lefebvre et al., 2004; Benson-Amram et al., 2016; but see: Healy & Rowe, 2007; MacLean et al., 2014). Nevertheless, given the high energetic cost of brain tissue (Expensive Brain Hypothesis: Aiello & Wheeler, 1995; Isler & van Schaik, 2006b; Heldstab et al., 2018), selection should only favour larger brains if the cognitive benefits outweigh the costs (Sol, 2009; Benson-Amram et al., 2016).

It is often hypothesized that larger brains will enable species to deal with more complex information, and will therefore be selected for in species with cognitive demanding lifestyles or habitats (Harvey & Krebs, 1990; Safi et al., 2005; Lefebvre & Sol, 2008; Sol, 2009; Sobrero et al., 2016). Especially those living in complex three-dimensional, heterogenous, environments (e.g. saxicolous or arboreal species), would be expected to evolve larger brains, in order to process a surplus of environmental information (Bennet & Harvey, 1985; Harvey & Krebs, 1990; Safi & Dechmann, 2005) and to find and exploit more diverse and heterogeneously distributed resources (Petren & Case, 1998; Pamela Delarue et al., 2015; Steck & Snell-Rood, 2018). Such species will also benefit from improved spatial memory (Safi & Dechmann, 2005; Shumway, 2008; Powell & Leal, 2014; White & Brown, 2015; Sobrero et al., 2016; Calisi et al., 2017), better motor coordination, navigation and manoeuvrability (Bennet & Harvey, 1985; Taylor et al., 1995; Calisi et al., 2017; Stankowich & Romero, 2017). Larger brains are indeed associated with structural habitat complexity in fish (Pollen et al., 2007; Shumway, 2008), frogs (Taylor et al., 1995), birds (Bennet & Harvey, 1985) and mammals (Harvey et al., 1980; Eisenberg & Wilson, 1981; Meier, 1983; Bertrand et al., 2017).

Environmental complexity may also include the social environment of an animal. Living in a group is cognitively demanding, due to the necessity to maintain and memorise social relationships, and may, therefore, select for larger brains (Byrne & Whiten, 1988; Dunbar, 1998; Dunbar & Shultz, 2007; Perez-Barberia et al., 2007; Dunbar, 2009; Dunbar & Shultz, 2017). This Social Brain Hypothesis (SBH) has found support in birds (Dunbar & Shultz, 2007; West, 2014), mammals (Shultz & Dunbar, 2006; Perez-Barberia et al., 2007; Fox et al., 2017) and especially in primates (Byrne & Whiten, 1988; Dunbar, 1998; Dunbar & Shultz, 2007; Dunbar & Shultz, 2017; Street et al., 2017).

Nevertheless, a large number of studies have also failed to find a positive association between brain size and either habitat (Clutton-Brock & Harvey, 1980; Schuck-Paim et al., 2008; Powell & Leal, 2014; Liao et al., 2015; Powell et al., 2017; Heldstab et al., 2018) or social complexity (Finarelli & Flynn, 2009; MacLean et al., 2014; Benson-Amram et al., 2016; DeCasien et al., 2017; Fedorova et al., 2017; Powell et al., 2017; Kverková et al., 2018). Which selective forces shape brain size variation is, therefore, still under discussion (Healy & Rowe, 2007; West, 2014). Given these diverse results, the context in which large brains evolve may differ among vertebrate taxa (Healy & Rowe, 2007). In particular, whether the SBH can be considered as a general rule for brain evolution, rather than being specific for primates has been brought into question (Holekamp, 2006; Finarelli & Flynn, 2009; van der Bijl & Kolm, 2016; Kverková et al., 2018). Unfortunately, most studies on brain size evolution appear to focus on either mammals or birds (Iwaniuk, 2017), a major weakness within the field of comparative cognition (Shettleworth, 2009).

The Squamata (lizards and snakes) provide an interesting opportunity to test the effect of environmental complexity on relative brain size. Squamata show immense ecological diversity and have adapted to a variety of lifestyles in a broad range of terrestrial ecosystems (Pianka & Vitt, 2003; Whiting et al., 2018).While often overlooked, Squamata also show varying levels of sociality, ranging from solitary species, over species that form transitory aggregations, to those living in stable associations with consistent membership across seasons or years (Mouton, 2011; Gardner et al., 2016; Halliwell et al., 2017; Whiting & While, 2017).

To date, brain evolution in Squamata has been studied in the context of sexual selection (Hoops et al., 2017a), communication (Robinson et al., 2015) and ecology (Powell & Leal, 2012; Powell & Leal, 2014; Allemand et al., 2017; Hoops et al., 2017b). Ecological studies, however, have mostly focused on brain morphology in specific taxa and rarely tested the differences in whole brain size. We hereby present the first large-scale comparative study investigating the effect of habitat complexity and sociality on brain size evolution within Squamata, using a dataset of 171 species. We hypothesize that arboreal and saxicolous species have relatively larger brains compared to fossorial and ground-dwelling species, and social species to have relatively larger brains than solitary squamates. In addition, as it is hypothesized that larger brains facilitate behavioural flexibility, large-brained species should be found in a broader range of habitats.

METHODS

Data collection

Data on body and brain masses from 171 Squamata (155 lizards & 16 snakes) were obtained from the literature, by searching for “Squamata”, “lizard”, “snake”, “amphisbaenia” or “reptile” in combination with “brains”, “brain mass”, “brain size”, “brain volume”, “brain weight”, “encephalization” or “brain-to-body ratio” in ISI Web of Science and Google Scholar (see Supplementary Table S2.1). Brain and body mass data from the tuatara (*Sphenodon punctatus*) was also included. Both published and unpublished data (e.g. unpublished thesis’s found in online university libraries) were used. Weighted averages were calculated if a species’ brain mass was available from multiple sources. When data was sourced via experimental studies (e.g. bioaccumulation of pesticides), only data from the control group was used for further analyses. We only retained data from studies in which brains were dissected and either weighed directly, sectioned and measured or scanned using magnetic resonance imaging. Brain volumes were converted to brain masses, following the general assumption that 1 cm^3 brain tissue weighs 1.036 gram (Northcutt, 2013). As the brain mass/body mass is known to vary with age (Patnaik & Jena, 1972) no data on juvenile specimen was used.

A common critique of comparative encephalisation studies is the potential bias introduced by collecting brain data from multiple sources (Healy & Rowe, 2007). However, we found no evidence for such bias in our dataset. Brain size was significantly repeatable across different sources (mixed effect model: R = 0.9704, 95% CI [0.9703; 0.9735]; log-likelihood ratio-test: $\chi^2 = 19.93$; df = 3; $p < 0.001$) and there was no significant influence of brain-measuring technique (wet weights v.s. MRI-scanning;

mixed effect model: $F_{1,7}$ =0.187; p = 0.68) within species for which brain data was available from multiple sources (N = 8).

Habitat complexity: ecological guilds

Using scientific literature, species were classified into four ecological guilds, based on whether they are primarily active underground and actively borrowing (fossorial, N = 7), on terrestrial surfaces (ground-dwelling, N = 96), on rock surfaces (saxicolous, N = 20) or in trees and shrubs (arboreal, N = 48). No brain data was found on completely aquatic species, and semi-aquatic species were classified according to their habitat use on land. Although these guilds are not always mutually exclusive, each species was classified according to how it was most commonly referred to in the literature.

Sociality

Information on sociality was taken from the datasets of Gardner et al. (2016) and Halliwell et al. (2017). Social species are species for which at least temporal aggregations have been reported in literature (N = 24). Species were only classified as solitary **(**N = 44) if a) no aggregations have been reported for a particular species and b) this species was well studied (see Halliwell et al. (2017) for criteria). Data on sociality was only available for a subset of our data (N = 68).

Habitat generalism

Using field guides and literature data, we noted the presence/absence of each species in 13 habitat categories **(**see Supplementary Table S2.2). The total number of categories in which a species occurred was used as an indicator for its ecological generalism (Stuart-Fox & Owens, 2003; Sol et al., 2005a; Ducatez et al., 2015).

Confounding variables

As already suggested by Platel (1979) and recently confirmed by Heesy et al. (2017), limb reduction in Squamata is associated with a decrease in relative brain size. Therefore, for each species we noted the status of the limbs (absent, reduced or present, see Supplementary Methods for details). A second possible confounding variable is the geographic origin of the specimen. Previous research suggested that selection for larger or smaller brains may differ among biogeographic regions in reptiles (Amiel et al., 2011). Biogeographical region of origin was, therefore, also included as an additional covariate **(**see Supplementary Methods for details).

Statistics

The software program R version 3.5.1. (Ihaka, R. & Gentleman, R., University of Auckland, New Zealand) was used for all statistical analyses.

The time-calibrated phylogenetic tree constructed by Tonini et al. (2016), which combines molecular tools and taxonomic assignment, represents the most complete and most recent phylogeny of the Squamata, and was, therefore, used as a basis for all further phylogenetic analyses. Prior to analyses, this tree was pruned to only include the 172 species of our dataset, and polytomies were randomly resolved using the function ‘multi2di’ in the R package ‘ape’ (Paradis et al., 2004).

Both body and brain mass were log10-transformed prior to all analyses and association between both variables was tested using a phylogenetic generalized least square (PGLS) regression with the ‘gls’ function in the ‘nlme’ package (Pinheiro et al., 2014) with Pagel correlation structure. The value for Pagel’s λ was determined through maximum likelihood. Pagel’s λ is a scaling parameter indicating how much similarity between species in a trait can be attributed to their relatedness (Pagel, 1999), and ranges from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). As brain and body mass were positively correlated (see results), body mass was controlled for by including it as a covariate in all further statistical models. Residuals of the brain to body mass regression were used for visualisation of the results.

The phylogenetic signals of absolute brain mass, absolute body mass and relative brain size (residuals from the brain on body mass regression**)** were calculated as Pagel's λ using the function 'phylosignal' in the R package 'phytools' (Revell, 2012). The phylogenetic signal for habitat generalism was calculated in the same way, but for ecological guild and sociality (categorical variables) the function 'fitDiscrete' in the R package 'geiger' (Harmon et al., 2008) was used. The evolution of relative brain size was visualized by estimating the maximum likelihood ancestral states using the function 'contMap' in the package 'phytools' (Revell, 2012).

To test which ecological (habitat generalism + complexity) and social variables influenced brain size, we ran PGLS models to take phylogenetic relatedness of species into account, with brain mass as the response variable and body mass as the covariate (both log10-transformed). Separate models were run for the ecological and social variables because of differences in sample size. Due to convergence problems with the social model when including limb status as covariate, we only tested the effect of sociality in fully limbed species (51/68). Limb status was, therefore, only included as fixed factor in the ecological model, while biogeographical realm was a covariable in both models. *Sphenodon punctatus* was excluded from these analyses.

More information on methods and statistics can be found in Supplementary Methods.

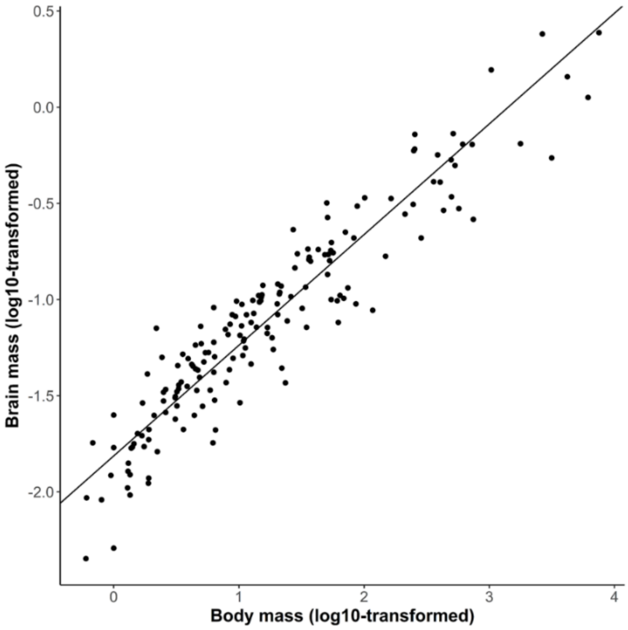

Figure 1. Correlation between body mass (log10-transformed) and brain mass (log10-transformed) in Squamata, using a phylogenetic generalized least square (PGLS) regression. N = 172 (including the tuatara outgroup).

RESULTS

Brain and body size data were obtained for 171 species of Squamata. Brain mass ranged from 0.0045 g (*Lerista muelleri*) to 2.44 g (*Varanus niloticus*). Relative brain size also exhibited considerable variability, with *Anolis stratulus* and *Lerista bipes* having respectively the largest and smallest brains relative to their body size. There was a significant positive correlation between body mass and brain mass (slope = 0.578 ± 0.016; $F_{1,170} = 1309$; $p < 0.001$, $\lambda = 0.87$; Figure 1).

All morphological traits carried a strong phylogenetic signal (brain mass: $\lambda = 0.94$; body mass: $\lambda = 0.91$; residual brain size: $\lambda = 0.87$; all $p < 0.001$). Both ecological guild and sociality showed a high phylogenetic signal (λ of respectively 0.95 and 1.00), while habitat generalism had a much lower (0.31) but still significant λ ($p < 0.001$) signal. Given these strong phylogenetic signals in our dataset, the use of PGLS-models seems appropriate.

Ancestral state reconstruction for relative brain size is visualised in Figure 2. A more detailed phylogenetic tree with ancestral state reconstruction and residual brain size per species is presented in Supplementary Figure S2.1.

On average, arboreal species had the largest and fossorial species the smallest brains relative to their body sizes (Figure 3). However, differences among ecological guilds were not statistically significant ($F_{3,157} = 1.98$; p = 0.12; Table 1). Neither was there an association between relative brain size and habitat generalism (slope = -0.007 + 0.005; $F_{1,157} = 2.84$; p = 0.09; Table 1).

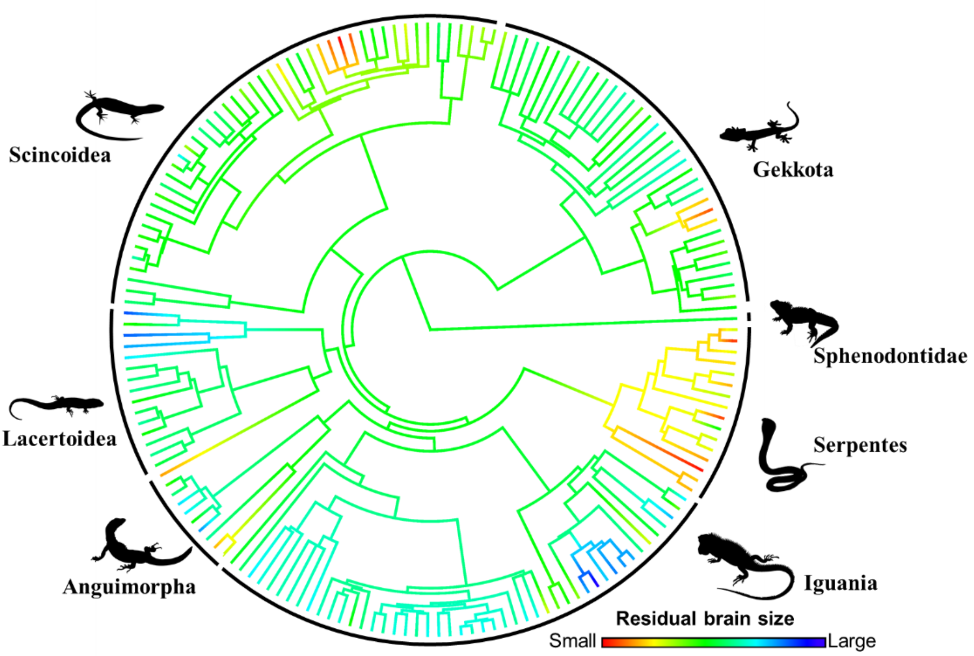

Figure 2. Ancestral state reconstruction of relative brain size (residuals of brain on body mass regression) along the nodes and branches of the phylogenetic tree of 171 species of Squamata. *Sphenodon punctatus* is included as outgroup. Species with positive residuals (blue) have large brains relative to their body size, while species with negative residuals (yellow-red) have small brains relative to their body size. Visualized using the 'contMap' function in R (package 'phytools'; Revell, 2012).

Table 1. Outcome of the Phylogenetic Generalized Least Square Regression for the model containing ecological variables (N = 171) and the model containing social variables (N = 51). Brain size and body size were both log10-transformed. Abbreviations for ecological guild: Ar = arboreal, Sa = saxicolous, GD = ground-dwelling and Fo = fossorial. Abbreviations for limb status: A = absent, R = reduced and P = present. Abbreviations for biogeographical realm: NT = Neotropics, AU = Australasian, NA = Nearctic, PA = Palearctic, AF = Afrotropics, OC = Oceania.

	Predictor	Effect	F-statistics	Significance	Λ
BRAIN SIZE **ecology*	Body size	b = 0.564 ± 0.012	$F_{1,157} = 2476$	p < 0.001	0.37
	Ecological guild	Ar > Sa & GD > Fo	$F_{3,157} = 1.98$	p = 0.12	
	Habitat generalism	b = -0.007 ± 0.005	$F_{1,157} = 2.84$	p = 0.09	
	Limb status	A < R < P	$F_{2,157} = 62.8$	p < 0.001	
	Biogeographical realm	NT > AU, NA	$F_{6,157} = 4.40$	p < 0.001	
BRAIN SIZE **sociality*	Body size	b = 0.568 ± 0.013	$F_{1,43} = 18*10^4$	p < 0.001	-0.88
	Sociality	Solitary > Social	$F_{1,43} = 20.00$	p < 0.001	
	Biogeographical realm	NT > AU, PA	$F_{5,43} = 7.00$	p < 0.001	

There was a significant effect of limb reduction on relative brain size ($F_{2,157} = 62.78$; $p < 0.001$), as species with reduced or absent limbs had smaller brains relative to their body size (Figure 4A). Relative brain size also differed significantly among biogeographical realms ($F_{6,157} = 4.40$; $p < 0.001$; see Figure 4B).

There was a significant effect of sociality on relative brain size in limbed Squamata ($F_{1,43} = 20$; $p < 0.001$; Table 1). Surprisingly, species with a 'solitary' life style had significantly larger brains relative to body size compared to 'social' species (Figure 5). Biogeographical realm also had a significant effect on relative brain size in this subset of the data (Table 1). Given the surprising result of a negative value for Pagel's λ in this model, we re-analysed the data using both the ‘gls’ function in the ‘nlme’ package with restricted maximum likelihood optimization for λ and the ‘pgls’ function in the ‘caper’ package (Orme et al., 2018). Both analyses suggested negative λ’s and gave similar results (Supplementary Table S2.3).

DISCUSSION

Decades of work have been dedicated to unravelling which ecological and social factors have driven the evolution of the brain, but the bulk of this work has focused on either mammals or birds. This taxonomic bias makes it difficult to understand whether the same selective forces have shaped brain size in different taxa and impedes a more complete picture of the evolution of the vertebrate brain.

Contrary to one of our main expectations, species living in more complex habitats did not have significant larger brains than species living in simple habitats. Older studies often reported a positive effect of arboreality on relative brain size (Harvey et al., 1980; Eisenberg & Wilson, 1981; Bennet & Harvey, 1985; Taylor et al., 1995) but more recent phylogenetically informed analyses have not (Liao et al., 2015; Powell et al., 2017; Heldstab et al., 2018; but see Stankowich & Romero, 2017). Such incongruity may arise if the variables considered exhibit strong phylogenetic signal, as was the case for our variables. Other aspects of habitat complexity, such as environmental variability, may be more important selective pressures for larger brains (Schuck-Paim et al., 2008; Sayol et al., 2018).

The lack of differences among ecological guilds can, however, be explained by two alternative hypotheses. Firstly, as predicted by the Mosaic Brain Hypothesis, selection may act independently on different parts of the brain (Barton & Harvey, 2000; Salas et al., 2003; Healy & Rowe, 2007; Powell & Leal, 2014). Indeed, studies on fish and anurans have shown a positive effect of habitat complexity on the size of the cerebellum (motor coordination) and telencephalon (spatial memory) independent of whole brain size (Pollen et al., 2007; Gonzalez-Voyer & Kolm, 2010; Liao et al., 2015). Unfortunately, for most species in our dataset only the size of the complete brain was available.

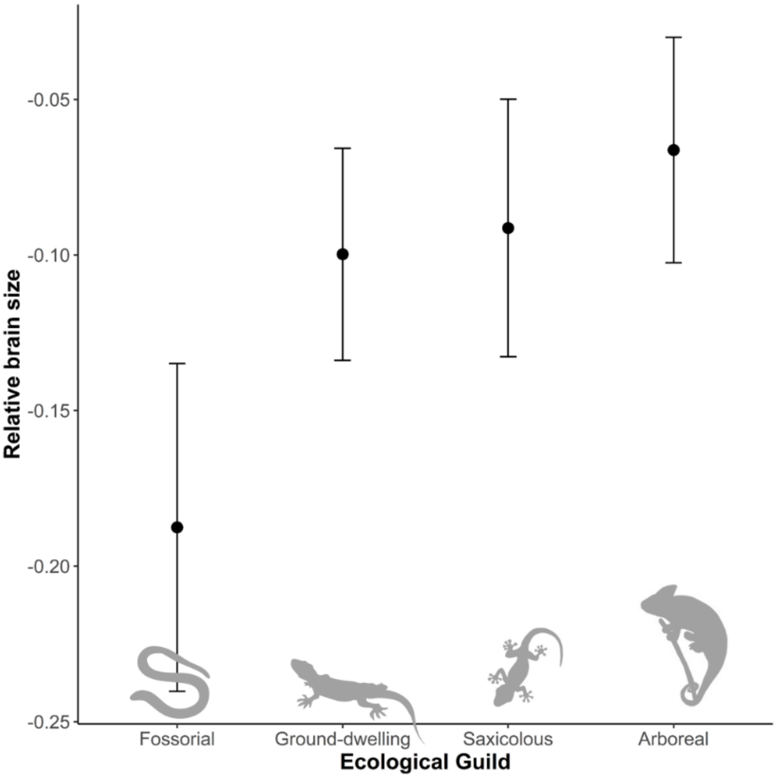

Figure 3. Relative brain size per ecological guild. Residuals of the brain to body mass regression were used for visualisation of results. The model also included limb status and biogeographical realm as confounding variables. There were no statistical differences among ecological guilds. Error bars indicate standard errors.

Secondly, it is also possible that membership of a particular guild may not adequately reflect the degree of habitat complexity each individual species is confronted with. For example, arboreal species, such as *Anolis*-lizards, are often specialized in specific micro-habitats, which can differ considerably in structural complexity (e.g. trunk versus canopy of trees) (Powell & Leal, 2014). Nevertheless, such differences in micro-habitat do not necessarily lead to interspecific differences in brain anatomy (Powell & Leal, 2012; Powell & Leal, 2014). It is also possible that the structural complexity of the environment is determined primarily at a broader ecological scale. For instance, whether a species is arboreal or ground-dwelling, a tropical forest remains a more complex environment compared to a desert (Pamela Delarue et al., 2015). Specific habitat data, both on micro- and macro-scale, was not available for our specimen, but further research incorporating those could provide interesting insights into the ecological factors influencing reptilian brain size.

Despite the general assumption that larger brains lead to higher behavioural flexibility, no association between brain size and habitat generalism was found (Iwaniuk, 2017). The ability to survive in a broader range of habitats may depend more on specific personality traits rather than cognitive skills (Chapple et al., 2012). Birds with greater colonising success were more willing to eat novel food items, but did not have larger brains (Ducatez et al., 2015). Bezzina et al. (2014) found no differences in learning ability between invasive and non-invasive skinks (*Lampropholis delicata* and *guichenoti*), although their results suggested higher explorative behaviour in the invasive species.

Limb reduction in our dataset was associated with a decrease in relative brain size, which is in line with previous findings (Platel, 1979; Heesy et al., 2017). This can be explained by a reduced need for motor coordination, as brain size reduction in limbless species is mainly the result of a smaller cerebellum (Black, 1983; Heesy et al., 2017). Our results clearly demonstrate the necessity to correct for limb reduction in further comparative studies on brain size in Squamata.

We found that Neotropical species had relatively larger brains than Nearctic and Australasian species. These results corroborates findings by Amiel et al. (2011), who noted that small-brained reptiles and amphibians were more successful invaders of Australian ecosystems. The Neotropical region is characterized by high net primary productivity and resource availability (Foley et al., 1996) and species living here may, therefore, afford to develop relatively large and energetically expensive brains (Aiello & Wheeler, 1995; Isler & van Schaik, 2006b). Large parts of the Nearctic and Australasian realm have low resource availability, leading to selection against expensive brains (Foley et al., 1996; Amiel et al., 2011). The complexity of neotropical ecosystems may also favour the evolution of larger brains (Pamela Delarue et al., 2015). However, a more detailed analysis using productivity and resource availability at the exact location where specimens were collected is required for more conclusive insights.

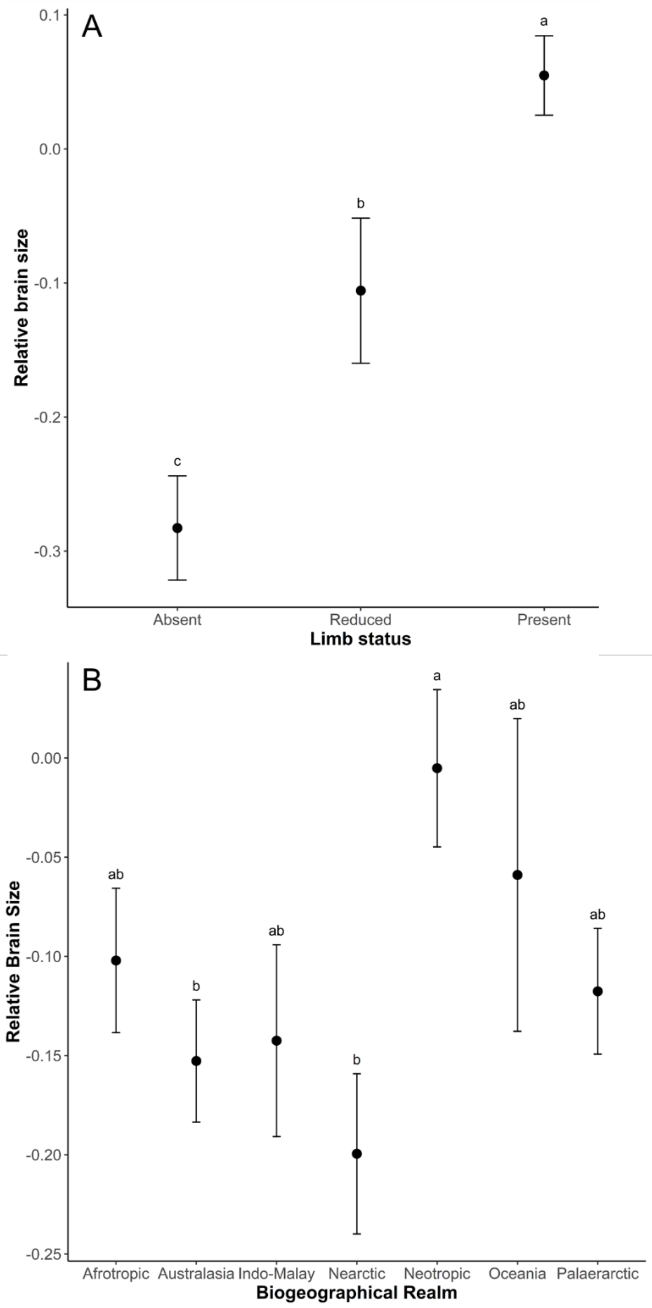

Figure 4. Effect of two ‘confounding’ variables on relative brain size: A) decrease in relative brain size with a higher degree of limb reduction and B) average relative brain size per biogeographical realm. Residuals of the brain to body mass regression were used for visualisation of results. Groups indicated by different letters differ significantly at $p < 0.05$. Error bars represent standard errors.

In sharp contrast to the expectations of the SBH, we found that, within limbed Squamata, solitary species had larger brains than social species. Surprisingly, all models run with the social data gave lambda values lower than or equal to zero, suggesting that related species resemble each other less than expected. Possibly, this is due to the limited number of Squamata for which sociality has been confirmed to be either present or absent (< 1 %, see Gardner et al., 2016). The SBH was initially proposed for and well-supported within primates (Byrne & Whiten, 1988; Dunbar, 1998; Dunbar & Shultz, 2007; Dunbar, 2009; Dunbar & Shultz, 2017). However, our study contributes to a growing list of literature failing to support the hypothesis in other taxa, and therefore questioning the validity of the SBH for species other than primates (Holekamp, 2006; Finarelli & Flynn, 2009; Reddon et al., 2016; Kverková et al., 2018).

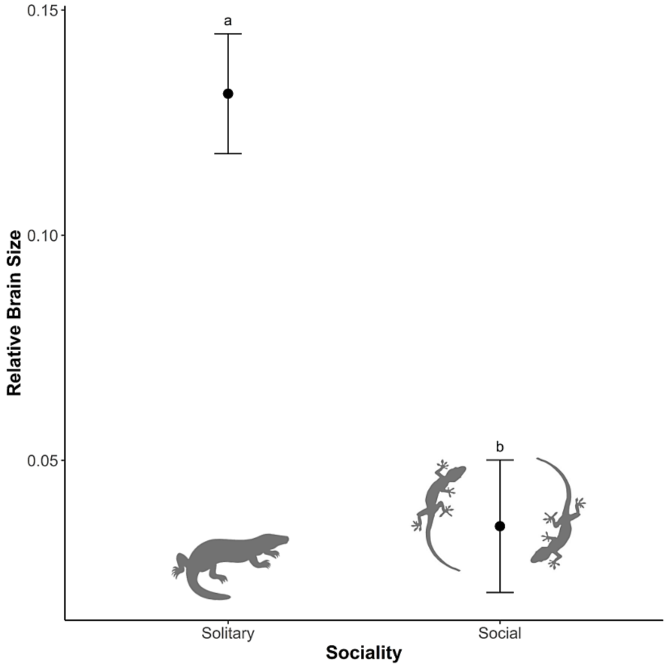

Figure 5. Relative brain size and sociality in Squamata. Residuals of the brain to body mass regression were used for visualisation of results**.** Groups indicated by different letters differ significantly at $p < 0.05$ Error bars represent standard errors.

But even within primates, it has been suggested that both sociality and large brains are consequences of other ecological variables, such as diet or predation pressure (van der Bijl & Kolm, 2016; DeCasien et al., 2017; Powell et al., 2017). Interestingly, Perez-Barberia et al. (2007) suggested that, in mammals, relatively simple social systems can evolve without an enlargement of the brain. Reptilian social systems are often believed to e.g. exhibit more modest levels of communication and cooperation compared to mammals or birds (Gardner et al., 2016) and group-living in reptiles is rarely obligatory or permanent (Whiting & While, 2017). Sociality in reptiles may be less cognitive demanding and, therefore, may not require larger brains. Interestingly in this context, social learning has been documented in both solitary (Noble et al., 2014; Damas-Moreira et al., 2018) and social (Whiting et al., 2018) lizards, but differences in e.g. learning speed between them have not been investigated yet. On the other hand, many solitary species are highly territorial and will thus benefit from e.g. improved spatial memory (Maille & Schradin, 2016; Araya-Salas et al., 2018) through larger brains. To our knowledge, this is the first study to test the SBH in Squamata. Future research should investigate the costs and benefits of sociality in Squamata, which will contribute to a better understanding of our results.

CONCLUSION

While it is generally hypothesized that evolution towards larger brains is driven by environmental complexity, it has recently been questioned whether the same selective forces act on the brain in different vertebrate taxa. In contrast to our expectations, our study found no effect of habitat complexity on relative brain size in Squamata, and solitary species had larger brains than social species. Nor was there a significant correlation between habitat generalism and relative brain size.

Our results might indicate that different selective forces drive brain size evolution in Squamata versus mammals or birds. Further research should incorporate more detailed ecological information (e.g. complexity at the micro- and macrohabitat level) and will benefit from a better understanding of Squamata sociality. We highly encourage comparative studies on brain size in understudied taxa, such as reptiles and amphibians, in order to get a more complete picture of how the vertebrate brain evolved.

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CHAPTER 3

LEARNING WITH LACERTIDS: STUDYING THE LINK BETWEEN ECOLOGY AND COGNITION WITHIN A COMPARATIVE FRAMEWORK.

Adapted from:

De Meester, G., Van Linden, L., Torfs, J., Pafilis, P., Šunje, E., Steenssens, D., Zulčić, T., Sassalos, T. & Van Damme, R. (2019). Learning with lacertids: studying the link between ecology and cognition within a comparative framework. Submitted at Evolution.

ABSTRACT

Cognition is considered essential for animals to deal with environmental challenges. Nonetheless, the ecological forces driving the evolution of cognition throughout the animal kingdom remain enigmatic. Plenty of research has proposed and tested hypotheses regarding the role of social and ecological factors on cognitive evolution, but these have yielded mixed results and thus the answer remains unclear. Large-scale comparative studies on multiple species and cognitive traits have been advanced as the best way to facilitate our understanding of cognitive evolution, but such studies are rare. Here, we test several of the common hypotheses regarding the role of ecology in cognitive evolution, using a dataset on 13 species of lacertid lizards (Reptilia: Lacertidae). We collected cognitive data using a battery of tests measuring inhibitory control, problem-solving, and spatial and reversal learning, and tried to link species' performance to interspecific variation in resource availability, complexity, and habitat variability, as well as their life-history. Although species differed markedly in their cognitive abilities, such differences were mostly unrelated to their ecology and life-history. The sole exception was that species living in temporally more variable environments seemingly performed worse on cognitive tasks typically associated with behavioural flexibility. The standardised approaches in our study provide opportunities for collaborative research which could increase sample size and replication, essential for moving forward in the field of comparative cognition.

INTRODUCTION

The ability to acquire, process, remember, and act upon information from the environment, i.e., cognition, is of vital importance to animals (Shettleworth, 2010). Cognitive skills, such as learning and problem-solving, help animals finding food (e.g., Cooper et al., 2019), avoiding predators (e.g., Font, 2019), locating and recognizing conspecifics and potential mates (Injaian & Tibbetts, 2014), and coping with changing environmental conditions (e.g., Tebbich and Teschke, 2014). Yet, despite its broad advantage, cognition differs greatly across species (e.g., Clarin et al., 2013), populations (e.g., Preiszner et al., 2017), and individuals within populations (e.g. Gatto et al., 2017). A general explanation for this intriguing variability is that local environmental conditions shift the trade-off between the benefits (ability to deal with environmental challenges e.g. via increased behavioural flexibility; Sol, 2009) and costs (developmental, maintenance and operational costs of neural tissue: Mink et al., 1981; Isler & van Schaik, 2006b; Kotrschal et al., 2019) of cognition, resulting in differential selection (Striedter, 2005). However, which exact environmental forces drive the evolution of cognition remains heavily debated (van Horik & Emery, 2011; Mettke-Hofmann, 2014; Holekamp & Benson-Amram, 2017; Henke-von der Malsburg et al., 2020).

The Social Intelligence Hypothesis (SIH) advances group size as the main factor: animals living in larger groups would require advanced cognitive skills in order to process and use all information related to the many social interactions with and between group members (Dunbar, 1998). The Ecological Intelligence Hypothesis (EIH) instead focuses on the non-social challenges that animals face: acquiring resources, evading predators, responding to climatological uncertainty, etc. (Parker & Gibson, 1977; Sol et al., 2005a; Henke-von der Malsburg et al., 2020). The SIH has been (partially) successful in explaining cognitive variability among species that clearly vary in sociality, such as primates (e.g., Dunbar & Shultz, 2017; but see e.g., DeCasien et al., 2017), but its relevance for non-social taxa is questionable (e.g., Kverková et al., 2018). For such lineages, the EIH seems more promising. However, even within the EIH it often remains unclear which exact non-social ecological challenges steer the evolution of cognition (Mettke-Hofmann, 2014; Henke-von der Malsburg et al., 2020).

One popular candidate-driver of cognitive evolution is habitat complexity or spatial complexity (Godfrey-Smith, 2002). The idea is that navigating and exploiting environments with high levels of structural complexity requires advanced cognitive skills, especially spatial learning abilities and spatial memory (Safi & Dechmann, 2005; Lefebvre & Sol, 2008; Shumway, 2008; Sol, 2009). Evidence for this idea is mixed, with some studies finding a clear relationship between habitat complexity and cognitive capacity (e.g., in bats: Safi & Dechmann, 2005; Clarin et al., 2013; in fish: Shumway, 2008; White & Brown, 2015) and others failing to do so (e.g., in reptiles: Powell & Leal, 2014; De Meester et al., 2019 ~ Chapter 2; in amphibians: Liao et al., 2015; in mice: Mackay & Pillay, 2017).

Another hypothesis claims that stronger cognitive skills are mainly required in harsh environments poor in resources. Under such conditions, animals are more likely to benefit from advanced cognitive skills if it helps them to obtain resources and thus survive (Freas et al., 2012; Rochais et al., 2022b). For instance, *Tropidurus*-lizards occupying harsh territories with fewer refuges and lower prey availability learn faster than those from milder territories (Rodrigues & Kohlsdorf, 2019). However, other authors have argued for the opposite case. Cognition is energetically expensive, and animals may need to maintain a continuously high food intake to grow and maintain the neural machinery required for behavioural flexibility (Isler & van Schaik, 2006b; Kotrschal et al., 2019). Thus, animals in environments with low resource availability (lower abundance of prey, limited rainfall, low temperatures) may economize on expensive neural tissue and undergo selection for lower cognitive performance.

A third environmental challenge that animals have to deal with is temporal variability in resource availability and habitat complexity (Godfrey-Smith, 2002). Dealing with unpredictable ecological conditions may require enhanced cognitive skills such as behavioural flexibility and superior learning abilities (Sol, 2009; Fristoe et al., 2017) to keep track of resources in a changing environment, or allow them to learn exploiting alternative resources when familiar ones become depleted. For instance, climate variability has been advanced as a possible driver of among-species variation in cognition: species subjected to erratic precipitation or temperature regimes may require enhanced cognitive capacity to deal with temporally fluctuating availability of resources (e.g., food, water, heat, shelter) and threats (e.g., predators, competitors) (Mettke-Hofmann, 2014). Support for this idea has been found, for example, across populations of chickadees (Roth et al., 2010b; Freas et al., 2012) and chimpanzees (Kalan et al., 2020). and among bird species (Sol et al., 2005a; Schuck-Paim et al., 2008; Fristoe et al., 2017; Sayol et al., 2018). However, other authors have claimed that environmental variability should constrain the evolution of cognition. Animals in highly variable environments may not be able to afford expensive cognitive abilities, as they will experience periods of food shortages and may thus prioritize investment in other functions such as growth or reproduction. This Expensive-Tissue Hypothesis (ETH; Aiello & Wheeler, 1995) has found empirical support in, for example, frogs (Luo et al., 2017) and strepsirrhine primates (Van Woerden et al., 2010).

Another school of thought has tried to link brain size and cognitive capacity to life-history pace (Pagel & Harvey, 1988; González-Lagos et al., 2010; Sol et al., 2016; Street et al., 2017). The premise here is that the energetic costs of developing large amounts of neural tissue force large-brained species to produce fewer, larger neonates that mature more slowly (Isler & van Schaik, 2006a; Isler & van Schaik, 2006b). Also, large brains and high cognitive performance, by their positive effects on e.g., foraging efficiency and predation evasion, are predicted to enhance survival and thus increase longevity (Deaner et al., 2003; Rushton, 2004; Sol, 2009; González-Lagos et al., 2010), further contributing to a slow pace of life. Support for these ideas also is mixed. Several studies have found that large brains and/or high cognitive performance are indeed linked to a slow pace of life (e.g. in mammals: Isler & van Schaik, 2009; in Euarchontoglires but not other mammals: DeCasien et al., 2018; in birds: Jiménez-Ortega et al., 2020), but other found quite the opposite (e.g. computer simulations: Liedtke & Fromhage, 2019b; in killifishes: Eckerström-Liedholm et al., 2021).

A fair number of studies have tested the above ideas by comparing the cognitive capacities of species inhabiting contrasting environments (e.g. in mammals and birds: MacLean et al., 2014; in Carnivora: Benson-Amram et al., 2016; in pit vipers: Krochmal et al., 2018; in skinks: Szabo et al., 2020b; in bees: Collado et al., 2021), but a number of issues complicate the interpretation of the results.

First, many of these studies have used relative brain size as an anatomical proxy of cognition, an approach that is increasingly being criticized (Cauchoix & Chaine, 2016; Healy & Rowe, 2007; Roth et al., 2010b). Brain size, whether absolute or relative, may be a poor predictor of cognitive performance in general (Cauchoix & Chaine, 2016) or of the specific cognitive skills under selection (Hartley et al., 2014). Hence, several authors have advocated the use of more direct, behavioural tests of cognitive performance (Healy & Rowe, 2007; Roth et al., 2010a). Then again, such assays face the difficult obligation of cross-species standardisation: they should be equally relevant for all species involved in the comparison (Roth & Dicke, 2005) or tailored per species (Bitterman, 1975; Shettleworth, 2010; Chittka et al., 2012). Cognitive tests should be carefully standardized to avoid that non-cognitive differences (e.g., in body size, power, agility, motivation) among species confound the interspecific comparison (Krasheninnikova et al., 2020).

Second, because measuring cognition in a sufficiently large number of individuals is time-consuming, many studies compared few species (often only two) and considered only one or two aspects of their cognitive abilities (Krasheninnikova et al., 2020; MacLean et al., 2012; notable exceptions include a study on inhibitory control across 36 mammal and bird species, MacLean et al., 2014; problem-solving in 39 carnivore species, Benson-Amram et al., 2016; and habituation in 13 pit vipers, Krochmal et al., 2018). Low taxon sampling hampers the identification of environmental drivers of among-species variation in cognitive capacity; focusing on single cognitive skills may produce a myopic view of species' cognition.

In this study, we test whether variation in cognitive performance across 13 lizard species (family Lacertidae) can be linked to differences in ecology and life-history. Lacertid lizards do not form complex social groups, so it seems unlikely that group complexity is a significant factor driving cognition in this taxon. Members of the Lacertidae live in a wide variety of habitats and microhabitats across most of Eurasia and Africa, yet are remarkably conservative in many aspects of their morphology, physiology, and behaviour (Arnold, 1989; Arnold et al., 2007), aiding the standardization of cognitive protocols across species. Lacertid species do vary in life-history traits (maturation, clutch size, hatchling size; Bauwens & Díaz-Uriarte, 1997; Bauwens, 1999). We used a battery of different cognitive tests, standardised across species, to gauge the animals' inhibitory control, problem-solving, spatial learning, and reversal learning abilities. We expected to find interspecific variation in cognitive performance, and specifically predicted superior cognitive performance in species living in more complex, harsh and/or variable environments, and/or in species with slower life-history strategies (longer development and lower fecundity).

MATERIALS AND METHODS

Study animals

We measured the cognitive performance of lizards belonging to 13 lacertid species (8 – 71 individuals per species). The animals were either wild-caught (by lasso), obtained via the pet trade, or captive-bred (Table 1). Lizards were sexed based on the presence of femoral pores and/or the hemipenes (Baeckens et al., 2015). Information about each species and its origin is provided in the Supplementary Material & Methods (Study animals and Table S3.3). The animals were housed at the facilities of the University of

Antwerp or associated universities (Supplementary Table S3.1), either in individual terraria or in groups of maximal six individuals. Each terrarium was equipped with sand, hiding spots (rocks and plastic plants), and a drinking bowl. Heat bulbs were suspended above the terraria allowing lizards to thermoregulate. Species-specific details regarding housing are provided in Supplementary Table S3.1. All animals were naïve to cognitive experiments, except for the second batch of *Acanthodactylus pardalis* which had been tested on their (colour) associative learning abilities five months prior to the start of these experiments. More details on the data collected on *Podarcis erhardii* can be found in Chapter 5, and data from *Podarcis siculus* were previously reported in Gavriilidi et al. (2022).

For each animal, the snout-vent length (mm) was measured with a CD-15CPX calliper (Mitutoyo Europe GmbH, Neuss, Germany) with 0.01 mm accuracy, and the sex was noted (Table 1).

Cognitive tests

Five tests were used to measure different aspects of cognition: an inhibitory control task, two problem-solving tests (lid-removal and an escape box), a spatial learning and a reversal learning assay (more details below). The timing of cognitive tests varied slightly among species (Supplementary Table S3.2) but lid-removal always followed upon the inhibitory control task, and reversal learning upon the spatial learning. Experimental trials were performed on weekdays (except during the spatial and reversal learning trials, see further) between 9:00 and 19:00 and test order of individuals was randomized each day. Testing started minimally two hours after the heat bulbs had been turned on, to allow the lizards sufficient time to reach preferred body temperatures.

Table 1. Overview of all species included in this study, total number (N°) of individuals, sex ratio (number of males, females, or unknown), mean snout-vent length (SVL) (mm) ± standard deviation, and origin of the individuals. Coordinates of the wild-caught specimens are found in Supplement.

Species	N°	Sex ratio	Mean SVL (± SD) (mm)	Origin
Acanthodactylus pardalis	26	All ♂	69.5 ± 2.7	Pet-trade from Egypt
Dalmatolacerta oxycephala	25	14 ♂, 9 ♀ 2 NA	53.8 ± 4.0	Wild-caught
Eremias brenchleyi	12	11 ♂, 1 ♀	55.3 ± 2.0	Pet-trade from Hebei Province (China)
Gastropholis prasina	15	8 ♂, 7 ♀,	63.3 ± 6.2	Pet-trade
Lacerta viridis	10	All ♂	116.9 ± 11.9	Wild-caught
Podarcis erhardii	71	35 ♂, 36 ♀	61.9 ± 3.2	Wild-caught
Podarcis melisellensis	19	All ♂	62.2 ± 7.4	Wild-caught from three locations
Podarcis muralis	15	All ♂	64.1 ± 5.2	Wild-caught
Podarcis siculus	22	All ♂	67.8 ± 5.1	Wild-caught
Podarcis ionicus	14	11 ♂, 3 ♀	60.9 ± 8.81	Wild-caught
Takydromus sexlineatus	16	10 ♂, 5 ♀, 1 NA	55.7 ± 3.7	Pet-trade
Timon lepidus	Adults: 2 Juveniles: 6	2 ♂, 6 NA	164.0 ± 17.5 99.8 ± 6.3	Captive-bred (originally from Southern France)
Zootoca vivipara	22	12 ♂, 10 ♀	52.2 ± 4.1	Wild-caught

Lizards were fed one prey item per day during the inhibitory control and lid removal trials, irrespective of task outcome; this strict diet regime was maintained to both increase and standardise hunger motivation within and among species (Amiel et al., 2014). For all tests, the dimensions of the materials (terraria, wooden blocks, petri dishes, escape box) and prey size were adjusted to the size of the species to standardise task difficulty and motivation respectively among species (Supplementary Table S3.2). All materials were cleaned (70% alcohol and water) in-between successive trials. Trials were recorded from above with a Casio EXILIM Pro EX-F1 digital camera (CASIO COMPUTER CO., LTD., Tokyo, Japan) or a JVC Everio GZ-HM400 camcorder (JVC, Yokohama, Japan) and scored manually afterwards. Different species were tested by different observers. Each observer was trained by GDM and used the same example video for scoring to minimise inter-observer variation. Analyses showed that the inter-observer reliability was high (Spearman's $\rho > 0.95$, $p < 0.05$; tested with the R package 'stats' v.3.6.1.). All experimental protocols and procedures, and field permits were ethically reviewed and approved (see Ethics approval).

Inhibitory control

Inhibitory control is the ability to inhibit an instinctive yet ineffective behaviour (Cookson, 1962; Bjorklund & Harnishfeger, 1995; Diamond, 2013) and is considered a crucial aspect of behavioural flexibility (Diamond, 2013; Griffin et al., 2016; Szabo et al., 2020a). Animals may need to exercise inhibitory control to, for example, attack prey at the right moment, avoid eating dangerous food, or stop responding to stimuli that are no longer relevant in a changing environment. Inhibitory control was tested in the lizards using a classical detour task (Diamond, 2013; Kabadayi et al., 2017; Storks & Leal, 2020; Szabo et al., 2020b; Gavriilidi et al., 2022). At the start of an inhibitory trial, a lizard was introduced into a blinded terrarium containing a sandy substrate with the feeding apparatus (a transparent petri dish taped on top of a wooden platform) already present (Figure 1a). A heat bulb was suspended above the arena to ensure that the lizard's body temperature was within the preferred range. After an acclimation period of two minutes, a prey item was introduced into the petri dish and the lizard was allowed 15 minutes to find and eat it. To gain access to the prey, the lizard had to inhibit its natural (but ineffective) tendency to directly attack the prey, and instead reach over the transparent wall (Cookson, 1962; Storks & Leal, 2020; Szabo et al., 2020b). Lizards were tested once a day, but a second attempt was allowed in case the lizard did not touch the dish during its first trial. All lizards were tested until they successfully reached the criterion of succeeding in three out of four consecutive trials (Gomes et al., 2020), or until they had completed ten valid trials (a trial was valid if lizards interacted with the petri dish as to eliminate trials in which lizards did not participate due to a lack of hunger motivation or neophobia). Only lizards that reached the learning criterion were allowed to participate in the lid-removal task (if they were close to reaching the criterion by trial 10, additional trials were run to allow participation in the lid-removal task, but these were not included in the analyses). For each lizard, the solving time (ST_{IC}) was calculated as the time difference between first contact with the dish and grabbing the prey (900 s in case of failure) in each of the trials and then averaged across all trials. In addition, for each individual, it was noted whether they reached the learning criterion within 10 trials or not (Y/N) ($CRIT_{IC}$).

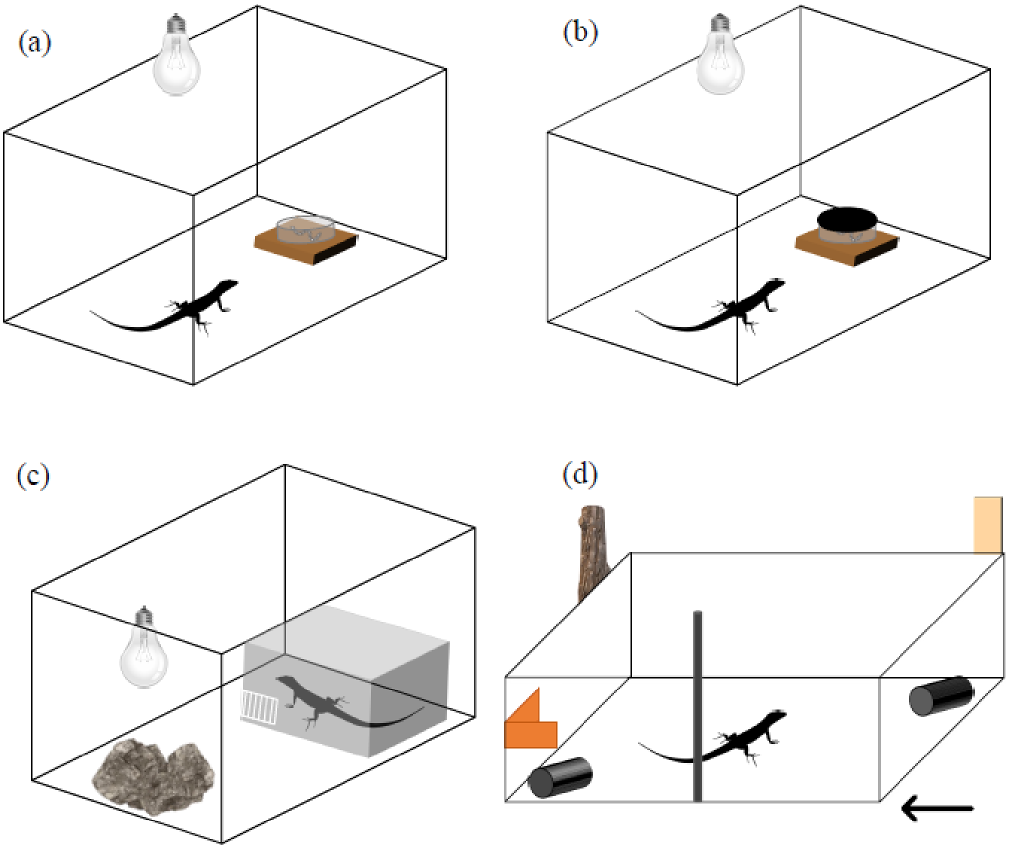


Figure 1. Experimental set-up of the cognitive tests. a) Inhibitory control b) Lid-removal, c) Escape box, d) Spatial and reversal learning (intramaze cue: a piece of orange paper in the bottom left corner of the arena; extramaze cues: a tree trunk at the top left corner, a piece of cardboard at the top right corner, the iron rod, the wall and the position of the observer, indicated by the arrow). The size of all materials was species-dependent (Supplementary Table S3.2).

Problem-solving 1: Lid-removal

The ability to develop new behaviours and/or use pre-existing behaviours in new contexts (i.e. problem-solving) can help animals to survive in unfamiliar and fluctuating environments, e.g., by gaining access to novel or difficult resources more efficiently (Griffin et al., 2016). We assessed our lizards' problem-solving skills by measuring their performance in a lid-removal task (Leal & Powell, 2012; Noble et al., 2014; De Meester et al., 2021 ~ Chapter 4; De Meester et al., 2022 ~ Chapter 5; Gavriilidi et al., 2022). The set-up and protocol closely resembled the inhibitory control trials, but now an opaque plastic disc was placed on top of the petri dish after introducing the mealworm (Figure 1b). The challenge was two-fold: the lizards needed to maintain the inhibitory control of the previous task, while also performing a novel motor action to gain access to the reward under a lid. A lizard was considered successful if it actively removed the disc (either by lifting or pushing it) and directly approached the prey upon doing so (Leal & Powell, 2012; Noble et al., 2014). Sometimes the lid fell off the dish by accident, and the lizard continued attacking the prey through the plastic wall. Such trials were considered invalid. Lizards were tested once a day but a second attempt was allowed in case the lizard did not touch the dish during its first trial. All lizards were tested until they had completed five valid trials. For each lizard, the mean solving time (ST_{LR}) over all valid trials and the proportion of solved trials (i.e., the success rate across five trials) (SR_{LR}) were calculated.

Problem-solving 2: Escape box

The escape box assay (De Meester et al., 2022 ~ Chapter 5; Gavriilidi et al., 2022) was another test used to measure the problem-solving ability of the lizards but offered heat and safety rather than food as a reward (Day et al., 1999b; Holtzman et al., 1999; Paulissen, 2008). A lizard was introduced in a transparent plexiglass box with a white plastic door (containing grooves for manipulation & already slightly opened), through a (sealable) hole in the top of the box (Figure 1c). To escape to a heated basking/hiding spot at the opposite side of the terrarium, the lizards needed to slide open the door (Kis et al., 2015; Siviter et al., 2017b; De Meester et al., 2022 ~ Chapter 5). The lizards had a maximum of 30 minutes to escape (a lizard was considered to have escaped when more than half of its body was outside the box). In case of failure, the door was opened and the lizard was gently directed outwards and allowed to bask for 5 minutes (as reinforcement for the next trials). Lizards were tested once a day, for three consecutive days. For each lizard, the mean solving time (ST_{ESC}) and the proportion of solved trials (i.e., the success rate across three trials, SR_{ESC}) were calculated.

Spatial cognition and reversal learning

Spatial cognition allows an individual to learn and remember the location of important resources such as food, water, and shelter or dangers (Dukas, 2004), which can be critical for survival. Lacertid lizards typically escape from predators by fleeing towards natural refuges (e.g., holes, under stones or logs, etc.). Being able to remember the location of an appropriate hiding spot would likely allow for a faster and more efficient escape and thus increase survival probability (Martín & López, 2003; Paulissen, 2008; Noble et al., 2012; Font, 2019). In a complex and dynamic environment, where the distribution and availability of resources change over time, lizards likely need to continuously update their spatial knowledge, thus requiring strong learning flexibility (Noble et al., 2012). Cognitive flexibility is generally measured using a reversal learning task (Brown & Tait, 2010; Noble et al., 2012), in which animals need to reverse a previously learnt association. This is deemed more difficult than learning something from scratch (Audet & Lefebvre, 2017; Buechel et al., 2018). We tested the learning abilities of our lizards using an ecologically relevant anti-predator protocol in which lizards needed to discriminate between a "safe" and "unsafe" hiding spot based on spatial cues (Noble et al., 2012; Carazo et al., 2014; Dayananda & Webb, 2017; Font, 2019; De Meester et al., 2021 ~ Chapter 4; De Meester et al., 2022 ~ Chapter 5; Gavriilidi et al., 2022).

Spatial learning was tested in large, blinded terraria provided with a sandy substrate and containing two identical hiding spots (black plastic cups cut in half vertically) in opposite corners, one of which was designated a priori as "safe" (left or right relative to the observer, counterbalanced within species). Both intra- and extramaze cues were provided for navigation and orientation (Figure 1d). At the start of a trial, a lizard was introduced into the arena underneath a transparent cover. After two minutes, the observer started simulating a predator attack, by horizontally tapping the base of the lizards' tail with a paintbrush. If the lizard fled into the safe hiding spot, it was left undisturbed for two minutes. If the lizard chose wrongly, the unsafe hiding spot was lifted and the chasing continued until the individual entered the safe hiding spot or until 120 s had passed (after which the lizard was caught and gently placed inside the safe shelter for two minutes). After each trial, the cups were cleaned and the sand was mixed to eliminate potential scent trails. The lizards performed three trials a day, for five consecutive days, after which the locations of the safe and unsafe hiding spots were switched, and the trials continued again for five consecutive days. This resulted in a total of 15 trials per phase (spatial and reversal learning). For each individual, it was noted whether it reached the learning criterion of the spatial learning and reversal learning task ($CRIT_{SL}$ and $CRIT_{RL}$), as well as how many trials were needed to reach the learning criterion (i.e., learning speed) (LS_{SL} and LS_{RL}). In case the learning criterion was not reached, a learning speed of 16 was given. Lizards were considered to be successful if their first choice was correct, and we used a learning criterion of five successes in six consecutive trials (Noble et al., 2014; Vardi et al., 2020; De Meester et al., 2021 ~ Chapter 4; Gavriilidi et al., 2022). However, an individual was only considered to have learned the task when it performed at the same level during the remainder of the trials or improved over the trials (in the number of errors they make), meaning their tally of correct/incorrect choices starting from the learning criterion needed to be $p < 0.10$ (the same level of chance as the five in six learning criterion) (Noble et al., 2012; Carazo et al., 2014; De Meester et al., 2021 ~ Chapter 4).

Reversal learning assays typically switch the reward contingency after animals have been trained either until a certain threshold of success (e.g. Tebbich & Teschke, 2014; Batabyal & Thaker, 2019; Bridgeman & Tattersall, 2019; Bensky & Bell, 2020; Szabo & Whiting, 2020) or after a fixed number of trials (e.g. Moldoff & Westneat, 2017; Madden et al., 2018; van Horik et al., 2018; van Horik et al., 2019b; Boussard et al., 2020; Aljadeff & Lotem, 2021). Here, we opted for the latter approach in order to standardize the experience with the spatial task and the opportunity to learn across species and individuals before moving on to the reversal (van Horik et al., 2018; van Horik et al., 2019b; Aljadeff & Lotem, 2021). Additionally, it is not necessarily guaranteed that reaching the same learning criterion brings all learners to the same level (Aljadeff & Lotem, 2021).

Nonetheless, to take into account that reversing an association requires learning it a priori, we also added a second measure for cognitive flexibility: a learning flexibility score. Lizards were considered to be "flexible learners" (score = 1) (i.e., indicative of high cognitive flexibility) when they succeeded in the spatial task and thereafter successfully reached criterion during the reversal ($CRIT_{SLRL}$) (Noble et al., 2012). Lizards who only learnt in one or neither phase were assigned a score of 0. Lastly, a total score on 30 was also noted as an indicator of overall performance over both phases (i.e., success rate; SR_{SLRL}), as individuals who show excellent general learning abilities will learn fast in both phases and are thus expected to make fewer errors overall.

Environmental variables and life history characteristics

Environmental quality and complexity

We used the Normalized Difference Vegetation Index (NDVI) as a proxy for the lushness of the lizards' habitat, and assume that lush habitats have higher complexity. The NDVI is an index of primary productivity (Pettorelli et al., 2011); higher NDVI values correspond to greener, healthier vegetation and higher plant biomass (Lafage et al., 2014) and have also been linked to arthropod abundance (Roiz et al., 2015; Sweet et al., 2015; Fernandez-Tizon et al., 2020), meaning that it can be used as an indicator of both resource availability (Pettorelli et al., 2011) and habitat complexity (Lassau et al., 2005; Miranda et al., 2018).

An estimation of the NDVI of the environment for each population was obtained with AppEEARS (AppEEARS Team, 2021) using the 250 x 250 m MODIS/Terra MOD13Q1 dataset collected at 16-days intervals (Didan, 2015) (Table 2). The NDVI values were averaged over the entire time period (2000 – 2021) but using only the data for the active season of the lizards (Supplementary Table S3.3). Data points with low quality (e.g., due to clouds or snow) were removed. Precipitation and NDVI were strongly correlated ($\rho > 0.80$, $p < 0.05$), hence only precipitation was retained in the models (see further).

Temperature and rainfall regimes are important determinants of both vegetation lushness (i.e., habitat complexity) (i.e. habitat complexity, Boisvenue & Running, 2006; Ortega et al., 2014) and arthropod abundance (i.e., resource availability) (Dunham, 1978; Stamps & Tanaka, 1981; Spiller & Schoener, 1995; Lessard et al., 2011; Kizito et al., 2017), two environmental factors that may drive cognitive evolution in lizards. In addition, temperature and precipitation can also directly affect the Umwelt of lizards by defining the time window during which lizards themselves can optimize their physiological performance (Adolph & Porter, 1996).

From the CRU-TS 4.03 dataset (Harris et al., 2014) downscaled with WorldClim 2.1 (Fick & Hijmans, 2017) (with a spatial resolution of 2.5 minutes), we extracted climatic variables for each of the locations where our lizards originated from, using the ‘raster’ R-package (Hijmans et al., 2021). In case the exact location of origin was unknown (pet trade animals) we narrowed it down as much as possible and averaged the climatic data of > five known populations of that species in that general region/country (see supplementary Materials & Methods).

As indices of local thermal and hydric conditions, we retrieved the monthly averages of daily minimal (T_{min}) and maximal temperatures (T_{max}), and the monthly precipitation. We disregarded monthly averages outside the species-specific activity season (obtained from literature, Supplementary Table S3.3) of the lizards and calculated the average precipitation and minimal and maximal temperatures experienced by the animals between 2000 – 2018 (as data between 2019 – 2021 was not available). In addition, we calculated the average air experienced by the lizards when active. From T_{min} and T_{max}, and assuming that air temperature follows a sinusoidal path, we calculated hourly estimates of air temperature (Monteith & Unsworth, 1990; Linvill, 2019) and averaged values between 8 am and 7 pm as this time window is most relevant for diurnal lizards (see Supplemental Materials & Methods), as an estimate of average daily temperature (T_{av}) experienced by the lizards between 2000 – 2018. All temperature measures (T_{min}, T_{max} and T_{av}) were highly correlated with each other (Spearman rank correlation tests: all rho > 0.85, $p < 0.05$) (R package 'Hmisc' v.4.3.; Harrel, 2021), thus we only retained T_{av} for further analyses.

Environmental variability

It has been argued that the variability, rather than the average condition of the environment could play a role in the evolution of cognitive capacity (Mettke-Hofmann, 2014). To gauge the temporal variability of the species' environment, we calculated the annual coefficients of variation (CV) in temperature, precipitation and NDVI within each year for the period 2000 – 2018 (Kalan et al., 2020; De Meester et al., 2021 ~ Chapter 4). The average coefficient of variation over the entire time period was then used as an indicator for the environmental variability each species experiences. The seasonality estimates for minimal, maximal, and average air temperature (CVT_{min}, CVT_{max}, CVT_{av}) were strongly intercorrelated ($\rho > 0.84$, $p < 0.05$), so we retained CVT_{av} for further analyses. Seasonality for NDVI and precipitation were also retained as they were not correlated with each other or with temperature (see further).

Life-history

To test the idea that cognitive performance is part of the pace-of-life syndrome (Pagel & Harvey, 1988), we correlated literature data available for the study species with our cognitive test results. The following life-history traits (averages per species) were obtained from the literature (Supplementary Table S3.4): SVL at hatchling stage and maturity as indicators of developmental time (larger individuals have a longer development time) (Adolph & Porter, 1996; Bauwens, 1999) and average clutch size and clutch frequency (n° of clutches per year) as indicators of fecundity (Bauwens, 1999). SVL at the hatchling stage, at maturity, and clutch size are all influenced by female body size (Bauwens, 1999), hence the residuals from a phylogenetic regression analysis with female body size were used (Supplementary Table S3.6) (Meiri et al., 2020). These life-history variables were not intercorrelated in our dataset (all $\rho < 0.40$, $p > 0.05$). For two species, *Gastropholis prasina* and *Eremias brenchleyi*, we were unable to find sufficient life history data, so these species were excluded from these analyses.

Statistical analyses

Data were analysed using Bayesian phylogenetic generalized linear mixed models based on a Markov Chain Monte Carlo algorithm, as implemented in the R-package ‘MCMCglmm’ (Hadfield, 2010). These models allow using the individual data to identify the variables predicting the success, while still accounting for phylogeny. The squamate phylogeny of Tonini et al. (2016), based on sequence data of 17 mitochondrial and nuclear genes was used to estimate phylogenetic interrelations. The tree was pruned to only include the 13 species in our study, using the ‘ape’ package (Paradis et al., 2004).

From each of the cognitive test results, two variables were extracted, both giving an indication of how well an individual performed in a certain test (see Cognitive tests; ST_{IC} and $CRIT_{IC}$, ST_{LR} and SR_{LR}, ST_{ESC} and SR_{ESC}, $CRIT_{SL}$ and LS_{SL}, $CRIT_{RL}$ and LS_{RL}, and $CRIT_{SLRL}$ and SR_{SLRL}). When the response variable was continuous (e.g., average solving time), we used a Gaussian error structure, with a weakly informative inverse γ-distribution prior (V = 1; μ = 0.002) for the residual variance. For count data (e.g., number of solved trials), we used a Poisson error structure, again with a weakly informative inverse γ-distribution prior (V = 1; μ = 0.002). When the response variable was binary (e.g., did or did not reach the learning criterion), we used a categorical error structure in the models, and the prior for residual variance was fixed to one (V = 1; fix = 1). Random effects for phylogeny, species and populations were included in all models with weakly informative inverse γ-priors with a low degree of belief (V = 1; μ = 0.002) for the random effect variance; but in case the priors were too weak, they were adjusted as appropriate. These alternative priors were more informative priors (e.g., V = 100 and μ = 2) and parameter-expanded priors (e.g., V = 1; μ = 1; αμ = 0; αV = 1000). The use of the different types of priors is indicated in the results.

The influence of the environmental quality, temporal variability, and life-history on success during the cognitive tests was assessed with three series of models. The first series of models assessed the influence of environmental quality: Cognition ~ T_{av} + prec. The second series of models tested the effect of temporal variability: Cognition ~ CV_{temp} + CV_{NDVI} + CV_{prec}. The final series of models investigated the link between cognition and life-history: Cognition ~ hatchling SVL + SVL at maturity + clutch size + clutch frequency. All three models also included individual SVL, sex, and side of the safe hiding spot (for spatial and reversal learning) as predictors. Random effects included phylogeny, species and population. Complete separation of the data sometimes led to the removal of a parameter (e.g., sex) (Supplementary Tables S3.8-3.10). We also reran the reversal learning models with only the RL data from individuals that passed the criterion during the spatial learning phase. The results, however, were largely identical to the results from the complete RL or SL+RL data, and are thus only reported in the supplementary material (Table S3.11).

All models were run for 5 million iterations with a burn-in of 5000 and a thinning interval of 500 to generate an effective sample size of minimally > 1000 for all parameters. Convergence of the models was assessed visually from the diagnostic plots, and autocorrelation of successively stored iterations was checked to ensure that it was < 0.1. For each parameter, the mean and 95% confidence intervals (CI) are provided. They were considered statistically significant when the 95% CI did not overlap zero and the p-value from Markov Chain Monte Carlo (pMCMC) was < 0.05 (Hadfield, 2010). In addition, we calculated how much of the variation in cognitive performance was explained by differences among species, by $V_{species} / V_{species} + V_{phylo} + V_{pop} + V_{res}$ from the null models. Similarly, we calculated the phylogenetic signal, Pagel's lambda (λ) (Pagel, 1999), as $V_{phylo} / V_{species} + V_{phylo} + V_{pop} + V_{res}$ (de Villemeuril, 2012).

Ethics approval

All experiments were approved by the Ethical Committee of the University of Antwerp for all but two species. Ethical clearance for the experiments on *Lacerta viridis* and *Podarcis ionicus* were given by the Ethical Committee of the University of Sarajevo (file ID: 01/01-1099/2-2021) and Greek Ministry of Environment and Energy (permit nr.

7M7T4653Π8-ΠΑ5) respectively. Additional ethical clearance was provided by the Dienst Dierenwelzijn (Vlaamse Overheid) for the use of wild-caught individuals of *Dalmatolacerta oxycephala* and *P. siculus* (DWZ/KF/20/1.15/41), and *P. muralis* and *Zootoca vivipara* (DWZ/EV/19/1.15/4). Field permits to capture wild-caught animals were obtained for *D. oxycephala*, *P. siculus* and, *Podarcis melisellensis* (Croatian Ministry of Nature Protection and Energetics, permit nrs.: 517-10-1-1-21-4, 517-10-1-1-21-4, and 517-07-1-1-1-18-5), *L. viridis* (Federal Ministry of Environment and Tourism in Sarajevo, permit nrs.: 04/2-19-2-126/21 and 04/2-19-2-257/21), *P. erhardii* and *P. ionicus* (Greek Ministry of Environment and Energy, permit nrs.: 7ΖΠΡ4653Π8-Ε76 and 7M7T4653Π8-ΠΑ5), *P. muralis* and *Z. vivipara* (Afwijking Soortbesluit van ANB: (permit nrs.: ANB/BL-FF/V19-00099 and ANB/BL-FF/V20-00010). All experiments were in accordance with national legislation.

RESULTS

Descriptive statistics for the cognitive performance per species and per test is shown in Figure 2 and summarized in Supplementary Table S3.5. The climate and life-history variables per species are shown in Table S3.6-3.7.

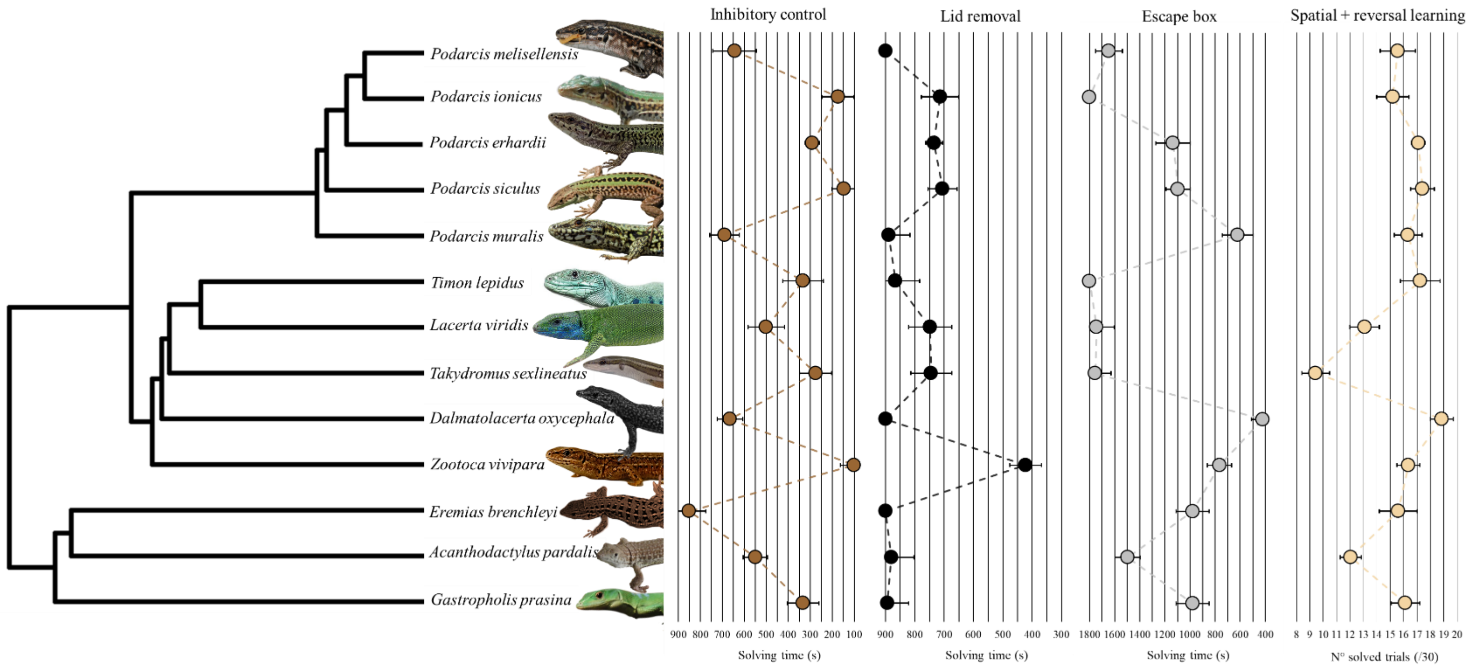


Figure 2. Overview of the results of the cognitive tests. See also Supplementary Table S3.5 for detailed results. Performance success increases along the x-axis. Photo credits: *Podarcis melisellensis*: Bjorn Briesen; *Podarcis ionicus*: Alexandros Bantounas; *Podarcis erhardii*: Soren Reynaert; *Podarcis siculus*: LVL; *Podarcis muralis*: GDM; *Timon lepidus*: Pixabay; *Lacerta viridis*: Adnan Zimić; *Takydromus sexlineatus*: GDM; *Dalmatolacerta oxycephala*: LVL; *Zootoca vivipara*: GDM; *Eremias brenchleyi*: GDM; *Acanthodactylus pardalis*: LVL; *Gastropholis prasina*: LVL

Environmental variables and life history characteristics

The species sampled in this study were taken from a broad diversity of ecological conditions, ranging from very dry (*A. pardalis*, average monthly precipitation: 3.01 ± SD: 1.60 mm) to very wet habitats (*Takydromus sexlineatus*, average monthly precipitation: 176.92 ± 64.89 mm) and from environments with modest (*P. muralis*, average temperature: 14.53 ± 0.55 °C) to very high temperatures (*A. pardalis*, maximal temperature: 29.69 ± 2.63 °C). Some environments had an overall low NDVI (*A. pardalis,* average NDVI: 0.15 ± 0.06), and others had high NDVI/primary productivity (*T. sexlineatus*, average NDVI: 0.76 ± 0.08) (Table S3.6).

Seasonality in the environmental variables also varied strongly from relatively stable habitats in time (*Z. vivipara,* seasonality precipitation: 42.01 (± SD: 8.53) %; *T. sexlineatus*, seasonality NDVI: 5.09 (± 2.81) %; *G. prasina*, seasonality temperature: 5.49 (± 1.29) %) to relatively variable environments (*E. brenchleyi*, seasonality precipitation: 121.13 ± (4.21) %, seasonality NDVI 42.01 (± 8.88) %, seasonality temperature: 97.81 (± 16.97) % (Table S3.6).

The lacertid lizards in our sample also vary in their life-history characteristics. *Acanthodactylus pardalis* has the largest hatchlings (30 mm) and longest SVL (59 mm) at maturity relative to their body size; they also have the most clutches within a year (4 per year). *Zootoca vivipara* has the largest clutch size (7.10 ± 3.82) relative to its size (Table S3.7).

Inhibitory control

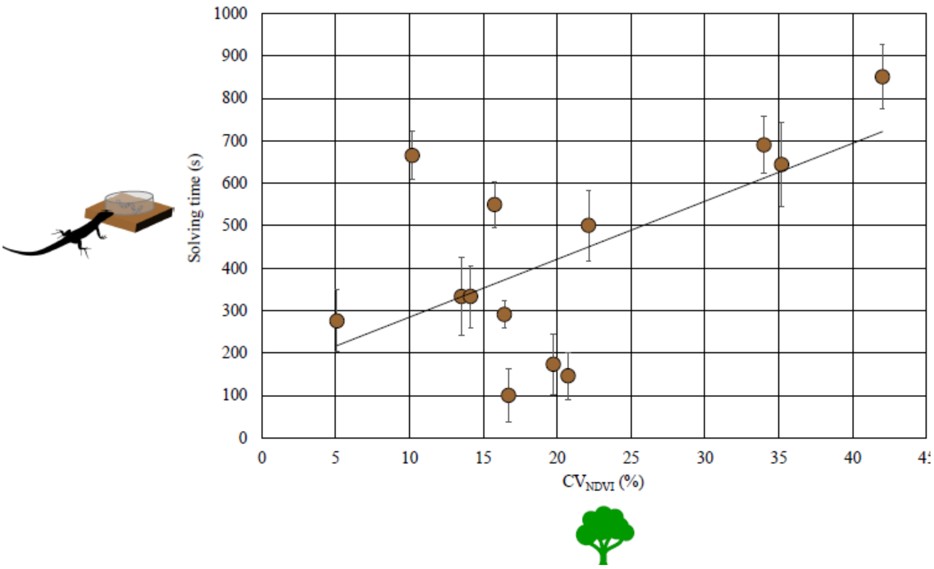
Across all species, 71% of test subjects succeeded in reaching the ($\mathrm{CRIT}_{\mathrm{IC}}$) criterion. The among-species variability in success rate was considerable: while in *Timon lepidus,* *L. viridis* and *P. ionicus* all individuals attained the criterion, only 17% of the *E. brenchleyi* did (Supplementary Table S3.5). Average solving time (ST_{IC}) during successful trials was 119.10 (± SD: 127.18) s, but species averages ranged 16-fold, from 30.28 (± 38.81) s in *Z. vivipara* to 494.33 (± 351.36) s in *E. brenchleyi* (Figure 2). Differences among species contributed to 39% (CI: [0.00, 88.65]) and 17% (CI: [0.00, 50.69]) of the overall variance in success rate and solving time, respectively. Both $CRIT_{IC}$ and ST_{IC} exhibited a weak phylogenetic signal ($\lambda = 0.027$, 95% confidence interval: [0.000, 0.12]; $\lambda = 0.010$ [0.00, 0.035]).

The physical environment, i.e., T_{av} and precipitation, did not predict success rate and solving time in the inhibitory control trials ($pMCMC > 0.58$) (Table S3.8). Lizards from environments with a high seasonality in NDVI were less successful ($CRIT_{IC}$~CV_{NDVI}: posterior mean [95% confidence interval]: -0.24 [-0.45, -0.05], $pMCMC < 0.05$) and solved the task slower (ST_{IC}~CV_{NDVI}: 23.80 [6.76, 40.45], $pMCMC < 0.05$) (Figure 3). None of the life-history variables were associated with inhibitory control performance ($pMCMC > 0.22$) (Table S3.10).

Lid removal

Our first measure of problem-solving ability, i.e., performance in the lid-removal task, also differed considerably among species. Across all species, the average success rate (SR_{LR}) was 22%. However, while individuals of *Z. vivipara* removed the lid in 61% of all trials, none of the *D. oxycephala*, *P. melisellensis* and *E. brenchleyi* individuals solved the task even once (Table S3.5). Across species, the average solving time ST_{LR} was 291s.

(a) Average solving time during the inhibitory control task vs. CV_{NDVI}



(b) Proportion successful individuals in the inhibitory control task vs. CV_{NDVI}

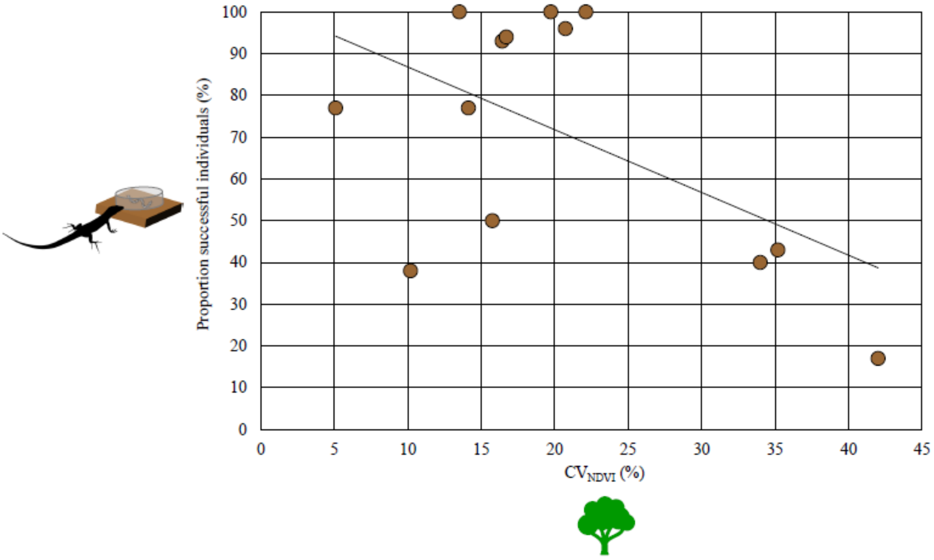


Figure 3. a) Solving time during the inhibitory control task (s) vs. CV_{NDVI} (%). Each dot represents a species. Species from environments with a high seasonality in NDVI solved the task slower (MCMCglmm results - posterior mean [95% confidence interval]: 23.80 [6.76, 40.45], pMCMC < 0.05). b) Mean CV_{NDVI} (%) of successful individuals (reaching the criterion of solving three in four consecutive trials) vs. the non-successful individuals. Each dot represents a species. Species from environments with a high seasonality in NDVI were less successful (MCMCglmm results: -0.24 [-0.45, -0.05], pMCMC < 0.05).

Individual *P. muralis* performed worst, (ST_{LR}= 691.00 ± 0 s), with individuals of *Z. vivipara* solving the problem almost 5 times faster (ST_{LR} = 142.60 ± 126.94 s; Figure 2). Among-species differences explained 19% ([0.00, 66.28]) of the variation observed in SR_{LR} and 5% ([0.00, 21.02]) in ST_{LR}. Both SR_{LR} and ST_{LR} had a weak phylogenetic signal ($\lambda = 0.018$ [0.00, 0.057]; $\lambda = 0.005$ [0.00, 0.013]).

None of the aspects of the physical environment of the lizards were associated with solving time. However, across species, larger lizards tended to remove the lid more often than smaller ones (SR_{LR}~SVL: 0.030 [-0.004, 0.065], pMCMC = 0.07) (Table S3.8). Also, lizards originating from areas with high NDVI seasonality tended to perform poorly in the lid-removal test: they needed more time (ST_{LR}~CV_{NDVI}: 11.13 [-0.53, 22.28], pMCMC = 0.06) and less often succeeded (SR_{LR}~CV_{NDVI}: -0.18 [-0.42, 0.034], pMCMC = 0.07) (Table S3.9). None of the life-history variables correlated with lid removal performance (all pMCMC > 0.47) (Table S3.10).

Escape box

Species differed in how often and how fast they solved the escape box task. Across all species, the average solving time for the successful trials (ST_{ESC}) was 550.08 (± 401.18) s, ranging from 269.95 (± 202.32) s in *D. oxycephala* to 1046.57 (± 504.39) s in *P. melisellensis*. The average proportion of solved trials (SR_{ESC}) was 46% (± 44) across all species, from 0% in individuals from *T. lepidus* and *P. ionicus* to 91% (± 4) in *D. oxycephala*. Among-species variation is 14% ([0.00, 57.35]) for ST_{ESC} and 53% ([0.00, 87.50]) for SR_{ESC}. The phylogenetic signal was weak for ST_{ESC} ($\lambda = 0.020$ [0.00, 0.053]), but moderate for SR_{ESC} ($\lambda = 0.15$ [0.020, 0.30]).

Larger individuals escaped slower (ST_{ESC}~ SVL: 8.18 [0.40, 15.29], pMCMC < 0.05) (Table S3.8). No other variables predicted escape time or success rate (pMCMC > 0.18) (Table S3.8-3.10).

Spatial cognition

Of all the specimens tested, 43% reached the spatial learning criterion ($CRIT_{SL}$). These animals required on average 8.27 (± 3.25) trials (learning speed, LS_{SL}) to learn the location of the safe hide. The number of individuals reaching the criterion ranged from 20% in *T. sexlineatus* to 56% in *D. oxycephala*, and average learning speed per species varied between 6.83 (± 1.47) trials in *L. viridis* and 11.50 (± 0.71) trials in *T. sexlineatus* (Figure 2). Differences among species explained 6% ([0.02,23.18]) of the variation in $CRIT_{SL}$ and 7% ([0.25, 22.33]) in LS_{SL}. The phylogenetic signal of LS_{SL} was weak (λ = 0.008 [0.002,0.08]), as was the one for $CRIT_{SL}$ (λ = 0.004 [0.00,0.012]).

Spatial learning exhibited laterality and sexual dimorphism. Lizards for which the safe hiding spot was positioned on the right side of the arena had lower LS_{SL} (LS_{SL} ~ Safe side: 0.13 [0.035, 0.22], pMCMC < 0.05), and were less successful in reaching the learning criterion ($CRIT_{SL}$~ Safe side: -0.53 [-1.17, 0.094], pMCMC < 0.05). Male lizards were less likely to succeed than females ($CRIT_{SL}$~Sex: -0.77 [-1.54, -0.012], pMCMC < 0.05). None of environmental or life-history variables were associated with LS_{SL} and $CRIT_{SL}$ (pMCMC > 0.20) (Table S3.8-3.10).

In the reversal learning task, 45% of the individuals successfully reached the learning criterion ($CRIT_{RL}$), needing on average 8.45 (± 3.01) trials (LS_{RL}). Individuals of *P. siculus* were most successful, with a 64% of individuals reaching the criterion. In sharp contrast, that percentage was a mere 3% in *E. brenchleyi* (Table S3.5). *Lacerta viridis* and *P. ionicus* individuals most rapidly adjusted their behaviour to the new situation, needing respectively 6.00 (± 1.00) and 6.00 (± 1.73) trials. At the other extreme, individuals *A. pardalis* on average required 10.75 (± 1.89) trials (Figure 2). Differences among species explained 6% ([0.01, 27.46]) of the variation in $\mathrm{CRIT}_{\mathrm{SL}}$ and 7% ([0.27, 23.31]) in $\mathrm{LS}_{\mathrm{SL}}$. The phylogenetic signals for $\mathrm{LS}_{\mathrm{RL}}$ and $\mathrm{CRIT}_{\mathrm{RL}}$ were $\lambda = 0.009$ ([0.002,0.020]) and $\lambda = 0.005$ ([0.0001,0.015]), respectively.

Precipitation, temperature, NDVI, and the seasonality in the latter two variables did not predict $\mathrm{LS}_{\mathrm{RL}}$ or $\mathrm{CRIT}_{\mathrm{RL}}$ (pMCMC > 0.40) (Table S3.8) (Table S3.9). However, lizards originating from environments with low precipitation seasonality tended to be more likely to reach the learning criterion ($\mathrm{CV}_{\mathrm{PREC}} \sim \mathrm{CRIT}_{\mathrm{RL}}$: -0.016 [-0.034, 0.003], pMCMC = 0.09) (Table S3.9). As with spatial learning, lizards presented with the safe hiding spot positioned on the right side of the arena were slower reversal learners (0.12 [0.02, 0.21], pMCMC < 0.05) and were less likely to reach the criterion (-0.83 [-1.49, -0.16], pMCMC < 0.05). None of the life-history characteristics correlated with performance in the reversal learning task (pMCMC > 0.37 (Table S3.10).

Across all specimens measured, only 12% of lizards reached the learning criteria of both spatial and reversal learning tasks. Among-species variation accounts for 20% ([0.00,63.43]) of the total variation in $\mathrm{CRIT}_{\mathrm{SLRL}}$ and for 47% ([5.16, 89.39]) of that in $\mathrm{SR}_{\mathrm{SLRL}}$. With 36% of its individuals reaching $\mathrm{CRIT}_{\mathrm{SLRL}}$, *D. oxycephala* proved the most flexible learning species. At the other extreme, none of the individuals of *A. pardalis, E. brenchleyi* and *P. melisellensis* managed to both learn and re-learn during both phases (Figure 2). Both $\mathrm{CRIT}_{\mathrm{SLRL}}$ and $\mathrm{SR}_{\mathrm{SLRL}}$ exhibited a weak phylogenetic signal ($\lambda = 0.092$ [0.00, 0.0037]; $\lambda = 0.096$ [0.004, 0.25]). Environmental quality did not predict performance in the spatial cognition tasks (pMCMC > 0.21). The same result was found for life-history characteristics (pMCMC > 0.17) (Table S3.10). Lizards from areas with high seasonality in precipitation and NDVI tended to perform more poorly in both spatial cognition tasks ($CRIT_{SLRL}$~CV_{prec}: -5.65 [-13.24, 0.56], pMCMC = 0.06; $CRIT_{SLRL}$~CV_{NDVI}:-18.85 [-45.68, 4.01], pMCMC = 0.10).

DISCUSSION

Our results indicated that species of the family Lacertidae, although similar in many aspects of their morphology, physiology and behaviour (Arnold, 1989; Arnold et al., 2007) differ markedly in their problem-solving skills and learning abilities. The origin of this variation remains obscure; we found little evidence for a link with life-history, climate or habitat characteristics. At the most, there was a weak trend for species originating from areas with high environmental seasonality to have relatively poor cognitive performance. The cognitive traits considered exhibit very little phylogenetic signal, suggesting that they may evolve rapidly. Below, we discuss the (lack of) support for each of the hypotheses proposed at the beginning of this paper.

The first hypothesis suggested that lizards living in spatially more complex habitats should exhibit superior cognitive skills (Godfrey-Smith, 2002; Safi & Dechmann, 2005; Mettke-Hofmann, 2014). Our data, however, lend no support to this idea, as none of the cognitive variables were related to habitat complexity. We should, however, be cautious with interpreting the lack of such a relationship. As NDVI and precipitation were highly correlated, we only retained precipitation in the final models, and thus did not test the effect of habitat complexity directly. Nonetheless, it can be assumed that environments with more rainfall will grow more dense and green vegetation and thus be structurally more complex (Lassau et al., 2005; Miranda et al., 2018; but see below).

Previous research on reptiles revealed that relative brain size (and the assumed concomitant cognitive skills, but see Cauchoix & Chaine, 2016) does not correlate with habitat complexity across species (Powell & Leal, 2014; De Meester et al., 2019 ~ Chapter 2). However, lesser earless lizards (*Holbrookia maculata*) and Aegean wall lizards (*P. erhardii*) from more complex habitats had respectively larger medial cortices (brain region involved with spatial cognition) and higher spatial learning success compared to conspecifics from more sparsely vegetated and simple environments (Calisi et al., 2017; De Meester et al., 2022 ~ Chapter 5). This suggests that habitat complexity shapes cognitive variation at the population-level, but that different factors are at hand driving cognitive divergence among species. Alternatively, it has been shown that juvenile bronze anoles (*Anolis aeneus*) defend smaller territories in more visually restricted (complex) environments (Eason & Stamps, 1992), and that many-spotted tree iguanas (*Liolaemus multimaculatus*) in forested areas have smaller home ranges than iguanas in open areas (Stellatelli et al., 2016). So perhaps species in more complex habitats compensate by reducing their space use, thus negating the need for higher (spatial) cognitive abilities (but see Perry & Garland, 2002).

On the other hand, a number of methodological limitations may have prevented us from establishing a relationship between habitat complexity and cognition in our study system. Precipitation may not be an adequate measure for structural habitat complexity, and even NDVI, although successfully used in previous studies (Lassau et al., 2005; Miranda et al., 2018), is probably but a crude proxy. NDVI measures the density of green vegetation of an area but ignores other components contributing to spatial complexity, such as rocks and walls, thermal heterogeneity, or the detailed 3D-geometry of the vegetation (e.g., number of layers, distance between branches etc.). NDVI-measures obtained for our populations did correspond with our 'gut-feeling' of habitat complexity (e.g., lowest value for the semi-desert environment of *A. pardalis*, highest value for the dense heathlands of *Z. vivipara*), but frankly, it remains highly unclear what makes a microhabitat 'simple' or 'complex' to a lizard. In addition, NDVI is highly correlated with precipitation, and both variables are associated with resource availability (primary productivity, arthropod abundance etc.) (Stamps & Tanaka, 1981; Spiller & Schoener, 1995; Boisvenue & Running, 2006; Pettorelli et al., 2011; Roiz et al., 2015; Sweet et al., 2015; Fernandez-Tizon et al., 2020; Kalan et al., 2020). Our current analyses thus do not allow us to detangle the effects of structural habitat complexity and resource availability (albeit it could be argued that higher prey availability implies higher prey diversity which also contributes to the complexity of the environment, see Mettke-Hofmann et al., 2002). This may be problematic as structural complexity and food availability could theoretically have opposite effects on cognitive ability, although due to their strong interconnectedness a more experimental approach may be needed to unravel their separate effects on cognitive evolution and development.

The second hypothesis proposed that species from resource-poor environments would have undergone selection for lower cognitive abilities due to the high costs associated with neural machinery (Mink et al., 1981; Brust et al., 2014; Munch et al., 2018). Alternatively, stronger cognitive abilities could actually help animals to acquire resources and survive in such harsh environments (Freas et al., 2012). Yet, our indicators for environmental quality (temperature and precipitation) were unrelated to any of the cognitive variables, in either direction. One intriguing possibility is that selection favours both high and low cognitive abilities simultaneously, as both may be equally viable strategies to deal with resource scarcity. Similarly, Fristoe and Botero (2019) demonstrated that bird species occurring in harsh and variable climates either have very large or very small brains (relative to their body size). Testing this hypothesis of possible disruptive selection in lizards using actual cognitive data would, however, require a more elaborate study with a larger number of species. Nevertheless, we should once again take into account that temperature and precipitation are only crude proxies for resource availability. How these variables influence arthropod abundance and the lizards' opportunities to prey upon them, is something that needs to be investigated in more detail.

A third hypothesis claimed that environmental variability would favour higher cognitive abilities and behavioural flexibility (Allman, 2000; Deaner et al., 2003; Sol, 2009; Kalan et al., 2020). Our data does not support this hypothesis and even points towards the opposite trend. Species experiencing higher variability in NDVI seemingly showed weaker inhibitory control, problem-solving and learning flexibility, while species exposed to more seasonal precipitation regimes tended to have reduced reversal learning abilities and learning flexibility. Inhibitory control, problem-solving and reversal learning are all considered indicators of behavioural flexibility (Tebbich & Teschke, 2014; Szabo et al., 2019b; Szabo et al., 2020a; but see Audet & Lefebvre, 2017). Hence, environmental variability appears to select for lower behavioural flexibility in lacertid lizards. Animals in more variable environments may frequently experience periods of food scarcity, and could thus struggle to uphold a sufficient high energy intake to maintain costly cognitive abilities. When food becomes more abundant again, it may be wiser to prioritize investing in growth, reproduction or building fat reserves instead of neural circuitry (Van Woerden et al., 2010; Luo et al., 2017). Additionally, if the environment becomes too variable, animals may never learn faster than their surroundings change, rendering higher cognition ultimately pointless (Niemela et al., 2013).

It is also surprising that seasonality constrained some, but not all (spatial learning, escape box), aspects of cognition within lacertids. A first explanation could be different costs of different traits. Inhibitory control, problem-solving and reversal learning are probably more expensive than spatial learning, as they require (higher rates of) adult neurogenesis (Burghardt et al., 2012; Zhang et al., 2012; Kalm et al., 2013; Swan et al., 2014; Audet et al., 2018) and may thus be more strongly selected against when resources are scarce. A second explanation may be that spatial learning is absolutely necessary for every species, e.g., to evade predation (Font, 2019), and should thus be maintained even if resources are scarce or variable. Thirdly, the curious fact that lid-removal performance was linked to environmental variability, but escape box performance was not, may indicate that these tasks did not measure the same cognitive ability (problem-solving) after all. Indeed, we previously reported that individual scores on both tests are not necessarily correlated (De Meester et al., 2022 ~ Chapter 5). Problem-solving assays are notoriously criticized because it is often unclear which exact cognitive processes are being measured, and to what extent test outcome is affected by non-cognitive factors such as stress, motivation or personality (Griffin & Guez, 2014; Audet & Lefebvre, 2017). Interestingly, body size positively affected the outcome of the lid-removal task, but had a negative impact on escape box performance. This may actually reflect motivational differences in both tasks. Larger species/individuals may behave bolder, as they are sometimes found to be less vulnerable to predation (Blomberg & Shine, 2000; Bajer et al., 2015; but see Samia et al., 2016). Bolder individuals will spend less time being vigilant and can thus investigate the lid-removal apparatus more intensively, thereby increasing their chance of success. Contrariwise, larger and bolder lizards may be less motivated to leave the escape box and find shelter. Nevertheless, it is also possible that it was simply more easy for larger species to reach over the petri dish and lift the disc, even despite our size-adjustments.

Lastly, it is interesting that different sources of environmental variability (NDVI seasonality vs. precipitation seasonality) affect different cognitive traits, albeit why is currently unclear to us. Taken together, our results imply that various aspects of cognition evolve independently from each other in response to different environmental pressures, rather than in conjecture as proposed by the idea of ‘general intelligence’ (Bräuer et al., 2020). Many ecological and evolutionary studies use either brain size or performance on a single cognitive task as proxy of ‘cognition’, but our results clearly highlight how important it is to consider a broad range of cognitive skills (Shaw & Schmelz, 2017).

The final prediction was that a slower pace of life (fewer but larger offspring, slower development and maturation) would be associated with higher cognitive abilities, due to energetic trade-offs (Isler & van Schaik, 2006; Isler & van Schaik, 2009; DeCasien et al., 2018; Jiménez-ortega et al., 2020). However, in our sample, no apparent relationship between life-history and cognition was found. We propose the following explanations. Firstly, perhaps species with a fast life-history are still able to afford high cognitive abilities because they limit energetic investment in other traits, such as immune function (Kotrschal et al., 2016) or somatic maintenance (Kotrschal et al., 2019; van der Woude et al., 2019). For instance, across killifish (Aplocheiloidei), fast-living species grow rapidly, have high reproductive rates and relative large brains, but this presumably comes at the price of very fast aging (Eckerström-Liedholm et al., 2021). But this scenario seems unlikely for our study system, as in Lacertidae fast-reproducing species may actually live longer (Bauwens & Díaz-Uriarte, 1997). Unfortunately, we lack data on the lifespan of our species to verify this hypothesis. Secondly, slower maturation may indeed permit the growth of larger brains in species with parental care, but in precocial species, juveniles need to be equipped with their full range of cognitive skills at the moment of birth (Szabo et al., 2019a). Pre-natal development may then be more important to take into consideration for our precocial lizards. Indeed, it has previously been reported that egg incubation time and relative brain size are positively associated in reptiles, at least at the family-level (Birchard & Marcellini, 1996). Lastly, the life-history traits used in our study are often species-averages, but such characteristics are known to vary considerably across the geographic range of a species (Sorci et al., 1996; Roitberg et al., 2015) and can be influenced by factors such as temperature and body size (Bauwens, 1999).

The low phylogenetic signals of cognition within our dataset suggest that cognitive performance is not constrained by phylogeny and can change rapidly between species. Nonetheless, our analyses failed to find strong support for either habitat complexity, climate, environmental variability, or life-history as drivers of this cognitive divergence among lacertids, meaning that it is likely that other, undocumented, (socio-)ecological forces must be responsible for the large amount of intraspecific variance observed in this study. One such force may be predation. Predation pressure in the environment strongly affects selective regimes on life-history (e.g. Schwarz et al., 2020), personality (e.g. Lapiedra et al., 2018) and likely cognition as well (e.g. Brown & Braithwaite, 2005; Burns & Rodd, 2008). Larger brain sizes have been linked to enhanced survival under high predation risk in eiders (*Somateria mollissima*, Jaatinen et al., 2019), guppies (*Poecilia reticulata*, Kotrschal et al., 2015a) and velvet geckoes (*Amalosia lesuerri*) with better spatial skills have been shown to survive longer in nature, presumably due to being more successful in locating shelter and evading predators (Dayananda & Webb, 2017). Predation pressure is notoriously difficult to estimate in the wild, but would nonetheless be a valuable factor to account for in future studies.

While our estimations for the amounts of interspecific variation were relatively large (5 – 53% of the total variance), their confidence intervals were also quite broad and overlapped with zero, and should thus be taken with some caution. This could of course be due to our limited sample sizes. On the other hand, it does suggest that a considerable portion of cognitive variation was due to intraspecific differences. Indeed, within lizard species, cognitive performance can be affected by learning biases (e.g. side bias: this study; Szabo et al., 2019b; De Meester et al., 2021 ~ Chapter 4; visual pattern bias: Paulissen, 2021), age (e.g., Noble et al., 2014), personality (e.g., Goulet et al., 2018), developmental conditions (e.g. Amiel & Shine, 2012; Amiel et al., 2014; Munch et al., 2018), microhabitat (Rodrigues & Kohlsdorf, 2019), and sex (e.g., this study; Carazo et al., 2014), and can vary across populations of the same species (e.g., Batabyal & Thaker, 2019; Pettit et al., 2021). Our data are not ideal for assessing the relative contribution of within and across species variation in cognition. Opportunistic sampling, resulting in highly unequal sample sizes per species and uneven sex-ratios, may have inflated within-species and reduced among-species variation in our study.

One factor explaining cognitive variation within species was sex. Currently, the link between cognition and sex in lizards has received little attention (Carazo et al., 2014; Szabo et al., 2019c; De Meester & Baeckens, 2021). In general, male animals are assumed to exhibit stronger spatial learning abilities due to the higher spatial demands associated with their reproductive strategies, e.g., larger home ranges, obtaining and defending territories, actively searching and remembering the location of females, male dispersal etc. (Gaulin & FitzGerald, 1986; Jones et al., 2003; Ecuyer-Dab & Robert, 2004; Carazo et al., 2014; Araya-Salas et al., 2018; Szabo et al., 2019c). However, female lacertid lizards exhibited faster spatial learning than males, which directly contradicts the scarce results from previous lizard studies (Carazo et al., 2014; Szabo et al., 2019c). There are a few possible explanations for this. A first possibility may be that within our species, females have larger home ranges. But this seems unlikely, as larger male home ranges are a general pattern across Lacertidae and Autarchoglossa (Perry & Garland, 2002). Secondly, females may face another kind of spatial challenges. Gravid female lizards, for instance, are extremely vulnerable to predation due to their reduced mobility (Shine, 1980). As such, females may actually need better knowledge about their immediate surroundings (e.g., hiding spots) because they lack the speed to correct mistakes when being attacked by predators. Thirdly, it has also been proposed that male spatial cognition is shaped by sexual selection and mostly requires spatial skills over a larger scale, while female spatial abilities are shaped by natural selection (prioritizing survival) and are more finetuned at a smaller spatial scale (Ecuyer-Dab & Robert, 2004). So perhaps male lizards would excel if they were tested on a spatial mate searching rather than antipredator task (as in Kotrschal et al., 2015b), or if we had measured long-range navigation rather than remembering local landmarks (Ecuyer-Dab & Robert, 2004). Lastly, these sex-differences in spatial learning may reflect differences in cognitive style (Sih & Del Giudice, 2012). The Cognitive Style Hypothesis predicts that fast learning comes at the cost of accuracy and flexibility. Males may indeed face stronger spatial demands, and therefore require more detailed and more accurate knowledge about their surroundings, and hence seem to learn slower. Females may then learn faster because they only learn superficially (Sih & Del Giudice, 2012; Dougherty & Guillette, 2018). Whether males and females differ in the precision of their spatial memory could be tested by comparing how their (post-criterion) performance changes when some of the spatial cues are removed from the set-up. We also propose that a more elaborate experiment, in which we consistently sample both sexes across multiple species, while collecting data on their territorial behaviour, sex-dependent dispersal and home range sizes, could greatly benefit our understanding of how sex-differences in cognition evolve.

Finally, we care to highlight some shortcomings of our study that may have clouded any relationships between ecology and cognition in Lacertidae. Firstly, although our current list of study animals includes species from a wide geographic and ecological distribution, it is nevertheless somewhat biased towards Mediterranean species of the genus *Podarcis*. In an ideal world, we would have included e.g., more desert and tropical species.

Secondly, we obtained several species via the pet trade, that were either wild-caught but with an unknown origin (two) or captive-bred (three). As a consequence, their environmental variables are probably less accurate. In fact, we should take into account that our environmental information in general was measured at scales that may be irrelevant for our lizards. For example, the complexity of an individual's environment may be determined at the microhabitat-level rather than the macrostructure (White & Brown, 2014; White & Brown, 2015). Lizards may also compensate for unfavourable climatic conditions by adjusting their thermoregulatory behaviour, although the argument could be made that this precisely requires cognitive flexibility. Thirdly, the cognitive abilities of the captive-bred species may not be a true reflection of their mental abilities in the wild, as being reared and raised in more simple and monotonous conditions (less temporal variation, structural simple, lack of social interactions, etc.) may have impaired their cognitive development (Vardi et al., 2020). The literature on the effect of captivity on reptile cognition is limited. Vardi et al. (2020) found that lab-raised delicate skinks (*Lampropholis delicata*) showed worse spatial learning compared to their wild-caught mothers, but Szabo et al. (2020b) found no differences in inhibitory control between captive-born and wild-caught sleepy lizards (*Tiliqua rugosa*). At last, a conceptual shortcoming is that interpretations regarding the link between ecology and cognition were hampered by the fact that we know very little about the role of these cognitive abilities during the day-to-day behaviour of our study species. Exactly how specific cognitive traits help these lizards escape predators, forage, or find partners, has not been established. Note, however, that such a limitation is far from unique for our study. In general, there is a dire need to better understand how cognition measures in the lab relate to ecological relevant behaviour in the wild (De Meester & Baeckens, 2021; Szabo et al., 2022).

One of the central goals of the field of comparative cognition is to unravel the selective pressures that have shaped cognitive variation across the animal kingdom (Krasheninnikova et al., 2020). The most promising approach to reach this objective is by conducting large scale comparisons in cognitive performance across multiple species, preferably on a series of tasks probing different cognitive domains (MacLean et al., 2012; Shaw & Schmelz, 2017; Krasheninnikova et al., 2020). Unfortunately, such comparative studies are scarce, and our understanding of cognitive evolution has been hindered by a lack of taxonomic diversity, standardised protocols and replications (Beran et al., 2014; Farrar et al., 2020; Krasheninnikova et al., 2020). We believe that our study both illustrates the merits of a comparative cognitive approach, and also provides a feasible and replicable protocol that could easily be extended towards other reptile taxa. Our methods require little to no training, and are easily standardisable, which opens the potential for international collaborations. Although most comparative research on cognition has focused on mammals and birds (Shettleworth, 2009; Szabo et al., 2021b), we think that reptiles have the potential to become an excellent study system within this field. Recent research has indeed revealed that reptiles are capable of problem-solving, rapid and flexible learning, response inhibition, and even social learning (reviewed in De Meester & Baeckens, 2021; Szabo et al., 2021b). Their broad ecological and taxonomic diversity (Vitt & Caldwell, 2014), in combination with their easy collection and housing in large numbers, can be used to address many questions regarding the role of ecology in cognitive evolution. Even the large ecological variation within species (e.g., *Z. vivipara* occurs from Southern France to just below the Artic circle, and from Western Europe to Japan) could be used to our advantage. Nevertheless, we end with a plea to collect and integrate more detailed ‘natural history’ data in such studies (e.g., foraging behaviour, predation pressure, thermal environment, food availability, etc.), ideally from the original population where species where collected. Taken together, we are convinced that such an comparative approach in combination with more ecological data could greatly move forward the field of comparative cognition.

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CHAPTER 4

DEALING WITH THE UNEXPECTED: THE EFFECT OF ENVIRONMENTAL VARIABILITY ON BEHAVIOURAL FLEXIBILITY IN A MEDITERRANEAN LIZARD

Adapted from:

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ABSTRACT

Harsh and variable environments have been hypothesized to both drive and constrain the evolution towards higher cognitive abilities and behavioural flexibility. In this study, we compared the cognitive abilities of island and mainland Aegean wall lizards (*Podarcis erhardii*), which were expected to live in respectively a more variable and a more stable habitat. We used four proxies of behavioural flexibility: a neophobia assay, a problem-solving test and a spatial + reversal learning task. Surprisingly, the two populations did not differ in neophobia or problem-solving. Insular lizards, however, outperformed mainland conspecifics in an initial spatial learning task, but were less successful during the subsequent reversal learning. Our results thus seem to indicate that the effect of environmental variability on cognition is complex, as it may favour some, but not all aspects of behavioural flexibility.

INTRODUCTION

Understanding how and why animals differ in their cognitive abilities is one of the major goals within the field of cognitive ecology. Cognition, broadly defined as the acquisition, retention and use of environmental information (Dukas, 2004), is considered to be an important mechanism behind behavioural flexibility, i.e. the ability of an individual to adjust its behaviour in response to changes in the environment (Sol, 2009; Tebbich & Teschke, 2014; Audet & Lefebvre, 2017). Previous research has demonstrated considerable variation in cognitive abilities both among and within species (see e.g. Roth et al., 2010b; MacLean et al., 2014; Tebbich & Teschke, 2014; White & Brown, 2014; Hermer et al., 2018; Qi et al., 2018; Szabo & Whiting, 2020), suggesting that the importance of behavioural flexibility depends on specific ecological conditions.

The Cognitive Buffer Hypothesis (CBH) claims that enhanced cognition and behavioural flexibility, via the development of larger brains, mainly evolved to buffer individuals against changes in environmental conditions (Sol, 2009; Fristoe et al., 2017). For example, fast and flexible learning will help an individual to keep track of the abundance and distribution of resources in a changing environment (Tebbich & Teschke, 2014; Morand-Ferron et al., 2019; Szabo et al., 2020a), and problem-solving skills may allow it to e.g. expand its dietary niche during periods of food scarcity (Greenberg, 2003; Griffin et al., 2016). Indeed, living in more variable and harsh habitats is associated with behavioural diversity in chimpanzees (Kalan et al., 2020), problem-solving ability in black-capped chickadees (Roth et al., 2010b), learning speed in climbing perch and *Tropidurus*-lizards (Sheenaja & Thomas, 2011; Rodrigues & Kohlsdorf, 2019) and learning flexibility in woodpecker finches and blue-tongued skinks (Tebbich & Teschke, 2014; Szabo & Whiting, 2020). Further evidence for the CBH comes from comparative brain studies on birds and primates, where a positive association is found between relative brain size and environmental variability (Schuck-Paim et al., 2008; DeCasien et al., 2017; Fristoe et al., 2017; Sayol et al., 2018).

However, other observations seem to oppose the CBH. Gobies from stable habitats learn a spatial task faster than species from unstable environments (White & Brown, 2014). Chickadees and great tits from high-elevations (which are considered harsher and more variable) are slower in reversing a previously learnt association compared to low-elevation conspecifics (Croston et al., 2017; Hermer et al., 2018; Tello-Ramos et al., 2018) and seasonality has a negative effect on relative brain size in primates (van Woerden et al., 2010) and anurans (Luo et al., 2017). One common explanation for these results is the high energetic cost associated with growing and maintaining a large brain (Expensive Brain Hypothesis - EBH - Aiello & Wheeler, 1995; Sol, 2009). Despite the apparent benefits of behavioural flexibility, species living in harsh variable environments may not be able to uphold the high energy intake required for larger brains due to frequently experiencing food shortages (van Woerden et al., 2010).

Thus, how exactly environmental variability and harshness influence the evolution of cognition remains poorly understood. The CBH and EBH are commonly tested by comparing brain sizes among species along an environmental gradient, and although useful, these studies provide little information on the specific cognitive abilities under selection (Healy & Rowe, 2007). Direct comparisons on cognition itself are still rare, especially within a single species. Intraspecific comparisons, however, have the benefit of easier standardization of cognitive assays among individuals inhabiting different environments (MacLean et al., 2012) while also providing more information on recent selection pressures (Roth et al., 2010b).

In this study, we quantify and compare cognitive abilities of Aegean wall lizards (*Podarcis erhardii* Bedriaga 1882) from a mainland and island habitat. Compared to the mainland, arthropod abundance and diversity on islands is often poor (Janzen, 1973; Andrews, 1979; Olesen & Valido, 2003) and more subject to seasonal variation (Karamaouna, 1987; Parashi, 1988; Trihas & Legakis, 1991; Adamopoulou et al., 1999). In accordance, many island lizards in the Mediterranean exhibit dietary versatility, switching to alternative food resources such as plants and ants to survive unfavourable periods (e.g. extremely dry summers with food scarcity) (Pérez-Mellado & Corti, 1993; Adamopoulou et al., 1999; Lo Cascio et al., 2001; Rodríguez et al., 2008; Sagonas et al., 2015). On the basis of the CBH, we expect that environmental variability on the island will select for behavioural flexibility and hence increased cognitive capacities. Alternatively, the EBH would predict that the low supply of energy resources on islands will results in smaller brains and reduced cognitive abilities compared to the mainland. Cognition was studied using four tasks that represent important aspects of behavioural flexibility (cfr. Tebbich & Teschke, 2014): a neophobia assay, a problem-solving test, a spatial learning task and a reversal learning task.

MATERIAL AND METHODS

Study species and populations

The Aegean wall lizard is a medium-sized insectivorous lizard that is widely distributed across the Greek mainland and the islands of the Aegean Sea (Valakos et al., 2008; Brock et al., 2014a). The species occupies a variety of habitats, from Mediterranean scrublands to open rock glades and sand dunes, and frequently inhabits urban environments as well (Valakos et al., 2008; Roca et al., 2009). It consumes a diversity of arthropods and snails, and occasionally fruits, eggs and even conspecifics (Brock et al., 2014b; Donihue, 2016; Madden & Brock, 2018). In these respects, it can be considered an ecological generalist.

For this study, adult males were collected from one island (Naxos, Cyclades, Greece) and one mainland location (Mt. Parnitha, Attica Peninsula, Greece). In May 2018, 21 wall lizards were caught either by lasso or by hand from two different sites on Naxos (Eggares: 37°07'49.1"N, 25°26'18.9"E and Rachi Polichnitou: 37°00'53.0"N, 25°24'10.7"E). Both sites were abandoned agricultural terraces, characterized by phrygana/maquis vegetation, dry stone walls and rocky outcrops. Fifteen lizards were collected from Parnitha (38 ° 09 '36.6 "N , 23 ° 43' 30.4" E) on the mainland in May 2019. The sampled area used to be covered with a forest of Greek fir (*Abies cephalonica*) until a fire in 2007. The habitat now consists of dense shrubland (Gkourtsouli-Antoniadou et al., 2017).

Resource availability

Although literature suggest that Naxos is the more variable environment in terms of food availability, we wanted to verify this assumption by collecting and analysing data on two frequently used proxies of resource availability.

First, we acquired monthly precipitation data for the period 2000-2018 from the WorldClim Database (Harris et al., 2014; Fick & Hijmans, 2017). Rainfall is often used as an indicator of ecosystem productivity (Schuck-Paim et al., 2008; Karameta et al., 2017; Kalan et al., 2020) and temporal variation in precipitation is known to correlate with fluctuations in arthropod abundances (Stamps & Tanaka, 1981; Spiller & Schoener, 1995). Precipitation data for Parnitha and the two sites on Naxos were extracted using the ‘raster’-package in R (Hijmans et al., 2015).

Secondly, we used the Normalized Difference Vegetation Index (NDVI), a common indicator of primary productivity in ecological studies (reviewed in Pettorelli et al., 2011). It is calculated based on surface reflectance patterns in red and near-infrared light, with higher positive values indicating healthier, greener vegetation and thus higher plant biomass (Lafage et al., 2014). Recent studies have shown that temporal changes in NDVI are often associated with temporal variation in arthropod abundance and diversity (Roiz et al., 2015; Sweet et al., 2015; Fernandez-Tizon et al., 2020; Uhey et al., 2020). NDVI data was acquired from the 250 x 250 m MOD13Q1 MODIS/Terra dataset collected at 16-day intervals (Didan, 2015). Data points with low quality (e.g. due to snow or cloud cover) were removed from the analyses.

For both variables, we calculated the coefficient of variation (CV) within each year (Kalan et al., 2020).

Husbandry and experiments

Animals were housed individually at the National and Kapodistrian University of Athens in plastic terraria (either 22 x 18 x 17 or 23 x 22 x 17 cm, l x w x h). Terraria contained a sandy substrate and small rocks for shelter and basking. Animals had *ad libitum* access to water and were fed thrice per week with mealworms (*Tenebrio molitor*) powdered with vitamin supplement (TerraVit Powder, JBL GmbH & Co. KG). In 2019, terraria were placed underneath incandescent lamps (60W) which allowed thermoregulation for nine hours per day. Lizards in 2018 had access to natural sunlight (filtered through glass) but no lamps were provided. Room temperature in both years was maintained around 28 ± 2 °C.

Experiments were conducted between May and July of the respective years. Testing typically started after 10:00, to provide lizards with ample time to obtain preferred body temperatures, and lasted until maximum 19:00. In addition, before each trial lizards were also allowed to bask underneath a heat bulb (100 W) for 20-30 minutes. During the neophobia trials and the problem-solving tests lizards were maintained on a restricted diet of a single mealworm per day in order to standardize hunger levels among individuals and increase motivation to participate (Amiel et al., 2014). Room temperature during the experiments was 28 ± 2 °C. Experiments started within a week after arrival in the lab, and were completed within ten weeks. All lizards were subjected to all tests in the same order: neophobia, problem-solving and spatial + reversal learning. Four lizards were unable to complete the entire test battery due to mortality.

Trials during the training, neophobia and problem-solving tests were filmed from above using a GoPro camera (Hero5 Black) and scored afterwards.

Training phase for neophobia and problem-solving tests

Prior to the start of the experiments, a training phase was conducted in order to habituate lizards to the experimental set-up, and train them to eat from the transparent petri dishes in which food was offered (which not all lizards were willing or able to do initially). Lizards had no prior experience with these transparent dishes, and were only exposed to them during the experimental trials.

Lizards were tested in separate glass arenas (30 x 30 x 30 cm) with a sandy substrate. A transparent petri dish (1.5 cm height, 5.5 cm diameter) taped on a wooden platform (10 x 10 x 1.5 cm) was placed at one side of the arena. A heat bulb of 100 W was suspended above the terraria to maintain temperature. At the start of each trial, the lizard was placed in the arena and allowed to accustom for two minutes, after which food was placed in the petri dish. We initially started in 2018 with two mealworms per trial, but changed this throughout the training (around day 5) as we noticed lizards becoming satiated. For mainland lizards, we used a single mealworm per trial consistently from the start. Lizards then received 15 minutes to grab the worm(s), and the latency to first contact the petri dish with their snout was recorded (‘feeding latency’). Individuals who did not contact the dish were assigned a latency of 900s. Lizards were tested up to two times per day. If a lizard successfully ate the worm(s) in three out of four consecutive trials, it moved on to the neophobia trials. The average feeding latency in the last three training trials was used as a control for the subsequent neophobia assay.

Neophobia

Neophobia, defined as the fear of novelty (Tebbich & Teschke, 2014), determines how likely individuals are to encounter and gather novel information, and thus influences their propensity to learn and to innovate (Tebbich et al., 2010; Tebbich & Teschke, 2014). The dietary shifts in insular lizards (see above) may (at least partially) be driven by lower levels of neophobia, either because less neophobic lizards are willing to exploit a more diverse range of resources (Greenberg, 1983; Greenberg 2003) or because they are more likely to innovate in order to access these (Overington et al. 2011; Daniels et al. 2019; but see Griffin & Guez, 2014).

Neophobia assays were performed one to ten days upon completion of the training, following a standard protocol (Greenberg, 1983; Candler & Bernal, 2014; Guido et al., 2017). Trials were largely identical to the training phase, but together with the mealworm a novel object was introduced next to the petri dish. Similar to Guido et al. (2017) neophobia was estimated as the relative change (%) in feeding latency when a novel object is present, compared to the control feeding latency. We used latency to make contact with the dish as this better reflects motivation to eat, while latency to grab the worm is influenced by an individual's ability to detour the transparent barrier. Each lizard received two trials on two consecutive days with different novel objects: either a bright red toy car (7.5 x 1.9 x 2.5 cm) or two yellow and orange glow sticks (diameter: 7cm) (Supplementary Figure S4.1). The objects were specifically chosen to be conspicuous and artificial to lower the probability that lizards had encountered them before (Damas-Moreira et al., 2019). The order of objects was randomized among individuals.

Problem-solving

The ability to solve new problems by inventing a new behaviour or applying an old behaviour in a new context, is considered an important indicator of behavioural flexibility (Griffin & Guez, 2014; Tebbich & Teschke, 2014; but see Audet & Lefebvre, 2017). Problem-solving abilities are expected to help individuals to exploit new resources or familiar ones in a more efficient way (Greenberg, 2003; Griffin et al., 2016). In species with an active foraging style, such as *Podarcis erhardii*, problem-solving may help individuals to increase their foraging efficiency e.g. by being able to extract otherwise inaccessible prey (Cooper et al. 2019; Henke-von der Malsburg et al. 2020). This may be particularly beneficial in periods of food scarcity.

In our study, problem-solving ability was assessed with a variation on the lid-removal task commonly used for lizards (Leal & Powell, 2012; Clark et al., 2013) and birds (Ducatez et al., 2014; Audet et al., 2015). Problem-solving tests started one to five days after the last neophobia trial. The protocol was similar to the training phase. However, after introduction of the mealworm, the petri dish was covered with an opaque plastic disc, which lizards had to remove in order to access the prey (Supplementary Figure S4.1). A lizard successfully solved the task if it 1) actively lifted or pushed away the disc and 2) grabbed the prey immediately afterwards (i.e. that disc removal and prey acquisition should constitute a single motor sequence without e.g. reverting back to attacking the transparent barrier or walking away from the apparatus in between). Trials in which the lizard didn’t interact with the petri dish, or accidentally opened it (e.g. by crawling over and dragging along the disc) were considered invalid. Trials lasted 15 minutes, and solving time was calculated as the time between first contacting the petri dish and obtaining the prey. If a lizard failed, it was assigned a maximum time of 900s. Individuals were tested once per day, but could be given a second chance in case they failed or did not participate during the first test. All lizards were tested until they solved the task three out of four consecutive times, or until they had participated in ten valid trials.

Each individual was classified as either a non-solver (never removing the disc), an occasional solver (solved at least once, but not consistent) or a consistent solver (successful in three out of four consecutive trials), and were accordingly assigned a problem-solving score from 0-2. We also calculated the average solving time per individual over a) all its trials and b) all its successful trials.

Spatial and reversal learning

Learning is an important mechanism that allows individuals to quickly adapt their behaviour to changes in the environment (Tebbich & Teschke, 2014). We have specifically chosen for a spatial learning task as most animals, including our study species, are expected to benefit from being able to learn and remember the location of resources such as food, mates and shelter (Dukas, 2004; Dayananda & Webb, 2017). For example, remembering where food can be found or which food patches have already been visited is likely to improve foraging efficiency (Winter & Stich, 2005), and could be especially beneficial in food-deprived habitats. Small lizards also typically respond to predatory threats by fleeing to a refuge, a strategy that may be more successful if lizards can directly flee towards a known hiding spot (Noble et al, 2012). Lizards in variable environments, however, may need to update spatial information frequently (e.g. because the distribution of resources changes) and will thus benefit from flexible learning skills (Noble et al., 2012). Hence, the spatial learning task was followed by a reversal phase, which is generally considered as cognitively more demanding (Tebbich & Teschke, 2014; Buechel et al., 2018).

We tested spatial learning in our lizards using a biologically relevant antipredator task, commonly used in reptiles (Paulissen, 2008; Amiel & Shine, 2012; Noble et al., 2012; Dayananda & Webb, 2017), in which lizards had to learn the location of a safe hiding spot within an experimental arena (60 x 60 x 30 cm). The spatial cognition task started seven to thirteen days after the last lid-removal trial for mainland lizards, and 21 – 34 days (two batches) for insular lizards. Walls of the test arena were blinded, but visual cues were provided in and around the arena to allow orientation and navigation (Supplementary Figure S4.2). The position of these spatial cues, as well as the position of the observer, remained consistent throughout the experiment. Two identical refuges (plastic cups covered in black tape) were placed in opposite corners of the arena and the location of the safe one (either left or right relative to the observer) was randomized among lizards within both groups (Munch et al., 2018).

At the start of each trial, an individual lizard was placed in the centre of the arena underneath a transparent cover. After two minutes, the cover was lifted and a predator attack was simulated by tapping the base of the lizard's tail with a paintbrush. In order to avoid influencing the direction in which the lizard fled, we always tried to poke the lizards from straight above. If a lizard entered the safe refuge, it was allowed to rest for two minutes. If a lizard entered the unsafe refuge, we lifted the plastic cup and continued chasing the lizard until it entered the safe refuge or until 120 s had passed (after which the lizard was gently placed inside the safe refuge). We recorded the latency to enter the safe refuge and the number of errors made by an individual. In between trials, sand in the arenas was mixed, refuges were cleaned with disinfecting wipes and water to eliminate chemical cues (Paulissen, 2008). Lizards were tested three times per day, with at least one hour in between trials, for five consecutive days. Thereafter, the reversal phase followed, during which safe and unsafe switched and lizards received five additional days in order to reverse the learnt association.

A lizard was considered to have made a successful escape when it entered the safe refuge first. Lizards were classified as learners if they were successful in five out of six consecutive trials (Noble et al., 2014; Vardi et al., 2020).

Statistics

Data were analysed in R version 3.5.1 (Ihaka, R. & Gentleman, R., University of Auckland, New Zealand). Where necessary, data were box-cox transformed to meet model assumptions, and non-significant interactions were stepwise removed. *Post-hoc* multiple comparisons were performed with the 'emmeans' package (Lenth et al., 2019) using Tukey's method. We used a significance level of $\alpha = 0.05$ unless stated otherwise. Behavioural data from both sites on Naxos were pooled together, as a preliminary analysis revealed no significant differences between them.

First, in order to verify whether Naxos was indeed more variable than Parnitha, we used a linear mixed-effect model (LMM) to compare the yearly CVs in NDVI and precipitation among the three study sites. The model included year as random factor. To test whether differences among sites in CV were consistent over time, we estimated the repeatability of 'study site' using the 'rptR' package (Stoffel et al., 2017). Seasonal variation was visualized by plotting a) the monthly precipitation means and b) the average relative changes in NDVI per time interval.

Differences in neophobia scores between populations were tested using a LMM. Site, lizard identity and novel object were included as random effects. Number of days between the last training trial and the first neophobia trial was initially also included, but as this did not affect neophobia scores in either population (all $p > 0.05$) it was dropped from the analyses. Based on the outcome of the LMM, adjusted repeatability of relative neophobia was calculated using the ‘rptR’ package (Stoffel et al., 2017). To see whether lizards reacted differently to each novel object, we reran the LMM but with object included as a fixed effect and an object*habitat interaction.

Differences in problem-solving scores were analysed using a generalized mixed-effect model (GLMM) following a Poisson distribution and including site as random factor. Average solving times were analysed using a mixed effect Cox proportional hazard model (‘survival’- and ‘coxme’ package; Therneau & Lumley 2020; Therneau 2015). A common critique of extractive foraging tasks is that the outcome may be influenced by other non-cognitive factors, such as morphology (Overington et al., 2011). As larger individuals may indeed have been more physically capable of removing the lid, SVL and an SVL*habitat interaction factor were included in both models. Two insular lizards did not complete ten valid trials. One of these individuals could still be classified as an occasional solver (as it only succeeded once in nine valid trials), but we were unable to assign the other a problem-solving score. Average solving times of both lizards were retained in the dataset.

For both the spatial and reversal learning task, we used separate GLMMs to test for population differences in learning success (binomial distribution). The models included an habitat*safe side interaction as lateralization may affect learning in lizards (Szabo et al., 2019b) Success on the reversal phase (Y/N) was also tested in a separate GLMM on the subset of lizards that passed the spatial phase (habitat and safe side as fixed factors). All three models included site and batch as random factor. Next, we tested whether lizards improved their performance over time, using separate GLMMs for both the spatial and reversal phase. These models contained: the ‘number of errors’ as response variable; habitat, safe side and trial number as independent variables; a habitat*trial and safe side*trial interaction; and site, batch and lizard ID as random factors. Similar LMMs were used to test whether the 'latency to enter the safe refuge' decreased over time. Initially, all models included a random intercept and slope for trial number within lizard ID, but this was dropped from the 'errors - reversal learning' model due to convergence issues. Where necessary, a negative binomial distribution was used to handle overdispersion.

Finally, the robustness of our learning criterion was tested in a subset of lizards, by calculating the significance of the tally (first trial of criterium until the last trial, minimum three trials post-criterium required) according to a binomial test (Noble et al., 2014). Here we used a significance level of $\alpha = 0.10$ as this is also the probability of reaching the 5/6 criterion by chance.

Ethical note

All experiments were approved by the Ethical Committee of the University of Antwerp (file number 2017-67) and by the Greek Ministry of Environment, Energy and Climate Change (Permit nr: Ω6314653Π9-ΤΒΞ and 7Μ7Τ4653Π8-ΠΑ5). Lizards from Parnitha were released upon completion of the experiments. Lizards from Naxos were re-used in a follow-up study (Chapter 5 - 7).

Table 1. Resource availability data for the three study sites. Monthly precipitation data were gathered from the WorldClim Database (Harris et al., 2014; Fick & Hijmans, 2017) for the period 2000-2018, Normalized Difference Vegetation Index (NDVI) data was acquired in 16-day intervals from 250 x 250 m MOD13Q1 MODIS/Terra dataset (Didan, 2015) for the period 2008-2018. For both precipitation and NDVI, the coefficient of variation (CV) within each year was calculated, and averaged over the entire time period to estimate seasonal variation (as the CV * 100). Mean + SE are given.

	Naxos		Parnitha
	Rachi P.	Eggares	
Mean driest month (mm)	1.1 ± 0.2	1.1 ± 0.2	5.6 ± 0.8
Mean wettest month (mm)	111.9 ± 6.8	110.2 ± 6.6	145.2 ± 8.7
Precipitation seasonality (%)	97.2 ± 3.1	97.2 ± 3.1	78.5 ± 2.2
Mean annual precipitation (mm)	454 ± 17	448 ± 17	653 ± 29
NDVI seasonality (%)	31.4 ± 1.2	30.6 ± 1.0	16.7 ± 1.7

RESULTS

Resource availability

Both sites on Naxos experienced higher seasonal variation in precipitation than Parnitha (Table 1; Figure 1b, $F_{2,36} = 125.59$; $p < 0.001$). Differences among sites in $CV_{precipitation}$ were significantly repeatable over time ($R = 0.488$; CI = [0.021; 0.784]; LRT: $p < 0.001$). Likewise, NDVI also showed higher seasonal variation in both sites on Naxos compared to Parnitha (Table 1; Figure 1b; $F_{2,30} = 38.29$; $p < 0.001$) and differences among sites in CV_{NDVI} were consistent over time ($R = 0.772$; CI = [0.000; 0.939]; LRT: $p < 0.001$).

Neophobia

For all cognitive tests, an overview of population means is given in Table 2.

All lizards learnt to eat from an open petri dish (mean + SE number of trials: 6 ± 3, range: 3-11; number of training trails did not affect performance in either of the subsequent tasks; all $p > 0.05$) and were allowed to the neophobia trials. Lizards took on average 102 ± 8s (range: 30 – 308s) to contact the Petri dish with food during the last three trials of the training phase, and on average 100 ± 15s (Range: 2 – 900s) during the neophobia trials. Island and mainland lizards did not differ in their latency to contact the Petri dish during the control trials ($F_{1,34} = 2.22$; $p = 0.145$).

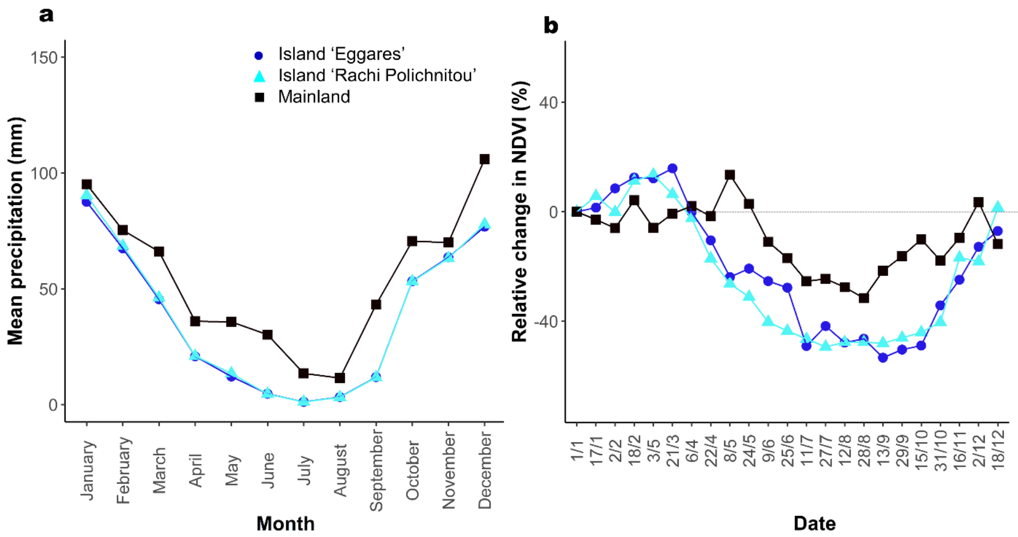

Figure 1. Seasonal variation in resource availability in two locations on Naxos (Eggares ● and Rachi Polichnitou ▲both in blue) and Parnitha (■ black). Resource availability is estimated by a) mean monthly precipitation for the period 2000 – 2018, and b) the relative change in Normalized Difference Vegetation Index (NDVI) per 16-day interval compared to the NDVI at the start of the year, averaged over the period 2008-2018. In case of missing values, relative change was calculated relative to the last NDVI value from the previous year.

We found no population-differences in relative neophobia ($N_{island} = 21$, $N_{mainland} = 15$; $F_{1,34} = 0.122$; $p = 0.730$). Detailed analyses revealed that lizards behaved neophobic towards the red car but slightly neophilic towards the rings (mean relative neophobia score red car: 88 ± 40 %, mean relative neophobia score rings: - 26 ± 40 %, $F_{1,35} = 12.93$; $p < 0.001$). This response was independent of population ($F_{1,34} = 0.68$, $p = 0.42$).

Neophobia scores were highly repeatable in island lizards (R = 0.518; CI = [0.156; 0.767]; LRT: p = 0.003) but not in mainland lizards (R = 0.063; CI = [0; 0.471]; LRT: p = 0.369). This was due to an higher interindividual variance on Naxos (variance = 0.56; CI = [0.112; 1.104]) compared to Parnitha (variance = 0.063; CI = [0; 0.515]).

Problem-solving

The majority of lizards failed to open the petri dish within ten trials (island: 15/20, mainland: 11/15). Three lizards (two island, one mainland) opened the petri dish at least once, while five animals were classified as consistent solvers (two island and three mainland lizards). Mainland and island lizards did not differ in their problem-solving score ($N_{island} = 20$, $N_{mainland} = 15$; LRT: $\chi^2 = 0.69$, $p = 0.407$). Average solving times did not differ either between populations ($N_{island} = 21$, $N_{mainland} = 15$; LRT: $\chi^2 = 0.03$, $p = 0.873$), even when only taking into account successful trials ($N_{island} = 5$, $N_{mainland} = 4$; $F_{1,6} = 2.15$, $p = 0.193$). Snout-vent length had no effect on problem-solving times and scores in either population (all $p > 0.05$).

Table 2. Overview of population means + SE for all cognitive tests. See main text for a description of the experiments.

	Naxos		Parnitha	
Trials required to pass training	4.9 ± 0.4		6.1 ± 0.8	
Control feeding latency (s)	116 ± 16		83 ± 13	
Neophobia	**Car**	**Rings**	**Car**	**Rings**
Feeding latency (s)	160 ± 45	75 ± 13	91 ± 16	58 ± 15
Relative neophobia (%)	140 ± 93	-7 ± 21	30 ± 24	-38 ± 12
Problem-solving				
Solving score	0.32 ± 0.15		0.47 ± 0.22	
Solving time (s)	784 ± 60		811 ± 42	
Solving time (s) (success)	204 ± 69		360 ± 51	
Spatial learning	**Left**	**Right**	**Left**	**Right**
Proportion of learners (%)	10/10	3/8	3/7	2/7
Number of errors	0.15 ± 0.04	0.97 ± 0.11	0.77 ± 0.12	0.76 ± 0.10
Latency to find safe refuge (s)	53 ± 3	47 ± 2	28 ± 3	22 ± 2
Reversal learning				
Proportion of learners	5/8	1/10	5/7	4/7
Number of errors	0.57 ± 0.09	1.56 ± 0.11	0.60 ± 0.09	0.75 ± 0.10
Latency to find safe refuge (s)	33 ± 2	77 ± 3	16 ± 2	22 ± 2
Success on both	3/13		4/5	

Spatial and reversal learning

Eighteen lizards (56%) were classified as learners during the spatial learning phase (island: 13/18, mainland: 5/14) and 15 lizards (47%) during the reversal (island: 6/18, mainland: 9/14). Most of the learners continued going to the correct refuge after reaching criterion (significant tally in 14/15 island and 11/14 mainland lizards). We thus consider our criterion to be valid.

During the spatial learning phase, island lizards were overall more likely to learn compared to mainland conspecifics (72 versus 36%). Nevertheless, a significant interaction between population and safe side was found (LRT: $\chi^2 = 4.38$; $p = 0.036$). A *post-hoc* test revealed that 100% of the island lizards learnt the task if the safe refuge was on the left side of the arena (relative to the observer), while only 38% (3/8) reached criterion if the rewarded refuge was on the right. A similar side bias was not found in mainland lizards ($Z = 0.56$, $p = 0.945$). Although island lizards still slightly outperformed mainland individuals when the safe refuge was on the right, this difference was not statistically significant (38 versus 29%; $Z = 0.37$, $p = 0.983$) (Figure 2a). In contrast, during the reversal phase, there was no significant interaction between population and safe side (LRT: $\chi^2 = 1.55$; $p = 0.214$). Lizards were overall more successful when the safe refuge was on the left (LRT: $\chi^2 = 4.59$; $p = 0.032$) and mainland lizards reached criterion more often, albeit not significantly (LRT: $\chi^2 = 2.89$; $p = 0.118$) (Figure 2b). In the subset of lizards that succeeded on the training, we found that mainland lizards were indeed better at the reversal task compared to insular lizards (island: 3/13, mainland: 4/5, LRT: $\chi^2 = 4.13$, $p = 0.042$; Figure 2c). There was no overall side bias during the reversal in this subgroup (LRT: $\chi^2 = 0.80$, $p = 0.37$).

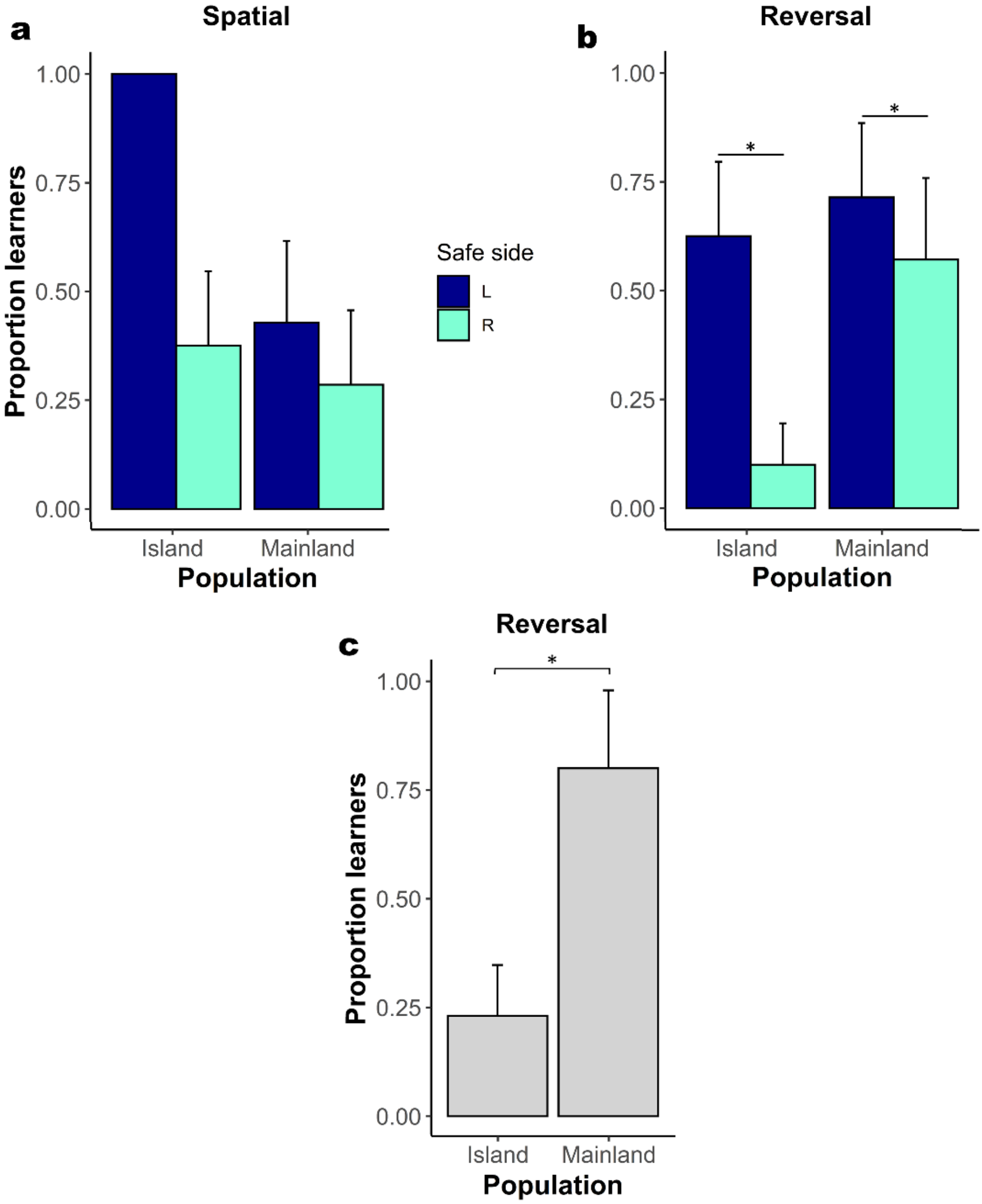

Figure 2. Proportion of lizards that reached the learning criterion (five correct in six consecutive trials) during a) the spatial learning phase, b) the reversal phase and c) the reversal phase (only the subset of lizards that succeeded on the initial spatial learning). Safe side is relative to the position of the observer (dark blue = left, light blue = right). For a and b: $N_{island} = 18$, $N_{mainland} = 14$, for c: $N_{island} = 13$, $N_{mainland} = 5$. Significance levels according to a *post-hoc* comparison using Tukey's method are indicated as follows: '.' $p < 0.1$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

Lizards made fewer errors over time during the reversal phase (LRT: $\chi^2 = 4.98$, $p = 0.026$; Figure 3a) but not during the initial spatial learning (LRT: $\chi^2 = 0.05$, $p = 0.831$; Figure 3a). In neither phase was there a difference in learning curve between populations (all $p > 0.05$). Island lizards made fewer errors during the spatial phase (LRT: $\chi^2 = 5.94$, $p = 0.015$) but they tended to make more mistakes during the reversal (LRT: $\chi^2 = 3.30$, $p = 0.069$). Lizards also made more mistakes when the safe hiding spot was on the right side of the arena, both during the training (LRT: $\chi^2 = 16.85$, $p < 0.001$) and the reversal (LRT: $\chi^2 = 12.07$, $p < 0.001$). Latency to find the safe refuge decreased during the spatial learning phase ($F_{1,31} = 4.99$; $p = 0.033$; Figure 3b) independent of population ($F_{1,29} = 0.82$; $p = 0.372$). During the reversal phase, however, only island lizards reduced their latency to find the safe refuge ($F_{1,29} = 5.27$; $p = 0.029$; Figure 3b). During the reversal, lizards were slower to make the correct choice when from the island ($F_{1,27} = 77.66$; $p < 0.001$) or when the safe refuge was on the right ($F_{1,29} = 22.23$ $p < 0.001$). This was not the case during the initial spatial learning (all $p > 0.05$). The decrease in latency or errors over time was independent of the side of the safe refuge, in both phases (all $p > 0.05$).

DISCUSSION

On the basis of both the CBH and the EBH, we expected to find differences in cognitive abilities between mainland and island lizards of the Aegean wall lizard. Our results paint a more complex picture. Against the expectations of both hypotheses, mainland and island populations did not differ in neophobia or problem-solving. Secondly, island lizards outperformed mainland conspecifics during the initial spatial learning task (lending support to the CBH), but the reverse was true for the reversal learning (corroborating the EBH). Below, we discuss these intriguing and conflicting results.

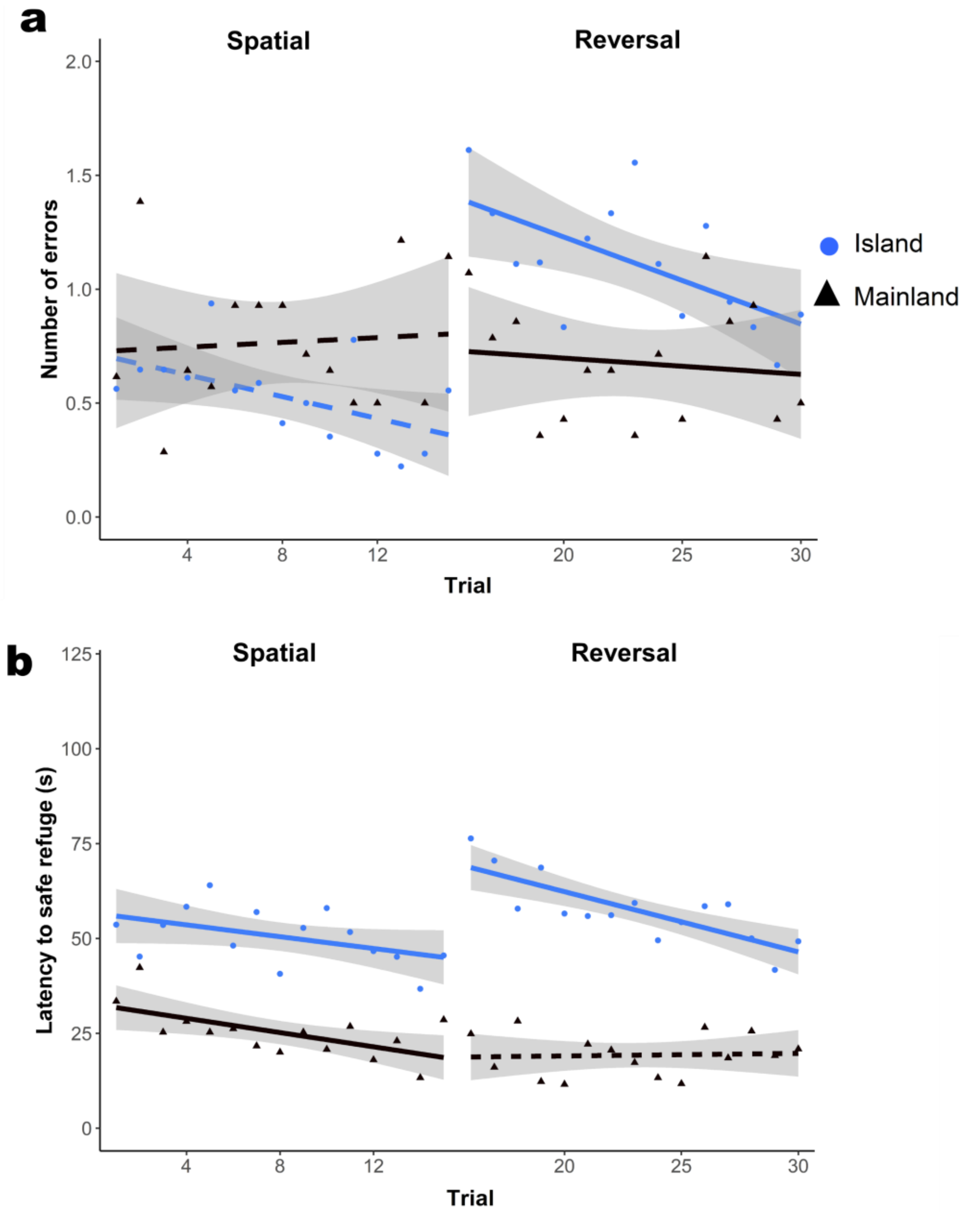

Figure 3. Changes in a) number of errors and b) latency to correct choice over time for both the spatial learning and reversal phase. Island lizards (N = 18) are indicated with blue dots, mainland lizards (N = 14) with black triangles. Solid lines represent statistically significant regressions. Grey areas indicate standard errors.

Cognition and environmental variability

An important assumption of both the CBH and EBH in this context, is that food availability on the island should be generally lower and more variable than on the mainland. Although we are unable to present data on food availability, we clearly demonstrated that Naxos experiences stronger seasonal variation in NDVI and precipitation, both of which are important indicators of resource availability. This seems to be in line with the strong seasonal fluctuations in arthropod abundances, characterized by a sharp drop during dry summers, typically observed on Mediterranean islands (Karamaouna, 1987; Parashi, 1988; Trihas & Legakis, 1991; Adamopoulou et al., 1999; Carpaneto & Fattorini, 2001; Sagonas et al., 2015; Mamou et al., 2019). In such a variable habitat with frequent periods of food scarcity the CBH predicts higher behavioural flexibility, while the EBH expects the opposite.

Our first indicator of behavioural flexibility was neophobia. Higher levels of neophobia are expected to limit behavioural flexibility, as neophobic individuals will be less likely to seek and gather novel information (Greenberg, 2003; Tebbich et al., 2010; Griffin & Guez, 2014; Tebbich & Teschke, 2014; Daniels et al., 2019). Contradicting both the CBH and EBH, we did not find any differences in average neophobia between island and mainland lizards. Previous studies have also yielded mixed results regarding the link between neophobia and either habitat variability (Roth et al., 2010b; Tebbich & Teschke, 2014; Feyten et al., 2019) or insularity (Mettke-Hofmann et al., 2002; De Meester et al., 2018).

One possible reason for this lack of difference may be that both our populations face a similar trade-off between the costs and benefits of neophobia. It is generally assumed that individuals should exhibit low neophobia in environments where the risk of seeking new information is low (e.g. due to a lack of predators and competitors) while the potential reward of discovering new resources is high (e.g. due to food scarcity) (Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002). Previous research, however, suggests that the predation rate on lizards is comparable between Naxos and Parnitha (Brock et al., 2014a), thus potentially equalizing the cost of neophobia in both populations.

Albeit no differences were found in average neophobia, it is interesting to note that neophobia was only repeatable on Naxos and not in Parnitha. Our data suggests that this is a consequence of lower interindividual variation in Parnitha compared to Naxos (Nakagawa & Schielzeth, 2010), which may indicate recent selection on neophobia. Whether this was due to the forest fire in 2007 or another ecological factor is yet unclear.

Our second indicator of behavioural flexibility was problem-solving ability. Here, we did not find differences between populations either, which once again challenges both the CBH and EBH. A first explanation may be that we did not find any differences due to the overall low success rate observed in both groups, which might indicate that our version of the lid-removal task was too difficult. Indeed, compared to previous studies (see e.g. Leal & Powell, 2012; Clark et al., 2013; Qi et al., 2018), our lizards did not receive a period of shaping, and the walls of the petri dish were intentionally left transparent to provide visual stimulation. The transparent barrier may imply an extra challenge: lizards were required to not only perform a novel motor act, but also to inhibit their response to directly attack the visible prey (Szabo et al., 2019b; Storks & Leal, 2020). Another explanation for the lack of population differences (and the low success rate) may be that, in contrast to birds (Sol et al., 2005a; Roth et al., 2010b; but see Tebbich & Teschke, 2014), lizards do not rely on problem-solving skills in order to access alternative food sources during periods of scarcity. Whether and how lizards benefit from problem-solving skills in the wild thus remains to be investigated.

Performance on a spatial reversal learning task was our third score of behavioural flexibility. Lizards demonstrated relatively good learning abilities, with 56 and 47% of the individuals reaching criterion during respectively the spatial learning and reversal phase. Neither group decreased the number of errors made during the initial spatial learning but did so during the reversal. Visual inspection of the data suggested that lizards did learn, but started making mistakes again towards to end of the first phase potentially due to overtraining and/or habituation to being attacked (Carazo et al., 2014; Munch et al., 2018).

Intriguingly, insular lizards were more successful during the initial learning (thus lending support to the CBH), while mainland lizards seemed more successful in reversing the learnt association (thus corroborating the EBH). We propose three alternative explanations to explain these seemingly paradoxical results. Note that these are not necessarily mutually exclusive.

Our first explanation relates to the energetic costs of cognition and behavioural flexibility. Reversal learning is often considered as cognitively more demanding than learning a new association de novo, given that the individual must inhibit and override a previously learnt response (Tebbich & Teschke, 2014; Buechel et al., 2018). Reversal learning may thus have a higher energetic cost, e.g. by requiring a higher rate of neurogenesis (Tello-Ramos et al., 2019). Indeed, in rodents, experiments suggest that neurogenesis is required for learning the reversal of a rule, but less so for its initial acquisition (Burghardt et al., 2012; Kalm et al., 2013; Swan et al., 2014). It is therefore possible that harsh, variable environments indeed favour enhanced learning to some extent, but limit more costly aspects of cognition, such as flexibility. Nevertheless, previous studies often found a positive link between reversal learning ability and habitat variability (Tebbich & Teschke, 2014; Szabo & Whiting, 2020; but see Croston et al., 2017; Hermer et al., 2018; Tello-Ramos et al., 2018).

Secondly, our results could also be explained as a trade-off between memory strength and flexibility. Strong memories will actively inhibit the replacement of old with new information – a phenomenon known as proactive interference (Croston et al., 2017). Studies on passerine birds suggest that harsh and variable environments may select for strong spatial memory, which consequently results in high proactive interference during reversal learning (Croston et al., 2017; Hermer et al., 2018; Tello-Ramos et al., 2018), similar to what may be the case for our insular lizards. Lizards on Naxos may revert to clumped, stationary food sources (e.g. ants or plants) during summer (Adamopoulou et al., 1999). Such a foraging strategy may select for a strong memory rather than behavioural flexibility. To validate this hypothesis, further studies could test whether insular lizards truly retain spatial information longer than mainland individuals.

Finally, it is also possible that Parnitha lizards show higher learning flexibility in response to other environmental variables. As a first example: lizards in Parnitha brumate during winter, while Naxian lizards are active throughout the entire year (Pafilis, P., personal communication). How brumation or hibernation affects cognition is unclear. One on hand, this may be a strategy to ‘evade’ harsh conditions, and thus lower the need for behavioural flexibility (Heldstab et al., 2018). On the other hand, brumation may require more flexible cognition if mainland lizards need to relearn the location of resources each spring (Hernández-Montero et al., 2020). As a second example of unaccounted environmental variation: it is possible that learning flexibility was selected for in Parnitha lizards, as it may have helped to handle the successive changes in vegetation structure (Capitanio & Carcaillet, 2008) and arthropod communities (Lazarina et al., 2016) following the forest fire in 2007 (Gkourtsouli-Antoniadou et al., 2017), or initially allowed lizards from nearby open areas to colonize this newly available habitat in the first place (Szabo et al., 2020a). Nevertheless, over the years, Naxos showed consistently higher seasonal variation compared to Parnitha, and such short-term variations within the lifetime of an individual are considered more important to select for behavioural flexibility than long-term variation (Snell-Rood, 2013; but see Sayol et al., 2018).

Object – and side bias

Our experiments revealed two interesting biases affecting the cognitive performance of our lizards: 1) a different behaviour towards each of the novel objects and 2) a side bias during the spatial learning test. Albeit we controlled for these biases during our tests, we nevertheless consider them worthy of a short discussion.

Firstly, during the neophobia assays, lizards behaved differently towards each novel object. On one hand, lizards may have been more neophobic towards the car due to its size or aposematic colour (Benes & Vesely, 2017; Ko et al., 2020). On the other hand, the lack of fear or higher curiosity towards the rings may be explained by the similarity of their colours with natural throat patterns in *P. erhardii* (Putman et al., 2017; Brock et al., 2020).

Secondly, during the spatial learning tests, insular, but not mainland, lizards exhibited a strong side bias, and reached the learning criterion more often if the safe refuge was on the left side of the arena. Lateralization of behaviour is well documented in reptiles (Bonati et al., 2010; Csermely et al., 2011; García-Muñoz et al., 2012; Bonati & Csermely, 2013) and is known to affect learning (Bridgeman & Tattersall, 2019; Szabo et al., 2019b). It is possible that our lizards relied more on egocentric cues (e.g. always turn left) (Odling-Smee & Braithwaite, 2003; Sheenaja & Thomas, 2011) rather than the visual cues provided. In such case, learning will be facilitated when learning to flee in a preferred direction, and constrained in the opposite case. Being rewarded for choosing the preferred side may also have strengthened memory consolidation, and thus have contributed to the possible proactive interference. Independent of the rewarded side, lizards became faster (both phases) and more accurate (during the reversal) over time, suggesting that learning did in fact occur.

Mainland lizards did not show a side bias initially, and only a weak one during the reversal, but it is currently unclear whether this population is less lateralized in general, or simply capable of overcoming a pre-existing bias.

CONCLUSION

Our results confirm neither the CBH or the EBH regarding the evolution of behavioural flexibility in variable and harsh environments. Rather, it seems that environmental variability may favour some aspects of behavioural flexibility, while not affecting or even limiting others. Our study hence illustrates the need to look beyond unidimensional measures of cognition, such as (relative) brain size or performance on a single task.

Future research on a larger number of populations alongside an environmental gradient will be necessary to both validate and generalize our results. In addition, we suggest that such studies will immensely benefit from more information on the ecological relevance of the cognitive skills under study, as well as their costs and benefits for animals in their natural environments.

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CHAPTER 5

BOLD AND BRIGHT – SHY AND SUPPLE?

THE EFFECT OF HABITAT TYPE ON PERSONALITY-COGNITION COVARIANCE IN THE AEGEAN WALL LIZARD (*PODARCIS ERHARDII*).

Adapted from:

De Meester, G., Pafilis, P. & Van Damme, R. (2022). Bold and bright – shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (*Podarcis erhardii*). — Animal Cognition, 1-23.

ABSTRACT

Animals exhibit considerable and consistent among-individual variation in cognitive abilities, even within a population. Recent studies have attempted to address this variation using insights from the field of animal personality. Generally, it is predicted that animals with "faster" personalities (bolder, explorative, neophilic) should exhibit faster but less flexible learning. However, the empirical evidence for a link between cognitive style and personality is mixed. One possible reason for such conflicting results may be that personality-cognition covariance changes along ecological conditions, a hypothesis that has rarely been investigated so far. In this study, we tested the effect of habitat complexity on multiple aspects of animal personality and cognition, and how this influenced their relationship, in five populations of the Aegean wall lizard (*Podarcis erhardii*). Overall, lizards from both habitat types did not differ in average levels of personality or cognition, with the exception that lizards from more complex habitats performed better on a spatial learning task. Nevertheless, we found an intricate interplay between ecology, cognition and personality, as behavioural associations were often habitat- but also year-dependent. In general, behavioural covariance was either independent of habitat, or found exclusively in the simple, open environments. Our results highlight that valuable insights may be gained by taking ecological variation into account while studying the link between personality and cognition.

INTRODUCTION

Broadly defined as the perception, acquisition, retention and use of environmental information (Dukas, 2004), cognition is clearly an important survival tool for many animals. However, animals can differ considerably in cognitive performance, both within and among populations and species. Both these types of variation are intriguing yet poorly understood.

Variation among species or populations is generally assumed to arise from local differences in the costs or benefits of high cognitive capacities. Unfortunately, exactly which environmental factors affect that balance is still highly debated (Henke-von der Malsburg et al., 2020). One potential driver that has received sizeable attention, is environmental complexity (Godfrey-Smith, 2002). Indeed, navigating through a spatially complex habitat, keeping track of resources and hazards, is likely to be cognitively demanding because it requires processing and storing large amounts of useful information (Safi & Dechmann, 2005; Powell & Leal, 2014; Calisi et al., 2017) while filtering out vast quantities of irrelevant background data (Shumway, 2008; Steck & Snell-Rood, 2018). As a consequence, structured habitats are believed to select for superior spatial cognition (White & Brown, 2014), learning flexibility (Clarin et al., 2013) and problem-solving abilities (Mettke-Hofmann, 2014; Cooper et al., 2019).

Previous studies have tested the idea that habitat complexity drives cognitive evolution by comparative research on the size of the brain or particular brain areas. The results were mixed: species or populations living in structured habitats had relatively larger brain (areas) in some taxa (chipmunks: Budeau & Verts, 1986; bats: Safi & Dechmann, 2005; cichlids: Shumway, 2008; lesser earless lizards: Calisi et al., 2017; pumpkinseed sunfish: Axelrod et al., 2018) but not in others (*Anolis* lizards: Powell & Leal, 2014; three-spined sticklebacks: Ahmed et al., 2017; Squamata: De Meester et al., 2019 ~ Chapter 2; *Anolis* lizards: Storks et al., 2020).

Brain size is, however, only a crude estimator for cognitive capacity (Smaers et al., 2021). More direct evidence for a role of habitat complexity in cognitive evolution comes from a limited number of studies, mostly on fish, that have tested cognitive ability through behavioural experiments. Superior spatial learning abilities are often found in fish which either originate from or are reared in more complex habitats (Odling-Smee et al., 2008; Shumway, 2008; White & Brown, 2014; 2015; Carbia & Brown, 2019; but see Roy et al., 2016). Studies on other taxa are rare and yielded mixed results. Damaralands (*Fukomus damarensis*) constructing more complex burrows learn a spatial task faster, but do not show enhanced long-term memory, compared to Cape mole-rats (*Georychys capensis*) living in simple linear tunnels (Costanzo et al., 2009). Bats (*Myotis* sp.) foraging in more open areas exhibit slower spatial learning than related species foraging in dense habitats, although these differences only became apparent in the most difficult spatial task (Clarin et al., 2013). Conversely, habitat complexity predicted neither spatial learning nor memory in three species of African striped mice (Mackay & Pillay, 2017). Only one study investigated problem-solving in relation to habitat complexity; one species of anole lizard (*Anolis evermanni*, a canopy-trunk ecomorph) proved better at solving a lid-removal task than another (*A. cristatellus*, adapted to simpler open trunk-ground microhabitat), although the difference was attributed to differences in dexterity rather than cognitive abilities (Storks et al., 2020).

The second level of variation in cognition, i.e. among individuals within populations, has recently enjoyed a surge of interest (Boogert et al., 2018). Interindividual differences in ecologically relevant performance are often thought to reflect alternative solutions to some internal trade-off. With respect to cognition, an often cited trade-off is that between fast-but-inaccurate or slow-but-attenuative information gathering and decision making (Sih & Del Giudice, 2012; Bensky et al., 2017; Dougherty & Guillette, 2018). According to this ‘Cognitive Style Hypothesis’, fast learners would learn to solve new problems and make associations readily, but this would come at the cost of reduced behavioural flexibility: initial fast learners are deemed less capable of changing a behavioural pattern they have previously acquired. The reverse would be true for ‘slow’ learners, whose more precise knowledge allows them to adjust to environmental changes more easily. These cognitive styles are often linked to the much better researched personality variation (Griffin et al., 2015). Animals with a ‘fast’ personality (bold, explorative, neophilic, aggressive) would seem more likely to exhibit a fast learning style, while those with a slow personality would show a slow learning style. This idea has found empirical support in diverse taxa (black-capped chickadees: Guillette et al., 2009; Carib grackles: Overington et al., 2011; Darwin’s finches: Tebbich et al., 2012; Florida scrub-jays: Bebus et al., 2016; great tits: Quinn et al., 2016; three-spined stickleback: Bensky et al., 2017; Chimango Caracaras: Guido et al., 2017; bank voles: Mazza et al., 2018), but other studies have reported opposite patterns or no correlation at all between cognition and personality (three-spined sticklebacks: Brydges et al., 2008; Bensky & Bell, 2020; Carib grackles: Ducatez et al., 2014; delicate skinks: Chung et al., 2017; Goulet et al., 2018; common mynas: Lermite et al., 2017; carpenter ants: Udino et al., 2017; common waxbills: Gomes et al., 2020). A recent meta-analysis by Dougherty & Guillette (2018) showed that the direction of cognition-personality relationships is highly variable among studies.

One possible explanation for this discrepancy in results may be that cognition-personality covariance is context-dependent (Liedtke & Fromhage, 2019a), e.g. differing among ages (Zidar et al., 2018), sexes (Mazza et al., 2018) and even years (Quinn et al., 2016). Nonetheless, how ecological conditions shape the association between personality and cognition has rarely been studied. One study showed that within eight populations of three-spined sticklebacks (*Gasterosteus aculeatus*) personality never predicted learning ability, despite varying levels of habitat stability and predation (Brydges et al., 2008). In pond snails (*Lymnaea stagnalis*), exploration and memory seemed to be negatively correlated in natural but not laboratory populations (Dalesman, 2018). This suggests a complex interplay between ecology, personality and cognition, which deserves to be investigated further in order to advance our understanding of cognitive evolution.

In this study, we tested the effect of habitat complexity on cognition, personality and their relationship within the Aegean wall lizard (*Podarcis erhardii* Bedriaga 1882). This ecological generalist can be found in a variety of habitats, from relatively simple open rock glades and sand dunes to Mediterranean scrublands with high structural complexity (Valakos et al., 2008; Lymberakis et al., 2018), making it a suitable study system for our research question. Our study specifically focusses on the role of habitat complexity, which will here be defined as structural spatial complexity (higher three-dimensionality & denser vegetation) in accordance with previous studies on this topic (see e.g. Clarin et al., 2013; Powell & Leal, 2014; White & Brown, 2014, 2015; Calisi et al., 2017; Braun et al., 2018). Our three main goals were to test 1) whether habitat complexity affects cognition and personality within the Aegean wall lizard, 2) how personality and cognition are related to each other in this species and 3) whether the strength and direction of such personality-cognition associations differ between habitat types. We predicted that lizards from more complex habitats would exhibit superior (spatial) cognitive abilities (Clarin et al., 2013; White & Brown, 2014, 2015; Calisi et al., 2017; Storks et al., 2020) and 'faster' (less neophobic and more explorative) personalities (Mettke-Hofmann et al., 2002; Harris et al., 2011; Crane et al., 2019; Garcia et al., 2020; Johnson et al., 2020). We also hypothesized that, in general, lizards with faster personalities would show fast initial learning and problem-solving but lower learning flexibility. Both the strength and (possibly) direction of such personality – cognition associations were expected to vary between habitat types.

MATERIAL AND METHODS

Study species and sites

The Aegean wall lizard is a medium-sized lacertid lizard, found in a variety of habitats across the Greek mainland and Aegean islands (Valakos et al., 2008; Brock et al., 2014a). Its diet mostly consists of arthropods, but occasionally includes snails, eggs, fruits and even conspecifics (Adamopoulou et al., 1999; Brock et al., 2014b; Donihue, 2016; Madden & Brock, 2018).

This study was conducted on Naxos, the largest island of the Greek Cyclades. Due to its relatively large size (429.8 km^2), Naxos offers a wide diversity of habitat types in which high densities of *P. erhardii* can be found (Donihue, 2016). Animals were collected from five locations (Figure 1a–e). The two complex sites (Eggares: 37°07'49.1"N, 25°26'18.9"E and Rachi Polichnitou: 37°00'53.0"N, 25°24'10.7"E) were abandoned agricultural terraces, characterized by dense phrygana and maquis vegetation. Human-built dry stone walls and rocky outcrops further increased the structural complexity at these locations. The three remaining locations were much more open and we will refer to them as the 'simple habitats'. Manto (37°05'22.0"N, 25°21'42.1"E) is a peninsula covered in small and scarcely distributed patches of grass with some rocks and trees present. Both Grotta (37°06'41.8"N, 25°23'09.8"E) and Alyko (36°58'45.3"N, 25°23'21.0"E) are coastal areas characterized by scattered but dense woody vegetation patches (of *Juniperus oxycedrus macrocarpa* and *Pistacia lentiscus*) with large open spaces of bare soil or sand in between. A total of 139 adult lizards of both sexes were collected over two consecutive years (2018 and 2019) and transported to the National and Kapodistrian University of Athens (sample sizes in Figure 1a-e).

Classification of our sites into simple and complex habitats was validated using yearly (2000-2018) Vegetation Continuous Fields data sets from NASA's EarthData website (DiMiceli et al., 2015). The percentage of ground covered in vegetation < 5 m height was estimated for each site plus a buffer zone of 200 meters. Estimates with low quality were removed. A linear mixed-effect model (LMM), with year as random effect, revealed that ground vegetation cover was significantly different among most of these populations (Figure 1f, $F_{4,69} = 301$; $p < 0.001$). More specifically, Eggares and Rachi P. were denser compared to the simple populations, but did not differ from each other. Among the simple habitats, Manto had a drastically lower vegetation cover compared to Grotta and Alyko.

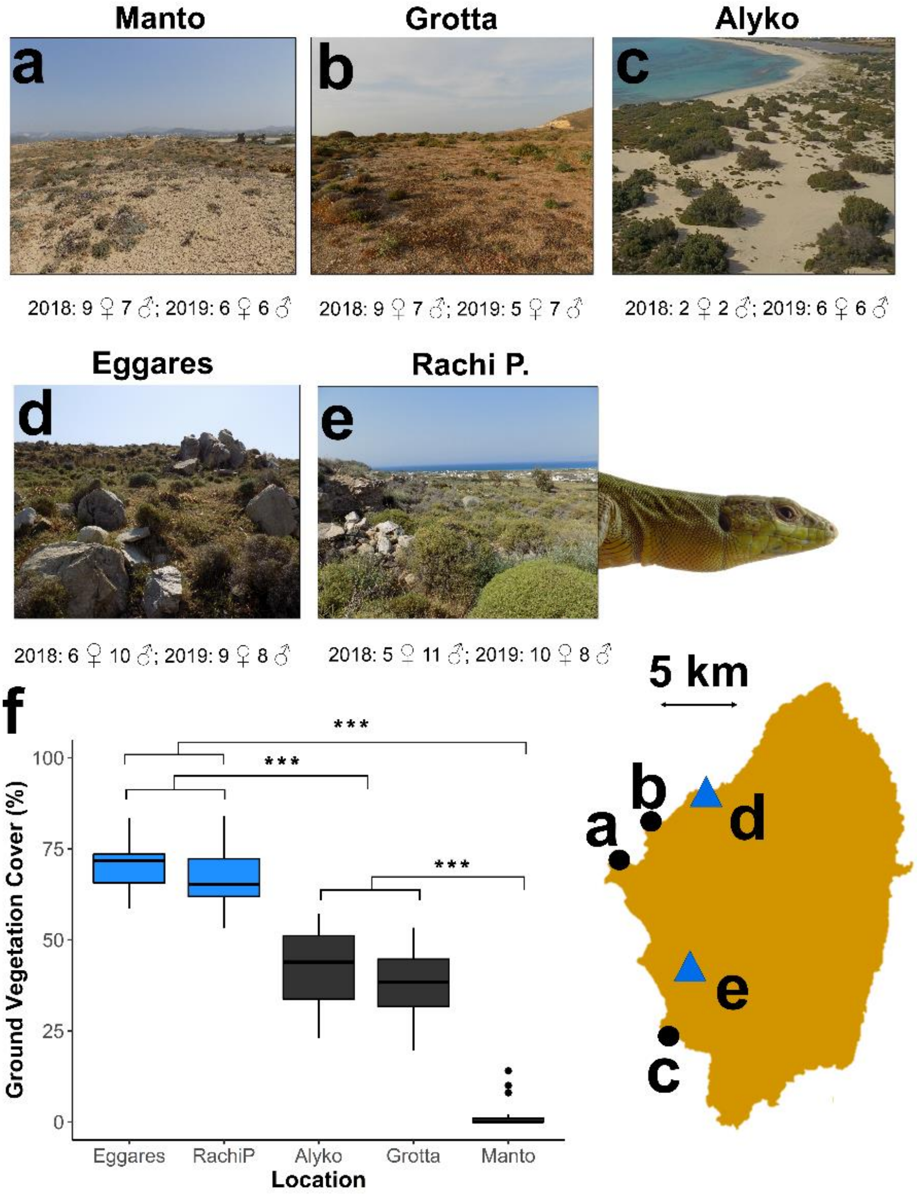

Figure 1. Overview of study sites on Naxos. Manto, Grotta and Alyko (a – c, black circles on map) were classified as simple habitats. Eggares and Rachi Polichnitou (d & e, blue triangles on map) were classified as complex habitats. For each location, a picture illustrating the general habitat structure is provided, as well as the sample sizes for both years. Sample size for Alyko is lower in 2018 as this location was initially not part of the study. The percentage of ground covered by vegetation is given per study site (f). Significance levels according to a post-hoc comparison using Tukey's method are indicated as follows: '°' $p < 0.1$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. Pictures belong to Gilles De Meester (a, b, d, e) and Colin Donihue (c).

Husbandry

Animals (female snout-vent length mean + SE: 60.36 ± 0.50 mm, range: 49.36 – 68.36 mm; male SVL: 61.83 ± 0.40, range = 53.54 – 68.92) were housed individually at the animal facilities of the National and Kapodistrian University of Athens in plastic terraria (22 x 20 x 17 l x w x h) containing sand, a water dish and stone bricks for shelter and basking. Fresh water was provided daily. Lizards were fed three times per week with mealworms (*Tenebrio molitor*) dusted with vitamin supplement (TerraVit Powder, JBL, GmbH & Co. KG). Terraria either had access to natural sunlight filtered through glass (2018) or were placed underneath incandescent lamps (60 W) (2019). Room temperature was 28 ± 2 °C during the day.

Experimental procedures

In total, lizards were tested on four cognitive tasks (two problem-solving tests and a spatial + reversal learning task) and three different personality assays (neophobia, exploration and aggression). In both years, experiments ran from May until July (4-9 weeks per lizard in 2018, 6 – 7 weeks in 2019) and were typically performed on weekdays between 10:00 and 19:00. Lizards were thus rarely tested longer than five consecutive days, except during the spatial cognition task (see below). Prior to each test, lizards were allowed to bask 20-30 minutes underneath a heat bulb (100 W) to reach preferred body temperatures (29 – 36.2 °C, which is within the range of field body temperatures measured on Naxos – Pafilis et al., 2019), upon which they were transferred to separate observational arenas. In the lid-removal and neophobia experiments food was offered as a reward, and hence hunger motivation was standardized among individuals by restricting lizards to a diet of a single mealworm per day (cfr. Amiel et al., 2014).

Lizards who obtained the food reward during these trials were allowed to immediately consume it, those who failed were given their mealworm at the end of the day.

In 2019 we took care to clean all cage equipment (petri dishes, novel objects, etc.) in between trials with 70% alcohol and water (Vicente & Halloy, 2017), a procedure that unfortunately was not followed during 2018 except for the spatial cognition protocol (see below). Room temperature during experiments was 28 ± 2 °C. All experiments were filmed from above using a GoPro (Hero5 Black) or digital camera (JVC Everio GZ-HM400) and scored afterwards. All videos were consistently scored by the same observer (GDM). The tests are described below in the same order as they were given to the animals.

Training for neophobia and problem-solving

To start, all lizards were habituated to the experimental set-up and trained to eat from a transparent petri dish (1.5 cm height, 5.5 cm diameter) positioned on a small wooden platform (10 x 10 x 1.5 cm l x w x h) within the experimental arenas. Arenas were made of Plexiglas (30 x 30 x 30 cm l x w x h) and contained a sand substrate. A heat bulb of 100 W was suspended above the arenas. Two minutes after introduction of a lizard in the arena, food (1-2 mealworms) was placed in the petri dish. The lizard then received fifteen minutes to find and eat the food. Lizards were tested once per day, albeit a second trial (minimal 50 minutes but up to 6.5 hours after the first one) was possible in case of failure or non-participation on the first one. Testing occurred five consecutive days per week and the order in which lizards were tested each day was randomized. Per trial, we recorded individual ‘attack latency’, i.e. the latency to contact the petri dish with their snout. Lizards who did not attack the dish received a maximum score of 900 s. All lizards were tested until they succeeded in three out of four consecutive trials (Gomes et al., 2020), or until they had participated in ten valid trials (trials in which lizards did not contact the petri dish were discarded).

Neophobia

Neophobia is defined as the fear of novelty and is thought to affect how eager individuals are to seek and gain new information (Tebbich & Teschke, 2014). Neophobia was measured using a standard procedure, by looking at how foraging behaviour changes when a novel, conspicuously coloured, and artificial object is introduced near a familiar food source (Greenberg, 1983; Candler & Bernal, 2014; Guido et al., 2017). Neophobia trials followed the same procedure as the training trials, with the exception that a novel object was placed next to the petri dish at the start of each trial. Per trial, we calculated a neophobia score as the relative change in attack latency (%): the attack latency during the neophobia trial minus the control attack latency, divided by the control attack latency (Guido et al., 2017; De Meester et al., 2021 ~ Chapter 4). Each lizard was exposed to novel objects twice (either a red toy car or two yellow and orange glow rings, order randomized) generally on two consecutive days.

Differences in neophobia scores were analysed using a linear mixed-effect model (LMM) which included habitat (simple vs. complex) and sex as fixed factors, as well as the status of the tail (complete or damaged) as the latter is known to affect a lizard's behaviour (Michelangeli et al., 2020). Snout-vent length (SVL, Z-transformed) was included as covariate, as well as year and its interactions with all other variables (excluding tail status due to low sample sizes per year). Population (nested in habitat: Eggares, Rachi P., Manto, Grotta & Alyko), novel object (rings or car) and lizard ID were included as additional random factor. Based on the outcome of this LMM, we calculated the (adjusted) repeatability of relative neophobia with the 'rptR' package (Stoffel et al., 2017), both per habitat type and pooled together. Best linear unbiased predictors (BLUPs) were extracted from these simplified models for further analyses (Henderson, 1975). BLUPs are standardized estimates for random effects (here: lizard ID) which are independent of other factors in the model and less sensitive to extreme outliers than average scores over multiple trials. Hence, they are considered to be more appropriate to use as individual (personality) scores (Pinheiro & Bates, 2000; Martin & Réale, 2008).

Problem-solving: lid-removal task

Cognition allows individuals to solve new problems by inventing a new behaviour or by expressing a familiar behaviour in a novel context (Griffin & Guez, 2014). Problem-solving was tested using the classical lid-removal paradigm for lizards (Leal & Powell, 2012; Clark et al., 2013; Storks et al., 2020) and birds (Ducatez et al., 2014; Audet et al., 2015). Trials followed the same protocol as the training trials, but lizards now had to remove an opaque plastic disc (6 cm diameter) from the petri dish to access the prey. A lizard successfully solved the task if it displaced the disc by either pushing or lifting it, and immediately grabbed the prey afterwards (i.e. removing the lid and grabbing the prey should constitute a single motor sequence). Trials in which the lid fell of due to a lizard dragging it along while moving over or near the dish were considered as accidental openings and discarded, given that lizards often continued to attack the transparent wall of the open dish in such cases, sometimes up to several minutes (De Meester et al., 2021 ~ Chapter 4). The time difference between first contact with the dish and grabbing the mealworm was taken as the ‘solving time’. Lizards received a maximum time of 900 s in case of a failed attempt. In 2018, lizards were tested until they solved the task in three out of four consecutive trials, or until they had participated in ten valid trials. In 2019, all lizards received ten valid trials, but for consistency between years we did not use data of post-criterion trials in further analyses. Trials in which lizards accidentally removed the disc or did not participate were discarded (as this reflects a lack of motivation rather than cognitive failure). Lizards were classified as non-solvers (never solved), occasional (at least once) or consistent (passed 3/4-criterion) solvers and received a lid-removal score (0-2) accordingly.

Differences in lid-removal score between habitats were tested using a generalized mixed-effect model (GLMM) following a zero-inflated negative binomial distribution, using the ‘glmmTMB’ function and (optim/BFGS) optimizer (Brooks et al., 2017). Independent variables were: habitat, sex, tail status, SVL, year and its interactions. Population was included as random effect. Solving times were analysed using Cox proportional hazard models ('coxme' and 'survival' packages, Therneau, 2015; Therneau & Lumley, 2020) as these are better suited for right-censored data.

Exploratory behaviour

The tendency to explore and sample novel environments is likely linked to how fast individuals solve new problems and learn new information (Sih & Del Giudice, 2012). Exploration was tested by introducing lizards into a novel environment (Carazo et al., 2014; McEvoy et al., 2015; Damas-Moreira et al., 2019). Two different novel environments were used to avoid habituation (cfr. McEvoy et al., 2015). Each environment was a Plexiglas arena (60 x 60 x 30 cm l x w x h) with either a plywood or sand substrate. Four identical plastic refuges (cups covered in either black or white isolation tape) were positioned along the four walls of the arena, with their entrance facing the centre, and four identical objects (either pine cones or stones) were placed in between them. A lizard was placed in the centre of the arena underneath an opaque cover for three minutes. After the cover was removed, it was free to explore the arena for ten minutes. Each lizard was tested once in each novel environment (order was randomized) generally with one day in between consecutive trials.

On the camera recordings, we divided the arena in four equal quadrants and scored the following behaviours: the first transition from one quadrant to another, the total number of transitions between quadrants, the latency to visit all four quadrants, the number of times an object was investigated (by contacting it with the snout or front legs), latency to first enter a refuge, number of times a refuge was entered and the total time spent inside refuges. The number of variables was reduced by performing a principal component analysis (PCA) with the ‘princomp’ function in R v 3.5.1. (R Core Team, 2018), using a correlation matrix to standardize variables. Principal components with an eigenvalue > 1 (Kaiser-Guttman criterion) were extracted and included as response variables in LMMs. Independent variables included: habitat, sex, SVL, and year and its interactions. Random factors were: population, arena and lizard ID. Repeatability of exploration was calculated as described above.

Aggression

Aggression was estimated by staging a series of pairwise agonistic encounters, similar to previous studies on lizard dominance (Abalos et al., 2016; Bruinjé et al., 2019; Names et al., 2019). Encounters took place in a separate Plexiglas arena (60 x 60 x 30 cm l x w x h), in order to avoid a residence-advantage effect. The arena had a sand substrate and was separated in two halves using an opaque divider. A heat bulb of 100 W was suspended above the centre of the arena. One lizard was placed at each side of the arena for three minutes. Thereafter, the divider was removed and a pile of stones was introduced in the centre of the arena as a basking spot for which lizards could compete. Encounters lasted ten minutes, but could be interrupted if fights escalated (e.g. biting and holding a rival for more than one minute – Abalos et al. 2016) in order to avoid injury. This was, however, never necessary.

Trials were videotaped and scored afterwards using a modified version of the ethogram in Names et al. (2019). For each agonistic behaviour lizards received a score of '+1' and for each evasive behaviour a '-1' (Table 1), which were then summed to calculate an individual's 'aggression score'.

Table 1. List of behaviours scored during the agonistic encounters, based on the ethogram of Names et al. (2019).

Behaviours		Description
Agonistic	Attacks	Fast strike to the opponent or touching rival with closed mouth
	Approach	Slow approach towards to opponent
	Bite	Grabbing part of the opponent's body with mouth
	Display	One or more of the following: mouth gaping, throat extension, back arching or turning its flank towards the opponent
Evasive	Bypass	Initially approaching, but then moving around rival
	Fleeing	Rapidly moving away from opponent
Aggression score		Sum of agonistic – sum of evasive

Lizards were paired with size-matched individuals (max 10% difference in SVL) of the same sex. Lizards were staged against three to five different opponents (with at least one rival from a simple and one from a complex habitat). Due to technical issues, we were only able to analyse two trials for ten individuals. We tested both males and females, but because true fights between females were rare we only analysed the data for male-male encounters.

Aggression scores were analysed using a GLMM with Poisson distribution. Independent variables included: habitat, tail status, SVL and year and its interactions. To account for the unequal number of contests among individuals, we also added the number of previous encounters (0 – 4) as covariable. Lizard ID, population, contest number and opponent ID were included as random effects. Repeatability of aggression was calculated as above.

Problem-solving: escape box

The escape box test differed from the other problem-solving task (lid-removal) in the nature of the reward offered: lizards were motivated by rewarding access to heat and safety rather than food. (e.g. Day et al., 2001; Noble et al., 2012; Carazo et al., 2014). The escape box, a Plexiglas transparent box (17.4 x 17.4 x 6.5 cm l x w x h), was placed inside a larger rectangular arena (46 x 30 x 30 cm l x w x h) containing sand and a pile of stones underneath a heat bulb (60 W). A lizard was introduced in the escape box through a small hole on the top (2.9 diameter) which was then immediately covered. In order to gain access to the basking/hiding spot, the lizard needed to slide open a white plastic door (3.2 x 2.4 cm l x h). This door was already slightly opened (4 mm) and contained grooves every 4 mm to facilitate grip. For this particular test, the camera was placed in front of the arena for better recordings.

Lizards received a single trial of 30 minutes to escape from the box, as most lizards managed to escape within the first trial (see results). Escape time was measured as the time between the first movement of an individual, and the moment that half of its body had passed through the door. Lizards received the maximum time of 1800 s in case of failure. Escape time could not be determined for ten lizards (3 complex, 7 simple) due to technical issues. In 2018, some individuals (N = 10) were tested in between their spatial learning trials and in 2019 lizards were tested in two batches (before and after spatial cognition) due to logistical reasons.

Differences in escape box success (Y/N – binomial distribution) and escape time were analysed using a GLMM and LMM respectively. Both models included the following independent variables: habitat, sex, tail status, and year and its interactions. Random effects were: population and batch.

Spatial and reversal learning

Spatial learning refers to an individual’s ability to learn and remember the location of resources in its environment (Dukas, 2004). Animals, however, also require the ability to update this spatial information frequently. Such learning flexibility is often tested using a reversal learning task (Noble et al., 2012). We estimated the lizards’ spatial learning and reversal learning capacities using a common protocol in which lizards needed to learn the location of a safe refuge during a simulated predator attack (Noble et al., 2012; Carazo et al., 2014; Vardi et al., 2020).

Lizards were tested in separate test arenas (60 x 60 x 30 cm l x w x h). Two identical refuges (plastic cups covered in black tape) were placed in opposite corners of the arena. The arena's walls were non-transparent, but visual cues were provided in and around the arena to facilitate spatial learning. For each lizard, we a priori designated either the left or right refuge (relative to the observer) as safe (randomized among lizards within each habitat). An individual lizard was placed in the centre of the arena underneath a transparent cover. After two minutes, the cover was lifted and the lizard was chased by tapping the base of its tail with a paintbrush. If a lizard entered the safe hiding spot, it was left alone for two minutes. Entering the unsafe refuge was penalized by lifting the refuge and continuing to chase the lizard until it had chosen correctly or 120 s had passed (after which the animal was gently placed inside the safe refuge). After two minutes underneath the safe refuge, lizards were returned to their home terrarium, and we recorded their number of incorrect choices. In between trials, refuges were cleaned with disinfecting wipes or 70 % alcohol and sand in arenas was mixed. We tested each individual thrice per day, with minimally one hour in between two trials, for five consecutive days. Immediately thereafter, a reversal phase of five consecutive days followed, in which lizards needed to reverse the learnt information (safe became unsafe and vice versa).

Trials were scored as successful if the lizard's first choice was the safe refuge, and individuals were considered to have learnt the task if they were successful in five out of six consecutive trials (Vardi et al., 2020) which was previously demonstrated to be a robust criterion for lizards (Noble et al., 2014; De Meester et al., 2021 ~ Chapter 4). Two lizards (one simple, one complex) that initially failed the spatial learning were able to reach the 5/6-criterion in the first trial of the reversal, and hence were still classified as learners. Lizards that succeeded on both phases were classified as 'flexible learners' as such consistent learning performance likely indicates high cognitive flexibility (Noble et al., 2012).

First, we performed a series of GLMMs to test for differences in learning success on the spatial learning, reversal learning and both phases (flexible learning) (all Y/N data). These models included habitat, sex, SVL, side of safe refuge (left/right, to account for lateralization - Szabo et al., 2019b) and year and its interactions. A habitat*safe side interaction was used in the reversal model but not in the spatial learning model due to convergence issues. Tail status was removed from the spatial model for the same reason. Population and batch were included as random factors. Thereafter, we also wanted to test whether learning curves differed between habitats, for which we fitted a GLMM (negative binomial distribution) per phase. Number or errors per trial was included as response variable. Independent variables were: habitat type, trial number, year and safe side, as well as a habitat*trial, habitat*year, year*trail and safe side*trial interaction. Lizard ID, batch ID and population were added as random factors. Initially, both models included a random slope and intercept for trial number in lizard ID, but this was removed from the reversal learning model to avoid convergence issues.

Cognitive-behavioural syndromes

Next, we were interested in covariance among personality and cognitive traits, and whether this differed between habitat types. First, we selected a single measure per test. For the personality traits (neophobia, exploration PC1 & PC2 and aggression) we used the BLUPs extracted from the (G)LMMs. For the cognitive tests, we preferred to use scores that would allow us to capture a large amount of individual variation, rather than solving or learning success (limited to either yes or no). Hence, we selected the solving time on the escape box task and mean number of errors per trial for both phases of the spatial cognition task (z-transformed per side and year in order to account for the side bias, cfr. Guillette et al. 2009, and year-effect). Solving times and number of errors are often used to indicate individual cognitive performance (e.g. Audet et al., 2015; Goulet et al., 2018; Branch et al., 2019). In addition, we added a 'flexibility-score', which was the mean number of errors lizards made over both phases of the spatial cognition task (individuals succeeding on both phases had a significantly lower mean number of errors compared to conspecifics who did not: LMM: $F_{1,126} = 30.20$, $p < 0.001$). We added 'flexibility-score' as it may be a stronger indicator of cognitive flexibility than performance on the reversal learning alone. For the lid-removal task, we initially wanted to include lid-removal times, but were unable to meet model assumptions due to highly skewed data. Hence, we assigned each lizard a binomial (LR) score depending on whether the lizard had solved the task consistently (1) or not (0). Other variables were transformed to improve normality if necessary, and all cognitive parameters except LR were multiplied with a factor of -1 so that higher scores would consistently reflect better cognitive performance. To test for the existence of a cognitive-behavioural syndrome, we ran a series of (G)LMMs for each pair of behavioural traits, with one trait as response variable, and the other as predictor. The interactions with habitat and year, as well as the three-way interaction between all independent variables, were included to test whether the association between two traits differed between habitat types and/or years (cfr. Michelangeli et al., 2019). Population nested in habitat was included as random effect. Significant trait*habitat*year interactions were further investigated by analysing the data for each year separately. No association was tested between Exploration PC1 and PC2 as these were derived from the same PCA analysis.

For these analyses, we only retained the scores of individuals that had participated in every test ($N_{complex}$ = 57 & N_{simple} = 60, 30 and 29 males respectively).

All data were analyzed in R version 3.5.1 (R Core Team, 2018). Where appropriate, data was transformed in order to meet model assumptions. Where necessary, the 'bobyqa' optimizer was used to ensure model convergence (Bates et al., 2015). Significance of fixed effects is reported based on F-tests calculated using Kenward-Roger Degrees of Freedom Approximation or Wald Chi-square tests for LMMs and GLMMs respectively.

Ethics approval

Experiments were approved by the Ethical Committee of the University of Antwerp (file ID: 2017-67) and permits were issued by the Greek Ministry of Environment and Energy (Permit Nrs: Ω6314653Π9-ΤΒΞ and 7ΖΠΡ4653Π8-Ε76). All experiments were in accordance with national legislation. Lizards were used for a follow-up experiment and thereafter released at site of capture.

RESULTS

Descriptive statistics for all cognitive and behavioural variables per habitat and per sex are presented in Supplementary Table S5.1. The outcome of all (G)LMMs is given in Table 2. Given the low degrees of freedom for the factor "habitat" in most of our models (due to low number of populations within each habitat type and the hierarchical structure of our data) we also tested the effect of habitat complexity on all behavioural parameters using equivalent models without population as random factor, and obtained largely identical results (Supplementary Table S5.2).

Training

Most lizards (91%, N = 138) successfully learned to eat from the transparent petri dish within ten trials (mean number of trials required + SE: 4.96 ± 0.22). Eight additional lizards reached the 3/4 – criterion during the neophobia trials and/or by including an additional trial. Six other lizards (three each year) did not reach criterion at all but participated in the lid-removal anyway.

Neophobia

Lizards took on average 113 ± 6 s (range: 6 – 493 s) to touch the petri dish during the last three trials of the training, compared to an average of 100 ± 10 s (range: 1 – 900s, car: 115 ± 16, rings: 85 ± 12) when a novel object was present. Lizards from simple and complex habitats did not differ in relative neophobia ($F_{1,2} = 0.28$, $p = 0.64$) and sex, year, SVL nor tail status ($N_{damaged} = 10$) affected neophobia (all $p > 0.05$). All interactions with year were non-significant (all $p > 0.05$).

Neophobia was highly repeatable in lizards from both the simple (R = 0.43) and complex habitats (R = 0.41), as well as when data was pooled (R = 0.43) (Figure 2).

Table 2. Outcome of the (G)LMMs testing the effect of habitat complexity and other variables on cognition and personality. Statistical significant differences are indicated as follows: '°' p < 0.10, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001 (see also main text).

Response	Predictor	F/Wald-stats	P
Relative neophobia (log)	Habitat	$F_{1,2} = 0.28$	0.64
	Sex	$F_{1,129} = 0.67$	0.41
	Year	$F_{1,130} = 0.00$	0.97
	Tail status	$F_{1,129} = 0.86$	0.36
	SVL	$F_{1,70} = 1.06$	0.31
	Habitat*Year	$F_{1,129} = 1.45$	0.23
	Sex*Year	$F_{1,127} = 1.60$	0.21
	SVL*Year	$F_{1,125} = 1.61$	0.21
LR Score	Habitat	$\chi^2_1 = 1.08$	0.30
	Sex	$\chi^2_1 = 0.10$	0.75
	Year	$\chi^2_1 = 4.84$	**0.03***
	Tail status	$\chi^2_1 = 0.00$	0.95
	SVL	$\chi^2_1 = 0.01$	0.93
	Habitat*Year	$\chi^2_1 = 0.05$	0.82
	Sex*Year	$\chi^2_1 = 0.03$	0.86
	SVL*Year	$\chi^2_1 = 0.18$	0.67
LR time (cox-proportional hazard model)	Habitat	$\chi^2_1 = 1.42$	0.23
	Sex	$\chi^2_1 = 1.15$	0.28
	Year	$\chi^2_1 = 3.75$	0.05°
	Tail status	$\chi^2_1 = 0.23$	0.63
	SVL	$\chi^2_1 = 0.05$	0.82
	Habitat*Year	$\chi^2_1 = 0.06$	0.81
	Sex*Year	$\chi^2_1 = 0.06$	0.80
	SVL*Year	$\chi^2_1 = 0.14$	0.71
Exploration PC1 (box-cox: $\lambda = 1.3$)	Habitat	$F_{1,2} = 1.91$	0.28
	Sex	$F_{1,130} = 0.54$	0.46
	Year	$F_{1,130} = 2.63$	0.11
	Tail status	$F_{1,129} = 0.53$	0.47
	SVL	$F_{1,52} = 0.30$	0.58
	Habitat*Year	$F_{1,129} = 0.54$	0.47
	Sex*Year	$F_{1,127} = 0.16$	0.69
	SVL*Year	$F_{1,125} = 0.03$	0.86
Exploration PC2	Habitat	$F_{1,2} = 2.51$	0.23
	Sex	$F_{1,129} = 2.28$	0.13
	Year	$F_{1,130} = 7.18$	**<0.01****
	Tail status	$F_{1,129} = 13.50$	**<0.001*****
	SVL	$F_{1,69} = 2.84$	0.10°
	Habitat*Year	$F_{1,129} = 2.75$	0.10°
	Sex*Year	$F_{1,127} = 1.18$	0.28
	SVL*Year	$F_{1,125} = 0.03$	0.87

Table 2. (Continued)

Response	Predictor	F/Wald-stats	P
Aggression	Habitat	$\chi^2_1 = 0.89$	0.35
	Year	$\chi^2_1 = 1.43$	0.23
	Tail status	$\chi^2_1 = 1.93$	0.17
	SVL	$\chi^2_1 = 0.18$	0.67
	Nr of previous trials	$\chi^2_1 = 2.48$	0.12
	Habitat*Year	$\chi^2_1 = 0.72$	0.40
	SVL*Year	$\chi^2_1 = 0.04$	0.83
ESC Success (Y/N)	Habitat	$\chi^2_1 = 0.12$	0.73
	Sex	$\chi^2_1 = 2.19$	0.14
	Year	$\chi^2_1 = 0.96$	0.33
	Tail status	$\chi^2_1 = 7.21$	<0.01**
	SVL	$\chi^2_1 = 0.24$	0.63
	Habitat*Year	$\chi^2_1 = 0.84$	0.36
	Sex*Year	$\chi^2_1 = 0.20$	0.66
	SVL*Year	$\chi^2_1 = 0.61$	0.43
ESC Time	Habitat	$F_{1,3} = 0.35$	0.60
(box-cox: $\lambda = 0.3$)	**Sex**	$F_{1,114} = 4.45$	**0.04***
	Year	$F_{1,1} = 0.28$	0.69
	Tail status	$F_{1,115} = 3.97$	**0.05***
	SVL	$F_{1,88} = 0.03$	0.86
	Habitat*Year	$F_{1,112} = 0.27$	0.60
	Sex*Year	$F_{1,113} = 1.36$	0.25
	SVL*Year	$F_{1,112} = 1.52$	0.22
SL Success (Y/N)	**Habitat**	$\chi^2_1 = 4.23$	**0.04***
	Safe side	$\chi^2_1 = 27.05$	**<0.001*****
	Sex	$\chi^2_1 = 0.57$	0.45
	Year	$\chi^2_1 = 0.93$	0.34
	SVL	$\chi^2_1 = 0.52$	0.47
	Habitat*Year	$\chi^2_1 = 2.91$	0.09°
	Sex*Year	$\chi^2_1 = 0.02$	0.88
	SVL*Year	$\chi^2_1 = 0.09$	0.76
SL Errors	Habitat	$\chi^2_1 = 1.67$	0.20
	Safe side	$\chi^2_1 = 276.79$	**<0.001*****
	Trail	$\chi^2_1 = 8.16$	**<0.01****
	Year	$\chi^2_1 = 6.61$	**0.01***
	Habitat*Year	$\chi^2_1 = 0.02$	0.90
	Trail*Year	$\chi^2_1 = 0.12$	0.73
	Habitat*Trail	$\chi^2_1 = 0.23$	0.64
	Safe side * Trail	$\chi^2_1 = 0.53$	0.47
RL Success (Y/N)	Habitat	$\chi^2_1 = 2.41$	0.12
	Safe side	$\chi^2_1 = 40.40$	**<0.001*****
	Sex	$\chi^2_1 = 0.21$	0.65
	Year	$\chi^2_1 = 0.83$	0.36
	Tail status	$\chi^2_1 = 0.05$	0.82
	SVL	$\chi^2_1 = 4.08$	**0.04***
	Habitat*Year	$\chi^2_1 = 1.87$	0.17
	Sex*Year	$\chi^2_1 = 0.25$	0.62
	SVL*Year	$\chi^2_1 = 0.25$	0.61
	Safe side * Habitat	$\chi^2_1 = 0.02$	0.88

Table 2. (Continued)

Response	Predictor	F/Wald-stats	P
RL Errors	Habitat	$\chi^2_1 = 1.04$	0.31
	Safe side	$\chi^2_1 = 223.55$	**<0.001*****
	Trail	$\chi^2_1 = 10.64$	**0.001*****
	Year	$\chi^2_1 = 0.36$	0.55
	Habitat * Year	$\chi^2_1 = 4.00$	**0.05***
	Trail * Year	$\chi^2_1 = 3.20$	0.07°
	Habitat * Trail	$\chi^2_1 = 0.53$	0.47
	Safe side * Trail	$\chi^2_1 =0.78$	0.38
Flexible learner (Y/N)	Habitat	$\chi^2_1 = 2.24$	0.13
	Safe side	$\chi^2_1 = 0.93$	0.34
	Sex	$\chi^2_1 = 0.02$	0.89
	Year	$\chi^2_1 = 1.03$	0.31
	Tail status	$\chi^2_1 = 3.85$	0.05*
	SVL	$\chi^2_1 = 0.94$	0.33
	Habitat * Year	$\chi^2_1 = 3.85$	0.05*
	Sex * Year	$\chi^2_1 = 0.17$	0.68
	SVL * Year	$\chi^2_1 = 1.67$	0.20
	Safe side * Habitat	$\chi^2_1 = 3.10$	0.08°

Problem solving: lid-removal task

Overall success on the lid-removal task was relatively low, with only 21.9 % of all lizards (complex: 12/66, simple: 18/71) learning to remove the disc consistently. Another 14.6 % opened the dish at least once (complex: 8/66, simple: 12/71) but failed to reach the 3/4 -criterion. Seven lizards only completed nine valid trials, but would have been unable to pass the 3/4-criterion even with an additional trial. Based on whether they had already solved the task at least once (N = 3) or not (N = 4) these lizards were classified as ‘occasional’ or ‘non-solver’ respectively. Two other lizards completed less than five valid trials, and were not assigned a lid-removal score. Average solving times of all these lizards were retained in the corresponding models.

Table 3. Principal Component Analysis of the behaviours observed during the exploration tests. Only loadings with an absolute value higher than 0.30 were considered to contribute to a principal component (indicated in bold). The first and second component were retained as exploration scores for further statistical analyses.

	Comp 1	Comp 2	Comp 3
Eigenvalue	1.62	1.41	0.90
% variance	37.38	28.35	11.59
First transition	- 0.21	**-0.46**	**0.56**
# transitions	**0.48**	0.25	0.20
Latency to explore all quadrants	**- 0.46**	**-0.30**	0.11
# touches	**0.34**	0.24	**0.65**
# refuges entered	**0.42**	**-0.42**	
Latency to enter first refuge	**-0.40**	0.26	**0.45**
Time spent hiding	0.26	**-0.59**	

Performance on the lid-removal (LR score or time) did not differ between lizards from different habitats or sexes, and was influenced by neither SVL or tail status, independent of year (all $p > 0.05$, Table 2). Nevertheless, lizards did acquire higher lid-removal scores in 2019 (2018: 0.41 ± 0.09; 2019: 0.76 ± 0.11; $\chi^2_1 = 4.84$, $p = 0.03$) and tended to be faster in 2019 ($\chi^2_1 = 3.75$, $p = 0.05$).

Exploration

The PCA of the exploration variables resulted in two principal components with an eigenvalue > 1, which together explained 65.73 % of the total variation (Table 3). Lizards scoring higher on the first component (PC1) made more transitions, investigated more objects, entered refuges faster and more often, and explored all quadrants of the arena in a shorter period of time. Higher scores on the second component (PC2) corresponded to lizards being faster in making the first transition and exploring all quadrants while entering less refuges and spending less time hiding inside them.

PC1-scores were influenced by neither habitat complexity, sex, SVL, tail status or year. None of the interactions with year were significant (all $p > 0.05$, Table 2).

Habitat complexity and sex did not affect PC2-scores either (all $p > 0.05$, Table 2). PC2-scores were higher in larger lizards (estimate: 0.18 ± 0.10; $F_{1,69} = 2.84$, $p = 0.10$) and in lizards with an intact tail ($N_{intact} = 123$, $N_{damaged} = 13$, intact: 0.12 ± 0.07, damaged: -1.18 ± 0.28, $F_{1,129} = 13.50$, $p < 0.001$). PC2-scores were lower in 2018 (-0.30 ± 0.12) than 2019 (0.28 ± 0.11; $F_{1,130} = 7.18$; $p < 0.01$). This year-effect was most pronounced in the simple habitats (habitat * year interaction: $F_{1,129} = 2.75$, $p = 0.10$), but this was likely due to the variable sample size for Alyko (habitat * year interaction if Alyko-lizards were excluded: $F_{1,112} = 1.60$, $p = 0.21$). No other interactions with year were significant (all $p > 0.05$).

Lizards showed consistent among-individual variation in PC1 in complex ($R = 0.26$) but not simple habitats ($R = 0.11$), while the opposite was found for PC2 ($R_{adj\text{-}complex} = 0.12$ $R_{adj\text{-}simple} = 0.34$). When pooled together, both PCs were repeatable (Figure 2).

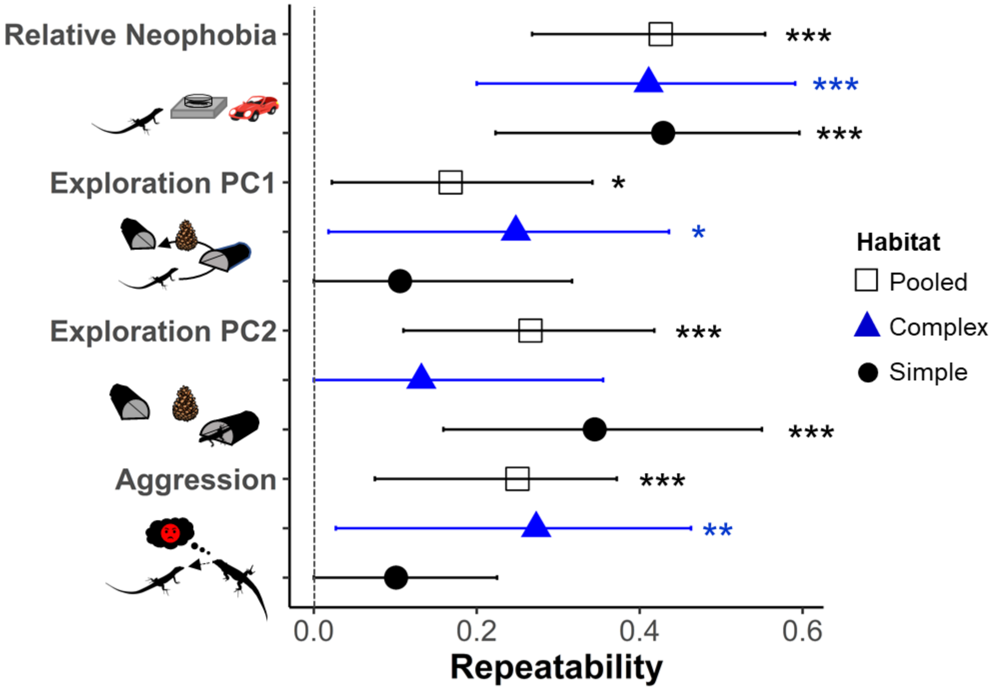

Figure 2. (Adjusted) repeatability of behavioural traits measured in this study. Repeatability was calculated using the 'rptR'-package (Stoffel et al. 2017) both for the pooled data (hollow squares) and for complex (blue triangles) and simple (black dots) habitats separately. For exploration PC2, adjusted repeatability was calculated, taking into account the effect of tail status and SVL. For a full explanation of the variables, see main text. The vertical grey line indicates R = 0 and error bars represent the 95% confidence interval estimated by parametric bootstrapping (n = 1000). Sample sizes were as follows: neophobia: $N_{complex}$ = 66, N_{simple} = 72, exploration: $N_{complex}$ = 65, N_{simple} = 71, aggression: $N_{complex}$ = 35, N_{simple} = 34. Significance levels according to a likelihood-ratio test are indicated as follows: : '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

Aggression

None of the main or nuisance factors affected aggression score (all $p > 0.05$, Table 2). Aggression scores varied consistently among lizards taken from complex (R = 0.27) but not simple (R = 0.10) habitats. When pooled together, aggression was repeatable (R = 0.25).

Problem-solving: escape box task

The majority of the lizards (78 %) was able to solve the escape box within a single trial. Habitat, SVL nor year affected escape probability or time (all $p > 0.05$, Table 2). Males and females were equally likely to escape ($\chi^2_1 = 2.19$, $p = 0.14$) although females were faster than males ($F_{1,114} = 4.45$, $p = 0.04$). Lizards with an intact tail escaped more often (intact = 94/115, damaged = 9/17, LRT: $\chi^2 = 7.21$, $p < 0.01$) and faster ($F_{1,114} = 3.97$; $p = 0.05$). The effect of all aforementioned variables did not differ between 2018 and 2019 (all $p > 0.05$).

Spatial and reversal learning

Seventy-two lizards (56 %) were classified as "learners" during the spatial learning phase (complex: 40/62, simple: 32/67), and sixty-two individuals (47 %) during the reversal learning phase (complex: 25/62, simple: 35/67). Only fifteen lizards (12 %) succeeded on both the spatial and reversal learning (complex: 8/62, simple: 7/67).

During the spatial learning phase, lizards from complex habitats were more likely to learn the location of the safe refuge than lizards from simple habitats (Figure 3a; $\chi^2_1 = 4.23$, $p = 0.04$) albeit there was a trend suggesting that this difference was more explicit in 2018 (2018: complex 68% vs simple 43%; 2019: complex 62% versus simple 57%; $\chi^2_1 = 2.91$, $p = 0.09$). Lizards were also more likely to learn if the safe refuge was positioned left in the arena (left: 61/64, right: 11/65, $\chi^2_1 = 27.05$, $p < 0.001$). Visual inspection of the data revealed that this side bias was identical in both habitat types. No other variables or interactions with year affected learning success (all $p > 0.05$, Table 2).

Habitat, sex, tail status nor year had an effect on reversal learning success (all $p > 0.05$, Figure 3b; Table 2). Larger lizards were less successful on the reversal learning (estimate: -0.61 ± 0.30, $\chi^2_1 = 4.08$, $p = 0.04$) and once again, lizards were more successful if the safe hiding spot was on the left (left: 53/65, right: 7/64; $\chi^2_1 = 36.69$, $p < 0.001$) independent of habitat ($\chi^2_1 = 0.02$, $p = 0.88$). No significant interactions with year were found (all $p > 0.05$).

During both the spatial and reversal phase, lizards clearly decreased the number of errors they made over time (Figure 3c; SL: $\chi^2_1 = 8.16$, $p < 0.01$; RL: $\chi^2_1 = 10.64$, $p < 0.001$), independent of habitat, safe side or year (all $p > 0.05$, Table 2). Nevertheless, for the reversal learning, there was a non-significant trend for a trial*year interaction ($\chi^2_1 = 3.20$, $p = 0.07$). Lizards decreased the number of errors in 2018 (estimate: -0.03 ± 0.01; $z = -3.57$, $p < 0.001$) but not in 2019 (estimate: -0.01 ± 0.01; $z = -1.04$, $p = 0.30$). In both phases, habitat had no effect on the number of errors made (all $p > 0.05$) but safe side did (SL: left: 0.26 ± 0.02, right: 1.23 ± 0.04, $\chi^2_1 = 276.79$, $p < 0.001$; RL: left: 0.38 ± 0.02, right: 1.44 ± 0.05, $\chi^2_1 = 223.55$, $p < 0.001$), independent of habitat (all $p > 0.05$). Lizards from both habitats made more errors during the spatial learning in 2019 ($\chi^2_1 = 6.61$, $p = 0.01$), but only lizards from simple habitats made fewer mistakes during the reversal in 2019 (habitat*year: $\chi^2_1 = 4.00$, $p = 0.05$).

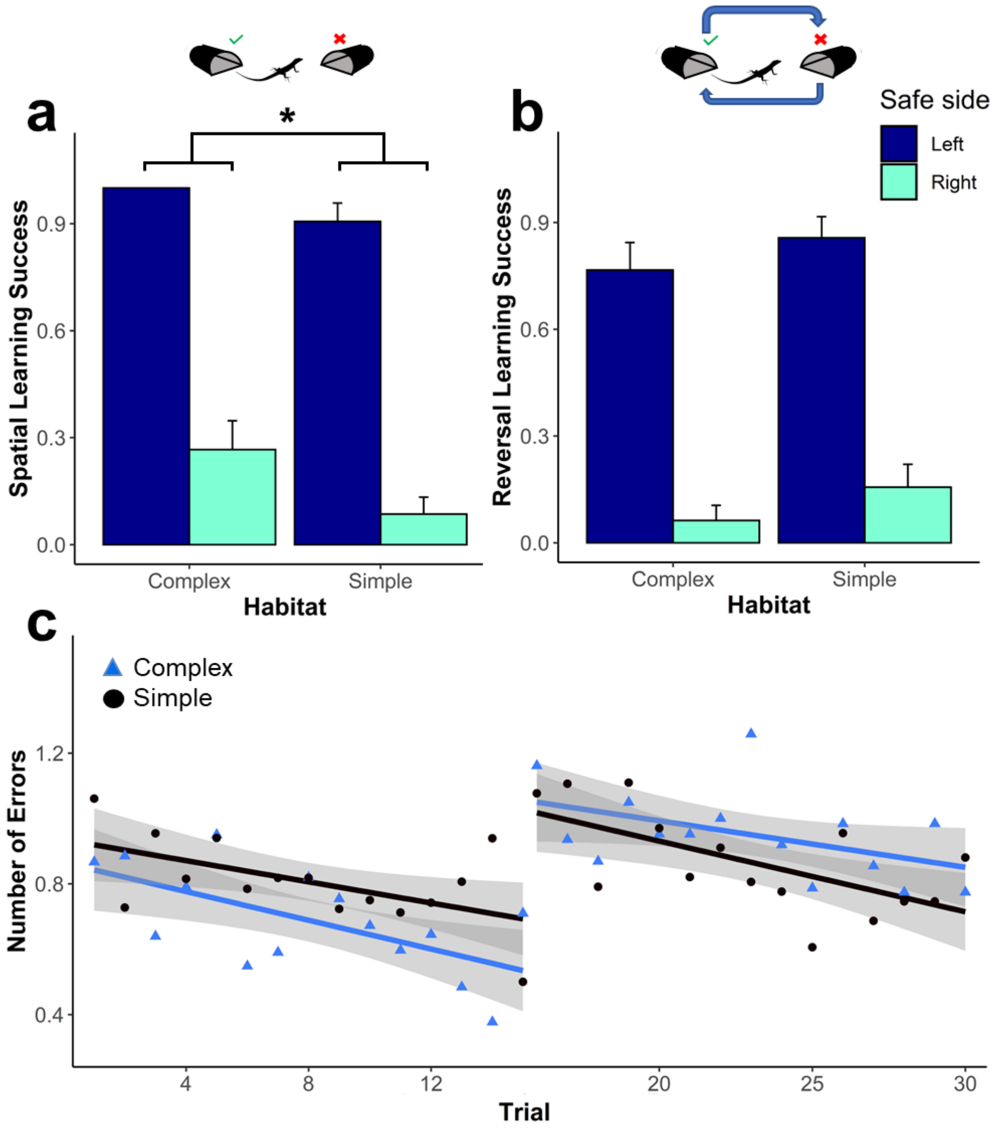

Figure 3. Proportion of lizards succeeding on a) the spatial learning task and b) the reversal learning task per habitat type and per side of the correct refuge (dark blue = left, light blue = right). Error bars indicate standard errors. Significance levels in a and b are indicated as follows: '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. c) changes in number of errors made by lizards over time, for both the spatial and reversal phase. Blue triangles represent means from complex habitats, black dots simple habitats. Significant regressions are indicated by a solid line, and grey areas represent standard errors. $N_{complex} = 62$, $N_{simple} = 67$.

The proportion of flexible learners (succeeding in both phases) did not differ between habitat types, although a significant interaction with year was found ($\chi^2_1 = 3.85$, $p = 0.05$). Although this interaction hinted that complex lizards were more flexible in 2018 and simple lizards in 2019 (Figure 4a), a post-hoc test revealed no significant differences (all pairwise comparisons $p > 0.10$). Such discrepancy may be due to the extremely low number of individuals succeeding on both phases (e.g. only one lizard in 2018 from the simple habitats). Post-hoc comparisons using the Tukey adjustment are known to be rather conservative.

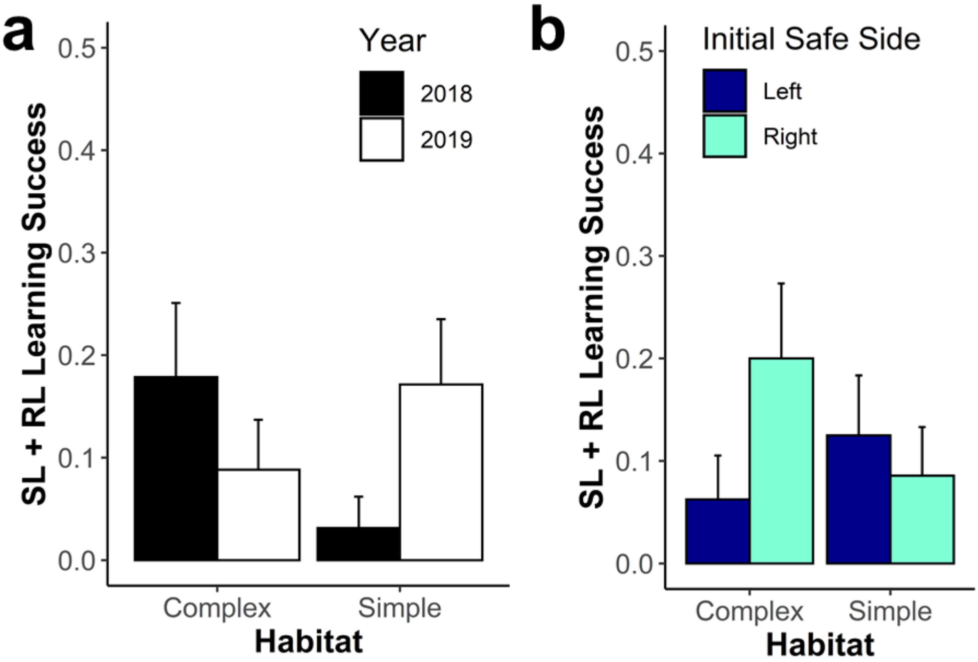

Figure 4. Proportion of lizards succeeding on both phases of the spatial cognition task per a) year (black = 2018, white = 2019). and b) initial safe side (dark blue = left, light blue = right). Error bars indicate standard errors Post-hoc pairwise comparisons did not reveal any significant differences or trends. $N_{complex\text{-}left} = 32$, $N_{complex\text{-}right} = 30$, $N_{simple\text{-}left} = 32$, $N_{simple – right} = 35$, $N_{complex -18} = 28$, $N_{complex – 19} = 34$, $N_{simple – 18} = 32$, $N_{complex – 19} = 35$.

Similarly, initial safe side did not affect learning success, but there was a trend that lizards from complex habitats were more likely to learn during both phases if they started with the safe refuge on the right (Fig. 4b, $\chi^2_1 = 3.10$, $p = 0.08$). Lizards with a broken tail were more likely to succeed on both phases (damaged: 5/17, intact: 10/112, $\chi^2_1 = 3.85$, $p = 0.05$).

Cognitive – behavioural syndromes

An overview of our results is given in Figure 5 (see also Table S5.3 for detailed results of all (G)LMMs). Overall, we did find significant associations among personality traits, among cognitive skills, and between personality and cognition, but often these relationships were habitat- and/or year-dependent, or both. We limit ourselves to highlighting those results that were consistent between both years.

First, our results suggest little evidence for the existence of a behavioural syndrome in either habitat type. Our analyses suggested a few links between personality traits in simple habitats, but these were inconsistent between years and involved traits that did not exhibit repeatable interindividual variation. In lizards from complex habitats such correlations were consistently absent (see Figure 5).

Secondly, there was stronger evidence for the existence of a cognitive syndrome. Across years and habitats, spatial and reversal learning capacity were inversely related (Figure 6a, $F_{1,113} = 6.02$, $p = 0.02$), and both measures correlated positively with flexibility scores (Figure 6b-c, SL-Flex: $F_{1,113} = 29.98$, $p < 0.001$, RL – Flex: $F_{1,112} = 70.25$, $p < 0.001$). One aspect of problem-solving, LR-score, was unrelated to either of these learning parameters in either year and/or habitat (all $p > 0.10$).

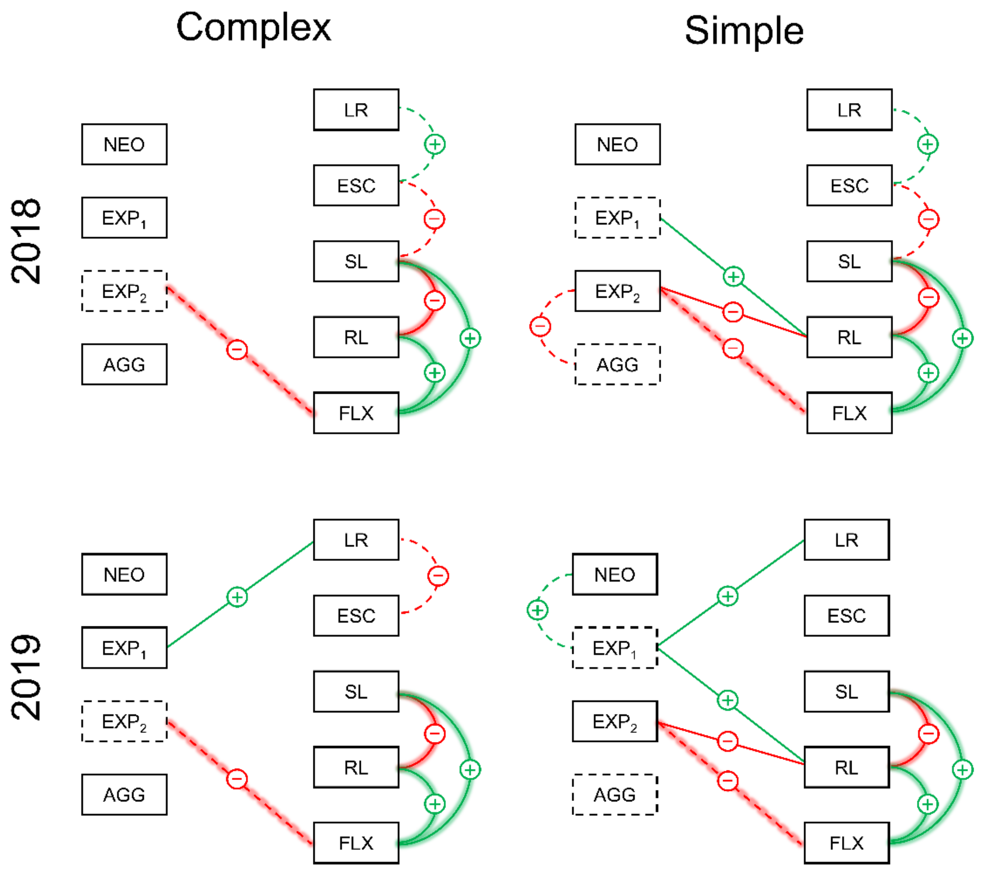

Figure 5. Overview of cognitive – behavioural syndromes per year and per habitat type. NEO = Neophobia BLUPs, Exp PC1 = Exploration PC1 BLUPs, Exp PC2 = Exploration PC2 BLUPs, AGG = Aggression BLUPs, LR = Lid removal success (Y/N), ESC = Escape Box Score (mean time * -1), SL = Spatial learning score (z-score errors * -1), RL = Reversal learning score (z-score errors * -1), FLEX = flexibility score (overall mean errors * -1). Higher scores on the cognitive traits represent higher cognitive performance (e.g. less errors, faster solving times). Green lines (+) represent a positive association, red lines (-) a negative association. A glow around the regression line indicates that this association was consistent both between years and habitat types. Solid lines represent statistical significant regressions ($p < 0.05$), while dotted lines represent trends ($p < 0.10$). Personality traits in a box with dotted lines were not repeatable within that habitat type. For more detailed results per regression, we refer to Table S5.3. Sample sizes were as follows: $N_{complex} = 57$ & $N_{simple} = 60$, 30 and 29 males respectively. Note that all regressions with aggression as predictor were solely performed using data of males.

Finally, aspects of personality and cognitive ability covaried in ways that were consistent over time but differed between habitats of origin. In particular, reversal learning performance was predicted by both exploration PC1 and PC2, but only in simple habitats (habitat*PC1: $F_{1,111} = 4.98$, $p = 0.03$; habitat*PC2: $F_{1,110} = 6.40$, $p = 0.01$), independent of year (year*trait: all $p > 0.10$). Lizards with high scores on exploration PC1 performed better on the reversal learning task (Figure 6d; $t = 2.28$, $p = 0.02$), but, unexpectedly, so did lizards with low scores on exploration PC2 (Figure 6e; $t = -3.29$, $p < 0.01$). Independent of year and habitat (all $p > 0.10$), lizards with high scores on the exploration PC2 axis tended to achieve low scores for flexibility (Figure 6f, exploration PC2: $F_{1,112} = 3.65$, $p = 0.06$). Consistent over both years and habitats, neophobia did not affect performance on any of the cognitive tests.

DISCUSSION

Ecological conditions are known to affect the evolution of animal cognition and personality, and may also shape their interaction (Brydges et al., 2008; Dalesman, 2018; Henke-von der Malsburg et al., 2020; Liedtke & Fromhage, 2019a). Our results add to the general observation that individual animals, including lizards, exhibit consistent differences in aspects of their behaviour. As expected, individual differences in cognitive performance were often related to personality variation in *P. erhardii*, and our study is one of the first to illustrate that such covariance can be highly variable across ecological conditions, and possibly in time. We also found that Aegean wall lizards originating from structured habitats outperformed conspecifics from simple habitats in a spatial learning test, but the effects of habitat complexity on other measures of cognitive performance and personality proved small.

Effect of habitat complexity on cognition and personality

In accordance with previous research on diverse taxa (bats: Clarin et al., 2013; mole-rats: Costanzo et al., 2009; fish: Shumway, 2008; White & Brown, 2014, 2015), *P. erhardii* lizards originating from structurally complex habitats scored better in the spatial learning task than conspecifics from simple open environments. To our best knowledge, this is the first study demonstrating this in surface-dwelling terrestrial vertebrates. Hence, the link between structural habitat complexity and spatial learning has now been demonstrated in aquatic (Shumway, 2008; White & Brown, 2014, 2015), aerial (Clarin et al., 2013), fossorial (Costanzo et al., 2009) and terrestrial animals (our study, but see Mackay & Pillay, 2017), implying this to be a general tenet in the evolution of spatial cognition.

Previous studies have mainly attributed these differences in spatial cognition to challenges associated with foraging in more structured habitats (Henke-von der Malsburg et al., 2020). Nevertheless, it should be noted that habitat complexity probably complicates other spatial tasks as well, such as territorial defence, finding mates and escaping to safe shelter. Field observations suggest that lizards tend to flee towards the same refuges in their habitat, even if these are not visible from their initial position (Martin et al., 2003; Paulissen, 2008; Font, 2019). To do so fast and efficiently in a dense visually restricted environment probably requires stronger spatial memories. Future studies could elaborate on this and test how exactly spatial cognition affects behaviour in a natural setting, and how this changes with vegetation density. Perhaps lizards from dense habitats, like gobies (White & Brown, 2014), use multiple types of cues to navigate their environment. But then again, the strong side-bias observed in our experiments suggests that lizards from both habitats rely heavily on egocentric cues (discussed in De Meester et al., 2021 ~ Chapter 4).

Neither problem-solving (both tests) nor reversal learning were related to habitat complexity in *P. erhardii*. The effect of habitat on learning flexibility seemingly varied between years, but we are cautious about this result due to the lack of significant post-hoc comparisons. Complex habitats are considered to be more variable in time and space and therefore to require higher cognitive flexibility (Roth et al., 2010b; Tebbich & Teschke, 2014; Tello-Ramos et al., 2019; Szabo & Whiting, 2020), of which both problem-solving and reversal learning are believed to be strong indicators (Tebbich & Teschke, 2014). We propose four alternative explanations for why our results did not align with this expectation.

A first plausible reason may be that structural complexity and habitat variability are not necessary related. Our populations of *P. erhardii* may all be exposed to comparable levels of temporal variation, or may experience variability in different ways, thus leading to similar levels of cognitive flexibility. Future studies on for example seasonal and spatial variation in habitat structure or arthropod abundance could confirm whether this is the case. Secondly, habitat complexity may require higher flexibility, but so do other environmental challenges that may be more prevalent in open environments, such as food scarcity (Tebbich et al., 2002; Roth et al., 2010b; Szabo & Whiting, 2020) or predation (Vila Pouca et al., 2021). Untangling the effect of multiple ecological factors will require sampling many more populations than in the current study. Thirdly, our tests may simply not be reliable indicators of cognitive flexibility, either because they do not reflect cognitive flexibility at all (Audet & Lefebvre, 2017) or because they are not ecologically relevant for Aegean wall lizards. For instance, whether and how problem-solving ability in the laboratory predicts performance in natural conditions has never been tested in lizards (but see Tebbich et al., 2002; Sol et al., 2005a for evidence in birds). Lastly, maybe lizards in neither habitat type are able to afford the high energetic cost of cognitive flexibility (Tello-Ramos et al., 2019) due to low resource availability on islands (Janzen, 1973; De Meester et al., 2021 ~ Chapter 4). This hypothesis seems to be supported by the overall low success rate on the lid-removal task and the limited number of lizards demonstrating flexible learning. All the same, our results show that habitat complexity does not affect all cognitive traits equally, thus highlighting how various aspects of cognition may evolve independently of each other in response to different ecological pressures.

Habitat complexity did not affect lizard personality either. This contradicts previous work on a variety of taxa where animals in more structured environments behave less neophobic, more explorative and bolder (Mettke-Hofmann et al., 2002; Harris et al., 2011; Crane et al., 2019; Garcia et al., 2020; Johnson et al., 2020). This is often believed to be due to the relative safety animals experience in more densely vegetated habitats, as predators are visually restricted and safe shelter is easily available (Keiser et al., 2018; Crane et al., 2019; Quadros et al., 2019). Nevertheless, we have little evidence that *P. erhardii* in complex habitats truly experiences less predation, as e.g. the foraging success of snakes, their common predators (Pafilis et al., 2009), is either unaffected or improved by increasing vegetation density (Mullin & Mushinsky, 1997; Mullin & Gutzke, 1999).

We found no effect of habitat complexity on aggressiveness. This goes against the general notion that territoriality may be more costly in cluttered areas (Eason & Stamps, 1992; Johnson et al., 2010; Church & Grant, 2018). Interestingly, some lizard species seemingly adjust their territorial behaviour to changes in habitat structure (Eason & Stamps, 1992; Calsbeek & Sinervo, 2002). Lizards from both habitat types may therefore exhibit different levels of aggression in their respective environments, but not when tested in the same standardized and simple arenas. For instance, a study by Church & Grant (2018) found that the complexity of the test enclosure, but not of the original habitat, predicted personality differences in juvenile salmon (*Salmo salar*). This could also explain the lack of differences in other personality traits, and requires future studies in (semi-)natural conditions to check if any ecological patterns went undetected.

While we found no differences between habitats in average personality traits, we did notice intriguing habitat-dependent shifts in the repeatability of those traits. Aggression and exploration PC1 (more transitions and investigations of refuges and objects) were only repeatable in complex habitats, suggesting higher plasticity for these traits in lizards from simple habitats (Damas-Moreira et al., 2019), while the opposite is found for exploration PC2 (less hiding and faster to start and end exploration of the entire arena). It is currently unclear why consistent interindividual differences would exist in one but not both habitat types, although this could be due differences in temporal and spatial variability (Hendry, 2016).

Behavioural associations

As predicted, we found numerous behavioural associations, both between personality traits, between cognitive traits and, finally, between personality and cognition. Nevertheless, the strength and direction of these correlations varied considerably between years and habitats.

Firstly, the existence of a behavioural syndrome (among personality traits, *sensu* Sih et al., 2004) was only weakly supported. No correlations were found in lizards from complex habitats. Potentially, behavioural syndrome structure has dissolved in these populations as a consequence of more relaxed predation pressure (Sih et al., 2004; Bell & Sih, 2007; Brydges et al., 2008; Harris et al., 2011). But then again, evidence for a behavioural syndrome in lizards from simple habitats was also unconvincing: the observed correlations were inconsistent over years, or involved traits with low repeatability. We tentatively conclude that *P. erhardii* on Naxos do not exhibit a stable behavioural syndrome. Why our study species differs in that respect from many previously studied species remains an open question.

Support for the existence of a cognitive syndrome was much stronger. Independent of year and habitat, we found a negative correlation between spatial and reversal learning, which is a general trend observed in various taxa (Griffin et al., 2013; Bebus et al., 2016; Mazza et al., 2018; Sorato et al., 2018; but see Bensky & Bell, 2020). This could reflect a trade-off between fast but superficial and slow but attenuative learning, as predicted by the Cognitive Style Hypothesis (Sih & Del Giudice, 2012). Alternatively, initial good learners may form stronger spatial memories, which actively inhibit the formation of new memories during the reversal (proactive interference: Croston et al., 2017). Probe tests in which spatial cues are manipulated in combination with memory retention tests could provide better insights in the neural mechanisms behind this learning – reversal learning trade-off.

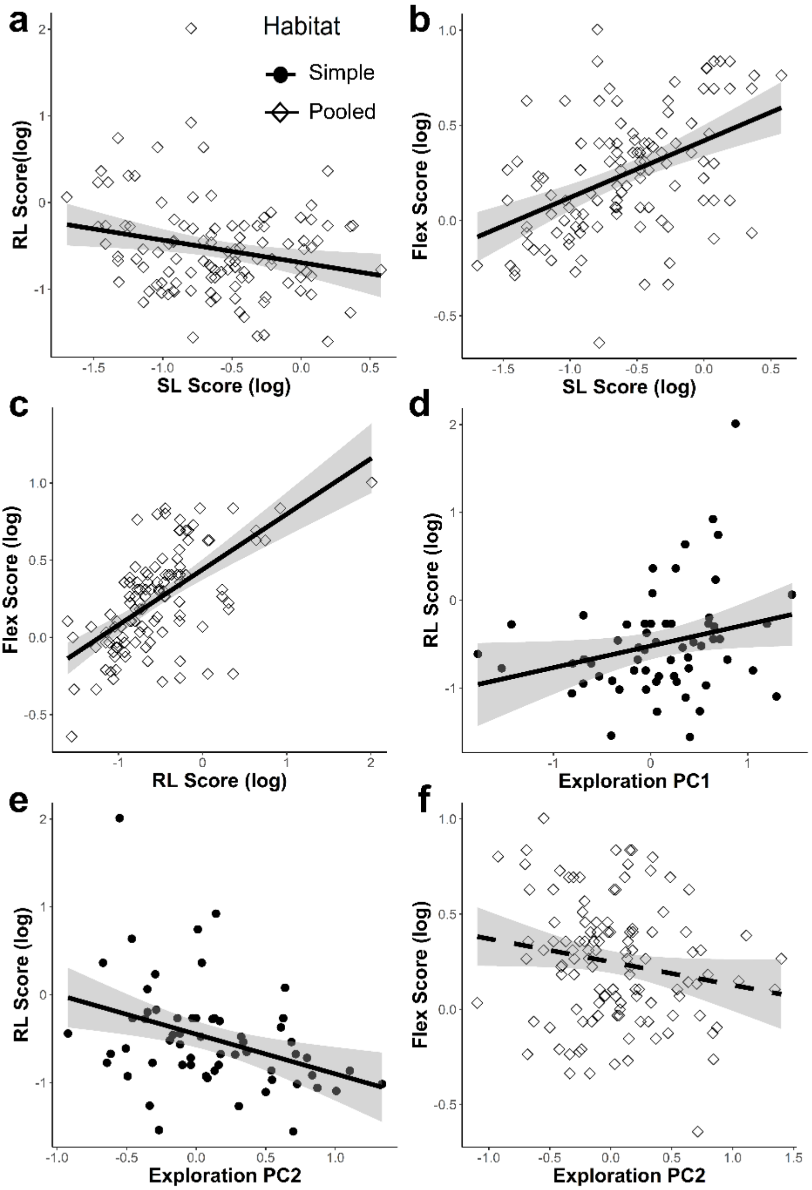

Figure 6. Associations between cognitive traits (a-c) and personality and cognition (d-e) in Aegean wall lizards. SL Score = spatial learning score (z-score errors *-1), RL Score = Reversal learning score (z-score errors *-1) and Flex Score = Flexibility score (overall mean errors * -1). Higher scores on the cognitive traits represent higher cognitive performance (e.g. less errors, higher flexibility). Black dots represent lizards from simple habitats (N = 60), hollow diamonds represent pooled data from both habitats (N = 117). Solid lines represent statistical significant correlations ($p < 0.05$). Dotted lines represent statistical trends ($p < 0.10$). Grey areas represent standard errors. For more detailed results per regression, we refer to Supplementary table S5.3.

The fact that this trade-off is found in both habitat types and years may indicate a general constraint for this species. Nevertheless, both spatial and reversal learning were strongly and positively associated with flexibility scores. Thus, despite this trade-off, some individuals performed well during both phases and thus exhibited true cognitive flexibility.

Other correlations between cognitive variables were consistently absent. Lid-removal, for instance, was never related to either reversal learning or flexibility scores, despite the common belief that these all reflect an individual's behavioural flexibility (Tebbich & Teschke, 2014). Our results add to a growing list of evidence suggesting that either problem-solving and reversal learning reflect flexibility in different cognitive domains, or novel motor tasks are simply not reliable indicators of cognitive flexibility (reviewed in Audet & Lefebvre, 2017). In that regard, it is worth noting that performance on both problem-solving tasks was weakly and inconsistently related. Whether this is due to differences in cognitive domain, motivation or task difficulty is currently unclear. While studying cognition in an ecological context, biologists often assume that individual performance is repeatable across time and context, but this result illustrates the need to verify such assumptions (see discussion in Griffin et al., 2015; Shaw & Schmelz, 2017).

Lastly, we also found considerable covariance between personality and cognition. Independent of year or habitat, more explorative lizards (PC2 – less time hiding, faster to start and finish exploration) tended to have lower flexibility scores. Although this seems to be perfectly in line with the Cognitive Style Hypothesis (Sih & Del Giudice, 2012), we also propose an alternative explanation which involved differences in motivation rather than information gathering. Individuals who consistently spent more time hiding may just have been more eager to find the safe refuge and thus learn in both phases. Contrariwise, more explorative individuals tend to habituate faster to predator attacks, and may thus have been less motivated to escape towards the end of the test (Rodriguez-Prieto et al., 2011). Individuals with a broken tail, who are supposedly more vulnerable to predation (Michelangeli et al., 2020), spent more time hiding during the exploration test and also showed higher learning flexibility, which seems to support the idea of motivational differences.

Other associations between personality and cognition were habitat-specific. In lizards from simple, but not in those from complex habitats, explorative behaviour predicted reversal learning ability. Paradoxically, lizards with higher exploration scores on PC1 (more transitions and investigating) performed better on the reversal learning, while those with higher PC2-scores performed worse. We doubt the ecological relevance of the former result, given that PC1 was not repeatable in lizards from simple habitats. The correlation between PC2 and reversal learning, on the other hand, mirrors the habitat-independent trend found between PC2 and flexibility. It is possible that this trend is thus mainly driven by the lizards from simple habitats.

Taking everything into account, there seemed to be an overall pattern that behavioural associations were either independent of habitat or solely found in the simple environments. The behavioural associations exclusively found in simple habitats (e.g. Exploration PC2 – RL) may have arisen because specific environmental challenges in these populations select for specific behavioural combinations/strategies (Sih et al., 2004; Brydges et al., 2008; Sih & Del Giudice, 2012; Liedtke & Fromhage, 2019a). Predation, for instance, is considered an important force shaping behavioural syndromes

(Bell & Sih, 2007; Dingemanse et al., 2007; Harris et al., 2011) and potentially cognitive styles (Sih & Del Giudice, 2012; Liedtke & Fromhage, 2019a). Consider the exploration PC2 – RL link in simple habitats, where there is presumably a higher predation risk. Fast exploration may result in high immediate gains (e.g. resources), but at the cost of increased mortality due to predation (Reale et al., 2010b; Sih & Del Giudice, 2012). Cognitive flexibility is costly, and a fast explorer may die before reaping its benefits. Slow explorers choose safety over short-terms gains (Reale et al., 2010b; Sih & Del Giudice, 2012; Mazza et al., 2019) and are thus more likely to experience environmental changes in their longer life. Flexibility may even help them to survive predation (Kotrschal et al., 2015a). A slow-inflexible individual, on the other hand, will neither be able to compete with fast explorers, nor will it gain the same survival-advantages as the flexible learners. Under predation such maladaptive combinations may be eliminated, while they may still be able to thrive in the relatively safe complex habitats. Indeed, pond snails obtained from the wild do show covariance among memory traits, and between exploration and memory, while captive bred individuals do not, most likely due to generations of relaxed selection (Dalesman et al., 2015; Dalesman, 2018). Nevertheless, Brydges et al. (2008) found no effect of predation pressure on personality-learning covariance in eight populations of stickleback. Other environmental factors may thus also play a role in shaping or breaking down such covariance. Our study is one of the first to specifically test how ecological conditions affect the personality-cognition link; clearly much remains to be learned.

The effect of year and sex

Another important finding of this study is that the strength and direction of cognition-personality associations (and those between themselves) can show considerable variation between years. In addition, we also found some differences between years in average levels of personality and cognition.

Such annual variation may simply be a consequence of deviations in methodology. For example, whether or not we cleaned the experimental equipment between trials may have affected how much time lizards would spent e.g. interacting with the problem-solving apparatus or hiding in the exploration arena (López et al., 1998). Different personality types may also react differentially to the scent of conspecifics (Aragón et al., 2006), which could affect the behavioural associations found. Nevertheless not all behavioural parameters showed annual variation and performance on the spatial cognition task, despite consistently controlling for chemical cues here, also differed between years. We therefore deem methodological deviations alone to be insufficient to explain the annual variation.

A second explanation may be that these differences between years are a consequence of temporal fluctuations in ecological conditions (Quinn et al., 2016), which could alter selection regimes on cognition and personality (Dingemanse et al., 2004; Le Cœur et al., 2015; Cauchard et al., 2017; Branch et al., 2019) or alter behavioural development during early life (Clark et al., 2013; Amiel et al., 2014; Dayananda & Webb, 2017; Siviter et al., 2017a; Siviter et al., 2017b; Munch et al., 2018; Beltrán et al., 2020; Vardi et al., 2020). Environmental changes can also shift the adaptive value of particular behavioural combinations, and thus alter such associations via selection and behavioural plasticity (Bell & Sih, 2007).

Independent of whether our year-differences were due to methodological or ecological variation, we would nevertheless argue that future studies on personality-cognition covariance would benefit immensely from collecting behavioural data over multiple years, and test whether such covariance is consistent across time within a population. Long-term studies could hence become a valuable approach to study how ecological variation shapes personality and cognition and their relationship.

Albeit outside our intended scope, we end with addressing the (lack of) sex-differences found in this study. In general, males are predicted to exhibit faster, more risk-taking, personalities and enhanced spatial cognition compared to females, due to differences in their reproductive strategies (Costanzo et al., 2009; King et al., 2013; Carazo et al., 2014; Szabo et al., 2019c). However, male and female *P. erhardii* did not differ in either personality nor cognitive traits, and evidence for sex-dependent learning is overall weak in lizards (Szabo et al., 2019c). Females escaping faster from the escape box could simply be a consequence of higher motivation to bask or hide. We suggest that further information on the spatial ecology and reproductive strategies of sexes in *P. erhardii* is required for a better understanding of our results.

CONCLUSION

Our results offer two interesting main insights, relevant for future studies on the evolution of cognition. First of all, the fact that habitat complexity affected only one aspect of cognition (spatial learning) does suggest that within Aegean wall lizards distinct cognitive abilities may evolve independently following different selective pressures. Thus, when studying the link between ecology and cognition, future studies should be aware of the dangers of using a single cognitive test as a general indicator of an animal's cognitive abilities.

Secondly, our study revealed an complex interplay between personality, cognition and ecology within *Podarcis erhardii*, showing that covariance between cognition and personality can vary both between years and between ecological conditions. Previous studies found a large mix of inconsistent results regarding the link between animal personality and cognition, but most have either studied this a) within a single year or b) within a single population. We suggest that expanding this line of research to include more populations over a broader ecological gradient and/or multiple years, could help us to identify the selective pressures shaping or breaking down cognition-personality covariance. A similar approach has certainly improved our understanding of behavioural syndromes, and is thus likely to advance the field of cognitive ecology as well.

ACKNOWLEDGEMENTS

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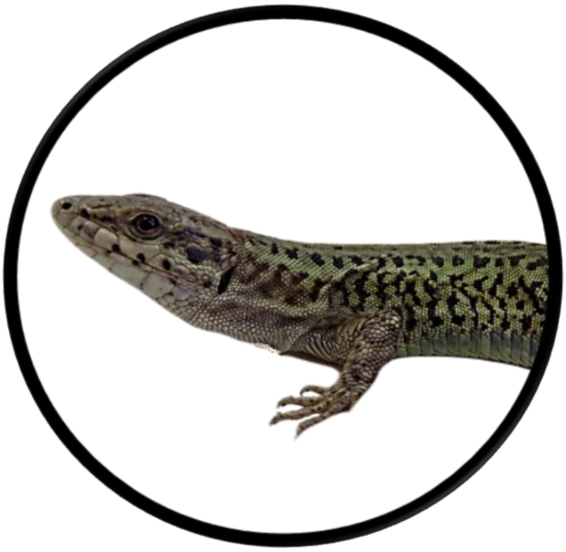
CHAPTER 6

EXPLORATION AND SPATIAL COGNITION SHOW LONG-TERM REPEATABILITY BUT NO HERITABILITY IN THE AEGEAN WALL LIZARD.



Adapted from:

De Meester, G., Pafilis, P., Vasilakis, G. & Van Damme, R. (2022). Exploration and spatial cognition show long-term repeatability but no heritability in the Aegean wall lizard. Accepted in Animal Behaviour.

ABSTRACT

Recently, biologists have become increasingly interested in cognitive variation among individuals, and how it relates to differences in fitness. However, very few studies so far have studied the long-term repeatability and heritability of cognitive performance in wild animals. This is nevertheless crucial information to fully understand the potential ecological and evolutionary impact of individual variation in cognitive performance. In 2019, we assessed exploration, problem-solving and spatial and reversal learning in 66 Aegean wall lizards (*Podarcis erhardii*), then released them in semi-natural enclosures consisting of either simple or complex habitat. One year later, we recaptured and retested the surviving lizards and their offspring to estimate the long-term repeatability and heritability of these behavioural and cognitive characteristics. We found that exploration and spatial learning were moderately repeatable, but reversal learning only marginally and learning flexibility and problem-solving not at all. Reversal learning ability declined over time in lizards kept in simple habitat, but not in those kept in complex habitats – suggesting habitat-dependent cognitive plasticity. To our knowledge, this is the first study demonstrating (long-term) consistency in cognitive traits within a non-avian reptile. The combination of modest repeatability and low heritability does suggest that within our study species, exploration and cognitive variation among individuals and populations is mostly moulded by environmental effects.

INTRODUCTION

The evolution of cognition, i.e. the acquisition, retention and use of environmental information (Dukas, 2004), is sometimes regarded as one of the most enigmatic topics within the study of biology (Thornton et al., 2014). The benefits of cognition seem obvious: learning and problem-solving equip animals with the necessary behavioural flexibility to deal with (changing) environmental conditions (Sol, 2009). However, cognition is also costly, as it requires energetically expensive neural processes and tissues (Aiello & Wheeler, 1995; Buechel et al., 2018). Recently, the field of cognitive ecology has started to adopt an individual-based approach to identify the drivers of cognitive evolution (Boogert et al., 2018). Individuals can differ remarkably in their cognitive abilities, and such variation can provide the raw material for natural and sexual selection to act on. Hence, a small, but growing, number of studies have tried to relate individual variation in cognition to individual differences in fitness (reviewed in: Morand-Ferron et al., 2016; Morand-Ferron, 2017; Boogert et al., 2018). Although valuable and informative, these studies have nonetheless been criticized for several reasons. To establish that a cognitive trait evolves by natural selection, one should not only prove its link with survival and/or reproduction, but also show that cognitive variation among individuals is consistent (i.e. repeatable) and heritable (Thornton et al., 2014; Griffin et al., 2015; Cauchoix & Chaine, 2016; Morand-Ferron, 2017; Boogert et al., 2018). Yet, few studies have verified these assumptions in non-human animals (but see references below).

Repeatability (R) is an estimate of how much of the phenotypic variation in a population can be explained by consistent differences among individuals (Boake, 1989; Bell et al., 2009; Nakagawa & Schielzeth, 2010). Behavioural repeatability does not necessarily exclude plasticity at the individual level. For instance, repeatability of cognitive performance would be demonstrated if over multiple repetitions of a learning task the relative order of fast to slow learners remains stable, even if intrinsic (e.g. age) or extrinsic (e.g. season) conditions influence individual performance (Griffin et al., 2015). Animals can either be retested on the same, slightly altered, task (temporal repeatability) or can be subjected to different protocols designed to measure the same cognitive ability (contextual repeatability) (Cauchoix et al., 2018).

Measuring the repeatability of cognitive performance, or behaviour in general, is deemed essential for various reasons. Firstly, repeatability sets the upper limit to heritability (h^2) (Boake, 1989; but see Dohm, 2002), and as such determines whether and how fast a trait may respond to selection (Boake, 1989; Croston et al., 2015; Morand-Ferron et al., 2016; Troisi et al., 2021). Secondly, measuring whether differences in cognitive traits are consistent is needed to understand the ecological and evolutionary relevance of their relation with a multitude of other biological traits (Soha et al., 2019), such as life-history (Cole et al., 2012), secondary sexual traits (Alvarez-Quintero et al., 2021) or personality (consistent interindividual differences in behaviour across time and context, Réale et al., 2007). There is currently a strong interest in exploring how personality and cognition covary (Dougherty & Guillette, 2018). However, interpretation of such relationships (or the lack thereof) often assumes that cognition is repeatable as well, yet this is rarely verified (Griffin et al., 2015; Sommer-Trembo & Plath, 2018). Last but not least, many authors have pointed out that performance on a cognitive task can be influenced by other, non-cognitive, factors, such as distraction, motivation or previous experience (Rowe &

Healy, 2014; Morand-Ferron et al., 2016). Repeated measurements are thus necessary to validate whether we are accurately quantifying cognitive variation.

While measuring repeatability of non-cognitive personality traits has almost become standard procedure in behavioural research (Bell et al., 2009), studies assessing the repeatability and consistency of animal cognition are much rarer in comparison (but see e.g. Cole et al., 2011; Rodríguez & Gloudeman, 2011; Brust & Guenther, 2017; Gibelli & Dubois, 2017; Schuster et al., 2017a; Schuster et al., 2017b; Shaw, 2017; Ashton et al., 2018; Cauchoix et al., 2018; Langley et al., 2018; Sommer-Trembo & Plath, 2018; Sorato et al., 2018; Tello-Ramos et al., 2018; Shaw et al., 2019; Soha et al., 2019; Reichert et al., 2020; Cooke et al., 2021; Mason et al., 2021; Troisi et al., 2021). A recent meta-analysis by Cauchoix et al. (2018) reported low to moderate values for repeatability of cognitive performance (temporal: R = 0.18 – 0.28, contextual: R = 0.20 – 0.27), albeit this was based on a small number of (mostly unpublished) datasets ($N_{temporal}$ = 22 studies, $N_{contextual}$ = 27 studies). Nevertheless, most of these past studies had three major limitations.

Firstly, repeatability of cognition, and personality, is commonly measured on relative short timescales, e.g. days or weeks in between repeated tests (estimates from > 1 year: 9 % in Bell et al., 2009; 31 % in Cauchoix et al., 2018 albeit only five species). Within a short timeframe, individuals are more likely to be tested under similar intrinsic and extrinsic conditions, leading to an inflation of repeatability estimates and potentially pseudo-repeatability (Dingemanse & Dochtermann, 2013). Over a longer period, plastic responses to differential environmental or developmental alterations may decrease the repeatability of the behavioural traits under study (Bell et al., 2009). Secondly, behavioural repeatability is frequently tested in animals raised and/or kept in controlled lab conditions. These will experience less environmental variation than their wild counterparts, which may result in biased repeatability estimates not representative for natural populations (Archard & Braithwaite, 2010; Stamps & Groothuis, 2010). Hence, verifying how consistent interindividual differences in cognition and personality are over longer timescales in natural conditions is critical information when trying to understand the role of such variation in ecological and evolutionary processes, but such data is largely lacking (but see e.g. Debeffe et al., 2015; Carlson et al ., 2020; Payne et al., 2021 for personality and e.g. Cole et al., 2011; Shaw, 2017; Ashton et al., 2018; Tello-Ramos et al., 2018 for cognition). Lastly, to our knowledge, no study to date investigated the long-term repeatability of cognition and personality within the same (wild) study system, despite the growing evidence that both aspects of behaviour are closely linked (Dougherty & Guillette, 2018).

Repeatability is often used as an estimation of heritability (Boake, 1989; but see Dohm, 2002), here defined in its narrow sense as the proportion of phenotypic variation in a population that can be explained by additive genetic effects (Falconer & Mackay, 1996). An alternative approach, however, is to measure behaviour of both parents and offspring and employ modern statistical methods to determine the amount of additive genetic variation (de Villemeuril, 2012: Colby et al., 2021). This also allows to determine the relative contribution of genetic versus permanent environmental effects in shaping phenotypic variation, which is key to understanding how a trait evolves (Croston et al., 2015). Although evidence for a genetic basis of cognition has been inferred by artificial selection studies (e.g. in fruit flies: Mery & Kawecki, 2002; in guppies: Buechel et al., 2018; in parasitoid wasps: Liefting et al., 2018), common garden experiments (e.g. in black-capped chickadees: Roth et al., 2010b) and genome-wide association studies (e.g. among dog breeds: Gnanadesikan et al., 2020), actual heritability estimations for cognition are rare. Cognitive abilities tend to be heritable in humans ($h^2 = 0.26 – 0.85$), primates ($h^2 = 0.21 – 0.91$) and laboratory mice ($h^2 = 0.21-0.50$) (reviewed in Croston et al., 2015) but data on non-traditional study taxa are scarce (Croston et al., 2015; but see: Smith et al., 2015; Quinn et al., 2016; Carrete et al., 2017; Langley et al., 2020a; Vardi et al., 2020). The few data available often come from laboratory populations (Croston et al., 2015), and thus heritability estimates may have been biased due to founder effects, inbreeding and artificial selection (Langley et al., 2018; Sorato et al., 2018; but see Dochtermann et al., 2019) and to all individuals being raised under the same standardized conditions (Croston et al., 2015; Smith et al., 2015; Vardi et al., 2020). More research on the heritability of cognitive traits in wild populations is needed (but see: Carrete et al., 2017; Quinn et al., 2016), in order to advance our understanding of their evolution in nature.

We aimed to test the long-term repeatability and heritability of spatial cognition, problem-solving and exploration within the Aegean wall lizard (*Podarcis erhardii* Bedriaga 1882). In 2019, we measured personality and cognition in 66 individual lizards and released them in semi-natural enclosures for a survival experiment. After one year, surviving lizards and their offspring were recaptured and re-subjected to the same behavioural assays. We specifically addressed some of the aforementioned limitations of previous research by 1) using a non-traditional study organism: to our best knowledge this is the first study to measure repeatability of cognition in a non-avian reptile, 2) measuring behavioural repeatability over a sufficient long timescale (20 % of this species' average lifespan, Valakos, 1990), 3) keeping and raising lizards in semi-natural environments and 4) studying both personality and cognition. This way, we hope to gain more ecologically relevant insights regarding the repeatability and heritability of cognition within this species. In addition, our lizards were kept in two contrasting habitats (either structural simple or complex). Habitat complexity is known to affect spatial learning within this species (Chapter 5), and by keeping adults and juveniles in two different environments, we hope to learn more regarding the role of selection and plasticity in shaping such variation.

MATERIAL AND METHODS

Study species and overall experimental design

The Aegean wall lizard is a medium-sized (40 -75 mm) insectivorous lizard, which is widespread across the Southern Balkans (Valakos et al., 2008; Lymberakis et al., 2018). It can be considered an ecological generalist, as demonstrated by its broad habitat use (e.g. Mediterranean scrublands, open sand dunes, urban habitats, ... - Valakos et al., 2008; Lymberakis et al., 2018) and its dietary flexibility (arthropods, snails, eggs, fruits and occassionally conspecifics – Adamopoulou et al., 1999; Brock et al., 2014b; Madden & Brock, 2018).

The initial batch of lizards was collected in May 2019 on Naxos Island (Cyclades, Greece), at five locations that differed in structural habitat complexity: two 'complex' sites (Eggares: 37°07'49.1"N, 25°26'18.9"E and Rachi Polichnitou: 37°00'53.0"N, 25°24'10.7"E), covered in dense phrygana and maquis vegetation, dry stone walls and rock outcrops and three 'simple' sites (Manto: 37°05'22.0"N, 25°21'42.1"E, Grotta:

37°06'41.8"N, 25°23'09.8"E and Alyko: 36°58'45.3"N, 25°23'21.0"E) that were characterized by small patches of vegetation in an overall open landscape. Seventy-one lizards were captured (by lasso, hand or pitfall) and transported to the National and Kapodistrian University of Athens for housing and behavioural experiments (see later). Lizards were kept in cotton bags in a cold cool box to reduce stress during transportation (Heathcote et al., 2014). Five of these lizards died in captivity. Upon completion of the experiments, the remaining 66 adults ($N_{female} = 32$, $N_{male} = 34$) were then released in four semi-natural enclosures on Naxos, in order to follow up their survival and reproduction over the course of one year. Lizards were released in July 2019 and recaptured in July 2020. We then transported the survivors ($N_{female} = 22$, $N_{male} = 21$) back to the National and Kapodistrian University of Athens and repeated a subset of the original behavioural experiments with them. The 2019 protocols were followed as closely as possible in order to measure the long-term temporal (rather than contextual) repeatability of personality and cognition. In addition, we collected and tested new individuals found within the enclosures, both juveniles ($N = 43$) and adults ($N_{female} = 9$, $N_{male} = 12$) for heritability estimations. These new adults were unmarked, and thus did not belong to the previous released batch. At the moment of capture, it was still unclear whether these ‘unknown adults’ were intruders or the full-grown offspring from a previous batch of lizards.

Housing

Lizards were housed at the animal facilities of the University of Athens, individually in plastic terraria (adults: 22 x 20 x 17 cm, juveniles: 18 x 9 x 13 cm l x w x h). Terraria contained a water bowl, sand and stone bricks (adults) or coconut fibre and a plastic refuge (juveniles), and were placed underneath 60 W incandescent lamps for thermoregulation. Animals were fed three times per week: adults with mealworms (*Tenebrio molitor*) and juveniles with either maggots (larva of a calliphorid fly) or small mealworms. Prey items were always dusted with Terravit Powder (JBL, GmbH & Co. KG). Room temperature was maintained around 28 ± 2 °C.

Behavioural experiments

Initially, in 2019, lizards were subjected to four cognitive tasks and three separate personality assays (described in Chapter 5). Due to time constraints, we only retested the surviving adults on a subset of these tasks in 2020: an exploration assay, a spatial + reversal learning task and a problem-solving task (in this order). Their offspring were submitted to the same tests, excluding the problem-solving task.

Experiments were conducted from May until July in 2019, and from August until September in 2020, and were performed between 10:00 and 19:00. Each individual received 20 – 30 minutes basking time underneath a 100 W heat bulb prior to transferring them to experimental arenas, in order to achieve sufficiently high body temperatures. All experiments were filmed using a digital camera (JVC Everio GZ-HM400) or a GoPro (Grundig HD 720P). Experimental equipment (e.g. refuges, novel objects, etc.) was cleaned between trials with 70 % alcohol and water (Vicente & Halloy, 2017).

Exploratory behaviour

Exploratory behaviour is the tendency of an individual to gather new environmental information (Verbeek et al., 1994). It facilitates the discovery and exploitation of novel habitats and resources, but may be costly due to e.g. an increased risk of predation and parasite infection (Bajer et al., 2015; Baxter-Gilbert et al., 2019). Aegean wall lizards on Naxos experience strong seasonal fluctuations in food availability (De Meester et al., 2021 ~ Chapter 4), during which they may benefit from more exploratory behaviour to find alternative food sources. In addition, explorative behaviour may be a key behaviour in successfully invading new environments (Damas-Moreira et al., 2019) and could thus be selected upon when our lizards where introduced in the enclosures. Exploration was tested using a classical novel arena test (cfr. McEvoy et al., 2015; Carazo et al., 2014; Damas-Moreira et al., 2019; De Meester et al., 2022 ~ Chapter 5). Two distinct novel arenas (60 x 60 x 30 cm l x w x h, either plywood or sand substrate), which contained four identical objects (either pinecones or stones, one in each corner) and four plastic refuges (either black or white) were used (Supplementary Figure S6.1a-b). We specifically used two different arenas to avoid a confounding effect of habituation (McEvoy et al., 2015). A lizard was put in the centre of the arena on a platform underneath an opaque container. After three minutes, the container was lifted and the animal was free to explore the arena for ten minutes. On the videos, we divided the arena in four equal quadrants and scored the following behaviours (starting from the moment the lizard left the platform): the latency until the first transition from one quadrant to another, total number of transitions between quadrants, number of times it investigated an object or refuge (by touching it with the snout or front legs), number of times it entered a refuge, the total time spent within refuges and the latency to explore all four quadrants of the arena. Lizards were tested once in each novel arena (random order – but 2019 adults retained the same order in 2020) with at least one day in between trials.

Spatial and reversal learning

Spatial cognition is the capacity of an animal to learn and remember the location of resources in its environment and is thus deemed a key aspect of an individual’s fitness

(Dukas, 2004; Tello-Ramos et al., 2018). Small lizards, including *P. erhardii*, tend to escape towards a refuge (e.g. a crevice in a rock wall, underneath a log, etc) when approached by a predator. This antipredator strategy is likely to be more successful if lizards are capable of remembering the location of adequate safe hiding spots (Noble et al., 2012). Field observations suggest that lacertid lizards often repeatedly flee towards the same shelter, thus implying an important role of spatial memory (Font, 2019)

We tested spatial learning in our lizards using an ecological relevant antipredator task, in which subjects needed to learn the difference between a safe and unsafe refuge in order to make a successful escape (following the methodology of Noble et al., 2012; Carazo et al., 2014; Font, 2019; Vardi et al., 2020; De Meester et al., 2021 ~ Chapter 4). Lizards were tested in a large arena (60 x 60 x 30 cm) with two identical refuges (black plastic cups) opposite of each other. In and around the arena, visual spatial cues were presented to allow orientation (Supplementary Figure S6.1c-e). At the start of each trial, a lizard was positioned in the centre of the arena underneath a transparent cover for two minutes. After lifting the cover, we ‘attacked’ the lizard by poking and chasing it with a paintbrush. We always tried to attack the animal from straight above in order to avoid influencing in which direction it fled. Subjects needed to escape either to the left or the right refuge (relative to the observer, counterbalanced among original populations). Entering the ‘safe’ refuge resulted in two minutes of undisturbed rest, after which the individual was brought back to its terrarium. Entering the ‘unsafe’ refuge was penalized by continuing the predator attack. Trials ended when the lizard entered the safe refuge or until 120 s had passed (after which it was captured and allowed to rest in the correct refuge for two more minutes). Trials were limited to 120 s to reduce the amount of stress inflicted on the animal and avoid exhaustion. Each lizard received three trials per day for five consecutive days, and per trial we noted how many times the lizard entered the unsafe refuge (‘errors’).

Lizards living in a dynamic environment need to keep track of changes in their environment, update their memories frequently, and adjust their behaviour accordingly (Noble et al., 2012). Replacing old obsolete with new information requires cognitive flexibility, which is commonly measured using a reversal learning task (Noble et al., 2012; Tebbich & Teschke, 2014; Audet & Lefebvre, 2017). Following previous reversal learning protocols (e.g. Bebus et al., 2016; Madden et al., 2018; van Horik et al., 2018; Boussard et al., 2020; Mason et al., 2021), we changed the identity of the refuges after a standardized number of trials (15) for each individual: safe became unsafe and vice versa. Immediately after the spatial learning, lizards received fifteen more trials over five days in order to relearn the location of the safe refuge. Adults retested in 2020 started the spatial learning phase with the same refuge designated as safe as in 2019 to make performances in both years comparable. Lizards were always tested in two batches because it was not feasible to test all lizards simultaneously.

Escape Box

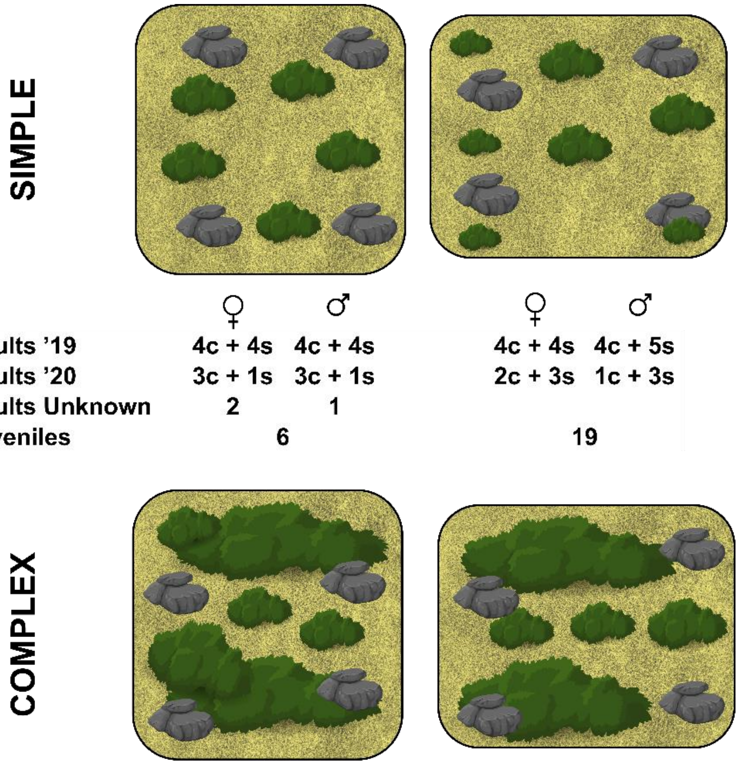
Problem-solving requires animals to express a new behaviour or apply an old behaviour in a novel context, and is therefore considered an indicator of behavioural flexibility (Griffin & Guez, 2014; Tebbich & Teschke, 2014; but see Audet & Lefebvre, 2017). Lizards with better problem-solving skills may increase their foraging efficiency, e.g. by being better at extracting hidden or difficult prey (Cooper et al., 2019). We tested problem-solving using an escape box task (Supplementary Figure S6.1f-g). A lizard was locked in a transparent Plexiglas box (17.4 x 17.4 x 6.5 cm l x w x h) which was placed opposite of a pile of stones underneath a 60 W heat bulb inside a larger arena. Hence, the lizard needed to escape from the box in order to get access to this hiding/basking spot. This was possible by performing a novel motor act i.e. sliding open a white opaque door (3.2 x 2.4 cm l x h). The door was already slightly opened and contained grooves to allow manipulation. Lizards received a single 30 min trial, and we recorded the time it took each lizard to escape. If lizards did not escape, we assigned them the maximum time as score.

In 2019, lizards were tested in two batches, either before or after the spatial cognition protocol for logistic reasons. In 2020, lizards were either tested on the same day as the spatial cognition protocol or later. Juveniles were not tested in the escape box as they proved to be unable to move the door in a few pilot trials. The video of one lizard in 2020 was lost.

Semi-natural enclosures

Upon completion of the experiments in 2019, 66 adult lizards were released in four semi-natural enclosures on Naxos as part of a survival experiment. Prior to release, each individual was photographed and individually marked by toe clipping for the purpose of identifying them upon recapture. Toe-clipping is a standard procedure to allow individual recognition in reptilian studies and is generally considered to have little to no negative effects either short- or long-term (Langkilde & Shine, 2006; reviewed in Perry et al., 2011). We removed maximum two toes per lizard (depending on already missing toes upon capture). In addition, we took small tail clips (± 1 cm) from each individual for parentage assignment (cfr. Huyghe et al., 2009; Huyghe et al., 2010). Tissues were stored in 96 % ethanol at 4 °C.

The four enclosures were located on a private field on Naxos, consisting of abandoned agricultural terraces with dense Mediterranean maquis and phrygana. Each enclosure was rectangularly shaped and constructed by fencing in approximately 100 m^2 of land with smooth metal fences (70 cm height and 30 cm deep). In two enclosures, we pruned the vegetation in order to mimic an open environment comparable to the structural simple sites where lizards were captured. The two other enclosures mimicked the more complex habitats (see Figure 1 and Supplementary Figure S6.2).



	♀	♂	♀	♂
Adults ’19	**4c + 4s**	**4c + 4s**	**4c + 4s**	**4c + 5s**
Adults ’20	**3c + 1s**	**3c + 1s**	**2c + 3s**	**1c + 3s**
Adults Unknown	**2**	**1**		
Juveniles	**6**		**19**	

	♀	♂	♀	♂
Adults ’19	**5c + 3s**	**3c + 6s**	**4c + 4s**	**4c + 4s**
Adults ’20	**4c + 2s**	**3c + 3s**	**3c + 4s**	**3c + 4s**
Adults Unknown	**4**	**5**	**3**	**6**
Juveniles	**8**		**12**	

Figure 1. Graphical representation of the four enclosures (structural simple on top, structural complex bottom). Per enclosure, sample sizes per group and per sex are given. Small letters next to the numbers represent whether the lizards originated from a complex (c) or simple (s) habitat.

Within each enclosure, we placed four piles of stones (± 30 cm high) for basking and shelter. We released 16 – 17 individuals in each enclosure based on their overall performance on the spatial cognition task (as to have more or less comparable numbers of good and bad learners in each enclosure) with approximately an equal number of a) males and females and b) lizards originating from complex and simple habitats (see Figure 1).

Terrestrial predators (e.g. snakes) were removed from the enclosures, although Megarian banded centipedes (*Scolopendra cingulata*), which are capable of catching and consuming *P. erhardii* (Deimezis-Tsikoutas et al., 2020), could not be entirely eliminated, and on one occasion a brown rat (*Rattus norvegicus*) intruded a complex enclosure, but was quickly removed. We also attempted to scare off avian predators by suspending reflective disks above the enclosures. Enclosures were normally checked biweekly by volunteers, who also placed leftover fruits and vegetables in each enclosure to attract flying insects. Vegetation around the enclosures was routinely cut down twice a year (early spring and mid-summer). Unfortunately, due to the Covid-19 pandemic, the enclosures were only irregularly checked throughout spring 2020, and early-spring maintenance had to be postponed until summer. Although this resulted in both enclosures growing denser vegetation, their relative differences in complexity did not change.

Sixty-six known lizards were released in the enclosures in July 2019. In July 2020, we recaptured every lizard in the enclosures during a seven-day recapture session. Survivors were identified based on toe clips and photographs of dorsal patterns. In total, we collected 43 survivors (59 – 71 mm snout-vent length SVL), 45 juveniles (29 – 37 mm) and 21 unknown adults (54 – 69 mm) from the enclosures (see Figure 1 for sample sizes per enclosure), all of which were then transported to the National and Kapodistrian University of Athens for subsequent personality and cognition tests (see above). We were unable to estimate the exact age of our animals at the time of capture, although the presence of umbilical scars in juveniles indicated that they had hatched relatively recent. Upon completion of the behavioural experiments in 2020, we also collected tail tissues for genetic analyses from unknown adults and juveniles (same protocol as described above for the adults in 2019).

Parentage assignment

Genetic analyses were conducted based on the protocol of Huyghe et al. (2010). DNA was extracted by placing ± 2 mm^3 of tail tissue in Chelex extraction buffer (consisting of 0.2 mL 10 % Chelex, 20 µL 1 % SDS and 2 µL of 20 mg/mL proteinase K), which was then put inside a stirring incubator (Eppendorf, thermomixer comfort), initially at 65°C for 60 minutes followed by 95°C for 15 minutes (modified from Small et al., 1998). Parentage was assessed using microsatellite genotypes from nine loci that have been successfully used in congeneric species before (B3, B4 and B6 from Nembrini & Oppliger, 2003; Pmeli-02, Pmeli-04, Pmeli-07, Pmeli-13, Pmeli-14 and Pmeli-19 from Huyghe et al., 2009). For each DNA-sample, we prepared three different primer mixtures, each of them containing fluorescently labelled primers for three of the nine loci. Next, we mixed 1.25 µL of each primer mix with 6.25 µL Qiagen multiplex PCR master mix 2x and 3.5 µL water, to which we then added 1.5 µL of DNA extract. Mixtures were centrifuged and placed in the thermocycler (Biometra, T-professional thermocycler) for PCR amplification. PCR conditions were as follows: 15 minutes of denaturation at 95°C, 30 cycles of 30 s denaturation at 72°C, 90 s of annealing at 57°C or 60°C (Huyghe et al., 2009; dependent on the primers, see Nembrini & Oppliger, 2003) and 60 s of extension at 72°C. This was followed by another 30 minutes of extension at 60°C. Success of the PCR was then visually checked via gel-electrophoresis. After appropriate dilution, successful PCR-products were sent to an external lab (Neuromics

Support Facility) for microsatellite detection on an AB 3130XL Genetic Analyser (Life Technologies, Carlsbad, CA, USA).

Microsatellite data was first processed in the Geneious Prime software version 2021.0.3. (http://www.geneious.com/) for loci identification and then in Cervus version 3.0.7. (Kalinowski et al., 2007) for parentage assignment. We conducted separate parentage analyses for each enclosure, and used the unknown adults both as potential offspring of the 2019 adults and as potential parents of the juveniles. Proportion of mistyped loci was set to 5 % and relaxed and strict (trio) confidence intervals were equal to 80 and 95 % respectively.

Statistical analyses

Statistical analyses were performed in R version 3.5.1. (R Core Team, 2018). Prior to analysis, data were transformed where necessary to meet model assumptions.

First, we reduced the number of variables measured in the exploration test using a principal component analysis (PCA) with the ‘princomp’ function (with a correlation matrix to standardize variables) (‘stats’ package, R Core Team, 2018). We retained the first two principal components as these both had an eigenvalue > 1 (Kaiser-Guttman criterion, Kaiser, 1991) (cfr. Petelle et al., 2015; Thys et al., 2021; Vanden Broecke et al., 2021).

Secondly, to verify that lizards did learn during our spatial + reversal learning task, we used two separate generalized mixed-effect models (GLMMs), with a negative binomial distribution ('glmer.nb' function in 'lmer4' package, Bates et al., 2015) for the spatial and reversal phase respectively. The number of errors per trial was fitted as response variable, while trial number, side of the safe refuge (left/right, relative to the observer) and lizard age group (adults 2019, adults 2020, unknown adults & juveniles) were included as predictors. To test whether learning was consistent across age groups and independent of the rewarded side, we added age*trial and safe side * trial interactions as well. Original population, batch (first half, second half) and lizard ID (with a random intercept and slope per individual for trial) were included as random effects. Model assumptions were checked using the 'RVAideMemoire' (Hervé, 2020) and 'performance' (Lüdecke et al., 2021) packages. Statistical significance of GLMMs was tested with Wald Chi-square tests using the 'Anova' function ('car' package, Fox & Weisberg, 2019). Interactions were removed if not-significant.

Next, we estimated long-term (temporal) repeatability in personality and cognition in the subset of lizards that were tested in both 2019 and 2020 (N = 43) using a series of linear mixed-effect models (LMMs) ('lmer' function, 'lmerTest' package, Kuznetsova, et al., 2017). For exploration, we used PC1 and PC2. Next, we used the mean number of errors made over 15 trials as scores for spatial (SL) and reversal learning (RL), as better learners should more quickly learn the location of the correct refuge and thus make fewer wrong entrees (cfr. Tello-Ramos et al., 2018; Sonnenberg et al., 2019). The mean number of errors over both stages of the task was used as an indicator of overall learning flexibility (FLEX score). For the repeatability of the escape box task, we used escape times (ESC time). Lower scores on the cognitive tasks generally reflect better cognitive performance (fewer errors, less time to escape). We started by fitting global full models including the following variables: year (2019/2020), original habitat (simple/complex), enclosure type (simple/complex), sex, SVL (scaled, as risk-taking behaviour may be size-dependent, e.g. Bajer et al., 2015), tail status (complete/damaged, as this can affect lizard behaviour, cfr. Michelangeli et al., 2020) and side of the safe refuge (left/right, for the spatial + reversal task only). We also included all two- and three-way interactions between year, original habitat and enclosure type to see whether cognitive performance and personality would change over time in a habitat-dependent way. The following random factors were added to the models: lizard ID, arena type (plywood/sand, only for exploration), original population, enclosure ID and batch (only for spatial cognition and escape box). Where necessary, the 'bobyqa' optimizer was used to ensure model convergence (Bates et al., 2015). Next, we adopted a model selection approach (Symonds & Moussalli, 2011). Starting from the full global model, we generated a set of candidate models with the 'dredge' function ('MuMIn' package, Barton, 2013). The top model with the lowest Akaike information criterion corrected for small sample sizes (AICc) was selected, as well as alternative candidate models within ≤ 2 AICc units from it (cfr. Symonds & Moussalli, 2011; Gomes et al., 2020). We then determined the relative importance (RI) of all predictors by calculating their summed Akaike weights over all candidate models. Variables with a RI ≥ 0.50 (Simpson & McGraw, 2018; Simpson & McGraw, 2019; Gardner et al., 2020; Gomes et al., 2020) were used to construct a final model to test which factors influenced personality and cognitive performance, and to calculate the (adjusted) repeatability with the 'rptR' package (Stoffel et al., 2017). We built a series of similar models to estimate the short-term repeatability of personality within each subgroup of lizards (all 2019 adults, surviving 2019 adults , 2020 adults, unknown adults and juveniles). Significance of predictors is based on F-tests calculated using Kenward-Roger Degrees of Freedom Approximation ('anova' function, 'stats' package).

Narrow-sense heritability (h^2) was estimated by employing Bayesian mixed-effect animal models with the 'MCMCglmm' package (Hadfield, 2010). Animal models use both phenotypic data (here behavioural measurements) and pedigree information (based on our paternity assignment) to calculate the additive genetic variance of a given trait (σ^2_a). For these analyses, we used the complete dataset of all lizards that were released and captured in the enclosures, including the repeated measures of the 2020 adults. All response variables were z-transformed, but given the strong side bias (see results), SL and RL scores were z-transformed per rewarded side, to make cognitive performance among individuals comparable (cfr. Guillette et al., 2009). We once again used a model selection approach, starting from full global models with the following predictors: enclosure type (simple/complex, as structural complexity of the environment may affect behavioural development of individuals e.g. Spence et al., 2011), age group (adults 2019/adults unknown/juvenile, to account for age-differences in mean levels of behaviour, e.g. Rohrer et al., 2020), SVL (standardized per age group), tail status, and an age group*enclosure type interaction. We included the following random effects: lizard ID linked to the pedigree (σ^2_a, additive genetic variance), lizard ID independent of pedigree (to account for repeated measurements and permanent environmental effects), enclosure ID, novel arena (exploration data only), batch (SL + RL + FLEX only) and mother ID (to avoid that maternal effects would inflate h^2). We calculated a dominance matrix using the 'nadiv' package (Wolak, 2012) and implemented this as an additional random factor in the MCMCglmms to account for (genetic) dominance effects. Heritability was calculated from the final models as σ^2_a / σ^2_p with σ^2_p being the total phenotypic variance (de Villemeuril, 2012). Each animal model was initially run for 1 000 000 iterations, with a burn-in period of 100 0000 iterations and a 200 iteration thinning interval, and a parameter expanded prior (v = 1, nu = 1, alpha.mu = 0, v.mu = 1) (de Villemeuril, 2012). We checked convergence of chains and autocorrelation of all models, and in case of high autocorrelation (>0.10) we increased the number of iterations, the burn-in period and/or the iteration thinning interval. One juvenile was removed from the animal models due to missing data.

For both the (G)LMMs and the MCMCglmms, post-hoc multiple comparisons between different levels of a significant fixed factor and/or different slopes were performed with the ‘emmeans’ and ‘emtrends’ functions respectively using Tukey’s method (Lenth et al., 2019).

Ethical note

All experiments and procedures were approved by the Ethical Committee of the University of Antwerp (file ID: 2017-67) and the Greek Ministry of Environment and Energy (permit IDs: 7ΖΠΡ4653Π8-Ε76, ΨΗ424653Π8-ΩΥ2 and 69Ι44653Π8-ΔΣ1). Experiments and procedures were conducted in accordance with national legislation and adhered to the ASASB/ABS guidelines for the use of animals in behavioural research and teaching. Animals were checked daily while in captivity to monitor their welfare. Adult lizards were released at the initial site of capture, juveniles and intruders were retained for a follow-up experiment. Five lizards died in captivity in 2019, one lizard in 2020, and another one escaped from captivity in 2020.

RESULTS

We identified parents of 37 (82 %) juveniles. We were unable to identify the parents of any of the unknown adults (neither when matched with the current or previous batch of released lizards), suggesting that these lizards originated from the surrounding field and somehow managed to get into the enclosures. Four of these 'intruders' interbred with known adults and sired/birthed five of the juveniles in our dataset. Hence, their data was retained for the analyses. From the 66 lizards initially released, 14 males (42 %) and 17 females (52 %) reproduced (parent of at least one juvenile). Within that subset, males fathered on average 2.50 ± 0.28 (SE) juveniles (max. 6) and females birthed on average 2.00 ± 0.32 young (max. 5). Of the 'intruders', only two males (17 %) and two females (22 %) reproduced. Each male fathered a single juvenile, while the females birthed one and two juveniles respectively.

Descriptive statistics for all behavioural tests are given for the subset of adults tested in both years and per age group in the Supplementary Table S6.1 and S6.2).

Exploration PCA

The results of the PCA on the explorative behaviours are summarized in Table 1. The first principal component (eigenvalue = 1.76) explained 44.33 % of the total variance. Higher scores on PC1 corresponded to a higher number of transitions in the arena, more frequently touching objects, more refuges entered and more time spent in them, a lower latency to explore the entire arena and to enter the first refuge, and thus to overall more explorative behaviour.

Table 1. Principal Component Analysis of exploration behaviours. Loadings with an absolute value > 0.3 (bold) were considered to substantially contribute to a principal component (Boon et al., 2007; Dammhahn, 2012; Thys et al., 2017b).

	Comp 1	Comp 2	Comp 3
Eigenvalue	1.76	1.29	1.00
% variance	44.33	23.60	14.16
First transition	-0.130	**-0.411**	**0.739**
# transitions	**0.422**	**0.357**	0.268
Latency all quadrants	**-0.347**	**-0.474**	0.156
# touches	**0.335**	0.287	**0.556**
# refuges entered	**0.462**	**-0.339**	
Latency to enter first refuge	**-0.432**	0.286	0.177
Time spent hiding	**0.413**	**-0.448**	-0.122

PC2 (eigenvalue = 1.29) explained 23.60 % of the total variance and represented a contrast between faster exploration (lower latency to first transition, more transitions, lower latency to explore the whole arena) versus more time spent inside the refuges (Table 1).

Exploration – short term repeatability within each group

Composition and output of the final models are reported in Table 2, as well as adjusted and unadjusted (short-term) repeatability estimates within each age group.

The short-term repeatability of exploration PC1 showed considerable variation across groups, e.g. being moderately high in 2020 adults but almost non-existent in intruders, 2019 adults and juveniles (see Table 2).

Table 2. Overview of the final models and their results for the short-term (within-year) repeatability of exploration within each age group. Models were constructed based on a model selection approach (see main text), using predictors with an relative importance (RI) ≥ 0.50. Repeatability (R) was calculated using the ‘rptR’ package in R (Stoffel et al., 2017). Both the adjusted and unadjusted repeatability are given, with their 95% confidence interval (square brackets). Their significance was tested using a log-likelihood ratio test. For the meaning of the exploration PCs, we refer to Table 1. Statistical significance is reported as: ‘°’ $p < 0.10$, ‘*’ $p < 0.05$, ‘**’ $p < 0.01$, ‘***’ $p < 0.001$.

Personality Trait	Age group	N	RI	Confounding factors	F-stats	P
Exploration PC1	Adults ‘19 (box-cox: λ = 1.4)	66	0.62	Tail	$F_{1,64} = 3.064$	0.085 °
				R_{adj}	0.085 [0.000; 0.310]	0.242
				R	0.101 [0.000; 0.314]	0.202
	Adults ‘19 (survivors only) (box-cox: λ = 1.3)	43	/	/	/	/
				R_{adj}	/	/
				R	0.079 [0.000; 0.370]	0.303
	Adults ‘20	43	0.79	Sex	$F_{1,37} = 4.071$	0.051 °
			1.00	**SVL**	$F_{1,52} = 6.465$	**0.014 ***
				R_{adj}	**0.333** [0.087; 0.602]	**0.007 *****
				R	**0.449** [0.167; 0.652]	**< 0.001 *******
	Intruders	21	/	/	/	/
				R_{adj}	/	/
				R	0.010 [0.000; 0.393]	0.480
	Juveniles	44	/	/	/	/
				R_{adj}	/	/
				R	0.005 [0.000; 0.237]	0.480

Table 2. (Continued)

Personality Trait	Age group	N	RI	Confounding factors	F-stats	P
Exploration PC2	Adults ‘19 (box-cox: $\lambda = 0.8$)	66	1.00	Habitat	$F_{1,3} = 6.134$	0.094 °
			1.00	**Tail**	$F_{1,61} = 8.731$	**0.004** **
				R_{adj}	**0.211** [0.000; 0.436]	**0.034** *
				R	**0.239** [0.022; 0.433]	**0.011** *
	Adults ‘19 (survivors only)	43	1.00	Habitat	$F_{1,3} = 4.183$	0.145
			1.00	**Tail**	$F_{1,38} = 6.215$	**0.017** *
				R_{adj}	0.130 [0.000; 0.410]	0.197
				R	0.169 [0.000; 0.430]	0.104
	Adults ‘20	43	1.00	**Sex**	$F_{1,35} = 5.970$	**0.020** *
				R_{adj}	0.162 [0.000; 0.445]	0.136
				R	0.227 [0.000; 0.465]	0.064 °
	Intruders	21	0.71	Tail	$F_{1,31} = 2.679$	0.111
				R_{adj}	**0.448** [0.038; 0.722]	**0.018** *
				R	**0.386** [0.000; 0.686]	**0.030** *
	Juveniles	44	0.68	SVL	$F_{1,40} = 3.776$	0.059 °
				R_{adj}	0.075 [0.000; 0.335]	0.280
				R	0.093 [0.000; 0.352]	0.228

Exploration PC1 increased with size in 2020 adults (est = 0.612 ± 0.224, $F_{1,52} = 6.465$, p = 0.014) and tended to be lower in 2019 adults with an intact tail (intact: 0.843 ± 0.133, damaged: 1.732 ± 0.216, $F_{1,64} = 3.064$, p = 0.085) and male 2020 adults (females: -0.024 ± 0.227, males: -0.405 ± 0.312, $F_{1,37} = 4.071$, p = 0.051).

Exploration PC2 was moderately repeatable within intruders but not in 2020 adults or juveniles. 2019 adults showed significant repeatability for PC2 in the entire dataset, but not in the subgroup of survivors (Table 2). Exploration PC2 was higher in 2019 adults (both complete dataset and survivors only) with an intact tail (intact: 0.290 ± 0.107, damaged: -1.069 ± 0.362, $F_{1,61} = 8.731$, $p = 0.004$), females in 2020 (females: 0.630 ± 0.210, males: -0.098 ± 0.190, $F_{1,35} = 5.970$, $p = 0.020$; Figure 2), and tended to be higher in larger juveniles (0.242 ± 0.123, $F_{1,40} = 3.3776$, $p = 0.059$) and 2019 adults originating from a simple habitat (complex: -0.194 ± 0.136; simple: 0.546 ± 0.151; $F_{1,3} = 6.134$, $p = 0.094$).

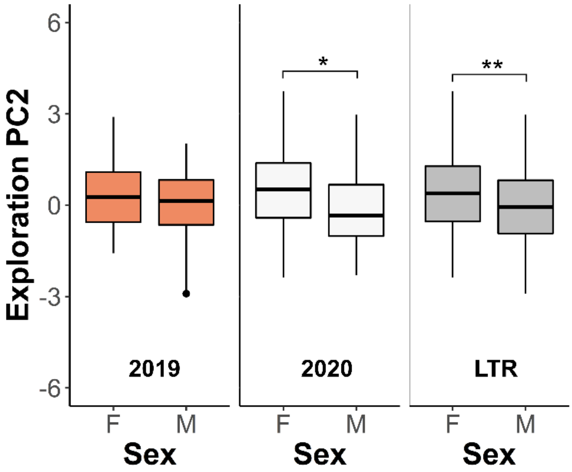


Figure 2. Exploration PC2 scores for surviving adults that were tested in both year ($N_{female} = 22$, $N_{male} = 21$). Orange boxplots represent exploration PC2 scores in 2019, light grey boxplots visualize PC2 scores when retested in 2020 and dark grey boxplots are the pooled data over both years (long-term repeatability – LTR). Statistical significant differences are indicted as follows: '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. Higher scores represent lizards that are faster in exploring a novel arena and spent less time hiding.

Exploration – long term repeatability

Final models for the long-term repeatability of exploration are given in Table 3. PC1 scores differed significantly between years ($F_{1,152}$ = 41.171, $p < 0.001$), with lizards having lower scores in 2020 than 2019 (682 ± 450 % decrease, t = -6.552, $p < 0.001$, Figure 3a), and larger lizards were more explorative (0.472 ± 0.150, $F_{1,134}$ = 8.812, p = 0.004). Sex and enclosure type did not affect exploration PC1 (all $p > 0.10$, Table 3). Interindividual variation in PC1 was moderately repeatable from 2019 to 2020 (R_{adj} = 0.280, CI = [0.091; 0.436], LRT: $p < 0.001$; Table 3).

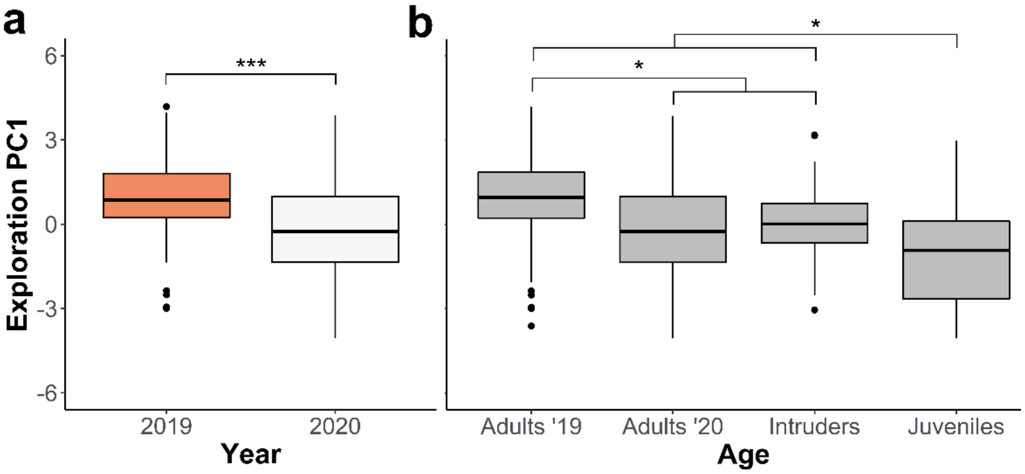


Figure 3. a) boxplots representing the exploration PC1 scores for adult Aegean wall lizards tested in both 2019 and 2020 (N = 43). Statistical significant differences are indicted as follows: '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. b) boxplots with the exploration PC1 scores per age group ($N_{adults\ '19}$ = 66, $N_{adults\ '20}$ = 43, $N_{intruders}$ = 21, $N_{juveniles}$ = 45). Age groups were considered different from each other if the 95 % credibility interval of their difference (as obtained from a MCMCglmm) did not overlap with zero, which is indicated with an '*'. In both graphs, higher scores represent more explorative behaviour, but see Table 1 for a more detailed explanation of the PC scores.

Male and female lizards differed in their exploration PC2 scores ($F_{1,35} = 9.032$, $p = 0.005$). Males obtained lower scores, meaning that they explored more slowly and spent more time hiding (females: 0.484 ± 0.134, males: -0.065 + 0.130; $t = -3.021$, $p = 0.005$; Figure 2). Original habitat type did not predict exploration PC2 scores ($F_{1,3} = 2.276$, $p = 0.237$). No other variable or interaction had sufficient high importance to be included in the final model. Lizards did not show long-term consistency in interindividual variation in PC2 ($R_{adj} = 0.060$, CI = [0.000; 0.201], LRT: $p = 0.178$, Table 3).

Exploration – heritability

The selected animal models (MCMCglmm) are reported in Table 4. The final model for exploration PC1 included age group and SVL (Table 4), albeit the latter did not affect explorative behaviour (posterior mean + 95% credibility interval: 0.057 [-0.044; 0.160]). Juveniles had lower exploration scores than adults (post-hoc pairwise comparisons: adults ’19 – juveniles: 1.135 [0.864; 1.423], adults ’20 - juveniles: 0.494 [0.185; 0.783], intruders - juveniles: 0.590 [0.204; 0.972]). Adults in 2019 behaved more explorative than intruders (intruders - adults ’19: -0.548 [-0.893; -0.209]) and 2020 adults (adults ‘19 – adults ’20: 0.642 [0.409; 0.858]). (Figure 3b; Supplementary Table S6.3). Heritability of exploration PC1 did not differ from zero ($h^2 = 0.031$, CI = [0; 0.110]), meaning that additive genetic variance contributed almost nothing to the observed phenotypic variation.

The best model explaining variation in exploration PC2 was the null model (Table 4), thus exploration PC2 was unaffected by age, enclosure type, SVL or tail status. Heritability for exploration PC2 scores was not different from zero either ($h^2 = 0.057$, CI = [0; 0.178]).

Table 3. Overview of the final models and their results for the long-term (across-year) repeatability of exploration and cognition. Models were constructed based on a model selection approach (see main text), using predictors with an relative importance (RI) ≥ 0.50. Repeatability (R) was calculated using the ‘rptR’ package in R (Stoffel et al., 2017). Both the adjusted and unadjusted repeatability are given, with their 95% confidence interval (square brackets). Their significance was tested using a log-likelihood ratio test. For the meaning of the exploration PCs, we refer to Table 1. Statistical significance is reported as: ‘°’ $p < 0.10$, ‘*’ $p < 0.05$, ‘**’ $p < 0.01$, ‘***’ $p < 0.001$.

Personality/Cognition Trait	N	RI	Confounding factors	F-stats	P
Exploration PC1	43	0.67	Enclosure	$F_{1,2} = 2.047$	0.284
		0.52	Sex	$F_{1,38} = 2.409$	0.129
		1.00	**Year**	$F_{1,152} = 41.171$	**< 0.001 *****
		1.00	**SVL**	$F_{1,134} = 8.812$	**0.004 ****
			R_{adj}	**0.280** [0.091; 0.436]	**< 0.001 *****
			R	**0.188** [0.021; 0.335]	**0.003 ****
Exploration PC2	43	0.83	Habitat	$F_{1,3} = 2.276$	0.237
		1.00	**Sex**	$F_{1,35} = 9.032$	**0.005 ****
			R_{adj}	0.060 [0.000; 0.201]	0.178
			R	**0.117** [0.000; 0.249]	**0.039 ***
SL Score (log)	42	0.77	Year	$F_{1,1} = 3.331$	0.317
		1.00	**Safe side**	$F_{1,37} = 106.93$	**< 0.001 *****
		0.86	Tail	$F_{1,63} = 3.602$	0.062 °
			R_{adj}	**0.398** [0.124; 0.622]	**0.004**
			R	**0.786** [0.515; 0.868]	**< 0.001 *****
RL Score (log)	42	1.00	Habitat	$F_{1,2} = 4.932$	0.141
		0.64	Enclosure	$F_{1,2} = 0.242$	0.672
		0.58	Sex	$F_{1,33} = 2.798$	0.104
		0.64	Year	$F_{1,2} = 2.006$	0.324
		1.00	**Safe side**	$F_{1,34} = 195.677$	**< 0.001 *****
		0.64	**Enclosure * Year**	$F_{1,39} = 7.924$	**0.008 ****
			R_{adj}	0.251 [0.000; 0.545]	0.061 °
			R	**0.805** [0.530; 0.874]	**< 0.001 *****

Table 3. (Continued)

Personality/Cognition Trait	N	RI	Confounding factors	F-stats	P
Flex Score	42	/	/	/	/
			R_{adj}	/	/
			R	0.192 [0.000; 0.460]	0.105
ESC Time **(box-cox** $\lambda = 0.2$)	41	/	/	/	/
			R_{adj}	/	/
			R	0.000 [0.000; 0.307]	1

Spatial + reversal learning – within-year performance

Full results of the GLMMs on learning performance over time are given in Supplementary Table S6.4 – 6.5 but summarized here. During the spatial learning task, lizards significantly decreased the number of errors they made over consecutive trials (-0.027 ± 0.008, $\chi^2 = 11.970$, df =1, $p < 0.001$) independent of safe side (safe side * trial: $\chi^2 = 2.063$, df =1, $p = 0.151$) and consistent across age groups (age * trial: $\chi^2 = 3.846$, df =3, $p = 0.279$) (Figure 4). Nevertheless, a side-bias was observed ($\chi^2 = 307.027$,df =1, $p < 0.001$) with lizards committing more errors when the safe refuge was on the right side of the arena (left: 0.230 ± 0.018, right: 1.253 ± 0.039, $z = -17.522$, $p < 0.001$). In addition, the age groups also differed in their overall number of errors ($\chi^2 = 28.202$, df =3, $p < 0.001$). Juveniles made fewer errors (0.519 ± 0.040) than 2019 adults (0.824 ± 0.041, $z = 5.204$, $p < 0.001$), 2020 adults (0.770 ± 0.050, $z = 3.615$, $p = 0.002$) and intruders (0.812 ± 0.061, $z = 3.497$, $p = 0.003$) (Supplementary Table S6.5)

During the reversal phase, learning curves differed among age groups (age * trial: $\chi^2 = 10.387$, df =3, $p = 0.016$). Within each group, the number of errors decreased significantly with trial number (adults' 19: -0.027 ± 0.012, z = -2.606, p = 0.009; adults '20: -0.073 ± 0.014, z = -2.767, p = 0.029; intruders: -0.036 ± 0.020, z = -2.319, p = 0.020; juveniles: -0.070 ± 0.017, z = -4.071, p < 0.001; Figure 4), but adults learnt faster (steeper slope) in 2020 than 2019 (z = -2.767, p = 0.029) and juveniles tended to learn faster than their parents in 2019 (z =2.325, p = 0.092) (Supplementary Table S6.5). Similarly, lizards improved over time independent of whether the safe refuge was left or right in the arena, but did so faster in case of the former (left: -0.069 + 0.015, z = -4.931, p < 0.001; right: - 0.034 ± 0.009, z = 4.007, p < 0.001; safe side * trial: $\chi^2 = 4.577$, df =1, p = 0.032).

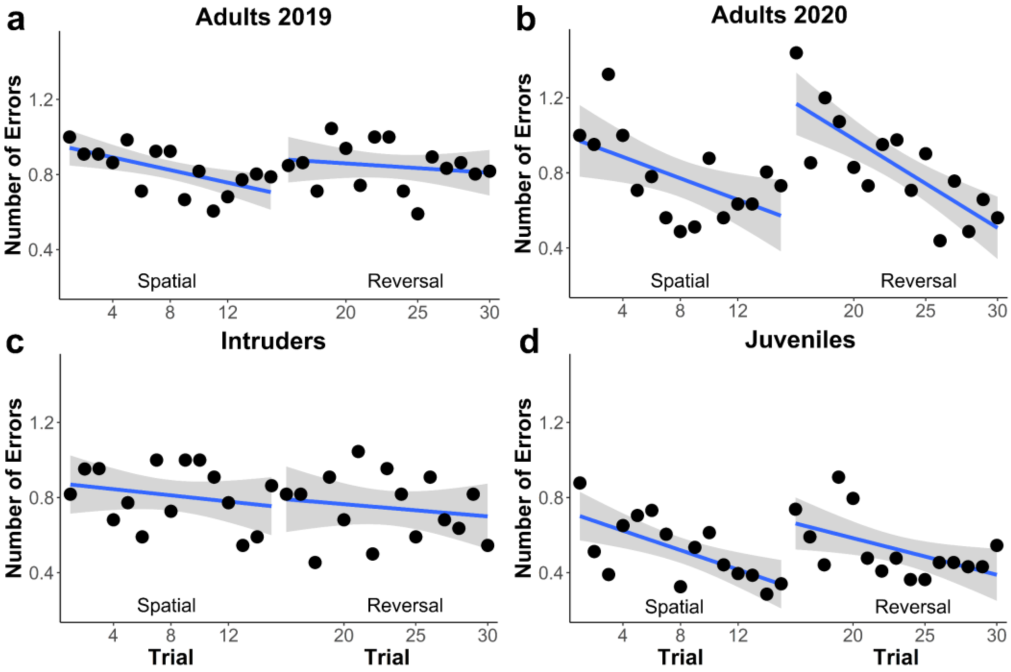


Figure 4. Performance of lizards (number of errors made) over consecutive trials in the spatial and reversal learning task. Significant regressions are indicated by a solid line, grey areas visualize the standard errors. Sample sizes are as follows: $N_{adults\ '19} = 66$, $N_{adults\ '20} = 42$, $N_{intruders} = 21$, $N_{juveniles} = 44$.

Spatial + reversal learning – repeatability

Adults did not differ in SL scores between both years ($F_{1,1}$ = 3.331, p = 0.317), independent of either original habitat and/or enclosure (neither included in final model, Table 3). We did find evidence for a side bias in cognitive performance ($F_{1,37}$ = 106.93, p < 0.001) with lizards making more errors if the safe refuge was on the right side of the arena (left: 0.305 ± 0.463, right: 1.376 ± 0.083, t = 10.806, p < 0.001), and there was a trend for lizards with an intact tail to make more errors (intact: 0.899 ± 0.084, damaged: 0.667 ± 0.168, $F_{1,63}$ = 3.602, p = 0.062). Lizards showed relatively modest consistency in their spatial learning performance across years, even when adjusting for this side bias (R_{adj} = 0.398, CI = [0.124; 0.622], LRT: p = 0.004; Table 3).

In contrast, RL scores differed between years depending on the enclosure in which lizards were kept (enclosure*year: $F_{1,39}$ = 7.924, p = 0.008). Nevertheless, post-hoc pairwise comparisons did not reveal any significant differences (all p > 0.10, see Supplementary Table S6.5). Visual inspection of the data suggested that lizards kept in simple enclosures made more reversal errors in 2020 compared to 2019 (75 ± 34 % increase), which was less prominent in the complex enclosures (12 ± 17 % increase) (Figure 5). Once again, lizards made fewer errors if the safe refuge was on the left side of the arena (left: 0.292 ± 0.032, right: 1.338 ± 0.074, $F_{1,34}$ = 195.677, p < 0.001). There was no overall effect of original habitat nor of sex, SVL or tail status, as these were either not included in the final model or non-significant (Table 3). Reversal learning, corrected for side bias and the enclosure*year interaction, showed moderate long-term repeatability, although this was only marginally significant (R_{adj} = 0.251, CI = [0.000; 0.545], LRT: p = 0.061) (Table 3).

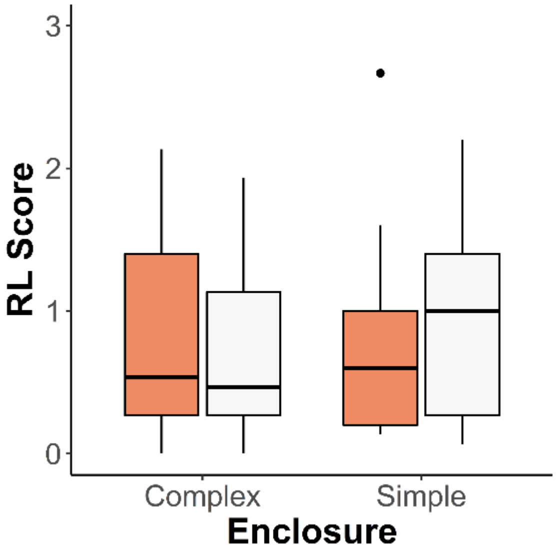


Figure 5. Boxplots visualising the reversal learning (RL) scores per year and per enclosure type. Higher scores indicate that lizards made more errors and thus correspond to lower cognitive performance. The same individual lizards were tested both in 2019 (orange) and 2020 (grey) after spending one year in semi-natural enclosures mimicking either a complex or simple habitat. Albeit a significant interaction was found between enclosure type and year, post-hoc pairwise comparisons did not reveal any significant differences among groups. Sample sizes were as follows: $N_{complex} = 25$, $N_{simple} = 17$

None of the variables or their interactions explained variation in FLEX scores, as the null model was the best model (Table 3). Long-term repeatability of learning flexibility was low and not significant (R = 0.192, CI = [0.000; 0.460], LRT: p = 0.105). (Table 3).

Spatial + reversal learning – heritability

Variation in SL scores was explained by neither age, nor enclosure type, nor SVL as none of these variables had sufficient high importance (all R < 0.50) to be included in the final (Bayesian) animal model (Table 4). Tail status was included in the final model but did not affect SL score (0.346, CI = [-0.026; 0.780]). The heritability of spatial learning performance did not differ from zero ($h^2 = 0.054$, CI = [0; 0.175]).

The final animal model for RL scores included the enclosure type * age interaction. A series of post-hoc pairwise comparisons (see Supplementary Table S6.3) revealed that: juveniles from simple enclosures made fewer errors than their parents (adults) in either 2019 or 2020 (adults$_{\text{simple}}$ ’19 – juveniles$_{\text{simple}}$: 0.692 [0.014; 1.449]; adults ’20$_{\text{simple}}$ – juveniles$_{\text{simple}}$: 1.187 [0.355; 1.946]). Juveniles from complex enclosures likewise performed better than their parents in either year (adults’ 19$_{\text{complex}}$ – juveniles$_{\text{complex}}$: 0.961 [0.266; 1.698]; adults$_{\text{complex}}$ ’20 – juveniles$_{\text{complex}}$: 0.833 [0.095; 1.530]) but also than the adults from the simple enclosures in 2020 (adults$_{\text{simple}}$ ’20 – juveniles$_{\text{complex}}$: 1.271 [0.264; 2.437]) (Figure 6). Curiously, RL scores from juveniles from simple and complex enclosures did not differ from each other, and neither from the RL scores of 2019 adults in the opposite enclosure type (Table 4, Table S6.3; Figure 6). Heritability of reversal learning was also not different from zero (h^2 =0.074, CI = [0.000; 0.249]).

Learning flexibility was not predicted by any of the aforementioned variables (Table 4), and did not show significant heritability (h^2 = 0.053, CI = [0; 0.167]).

Escape box – repeatability

Most lizards succeeded in escaping from the box (2019: 34/41, 2020: 38/41). Neither year, original habitat, enclosure, SVL, sex or any of their interactions was included in the final model, and thus did not explain variation in escape times among individuals. Overall, long-term consistency of escape time was non-existent (R_{adj} = 0.000, CI = [0.000; 0.307], LRT: p = 1) (Table 3).

Table 4. Overview of the final animal models (MCMCglmm) and their results for the heritability of exploration and cognition. Models were constructed based on a model selection approach (see main text), using predictors with an relative importance (RI) ≥ 0.50. Posterior means + 95% credible intervals (between square brackets) are reported. Predictors were considered to be important if the 95 % credible interval did not overlap with zero (bold). Heritability was calculated from both the final and null models. Higher exploration scores correspond to more explorative behaviour, while higher scores for spatial learning (SL), reversal learning (RL) and learning flexibility (FLEX) reflect more errors and thus worse cognitive performance.

Personality/Cognitive trait	RI	Confounding factors	Posterior mean + CI
Exploration PC1	/	Intercept	-0.035 [-1.616; 1.268]
	1.00	**Age (Adult ’19)**	**0.549 [0.209; 0.893]**
		Age (Adult ’20)	-0.093 [-0.450; 0.282]
		Age (Juv)	**-0.587 [-0.972; -0.204]**
	0.65	SVL	0.057 [-0.044; 0.160]
		h^2	0.031 [0.000; 0.110]
		$h^2_{\text{null model}}$	0.027 [0.000; 0.092]
Exploration PC2	/	Intercept	-0.001 [-1.376; 1.581]
		h^2	/
		$h^2_{\text{null model}}$	0.057 [0.000; 0.178]
SL Score (log)	/	Intercept	-0.378 [-1.046. 0.307]
	0.72	Tail (intact)	0.346 [-0.026. 0.780]
		h^2	0.054 [0.000; 0.175]
		$h^2_{\text{null model}}$	0.056 [0.000; 0.184]
RL Score (log)	/	Intercept	-0.077 [-0.870; 0.617]
	0.65	Enclosure (Simple)	0.558 [-0.828; 2.003]
	0.65	Age (Adult ’19)	0.367 [-0.368; 1.000]
		Age (Adult ’20)	0.245 [-0.358; 0.808]
		Age (Juvenile)	-0.586 [-1.366; 0.200]
	0.65	Enclosure (Simple)*Age (Adult ‘19)	-0.748 [-2.022; 0.588]
		Enclosure (Simple)*Age (Adult ‘20)	-0.122 [-1.487; 1.227]
		Enclosure (Simple)*Age (Juveniles)	-0.476 [-1.842; 0.968]
		h^2	0.074 [0.000; 0.249]
		$h^2_{\text{null model}}$	0.063 [0.000; 0.218]
Flex Score	/	Intercept	-0.103 [-0.701. 0.623]
		h^2	/
		$h^2_{\text{null model}}$	0.053 [0.000; 0.167]

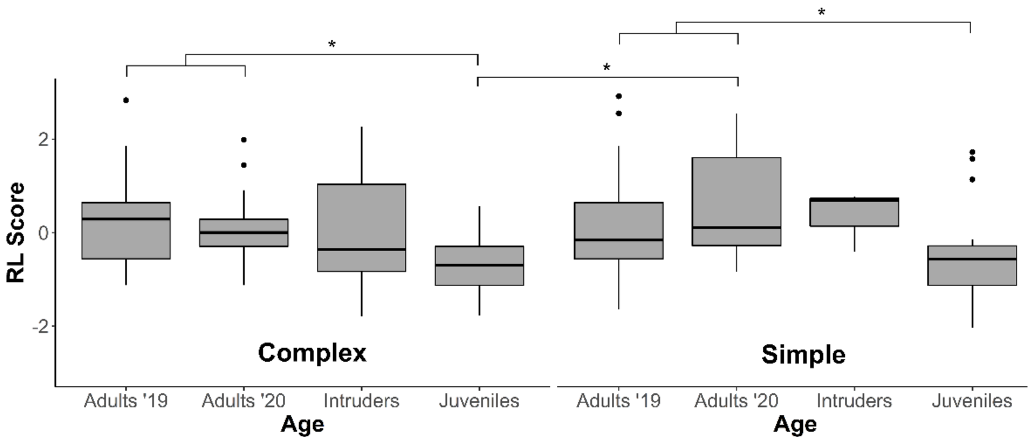


Figure 6. Boxplots with the reversal learning (RL) scores per age group in enclosures with a complex habitat (left: $N_{adults\ '19} = 33$, $N_{adults\ '20} = 25$, $N_{intruders} = 18$, $N_{juveniles} = 21$) and simple habitat (right: $N_{adults\ '19} = 33$, $N_{adults\ '20} = 17$, $N_{intruders} = 3$, $N_{juveniles} = 22$). Age groups were considered different from each other if the 95 % credibility interval of their difference (as obtained from a MCMCglmm) did not overlap with zero, which is indicated with an '*'. In both graphs, higher scores represent more errors and thus worse cognitive performance.

DISCUSSION

In the last few years, a growing number of studies has focused on interindividual variation in cognition. Despite this interest, information on the long-term consistency of such individual differences, as well as on their heritability, is still lacking. Here, we report moderate repeatability in explorative behaviour (PC1) and spatial learning in Aegean wall lizards kept in semi-natural conditions for one year (20 % of their average lifespan). In contrast, reversal learning was only marginally repeatable, and showed habitat-dependent plasticity. Problem-solving and learning flexibility were not repeatable. Last, heritability estimates were not different from zero for any of the traits.

Exploration

Our lizards displayed repeatable individual variation in exploration PC1 (general exploratory behaviour) across years (R_{adj} = 0.280). This result corroborates previous findings that personality variation can be consistent over long and considerable portions of a species life (zebra finches: Wuerz & Krüger, 2014; roe deer: Debeffe et al., 2015; European starlings: Thys et al., 2017a; eastern box turtles: Carlson et al., 2020; zebra fishes: Thomson et al., 2020; sleepy lizards: Payne et al., 2021); although not always (collared flycatchers: Garamszegi et al., 2015). In contrast, exploration PC1 did not show significant heritability (h^2 = 0.031). Explorative behaviour is generally found to be moderately heritable (Dochtermann et al., 2019) albeit this varies greatly among studies (h^2 = 0.22 - 0.37 in great tits: Dingemanse et al., 2002; h^2 = 0.08 in red squirrels: Taylor et al., 2012; R^2 = 0.019 - 0.25 in European green lizards: Bajer et al., 2015; h^2 = 0.355 - 0.362 in yellow-bellied marmots: Petelle et al., 2015).

Thus, the consistent individual variation in exploration PC1 could not be explained by additive genetic differences among individuals. We should, however, take into account that our sample size (37 juveniles, 16 fathers, 19 mothers) was relatively small compared to former studies on heritability (median N = 336, range = 6 - 11 092, only 14 % with N < 100 in the meta-analysis of Dochtermann et al., 2019) Hence, it is not impossible that additive genetic variance does contribute to behavioural variation in *P. erhardii*, but we were simply unable to detect it (Blanckenhorn & Perner, 1994). Nonetheless, the low genetic variation in our lizards could also be due to going through a genetic bottleneck when introduced in our enclosures (Carrete et al., 2017) or could be a consequence of strong directional selection on explorative behaviour in the past (Boake, 1989; Falconer

& Mackay, 1996; Wheelwright et al., 2014). Large seasonal fluctuations in precipitation and accordingly arthropod abundances on Naxos (Karamaouna, 1987; Parashi, 1988; Adamopoulou et al., 1999; De Meester et al., 2021 ~ Chapter 4) may exert strong selection on explorative behaviour within Aegean wall lizards if it facilitates the discovery and acquisition of resources (Bajer et al., 2015; Baxter-Gilbert et al., 2019). However, we did observe negative selection on exploration in a previous batch of lizards from 2018 to 2019, but not in the current batch (Chapter 7). Ideally, we should thus verify the heritability of personality (and cognition) in completely natural populations.

Regardless of the reasons, low heritability (if accurate) but moderate repeatability does imply that personality variation in *P. erhardii* mostly arises due to strong environmental effects (Petelle et al., 2015; Quinn et al., 2016; Vardi et al., 2020). This is further supported by the extremely low short-term repeatability of exploration PC1 within juveniles (R = 0.005). In hindsight, juveniles were captured and transferred to captive lab conditions too soon after hatching (as indicated by the presence of umbilical scars) and thus effectively grew up in the same standardized environment. A lack of genetic differences plus little divergence in personal experiences may explain their low behavioural repeatability (Archard & Braithwaite, 2010; Stamps & Groothuis, 2010). Short-term repeatability is slightly higher (but not significant) in 2019 adults (R_{adj} = 0.079 - 0.085) and moderate in 2020 adults (R_{adj} = 0.333), giving additional support for the hypothesis that personality variation develops over time. Behavioural repeatability is often predicted to change with age, although in which direction is highly debated (Carlson et al., 2020). Both within- and among- individual variance in a population can increase or decrease over time due to a multitude of processes (overview in Carlson et al., 2020), including selection (Bell et al., 2009), divergence in personal experiences (Stamps & Groothuis, 2010), state-behaviour feedback loops (Sih et al., 2015; Kok et al., 2019), canalization (Kok et al., 2019), changes in the costs of behavioural flexibility (Polverino et al., 2016) or in the developmental dynamics of the physiological mechanisms underlying behaviour (Bell et al., 2009; Stamps & Groothuis, 2010). Such changes are not necessarily monotonic over time (Thys et al., 2021). A valuable follow-up experiment would be to measure personality multiple times across the lifetime of the same cohort of lizards starting from birth, to test more explicitly how and when personality variation develops in this species.

Following up on this, we did find evidence for changes in (average) explorative behaviour with age. Adult lizards behaved more explorative in 2019 than 2020, which could simply reflect senescence (Brommer & Class, 2015). In addition, juveniles had lower PC1 scores than adults, which is in line with the idea that younger animals should behave more cautiously to allow future reproduction, while adults should take more risks to increase current reproduction (Wolf et al., 2007; Schuster et al., 2017a). Nevertheless, we should note that all lizards tested in 2020 (intruders included) behaved less explorative than the 2019 adults. Lizards were tested in May and August during 2019 and 2020 respectively, thus seasonal fluctuations in behaviour (Jenssen et al., 1995; Aragón et al., 2001; Kerr & Bull, 2006) may explain the differences between years. Indeed, Naxian *P. erhardii* become less active as ambient temperatures rise during summer (Catsadorakis, 1984). Alternatively, restricted space use and physical activity within the enclosures compared to a natural environment could also have led to a plastic decrease in explorative behaviour over time in every group (Oosthuizen et al., 2013).

In sharp contrast, individual differences in exploration PC2 (fast exploration versus hiding) were not consistent across years (R = 0.060), nor did they show significant heritability ($h^2 = 0.057$). Interestingly, exploration PC2 showed considerable short-term repeatability within the complete dataset of 2019 adults ($R_{adj} = 0.211$), but not within the subset of survivors in either 2019 ($R_{adj} = 0.130$) or 2020 ($R_{adj} = 0.162$). Lower repeatability among survivors may be a consequence of strong directional selection on exploration PC2 (Bell et al., 2009). Indeed, female PC2 scores were higher in the survivors than in the complete batch of released adults (survivors: 0.339 ± 0.167; all: 0.212 ± 0.142) while the opposite occurred in males (survivors: -0.031 ± 0.180; all: 0.165 ± 0.160). Interestingly, male and female survivors differed in PC2-scores in 2020 but not 2019. This implies that sex-dependent plasticity also occurred across years. Male and female lizard can indeed differ in how their behaviour changes over the breeding season (Aragón et al., 2001). Sex-dependent selection and plasticity would have respectively decreased inter-individual and increased within-individual variance (Carlson et al., 2020), and thus both contributed to overall lower behavioural repeatability of PC2 on the long-term.

Cognition

Adult lizards showed moderate repeatability in spatial learning performance across years ($R_{adj} = 0.398$). Our study hence adds to a small body of evidence that individual variation in spatial learning abilities can be repeatable over longer timescales (Eurasian harvest mice: Schuster et al., 2017b; pheasants: Langley et al., 2018; mountain chickadees: Tello-Ramos et al., 2018; but see Soha et al., 2019 on song sparrows). To our best knowledge, this is the first study demonstrating cognitive repeatability (either short- or long-term) in a non-avian reptile. On the other hand, heritability for spatial learning was not different from zero ($h^2 = 0.054$). While heritability estimates for spatial learning vary greatly across literature ($h^2 = 0.27$ in chimpanzees: Hopkins et al., 2014; $h^2 = 0.27$ in rose bitterlings: Smith et al., 2015; $h^2 = 0.09 - 0.23$ in pheasants: Langley et al., 2020a), our results are in line with the only other study investigating heritability of (spatial) cognition in lizards (no significant mother-offspring regression in delicate skinks: Vardi et al., 2020).

Whether this low heritability is a consequence of directional selection, founder effects or too low sample sizes can unfortunately not be verified with our current dataset. It would not be unreasonable to expect selection for spatial learning in *P. erhardii*, as it may contribute to successfully escaping predators (Font, 2019) and remembering the location of resources during periods of food scarcity (De Meester et al., 2021 ~ Chapter 4). We did indeed observe selection on spatial learning in our enclosures, although in the opposite direction and only in females (Chapter 7).

We previously reported differences in spatial learning performance between lizards originating from structurally simple and complex habitats (De Meester et al., 2022 ~ Chapter 5). Assuming that spatial learning is not heritable, then such intraspecific variation would be entirely due to plasticity (Morand-Ferron et al., 2016), as also hypothesized for the lizards in Vardi et al. (2020). Indeed, being reared in structural complex environments has a positive effect on brain (size) and cognitive development in fish and lizards (Spence et al., 2011; LaDage et al., 2016; Carbia & Brown, 2019; Vardi et al., 2020). Our juveniles made fewer errors during the spatial learning compared to adults, which indicates that spatial cognition may indeed be plastic in *P. erhardii*.

Higher learning abilities in juveniles could be a consequence of the higher need for behavioural plasticity in early life (Fischer et al., 2014; Szabo et al., 2019a) or of cognitive decline with age (Bonte et al., 2014). Alternatively, juvenile lizards should be more motivated to find the safe refuge due to an higher vulnerability to predation (Martín & López, 1995). Interestingly, in contrast to reversal learning, spatial learning performance did not show habitat-dependent plastic changes across years. This implies that if variation in spatial learning is caused by permanent environmental effects, such effects may be limited to a critical period during early life. It could thus be an interesting follow-up experiment to test the cognitive performance of newly born lizards, release them in our enclosures, and follow up their cognitive development in both habitat types.

Demonstrating that individual variation in learning is repeatable validates that we are truly measuring cognitive variation (Thornton et al., 2014; Ashton et al., 2018) and helps us to understand its ecological and evolutionary relevance (Boake, 1989; Morand-Ferron et al., 2016; Soha et al., 2019). Nevertheless, we should be aware of the possibility of pseudo-repeatability (Dingemanse & Dochtermann, 2013; Cooke et al., 2021; Mason et al., 2021), i.e. behavioural repeatability could be a consequence of consistent differences in other non-cognitive variables among individuals. For example, Cooke et al. (2021) demonstrated that problem-solving performance in great tits (*Parus major*) was highly repeatable, until corrected for hunger motivation and experience. Nonetheless, the long time-interval between repeated tests should have drastically reduced the chances of pseudo-repeatability (Niemelä & Dingemanse, 2017). Spatial learning was also unaffected by lizard personality in this dataset (Chapter 5), and tail status was corrected for, thus it is also unlikely that individuals simply differed consistently in their willingness to seek shelter. Biases for certain stimuli, such as a colour (Mason et al., 2021) or a side preference (our results) could also increase repeatability estimates if test subjects differ consistently in whether they are trained to pick the preferred or unpreferred cue. However, learning performance remained significantly repeatable even after adjusting for the side bias of our lizards. Lastly, behavioural repeatability could as well be influenced by memories from a previous testing round (Griffin et al., 2015). Yet, if lizards remembered the location of the safe refuge from the previous year, they should have made fewer errors or learnt faster in 2020, which was not the case. Nonetheless, it would be good to test the contextual repeatability of spatial learning in *P. erhardii* as well. Using various tasks aimed at measuring the same cognitive ability, e.g. training lizards to locate food or mates instead of shelter, or testing spatial learning at different scales, may help to minimize the influence of pseudo-repeatability and memory (Griffin et al., 2015; Brust & Guenther, 2017; Cauchoix et al., 2018; Troisi et al., 2021).

Next, we found that reversal learning was only marginally repeatable ($R_{adj} = 0.251$) and learning flexibility not at all ($R = 0.192$), and that neither showed significant heritability ($h^2_{RL} = 0.074$, $h^2_{FLEX} = 0.053$). Previous studies reported reversal learning to be both repeatable (song sparrows: Soha et al., 2019) and not repeatable (mountain chickadees: Tello-Ramos et al., 2018), while overall being modestly heritable ($R^2 = 0.31$ among 51 strains of lab mice: Laughlin et al., 2011; $h^2 = 0.26$ in red junglefowl: Sorato et al., 2018). The low repeatability of reversal learning and learning flexibility is in sharp contrast with the rather high repeatability of spatial learning. A similar result was obtained for wild mountain chickadees by Tello-Ramos et al. (2018). One possible explanation may be that cognitive flexibility is more plastic and sensitive to environmental changes

(Tello-Ramos et al., 2018). Indeed, lizards kept in simple enclosures seemingly made more errors during the reversal in 2020 than in 2019. If individuals within a group change their behaviour inconsistently from each other, due to differential personal experiences, then behavioural repeatability is indeed expected to decrease (Brommer & Class, 2015).

Changes in reversal learning performance may be a consequence of deviations in neurogenesis rates, a process known to be stimulated by spatial complexity and impaired by structural simplicity, even in adults (Kempermann et al., 1997; LaDage et al., 2013; Dunlap, 2016). Neurogenesis facilitates reversal learning but importantly, appears to be less relevant for the initial acquisition of information (Burghardt et al., 2012; Kalm et al., 2013; Swan et al., 2014). In addition, stress is known to down-regulate neurogenesis (Mirescu & Gould, 2006). Lizards in the simple open enclosures may have experienced more stress, due to e.g. feeling more exposed to aerial predators or more intense competition for the fewer resources. Thus, stress and habitat simplicity may have inhibited the rate of neurogenesis, leading to reduced reversal learning in lizards kept in simple enclosures. Importantly, the fact that changes in neurogenesis are not expected to influence the capacity to learn an initial (spatial) association may explain why habitat complexity did not lead to differential changes in spatial learning performance.

The rate of neurogenesis is also often believed to decline with age (Molowny et al., 1995; Amrein et al., 2004), which possibly explains why juvenile lizards showed better reversal learning than adults. Yet, strangely enough, juveniles only outperformed the adults in their own enclosure, but did not differ from adults in the opposite enclosure type (with the exception of juveniles from complex enclosures making fewer errors than 2020 adults in simple enclosures). Why these age-differences seem habitat-specific is unclear to us, especially given that 2019 adults were tested prior to release into the enclosures.

Finally, problem-solving ability, here measured with an escape box task, showed the lowest repeatability (R = 0) of all cognitive traits. Long term consistency of problem-solving is very rarely tested, and previous studies have demonstrated both low (R = 0.002 - 0.02 in North Island robins: Shaw, 2017) and relative high temporal repeatability (R = 0.27 - 0.54 in great tits: Cole et al., 2011). Cauchoix et al. (2018) found that (contextual) repeatability of cognition was significantly lower for latency measures, such as our escape times, likely due to ceiling or floor effects. Among-individual variation may be lowered because all failing individuals were assigned the same maximum score, or because most lizards solved the task within a comparable short time due to its apparent ease.

Problem-solving assays have been criticized, as it is often unclear whether individual variation in performance truly reflects cognitive variation or is due to non-cognitive differences (e.g. hunger, motivation, …) among test subjects (Morand-Ferron et al., 2016; Audet & Lefebvre, 2017; Shaw, 2017). Especially when only measured once, the outcome of a problem-solving task can be strongly influenced by intrinsic and extrinsic conditions (Cauchoix et al., 2018). The fact that escape times were not repeatable in our study seems to validate such concerns, and illustrates the danger of linking performance in a (single) problem-solving task to e.g. personality, life-history or fitness without any information regarding its repeatability. Following the suggestion of Thornton et al. (2014), problem-solving should have been tested over multiple trials within each year, and measure the repeatability of lizards' improvement or the mean solving time (Cauchoix et al., 2018).

CONCLUSION

Very few studies so far have tested the long-term consistency and heritability of personality and cognition, especially so for wild animals, despite the fact that this information is crucial to understand the potential evolutionary and ecological impact of such behavioural variation (Dukas, 2004; Griffin et al., 2015; Morand-Ferron et al., 2016; Cauchoix & Chaine, 2016; Boogert et al., 2018). Our study showed that individual differences in some, but not all, aspects of exploration and cognitive performance were consistent in semi-wild Aegean wall lizards across years, but neither cognition nor personality were heritable.

The low heritability estimates would imply that all of our behavioural traits have very little evolutionary potential, even if selection would act upon them, although this needs to be verified in natural populations. Our results do suggest that both cognition and personality within Aegean wall lizards are at least partially plastic, changing with age, depending on both sex and habitat complexity. Our study thus illustrates that long-term studies on the repeatability of cognition in wild animals can advance our understanding of the role of both genetic and environmental factors in shaping cognitive variation.

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CHAPTER 7

DOES BEING SMART PAY OFF?

THE FITNESS CONSEQUENCES OF COGNITION IN AEGEAN WALL LIZARDS LIVING IN DIFFERENT HABITAT TYPES.

Adapted from:

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ABSTRACT

How cognition evolves is one of the most intriguing questions within biology. Traditionally, comparative studies across species and populations were employed to identify the (socio-)ecological forces driving the evolution of the brain, and, occasionally, cognitive performance. Lately, cognitive research has shifted its attention to the individual level, and in particular to how individual variation in cognitive traits translates into differences in fitness. Studying selection on cognition across environmental contexts could become a powerful approach to gain new insights in the role of ecology in shaping cognitive variation. Unfortunately, studies linking cognition and fitness in wild animals, even in a single ecological context, remain scarce. Here, we investigated the relation between cognitive performance, personality and fitness within Aegean wall lizards (*Podarcis erhardii*) kept in either structural simple or complex enclosures for one year. Using two different enclosure types allowed us to test the widely held hypothesis that environmental complexity would favour higher cognitive abilities. Cognition was indeed associated with survival, but in unpredicted ways. Better spatial learning was negatively associated with female, but not male, survival. The link between problem-solving and survival was non-linear, with moderate solvers suffering the highest mortality. Cognition was unrelated to reproductive success. In contrast to our expectations, results were independent of habitat type, thus refuting the hypothesis that higher environmental complexity selects for higher cognition. The personality-fitness relationship was, however, often year – and habitat-dependent. Selection studies on cognition, preferably across an ecological gradient, can thus lead to interesting novel insights in the evolution of animal cognition.

INTRODUCTION

Cognition (i.e. learning, remembering and using environmental information cfr. Dukas, 2004) is quintessential to most animals because it enables them to adjust their behaviour in response to an ever-changing environment (Sol, 2009). The fact that species, populations and even individuals within populations can differ considerably in cognitive abilities (Morand-Ferron, 2017; Boogert et al., 2018) raises the question of which factors promote and constrain the evolution of cognition. This issue ranks among the least understood within current biology (Thornton et al., 2014; Boogert et al., 2018). A general answer would be that variation in cognitive capacity is caused by local environmental conditions shifting the balance between the benefits of cognitive competence (behavioural flexibility; Sol, 2009) and its costs (development and maintenance of expensive neural circuitry; Aiello & Wheeler, 1995; Kotrschal et al., 2013; Buechel et al., 2018; Kotrschal et al., 2019). However, exactly which socio-ecological forces shape cognitive variation remains poorly known (Cauchoix & Chaine, 2016; Morand-Ferron, 2017; Henke-von der Malsburg et al., 2020).

One often proposed candidate driver of cognitive evolution is environmental complexity (Godfrey-Smith, 2002). To find resources and avoid predators, animals living in complex habitats must be able to process large quantities of environmental information rapidly, and efficiently sift useful cues from irrelevant noise (Safi & Dechmann, 2005; Shumway, 2008; Powell & Leal, 2014; White & Brown, 2014; Calisi et al., 2017; Steck & Snell-Rood, 2018). Past research has indeed demonstrated that species and/or populations inhabiting spatially more complex habitats possess relatively larger brains (chipmunks: Budeau & Verts, 1986 ; fish: Shumway, 2008; Axelrod et al., 2018). In particular, brain regions associated with spatial cognition (bats: Safi & Dechmann, 2005; lesser earless lizards: Calisi et al., 2017), improved spatial learning (fish: Shumway, 2008; White & Brown, 2014; mole-rats: Costanzo et al., 2009; *Myotis* bats: Clarin et al., 2013; Aegean wall lizards: De Meester et al., 2022 ~ Chapter 5) and problem-solving (*Anolis* lizards: Storks et al., 2020) increase with habitat complexity. On the other hand, habitat complexity does not affect brain morphology across *Anolis*-species (Powell & Leal, 2014) or populations of three-spined sticklebacks (*Gasterosteus aculeatus,* Ahmed et al., 2017), nor spatial learning or memory in three species of African striped mice (*Rhabdomys* sp., Mackay & Pillay, 2017).

Thus, variation in cognition among populations is expected to result from geographic variation in selection pressures (but see e.g. Shumway, 2008; Spence et al., 2011; Carbia & Brown, 2019 for the role of phenotypic plasticity). However, actual evidence for differential selection on cognition in the wild remains scarce (Branch et al., 2019). In fact, the link between cognition and fitness in general remains underexplored, probably because collecting such data in free-ranging animals is challenging (Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016; Morand-Ferron, 2017; Boogert et al., 2018; Rochais et al., 2022a). The few studies that have tackled the issue so far have yielded mixed results. Some have found that individuals with high cognitive abilities survive better. Tool-using Indo-pacific bottlenose dolphins (*Tursiops aduncus*) were more likely to survive an extreme marine heatwave (Wild et al., 2019), and better spatial learning was positively associated with survival in mountain chickadees (*Poecile gambeli*, Sonnenberg et al., 2019) and hatchling velvet geckoes (*Amalosia lesueurii,* Dayananda & Webb, 2017). On the other hand, neither spatial learning nor problem-solving ability predicted survival in grey mouse lemurs (*Microcebus murinus*, Huebner et al., 2018); and pheasant chicks (*Phasianus colchicus*) with higher cognitive flexibility suffered higher mortality upon release in the wild (Madden et al., 2018). Fast learning bumble bees (*Bombus terrestris*) surprisingly had a lower lifetime foraging success due to a reduced lifespan (Evans et al., 2017).

Enhanced cognition also seems to benefit individuals' mating success (satin bowerbirds: Keagy et al., 2009; guppies: Shohet & Watt, 2009; three-spined sticklebacks: Minter et al., 2017; budgerigars: Chen et al., 2019) and reproductive output (great tits: Cauchard et al., 2017; Preiszner et al., 2017; house sparrows: Wetzel & Koenig, 2017; Australian magpies: Ashton et al., 2018; male New Zealand robins: Shaw et al., 2019), albeit not always (great tits: Cole et al., 2012; spotted bowerbirds: Isden et al., 2013; spotted hyenas: Johnson-Ulrich et al., 2019).

Interestingly, these studies show that the fitness consequences of the same cognitive skills can vary greatly, even between related species (e.g. satin and spotted bowerbirds: Keagy et al., 2009; Isden et al., 2013) or populations of the same species (e.g. great tits: Cole et al., 2012; Cauchard et al., 2017; Preiszner et al., 2017). Additionally, within the same population, the fitness consequences of cognition can differ between sexes (guppies: Kotrschal et al., 2015a; African striped mice: Maille & Schradin, 2016), body sizes (pheasants: Madden et al., 2018), mating strategies (rose bitterlings: Smith et al., 2015), group sizes (pheasants: Langley et al., 2020b), or vary across years due to temporal variation in resource availability (great tits: Cauchard et al., 2017; mountain chickadees: Branch et al., 2019) or predation risk (eiders: Jaatinen et al., 2019).

Hence, the fitness consequences of cognition do not seem to be universal, and understanding when and how selection acts on cognition is an important step to advance our understanding of its evolution. To our best knowledge, only three studies so far have explicitly tested the fitness consequences of cognition across environmental conditions. Female guppies (*Poecilia reticulata*) with smaller brains experience greater mortality in the presence of a predator, but live longer in a safe environment (Kotrschal et al., 2015a; Kotrschal et al., 2019). Problem-solving increases reproductive success equally in both urban and forest great tits (Preiszner et al., 2017) and in black garden ants (*Lasius niger*) individual learning ability correlates with colony foraging success only in rich, complex environments (Pasquier & Grüter, 2016). Comparing the link between cognition and fitness across populations of the same species living under different ecological conditions can nonetheless become a powerful approach to gain new insights in the costs and benefits of cognition, and identify the selective drivers of its evolution (Morand-Ferron et al., 2016; Preiszner et al., 2017; Branch et al., 2019).

The relative benefits and costs of cognition may also vary across the lifetime of an individual. In particular, learning and higher behavioural flexibility may be more advantageous in early life, especially in species lacking parental care, when individuals still need to learn a lot about their environment (Fischer et al., 2014; Noble et al., 2014; Szabo et al., 2019a). Indeed, in some fish and lizard species it was shown that juveniles are more willing to copy information from conspecifics than adults (Hoppitt & Laland, 2013; Noble et al., 2014; but see Leris & Reader, 2016). Juveniles are often more vulnerable to predation, and hence may require faster learning abilities to directly avoid/escape predators (Kotrschal et al., 2015a; Dayananda & Webb, 2017) or to obtain sufficient resources to maximize their growth rate (Bajer et al., 2015; Cauchard et al., 2017). On the other hand, juveniles may face an energetic trade-off between body growth and neural development (Kotrschal et al., 2015c). If juveniles need to grow fast to become less vulnerable to predation (Bajer et al., 2015), then perhaps higher cognitive abilities may be a disadvantage in this life stage. Although some work has tested the fitness consequences of cognitive performance in juvenile animals (see e.g. Dayananda & Webb, 2017), we are not aware of a single study measuring the cognition-fitness link in both juveniles and adults of the same species.

In order to improve our understanding regarding the role of habitat complexity in shaping cognitive variation, we investigated the link between individual cognitive abilities and fitness within Aegean wall lizards (*Podarcis erhardii*), and tested whether selection on cognition would differ between structural simple and complex habitats. Wild-caught lizards were tested on several cognitive abilities and released in large outdoor semi-natural enclosures. Their survival and reproduction was monitored in the next 9-12 months. As it has become evident that cognition and personality are closely intertwined (Sih & Del Giudice, 2012; Dougherty & Guillette, 2018) and should thus be studied in conjunction (Rochais et al., 2022a), we also collected data on several personality traits in our lizards and tested their effect on fitness as well. We specifically hypothesized that selection for cognition, especially spatial learning, will be stronger in enclosures consisting of complex habitat, while cognition will either have no effect or a negative impact on fitness in the simple enclosures. We also tested the effect of cognition in a smaller subset of juvenile lizards, as cognition should be particularly useful for juvenile lizards due to a lack of parental care (Szabo et al., 2019a).

MATERIAL AND METHODS

Study species and general experiment design

The Aegean wall lizard is a diurnal, heliothermic lacertid lizard (40 – 70 mm snout-vent length) inhabiting the Southern Balkans and the islands of the Aegean Sea (Valakos, 1990; Lymberakis et al., 2018). Aegean wall lizards occupy a broad diversity of habitats (Valakos et al., 2008; Lymberakis et al., 2018) and feed on a variety of arthropods but occasionally also on gastropods, fruits and conspecifics (Adamopoulou et al., 1999; Brock et al., 2014b; Donihue et al., 2016; Madden & Brock, 2018). Previous research has shown that individuals of this species do well in spatial learning and problem-solving tasks, although cognitive performance varies both within and among populations (De Meester et al., 2021 ~ Chapter 4; De Meester et al., 2022 ~ Chapter 5)

We captured 125 adult lizards on Naxos Island (Cyclades, Greece) during spring 2018 and 2019. Animals were collected from five sites that differed in structural habitat complexity (previously described in De Meester et al., 2022 ~ Chapter 5): two ‘complex’ and three ‘simple’ environments ($N_{male-complex}$ = 39, $N_{female-complex}$ = 27, $N_{male-simple}$ = 34, $N_{female-simple}$ = 32). Lizards were caught by hand, lasso or pitfall, and transported to the National and Kapodistrian University of Athens in individual cotton bags kept in a cool box to minimize stress. In the lab, lizards were tested on several personality traits and cognitive abilities (see below). Upon completion of these tests, lizards were individually marked and released into four semi-natural enclosures on Naxos with either a complex or simple habitat structure in order to follow up their survival and reproductive success over the course of 11 – 12 months. Two batches of adult lizards were released in the enclosures and kept there from 2018 to 2019 (year 1) and from 2019 to 2020 (year 2) respectively. In addition, we estimated aspects of cognition and personality in 44 juvenile lizards, released them in the enclosures in 2020 and recaptured them after 9 months.

Husbandry during behavioural testing

Lizards were kept in individual plastic terraria (22 x 20 x 17 cm l x w x h) at the facilities of the National and Kapodistrian University of Athens. Terraria received natural sunlight (2018) or were equipped with an incandescent lamp (60 W) that allowed lizards to thermoregulate (2019). Each terrarium contained a sand substrate, a water dish (refreshed daily) and stone bricks for basking and shelter. Lizards were offered mealworms (*Tenebrio molitor*) dusted with TerraVit Powder (JBL, GmbH & Co. KG) thrice per week. Room temperature was maintained around 28 ± 2 °C during the day. Lizards were kept in captivity from the beginning of May until the end of July (2019) or beginning of August (2018).

Behavioural experiments

Lizards were subjected to four cognitive tasks (two problem-solving test and a spatial + reversal learning task) and three personality assays (neophobia, exploration and aggression). All these tests and their results have been previously described in De Meester et al. (2022) (~ Chapter 5) in more detail but experimental procedures are briefly summarized below in the same order as they were conducted. One problem-solving task (an escape box) was excluded from this study, as performance on this task was not repeatable (Chapter 6).

All observations were performed between 10:00 and 19:00. Lizards were given 20 – 30 minutes basking time underneath a 100 W heat bulb before each trial allowing them to achieve preferred body temperatures. Thereafter they were transferred to the observational arenas. Experimental equipment was washed in between trials with 70 % alcohol and water (Vicente & Halloy, 2017) during both years for the spatial cognition task, but not in 2018 for the other assays. Behavioural trials (except the spatial cognition task) were recorded using either a GoPro (Hero5 Black) or digital camera (JVC Everio GZ-HM400) and analysed afterwards.

Training for neophobia and problem-solving

As a first step, lizards were trained to eat from an experimental set-up (a 1.5 cm hight transparent petri dish taped on a 10 x 10 x 1.5 cm l x w h wooden platform) within the observational arenas (30 x 30 x 30 cm). A lizard was released in the arena and left undisturbed for two minutes. Then, a food reward (1 – 2 mealworms) was placed inside the petri dish, and the lizard was given fifteen minutes to obtain and consume it. Lizards received one (in case of success) or two trials per day, until they had succeeded to consume the reward in three out of four consecutive trials (cfr. Gomes et al., 2020) or until they had participated in ten trials. The average ‘attack latency’ (time to contact the petri dish with the snout) of the last three trials was used as a control for the neophobia assays.

Neophobia

Neophobia, or the fear of novelty, affects how likely individuals are to encounter and gather new information. Less neophobic individuals may profit from discovering novel resources, but also face higher risks e.g. due to dangerous food or predation (Greenberg, 1983; Greenberg, 2003; Mettke-Hofmann, 2014; Tebbich & Teschke, 2014). The procedure for the neophobia assays was identical to the training sessions, but now a novel object (either a pair of orange and yellow glow rings or a red toy car - random order) was placed next to the petri dish after introduction of the mealworm. Neophobia was then measured as the relative change (%) in attack latency compared to the training (Greenberg, 1983; Candler & Bernal, 2014; Guido et al., 2017). Neophobia was measured twice, generally on two consecutive days. As neophobia was found to be highly repeatable in another study (De Meester et al., 2022 ~ Chapter 5), we used the average of the two trials as neophobia score for statistical analyses. One individual was not assigned a neophobia score as it was accidentally tested twice with the same object.

Problem-solving: lid-removal

Problem-solving is the cognitive ability to solve new problems by demonstrating a novel behaviour or applying an existing behaviour within a new context (Griffin & Guez, 2014). Lizards may profit from problem-solving if it allows them to exploit new resources, or utilize familiar resources in a more efficient way (Griffin et al., 2016), e.g. by allowing extraction of hidden prey (Mendyk & Horn, 2011; Cooper et al., 2019). Our problem-solving test was based on the standard lid-removal task often used in studies on lizard cognition (Leal & Powell, 2012; Storks et al., 2020; De Meester et al., 2021 ~ Chapter 4). The procedure was identical to the training sessions, but access to the prey was blocked by an opaque plastic disc (6 cm diameter) placed on top of the petri dish. A lizard could solve the task by either pushing or lifting the disc, and was considered successful if it grabbed the prey immediately afterwards (as to eliminate potential accidental and thus invalid openings). In 2018, lizards were tested until they opened the apparatus in three out of four consecutive trials (Gomes et al., 2020) or until they had completed ten valid trials. In 2019, all lizards, regardless of their success, received ten valid trials, in order to measure whether consistent solvers would become more efficient over time. During the lid-removal experiment, lizards were kept on a diet of a single mealworm per day in order to both increase and standardize hunger motivation among individuals (Amiel et al., 2014). For further analyses, we assigned each individual a lid-removal (LR) score: 0 - non-solvers (those which never opened the dish), 1 - occasional solvers (at least once) and 2 - consistent solvers (passed the ¾-criterion). Two individuals could not be assigned lid-removal scores as they did not complete sufficient valid trials.

Spatial exploration behaviour

Spatial exploration is the tendency of an animal to gather information from the environment (Verbeek et al., 1994). Fast explorers are generally assumed to be faster in acquiring resources, but at the cost of increased mortality (Wolf et al., 2007). We tested exploration using a standard novel arena test (e.g. Carazo et al., 2014; McEvoy et al., 2015; Damas-Moreira et al., 2019). An individual was placed in the centre of an experimental arena (60 x 60 x 30 cm l x w x h) underneath an opaque cover for three minutes. Thereafter, the animal was allowed to explore the environment for ten minutes. Each lizard was tested twice (at least one day in between trials) in two distinct arenas with different lay-outs (arena 1: sand, four black plastic refuges and four pinecones; arena 2: plywood substrate, four white plastic refuges and four stones). On the recordings, we divided the arena in four equal quadrants and scored the following behaviours: latency until the first transition between quadrants, total number of transitions made, number of times it touched an object or refuge with the snout or front legs, number of entries in a refuge, total time hiding in the refuges and the latency to explore all four quadrants. Subsequently, the number of variables was reduced using a principal component analysis (PCA) ('princomp' function in R). This PCA gave two principal components with an eigenvalue > 1, explaining together 65.72 % of the total variance (Table 1). Higher scores on PC1 (eigenvalue = 1.62, 37.15 % of total variance) indicated that lizards made more transitions and touched more objects, and took less time to enter the first refuge and explore all quadrants. Scores on PC2 (eigenvalue = 1.42, 28.62 % of variance) represented a trade-off between fast exploration (latency for first transition and to explore all quadrants) and hiding (number of refuges visited and time spent within these). We only retained PC1 scores, as individual variation in this aspect of exploration was previously shown to be repeatable across years, while intra-individual variation in PC2 was not (Chapter 6). Average PC1 scores were used for further analyses.

Table 1. Principal Component Analysis of the behaviours observed during the exploration tests. Only loadings with an absolute value higher than 0.30 were considered to contribute to a principal component (indicated in bold). The first component was retained as exploration score for further statistical analyses.

	Comp 1	Comp 2	Comp 3
Eigenvalue	1.62	1.40	0.91
% variance	37.56	28.12	11.94
First transition	-0.15	**-0.49**	**0.54**
# transitions	**0.45**	0.29	0.19
Latency to explore all quadrants	**-0.43**	**-0.35**	0.14
# touches	0.29	0.27	**0.72**
# refuges entered	**0.45**	**-0.38**	
Latency to enter first refuge	**-0.43**	0.20	**0.38**
Time spent hiding	**0.33**	**-0.54**	

Aggression

Competition for resources in lizards is likely to favour more aggressive individuals (Marco & Pérez-Mellado, 1999; Ancona et al., 2010; Names et al., 2019). We scored aggression by using a series of staged encounters (Abalos et al., 2016; Bruinjé et al., 2019; Names et al., 2019). Two same-sex lizards of similar size (max 10 % difference in SVL) were introduced within a large arena (60 x 60 x 30 cm l x w x h) separated from each other by an opaque divider. After three minutes, the divider was removed, and a basking spot (pile of stones underneath a 100 W heat bulb) was introduced in the centre of the arena for which lizards could compete. Trials lasted ten minutes and each lizard was intended to be staged against three different opponents (one/day). Nevertheless, due to camera issues, and the need to reuse some individuals > 3 times to allow size-matching, the actual number of encounters varied from two to five across individuals.

As the majority of animals (83 %) had maximum three encounters, we only used data from the first three trials per individual for further analyses. Trials were scored on video following an ethogram similar to the one described in Names et al. (2019) (see also Chapter 5: Table 1). For each agonistic action (attacks, approaches, bites, display behaviours) the focal lizard received a score of '+1', and for each evasive behaviour (bypassing or fleeing from the opponent) it received a score of '-1'. Aggression scores were then calculated as the difference between agonistic and evasive behaviours. Aggression between females was rare, and hence we only retained aggression scores for males.

Spatial and reversal learning

Spatial cognition allows animals to learn and remember the location of resources (e.g. food or shelter) in their environment and is therefore believed to be an ecological relevant ability (Dukas, 2004; Noble et al., 2012; Dayananda & Webb, 2017). We quantified the spatial learning ability of our lizards using a standard antipredator task, in which lizards needed to learn the position of a safe refuge (Paulissen, 2008; Noble et al., 2012; Font, 2019; Vardi et al., 2020; De Meester et al., 2021 ~ Chapter 4).

Lizards were placed in the centre of an experimental arena (60 x 60 x 30 cm l x w x h) underneath a transparent container. The arena contained two identical refuges (black plastic cups) in opposite corners, one of which was a priori assigned as safe (counterbalanced among original populations). Visual cues were provided both in and around the arena as to facilitate orientation and navigation. After two minutes, we lifted the container and simulated a predator attack by poking the lizards' tail repeatedly with a paintbrush (always from straight above). Each trial lasted two minutes, or until the lizard entered the safe refuge (in which case it was allowed to rest for two minutes before being returned to its home terrarium). Entering the wrong refuge was penalized by lifting the hiding spot and continuing chasing the lizard. If a lizard had not yet entered the safe refuge after two minutes, it was captured and gently placed underneath the safe spot for two minutes. We took care to mix the sand substrate in between trials and clean all refuges with 70 % alcohol and water. Lizards were tested three times per day for five consecutive days, and were considered to have learnt the task if the safe refuge was their first choice in five out of six consecutive trials (cfr. Noble et al., 2014; Vardi et al., 2020; De Meester et al., 2021 ~ Chapter 4).

Animals living in more dynamic environments will need to continuously update their knowledge regarding the distribution and abundance of resources in their habitat, and adjust their behaviour in response to environmental changes (Noble et al., 2012). Such cognitive flexibility is typically measured using a reversal learning task (Noble et al., 2012; Audet & Lefebvre, 2017; Buechel et al., 2018), in which animals are initially trained until a certain level of success or for a fixed number of trials (Boussard et al., 2020), after which rewarded and unrewarded stimulus are switched and test subjects need to relearn the association. Cognitive flexibility may be useful for Naxian lizards, as they experience strong seasonal fluctuations in resource availability due to the harsh and dry summers typical for Mediterranean insular ecosystems (Adamopoulou et al., 1999; Sagonas et al., 2015). The spatial learning task was hence followed by a reversal phase, in which safe and unsafe were switched. Lizards then received an additional fifteen trials to relearn the spatial association.

For subsequent analyses, we assigned each lizard a spatial learning and reversal learning score (the mean number of wrong choices per trial in each phase respectively). We also assigned lizards a score for overall learning flexibility: 0 – reaching criterion in neither phase, 1 – reaching criterion during either spatial or reversal and 2 – learning during both phases.

Semi-natural enclosures

The survival and reproductive success of each individual lizard, was monitored in four semi-natural enclosures on a private domain on the island of Naxos. Enclosures were constructed by fencing in ± 100 m² of land with smooth metal sheets (100 cm high, 30 cm of which was dug in). Two enclosures were characterized by dense Mediterranean maquis and phrygana (complex) while the other two were pruned to be more open and structurally simple, therefore mimicking the habitat structure of the populations from which the lizards originated (Figure 1). Within each enclosure we placed four piles of rocks (± 30 cm high) for basking and shelter. An attempt was made to remove terrestrial predators (such as snakes) although Megarian banded centipedes (*Scolopendra cingulate*) – known to predate on *P. erhardii* (Deimezis-Tsikoutas et al., 2020) – were occasionally found within the enclosures, and at one point a brown rat (*Rattus norvegicus*) intruded a complex enclosure, albeit it was quickly removed.

	Complex 1	Complex 2	Simple 1	Simple 2
Adults ‘18	7 ♀ 8 ♂	6 ♀ 8 ♂	7 ♀ 8 ♂	7 ♀ 7 (8) ♂
Survivors ’19	7 ♀ 6 ♂	6 ♀ 8 ♂	6 ♀ 5 ♂	4 ♀ 4 ♂
Adults ’19	8 ♀ 9 ♂	8 ♀ 8 ♂	8 ♀ 7 (8) ♂	8 ♀ 9 ♂
Survivors ‘19	6 ♀ 6 ♂	7 ♀ 7 ♂	5 ♀ 4 ♂	5 ♀ 5 ♂

Figure 1. Overview of the number of adult lizards released and recaptured in each enclosure per year. Complex enclosures (photo left) were characterized by dense Mediterranean phrygana and maquis vegetation, while simple enclosures (photo right) were more open with fewer bushes. We had two lizards (one in simple 2 in 2018, one in simple 1 in 2019) which were initially released in the enclosures but died while in captivity during a first recapture session ten days after initial release. These two individuals were removed from the dataset. Pictures belong to Reynaert, S. & Gonnissen, V.

Initially, reflective discs were suspended above each enclosure to deter avian predators, but these wore down fast due to weather conditions. For consistency's sake, we nevertheless suspended new disks above the enclosures after each recapture session.

Local volunteers checked the enclosures biweekly – except during two periods of interruption (± 1.5 months) in spring of each year due to logistic reasons - and placed leftover fruits and vegetables in the enclosures to attract flying insects. Originally, vegetation near the fences was trimmed twice per year (early spring and summer) as to avoid lizards getting in or out of the enclosure. Unfortunately, the Covid-19 pandemic hindered the planned workflow from spring 2020 onwards, resulting in fewer checks and postponing of early spring maintenance. The latter resulted in higher than usual vegetation near the fences by the summer of 2020, and concurrently a high number of unknown adults (21) was found within the enclosures. None of these could be genetically identified as the offspring of our released lizards, and therefore it is possible that these 'intruders' managed to get into the enclosures by climbing the vegetation near the fences.

Measuring fitness

Upon completion of the behavioural experiments, each lizard was weighed, measured (SVL), photographed and toe-clipped to allow individual recognition upon recapture. Toe-clipping is a commonly used procedure in reptiles for individual marking due to its reliability and negligible impact on the health, survival (in species not using toe pads for climbing) and stress-levels of the animal compared to other permanent marking methods (Langkilde & Shine, 2006; Perry et al., 2011). Nevertheless, to minimize stress inflicted upon our animals, we removed a maximum of two toes per individual and avoided to do so for those presenting natural toe loss. In addition, small tail clips (± 1 cm) from each lizard were collected for later parentage assignment (see below). Tissues were stored in 96 % alcohol at 4°C.

We released two batches of lizards in the enclosures over two consecutive years. A first batch was released in August 2018 and recaptured in July 2019. A second batch was released in July 2019 and recaptured in July 2020. We released 14 – 17 individuals per enclosure (see Figure 1 for sample sizes), and assorted lizards based on their sex, original habitat, problem-solving score and spatial cognition performance. We initially planned to recapture lizards at three points in time: eight days after initial introduction, early spring (~8 months) and summer (~11 – 12 months), but were unable to do the early spring recapture for the second year due to the Covid-19 pandemic.

Survival was quantified as whether lizards were still alive (1) or not (0) the next summer. Lizards were recaptured from the enclosure by hand, lasso or pitfall (baited with tomatoes) and immediately identified based on their unique toe-code (and verified using pictures in case of doubt). Captured lizards were then transported to the field lab in order to measure snout-vent length (SVL) and body mass, using a digital calliper (Mitutoyo, precision: 0.01 mm) and an electronic balance (Pesola PPS200, precision: 0.01 g). Juveniles in the enclosures (mostly found during summer) were also captured, weighed and measured and tail clips were collected for further parentage analyses (see below). During a recapture session, enclosures were checked daily to lower the probability of missing any survivors and/or offspring. Each recapture session lasted on average a week, by the end of which we usually had captured (or identified) all remaining lizard and observed no new individuals. We also had the opportunity to detect any missed individuals during future recapture/release sessions: two individuals from the 2018-

batch were recovered ten days later during the first recapture of the 2019-batch, and two individuals of the 2019-batch were found during the release and recapture of the juveniles respectively. Missing lizards were hence only classified as “dead” if they were neither captured nor observed in subsequent sessions. We were unable to capture two individuals because of their extreme shyness in 2018, but still managed to confirm their identity by reading their toeclip using binoculars. These individuals were left in the enclosures (complex 1) and were eventually recaptured in 2020.

Parentage assignment

The protocol for the parentage assignment largely followed Huyghe et al. (2010). First, DNA-extraction was conducted by placing ± 2 mm² of tail tissue in Chelex extraction buffer (0.2 mL 10 % Chelex + 20 µL 1 % SDS + 2 µL 20 mg/ mL proteinase K) and putting it inside a stirring incubator (Eppendorf, thermomixer comfort) for 60 minutes at 65°C followed by 15 minutes at 95°C (Small et al., 1998). Thereafter, we prepared three different primer mixtures for each DNA-sample, each containing an unique mix of fluorescently labelled primers for three different loci (so nine in total) which have been successfully used for genetic analyses in congeneric species (B3, B4 and B6 from Nembrini & Oppliger, 2003; Pmeli-02, Pmeli-04, Pmeli-07, Pmeli-13, Pmeli-14 and Pmeli-19 from Huyghe et al., 2009). We then mixed 1.25 µL of each primer mix with 6.25 µL Qiagen multiplex PCR master mix 2x and 3.5 µL water, to which 1.25 - 1.5 µL of DNA-extract was added. After centrifugation, mixtures were placed in a thermocycler (Biometra, T-professional thermocycler) for PCR amplification, with the following conditions: denaturation for 15 minutes at 95°C followed by 30 cycles of 30 s, at 72°C, annealing for 90 s at either 57°C or 60°C (depending on the primers) and finally extension for 60 s at 72 °C and 30 minutes at 60°C. Gel-electrophoresis was used to visually check PCR success. Successful PCR-products were diluted and sent to an external lab (Neuromics Support Facility) for microsatellite detection (AB 3130XL Genetic Analyser, Life Technologies, Carlsbad, CA, USA).

Loci were identified in the resulting microsatellite data using the Geneious Prime software (versions 2019.2.1. & 2021.0.3., http://www.geneious.com/) and parentage assignment was performed in Cervus version 3.0.7. (Kalinowski et al., 2007). Separate analyses were conducted per year and per enclosure, and the unknown adults in 2019 were included both as potential offspring of the 2018 and 2019 adults, and as potential parents of the juveniles. Proportion of mistyped loci was set to 5 % and relaxed and strict (trio) confidence intervals were equal to 80 and 95 % respectively.

Effect of cognition on juvenile fitness

In July 2020, 44 of the juveniles found within the enclosures ($N_{complex} = 21$, $N_{simple} = 23$) were transported to the animal facilities of the National and Kapodistrian University of Athens for further behavioural testing. Juveniles were collected soon after hatching, as indicated by the presence of umbilical scars. They were individually housed in plastic terraria (18 x 9 x 13 cm l x w x h) containing a coconut fibre substrate, a plastic refuge, a water bowl and had access to heat provided by a 60 W incandescent lamp for thermoregulation. Lizards were fed three times per week with either small mealworms or maggots (larvae of calliphorid flies).

All juveniles were subjected to the exploration test and spatial cognition task following the exact same procedures as described above. Upon completion of the experiments, juveniles were measured, weighed and individually marked by toe-clipping. Given the lower sample size, we decided to distribute the juveniles over only two enclosures: all juveniles originating from complex enclosures were released in complex enclosure 1; all juveniles originating from simple enclosures were released in simple enclosure 1 (safe for one juvenile that was accidentally released in the wrong – simple – enclosure). Albeit this means that we had a higher number of individuals per enclosure compared to the adult experiments, we argue that in natural populations lizard density also strongly increases after hatching. Juveniles were released in the enclosures in September 2020 and recaptured in June 2021.

Statistical analyses

The following behavioural variables were retained for analyses: neophobia scores, exploration PC1 scores, aggression scores (males only), lid-removal (LR) scores (never – occasional – consistent), spatial learning errors, reversal learning errors and learning flexibility (never – once – both). In previous studies, we reported a strong side bias in *P. erhardii* (Chapter 3 – 6) with lizards learning the spatial cognition task more readily if the safe refuge was located on the left side of the arena (relative to the observer). Hence, to make individual performances more comparable, we standardized the number of spatial and reversal errors per rewarded side (cfr. Guillette et al., 2009) and per year to account for annual differences in average cognitive performance (De Meester et al., 2022). For juveniles, we obtained spatial learning (SL) and reversal learning (RL) scores in a similar way. As only a single juvenile failed at both phases of the spatial cognition task, we classified juveniles as either flexible learners (during both phases) or not (once or never). As exploration was non-repeatable on the short-term within juveniles (Chapter 6), we did not further analyse these data.

In order to score individual fitness, we used the following parameters: whether an individual survived until the next summer (Y/N), its growth rate, its change in body condition and its reproductive success (number of offspring). Growth rate was calculated as ($SVL_{post\text{-}enclosure}$ - $SVL_{pre\text{-}release}$)/(days in between measures) (Rozen-Rechels et al., 2020) and body condition change by taking the residuals from a log(SVL) – log(body mass) regressions pre- and post-release and subtracting them from each other (Rodríguez-Prieto et al., 2010). As explained earlier, four lizards were confirmed to be alive during the final recapture session of their batch, but were only caught during a later session. Hence, their growth rate and body condition change was not used for further analyses due to not being comparable with those of the other lizards within their batch. Individuals with a negative growth rate (N = 5) were also removed from the growth rate analyses as these likely represent measurement errors. The effect of behaviour on reproductive success was tested only in the subset of surviving lizards in order to not confound the survival- and reproductive consequences of cognition and personality.

Our main research question was whether the effect of cognition and personality on fitness would differ between simple and complex habitats. Nevertheless, other factors may affect the behaviour – fitness link as well. The fitness consequences of a certain behavioural phenotype may for instance differ between males and females (Maille & Schradin, 2016) or fluctuate across years (Cauchard et al., 2017). To account for so many different possible interactions, we adopted a model selection approach (Symonds & Moussalli, 2011). We started by fitting global models, to each fitness measure, with one behavioural variable, year, enclosure type and sex as independent variables. As the relationship between behaviour and fitness may not necessary be linear (e.g. disruptive selection as in Bergeron et al., 2013), we also fitted each behavioural variable (except LR and FLEX scores) as quadratic terms. Finally, we added two-way interaction effects between behaviour (linear or quadratic) and the other variables, although not all full models could be fitted due to overfitting and convergence issues (see Supplementary Tables S7.1-S7.5). Snout-vent length (z-transformed) was also included as covariate, and enclosure ID and original population were entered as random factors. For one particular model (aggression – reproductive success) we had to drop the random factor "population" from the global model as it lead to otherwise unsolvable convergence issues. Linear mixed-effect models (LMMs) were used for growth rate and body condition change ('lmer' function'), generalized mixed-effect models (GLMMs) with binomial distribution for survival ('glmer' function) and GLMMs with a zero-inflated negative binomial distribution ('glmmTMB' function; Brooks et al., 2017) for reproductive success. A set of candidate models was then generated using the 'dredge' function ('MuMIn' package, Barton, 2013) and model fit and explanatory power was evaluated based on the Akaike information criterion corrected for small sample sizes (AICc). Models within ≤ 2 AICc units from the top-model are not considered different from each other (Symonds & Moussalli, 2011; Gomes et al., 2020) and were thus selected for model-averaging and final model construction. For each model, we determined the relative importance values of each predictor by calculating the summed Akaike weights over all candidate models within ≤ 2 AICc units (Symonds & Moussalli, 2011). We then constructed a final model using only those predictors with a relative importance of ≥ 0.50 (Simpson & McGraw, 2018; Simpson & McGraw, 2019; Gardner et al., 2020; Gomes et al., 2020). The final mixed model was used to test the effect of the selected variables on fitness. We ran separate model-averaging procedures for each combination of a fitness and behavioural variable, as combining multiple behavioural variables and all their potential interactions in a single model lead to overfitting. A similar series of models was ran for the juvenile fitness data, with each model containing one behavioural variable (linear and quadratic), enclosure and their interaction as fixed effects, SVL as a covariate and original enclosure as random effect. In total, we conducted model-averaging for 34 models (presented in Supplementary Tables S7.1 – 7.5).

Lastly, we aimed to better understand the difference between the three categories of lizards during the lid-removal task. In particular, we wanted to know whether solvers and non-solvers differed in their motivation to participate and how this changes over consecutive trials, and whether consistent solvers became more efficient in opening the dish. These analyses were only performed on the 2019-lizards. First, we tested how the attack latency changed over consecutive trials within each group, using a LMM with attack latency as response variable and trial, LR score (never, occasional or consistent) and their interaction as predictors. Population and lizard ID, with a random intercept and slope for trial number within lizard ID, were included as random factors. Secondly, we tested whether consistent solvers would improve over time. Due to the right-censored nature of the solving time data, we used a mixed-effects Cox proportional hazard model (Therneau, 2015; Therneau & Lumley, 2020) which included trial as predictor and population and lizard ID (with a random intercept and slope for trial) as random effects.

Statistical analyses were performed in R version 3.5.1. (Ihaka, R. & Gentleman, R., University of Auckland, Auckland, New Zealand). Data were transformed where necessary to meet model assumptions and the “bobyqa” optimizer was used if needed to solve convergence issues (Bates et al., 2015). Significance of fixed effects was based on F-tests (with Kenward-Roger Degrees of Freedom Approximation) for LMMs and Wald Chi-square tests for GLMMs. Post-hoc pairwise comparisons were performed using Tukey’s method ('emmeans' and 'emtrends' functions, Lenth et al., 2019). Non-significant interactions were removed from the model.

Ethical note

Experiments and procedures were approved by the Ethical Committee of the University of Antwerp (file ID: 2017-67). Field permits were issued by the Greek Ministry of Environment and Energy (permit IDs: Ω6314653Π9-ΤΒΞ, 7ΖΠΡ4653Π8-Ε76, ΨΗ424653Π8-ΩΥ2 and 69Ι44653Π8-ΔΣ1). All experiments were conducted in accordance with national legislation and the ASASB/ABS guidelines for the use of animals in behavioural research and teaching. Upon completion of the experiments, we released all surviving lizards at the initial site of capture.

RESULTS

Survival

In total, 91 of the 123 (74 %) adult lizards survived until the next year. Two lizards (one in both years) died while in captivity during the first recapture session, and were thus removed from the dataset.

All final models showed that adult survival was higher in the complex (85 %: 27/29 lizards in 2018, 26/33 lizards in 2019) than the simple enclosures (62 %: 19/29 lizards in 2018, 19/32 lizards in 2019) (Table 2). In contrast, there was moderate model uncertainty regarding the influence of other predictors (4 – 17 top models, averaged estimates presented in Table S7.1). Sex, year and SVL did either not make it to the final models or turned out to be non-significant, and therefore had no effect on survival (Table 2). Only a few behavioural variables were related to survivorship. The effect of exploration (PC1) varied between years (exp * year: $\chi^2 = 5.674$, df = 1, p = 0.017). More explorative individuals were less likely to survive in 2018 (estimate + SE = -0.959 ± 0.377, z = -2.547, p = 0.011) but not in 2019 (0.103 ± 0.243, z = 0.425, p = 0.671) (Figure 2a). The effect of aggression depended on the complexity of the enclosure's habitat (aggression * habitat: $\chi^2 = 4.407$, df = 1, p = 0.036), with more aggressive males having lower survival rates in complex (-2.269 ± 0.976, z = -2.325, p = 0.020) but not in simple enclosures (-0.026 ± 0.433, z = -0.059, p = 0.953) (Figure 2b). Problem-solving ability, as measured in a lid-removal task, predicted survival ($\chi^2 = 7.008$, df = 1, p = 0.030) independently of year and habitat (not included in final model). Surprisingly, lizards with low problem-solving skills ('non-solvers', 86.6 %) survived better than lizards with high (consistent solvers, 77.5 %) and intermediate problem-solving skills (occasional solvers, 50.4 %), although only the difference between occasional and non-solvers was significant (z = 2.646, p = 0.022) (Figure 3a).

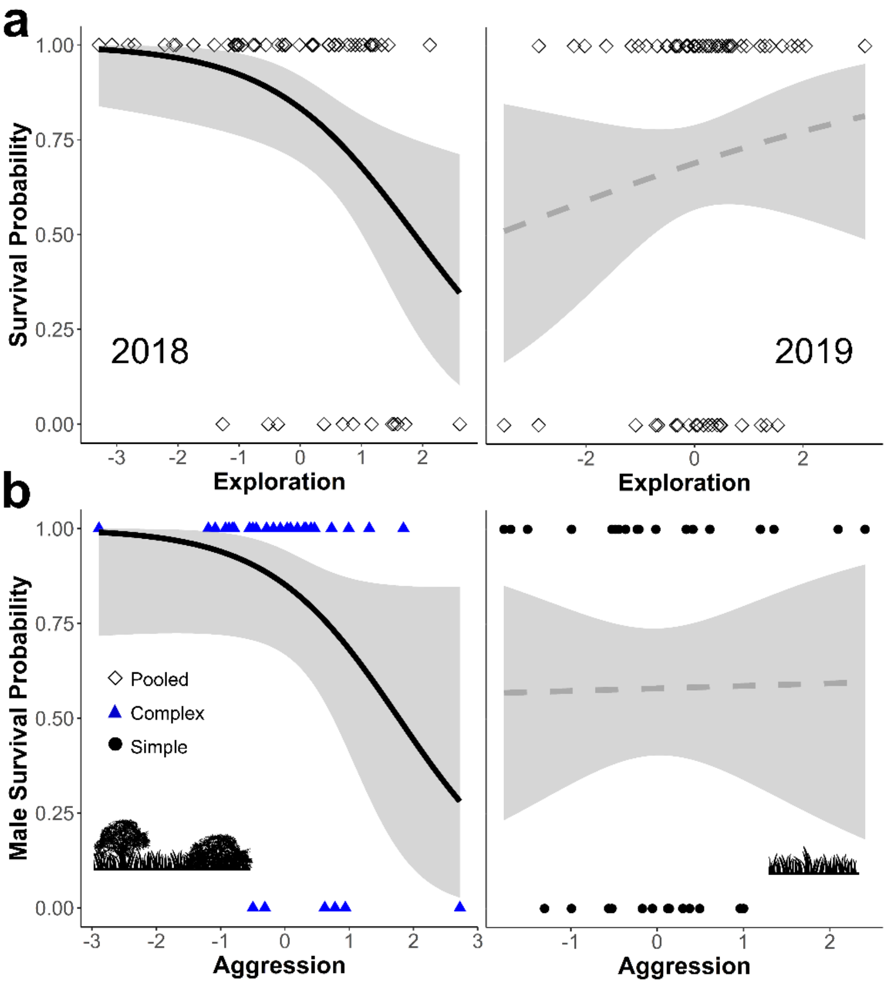

Figure 2. Effect of personality on adult survival: A) more explorative lizards were less likely to survive until the next summer from 2018 until 2019 (left, N = 58) but not from 2019 until 2020 (right, N = 65). B) More aggressive males had lower survival chances in complex (left, blue triangles, N = 33) but not simple enclosures (right, black dots, N = 31). Black solid lines indicate significant associations ($p < 0.05$), black dashed lines represent trends ($p < 0.10$) while grey lines are not statistically significant ($p > 0.10$). Grey areas represent standard errors. See main text for more explanation about the behavioural parameters.

The effect of spatial learning performance on survival slightly differed between sexes (SL * sex: $\chi^2 = 3.204$, df = 1, $p = 0.073$).Against our initial expectations, females with worse spatial learning (more errors) had a higher chance of survival (1.200 ± 0.533, $z = 2.249$, $p = 0.025$) while male survival was not associated with SL scores at all (0.128 ± 0.290, $z = 0.442$, $p = 0.658$) (Figure 3b). The effect of spatial learning on survival was independent of habitat or year (neither interaction included in final model, Table 2). In contrast, neither reversal learning nor overall learning flexibility affected survival (Table 2).

Survival was lower in juveniles (61 %, 27 out of 44) than in adults, and independent of habitat type (complex: 14/20; simple: 13/24, $p = 0.276$). Spatial learning did not predict juvenile survival ($\chi^2 = 2.686$, df = 1, $p = 0.101$). Neither RL score, nor SVL had sufficient high importance to be included in the final models, and thus did not explain variation in juvenile survival (Table 3, Table S7.5). The separate GLMM for learning flexibility did not find an effect of learning flexibility, habitat type or SVL on juvenile survival either ($0.276 \leq p \leq 0.989$).

Growth and body condition

Model certainty was relatively high for growth rate (2 – 5 top models, averaged estimates presented in Table S2). Most models for adult growth rate indicated that larger lizards grew slower, and half of the models suggested that males had a faster growth rate than females (females: $8.700 \pm 0.887 * 10^{-3}$ mm/day, males: $10.500 \pm 1.161 * 10^{-3}$ mm/day) (Table 2). Growth rate did not differ between years or enclosures (Table 2). None of the behavioural variables turned out to be sufficiently important (RI < 0.50) to be included in the full models, and thus none of them explained variation in growth rate (Table 2).

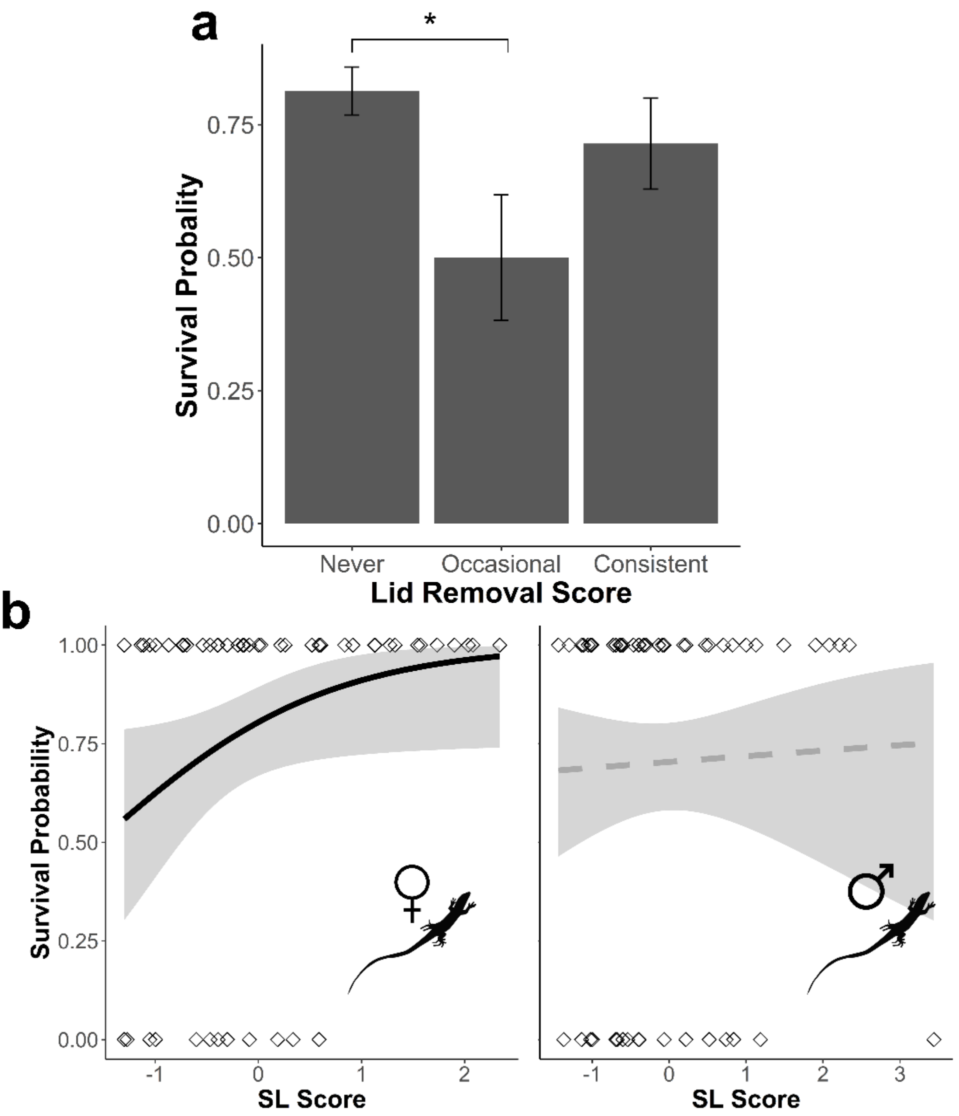

Figure 3. Effect of cognitive performance on the fitness of adult lizards. a) survival probability for non-solvers (N = 75), occasional solvers (N = 18) and consistent solvers (N = 28), as measured in a lid-removal task. b) Better spatial learners (lower number of errors and thus SL scores) have a lower chance of survival than conspecifics with higher spatial learning scores in females (N = 59, left) but not in males (N = 64, right). See main text for more explanation about the cognitive variables. In A, statistical significant differences between groups, as reported by a post-hoc pairwise comparison using Tukey's method, are indicated as follows: '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$. In B, black solid lines indicate statistical significance at $p < 0.05$, black dashed lines indicate trends at $p < 0.10$ and grey lines are not statistically significant ($p > 0.10$). Grey areas represent standard errors.

Table 2. Effect of cognition and personality on adult fitness, as the outcome of the final models obtained by model averaging. Only the predictors with a relative importance value (RI) ≥ 0.50 were included in the final models. For enclosure, the intercept is set at ‘complex’, for year at ‘2018’. Sample sizes may vary among models due to missing data. Statistical significance is indicated as follows: ‘°’ $p < 0.10$, ‘*’, $p < 0.05$, ‘**’, $p < 0.01$, ‘***’ $p < 0.001$. See main text for a full explanation about the procedure to build the full models. Response variables were transformed where necessary to meet model assumptions.

Behaviour	N	Predictors	RI	Wald/F-stats	P
		SURVIVAL			
Neophobia	122	**Enclosure**	1.00	$\chi^2_1 = 7.607$	0.006 **
Exploration PC1	123	**Exploration**	1.00	$\chi^2_1 = 6.460$	0.011 *
		Enclosure	1.00	$\chi^2_1 = 7.969$	0.005 **
		Year	1.00	$\chi^2_1 = 2.716$	0.099 °
		Exp * Year	1.00	$\chi^2_1 = 5.674$	0.017 *
Aggression	64	**Aggression**	0.73	$\chi^2_1 = 5.407$	0.020 *
		Aggression^2	0.50	$\chi^2_1 = 1.214$	0.271
		Enclosure	1.00	$\chi^2_1 = 6.628$	0.010 *
		Aggression *Enclosure	0.63	$\chi^2_1 = 4.407$	0.036 *
LR score	121	**LR Score**	1.00	$\chi^2_1 = 7.008$	0.030 *
		Enclosure	1.00	$\chi^2_1 = 7.432$	0.006 **
		Year	0.56	$\chi^2_1 = 2.189$	0.139
SL score	123	SL Score	1.00	$\chi^2_1 = 5.057$	0.025 *
		Enclosure	1.00	$\chi^2_1 = 10.112$	0.001 **
		Year	0.53	$\chi^2_1 = 1.432$	0.232
		Sex	0.67	$\chi^2_1 = 2.307$	0.129
		SL * Sex	0.54	$\chi^2_1 = 3.204$	0.073 °
RL score	123	RL Score	0.53	$\chi^2_1 = 2.087$	0.149
		Enclosure	1.00	$\chi^2_1 = 8.322$	0.004 **
		Year	0.50	$\chi^2_1 = 2.037$	0.154
Learning Flexibility	123	**Enclosure**	1.00	$\chi^2_1 = 7.929$	0.005 **
		Year	0.62	$\chi^2_1 = 1.897$	0.168
		GROWTH RATE			
Neophobia	80	Sex	0.65	$F_{1,75} = 2.657$	0.107
		SVL	1.00	$F_{1,45} = 27.061$	< 0.001 ***
Exploration PC1	81	Sex	0.66	$F_{1,76} = 2.700$	0.105
		SVL	1.00	$F_{1,45} = 27.291$	< 0.001 ***
Aggression	39	**SVL**	1.00	$F_{1,31} = 17.011$	< 0.001 ***
LR score	80	Sex	0.63	$F_{1,74} = 2.478$	0.120
		SVL	1.00	$F_{1,53} = 27.346$	< 0.001 ***
SL score	81	**Sex**	1.00	$F_{1,75} = 5.893$	0.018 *
		SVL	1.00	$F_{1,69} = 40.232$	< 0.001 ***
RL score	81	**Sex**	1.00	$F_{1,75} = 5.893$	0.018 *
		SVL	1.00	$F_{1,69} = 40.232$	< 0.001 ***
Learning Flexibility	81	**Sex**	1.00	$F_{1,75} = 5.893$	0.018 *
		SVL	1.00	$F_{1,69} = 40.232$	< 0.001 ***

Table 2. (Continued)

		BODY CONDITION CHANGE			
Neophobia	86	Enclosure	0.66	$F_{1,2} = 1.548$	0.338
		Sex	1.00	$F_{1,82} = 13.641$	< 0.001 ***
Exploration PC1	87	Exploration²	0.81	$F_{1,74} = 2.613$	0.110
		Enclosure	0.76	$F_{1,2} = 2.009$	0.293
		Sex	1.00	$F_{1,81} = 12.590$	< 0.001 ***
Aggression	42	Enclosure	0.55	$F_{1,2} = 2.668$	0.243
LR score	86	**Sex**	1.00	$F_{1,81} = 11.878$	< 0.001 ***
SL score	87	**Sex**	1.00	$F_{1,82} = 12.644$	< 0.001 ***
RL score	87	RL Score²	0.72	$F_{1,82} = 2.141$	0.147
		Enclosure	0.65	$F_{1,2} = 1.887$	0.302
		Sex	1.00	$F_{1,81} = 11.481$	0.001 **
Learning flexibility	87	Enclosure	0.50	$F_{1,2} = 1.638$	0.328
		Sex	1.00	$F_{1,82} = 13.241$	< 0.001 ***
		NUMBER OF OFFSPRING			
Neophobia	90	**Year**	1.00	$\chi^2_1 = 6.903$	0.009 **
		SVL	0.88	$\chi^2_1 = 3.774$	0.052 °
Exploration PC1	91	**Year**	1.00	$\chi^2_1 = 7.412$	0.006 **
		SVL	0.82	$\chi^2_1 = 3.810$	0.051 °
Aggression	45	Enclosure	0.54	$\chi^2_1 = 3.005$	0.083 °
		SVL	0.90	$\chi^2_1 = 4.507$	0.034 *
LR score	90	**Year**	1.00	$\chi^2_1 = 7.719$	0.005 **
		SVL	0.81	$\chi^2_1 = 3.777$	0.052 °
SL score	91	**Year**	1.00	$\chi^2_1 = 7.412$	0.006 **
		SVL	0.77	$\chi^2_1 = 3.810$	0.051 °
RL score	91	**Year**	1.00	$\chi^2_1 = 7.412$	0.006 **
		SVL	0.84	$\chi^2_1 = 3.810$	0.051 °
Learning Flexibility	91	**Year**	1.00	$\chi^2_1 = 7.412$	0.006 **
		SVL	0.77	$\chi^2_1 = 3.810$	0.051 °

Very similar results were obtained for body condition change (2-8 top models, averaged estimates in Table S3). Overall, males had improved their body conditions after one year in the enclosures, while females ended up with poorer body conditions (females: -0.045 ± 0.023, males: 0.073 ± 0.022; Table 2). Body condition changes were unaffected by enclosure, SVL, year or any of the behavioural variables (Table 2).

Table 3. Effect of cognition on juvenile fitness. For SL and RL, these are the outcomes of the final models obtained by model averaging. Only the predictors with a relative importance value (RI) ≥ 0.50 were included in the final models to test the effect of cognition on individual fitness. "/" indicates that no variables had a sufficient high relative importance and hence no final model was built. For learning flexibility, we only fitted one model from which the interaction was removed in case of non-significance. Sample sizes may vary among models due to missing (fitness or behavioural) data. Statistical significance is indicated as follows: '°' $p < 0.10$, '*', $p < 0.05$, '**', $p < 0.01$, '***' $p < 0.001$. See main text for a full explanation about the procedure to build the full models. Response variables were transformed where necessary to meet model assumptions.

Behaviour	N	Predictors	RI	Wald/F-stats	P
SURVIVAL					
SL score	44	SL Score	0.75	$\chi^2_1 = 2.686$	0.101
RL score	44	/	/	/	/
Learning Flexibility	44	Flex Score	/	$\chi^2_1 = 0.031$	0.860
		Enclosure	/	$\chi^2_1 = 1.188$	0.276
		SVL	/	$\chi^2_1 = 0.051$	0.821
		Flex Score * Enclosure	/	$\chi^2_1 = 0.000$	0.989
GROWTH RATE					
SL score	26	Enclosure	1.00	$F_{1,1} = 5.960$	0.318
RL score	26	Enclosure	1.00	$F_{1,1} = 5.960$	0.318
Learning Flexibility	26	Flex Score	/	$F_{1,22} = 0.037$	0.850
		Enclosure	/	$F_{1,1} = 4.853$	0.354
		SVL	/	$F_{1,21} = 1.404$	0.250
		Flex Score * Enclosure	/	$F_{1,21} = 0.175$	0.680
BODY CONDITION CHANGE					
SL score	26	SL Score²	0.50	$F_{1,23} = 2.561$	0.123
RL score	26	/	/	/	/
Learning Flexibility	26	Flex Score	/	$F_{1,22} = 1.331$	0.261
		Enclosure	/	$F_{1,1} = 0.004$	0.962
		SVL	/	$F_{1,21} = 0.068$	0.798
		Flex Score * Enclosure	/	$F_{1,21} = 0.087$	0.771

For juvenile growth rate, neither SL or RL scores or SVL were included in the final models (Table 3, Table S5). The separate model with learning flexibility as predictor did not find an effect of learning flexibility, SVL or enclosure on juvenile growth either (all $0.250 \leq p \leq 0.850$). Similar results were obtained for juvenile changes in body condition (Table 3, Table S5).

Reproductive success

We captured a total of 156 juveniles in the experimental enclosures, 133 of which could be assigned parents ($N_{year1 – complex} = 46$, $N_{year1 – simple} = 41$, $N_{year2 – complex} = 33$, $N_{year2 – simple} = 36$). Note, however, that eleven of these juveniles were the offspring of a known parent (2019-batch) and an "intruder".

Reproductive success varied greatly among individuals. Around 39 % of the released lizards produced no offspring (21/59 females and 27/64 males). Among those that did leave offspring, females birthed on average 3.34 ± 0.36 (range: 1-12) and males fathered on average 3.62 ± 0.46 (range: 1 -15) juveniles. Females had offspring with on average 1.55 ± 0.12 (1 – 4) different males, while males fathered offspring with on average 1.70 ± 0.14 (1-4) different females. Very few deceased lizards left offspring (6/32 non-survivors versus 69/91 survivors), and those who did produced fewer offspring (2.00 ± 0.68) than lizards surviving until the next year (3.61 ± 0.30). There was a strong positive correlation between the number of offspring and number of confirmed partners, both for males (Spearman Rank correlation test: $\rho = 0.701$, $p < 0.001$) and females ($\rho = 0.437$, $p = 0.006$).

There was moderate model uncertainty in explaining this variation in reproductive success (3-7 top models, see Table S4). Most final models agreed that the lizards had a higher reproductive output in year 1 (average of 2.66 ± 0.41 juveniles/lizard) than year 2 (1.65 ± 0.24 juveniles/lizard) and suggested that larger lizards produced more offspring (Table 2). The aggression model revealed that for males, there was a significant positive effect of SVL (0.316 ± 0.149, $\chi^2 = 4.507$, df = 1, p = 0.034) and a slightly higher number of offspring in the simple enclosures (0.488 ± 0.282, $\chi^2 = 3.005$, df = 1, p = 0.083).

Neither sex nor any behavioural variable affected how many offspring an individual produced (Table 2).

Additional problem-solving analyses

Over the course of the lid-removal task, lizards changed their behaviour in multiple ways. First of all, the latency to attack the experimental apparatus changed over consecutive trials, albeit in opposite directions for solvers and non-solvers (trial * LR Score: $F_{2,67} = 11.959$, $p < 0.001$). Specifically, attack latencies increased over time in non-solvers (est = 0.087 ± 0.018, t = 4.936, $p < 0.001$, N = 37) but less so in occasional solvers (est = 0.070 ± 0.035, t = 1.87, p = 0.051, N = 9) while consistent solvers became progressively faster in attacking the petri dish over consecutive trials (est = - 0.056 ± 0.024, t = -2.356, p = 0.022, N = 20) (Figure 4a). Consistent solvers also decreased their solving times over consecutive trials, thus becoming more efficient over time ($\chi^2 = 6.510$, df = 1, p = 0.011, Figure 4b).

DISCUSSION

Very little is known about whether, how and when selection acts on cognition in wild animals, yet such information is critical for our understanding of how cognition evolves. In this study, we showed that cognition (and personality) was related to several aspects of fitness within Aegean wall lizards living in semi-natural enclosures for 9-12 months, albeit less so than expected and rarely in the predicted directions. In contrast to our main hypothesis, the relationship between cognitive capacity and fitness was unaffected by habitat complexity.

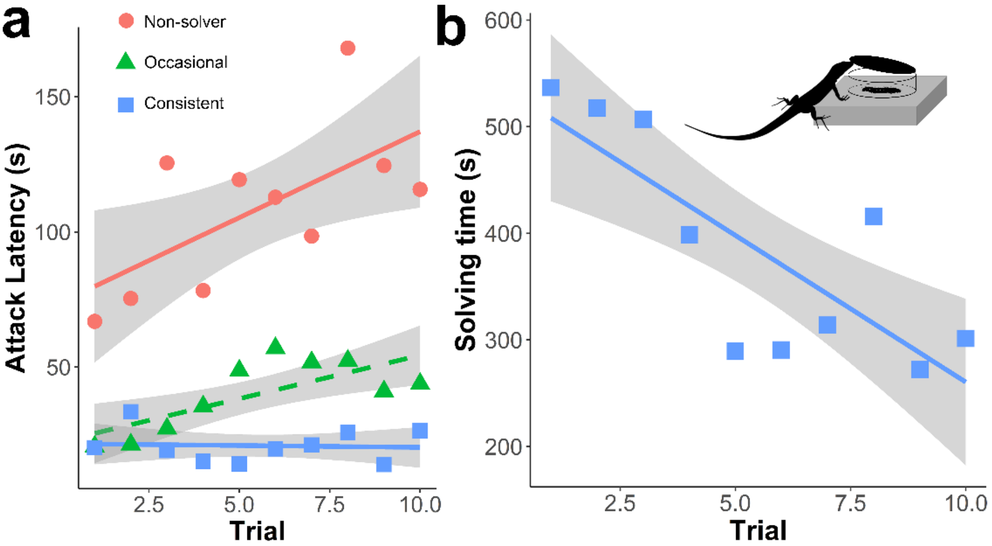

Figure 4. Behaviour of adult lizards (2019) over consecutive trials of the lid-removal task. A) changes in attack latency (i.e. latency to touch the experimental apparatus with the snout) over time in non-solvers (red dots, N = 37), occasional solvers (green triangles, N = 9) and consistent solvers (blue squares, N = 20). See main text for more information regarding these problem-solving scores. B) consistent solvers improve their solving times (time between contacting the apparatus and grabbing the prey) over consecutive trials. solid lines indicate statistical significance at $p < 0.05$, dashed lines indicate trends at $p < 0.10$ and grey areas represent standard errors.

Cognition and survival

Our study revealed interesting patterns regarding the link between cognition and survival, which do not always seem to be in line with the preceding literature. In the next paragraphs, we will discuss our results one by one and offer possible explanations.

A first rather surprising result was the non-linear effect of problem-solving on survival, selection seems to favour individuals with either very strong or very weak problem-solving skills, independent of habitat complexity. Our results contradict previous studies where problem-solving/innovation either increased survival (Indo-Pacific bottlenose dolphins, Wild et al., 2019) or had no effect at all (great tits, Cole et al., 2012; grey mouse lemurs, Huebner et al., 2018). However, earlier studies typically quantified problem-solving in a binary way: individuals are either successful or not (e.g. Cole et al., 2012; Johnson-Ulrich et al., 2019; Wild et al., 2019), so disruptive selection may have simply gone unnoticed. This clearly illustrates the necessity of testing and scoring consistency in problem-solving performance, as has been often pleaded for (Rowe & Healy, 2014; Thornton et al., 2014; Morand-Ferron et al., 2016; Shaw, 2017).

This disruptive selection could be explained if both extreme cognitive phenotypes experience different benefits. Consistent solvers solve the task repeatedly and improve (‘learn’) over consecutive trials. The ability to discover and learn new motor actions may increase their foraging efficiency (Cauchard et al., 2017; Wetzel & Koenig, 2017), e.g. by being able to extract food from otherwise inaccessible locations (e.g. rock crevices, inside rotting wood, hollow trees, burrows ... Mendyk & Horn, 2011; Cooper et al., 2019) or by figuring out how to handle dangerous or difficult prey (Castilla et al., 2008; Herr et al., 2016; Whitford et al., 2022). Eastern fence lizards (*Sceloporus undulatus*), for instance, increase their consumption of venomous ants with repeated exposures, potentially because they become more adept in catching such prey without being bitten (Herr et al., 2016). In our experiments, we also observed that non-solvers became less eager to participate in the task over time, which might imply a form of learning as well. If a certain action is no longer rewarding, individuals should refrain from it (i.e. inhibitory control, Kabadayi et al., 2018). During foraging and prey handling, lizards are more vulnerable to predation or competition (Verwaijen et al., 2002; Hawlena & Perez-Mellado, 2009), so selection may favour those who quickly learn to avoid ‘high risk – low reward’ foraging opportunities. In contrast, occasional solvers did not learn the lid-removal (13/20 lizards only solved the task once, 6/20 only twice), and exhibited slower inhibitory control. Their low survival rate may thus be a consequence of general lower learning abilities and/or an tendency to persist in risky actions yielding few gains. To evaluate how likely these conjectures are, we need to learn more on the exact pathways by which problem-solving ability, e.g. through its effects on foraging decisions, translates into fitness.

A second surprising results was found for spatial learning ability. In theory, strong spatial learning should increase survival rates, because it allows individuals to quickly memorize the location of rewarding or dangerous places within their habitat. Recent studies have indeed confirmed this idea in velvet geckoes (Dayananda & Webb, 2017) and mountain chickadees (Sonnenberg et al., 2019), although no effect was found in grey house lemurs (Huebner et al., 2018). Our results show a remarkable sex-dependent effect: spatial learning ability has no effect on male survival, and decreased survival probability in female lizards. Both observations are puzzling. The finding of sex-dependent selection on cognition is rare (but see e.g. Kotrschal et al., 2015a), although Maille and Schradin (2016) have reported that better spatial memory increased survival of male African striped mice and decreases it in females of the same species, which they related to the higher territoriality of males and a trade-off with reaction times (to predators) in females.

The lack of a positive relationship between spatial learning and survival is unexpected because lacertid lizards typically exhibit an obvious awareness of their physical surroundings, e.g. fleeing consistently and directly to the same refuges, even if these are not visible from their starting point (Martin et al., 2003; Font, 2019; personal observations). Good spatial memory would also aid *P. erhardii* to retrieve locations with food resources, such as plants or ant nests, on which they rely during dry periods in summer (Adamopoulou et al., 1999). Moreover, spatial awareness was expected to benefit male *P. erhardii* in particular, as they lay-out and defend individual territories at least during the mating season (Gruber & Schultze-Westrum, 1971). Perhaps males with low spatial learning abilities compensate for their limitation by adopting alternative foraging, anti-predator and mate acquisition strategies.

The negative relationship between spatial learning ability and survival rate in females suggests that overinvesting in brain tissue dedicated to spatial awareness was penalized in our set up. Cognition is energetically expensive, and larger brains are often associated with reduced growth and lower fecundity (Kotrschal et al., 2013; Kotrschal et al., 2015c; Ebneter et al., 2016). Female lizards seemed to have higher difficulties coping with the circumstances in our enclosures than males; perhaps because they allocated more energy into reproduction, they grew slower and tended to exhibit a reduction in body condition. Investing in non-essential, expensive spatial cognition may be a wrong choice in such conditions. Strangely enough, we found no sex-differences in spatial learning within wild-caught *P. erhardii* (De Meester et al., 2022 ~ Chapter 5) which implies that spatial learning has at least some benefits for females in nature to counter the survival-cost. Yet, our results did not show any effect of spatial learning on female growth, body condition or reproduction.

Alternatively, the results observed here may be an artefact of our experimental design. Although they were designed to mimic natural conditions as close as possible, our enclosures may differ from the real world in several aspects. First, reduced predation risk and high food availability may have made them a somewhat less challenging environment, while cognition is predicted to be mostly useful under demanding conditions (Sol, 2009). Albeit the size of the enclosures exceeded the average home range size of *P. erhardii* on Naxos (BeVier et al., 2021), a restriction in space use may still have reduced the need for spatial processing and memory in our animals (du Toit et al., 2012; LaDage et al., 2013; Vardi et al., 2020). Altogether, a lack of ecological challenges in the enclosures may have eliminated the benefits of spatial learning, and particularly for females the energetic costs may then have outweighed the reduced benefits. Likewise, large-brained female guppies outlived their small-brained counterparts when a predator was present, but died faster under safe conditions (Kotrschal et al., 2015a; Kotrschal et al., 2019). Future field studies could reveal whether the observed sex-dependent selection is due to our experimental design, or occurs in natural populations as well.

A third noteworthy results was that neither reversal learning, nor learning flexibility, predicted survival in either habitat type or sex. This is surprising, as both measures reflect an individual's cognitive/behavioural flexibility (Audet & Lefebvre, 2017; Buechel et al., 2018), a trait that would have been particularly valuable upon introduction in a new environment (Sol, 2009; Wright et al., 2010; Griffin et al., 2017; Szabo et al., 2020a). It is, however, possible that cognitive flexibility was mostly beneficial directly after lizards were introduced in their new environment, when there was a strong need to replace old irrelevant with new information (Wright et al., 2010; Griffin et al., 2017). Over time, when lizards were familiarized with their new habitat and faced no novel challenges, such flexibility may have become less useful and even too costly (Madden et al., 2018). Periods of positive and negative selection following each other may have led to no net impact of cognitive flexibility on survival when taken over the entire time period, but this should be tested by measuring survival multiple times over shorter time intervals. Additionally, we previously described habitat-dependent plastic changes in reversal, but not spatial, learning performance in lizards kept in these exact enclosures for one year (Chapter 6). Such plasticity may have countered selection on reversal learning ability (Croston et al., 2015). Lastly, it should be noted that reversal learning specifically measures the ability of individuals to reverse previously learnt contingencies. This may indeed be important in order to deal with (seasonal) changes in a familiar environment (Tebbich & Teschke, 2014), but perhaps less so for invading new environments where these previous contingencies are not present and thus do not need to be reversed. Rather, lizards introduced in the enclosures need to learn again from scratch, or will have to learn to associate a completely new set of cues with familiar outcomes (Greggor et al., 2019). The latter ability is often measured using a ‘set shifting’ task (Szabo et al., 2018; Greggor et al., 2019), which could be a valuable addition to our cognitive test battery for future work.

Neither spatial nor reversal learning predicted juvenile survival, despite the assumption that learning would be especially helpful during earlier stages of life in species without paternal care (Szabo et al., 2019a). This may again be a consequence of a lack of environmental challenges, albeit juveniles experienced higher mortality than adults. Unfortunately, we could not sex the juveniles prior to their release in the enclosures, so it is possible that similar sex-dependent selection on cognition may have occurred which we are unable to detect.

Cognition and reproductive success

None of the cognitive abilities were directly associated with lizards' reproductive success, despite previous research generally reporting higher mating success and/or reproductive output in more cognitively able individuals (Keagy et al., 2009; Shohet & Watt, 2009; Cauchard et al., 2013; Cauchard et al., 2017; Minter et al., 2017; Preiszner et al., 2017; Wetzel & Koenig, 2017; Ashton et al., 2018; Branch et al., 2019; Chen et al., 2019; Shaw et al., 2019), although not always (Cole et al., 2012; Isden et al., 2013; Johnson-Ulrich et al., 2019; Wild et al., 2019). Many of these studies were conducted on birds or fish, where higher cognitive abilities probably facilitated better parental care (e.g. Cauchard et al., 2013; Cauchard et al., 2017; Minter et al., 2017; Wetzel & Koenig, 2017; Shaw et al., 2019). The lack of parental care in *P. erhardii* may be a first reason why cognitive performance was unrelated to reproductive success. Secondly, it is often proposed that females should choose cognitively superior males due to their "good genes" and to have "smarter" offspring (Keagy et al., 2009; Isden et al., 2013). However, given the limited fitness-advantages of cognition in our species, selecting "smarter" mates may not really be a rewarding strategy. In addition, the importance of female choice during lizard mating is quite disputed (Huyghe et al., 2012). Thirdly, males are generally believed to profit principally from spatial cognition in order to locate potential mates (Kotrschal et al., 2015b; Smith et al., 2015) or to acquire and defend territories necessary for breeding (Araya-Salas et al., 2018). Once again, such benefits of spatial cognition may have been reduced due to restricted space use in our enclosures. Fourthly, the effect of cognition on reproductive success may depend on an individual's mating strategy. In rose bitterlings, better spatial learning increased the fertilization success of sneaker but not territorial males (Smith et al., 2015). Different colour morphs of *P.*

erhardii co-exist on Naxos (Brock et al., 2020), which in other lizard species is often associated with differential behavioural strategies (Sinervo & Lively, 1996; Galeotti et al., 2013) varying in their reliance on spatial cognition (LaDage et al., 2013; LaDage et al., 2016). Unfortunately, the sample size of alternative (yellow and orange) morphs was too low in our current dataset to test this possibility. Lastly, cognitive performance of parents could affect the quality rather than quantity of offspring (Branch et al., 2019), but this should be measured under more standardized conditions preferably directly after hatching.

Cognition, growth rate and body condition

No behavioural variables affected growth rate and body condition, in neither sex, and neither in adults nor juveniles. We should firstly realize that we only obtained such measures for the survivors, and that the deceased occasional solvers or bad spatial learners may have been the slowest growers or those with the worst body conditions. Secondly, measuring changes in body condition over a period of 9-12 months may give unreliable results, as body condition can fluctuate strongly throughout the year (Van Sluys, 1998). It would be more informative to look at how cognition affects body condition changes over shorter time-intervals, e.g. before and after the dry summer, hibernation, breeding season etc.

Personality and fitness

It is often assumed that different personality types correspond to different life-history strategies. Risk-prone individuals invest in current reproduction at the expense of survival, while risk-averse personalities prioritize survival and future reproduction. (pace-of-life syndrome hypothesis, Wolf et al., 2007; Smith & Blumstein, 2008; Reale et al., 2010b; Sih & Del Giudice, 2012). Following these predictions, we would have expected less neophobic, more explorative and more aggressive lizards to have a higher growth rate and more offspring but lower survival. In the next paragraphs, we will discuss how our results align with these predictions.

First of all, neophobia was unrelated to either reproduction, growth or survival. Once again, this result could have been a consequence of our experimental design. Neophobia is predicted to be mostly beneficial when foraging under dangerous circumstances, such as high predation pressure, but will become costly if it prevents an individual from seizing novel resources (Mettke-Hofmann, 2014). Perhaps lizards faced both lower levels of predation and fewer novel resources in our enclosures (due to being more restricted in space), thus simultaneously eliminating both pros and cons of neophobia and resulting in no nett selection.

Secondly, more explorative lizards suffered higher mortality in the first but not the second experimental year. Annual variation in selection on exploration has previously been described in mammals and birds, and is often due to temporal fluctuations in food availability (Dingemanse et al., 2004; Le Cœur et al., 2015; Mouchet et al., 2021) or predation pressure (Réale & Festa-Bianchet, 2003). Such environmental stochasticity may also have occurred in our study system. Naxos experienced unusual high precipitation during the winter of 2018-2019, which might have increased arthropod abundances (Stamps & Tanaka, 1981; Spiller & Schoener, 1995). If food is plentiful, then more explorative individuals may no longer be more efficient in acquiring resources than less explorative conspecifics (Le Cœur et al., 2015). Predation pressure may also have varied across years, as open areas in the newly constructed enclosures in 2018 had been covered by grasses and herbs by 2019, and the lack of maintenance in 2020 also further increased vegetation density. Lizards in our first experimental year thus lived in relatively more open enclosures where more explorative individuals may have suffered more predation (Wolf et al., 2007; Rödel et al., 2014; Lapiedra et al., 2018). However, this is not in line with the fact that overall survival was actually higher in the first than second experimental year, and that the exploration – survival link did not differ likewise between simple and complex enclosures. Running this experiment for multiple years while also collecting data on resource availability could provide further insights in what drives temporal variation in selection, and thus ultimately how personality variation within populations is maintained.

Thirdly, in accordance with the predictions of the POLS-hypothesis, aggressive individuals suffered higher mortality albeit only in the complex enclosures. Possibly, aggressive males expend more energy (Marler et al., 1995), have less time to forage (Ancona et al., 2010) and are more susceptible to predation (Jakobsson et al., 1995), injury (Donihue et al., 2016) and infection (Salvador et al., 1996). All these factors may have jeopardized survival specifically in the complex enclosures, as territorial defence is expected to be more difficult, and thus costly, in cluttered habitats with lower visibility (Eason & Stamps, 1992; Höjesjö et al., 2004; Johnson et al., 2010; Church & Grant, 2018). Yet, this contradicts a previous study in which we reported that Aegean wall lizards originating from complex and simple habitats did not differ in aggressiveness (De Meester et al., 2022 ~ Chapter 5). Perhaps it was not habitat complexity per se that explains the differential survival of aggressive males, but rather, variation in population density. Higher survival rates in complex enclosures likely resulted in more intense, and thus costly, competition (Stamps & Buechner, 1985; Donihue et al., 2016).

Finally, the POLS-hypothesis predicts that the lower survival of more explorative and more aggressive lizards should be compensated by a higher reproductive output. However, neither exploration nor aggression were positively related to lizards' reproductive success. For exploration, it is possible that being more explorative was no longer an advantage during mate search, given the small size of the enclosures and the high densities of lizards in it. For aggression, it could be that non-aggressive males were still able to achieve a high reproductive success by adopting a sneaker-strategy (Sinervo & Lively, 1996; Sinervo & Zamudio, 2001). It could be a nice follow-up experiment to determine the relative importance of cognition versus personality in determining the reproductive success of male lizards with alternative mating strategies. Another explanation may be that aggressive lizards indeed outcompete submissive individuals for territories and mates, but this advantage is countered by females preferring less aggressive partners (Huyghe et al., 2012) due to the potential fatal consequences of male harassment (Le Galliard et al., 2005). We should note that we only tested the personality – reproductive output link within the subset of survivors, but deceased lizards rarely reproduced and left fewer offspring if they did. So even if we had included these individuals in our analyses, we would have likely still failed to find support for the POLS-hypothesis.

Intruders?

One issue of concern is the presence of unknown adults within our enclosures in 2020. Genetic analyses confirmed that these individuals were not the offspring of our own lizards, meaning that they were indeed 'intruders' who managed to get into the enclosures somewhere between 2019 and 2020, perhaps helped by the higher vegetation in 2020. This implies that, in year 2 at least, lizards may also have been able to get out of the enclosures. Nevertheless, we do not think this compromises our results and interpretation thereof. Firstly, selection studies, especially those within natural population, always have to accept a certain level of uncertainty regarding the ultimate fate of their test subjects (Dingemanse et al., 2004; Madden et al., 2018; Abalos et al., 2022; Rochais et al., 2022a). Secondly, we believe that the number of escaped individuals, if any, to be negligible compared to the number of truly deceased lizards. The survival rate in the second year was only slightly (and non-significantly) lower than in the first year, and this could also be due to higher competition (influx of intruders) or a harsher winter (see above). Thirdly, we only found intruders in 2020, meaning that the enclosures were probably very efficient in keeping lizards out and in during the first year (indeed, in one complex enclosure we recovered 100 % of all individuals). Thus, if lizards escaped rather than died, we would likely observe different results across years. Nevertheless, most of our results were very consistent across experimental years.

Is selection on cognition context-dependent?

In contrast to our expectations, we did not find stronger positive selection for cognition in structural more complex habitats. In fact, selection on cognition and personality (or the lack thereof) was largely independent of habitat type. This seems to suggest that habitat complexity, at least in this species, is not an important environmental factor shaping cognitive variation. In a previous study on *P. erhardii* we did not find any differences in problem-solving or reversal learning between populations originating from naturally simple and complex habitats, but nevertheless lizards from complex environments were more successful in a spatial learning task (De Meester et al., 2022 ~ Chapter 5). Possibly, such variation in spatial learning is a consequence of developmental plasticity, as often observed in fish (Spence et al., 2011; Carbia & Brown, 2019), rather than selection. Alternatively, habitat complexity may in fact select for stronger spatial learning in natural populations, but not under the relaxed conditions in our enclosures.

It would be interesting to adapt our set-up in order to test how other types of ecological variation would affect the cognition – fitness link. Enclosures could be adjusted to differ in e.g. resource variability (Szabo & Whiting, 2020), predation pressure (Jaatinen et al., 2019), social complexity (Langley et al., 2020b) etc., all of which are predicted to be important drivers of cognitive variation.

CONCLUSION

Overall, the effect of cognition on lizards' fitness was relatively limited and often in conflict with the trends described in literature. Albeit this could be an artefact of our experimental design, it is also plausible that our results do not align with earlier studies since these were mainly conducted on birds with completely different (socio-)ecological lifestyles (e.g. parental care). Expanding research regarding the fitness consequences of cognition to non-traditional taxa may thus lead to novel and fresh insights.

One shortcoming of our study is that the exact pathways of how these cognitive abilities affect fitness remain unclear, i.e. more information is needed regarding the role of spatial cognition and problem-solving in the natural behaviour of our study species. How does spatial learning performance in the lab relate to spatial behaviour of individual lizards in the wild? How do lizards use these cognitive skills during foraging, mate search and predator evasion? This limitation is, however, not unique to our own work, as cognitive research in general will benefit from a better understanding of the role of cognition within the daily life of their study animals, to understand its fitness-outcomes. Modern techniques (e.g. camera-trapping, radio-tracking, etc) are currently expanding our potential to collect such data.

Although we failed to find habitat-dependent selection on cognition within our study system, we nevertheless believe that comparing selection gradients on cognition within the same species under different ecological conditions can become a very powerful approach to identify the drivers of cognitive evolution. We hence recommend future research to study selection on cognition and personality across (natural or experimental) populations exposed to different environmental factors, preferably across multiple years. Albeit this remains challenging, modern technological advancements are making these kind of studies more and more feasible.

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CHAPTER 8

GENERAL DISCUSSION

OUTLINE

The goal of this thesis was to understand the role of ecology in shaping cognitive variation, both among species, among populations of the same species and among individuals. By combining a comparative and individual-based approach, I hoped to gain deeper insights in how cognition evolves. In the first part of this discussion, I will consider whether and how differences in habitat complexity and variability instigate variation in cognitive abilities at the individual, population and species level, and what this tells us about the evolution of (reptile) cognition. In the second part of the discussion, I will highlight some important shortcomings of my thesis and the field in general, but also suggest how these could be addressed in future research.

THE ROLE OF ECOLOGY IN LIZARD COGNITIVE EVOLUTION

Ecological challenges posed by the physical environment, typically those involved with the acquisition of food, are often proposed to drive the evolution of animal cognition. Throughout this thesis, I have looked at two aspects of the physical environment in particular; structural habitat complexity and environmental variability, and both of them were studied at different taxonomic levels. An overview of the most important results is given in Table 1.

Table 1. Summary of the results obtained across all research chapters (2-7). RBS = relative brain size, IC = inhibitory control, LR = lid-removal, SL = spatial learning, RL = reversal learning and FLEX = learning flexibility.

	Among species	**Among populations**	**Among individuals**
Social Complexity ↑	↓ RBS Solitary squamata have relative larger brains than social species (Chapter 2)	/	/
Habitat complexity ↑	(0) RBS Arboreal squamata have relative larger brains than fossorial species, but not significantly (Chapter 2).	↑ SL Aegean wall lizards from complex habitats are more likely to learn a spatial learning task than those from a simple habitat (Chapter 3).	↑ RL Individual lizards housed in simple enclosures for one year show reduced reversal learning, but no differences in spatial learning or problem-solving (Chapter 6).
	(0) No link between performance in any cognitive task and structural habitat complexity (NDVI) across 13 species of Lacertidae (Chapter 3).	(0) No differences in other cognitive traits (Chapter 3)	(0) No habitat-dependent selection on cognition or personality (Chapter 7)
Environmental variability ↑	↓ RBS Squamata from the Neotropics have relative larger brains than those from more temperate regions (Chapter 2).	↑ SL Aegean wall lizards from a more seasonal habitat show better spatial learning.	/
	↓ IC, LR, RL, FLEX Lacertid lizards from more seasonal habitats have worse inhibitory control, and tend to be less successful in problem-solving and reversal learning (Chapter 3)	↓ RL, FLEX Aegean wall lizards from a more seasonal habitat show lower cognitive flexibility and reversal learning. (Chapter 4).	

Habitat complexity and cognition

According to literature, living in structural complex habitats should select for enhanced cognitive abilities and larger brains, due to increased demands for processing and storing environmental information (Safi & Dechmann, 2005; Shumway, 2008; Mettke-Hofmann, 2014; Powell & Leal, 2014; Pamela Delarue et al., 2015; Steck & Snell-Rood, 2018). The results obtained during my PhD are mixed in this respect (see Table 1). Habitat complexity does not explain variation in relative brain size across squamate reptiles (Chapter 2), nor in cognitive performance (inhibitory control, problem-solving, spatial and reversal learning) across Lacertidae (Chapter 3). At the intraspecific level, however, I found that Aegean wall lizards (*Podarcis erhardii*) from complex habitats were more successful in learning a spatial task than conspecifics from open, simple areas (although no differences were found in problem-solving or reversal learning, Chapter 5). At the individual level, however, I observed that lizards kept in structurally simple enclosures experienced a greater reduction in reversal learning capacity than conspecifics in more complex enclosures. Lastly, there was no evidence for habitat-dependent selection on spatial learning or any other cognitive ability in the semi-natural enclosures (Chapter 7).

Firstly, **problem-solving** ability seemed to be consistently unaffected by habitat complexity both across and within species. I predicted that lizards from more complex environments would be more proficient in problem-solving, due to more frequently encountering hidden, cryptic or dangerous prey and/or physical barriers while trying to obtain resources (Mendyk & Horn, 2011; Mettke-Hofmann, 2014). Nonetheless, complex habitats are also likely to offer a high abundance and diversity of prey (Gardner et al., 1995; Steck & Snell-Rood, 2018; Fernandez-Tizon et al., 2020; Peng et al., 2020). As long as more ‘easy’ prey are available, there might be no pressure for lizards to resort to complicated extractive foraging techniques. Similarly, woodpecker finches (*Cactospiza pallida*) are more frequently observed using tools for extractive foraging during the dry season when more accessible prey items become scarce (Tebbich et al., 2002). Hence, problem-solving may be more important in harsh and temporally variable, rather than spatially complex, habitats (but see below).

Secondly, I initially predicted a particularly strong effect of habitat complexity on **spatial learning** (see introduction and literature e.g. Safi & Dechmann, 2005; Shumway, 2008; Costanzo et al., 2009; White & Brown, 2014), but results were highly incongruent across taxonomic levels (and hence chapters) (Table 1). A first possible explanation for this discrepancy in results across chapters may be that different environmental forces shape cognitive variation across and within species. In that respect, my results do seem to be in line with previous comparative brain studies on lizards, showing that habitat structure was unrelated to the relative size of either the whole brain or specific brain regions across anole species (Powell & Leal, 2014) but positively associated with the relative size of the medial cortices (reptilian brain areas involved in spatial cognition) between populations of lesser earless lizards (*Holbrookia maculata*, Calisi et al., 2017). It is worth remembering that the current variation across species, both in brain size and cognitive abilities, is shaped by a long evolutionary history, and are therefore sometimes considered less informative regarding the influence of current environmental conditions on cognition (Roth et al., 2010b).

Alternatively, discrepancy in results across chapters may be due to the different approaches used to define habitat complexity. Habitat complexity was scored using microhabitat/ecological guild data (fossorial, ground-dwelling, saxicolous, arboreal) taken from literature in Chapter 2, using NDVI and precipitation data obtained via remote sensing in Chapter 3, and by actually visiting the field sites in Chapter 5 – 7 (and verifying this using remote sensing data on ground vegetation cover). The latter approach is likely the most informative and accurate. For instance, being ground-dwelling in an open desert or in a dense grassland is a considerable difference in terms of environmental complexity, but the ecological guilds defined in Chapter 2 are too broad to take this into account. Likewise, NDVI-data is mainly based on vegetation density, and does not consider other aspects of structural complexity such as rocks, stone walls, etc. In addition, NDVI also correlates with precipitation and resource availability (Chapter 3, Pettorelli et al., 2011; Sweet et al., 2015; Fernandez-Tizon et al., 2020) and thus does not solely reflect structural habitat complexity. This inconsistency in measures of habitat complexity was due to logistic and conceptual issues. For instance, we did not know the exact origin of the many species featuring in Chapters 2 and 3, and/or were unable to visit those places of origin to evaluate habitat complexity. Ground vegetation cover used in Chapter 5 may accurately reflect habitat complexity for populations of a ground-dwelling species (such as *P. erhardii*) but less so for arboreal or fossorial species.

Hence, future work could benefit from using more detailed measures for habitat complexity. This does raise the important question of what exactly constitutes a complex habitat from the perspective of a lizard? Throughout this thesis, and much of literature, it is assumed that visually restricted habitats (e.g. denser vegetation) with higher three-dimensionality (e.g. rock outcrops, trees) and a higher diversity of microhabitats (and thus resources) are more complex because they require the processing and storage of considerable more environmental information and a greater capacity to distinguish between relevant and irrelevant environmental cues (Safi & Dechmann, 2005; Shumway, 2008; Mettke-Hofmann, 2014; Powell & Leal, 2014; Pamela Delarue et al., 2015; Calisi et al., 2017; Steck & Snell-Rood, 2018). For instance, if an animal wishes to return to a previously visited location (food patch, hiding spot, …) it will have to memorize more landmarks to find its way within a visually restricted habitat compared to a more open environment (where the goal is already visible from a greater distance). Nonetheless, it would be good if future studies were able to actually quantify whether such complex environments are truly richer in information. For instance, Powell and Leal (2014) measured habitat complexity by quantifying how many possible paths *Anolis*-lizards could take while moving around in their home range, and how many branches they needed to cross to get from one point to another. Other options are to take more rigorous field measurements of habitat structure in terms of e.g. shrub/rock/tree/… cover (Ferreira & Faria, 2021), or even to quantify the three-dimensional structure of the habitat in great detail using LiDAR (light detection and ranging) technology (Bradley et al., 2022). These could be combined with collecting field data on the abundance and diversity of arthropods, other resources, competitors, predators etc. as. Of course, all of these require actually visiting the original populations, which was not always feasible during this project.

But even at the intraspecific level, results are incongruent. While habitat complexity is associated with spatial learning performance across natural populations of *P. erhardii*

(Chapter 5), selection on this ability did not differ between simple or complex enclosures (Chapter 7). There are two possible, non-exclusive, explanations for these divergent results. First, these cognitive differences across populations of *P. erhardii* may arise due to phenotypic plasticity, rather than selection. Many previous studies have indeed observed that structural complexity of the (rearing) environment promotes spatial cognition and brain development in various taxa (e.g. rats: Leggio et al., 2005; fish: Spence et al., 2011; Carbia & Brown, 2019; mole-rats: du Toit et al., 2012; Carbia & Brown, 2019; lizards: LaDage et al., 2013; LaDage et al., 2016; Vardi et al., 2020). In Chapter 6, I also reported a low heritability for spatial learning in *P. erhardii,* which may indeed indicate that most of the variation across individuals arises due to environmental effects (Morand-Ferron et al., 2016; Vardi et al., 2020). However, adult *P. erhardii* did not change their spatial learning performance after being housed in either a structural simple or complex enclosure for one year (Chapter 6). This could of course mean that the effect of environmental complexity on spatial cognitive development may be restricted to early life in this species (Chandler et al., 2020).

Secondly, as discussed in Chapter 7, the lack of differential selection on spatial cognition between simple and complex enclosures could be an artefact of our experimental design. Lizards in our enclosures probably experienced reduced predation risk (Kotrschal et al., 2019), high and predictable food availability (Henke-von der Malsburg et al., 2020) and restricted space use (du Toit et al., 2012). These more ‘easy’ conditions may have negated the benefits from spatial cognition compared to a more natural (complex) environment, hence why there was no (males) or negative (females) selection on spatial learning within the enclosures. Using larger enclosures, limiting food availability, introducing predators, or following survival in the original complex and simple habitats (albeit challenging) may have yielded more consistent results across chapters.

Aegean wall lizards kept in structurally simple semi-natural enclosures for ± 1 year showed a stronger reduction in **reversal learning** performance compared to conspecifics kept in enclosures with complex habitat. Yet, despite this habitat-dependent plasticity, lizards originating from natural complex and simple habitats did not differ in their reversal learning scores (Chapter 5). The most likely explanation is that lizards suffered a reduction in reversal learning abilities in our simple semi-natural enclosures due to a combination of increased stress, restricted space use and lower habitat complexity impairing adult neurogenesis, while the enriched vegetation structure in the complex enclosures buffered this effect to some extent (du Toit et al., 2012; LaDage et al., 2013; Powers, 2016; see also Chapter 6).

Lizards were nonetheless expected to show better reversal learning in more complex environments due to a higher likelihood of encountering novel situations and resources (Mettke-Hofmann et al., 2002). However, reversal learning was unrelated to habitat complexity both across and within species (Table 1). A lizard in a complex environment may indeed e.g. have a higher probability of discovering a new food source, but this does not mean that familiar food sources are no longer available and a lizard should forget about them. Hence, structural complex environment may require lizards to learn and retain a greater diversity of information, but not necessary to be cognitively more flexible. A similar reasoning could also explain why inhibitory control was unaffected by habitat complexity.

One thing that should be addressed in future studies, and may even explain why my results did not align with common expectations, is the possibility of correlated selection between cognition and other behavioural traits, such as personality type (boldness, exploration, aggressiveness, activity and sociability). Perhaps habitat complexity selects for specific behavioural combinations. The results presented in Chapter 5 seem to imply this. Behavioural associations between personality and cognition were either habitat-independent, or solely found within the simple, open, habitats. I suggested the possibility that high predation pressure in the simple habitats eliminates certain maladaptive behavioural combinations, thus giving rise to stronger personality-cognition correlations (Bell & Sih, 2007; Sih & Del Giudice, 2012; Liedtke & Fromhage, 2019a), while the same behavioural combinations may persist in more safe complex habitats. This was indeed demonstrated by Bell and Sih (2007) in a study on behavioural syndromes in three-spined sticklebacks (*Gasterosteus aculeatus*). Boldness and aggressiveness were unrelated in sticklebacks prior to being released in artificial pools with a predator, but were positively correlated when the surviving fish were re-tested at the end of the experiment. This correlation arose partially due to phenotypic plasticity, but was also due to the higher mortality of individual fish who were both bold and unaggressive. It would thus have been interesting to check whether the same behavioural associations would emerge within the surviving lizards in the simple enclosures, as in the original simple habitats.

Environmental variability and cognition

There are two conflicting hypotheses regarding the effect of environmental variability on cognition. The Cognitive Buffer Hypothesis (CBH) predicts that variability selects for higher cognitive abilities, as the ensuing behavioural flexibility will help animals to survive environmental changes (Deaner et al., 2003; Sol, 2009). The Expensive Brain Hypothesis (EBH), on the other hand, states that energetic limitations in variable environments will favour lower cognitive abilities and smaller brains (Aiello & Wheeler, 1995; van Woerden et al., 2010; Niemela et al., 2013). The results obtained during my PhD seem to support both the CBH and the EBH to some extent.

Across species, there are some trends implying that environmental variability indeed impairs evolution towards higher cognitive abilities. Lacertid lizards sampled from more variable environments showed worse inhibitory control, and tended to be less adept in solving new problems and reversing a spatial association (Table 1). They were also slightly less likely to learn across both phases of the spatial + reversal learning task (Chapter 3). Interestingly, all these traits are generally considered indicators of high behavioural flexibility (Tebbich & Teschke, 2014; Szabo et al., 2019b; Szabo et al., 2020a; Szabo et al., 2020b; but see Audet & Lefebvre, 2017). On the other hand, spatial learning was unaffected by seasonality. Similar patterns were observed within species. *Podarcis erhardii* from Naxos (high seasonality in precipitation and NDVI) were better in learning a spatial task, but seemingly worse in reversing it, compared to conspecifics from a more stable mainland habitat (Chapter 4). A final piece of evidence comes from Chapter 2: Neotropical Squamata were found to have relatively larger brains than Nearctic or Australasian species. The high food availability in Neotropical systems was given as a possible explanation (Foley et al., 1996). Tropical regions are also considered more climatically stable compared to more seasonal temperate zones (Whitton et al., 2012; Pamela Delarue et al., 2015; but only in temperature and not precipitation according to Jetz & Rubenstein, 2011).

Thus, both among and within species, environmental variability seems to be negatively associated with (one or several aspects of) behavioural flexibility. As already discussed in Chapter 3 and 4, reversing a (spatial) association requires (higher rates of) neurogenesis, but initially acquiring the association less so (Burghardt et al., 2012; Kalm et al., 2013; Swan et al., 2014; Epp et al., 2016; Guitar & Sherry, 2018). Likewise, neurogenesis may also facilitate inhibitory control (Zhang et al., 2012) and problem-solving (Audet et al., 2018). It seems logical that the more costly cognitive abilities will be more restricted by fluctuating levels of resource availability and food intake. The higher energetic cost of reversal learning was also given as a possible explanation for its decline in lizards kept in structural simple habitats for a year (Chapter 6). Taken together, my results strongly suggest that environmental variability constrains the evolution of the more 'expensive' cognitive abilities, but has no impact on or may even promote presumably 'cheaper' cognitive traits.

Nonetheless, whether reversal learning, problem-solving and inhibitory control are truly energetically more expensive than simple spatial learning should be validated. This can be done in two different ways. Firstly, artificial selection experiments on any of these cognitive traits could be highly informative in this regard (Kotrschal et al., 2013; Kotrschal et al., 2015c; van der Woude et al., 2019), but would probably require working on species with a shorter generation time (e.g. side-blotched lizards mature in < 1 year, Ferguson & Fox, 1984). Secondly, uncovering the neural mechanisms underlying lizard cognition (e.g. link with brain size, neurogenesis rate, …) can also advance our understanding of the costs and thus evolution of behavioural flexibility (see further in discussion) (Roth et al., 2019; LaDage, 2020). Apart from that, it should also be verified whether environmental variability truly selects against these cognitive traits. Environmental variability could be simulated in my enclosures by manipulating food availability, e.g. frequently switching periods of high and low food provision (Kotrschal & Taborsky, 2010) or regularly changing the location of food sources in the enclosures (van Horik et al., 2019a). Lastly, while I have put a lot of emphasis on the energetic costs of cognition in habitats with fluctuating levels of food availability, it should be noted that other sources of environmental variation can also impact cognition. Seasonal changes in NDVI and precipitation are also likely to impact habitat structure (Irteza et al., 2020) and consequentially thermal environment (Hacking et al., 2013), predation risk (Ferreira & Faria, 2021) and social interactions (Leu et al., 2016). For instance, if the structure of the habitat (e.g. distribution of hiding spots) changes much faster than lizards can (re-)learn, than learning may simply not be an advantage for lizards, independent of whether there is sufficient food available or not (Niemela et al., 2013; Mettke-Hofmann, 2014). Whether the reduced cognitive performance in more variable habitats is thus truly due to unpredictability in food sources, rather than in other aspects of the environment, should be further investigated in future experiments.

General intelligence or adaptive specialization

Overall, the associations with habitat complexity/variability were not consistent across different cognitive abilities. Habitat complexity was associated with spatial learning, while variability was mostly linked to inhibitory control, problem-solving and reversal learning. This does seem to suggest that different ecological factors will target specific cognitive abilities, rather than selecting for a ‘general cognitive ability’(Magphail & Bolhuis, 2001; Bräuer et al., 2020; Poirier et al., 2020). The results presented in Chapter 5 also do not seem to support the idea of a general intelligence factor ‘g’ in the Aegean wall lizard. Spatial and reversal learning were negatively associated with each other, the link between performance on the two problem-solving tasks was inconsistent across years, and problem-solving and spatial/reversal learning were also only weakly and inconsistently related. In this respect, my thesis illustrates the potential pitfall of using a single proxy (brain size or performance on a single task) to answer questions about the evolution of animal cognition, which is still too often done in cognitive research.

It is possible, however, that the inconsistencies in cognitive performance across tasks are (partially) due to differences in the rewards used (safety in the escape box task, spatial + reversal learning; food in the inhibitory control and lid-removal task). Individuals may react differently in response to various rewards. A lizard bold enough to feed in an experimental arena, may also feel less threatened by a predator attack and will thus be less motivated to seek shelter during the spatial learning task. Whether lizards are more motivated to find shelter or find food could also depend on the ecological conditions in their natural environment (e.g. resource availability, predation pressure). My results do not seem to support the idea that food-rewarded and safety-rewarded tasks are oppositely related. Lid-removal (food) and escape box (safety) performance were positively associated in *P. erhardii* in 2018, while escape box performance and spatial learning (both safety) were negatively associated that year. Nonetheless, it would be interesting to validate this in future work, e.g. by testing the cross-contextual repeatability of spatial learning performance across different spatial tasks using different rewards (e.g. food, shelter, mates, basking spots, etc.).

LIMITATIONS AND FUTURE DIRECTIONS

This thesis reported some interesting relationships (or the lack thereof) between cognition, ecology and fitness. However, I often found that the interpretation of my results in an evolutionary context was hampered by two major gaps in our current knowledge: 1) what are the *mechanisms* underlying reptilian cognition and 2) what are the *functions* of reptile cognition?

The (neural) mechanisms behind cognition

Cognition is generally considered energetically expensive due to the high need to maintain costly neural machinery (Aiello & Wheeler, 1995). Identifying the exact neural mechanisms underlying a particular cognitive trait will help us gauging the energetic costs of this trait, making it easier to interpret why it would be selected for or against under certain ecological conditions. However, few studies so far have tried to link reptilian cognition to neuro-anatomy (Roth et al., 2019).

As a first step, future studies could try to investigate the link between cognitive performance and the size of either the whole brain or specific brain regions. Some pioneering work has been done with regards to reptile spatial cognition. The dorsal and/or medial cortices (DC and MC), the reptilian homologues of the hippocampus, are often larger in reptiles facing higher spatial demands, e.g. those that are active foragers (Day et al., 1999a), are territorial (Ladage et al., 2009) or live in more densely vegetated areas (Calisi et al., 2017). Lesions in the DC and/or MC also impair spatial (reversal) learning and memory in lizards and turtles, but do not affect other types of learning (Day et al., 2001; López et al., 2003a; López et al., 2003b). Manipulating space use (e.g. changing enclosure size, translocations, captivity) often leads to plastic changes in the volume of one or both of these regions (northern Pacific rattlesnakes: Holding et al., 2012; side-blotched lizards: LaDage et al., 2016) or in their neurogenesis rate (Tenerife lizards: Delgado-Gonzalez et al., 2008; side-blotched lizards: LaDage et al., 2013; painted turtles: Powers, 2016). Nonetheless, the MC/DC – spatial cognition link is not always straightforward. Two species of fringe-toed lizards (*Acanthodactylus boskianus*, an active forager, and *A. scutellatus*, a sit-and-wait forager) differ in the relative size of their MC and DC (Day et al., 1999a), but not in their spatial learning performance (Day et al., 1999b). Whether better spatial learners also have larger MC/DCs at the individual level has not been tested yet.

Studies on the neural basis of cognitive traits outside the spatial domain are, however, practically non-existent in reptiles. The only exception, to my best knowledge, is a recent paper by Storks et al. (2020) in which problem-solving and brain cell count was compared between two anole species. The superior problem-solver did have a higher number of non-neuron brain cells, but did not differ in neuron number or density from the less innovative species.

Apart from brain size, future research could also look at the process of neurogenesis. Throughout this thesis, I have also proposed neurogenesis as a potential reason for why some cognitive abilities were negatively impacted by environmental variability (Chapter 3, Chapter 4) and habitat simplicity (Chapter 6), while others were not. Albeit adult neurogenesis is high in reptiles, its link with cognitive/behavioural flexibility within this group has yet to be proven (Roth et al., 2019; LaDage, 2020). Comparing the rate of neurogenesis among populations/species differing significantly in e.g. reversal learning ability (e.g. *Podarcis siculus* versus *Eremias brenchleyi*, Chapter 3) or in the environmental variability to which they are exposed (e.g. Naxos versus Parnitha, Chapter 4) can be a highly informative first step (Tello-Ramos et al., 2019). To support a causal link between neurogenesis and cognition, one could experimentally test how supressing or promoting neurogenesis, e.g. by pharmaceutical agents, would affect a lizards' cognitive performance (Guitar & Sherry, 2018; Roth et al., 2019).

A final promising approach to understand the mechanisms behind reptilian cognition would be to look at and compare brain gene expression levels between e.g. solvers and non-solvers, or lizards succeeding and failing the reversal learning. Such an approach was followed for instance by Audet et al. (2018), who described differences in the expression of genes associated with neuronal and synaptic plasticity, and glutamate receptors between innovative (problem-solving) Barbados bullfinches (*Loxigilla barbadensis*) and more conservative black-faced grassquit (*Tiaris bicolor*).

The functions of cognition

Comparative studies may demonstrate a link between a cognitive trait and an environmental factor, but this evidence remains purely correlational (Healy et al., 2009; Cauchoix & Chaine, 2016). Demonstrating the fitness consequences of the same trait under different levels of that environmental factor may provide more direct proof for selection, but leaves open a crucial question: exactly how does this particular trait help individuals to deal with environmental challenges? This is an important question to answer, as a single cognitive ability can help an animal to increase its fitness via multiple possible pathways (or a combination thereof), e.g. foraging, predator avoidance, mate acquisition, territorial defence, migration etc. This should also control for the possibility that selection is not directly targeting this cognitive trait, but another correlated one instead (Morand-Ferron et al., 2016). More information is thus desperately needed on the functional mechanisms linking cognitive abilities to fitness, a shortcoming that is not unique to my own study system (Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016; Szabo et al., 2022).

Problem-solving has been advanced as an important tool enabling animals to gain access to novel food sources or to exploit familiar ones more efficiently (Parker & Gibson, 1977; Tebbich et al., 2002; Greenberg, 2003; Griffin et al., 2016). Bird species known to show more foraging innovations in the wild have indeed demonstrated higher problem-solving abilities in the lab (Webster & Lefebvre, 2001; Griffin & Diquelou, 2015). Likewise, free-ranging individual great tits (*Parus major*) with higher problem-solving skills fed their young at higher rates, indicative of being more efficient foragers (Cauchard et al., 2017). For other taxa, however, the link between problem-solving and foraging is less clear.

In lizards, there is some circumstantial evidence that problem-solving skills may be related to their foraging behaviour. The excellent problem-solving skills of monitor lizards (Varanidae) have been attributed to their natural tendency to excavate hidden prey from tree holes, rotting wood, burrows, crevices etc. (Manrod et al., 2008; Mendyk & Horn, 2011; Cooper et al., 2019; Cooper et al., 2020; Pettit et al., 2021). Of course, whether species showing such extractive foraging behaviour are indeed better problem-solvers should be confirmed by a more robust comparative study. Another possibility could be that problem-solvers are more adept in learning how to handle difficult or dangerous prey (see Chapter 7), e.g. very agile insects, large prey or venomous arthropods. This hypothesis could be tested in two different ways. Firstly, individual lizards could be tested on their efficiency to handle and consume a series of prey varying in ‘difficulty’ (e.g. mobility, hardness, size and 'riskiness', cfr. Díaz & Carrascal, 1993; Verwaijen et al., 2002; Whitford et al., 2022). Prey handling time, and the improvement over consecutive trials, can then be directly linked to their problem-solving scores. Secondly, it may be interesting to check whether problem-solvers indeed differ in diet from non-solvers, specifically in the proportion of difficult, hidden or dangerous prey. This could be measured in semi-natural enclosures, either by regularly recapturing animals and stomach-flushing them to score individuals’ dietary niche (Donihue, 2016), or by providing such prey at fixed locations in the enclosures and observing which individuals more frequently visit and consume prey here, which could be done using camera traps (Bennett & Clements, 2014; Welbourne et al., 2020) or a PIT-tag system (Sonnenberg et al., 2019). Doing so multiple times over a sufficient long-time scale may be necessary, as innovative lizards may only switch to such alternative prey in times of food scarcity (Tebbich et al., 2002).

The role of spatial cognition in the day-to-day life of lizards should also be further investigated. How are spatial learning and memory involved in lizards’ foraging, territorial and antipredator behaviour? One possible approach may be to (temporary) impair spatial learning and memory in lizards, e.g. by lesions in the MC and/or DC (Day et al., 2001; López et al., 2003a; López et al., 2003b) or by administering memory-blocking drugs (Roth & Krochmal, 2018) and see how this affects their ability to locate familiar shelter and food sources, and maintain territories under (semi-)natural conditions. For instance, Roth and Krochmal (2018) reported that individual painted turtles (*Chrysemys picta*) treated with a memory-inhibiting pharmaceutical agent (scopolamine) lost the ability to follow their usual very precise and consistent migration paths, but would regain it after the drug wore off. In my set-up, it could be an elegant experiment to confirm the role of spatial learning in efficient escape behaviour (Martin et al., 2003; Font, 2019), by testing whether memory-impaired and control lizards differ in catchability (by a human predator).

Luckily, less invasive methods are nowadays provided by modern tracking technology. Tracking systems have previously been employed in a variety of wild-ranging animals, to test the role of spatial learning (common carps: Bajer et al., 2010; roe deer: Ranc et al., 2021) and the use of cognitive maps (Weddell's saddleback tamarins: Porter & Garber, 2012; African elephants: Presotto et al., 2019; Egyptian fruit bats: Toledo et al., 2020) during foraging. It could be a very valuable experiment to equip individual lizards with such tracking devices, release them in a semi-natural enclosure, and test whether learning abilities measured in the lab correlate with how fast they familiarize with resources in their new environment. For instance, this data could reveal whether lizards indeed flee repeatedly towards the same refuges when attacked, and whether these escape routes become more consistent and shorter over time. Tracking technology, such as radio-telemetry or GPS-data loggers, have already been successfully used to quantify space use and home-range sizes in some lizard species (Texas horned lizards: Miller et al., 2019; sand lizards: Wieczorek et al., 2020; sleepy lizards: Michelangeli et al., 2022; bearded dragons: Wild et al., 2022), demonstrating the potential of such technology. By using smart feeders and PIT-tags, we could also directly test whether better spatial learners return more often to rewarded food locations (Sonnenberg et al., 2019), and whether better reversal learners adjust their behaviour faster when environmental conditions (e.g. location of resources) change (Ranc et al., 2021).

A lack of information on the functional significance of cognition is a major issue within the entire field of animal cognition, but this knowledge is particularly lacking for non-traditional model species such as reptiles. Most recent work on reptile cognition has focused on simply documenting the extent of their cognitive abilities (see e.g. Miletto Petrazzini et al., 2018; Font, 2019; Szabo et al., 2019b; Ko et al., 2020; Szabo et al., 2021a; Szabo et al., 2021c; Szabo & Whiting, 2022), but very little attention has been given on how reptiles use cognition to deal with environmental challenges (but see e.g. Roth & Krochmal, 2015; Ward-Fear et al., 2016; Roth & Krochmal, 2018).

Lizards as models in cognitive research

I will end this thesis with a short re-evaluation of the potential of (lacertid) lizards in cognitive research, and by making some last suggestions on how to capitalize more on this potential.

The main advantage of using lizards is without a doubt their broad ecological and social diversity, both among and within species. Lizards can be found in a broad variety of terrestrial ecosystems, from complex tropical jungles to arid deserts, and in many different microhabitats, from being arboreal to fossorial (Arnold, 1989; Pianka & Vitt, 2003; Arnold & Ovenden, 2004; Arnold et al., 2007; Powell & Leal, 2014; Whiting & While, 2017; Horreo et al., 2021). Some species are able to thrive in seemingly inhospitable environments, such as small remote and food-deprived islets (e.g. Pérez-

Mellado et al., 2008) or urban areas (Putman & Tippie, 2020). Many species are successful invaders of novel environments (Amiel et al., 2011; Damas-Moreira et al., 2018; Damas-Moreira et al., 2019), possibly helped by a high degree of behavioural flexibility (Szabo et al., 2020a). Within species, it is often easy to find populations exposed to different levels of e.g. predation (e.g. Brock et al., 2014a) or novel invasive prey (e.g. Herr et al., 2016; Pettit et al., 2021). Lizard also show great variety in their behaviour and lifestyles,, e.g. in territoriality and mating strategy (e.g. Sinervo & Lively, 1996; Zamudio & Sinervo, 2000; Perry & Garland, 2002) and foraging behaviour (Reilly et al., 2009), sometimes even within species. Lizard species also vary in the degree of their sociality, ranging from solitary species, to those forming temporary associations to those living in stable aggregations and families (Shah et al., 2003; Gardner et al., 2016; Halliwell et al., 2017; Vasconcelos et al., 2017; Whiting & While, 2017). This ecological and social diversity represents a valuable, yet largely unexplored, resource to address many of the emergent questions within comparative cognition and cognitive ecology. This ecological diversity is present within lacertid lizards as well, but the rather conservative nature of other aspects of their biology (e.g. body plan) makes standardization across tasks feasible (Arnold, 1989; Arnold et al., 2007; Horreo et al., 2021).

There also several practical advantages of working with lizards. Many species, and lacertids specifically, are found in populations with high densities (Amaral et al., 2012) and can easily be caught in sufficient large sample sizes. Lacertids can also be housed with relative ease and in sufficient large sample sizes in the lab (Amaral et al., 2012). Another major advantage is that there are already several cognitive protocols available in literature that have been successfully employed on lizards from various taxa. For instance, the colour discrimination assay (Iguania: Leal & Powell, 2012; Scincoidea: Clark et al., 2013; Lacertoidea: Pérez i de Lanuza et al., 2018) and spatial antipredator task (Scincoidea: Noble et al., 2012; Gekkota: Dayananda & Webb, 2017; Iguania: Batabyal & Thaker, 2019; Lacertoidea: Font, 2019; this thesis) have both become prevalent within reptile cognition literature. These protocols are low-cost, require little to no training of the experimenter, and seem easy to standardize across species, meeting all necessary requirements for comparative research (MacLean et al., 2012; Krasheninnikova et al., 2020).

However, working with lizards also presents some challenges. Firstly, it remains a time-consuming endeavour. Due to their low metabolic rate, lizards are quickly satiated, thus only allowing for a few trials per day if food is used as motivator (Burghardt, 1977; Whiting & Noble, 2018; Szabo & Whiting, 2022). This is very different from studies on birds where entire cognitive tasks can be completed within a day (Ashton et al., 2018). Using alternative motivators, such as safety, could be a solution, but even then the number of daily trials is better kept limited to avoid trial fatigue and/or too much stress in the animals (Whiting & Noble, 2018). Alternative protocols have been suggested, such as training animals to consume smaller prey items which would allow more trials in a shorter timeframe (Emer et al., 2015; Szabo & Whiting, 2022), but this approach becomes less feasible in smaller species. Another difficulty I faced was that some species more readily than others adjusted to conditions in the lab and seemed more motivated to participate in the cognitive tasks, but this is not an issue unique to reptiles (MacLean et al., 2012). In addition, this was controlled for by removing trials in which lizards did not engage with the experimental apparatus. A more conceptual limitation of working with reptiles is the currently meagre comprehension of the mechanisms behind and functions of their cognitive abilities (see previous paragraphs).

The use of *P. erhardii*, a medium-sized lizard, as focal species for my selection study also provided some challenges. At the start of my PhD, I deemed it too difficult to measure survival and reproductive success in (multiple) wild populations of this species. While *P. erhardii* does have a relative small home range (BeVier et al., 2021), it is not yet known how consistent this home range is across seasons or years. As I could not check these populations regularly throughout the year for logistic reasons, and because I did most of this monitoring on my own, there would have been a too high risk that missing individuals had dispersed, rather than died, or would simply be overlooked (especially in the complex habitats) (Rochais et al., 2022a). Measuring reproductive success may have been even more difficult, as in at least some lacertid species juveniles disperse, and the propensity for dispersal can be personality- and context-dependent (Galán, 2006; Cote & Clobert, 2007). Due to these issues, I had to resort to studying selection within semi-natural enclosures, a situation that may not be entirely comparable with more natural conditions (see Chapter 7).

Previous cognition-fitness studies have benefitted from working in already extensively monitored bird-populations (see e.g. Cole et al., 2012; Cauchard et al., 2013; Cauchard et al., 2017; Preiszner et al., 2017; Branch et al., 2019) or by using animals that are unlikely to disperse, either due to high site-fidelity (Maille & Schradin, 2016; Dayananda & Webb, 2017; Sonnenberg et al., 2019) or because of their more or less enclosed habitat (Madden et al., 2018; Colby et al., 2021). Nonetheless, we should be able to find a lizard study species meeting these criteria as well. For instance, individual survival and reproductive success of individual side-blotched lizards (*Uta stansburiana*) has been successfully monitored consistently since 1988 in four populations on rocky outcrops surrounded by unfavourable grassland (Sinervo & Lively, 1996; Zamudio & Sinervo, 2000; Sinervo & Zamudio, 2001; Hazard et al., 2019). Introducing lizards on small islets (Lapiedra et al., 2018; Donihue et al., 2022) or employing tracking devices (Ward-Fear et al., 2016; Wild et al., 2022) may also increase the accuracy of survival estimates in the wild.

Although there are challenges with using reptiles in cognitive research, I believe that as our knowledge of reptile cognition progresses, more adequate methods and protocols will arise with which we will be able to overcome these limitations. One important avenue for future research, is to study reptile cognition in a natural setting, where the animals have full access to all ecological relevant cues needed to learn, and are more likely to express natural behaviours (Pritchard et al., 2016). Bringing animal cognition to the field has advanced our understanding of its functions and adaptive value in other taxa (Pritchard et al., 2016) and doing so for reptiles will advance our understanding, not only of reptilian cognition, but also of the evolution of cognition throughout the entire animal kingdom.

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APPENDIX CHAPTER 2

SUPPLEMENTARY DATA CHAPTER 2

Supplementary Table S2.1. Overview of all data used for the comparative study on relative brain size in Squamata. N = sample size (NA indicates that the original source did not report the sample size), BoM = body mass (in gram), BrM = brain mass (in gram). The column 'Limbs' indicates the limb status of the species (P = present, A = absent and R = reduced), Bio indicates the biogeographical realm from which the species originates (AF = Afrotropics; AU = Australasian; NEA = Nearctic; NT = Neotropics; PA = Palaearctic, OC = Oceania). Eco indicates the ecological guild (Ar = arboreal, Sa = saxicolous, GD = ground-dwelling and Fo = fossorial). Hg is the score for habitat generalism (number of habitat categories in which the species can be found) and Soc = sociality (Y = social, N = solitary, NA = no data available). See main text (Chapter 2) for more information regarding this data. Sources from which brain and ecological data was taken are reported below. Body mass was taken from the same source as brain mass unless states otherwise.

Species	N	Seks	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Acanthosaura armata	NA	NA	43	0.182 (i)	P	IND	Ar (*f*)	2	NA
Agama agama	80	M+F	29.3	0.173 (c,d)	P	AF	Sa (θ)	4	Y
Agkistrodon piscivorus	1	F	728	0.64 (b)	A	NT	GD (g)	4	Y
Amalosia rhombifer	1	NA	1.68	0.0196 (f)	P	AU	Ar (€)	1	NA
Amblyrhynchus cristatus	1	F	4190	1.44 (f)	P	NT	GD (m,u)	2	Y
Ameiva ameiva	3	M+F	27.1	0.231 (c,d)	P	NT	GD (v)	4	N
Amphibolurus muricatus	1	NA	28	0.146 (f)	P	AU	Ar (€)	3	NA
Anguis fragilis	31	M+F	22	0.044 (c,d)	A	PA	GD (λ)	4	Y
Anolis auratus	1	M	10.5	0.073 (c,d)	P	NT	Ar (p)	3	N
Anolis carolinensis	10	M	4.08	0.028 (q)	P	NEA	Ar (Σ)	3	Y
Anolis cristatellus	10	M+F	9.56	0.098 (o)	P	NT	Ar (d,z)	3	N
Anolis evermanni	10	M+F	4.95	0.073 (o)	P	NT	Ar (d,i)	2	N
Anolis gundlachi	10	M+F	6.29	0.091 (o)	P	NT	Ar (d,z)	1	N

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Anolis krugi	10	M+F	2.43	0.050 (o)	P	NT	Ar (f, φ)	1	N
Anolis pulchellus	8	M+F	1.86	0.041 (o)	P	NT	Ar (f, φ)	2	N
Anolis stratulus	10	M+F	2.19	0.071 (o)	P	NT	Ar (z, φ)	2	N
Aspidoscelis gularis	10	M	17.68	0.067 (q)	P	NEA	GD (κ)	3	N
Boa constrictor	2	M+F	3144.5	0.545 (c,d)	A	NT	GD (x,ψ)	9	N
Bronchocela cristatella	NA	NA	1.7	0.029 (i)	P	IND	Ar (ƒ)	2	NA
Callopistes maculatus	1	M	50.3	0.318 (c,d)	P	NT	GD (b)	2	N
Calotes versicolor	1	M	14.6	0.097 (c,d)	P	AF	Ar (ƒ)	2	N
Carlia amax	2	NA	1	0.017 (f)	P	AU	GD (o,€)	4	NA
Carlia bicarinata	3	NA	2.23	0.0162 (f)	P	AU	GD (r)	3	NA
Cerastes vipera	1	F	62.1	0.076 (c,d)	A	PA	GD (y)	2	NA
Chalarodon madagascariensis	80	M+F	6.3	0.06 (c,d)	P	AF	GD (π, §)	5	NA
Chalcides chalcides	1	F	18.8	0.055 (c,d)	R	PA	GD (λ)	4	N
Chalcides mionecton	1	F	6.4	0.03 (c,d)	R	PA	GD (y)	4	NA
Chalcides ocellatus	3	M+F	32	0.09 (c,d)	P	PA	GD (y)	4	NA
Chalcides polylepis	NA	NA	7.9	0.037 (i)	P	PA	GD (y)	4	NA
Chondrodactylus turneri	45	F	20.2	0.095 (p)	P	AF	Sa (θ)	2	NA
Christinus marmoratus	3	NA	3.09	0.0309 (f)	P	AU	Ar (€)	2	Y
Coluber constrictor	3	M+F	431	0.291 (b)	A	NEA	GD (κ)	4	NA
Concinnia queenslandiae	1	NA	8.4	0.0432 (f)	P	AU	GD (€)	1	Y
Cordylus cordylus	1	M	56.5	0.175 (c,d)	P	AF	Sa (α)	1	Y

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Coronella girondica	1	M	117	0.088 (c,d)	A	PA	GD (ε, λ)	5	NA
Crotalus oreganus	14	M	745.14	0.261 (m)	A	NEA	GD (κ)	7	N
Cryptoblepharus litoralis	1	NA	1.41	0.0171 (f)	P	AU	Sa (€)	3	NA
Cryptoblepharus plagiocephalus	2	NA	1.3	0.0128 (f)	P	AU	Ar (o,q)	3	NA
Cryptoblepharus virgatus	5	NA	0.95	0.0122 (f)	P	AU	Ar (€)	4	NA
Ctenophorus caudicinctus	19	M+F	15.28	0.106 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus cristatus	20	M+F	35.57	0.183 (t,u)	P	AU	GD (€)	1	NA
Ctenophorus decresii	20	M+F	16.026	0.112 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus fionni	21	M+F	14.93	0.099 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus fordi	21	M+F	3.919	0.046 (t,u)	P	AU	GD (€)	1	N
Ctenophorus gibba	19	M+F	15.07	0.103 (t,u)	P	AU	GD (€)	1	NA
Ctenophorus isolepis	20	M+F	8.19	0.066 (t,u)	P	AU	GD (€)	2	NA
Ctenophorus nuchalis	18	M+F	27.429	0.149 (f,t,u)	P	AU	GD (€)	2	NA
Ctenophorus ornatus	17	M+F	21.75	0.118 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus pictus	30	M+F	9.564	0.083 (f,t,u)	P	AU	GD (€)	1	NA
Ctenophorus rufescens	20	M+F	20.44	0.120 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus salinarum	20	M+F	8.84	0.083 (t,u)	P	AU	GD (€)	1	NA
Ctenophorus tjantjalka	19	M+F	10.56	0.094 (t,u)	P	AU	Sa (€)	1	NA
Ctenophorus vadnappa	18	M+F	14.35	0.105 (t,u)	P	AU	Sa (€)	1	NA
Ctenotus inornatus	1	NA	11	0.0623 (f)	P	AU	GD (Γ)	8	NA
Ctenotus regius	1	NA	6.3	0.0419 (f)	P	AU	GD (€)	3	NA

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Ctenotus robustus	1	NA	20.4	0.0836 (f)	P	AU	GD (€)	5	N
Cyclodomorphus casuarinae	1	NA	13.8	0.0718 (f)	P	AU	GD (€)	4	NA
Delma australis	1	NA	1.9	0.0118 (f)	A	AU	GD (l,€)	4	N
Diplodactylus conspicillatus	1	NA	4.4	0.025 (f)	P	AU	GD (χ,€)	4	NA
Diplodactylus tessellatus	1	NA	3.1	0.0313 (f)	P	AU	GD (η, €)	2	NA
Diporiphora bilineata	3	NA	3.93	0.0493 (f)	P	AU	GD (€)	4	NA
Diporiphora lalliae	1	NA	8.5	0.0744 (f)	P	AU	GD (€)	3	NA
Draco volans	NA	NA	4.5	0.058 (f)	P	IND	Ar (*f*)	2	NA
Egernia cunninghami	1	NA	246	0.3122 (f)	P	AU	Sa (€)	1	Y
Egernia striolata	1	NA	36.4	0.166 (f)	P	AU	Ar (¢)	3	Y
Emoia atrocostata	1	NA	13.14	0.0847 (f)	P	AU	GD (t)	4	NA
Emoia pallidiceps	2	NA	4.51	0.0436 (f)	P	AU	GD (t)	4	NA
Emoia submetallica	1	NA	3.31	0.03595 (f)	P	AU	GD (t)	1	NA
Eremias argus	6	M	3.56	0.052 (s)	P	PA	GD (▼)	3	NA
Eremiascincus isolepis	1	NA	12.5	0.0462 (f)	P	AU	GD (€)	2	NA
Eublepharis macularius	3	NA	28.64	0.091 (v)	P	IND	GD (■)	7	N
Eugongylus albofasciolatus	1	NA	53	0.1592 (f)	P	AU	GD (δ)	2	NA
Eumeces schneideri	1	M	51.7	0.172 (c,d)	P	PA	GD (y)	5	N
Furcifer lateralis	80	M+F	10.9	0.061 (c,d)	P	AF	Ar (ø)	4	N
Gallotia galloti	10	NA	54.12 (#)	0.18 (h)	P	PA	GD (β, λ)	3	N
Gehyra australis	1	NA	3.2	0.0332 (f)	P	AU	Ar (€)	4	NA

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Gehyra mutilata	1	NA	2.6	0.0341 (f)	P	AU	Ar (€)	5	NA
Gehyra oceanica	1	NA	14.6	0.0973 (f)	P	OC	Ar (£)	4	NA
Gehyra punctata	1	NA	2.6	0.0259 (f)	P	AU	Sa (€)	1	NA
Gehyra variegata	2	NA	5.25	0.0474 (f)	P	AU	Ar (e,€)	5	NA
Gehyra vorax	2	NA	36.1	0.1615 (f)	P	OC	Ar (£)	2	NA
Gekko gecko	1	M	54.8	0.198 (c,d)	P	IND	Sa (*f*)	2	Y
Glaphyromorphus fuscicaudis	2	NA	10.75	0.0512 (f)	P	AU	GD (€)	2	NA
Heloderma suspectum	1	F	514	0.729 (b)	P	NEA	GD (κ)	4	N
Hemidactylus brookii	4	M+F	4.7	0.043 (a)	P	IND	Ar (*f*)	2	NA
Hemidactylus frenatus	3	NA	4.85	0.0394 (f)	P	AU	Ar (€)	8	N
Hemidactylus mabouia	1	M	2.5	0.033 (c,d)	P	AF	Sa (ζ, θ)	3	NA
Hemidactylus turcicus	10	M	2.68	0.021 (q)	P	NEA	Sa (λ)	2	Y
Hemiergis peronii	1	NA	1.29	0.0105 (f)	R	AU	Fo (€)	1	NA
Hemiphyllo-dactylus typus	1	NA	0.607	0.0093 (f)	P	IND	Ar (£)	3	NA
Heteronotia binoei	1	NA	4.6	0.0337 (f)	P	AU	GD (e,€)	5	NA
Hierophis viridiflavus	3	M+F	285.1	0.209 (c,d)	A	PA	GD (λ)	5	Y
Hypsilurus boydii	1	NA	101	0.338 (f)	P	AU	Ar (€)	1	NA
Hypsilurus papuensis	1	NA	88	0.306 (f)	P	AU	Ar (Đ)	1	NA
Iguana iguana	1	F	253.5	0.606 (c,d)	P	NT	Ar (a,w)	6	Y
Lacerta agilis	2	M+F	12.507	0.076 (a)	P	PA	GD (β,λ)	5	N
Lacerta viridis	88	M+F	21.2	0.109 (c,d)	P	PA	Ar (β,λ)	4	N

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Lampropholis guichenoti	1	NA	1.55	0.0201 (f)	P	AU	GD (€)	4	NA
Leiocephalus carinatus	10	M	16.79	0.072 (q)	P	NT	GD (ι,Þ)	3	NA
Lepidodactylus lugubris	3	NA	1.38	0.0169 (f)	P	AU	Ar (£)	4	NA
Lepidodactylus orientalis	3	NA	1.45	0.0178 (f)	P	AU	Ar (k)	2	NA
Lerista bipes	1	NA	1	0.0051 (f)	A	AU	Fo (€)	2	NA
Lerista bougainvillii	1	NA	1.89	0.0111 (f)	R	AU	Fo (€)	3	NA
Lerista muelleri	1	NA	0.6	0.0045 (f)	R	AU	Fo (€)	4	NA
Lerista punctatovittata	1	NA	6.2	0.018 (f)	R	AU	Fo (€)	4	NA
Lialis burtonis	1	NA	23.5	0.0369 (f)	A	AU	GD (€)	4	N
Liolaemus chiliensis	1	M	26	0.104 (c,d)	P	NT	Ar (ς)	2	NA
Lobulia elegans	1	NA	3.46	0.0373 (f)	P	AU	Ar (n)	2	NA
Lophognathus temporalis	1	NA	48.5	0.171 (f)	P	AU	Ar (€)	4	NA
Lucasium damaeum	1	NA	2.5	0.0297 (f)	P	AU	GD (€)	2	NA
Lygisaurus foliorum	1	NA	1	0.0251 (f)	P	AU	GD (€)	3	NA
Lygisaurus novaeguineae	1	NA	1.31	0.0141 (f)	P	AU	GD (ω)	2	NA
Moloch horridus	1	NA	61	0.0985 (f)	P	AU	GD (€)	3	Y
Morethia boulengeri	1	NA	1.91	0.0211 (f)	P	AU	GD (€)	3	NA
Nactus pelagicus	2	NA	5.89	0.0338 (f)	P	AU	GD (£,€)	3	NA
Naja melanoleuca	1	NA	1770	0.646 (a)	A	AF	GD (θ)	4	N
Natrix maura	6	F	86	0.095 (c,d)	A	PA	GD (λ)	3	NA
Natrix natrix	31	M+F	74.1	0.115 (c,d)	A	PA	GD (λ)	2	N

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Nephrurus levis	1	NA	11.5	0.0834 (f)	P	AU	GD (e,€)	4	NA
Notoscincus ornatus	1	NA	0.8	0.0091 (f)	P	AU	GD (€)	4	NA
Oedura marmorata	1	NA	24.3	0.0774 (f)	P	AU	Ar (€)	2	NA
Oedura monilis	1	NA	10.2	0.0652 (f)	P	AU	Ar (€)	2	NA
Oplurus cuvieri	1	M	51	0.267 (c,d)	P	AF	Ar (ζ)	1	NA
Papuascincus stanleyanus	3	NA	3.86	0.0354 (f)	P	AU	GD (n)	6	NA
Phelsuma cepediana	1	M	5	0.059 (c,d)	P	AF	Ar (Ω)	1	NA
Phrynocephalus przewalskii	15	M+F	5.4	0.053 (j)	P	PA	GD (æ)	3	NA
Phyllodactylus gerrhopygus	NA	NA	0.68	0.018 (i)	P	NT	GD (#)	2	NA
Podarcis liolepis	100	M+F	3.3	0.034 (k,r)	P	PA	Sa (λ)	2	NA
Podarcis muralis	73	M+F	4.2 (*)	0.046 (c,d)	P	PA	Sa (β, λ)	3	N
Podarcis siculus	8	NA	8.99	0.0495 (e)	P	PA	GD (λ)	4	NA
Pogona vitticeps	10	NA	315	0.398 (f,g)	P	AU	GD (€)	5	Y
Prasinohaema flavipes	1	NA	11.25	0.056 (f)	P	AU	Ar (s)	1	NA
Psammodromus algirus	1	F	4.3	0.045 (c,d)	P	PA	GD (λ)	2	N
Psammodromus hispanicus	1	F	2.1	0.025 (c,d)	P	PA	GD (λ)	3	NA
Pseudemoia entrecasteauxii	3	NA	3.1	0.0239 (f)	P	AU	GD (€)	3	NA
Pseudopus apodus	NA	NA	498	0.342 (i)	A	PA	GD (λ)	3	NA
Pygopus nigriceps	2	NA	10.2	0.0291 (f)	A	AU	GD (€)	4	N
Python molurus	1	M	6140	1.123 (b)	A	AF	GD (ƒ)	4	N
Python regius	26	M	570.26	0.2973 (n)	A	AF	GD (σ)	6	N

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Saltuarius cornutus	1	NA	51	0.1351 (f)	P	AU	Ar (€)	1	NA
Saproscincus challengeri	1	NA	1.9	0.0187 (f)	P	AU	GD (€)	1	NA
Sceloporus occidentalis	30	M	18.386	0.067 (f, l)	P	NEA	GD (κ)	4	Y
Sceloporus olivaceus	10	M	19.25	0.072 (q)	P	NEA	Ar (c)	3	NA
Scincella lateralis	9	M	1	0.010 (q)	P	NEA	GD (Δ)	2	NA
Scincus scincus	80	M+F	34.1	0.116 (c,d)	P	PA	GD (y)	2	NA
Sphenodon punctatus	2	NA	584.5	0.616 (i)	P	AU	GD(j)	3	N
Sphenomorphus fragilis	3	NA	1.35	0.0123 (f)	R	AU	Fo (h)	4	NA
Strophurus ciliaris	1	NA	6.4	0.0504 (f)	P	AU	Ar (e,€)	5	NA
Strophurus elderi	1	NA	1.75	0.0172 (f)	P	AU	Ar (e,€)	3	NA
Tarentola mauritanica	11	M+F	7.8	0.07 (c,d)	P	PA	Sa (y)	2	Y
Thamnophis sirtalis	2	F	54.5	0.1 (b)	A	NEA	GD (κ)	6	Y
Tiliqua gigas	1	NA	532	0.498 (f)	P	AU	GD (υ)	2	NA
Tiliqua multifasciata	2	NA	404.5	0.4078 (f)	P	AU	GD (€)	2	NA
Tiliqua rugosa	2	NA	495	0.533 (f)	P	AU	GD (€)	5	Y
Timon lepidus	1	F	70.8	0.224 (c,d)	P	PA	GD (λ)	4	N
Trapelus mutabilis	46	M+F	12.9	0.099 (c,d)	P	NEA	GD (y)	5	NA
Trogonophis wiegmanni	NA	NA	6.5	0.021 (c,d)	A	PA	Fo (y)	3	Y
Tupinambis teguixin	NA	NA	1034	1.563 (i)	P	NT	GD (¤)	4	N
Underwoodi-saurus milii	2	NA	5.72	0.0531 (c,d)	P	AU	GD (€)	2	Y
Uromastyx acanthinura	3	M+F	164	0.335 (f)	P	AU	GD (y)	2	N

Supplementary Table S2.1. (Continued)

Species	N	Sex	BoM (g)	BrM (g)	Limbs	Bio	Eco	Hg	Soc
Varanus acanthurus	1	NA	212	0.278 (f)	P	AU	Sa (€)	1	N
Varanus gilleni	1	NA	21	0.107 (f)	P	AU	Ar (μ,€)	2	N
Varanus griseus	3	F	254.2	0.722 (c,d)	P	PA	GD (μ)	3	N
Varanus niloticus	1	NA	7500	2.44 (a)	P	AF	GD (μ)	7	N
Varanus prasinus	1	NA	249	0.594 (f)	P	AU	Ar (μ)	3	N
Varanus salvadorii	1	NA	2650	2.402 (f)	P	AU	Ar (μ)	2	N
Vipera aspis	46	M+F	68.7	0.1015 (c,d)	A	PA	GD (λ)	4	N
Vipera berus	7	NA	64.2	0.105 (a)	A	PA	GD (λ)	5	Y
Zamenis longissimus	1	F	148.2	0.168 (c,d)	A	PA	Ar (λ)	4	NA
Zonosaurus maximus	2	M+F	386.4	0.565 (c,d)	P	AF	GD (*)	3	NA
Zonosaurus quadrilineatus	1	M	82.7	0.209 (c,d)	P	AF	GD (τ)	2	N
Zootoca vivipara	1	F	3.2	0.028 (c,d)	P	PA	GD (β, λ)	7	Y

Brain data was taken from: a - Dubois (1913); b - Crile and Quiring (1940); c - Platel (1975); d - Platel (1979); e - Wächtler (1980); f - Black (1983); g - Else (1984); h - Molowny et al. (1987); i - Platel (1989); j - Shen et al. (2005); k - Sampedro et al. (2008); l - Suski et al. (2008); m - Holding et al. (2012); n - Bales (2014); o - Powell and Leal (2014); p - Barabanov et al. (2015); q - Robinson et al. (2015); r - Sampedro (2015); s - Chang et al. (2017); t - Hoops et al. (2017a); u - Hoops et al. (2017b) and v - shared by Matthew Vickaryous.

Body mass was taken from * - Angelini et al. (1986); # - Huyghe et al. (2005)

Ecological data was taken from: a - Swanson (1950); b - Donoso-Barros (1960); c - Dutton et al. (1975); d - Huey and Webster (1976); e - Pianka and Pianka (1976); f - Gorman and Harwood (1977); g - Kofron (1978); h - Greer and Parker (1979); i - Lister (1981); j - Walls (1981); k - Pernetta and Black (1983); l - Chapman and Dell (1985); m - Rauch (1985); n - Allison and Greer (1986); o - Braithwaite (1987); p - Fleishman (1988); q - Martin and Freeland (1988); r - Ingram and Covacevich (1989); s - Hyndman and Menzies (1990); t - Brown (1991); u - Buttemer and Dawson (1993); v - Vitt and Colli (1994); w - Alvarado et al. (1995); x - Henderson et al. (1995); y - Schleich et al. (1996); z - Fleishman et al. (1997); α - Branch (1998); β - Vanhooydonck and Van Damme (1999); Γ - Woinarski et al. (1999); δ - Buden (2000); ε - Luiselli et al. (2001); ζ - Rodda et al. (2001); η - Read (2002); θ - Spawls et al. (2002); ι - Smith and Engeman (2003); κ - Stebbins (2003); λ - Arnold and Ovenden (2004); μ - Pianka et al. (2004); ζ - Randriamahazo and Mori (2004); π - D'Cruze and Sabel (2005); Σ - Irschick et al. (2005); σ - Luiselli et al. (2005); ς - Pincheira-Donoso and y Núñez (2005); τ - Yoder et al. (2005); υ - Allison (2006); φ - Cooper (2006); χ - Greer (2006); ψ - Romero-Nájera et al. (2006); Ω - Harmon et al. (2007); ω - Kraus (2007); * - Ramanamanjato (2007); Δ - Paulissen (2008); § - Bora et al. (2009); ø - Randrianantoandro et al. (2009); ¢ - Michael et al. (2010); # - Pérez and Balta (2011); ¤ - Passos et al. (2013); £ - Zug (2013); € - Cogger (2014); Þ - Torres et al. (2014); ▼ - Zeng et al. (2014); ƒ - Das (2015); Đ - Oliver and Tallowin (2015); æ - Li et al. (2017); ■ - Ali et al. (2018)

CHAPTER 2: SUPPLEMENTARY METHODS

Categories for habitat generalism

Table S2.2 gives the 13 habitat categories used to estimate habitat generalism. Per species, we noted the presence/absence in each category. The total number of categories in which a species occurred was then used as an indicator for ecological generalism. Habitat data was taken from field guides and literature (see above).

Supplementary Table S2.2. Habitat categories used in this study to estimate habitat generalism. For each category, examples of habitat descriptions in field guides are given that fell within this category.

Habitat category	Examples
Aquatic	Ponds; mountain streams; prairie swales;
Wetland	Mangroves; marshes; bogs; wetlands; swamp forest; littoral forest
Sandy desert/dune	Sandy desert; coastal desert; beaches; sand flats; wadi; succulent desert, sand dunes;
Rocky desert	Gibber plains; hamada; rocky desert;
Rocky habitat	Rock cliffs; rock outcrops; caves; boulders; rock crevices; mountain slopes;
Grassland	Pasture; grassland; prairie; meadow; spinifex grasslands; steppe
Shrubland	Different types of scrubland; heathland; chaparral, scrub forests; sagebrush; shrubland; bushland;
Savanna	Savanna
Thicket	Thicket
Woodland	Woodland; open wood/forest; pindan; mallee
Forest	Dry deciduous forest; open secondary forest; (sub)montane forest; rainforest, tropical forest;
Rural and urban	Parks; urban habitats; gardens; agricultural land; buildings; vineyards; ruins
Ecotone	Forest clearings; forest edge; wood glade; oases; intertidal areas; hedgerows; field edges;

Confounding variables

In order to account for the effect of limb reduction on relative brain size, we assigned each species to one of the following categories: 1) all four limbs fully developed (n = 142), 2) limbs distinctly reduced relative to body size (n = 7), and 3) at least one pair of limbs lacking entirely (n = 23). Data on limb status was taken from morphological descriptions in field guides and literature (same as used for habitat generalism, see Supplementary Table S2.1).

As selection for larger or smaller brains might depend on the geographic location, as suggested by Amiel et al. (2011), we included the biogeographical realm of each species as covariate in further statistical analyses. Biogeographical realm was based upon the location where the species was sampled in the original paper where brain size was taken from. If not specified, we based ourselves on distribution data from the Reptile Database (Uetz et al., 2018). Our data included 15 Afrotropical, 88 Australasian, 9 Indo-Malayan, 11 Nearctic, 17 Neotropic, 2 Oceanic and 31 Palaerarctic species.

Statistical analyses for social data

The effect of sociality on relative brain size was tested using phylogenetic generalized least squares (PGLS) models, in order to take the phylogenetic relatedness of species into account. Brain mass (log10-transformed) was the response variable, while body mass (log10-transformed) and biogeographic realm were included as covariates. Due to convergence problems with the social model when including limb status as covariate, we only tested the effect of sociality in fully limbed species (51/68). At first, we used the ‘gls’ function in the ‘nlme’ package in R (Pinheiro et al., 2014), with Pagel correlation structure and Pagel’s λ optimized by maximum likelihood. As this model returned a negative value for lambda (see main results), we verified our results using a) the same model, but now with restricted maximum likelihood methods and b) the ‘pgls’ function in the ‘caper’ package (Orme et al., 2018).

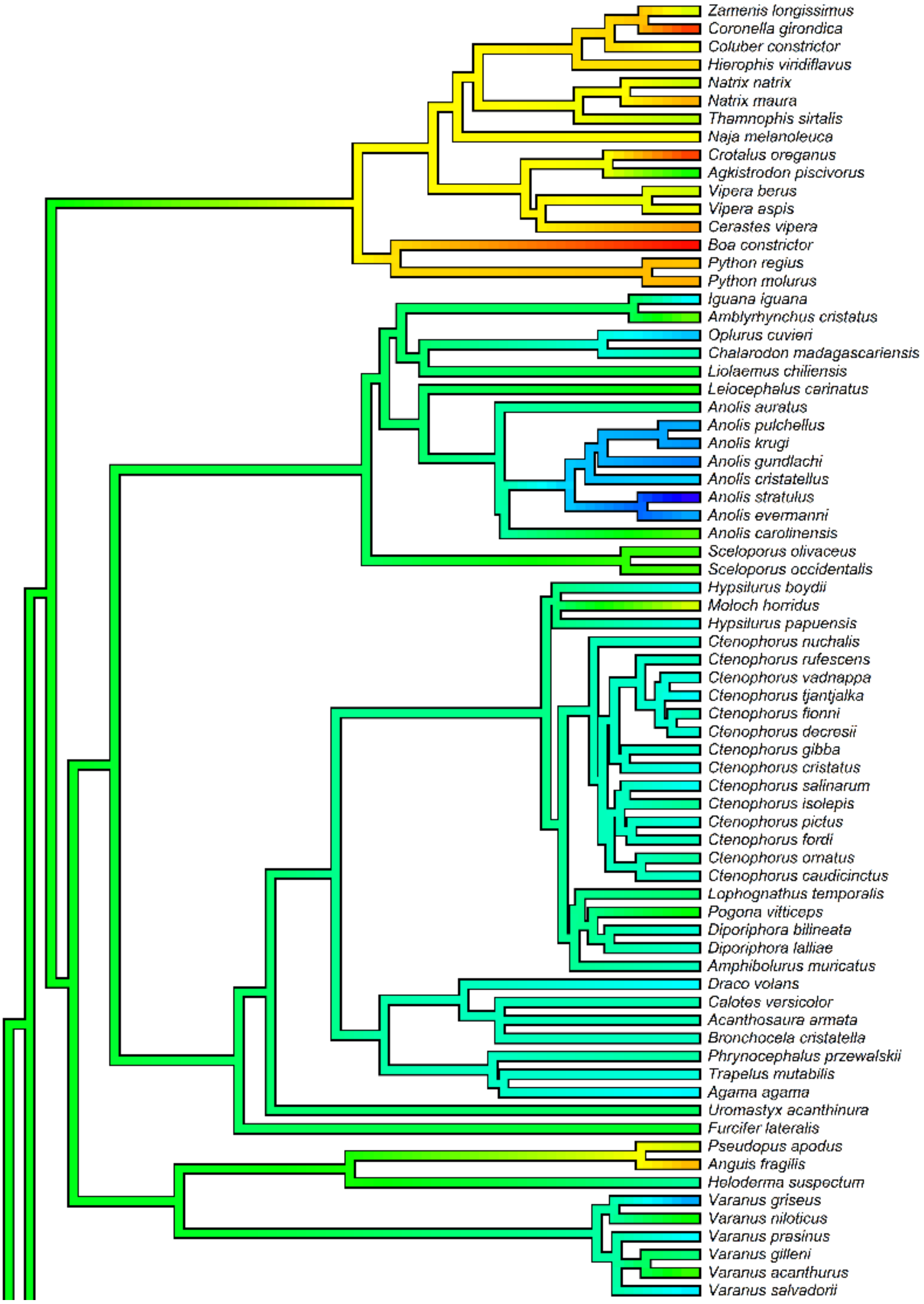
CHAPTER 2: SUPPLEMENTARY RESULTS

Effect of sociality on brain size

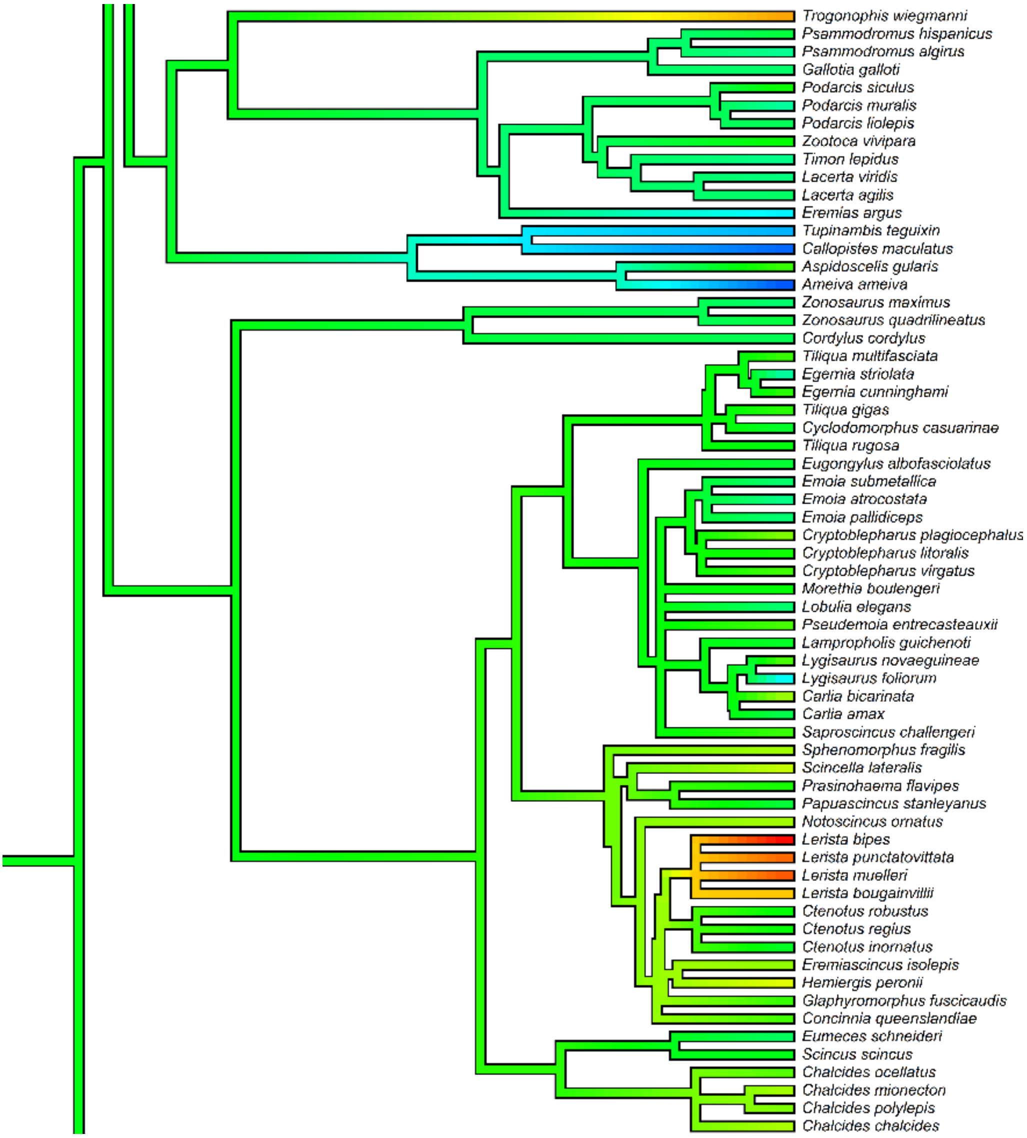
All three approaches give very similar results (see Table S2.3. and Table 1 in main text). There was always a significant effect of sociality, with relative brain size being higher in solitary species compared to social species. Pagel’s λ was either estimated to be negative, or zero. Note that the ‘pgls’ function in caper is automatically restricted to values between 0 and 1 for Pagel’s λ.

Supplementary Table S2.3 Outcome of the Phylogenetic Generalized Least Square Regressions for the social data. In all models, only fully limbed species were included (N=51). Brain size and body size were both log10-transformed. Abbreviations: AF = Afrotropics, AU = Australasia, IM = Indo-Malayan, NA = Nearctic, NT = Neotropics, AU = Australasian, NA = Nearctic, PA = Palearctic, OC = Oceania.

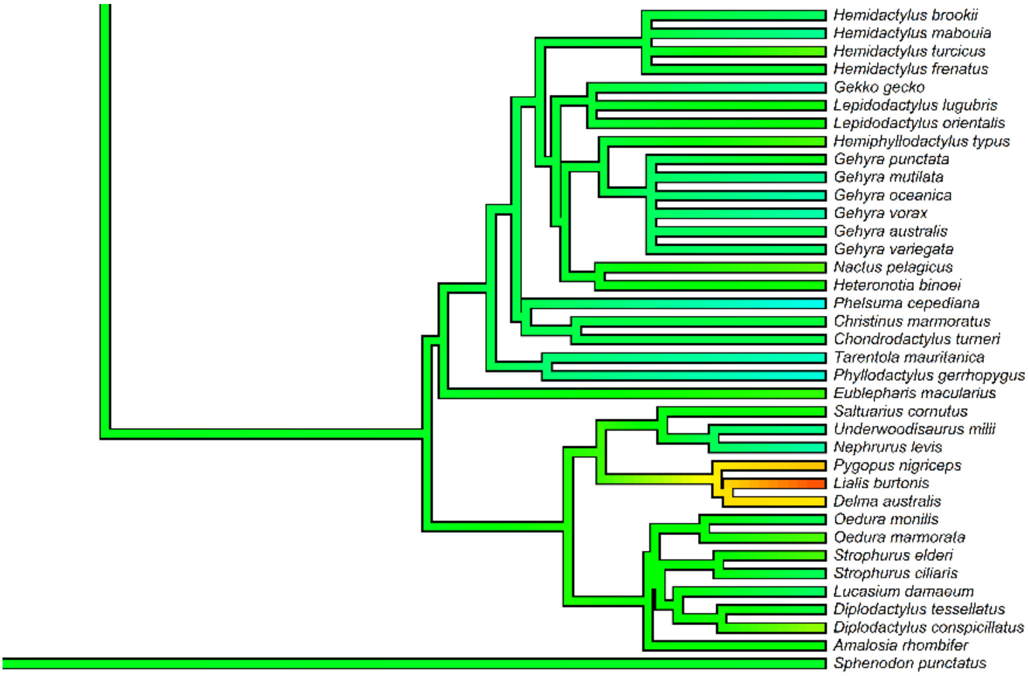
	Predictor	Effect	F-statistics	Significance	Λ
Brain size gls – ML	Body size	b = 0.568 ± 0.013	$F_{1,43}$ = 18*10^4	$p < 0.001$	-0.88
	Sociality	Solitary > Social	$F_{1,43}$ = 20.00	$p < 0.001$	
	Biogeographical realm	NT > AU, PA	$F_{5,43}$ = 7.00	$p < 0.001$	
Brain size gls - REML	Body size	b = 0.563 ± 0.017	$F_{1,43}$ = 1132	$p < 0.001$	-0.06
	Sociality	Solitary > Social	$F_{1,43}$ = 18.91	$p < 0.001$	
	Biogeographical realm	NT > AF, AU, NA, PA	$F_{5,43}$ = 6.24	$p < 0.001$	
Brain size pgls - ML	Body size	b = 0.560 ± 0.018	$F_{1,43}$ = 1016	$p < 0.001$	0
	Sociality	Solitary > Social	$F_{1,43}$ = 5.24	$p = 0.027$	
	Biogeographical realm	NT > AF, AU, NA, PA, IM	$F_{5,43}$ = 7.82	$p < 0.001$	



Supplementary Figure S2.1. Ancestral state reconstruction of relative brain size (residuals of brain on body mass regression) along the nodes and branches of the phylogenetic tree of 171 species of Squamata. *Sphenodon punctatus* is included as outgroup. Species with positive residuals (blue) have large brains relative to their body size, while species with negative residuals (yellow-red) have small brains relative to their body size. Visualized using the 'contMap' function in R (package 'phytools'; Revell, 2012).



Supplementary Figure S2.1. (Continued)



Supplementary Figure S2.1. (Continued)

APPENDIX CHAPTER 3

CHAPTER 3: SUPPLEMENTARY METHODS

Species description

In the following paragraphs, a short species description is provided, including information on the geographic range and origin of the individuals obtained for this study.

Acanthodactylus pardalis

Acanthodactylus pardalis Lichtenstein, 1823, more commonly known as the leopard fringe-fingered lizard. is endemic to North-Africa, with a distribution from Libya to Israel (Salvador, 1982). It is a ground-dwelling species, mostly found in open habitats with a dry and sandy substrate (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Van Damme & Vanhooydonck, 2002). The individuals used in this study were obtained from pet-trade, after being wild-caught in their native range in Egypt. Two different batches (2019 and 2020) were used in this study.

Dalmatolacerta oxycephala

Dalmatolacerta oxycephala Duméril & Bibron, 1839, is a small to medium-sized lizard. The sharp-snouted rock lizard is, as the name implies, mostly found in rocky areas (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Speybroeck et al., 2018). It is found along the East-Adriatic coast and on many small islands (Speybroeck et al., 2018). The individuals in this study were wild-caught in Vis (43°04'26.3"N 16°11'48.9"E), Croatia, on the remains of an old fortress.

Eremias brenchleyi

Eremias brenchleyi Günther, 1872, or Ordos racerunner, is found in North-East China (Guo et al., 2011). It is a ground-dwelling species, inhabiting dry habitats with sandy substrates (Arnold, 1998) and rocky slopes with bare rocks (Du et al., 2005). The individuals were obtained from the pet-trade, after being caught in their natural habitat in Hebei, China.

Gastropholis prasina

Gastropholis prasina Werner, 1904, is a slim, bright green lizard. The green keel-bellied lizard is an arboreal species, spending most of its time in the dense canopy layer of trees (Arnold, 1998). It inhabits areas with moist woodland and lowland grasslands of the coastal plains of Kenya and Tanzania (Spawls & Rotich, 1997). The individuals in this study were obtained via pet-trade and bred in captivity for an unknown number of generations.

Lacerta viridis

Lacerta viridis Laurenti, 1768, more commonly known as the European green lizard, is a medium- to large-sized lizard. It lives in habitats with dense vegetation, where it is often observed climbing in bushes and hedges (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Speybroeck et al., 2018). It is found in East-Germany, South-Austria, Czech Republic, Hungary, South-Ukraine, and the Balkan region (Speybroeck et al., 2018). The individuals were wild-caught in Dariva (43°51'25.1"N 18°26'53.2"E), near Sarajevo (Bosnia and Herzegovina) in a park close to a river canyon. Two batches were used in this study, with the batch from 2019 for IC, LR and ESC, and the second batch from 2021 for SL and RL.

Podarcis erhardii

Podarcis erhardii Bedriaga, 1876, Erhard's wall lizard, is a small to medium-sized lizard. This species is found in sunny areas with low vegetation (Vanhooydonck & Van Damme, 1999; Speybroeck et al., 2018). This wall lizard is found in the Balkan peninsula and the Aegean islands (Speybroeck et al., 2018). Individuals from this species were wild-caught from five different locations on Naxos Island (37°06'07.8"N 25°22'34.5"E) (Cyclades, Greece), ranging from more open areas with sparse vegetation to densely vegetated abandoned agricultural terraces with dry stone walls and rocky outcrops present.

Podarcis melisellensis

Podarcis melisellensis Braun, 1877, is a medium-sized lizard, mostly found in sunny areas. It inhabits environments with many vertical elements such as rocks (Arnold, 1998; Van Damme & Vanhooydonck, 2002; Meiri, 2018; Speybroeck et al., 2018). The Dalmatian wall lizard is found along the East-Adriatic coast. reaching from North Italy until Montenegro (Speybroeck et al., 2018). Individuals were captured from Brusnik (43°00'23.6"N 15°48'02.6"E), Mali Bariak (43°03'09.4"N 16°02'22.9"E), and Vis (43°02'47.9"N 16°09'14.1"E), Croatia.

Podarcis muralis

Podarcis muralis Laurenti, 1768, is a small to medium-sized lizard that lives mostly in sunny, often rocky, areas (Arnold, 1998; Vanhooydonck & Van Damme, 1999;

Speybroeck et al., 2018). The distribution of the common wall lizard comprises central and Southern Europe (Speybroeck et al., 2018). Individuals were wild-caught from Muizen (51°01'05.7"N 4°30'51.3"E) (Belgium) in a densely vegetated railroad berm with stones (an urbanised area).

Podarcis siculus

Podarcis siculus Rafinesque-Schmaltz, 1810, more commonly known as the Italian wall lizard, lives in places with a lot of dense vegetation and is mostly terrestrial (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Speybroeck et al., 2018). *Podarcis siculus* is originally from central Italy but has been introduced outside its native range: throughout the Mediterranean basin and even as far as North-America (Speybroeck et al., 2018). The individuals caught for this study were from an invasive population in Nin (44°14'09.1"N 15°11'01.5"E), Croatia.

Podarcis ionicus

Podarcis ionicus Lehrs, 1902, or the Ionian wall lizard, was formerly considered a subspecies of *Podarcis tauricus* (Psonis et al., 2017; Psonis et al., 2021). It is a terrestrial lizard inhabiting open habitats (Speybroeck et al., 2018) and can be found on the Western Greek mainland (e.g. Peloponnese), several western Greek Islands and Southwestern Albania (Psonis et al., 2017; Psonis et al., 2021) The individuals were wild-caught at Lake Doxa (37°55'44.6"N 22°17'09.2"E), Greece.

Takydromus sexlineatus

Takydromus sexlineatus Daudin, 1802, is more commonly known as the six-striped long-tailed grass lizard. As the name implies, it is found in areas with low but dense, grassy vegetation (Arnold, 1998; Vanhooydonck & Van Damme, 1999). *Takydromus sexlineatus* is found in large areas of South-East Asia (Arnold, 1997). The individuals were obtained from pet-trade, and captive-bred for an unknown number of generations.

Timon lepidus

Timon lepidus Daudin, 1802, is one of the largest lizards found in Europe. It is a terrestrial species inhabiting densely vegetated areas (rocks and bushes) (Van Damme & Vanhooydonck, 2002; Speybroeck et al., 2018). The jewelled lizard is found on the Iberian peninsula and a few areas in Southern France and North-West Italy (Speybroeck et al., 2018). The individuals in this study were provided by a hobbyist breeder for the duration of the experiment. These individuals were the second- or third generation descendants bred in captivity from wild-caught specimen from Southern-France.

Zootoca vivipara

Zootoca vivipara Lichtenstein, 1823, more commonly known as the viviparous or common lizard, is a small Eurasian lizard. It is found in moist areas with a lot of low vegetation; it is a ground-dwelling species (Arnold, 1998; Vanhooydonck & Van Damme, 1999; Speybroeck et al., 2018). *Zootoca vivipara* has the largest distribution of all reptiles, longitudinally from Ireland to Japan, and latitudinally from the Pyrenees to northern Scandinavia. It is absent in most parts of Southern Europe (Speybroeck et al., 2018). The individuals were wild-caught from a moist, dense heathland in Het Marum, Wuustwezel (51°22'46.0"N 4°36'43.6"E), Belgium.

Environmental variables and life history characteristics – extra methodology

We always tried to extract climate and NDVI data from the exact location where animals were collected. For wild-caught species obtained via the pet trade we were often unable to get data on the exact capture site, but could limit it down to a specific county or region. In such cases, we took the average climatic variables of several known populations of the particular species within this limited range (coordinates obtained via literature or sighting websites). For species bred in captivity, we tried to gain information about the origin of the wild-caught ancestors and followed the protocol above where possible. If the individuals from one species were captured from different locations, the climate and NDVI data was also averaged across these different populations. For *P. melisellensis*, climate and NDVI data could not be collected for the populations from Brusnik and Mali Bariak due to the small size of these islands. See Supplementary Table S3.3 for details about the origin, coordinates of capture locations/sightings, and the activity season. Climate data was only available between 2000 and 2018, and NDVI between 2000 and 2021. To get the most accurate representation, the maximal time period was used for both (until 2018 for climate data, and until 2021 for NDVI).

We calculated the average temperature the lizards experience in their natural environment. Because lacertids are diurnal lizards, we consider environmental temperatures between 8 am and 7 pm most relevant. Therefore, assuming that air temperature follows a sinusoidal path, we calculated hourly estimates of temperature and averaged values between 8 am and 7 pm. Hourly estimates were calculated using minimal and maximal temperature values (Monteith & Unsworth, 1990; Linvill, 2019) and the formula $T_{average}(t) = T_{max}*(0.44 - 0.46*\sin(\pi/12t+0.9) + 0.11*\sin(\pi/6t+0.9))(t) +$

T_{min}* [1 - (0.44 - 0.46*sin(π/12t+0.9) + 0.11*sin(π/6t+0.9))] presented in Monteith and Unsworth (1990). The average temperature experienced between 8 am and 7 pm was then used as an estimate of average daily temperature experienced by the lizards during their activity period between 2000 – 2018.

Supplementary Table S3.1. Overview of the institutions where the species were housed, the respective housing conditions, the timing of each cognitive test and who performed the experiments. Mealworms and crickets were dusted in calcium (e.g.. Zoo Med REPTI CALCIUM®). During the inhibitory control and lid-removal trials, a different dietary regime was followed (i.e. one mealworm per day). HC = house cricket (*Acheta domesticus*), FC = field cricket (*Gryllus campestris*), MW = meal worm (*Tenebrio molitor*), MoW = morioworms ((*Zophobas morio*), WM = larvae of the greater wax moth (*Galleria mellonella*).

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Acanthodactylus pardalis	University of Antwerp	50 x 25 x 30 cm 57 x 39 x 28 cm (individually)	HC + TM 3/week	20.7 ± 0.1 °C	12:12	IC, LR, ESC: JT + LK SL, RL: GDM
Timing	Batch 1 (N = 10): IC: 18/03/2019 – 3/04/2019; LR: 21/03/2019 – 2/04/2019; ESC: 25/02/2019 – 3/04/2019; SL: 1/02/2019 – 5/02/2019; RL: 6/02/2019 – 10/02/2019 Batch 2 (N = 16): IC: 15/06/2020 – 3/07/2020; LR: 29/06/2020 – 16/07/2020; ESC: 9/06/2020 – 12/06/2020; SL: 6/07/2020 – 10/07/2020; RL:11/07/2020 – 15/07/2020					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Dalmatolacerta oxycephala	University of Antwerp	57 x 39 x 28 cm (1 – 2 individuals)	HC + MW 3/week	23.80 ± 0.03 °C	12:12	LVL
Timing	IC: 31/07/2020 – 10/09/2020; LR: 5/08/2020 – 23/08/2020; ESC: 27/08/2020 – 10/09/2020; SL: 14/09/2020 – 18/09/2020; RL: 19/09/2020 – 23/09/2020					
Eremias brenchleyi	University of Antwerp	57 x 39 x 28 cm (individually)	HC + MW 3/week	20.7 ± 0.1 °C	12:12	IC, LR, ESC: LK SL, RL: GDM
Timing	IC: 18/11/2019 – 7/12/2019; LR: 26/11/2019 – 12/12/2019; ESC: 11/12/2019 – 20/12/2019; SL: 7/01/2020 – 11/01/2020; RL: 12/01/2020 – 16/01/2020					
Gastropholis prasine	University of Antwerp	41 x 41 x 71 cm (individually)	HC + MW 3/week	20.0 ± 0.4 °C	12:12	IC, LR: LVL ESC, SL, RL: GDM
Timing	IC: 1/02/2021 – 16/02/2021; LR: 4/02/2021 – 3/03/2021; ESC: 22/02/2021 – 5/03/2021; SL: 4/03/2021 – 8/03/2020; RL: 9/03/2021 – 13/03/2021					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Lacerta viridis	Herpetological Association in Bosnia and Herzegovina	48 x 27 x 32 cm 58.5 x 23 x 48.5 cm 58.5 x 21 x 48.5 cm (individually)	MoW 3/week	17 °C - 24 °C	12:12	IC, LR, ESC: TZ SL, RL: AH+AT+VM
Timing	Batch 1 (N = 10): IC: 20/06/2019 – 19/09/2019; LR: 27/06/2019 – 16/09/2019; ESC: 24/7/2019 – 12/10/2019 Batch 2 (N = 10): SL: 28/05/2021 – 1/06/2021; RL: 2/06/2021 – 6/06/2021					
Podarcis erhardii	National & Kapodistrian University of Athens	22 x 20 x 17 cm (individually)	MW 3/week	28.0 ± 2.1°C	12:12 8h basking	All: GDM
Timing	IC: 6/05/2019 – 21/05/2019; LR: 14/05/2019 – 3/06/2019; ESC: 19/06/2019 – 21/06/2019; SL: 13/06/2020 – 27/06/2020; RL: 18/06/2020 – 2/07/2019					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Podarcis melisellensis	University of Antwerp	57 x 39 x 28 cm (individually)	HC 3/week	23.80 ± 0.03 °C	12:12	IC, LR, ESC: JT + GDM SL, RL: AV
Timing	IC: 18/02/2019 – 5/03/2019; LR: 25/02/2019 – 18/03/2019; ESC: 13/02/2019 – 13/03/2019; SL: 15/04/2019 – 19/04/2019; RL: 22/04/2019 – 26/04/2019					
Podarcis muralis	University of Antwerp	57 x 39 x 28 cm (individually)	HC + MW 3/week	23.7 ± 0.2 °C	12:12	IC, LR, ESC: LK + LVL SL, RL: LVL
Timing	IC: 22/06/2020 – 19/09/2020; LR: 26/08/2020 – 16/07/2020; ESC: 8/07/2020 – 4/08/2020; SL: 17/08/2020 – 21/08/2020; RL: 22/08/2020 – 26/08/2020					
Podarcis siculus	University of Antwerp	57 x 39 x 42 cm (individually)	HC + MW + WM 3/week	23.80 ± 0.03 °C	12:12	All: LVL
Timing	IC: 3/08/2020 –19/08/2020; LR: 6/08/2020 – 20/08/2020; ESC: 13/08/2020 – 27/08/2020; SL: 31/08/2020 – 4/09/2020; RL: 5/09/2020 – 9/09/2020					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Podarcis ionicus	National and Kapodistrian University of Athens	23 x 30 x 17 cm	MW 3/week	28.0 ± 2.1°C	12:12 8h basking	All: AS
Timing	IC: 29/08/2020 – 08/09/2020; LR: 13/09/2020 – 19/09/2020; ESC: 21/09/2020 – 28/09/2020; SL: 29/09/2020 – 03/10/2020; RL: 08/10/2020 – 12/10/2020					
Takydromus sexlineatus	University of Antwerp	55 x 39 x 27 cm (4 to 5 individuals together)	HC 3/week	20.7 ± 0.1 °C	12:12	IC, LR, ESC: JT SL, RL: GDM
Timing	IC: 1/02/2019 – 11/02/2019; LR: 11/02/2019 – 4/03/2019; ESC: 27/02/2019 – 28/03/2019; SL: 13/03/2019 – 17/03/2019; RL: 18/03/2019 – 22/03/2019					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Timon lepidus Adults	University of Antwerp	100 x 40 x 50 cm (individually)	FC 3/week	20.7 ± 0.1 °C	12:12	IC, LR, ESC: JT SL, RL: GDM
Timing	IC: 25/03/2019 – 29/03/2019; LR: 28/03/2019 – 9/04/2019; ESC: 8/04/2019 – 10/04/2019; SL: 13/03/2019 – 17/03/2019; RL: 18/03/2019 – 22/03/2019					
Timon lepidus Juveniles	University of Antwerp	100 x 40 x 50 cm (6 individuals together)	HC 3/week	20.7 ± 0.1 °C	12:12	IC, LR, ESC: JT SL, RL: GDM
Timing	IC: 25/03/2019 – 29/03/2019; LR: 5/03/2019 – 3/04/2019; ESC: 8/04/2019 – 10/04/2019; SL: 13/03/2019 – 17/03/2019; RL: 18/03/2019 – 22/03/2019					

Supplementary Table S3.1. (Continued)

Species	Institution	Terrarium size (l x w x h)	Diet	Room temperature	L:D cycle	Observer
Zootoca vivipara	University of Antwerp	57 x 39 x 28 cm (individually)	HC 3/week	20.7 ± 0.1 °C	12:12	All: DS
Timing	IC: 29/08/2019 – 20/09/2019; LR: 3/09/2019 – 20/09/2019; ESC: 16/09/2019 – 9/10/2019; SL: 23/09/2019 – 27/09/2019; RL: 28/09/2020 – 2/10/2019					

Supplementary Table S3.2. Overview materials and prey types used in the cognitive tests for each species.

	Dimensions terrarium (l x w x h)	Prey type and weight	Height and diameter petri dish	Dimensions wooden platform (l x w x h)	Dimensions escape box (l x w x h) and door (h x l)	Dimensions arena (l x w x h)
TEST	IC, LR	IC, LR	IC, LR	IC, LR	ESC	SL, RL
Acanthodactylus pardalis	30 x 28 x 28 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Dalmatolacerta oxycephala	30 x 28 x 28 cm	Mealworm of 0.05 – 0.10 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Eremias brenchleyi	30 x 28 x 28 cm	Mealworm of 0.05 – 0.10 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Gastropholis prasina	30 x 28 x 28 cm	Mealworm of 0.05 – 0.10 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Lacerta viridis	58 x 39 x 31 cm	Larvae *Zophobas morio* of 0.50 g	Height: 3 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm

Supplementary Table S3.2. (Continued)

	Dimensions terrarium (l x w x h)	Prey type and weight	Height and diameter petri dish	Dimensions wooden platform (l x w x h)	Dimensions escape box (l x w x h) and door (h x l)	Dimensions arena (l x w x h)
Podarcis erhardii	30 x 30 x 30 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Podarcis melisellensis	30 x 28 x 28 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Podarcis muralis	30 x 28 x 28 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Podarcis siculus	30 x 28 x 28 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Podarcis tauricus	30 x 30 x 30 cm	Mealworm of 0.10 – 0.20 g	Height: 1.5 cm Diameter: 5.5 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm
Takydromus sexlineatus	30 x 28 x 28 cm	Mealworm of 0.05 – 0.10 g	Height: 1 cm Diameter: 3 cm	10 x 10 x 1.5 cm	Box: 40 x 40 x 50 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm

Supplementary Table S3.2. (Continued)

	Dimensions terrarium (l x w x h)	Prey type and weight	Height and diameter petri dish	Dimensions wooden platform (l x w x h)	Dimensions escape box (l x w x h) and door (h x l)	Dimensions arena (l x w x h)
Timon lepidus **Adults**	66 x 43 x 36 cm	Larvae *Zophobas morio* of 0.50 g	Height: 3 cm Diameter: 7 cm	28 x 11 x 3 cm	Box: 22 x 22 x 8 cm Door: 12 x 9 cm	100 x 100 x 30 cm
Timon lepidus Juveniles	39 x 27 x 27 cm	Mealworm of 0.15 – 0.20 g	Height: 2.5 cm Diameter: 4 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 12 x 9 cm	100 x 100 x 30 cm
Zootoca vivipara	30 x 28 x 28 cm	Mealworm of 0.05 – 0.10 g	Height: 1 cm Diameter: 3 cm	10 x 10 x 1.5 cm	Box: 22 x 22 x 8 cm Door: 5.5 x 7.5 cm	60 x 60 x 30 cm

Supplementary Table S3.3. The origin of the species used in this study, the coordinates of their capture locations or of known populations within their native range (obtained via literature, observation.org and iNaturalist) and the period of the year the species are active. For all information, the literature (or other) sources are given.

Species	Origin	Coordinates (Lat, Long)	Source	Activity period	Source
Acanthodactylus pardalis	Pet-trade from Egypt	31.301389, 26.979444 31.468715754912527, 26.390516927734136 30.518371134247023, 30.276201480733963 29.82731958537036, 31.301975610076497 30.900969709501066, 29.55160048106914 30.929273269689368, 29.568341297057405 30.91179214619455, 30.171899733726466 31.574524893440067, 25.15949263226295 31.609192715506595, 25.92484544160242 29.45249814617522, 30.91266747869165	1	Apr - Nov	1
Dalmatolacerta oxycephala	Vis (Croatia)	43.073983, 16.196924	NA	Feb – Mar	2
Eremias brenchleyi	Pet-trade from Hebei Province (China)	40.677835, 117.255969 39.57005020679096, 115.5108504027994 39.612301, 115.580983 40.258557, 115.931396 40.969275, 117.815973	2, 3	Mar - Oct	3

Supplementary Table S3.3. (Continued)

Species	Origin	Coordinates (Lat, Long)	Source	Activity period	Source
Gastropholis prasine	Pet-trade from coastal regions Kenya and Tanzania	-3.355171, 40.013975 -3.331233748323525, 39.87838241448717 -4.257575271500067, 39.385610555218655 -5.144564136042722, 38.635397912197234 -5.073491530778728, 39.12655403069819 -5.998266314495584, 38.75413364688048 -6.434203616668318, 38.904946748719155 -6.000298591696631, 37.49991413237952	4	Aug – Apr	NA
Lacerta viridis	Dariva, Bosnia & Herzegovina	43.860278, 18.448750	NA	Feb – Sep	2
Podarcis erhardii	5 locations on Naxos (Greece)	36.979250, 25.389167 37.089444, 25.361694 37.111611, 25.386056 37.130306, 25.438583 37.014722, 25.402972	NA	Feb - Nov	2
Podarcis melisellensis	Brusnik, Mali Bariak, and Vis (Croatia)	43.006417, 15.800944 43.052611, 16.039694 43.0466612499245, 16.15427258864697	NA	Feb - Nov	2
Podarcis muralis	Muizen (Belgium)	51.01397437563141, 4.506916673312601	NA	Feb - Nov	2

Supplementary Table S3.3. (Continued)

Species	Origin	Coordinates (Lat, Long)	Source	Activity period	Source
Podarcis siculus	Nin (Croatia)	44.232262274450434, 15.18541273891122	NA	Feb - Nov	2
Podarcis ionicus	Lake Doxa (Greece)	37.92678300912619, 22.28645064601946	NA	Feb - Oct	2
Takydromus sexlineatus	Pet-trade	24.779860688713157, 113.60323002237655 22.788602791897674, 108.39688483972023 14.408889, 103.453056 -6.5964828735321595, 106.79993202131229 1.0715022808579726, 104.42930515861168	3, 5-9	Feb - Nov	NA
Timon lepidus	Captive-bred (originally from Southern France)	43.501441, 2.668679 43.647469, 3.999620 43.007154, 1.064630 42.912557, 2.878350 43.421346, -1.436474 42.684380, 2.860660 43.571522, 4.940472 43.394807, 6.208115 43.204002, 6.448390 43.756467, 7.091883	3, 10	March - October	2
Zootoca vivipara	Wuustwezel (Belgium)	51.378861, 4.613333	NA	Feb – Oct	2

References for the coordinates: 1 - Moravec et al. (1999), 2 - Zhao et al. (2011), 3 – iNaturalist, 4 - Spawls et al. (2018), 5 - Zhang and Ji (2004), 6 - Qin et al. (2015), 7 - Patawang et al. (2018), 8 - Trobisch and Glässer-Trobisch (2008), 9 - Tay (2016), 10 - Jorcin et al. (2019), references for activity period: 1 - Akiki et al. (2015), 2 - Speybroeck et al. (2018), 3 - Feng et al. (2004).

Supplementary Table S3.4. The life-history characteristics of each species: mean female SVL, hatchling SVL, SVL at maturity, average maximal clutch size, and clutch frequency (all raw values). For all characteristics, the literature (or other) references are given (see below table). All female SVL data was taken from Meiri, 2018.

Species	Mean female SVL (mm)	Hatchling SVL (mm)	Ref	Maturity SVL (mm)	Ref	Average clutch size	Ref	Clutch Frequency	Ref
Acanthodactylus pardalis	61	30	1	59	1	4.8	1	4	2
Dalmatolacerta oxycephala	57.9	25.85 ± 3.46	3, 4	55.68	5	3.49	5	1.5	2, 5
Eremias brenchleyi	49.3	NA	/	NA	/	4	3	NA	/
Gastropholis prasine	71.67	21	7	NA	/	8.5	7	NA	/
Lacerta viridis	102.4	33.75 ± 1.77	3, 8	93.73 ± 15.68	9-11	10.51 ± 3.41	9-11	1.5	12

Supplementary Table S3.4. (Continued)

Species	Mean female SVL (mm)	Hatchling SVL (mm)	Ref	Maturity SVL (mm)	Ref	Average clutch size	Ref	Clutch frequency	Ref
Podarcis erhardii	61.4	28.9 ± 1.1	3, 13, 14	48	15	2.32 ± 0.45	14, 15	2	2
Podarcis melisellensis	59.4	24.50	3	48.5 ± 0.71	6	4.60 ± 0.42	3, 6	3	2
Podarcis muralis	63.8	24.65 ± 0.21	3, 16	49	16	5.75 ± 0.78	3, 16	2	16
Podarcis siculus	61.9	30.00 ± 2.65	3, 17	50.43 ± 2.70	17, 18	6.0 ± 1.04	3, 17, 18	3	17
Podarcis ionicus	62.1	28.05 ± 1.91	3, 13	58.15 ± 4.50	15, 19	4.07 ± 1.45	3, 15, 20; 21	2	20

Supplementary Table S3.4. (Continued)

Species	Mean female SVL (mm)	Hatchling SVL (mm)	Ref	Maturity SVL (mm)	Ref	Average clutch size	Ref	Clutch frequency	Ref
Takydromus sexlineatus	55.8	17.70 ± 1.84	22	48.8	23	2.2	3	2.83	23
Timon lepidus	150	41.25 ± 2.19	16	132	16	16.9	3	1	16
Zootoca vivipara	61	19.65 ± 1.63	16	44	16	7.10 ± 3.82	3, 16	1	16

References for life-history data: 1 - Schleich et al. (1996), 2 -Scharf et al. (2015), 3 – Meiri (2018), 4 - Aleksic and Tucic (1994), 5 - Bejaković et al. (1955), 6 - Bejakovic et al. (1995), 7 - Ashe et al. (1999), 8 - Elbing (2001), 9 - Brana et al. (1991), 10 - Karmyshev and Yarigin (2013), 11 - Sagonas et al. (2018), 12 - Fitch (1970), 13 - in den Bosch and Bout (1998), 14 - Gruber (1986), 15 - Maragou et al. (1999), 16 - Bauwens and Díaz-Uriarte (1997), 17 - Henle and Klaver (1986), 18 - Radočaj et al. (2011), 19 - Altunışık et al. (2016), 20 - Chondropoulos and Lykakis (1983), 21 - Ljubisavljević et al. (2010), 22 - Xu et al. (2007), 23 - Mumpuni (2011)

CHAPTER 3: SUPPLEMENTARY RESULTS

Supplementary Table S3.5. Descriptive statistics per species for the different cognitive tests. Two variables were extracted for each test, both giving an indication of how well individuals performed. See the text for an explanation of these variables. Averages across all species are given in the result section. Note: for solving time and learning speed, both the overall solving times/learning speed (including non-successful trials that were given 900 s/16 trials) and solving times/learning speed in the successful trials are given (the latter between parentheses).

Species		
Inhibitory control	***Solving time (s)***	***% learners***
Acanthodactylus pardalis	549.78 ± 54.61 (48.98 ± 56.59)	50
Dalmatolacerta oxycephala	665.33 ± 57.15 (126.49 ± 119.41)	38
Eremias brenchleyi	850.75 ± 75.61 (494.33 ± 351.36)	17
Gastropholis prasine	333.1 ± 72.64 (55.84 ± 29.21)	77
Lacerta viridis	500.80 ± 82.80 (208.00 ± 122.02)	100
Podarcis erhardii	290.84 ± 31.30 (129.90 ± 103.47)	93
Podarcis melisellensis	644.00 ± 99.00 (122.67 ± 41.79)	43
Podarcis muralis	690.27 ± 67.62 (307.08 ± 187.60)	40
Podarcis siculus	146.14 ± 55.84 (64.71 ± 71.73)	96
Podarcis ionicus	173.46 ± 72.64 (93.23 ± 99.29)	100
Takydromus sexlineatus	275.77 ± 72.64 (98.15 ± 94.05)	77
Timon lepidus	333.13 ± 92.6 (229.87 ± 153.18)	100
Zootoca vivipara	100.39 ± 61.73 (30.28 ± 38.81)	94
Lid-removal	***Solving time (s)***	***Prop. solved trials***
Acanthodactylus pardalis	880.22 ± 76.64 (9.00)	0.024 ± 0.038
Dalmatolacerta oxycephala	900 (NA)	0
Eremias brenchleyi	900 (NA)	0
Gastropholis prasine	894.00 ± 73.00 (602)	0.02 ± 0.03
Lacerta viridis	748.00 ± 73.00 (278.33 ± 338.58)	0.21 ± 0.1
Podarcis erhardii	734.91 ± 28.52 (213.50 ± 164.25)	0.24 ± 0.038
Podarcis melisellensis	900 (NA)	0
Podarcis muralis	889.50 ± 72.70 (691.00)	0.041 ± 0.04
Podarcis siculus	705.81 ± 50.17 (325.17 ± 83.83)	0.33 ± 0.074

Supplementary Table S3.5.

Species	***Solving time (s)***	***Prop. solved trials***
Podarcis ionicus	713.77 ± 63.77 (268.45 ± 276.57)	0.25 ± 0.086
Takydromus sexlineatus	744.18 ± 69.32 (384.23 ± 316.68)	0.22 ± 0.09
Timon lepidus	865.75 ± 81.29 (381.00 ± 264.46)	0.075 ± 0.067
Zootoca vivipara	422.17 ± 54.19 (142.60 ± 126.94)	0.61 ± 0.084
Escape box	***Solving time (s)***	***Prop. solved trials***
Acanthodactylus pardalis	1497.50 ± 101.40 (559.71 ± 315.38)	0.2 ± 0.07
Dalmatolacerta oxycephala	421.72 ± 90.67 (269.95 ± 202.32)	0.91 ± 0.043
Eremias brenchleyi	978.17 ± 130.87 (507.90 ± 340.85)	0.6 ± 0.1
Gastropholis prasine	1386.13 ± 117.05 (674.13 ± 472.98)	0.36 ± 0.091
Lacerta viridis	1743.80 ± 143.35 (957.00 ± 83.44)	0.067 ± 0.058
Podarcis erhardii	1135.00 ± 136.69 (738.44 ± 443.85)	0.58 ± 0.11
Podarcis melisellensis	1645.67 ± 106.85 (1046.57 ± 504.39)	0.19 ± 0.068
Podarcis muralis	620.5 ± 121.16 (503.23 ± 180.27)	0.9 ± 0.06
Podarcis siculus	1095.27 ± 96.65 (540.23 ± 469.87)	0.51 ± 0.079
Podarcis ionicus	1800 (NA)	0
Takydromus sexlineatus	1754.54 ± 125.73 (26)	0.025 ± 0.032
Timon lepidus	1800 (NA)	0
Zootoca vivipara	764.64 ± 96.65 (628.25 ± 403.52)	0.85 ± 0.057
Spatial learning	***Learning speed (N° of trials)***	***Success (%)***
Acanthodactylus pardalis	13.09 ± 1.03 (8.38 ± 2.92)	29
Dalmatolacerta oxycephala	11.64 ± 0.89 (8.73 ± 3.63)	56
Eremias brenchleyi	12.00 ± 2.00 (8.80 ± 4.09	22
Gastropholis prasine	13.20 ± 1.20 (10.00 ± 4.16)	33
Lacerta viridis	10.50 ± 1.30 (6.83 ± 1.47)	50
Podarcis erhardii	10.88 ± 0.52 (7.39 ± 3.16)	54
Podarcis melisellensis	12.59 ± 0.89 (7.64 ± 3.23)	37
Podarcis muralis	12.33 ± 1.19 (9.89 ± 3.69)	33
Podarcis siculus	12.18 ± 0.98 (7.60 ± 2.37)	41
Podarcis ionicus	11.80 ± 1.30 (10.44 ± 3.50)	50
Takydromus sexlineatus	15.10 ± 1.61 (11.50 ± 0.71)	20
Timon lepidus	12.75 ± 1.65 (9.50 ± 1.29)	50
Zootoca vivipara	12.45 ± 0.99 (7.33 ± 2.50)	36

Supplementary Table S3.5.

Species		
Reversal learning	***Learning speed (N° of trials)***	***Success (%)***
Acanthodactylus pardalis	15.00 ± 1.00 (10.75 ± 1.89)	14
Dalmatolacerta oxycephala	11.16 ± 0.85 (9.63 ± 3.17)	60
Eremias brenchleyi	11.33 ± 1.42 (9.00 ± 1.26)	3
Gastropholis prasine	10.40 ± 1.10 (8.36 ± 1.75)	40
Lacerta viridis	13.00 ± 1.00 (6.00 ± 1.00)	30
Podarcis erhardii	11.81 ± 0.52 (7.74 ± 3.10)	48
Podarcis melisellensis	13.00 ± 2.00 (9.25 ± 3.30)	33
Podarcis muralis	11.4 ± 1.1 (8.33 ± 3.16)	53
Podarcis siculus	11.36 ± 0.91 (9.20 ± 3.51)	64
Podarcis ionicus	13.00 ± 1.00 (6.00 ± 1.73)	30
Takydromus sexlineatus	12.33 ± 1.48 (7.75 ± 2.06)	33
Timon lepidus	10.88 ± 1.48 (9.17 ± 3.43)	38
Zootoca vivipara	11.10 ± 0.90 (7.69 ± 3.45)	55
Spatial + reversal learning	***Score (/30)***	***Success (%)***
Acanthodactylus pardalis	12.05 ± 0.78	0
Dalmatolacerta oxycephala	18.68 ± 0.86	36
Eremias brenchleyi	15.60 ± 1.40	0
Gastropholis prasine	16.14 ± 1.07	7
Lacerta viridis	13.10 ± 1.10	10
Podarcis erhardii	17.10 ± 0.50	12
Podarcis melisellensis	15.56 ± 1.31	0
Podarcis muralis	16.33 ± 1.04	13
Podarcis siculus	17.41 ± 0.89	18
Podarcis ionicus	15.20 ± 1.20	10
Takydromus sexlineatus	9.44 ± 1.02	22
Timon lepidus	17.25 ± 1.47	13
Zootoca vivipara	16.36 ± 0.86	5

Supplementary Table S3.6. Climate variables as proxies of resource availability and habitat complexity, calculated per species. See text for details on how these were obtained. Averages ± SE per species are given.

Species	NDVI	NDVI seasonality (%)	Monthly precipitation (mm)	Precipitation seasonality (%)	Min. temperature (°C)
Acanthodactylus pardalis	0.15 ± 0.06	15.76 ± 7.99	3.01 ± 1.60	138.39 ± 11.03	18.98 ± 1.19
Dalmatolacerta oxycephala	0.52 ± 0.07	10.19 ± 4.89	51.85 ± 9.85	57.97 ± 13.96	14.67 ± 0.53
Eremias brenchleyi	0.58 ± 0.23	42.01 ± 8.88	57.92 ± 2.08	121.13 ± 4.21	10.57 ± 0.93
Gastropholis prasine	0.62 ± 0.19	14.13 ± 11.33	79.29 ± 16.84	77.84 ± 4.86	21.18 ± 2.97
Lacerta viridis	0.64 ± 0.14	22.12 ± 2.24	90.06 ± 22.54	45.92 ± 10.36	7.71 ± 0.62
Podarcis erhardii	0.33 ± 0.13	16.42 ± 250.94	27.85 ± 0.90	97.56 ± 0.55	17.26 ± 0.13
Podarcis melisellensis	0.63 ± 0.21	35.19 ± 8.24	49.51 ± 9.65	57.54 ± 13.94	14.99 ± 0.54
Podarcis muralis	0.49 ± 0.14	33.99 ± 9.42	66.27 ± 8.57	42.16 ± 9.20	8.41 ± 0.47
Podarcis siculus	0.57 ± 0.13	20.73 ± 4.17	73.71 ± 14.29	55.26 ± 12.66	12.18 ± 0.49
Podarcis ionicus	0.51 ± 0.12	19.74 ± 7.77	61.98 ± 14.56	72.17 ± 6.96	7.78 ± 0.42
Takydromus sexlineatus	0.76 ± 0.08	5.09 ± 2.81	176.92 ± 64.89	67.27 ± 20.87	21.44 ± 2.08
Timon lepidus	0.64 ± 0.18	13.51 ± 8.20	57.74 ± 16.90	59.83 ± 7.38	12.53 ± 1.76
Zootoca vivipara	0.75 ± 0.12	16.71 ± 2.21	68.35 ± 8.58	42.01 ± 8.53	8.33 ± 0.52

Supplementary Table S3.6. (Continued)

Species	Min. temperature seasonality (%)	Max. temperature (°C)	Max. temperature seasonality (%)	Average temperature (°C)	Average temperature seasonality (%)
Acanthodactylus pardalis	32.67 ± 2.29	29.69 ± 2.63	18.67 ± 1.38	26.13 ± 2.32	21.85 ± 2.36
Dalmatolacerta oxycephala	40.16 ± 4.57	21.31 ± 0.53	33.16 ± 2.88	19.47 ± 0.52	34.58 ± 3.18
Eremias brenchleyi	307.40 ± 99.87	22.42 ± 0.94	69.87 ± 5.92	18.16 ± 2.13	97.81 ± 16.97
Gastropholis prasine	6.90 ± 2.39	29.46 ± 2.63	5.32 ± 1.18	26.72 ± 3.06	5.49 ± 1.29
Lacerta viridis	118.12 ± 19.26	18.73 ± 0.72	54.56 ± 4.76	15.67 ± 0.68	61.93 ± 5.98
Podarcis erhardii	31.25 ± 0.48	22.55 ± 0.16	24.98 ± 0.41	20.38 ± 1.52	31.11 ± 9.16
Podarcis melisellensis	40.62 ± 4.68	21.53 ± 0.54	33.68 ± 2.97	19.72 ± 0.53	35.09 ± 3.28
Podarcis muralis	62.94 ± 11.66	16.88 ± 0.62	41.26 ± 5.44	14.53 ± 0.55	44.44 ± 6.25
Podarcis siculus	57.06 ± 6.89	21.99 ± 0.54	36.79 ± 3.20	19.26 ± 0.52	40.19 ± 3.73
Podarcis ionicus	90.54 ± 10.21	17.75 ± 0.54	50.69 ± 3.29	14.98 ± 0.49	55.89 ± 3.98
Takydromus sexlineatus	16.86 ± 17.18	29.13 ± 2.01	12.19 ± 11.86	26.47 ± 1.54	13.18 ± 12.94
Timon lepidus	57.31 ± 12.98	22.06 ± 2.13	33.32 ± 5.23	18.93 ± 2.75	38.48 ± 7.42
Zootoca vivipara	66.56 ± 12.91	17.72 ± 0.64	42.61 ± 5.42	15.11 ± 0.58	45.92 ± 6.33

Supplementary Table S3.7. Follow-up from the previous table. Life-history characteristics of each species. For hatchling snout-vent length (SVL), SVL at maturity, and clutch size residuals from a phylogenetic analysis with female SVL are reported and used in the analyses. See Supplementary Table S3.4 for the raw values and information on literature sources.

Species	Res. SVL hatchling	Res. SVL maturity	Res. clutch size	Clutch frequency
Acanthodactylus pardalis	0.18	0.13	0.13	4
Dalmatolacerta oxycephala	0.063	0.13	-0.11	1.5
Eremias brenchleyi	NA	NA	NA	NA
Gastropholis prasina	NA	NA	NA	NA
Lacerta viridis	-0.052	0.047	0.057	1.5
Podarcis erhardii	0.14	-0.082	-0.61	2
Podarcis melisellensis	-0.0077	-0.037	0.13	3
Podarcis muralis	-0.049	-0.10	0.23	2
Podarcis siculus	0.17	-0.042	0.33	3
Podarcis ionicus	0.098	0.097	-0.068	2
Takydromus sexlineatus	-0.29	0.035	-0.52	2.8
Timon lepidus	-0.11	-0.013	-0.097	1
Zootoca vivipara	-0.25	-0.16	0.52	1

Supplementary Table S3.8. MCMCglmm results for the environmental quality models. Significant p-values (pMCMC) and non-overlap of the 95% CI with zero are indicated in bold, as are trends close to significance. Sex was removed in multiple models due to complete separation of the data. The results reported here are those of the models with the priors leading to sample sizes > 1000 and autocorrelations < 0.1. These priors are either weakly informative inverse γ-distribution (V = 1; μ = 0.002), fixed to one (V = 1; fix = 1), informative (V = 100 and μ = 2), or parameter-expanded (V = 1; μ = 1; αμ = 0; αV = 1000), as indicated in the table. ST = solving time, CRIT = whether an animal reached the learning criterion (Y/N), SR = success rate, LS = learning speed (see main text for a more detailed explanation of all tests and cognitive traits).

INHIBITORY CONTROL

1. ***ST$_{IC}$***

Parameter-expanded priors

	Effective sample size	Posterior mean [95% CI]	Pmcmc
Random effect			
Phylogeny	9990	1411 [0, 4220]	-
Species	9990	25620 [0, 96614]	-
Population	9990	6384 [0.0002, 31677]	-
Units	9990	67497 [55348, 81388]	-
Fixed effect			
Intercept	10305	637.86 [-427.86, 1668.42]	0.20
Average temperature	9990	-6.49 [-46.89, 39.48]	0.75
Precipitation	9652	-0.92 [-5.74, 3.78]	0.67
Sex – juvenile	10349	-49.16 [-477.13, 364.13]	0.82
Sex – male	9990	-69.66 [-155.82, 14.76]	0.11
SVL	10332	0.83 [-3.69, 5.53]	0.72

Supplementary Table S3.8. (continued)

2. CRIT$_{IC}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	8105	0.08 [0.0001, 0.34]	-
Species	8130	4.28 [0.0002, 14.8]	-
Population	7402	1.56 [0.0002, 7.45]	-
Units	-	-	-
Fixed effect			
Intercept	9990	0.006 [-11.73, 11.63]	0.96
Average temperature	9188	-0.12 [-0.62, 0.35]	0.58
Precipitation	9990	0.009 [-0.04, 0.06]	0.67
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	7976	0.06 [-0.027, 0.14]	0.16

LID REMOVAL

1. ST$_{LR}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	8860	204 [0.0001, 848.8]	-
Species	8422	9244 [0.0002, 33933]	-
Population	8857	1175 [0.0002, 7572]	-
Units	9432	54813 [43450, 67045]	-
Fixed effect			
Intercept	**9990**	**629.17 [57.43, 1203.92]**	**0.023**
Average temperature	9990	11.03 [-12.00, 33.37]	0.30
Precipitation	9990	-0.66 [-3.06, 1.75]	0.55
Sex – juvenile	9990	111.54 [-190.33, 397.93]	0.45
Sex – male	9990	-19.81 [-107.70, 63.54]	0.64
SVL	9990	-0.15 [-3.54, 2.92]	0.94

Supplementary Table S3.8. (continued)

2. SR_{LR}

Non-informative priors	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9612	0.074 [0.0002, 0.24]	-
Species	9417	2.15 [0.0002, 8060]	-
Population	9990	0.11 [0.0002, 0.48]	-
Units	9990	1.53 [0.71, 2.50]	-
Fixed effect			
Intercept	9990	-4.13 [-13.59, 3.67]	0.29
Average temperature	9990	-0.06 [-0.43, 0.30]	0.69
Precipitation	9990	0.016 [-0.024, 0.053]	0.34
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	**10431**	**0.030 [-0.004, 0.065]**	**0.068**

ESCAPE BOX

1. ST_{ESC}

Parameter-expanded priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	3139 [0, 9796]	-
Species	9990	51995 [0, 230518]	-
Population	9990	28398 [0, 153824]	-
Units	9990	206829 [163297, 250904]	-
Fixed effect			
Intercept	10286	-340.87[-1995.49, 1280.47]	0.63
Average temperature	9263	35.10 [-32.24, 101.45]	0.28
Precipitation	9990	3.37 [-4.38, 10.56]	0.34
Sex – juvenile	**9990**	**591.58 [-81.90, 1311.93]**	**0.094**
Sex – male	8108	112.04 [-79.70, 326.11]	0.28
SVL	**9575**	**8.18 [0.40, 15.29]**	**0.035**

Supplementary Table S3.8. (continued)

2. SR$_{ESC}$

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	3092	29.4 [8.46, 60.73]	-
Species	9147	138.1 [13.59, 401.2]	-
Population	9990	58.42 [11.22, 148.3]	-
Units	9990	3.05 [2.17, 4.02]	-
Fixed effect			
Intercept	7279	-18.49 [-151.02, 104.19]	0.75
Average temperature	6622	0.84 [-4.57, 6.76]	0.76
Precipitation	8393	-0.012 [-0.61, 0.57]	0.96
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	9990	-0.036 [-0.11, 0.04]	0.35

SPATIAL LEARNING

1. LS$_{SL}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10249	0.0007 [0.0001, 0.0016]	-
Species	9642	0.007 [0.0002, 0.024]	-
Population	9990	0.004 [0.0002, 0.013]	-
Units	9990	0.06 [0.033, 0.090]	-
Fixed effect			
Intercept	**9990**	**2.31 [1.50, 3.10]**	**< 0.0001**
Average temperature	9990	0.006 [-0.027, 0.038]	0.69
Precipitation	10295	0.001 [-0.002, 0.005]	0.45
Sex – juvenile	9990	0.067 [-0.44, 0.55]	0.78
Sex – male	**9990**	**0.11 [-0.011, 0.23]**	**0.07**
SVL	9990	-0.003 [-0.007, 0.002]	0.26
Safe side - right	**8737**	**0.13 [0.035, 0.22]**	**0.007**

Supplementary Table S3.8. (continued)

2. ***CRIT$_{SL}$***

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.005 [0.0002, 0.015]	-
Species	9026	0.069 [0.0002, 0.31]	-
Population	9990	0.051 [0.0002, 0.23]	-
Units	-	-	-
Fixed effect			
Intercept	9990	0.45 [-3.04, 3.81]	0.78
Average temperature	9990	-0.026 [-0.15, 0.10]	0.67
Precipitation	9990	-0.008 [-0.023, 0.0053]	0.24
Sex – juvenile	9990	0.55 [-2.13, 3.35]	0.71
Sex – male	**9990**	**-0.77 [-1.54, -0.012]**	**0.048**
SVL	10231	0.012 [-0.013, 0.037]	0.35
Safe side – right	**10727**	**-0.53 [-1.17, 0.094]**	**0.098**

REVERSAL LEARNING

1. ***LS$_{RL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.0007 [0.0001, 0.002]	-
Species	9990	0.007 [0.0001, 0.023]	-
Population	9996	0.004 [0.0002, 0.014]	-
Units	9990	0.054 [0.0002, 0.014]	-
Fixed effect			
Intercept	**9990**	**2.23 [1.45, 3.06]**	**< 0.0001**
Average temperature	9990	0.004 [-0.030, 0.035]	0.82
Precipitation	10540	-0.0006 [-0.004, 0.003]	0.70
Sex – juvenile	9701	-0.15 [-0.65, 0.35]	0.56
Sex – male	9937	-0.024 [-0.14, 0.098]	0.69
SVL	9990	0.002 [-0.0022, 0.0068]	0.35
Safe side – right	**9990**	**0.12 [0.020, 0.21]**	**0.016**

Supplementary Table S3.8. (continued)

2. ***CRIT$_{RL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10384	0.006 [0.0001, 0.021]	-
Species	9990	0.11 [0.0002, 0.50]	-
Population	9990	0.11 [0.0002, 0.47]	-
Units	-	-	-
Fixed effect			
Intercept	9990	2.19 [-1.58, 5.88]	0.24
Average temperature	9990	-0.06 [-0.20, 0.086]	0.40
Precipitation	9990	0.003 [-0.011, 0.018]	0.64
Sex – juvenile	10470	0.22 [-2.79, 3.02]	0.86
Sex – male	9990	0.16 [-0.62, 0.96]	0.69
SVL	9990	-0.02 [-0.05, 0.0077]	0.13
Safe side – right	**9990**	**-0.83 [-1.49, -0.16]**	**0.015**

SPATIAL + REVERSAL LEARNING

1. ***SR$_{SLRL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.0008 [0.0002, 0.0019]	-
Species	9990	0.0083 [0.0002, 0.029]	-
Population	9990	0.0032 [0.0002, 0.010]	-
Units	9000	0.0017 [0.0002, 0.0043]	-
Fixed effect			
Intercept	**9990**	**3.23 [2.47, 4.02]**	**< 0.0001**
Average temperature	9990	-0.013 [-0.045, 0.020]	0.40
Precipitation	9990	-0.002 [-0.0059, 0.0014]	0.21
Sex – juvenile	9990	0.26 [-0.13, 0.62]	0.18
Sex – male	9322	-0.021 [-0.11, 0.058]	0.60
SVL	9698	-0.0017 [-0.005, 0.0015]	0.30

Supplementary Table S3.8. (continued)

2. ***CRIT*$_{SLRL}$**

Parameter-expanded priors

	Effective sample size	***Posterior mean [95% CI]***	***pMCMC***
Random effect			
Phylogeny	2442	0.069 [0.00, 0.29]	-
Species	3654	2.81 [0.00, 11.43]	-
Population	3970	3.04 [0.00, 10.38]	-
Units	-	-	-
Fixed effect			
Intercept	9990	-0.49 [-10.60, 10.19]	0.91
Average temperature	7103	-0.98 [-0.60, 0.33]	0.65
Precipitation	4859	0.022 [-0.023, 0.083]	0.32
Sex – juvenile	6314	2.45 [-3.37, 8.90]	0.39
Sex – male	9587	-0.44 [-1.58, 0.66]	0.45
SVL	9990	-0.037 [-0.093, 0.018]	0.18

Supplementary Table S3.9. MCMCglmm results for the temporal variability models. Significant p-values (pMCMC) and non-overlap of the 95% CI with zero are indicated in bold, as are trends close to significance. Sex was removed in multiple models due to complete separation of the data. The results reported here are those of the models with the priors leading to sample sizes > 1000 and autocorrelations < 0.1. These priors are either weakly informative inverse γ-distribution (V = 1; μ = 0.002), fixed to one (V = 1; fix = 1), informative (V = 100 and μ = 2), or parameter-expanded (V = 1; μ = 1; αμ = 0; αV = 1000), as indicated in the table. ST = solving time, CRIT = whether an animal reached the learning criterion (Y/N), SR = success rate, LS = learning speed (see main text for a more detailed explanation of all tests and cognitive traits).

INHIBITORY CONTROL

1. ***ST_{IC}***

Parameter-expanded priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10296	954 [0, 2317]	-
Species	9990	6266 [0.0005, 34001]	-
Population	9990	3718 [0, 16569]	-
Units	9990	67239 [54781, 90381]	-
Fixed effect			
Intercept	9990	21.59 [-705.20, 704.04]	0.94
Seasonality temperature	9814	-3.46 [-11.21, 4.38]	0.35
Seasonality precipitation	9990	1.08 [-4.31, 6.23]	0.66
Seasonality NDVI	**9990**	**23.80 [6.76, 40.45]**	**0.0094**
Sex – juvenile	9990	-35.36 [-423.95, 352,36]	0.85
Sex – male	**9990**	**-79.07 [-165.13, 6.56]**	**0.073**
SVL	9990	0.76 [-3.18, 5.02]	0.72

Supplementary Table S3.9. (Continued)

2. CRIT$_{IC}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9126	0.076 [0.0002, 0.24]	-
Species	9457	1.26 [0.0002, 5.85]	-
Population	8380	0.67 [0.0002, 3.22]	-
Units	-	-	-
Fixed effect			
Intercept	8996	0.15 [-8.14, 8.26]	1.00
Seasonality temperature	8742	0.071 [-0.019, 0.17]	0.11
Seasonality precipitation	9990	-0.016 [-0.073, 0.38]	0.52
Seasonality NDVI	**8813**	**-0.24 [-0.45, -0.045]**	**0.017**
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	**7101**	**0.07 [-0.011, 0.16]**	**0.077**

LID REMOVAL

1. ST$_{LR}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9193	197.9 [0.0002, 694.8]	-
Species	9031	4759 [0.0002, 22193]	-
Population	8929	814.4 [0.0002, 5165]	-
Units	9990	54731 [43536, 67310]	-
Fixed effect			
Intercept	**9990**	**638.31 [251.33, 1081.69]**	**0.004**
Seasonality temperature	9490	-4.03 [-9.15, 1.21]	0.12
Seasonality precipitation	9205	1.24 [-1.75, 4.33]	0.37
Seasonality NDVI	**9468**	**11.13 [-0.53, 22.28]**	**0.057**

Supplementary Table S3.9. (Continued)

	Effective sample size	Posterior mean [95% CI]	pMCMC
Sex – juvenile	9990	148.74 [-125.96, 443.71]	0.28
Sex – male	9990	-30.36 [-117.38, 54.86]	0.48
SVL	9990	0.16 [-2.90, 3.41]	0.88

2. SR_{LR}

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	7214	0.093 [0.0004, 0.029]	-
Species	9616	1.42 [0.0001, 6.54]	-
Population	9990	0.10 [0.0002, 0.39]	-
Units	9908		-
Fixed effect			
Intercept	8803	-0.69 [-8.89, 7.46]	0.819
Seasonality temperature	9296	0.025 [-0.076, 0.13]	0.543
Seasonality precipitation	9068	-0.018 [-0.084, 0.042]	0.504
Seasonality NDVI	**9638**	**-0.18 [-0.42, 0.034]**	**0.069**
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	**9038**	**0.030 [-0.0050, 0.066]**	**0.075**

Supplementary Table S3.9. (Continued)

ESCAPE BOX

1. ST$_{ESC}$

Parameter-expanded priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	4305 [0.00, 12980]	-
Species	9990	68080 [0.00, 293658]	-
Population	9990	27929 [0.00, 167866]	-
Units	9990	206347 [164127, 251366]	-
Fixed effect			
Intercept	10527	481.40 [-977.81, 2080.89]	0.48
Seasonality temperature	9990	-2.71 [-20.43, 14.43]	0.74
Seasonality precipitation	10311	3.99 [-8.83, 15.33]	0.46
Seasonality NDVI	9990	-3.17 [-37.87, 35.89]	0.86
Sex – juvenile	9990	545.38 [-207.54, 1261.73]	0.14
Sex – male	9990	105.58 [-101.19, 306.12]	0.31
SVL	**10297**	**7.85 [0.078, 15.80]**	**0.056**

2. SR$_{ESC}$

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	1020	33.36 [8.90, 71.96]	-
Species	8735	148.3 [11.32, 443.4]	-
Population	9867	59.42 [9.16, 148.1]	-
Units	9990	3.06 [2.20, 4.03]	-

Supplementary Table S3.9. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	9990	-5.41 [-119.96, 106.27]	0.93
Seasonality temperature	2372	-0.40 [-1.85, 0.93]	0.54
Seasonality precipitation	9990	0.030 [-0.94, 0.95]	0.95
Seasonality NDVI	2367	0.86 [-1.87, 3.77]	0.53
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	9990	-0.036 [-0.11, 0.039]	0.34
SPATIAL LEARNING			
1. LS$_{SL}$			
Non-informative priors			
	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.023 [0.00, 0.089]	-
Species	9990	1.04 [0.00, 3.90]	-
Population	9990	0.47 [0.00, 1.76]	-
Units	9990	19.48 [16.2, 23.14]	-
Fixed effect			
Intercept	**9990**	**13.73 [8.27, 19.20]**	**0.00020**
Seasonality temperature	9990	-0.020 [-0.082, 0.046]	0.51
Seasonality precipitation	9990	-0.0043 [-0.047, 0.034]	0.82
Seasonality NDVI	9299	-0.0065 [-0.14, 0.13]	0.94
Sex – juvenile	10360	1.02 [-4.00, 6.25]	0.68
Sex – male	**10690**	**1.38 [-0.02, 2.78]**	**0.051**
SVL	10882	-0.030 [-0.076, 0.020]	0.23
Safe side - right	**9990**	**1.45 [0.34, 2.51]**	**0.0082**

Supplementary Table S3.9. (Continued)

2. $CRIT_{SL}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9989	0.0069 [0.0002, 0.022]	-
Species	9693	0.11 [0.0002, 0.49]	-
Population	9990	0.06 [0.0001, 0.28]	-
Units	-	-	-
Fixed effect			
Intercept	9990	-0.37 [-3.31, 2.35]	0.80
Seasonality temperature	9990	0.0032 [-0.030, 0.036]	0.83
Seasonality precipitation	9990	-0.0004 [-0.020, 0.019]	0.95
Seasonality NDVI	9990	-0.018 [-0.082, 0.050]	0.56
Sex – juvenile	9990	0.74 [-2.20, 3.57]	0.62
Sex – male	**8667**	**-0.68 [-1.49, 0.099]**	**0.093**
SVL	9990	0.012 [-0.014, 0.040]	0.39
Safe side – right	**9990**	**-0.54 [-1.20, 0.060]**	**0.090**

REVERSAL LEARNING

1. LS_{RL}

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10110	0.012 [0.0015, 0.043]	-
Species	9990	0.22 [0.0002, 1.02]	-
Population	9990	0.15 [0.0001, 0.71]	-
Units	9990	18.75 [15.35, 22.31]	-

Supplementary Table S3.9. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	**10564**	**7.56 [3.32, 11.82]**	**0.0014**
Seasonality temperature	9990	-0.0017 [-0.058, 0.050]	0.95
Seasonality precipitation	9990	0.021 [-0.0068, 0.050]	0.14
Seasonality NDVI	9990	0.0063 [-0.11, 0.14]	0.92
Sex – juvenile	9990	-1.94 [-6.72, 2.40]	0.40
Sex – male	9654	-0.069 [-1.48, 1.27]	0.93
SVL	10089	0.032 [-0.009, 0.075]	0.14
Safe side - right	**9990**	**1.37 [0.24, 2.47]**	**0.019**

2. CRIT_{RL}

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.0052 [0.0002, 0.017]	-
Species	9990	0.10 [0.0002, 0.44]	-
Population	9990	0.087 [0.0001, 0.39]	-
Units	-	-	-
Fixed effect			
Intercept	**9498**	**2.74 [-0.038, 5.53]**	**0.056**
Seasonality temperature	9990	0.003 [-0.030, 0.039]	0.85
Seasonality precipitation	**9990**	**-0.016 [-0.034, 0.0034]**	**0.086**
Seasonality NDVI	9990	-0.018 [-0.092, 0.057]	0.61
Sex – juvenile	10567	0.082 [-2.77, 3.00]	0.95
Sex – male	9990	0.20 [-0.63, 0.96]	0.61
SVL	9501	-0.023 [-0.052, 0.0052]	0.11
Safe side - right	**9990**	**-0.84 [-1.51, -0.20]**	**0.013**

Supplementary Table S3.9. (Continued)

Spatial and reversal learning

1. ***SR$_{SLRL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10843	0.11 [0.0002, 0.33]	-
Species	9990	2.53 [0.0002, 10.02]	-
Population	9990	0.23 [0.0002, 1.06]	-
Units	9990	11.16 [9.25, 13.41]	-
Fixed effect			
Intercept	**9542**	**17.63 [9.71, 25.43]**	**0.0010**
Seasonality temperature	10148	0.013 [-0.087, 0.11]	0.76
Seasonality precipitation	9636	-0.018 [-0.082, 0.044]	0.53
Seasonality NDVI	9990	0.025 [-0.19, 0.23]	0.82
Sex – juvenile	**9990**	**4.60 [-0.37, 9.57]**	**0.067**
Sex – male	9990	-0.39 [-1.49, 0.72]	0.48
SVL	9306	-0.031 [-0.074, 0.014]	0.17

2. ***CRIT$_{SLRL}$***

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9588	414.4 [10.77, 1456]	-
Species	9990	779.6 [12.5, 2261]	-
Population	9990	1120 [10.38, 3172]	-
Units	7961	233194 [27881, 495005]	-

Supplementary Table S3.9. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	9990	470.16 [-364.04, 1437.16]	0.27
Seasonality temperature	9990	0.63 [-11.83, 13.40]	0.90
Seasonality precipitation	**9242**	**-5.65 [-13.24, 0.56]**	**0.062**
Seasonality NDVI	**9635**	**-18.85 [-45.68, 4.01]**	**0.096**
Sex – juvenile	9608	111.75 [-699.67, 903.97]	0.74
Sex – male	9990	-64.54 [-321.58, 183.36]	0.58
SVL	9990	-5.31 [-15.66, 3.81]	0.24

Supplementary Table S3.10. MCMCglmm results for the life-history models. Significant p-values (pMCMC) and non-overlap of the 95% CI with zero are indicated in bold, as are trends close to significance. Sex was removed in multiple models due to complete separation of the data. The results reported here are those of the models with the priors leading to sample sizes > 1000 and autocorrelations < 0.1. These priors are either weakly informative inverse γ-distribution (V = 1; μ = 0.002), fixed to one (V = 1; fix = 1), informative (V = 100 and μ = 2), or parameter-expanded (V = 1; μ = 1; αμ = 0; αV = 1000), as indicated in the table. ST = solving time, CRIT = whether an animal reached the learning criterion (Y/N), SR = success rate, LS = learning speed (see main text for a more detailed explanation of all tests and cognitive traits).

INHIBITORY CONTROL

1. *ST*$_{IC}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	8699	1409 [0.0002, 6775]	-
Species	8983	0.0003, 273447]	-
Population	8542	6950 [0.0002, 43473]	-
Units	9422	67990 [54619, 82437]	-
Fixed effect			
Intercept	9990	415.56 [-540.99, 1361.21]	0.32
SVL hatchling	9990	-118.16 [-2023.36, 1690.57]	0.91
SVL maturity	9990	331.58 [-2561.56, 3169.57]	0.76
Clutch size	9614	64.16 [-644.27, 745.82]	0.82
Clutch frequency	9990	1462 [-273.36, 340.64]	0.92
Sex - juvenile	9990	-67.29 [-525.26, 401.54]	0.77
Sex - male	9990	-64.17 [-159.90, 26.21]	0.18
SVL	9990	-0.21 [-5.46, 4.93]	0.95

Supplementary Table S3.10. (Continued)

2. *CRIT*$_{IC}$

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9254	471.3 [12.11, 1405]	-
Species	9990	1491 [10.78, 7345]	-
Population	9990	830.5 [13.84, 3592]	-
Units	7372	11431 [725.8, 25492]	-
Fixed effect			
Intercept	9990	68.58 [-367.16, 535.25]	0.79
SVL hatchling	9990	213.38 [-535.73, 981.72]	0.53
SVL maturity	9990	157.45 [-1031.02, 1440.41]	0.81
Clutch size	9990	-31.25 [-264.52, 225.05]	0.74
Clutch frequency	9659	-66.92 [-198.09, 56.28]	0.22
Sex - juvenile	-	-	-
Sex - male	-	-	-
SVL	9990	2.72 [-0.55, 5.96]	0.11

LID REMOVAL

1. *ST*$_{LR}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	328.9 [0.0002, 1574]	-
Species	9444	14290 [0.0002, 28144]	-
Population	9173	1220 [0.0001, 7335]	-
Units	9990	59215 [46495, 73606]	-

Supplementary Table S3.10. (Continued)

Fixed effect			
Intercept	**9990**	**682.4 [160.5, 1217]**	**0.013**
SVL hatchling	9990	88.11 [-782.9, 971.5]	0.75
SVL maturity	9990	384.5 [-1028, 1697]	0.47
Clutch size	9990	-40.85 [-337.4, 302.22]	0.70
Clutch frequency	9686	44.12 [-106.1, 197.7]	0.48
Sex - juvenile	9990	148.7 [-188.5, 483.7]	0.36
Sex - male	9648	-26.53 [-121.7, 68.79]	0.58
SVL	9990	-0.099 [-3.85, 3.75]	0.99

2. SR_{LR}

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	8473	0.22 [0.0002, 0.86]	-
Species	4470	8.65 [0.0002, 33.35]	-
Population	8733	0.13 [0.0002, 0.51]	-
Units	9765	1.59 [0.73, 2.58]	-
Fixed effect			
Intercept	9030	-5.00 [-16.66, 4.46]	0.22
SVL hatchling	9990	-0.66 [-21.71, 19.92]	0.91
SVL maturity	9002	-9.12 [-43.81, 21.88]	0.49
Clutch size	9990	-0.84 [-8.47, 6.59]	0.78
Clutch frequency	9990	0.15 [-3.71, 3.66]	0.89
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	**9322**	**0.038 [0.001, 0.080]**	**0.041**

Supplementary Table S3.10. (Continued)

ESCAPE BOX

1. ***ST$_{ESC}$***

Parameter-expanded priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	5816 [0.001, 16369]	-
Species	9990	39906 [0.00, 220472]	-
Population	9990	12019 [0.00, 65911]	-
Units	9990	194032 [150778, 239878]	-
Fixed effect			
Intercept	10663	154.14 [-1246.81, 1662.77]	0.85
SVL hatchling	9990	-1433.21 [-4082.3, 1246.1]	0.24
SVL maturity	9990	2522.98 [-1434.9, 6543.5]	0.18
Clutch size	10945	-269.52 [-1206.33, 609.46]	0.50
Clutch frequency	9990	228.76 [-200.35, 648.87]	0.25
Sex - juvenile	9990	521.32 [-233.87, 1279.46]	0.18
Sex - male	10687	78.53 [-148.37, 291.94]	0.48
SVL	9990	6.49 [-2.05, 14.70]	0.13

2. ***SR$_{ESC}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9665	98.4 [72.45, 126.6]	-
Species	9990	101.8 [73.73, 129.6]	-
Population	9990	99.61 [72.44, 127.1]	-
Units	9990	57.78 [45.96, 69.92]	-

Supplementary Table S3.10. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	6234	-46.83 [-204.20, 108.87]	0.56
SVL hatchling	9990	35.34 [-268.77, 346.08]	0.83
SVL maturity	3907	-240.43 [-773.18, 247.47]	0.36
Clutch size	9990	-3.81 [-101.29, 97.73]	0.95
Clutch frequency	5001	18.69 [-33.44, 67.94]	0.49
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	9990	-0.056 [-0.37, 0.23]	0.73

SPATIAL LEARNING

1. LS$_{SL}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.0013 [0.0001, 0.036]	-
Species	9990	0.014 [0.0002, 0.050]	-
Population	9990	0.0053 [0.0002, 0.017]	-
Units	9990	0.063 [0.033, 0.096]	-
Fixed effect			
Intercept	**9990**	**2.40 [1.70, 3.09]**	**<1e-04**
SVL hatchling	9700	-0.50 [-1.85, 0.94]	0.41
SVL maturity	10172	0.53 [-1.39, 2.75]	0.57
Clutch size	9990	0.028 [-0.42, 0.50]	0.90
Clutch frequency	10384	0.034 [-0.19, 0.25]	0.72
Sex – juvenile	9990	0.012 [-0.56, 0.53]	0.96
Sex – male	8745	0.10 [-0.042, 0.24]	0.15
SVL	9990	-0.002 [-0.007, 0.003]	0.40
Safe side – right	**9990**	**0.15 [0.050, 0.25]**	**0.003**

Supplementary Table S3.10. (Continued)

2. CRIT$_{SL}$

Non-informative priors

	Effective sample size	**Posterior mean [95% CI]**	**pMCMC**
Random effect			
Phylogeny	9990	0.009 [0.0001, 0.029]	-
Species	9990	0.15 [0.0002, 0.58]	-
Population	9990	0.064 [0.0001, 0.27]	-
Units	-	-	-
Fixed effect			
Intercept	9990	0.42 [-2.46, 3.16]	0.72
SVL hatchling	10172	3.01 [-1.72, 7.91]	0.20
SVL maturity	9990	-0.79 [-7.49, 6.51]	0.80
Clutch size	9990	-0.15 [-1.81, 1.45]	0.83
Clutch frequency	9701	-0.35 [-1.09, 0.49]	0.36
Sex - juvenile	9990	0.70 [-2.34, 3.84]	0.67
Sex - male	9990	-0.67 [-1.56, 0.19]	0.13
SVL	9990	0.011 [-0.016, 0.039]	0.44
Safe side - right	**9990**	**-0.82 [-1.49, -0.16]**	**0.016**

REVERSAL LEARNING

1. LS$_{RL}$

Non-informative priors

	Effective sample size	**Posterior mean [95% CI]**	**pMCMC**
Random effect			
Phylogeny	10199	0.0013 [0.0001, 0.004]	-
Species	8172	0.015 [0.0002, 0.054]	-
Population	9990	0.006 [0.0002, 0.019]	-
Units	9730	0.057 [0.027, 0.091]	-

Supplementary Table S3.10. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	**10586**	**2.23 [1.49, 2.94]**	**<1e-04**
SVL hatchling	10771	-0.052 [-1.41, 1.37]	0.93
SVL maturity	9990	0.37 [-1.67, 2.52]	0.68
Clutch size	9990	0.008 [-0.47, 0.49]	0.97
Clutch frequency	9990	0.053 [-0.17, 0.28]	0.60
Sex - juvenile	9990	-0.11 [-0.68, 0.44]	0.69
Sex - male	9990	-0.054 [-0.19, 0.074]	0.43
SVL	9990	0.002 [-0.004, 0.0064]	0.53
Safe side - right	**9990**	**0.13 [0.034, 0.24]**	**0.009**

2. *CRIT*$_{RL}$

Non-informative priors

	Effective sample size	**Posterior mean [95% CI]**	**pMCMC**
Random effect			
Phylogeny	9990	0.015 [0.0002, 0.053]	-
Species	9990	0.27 [0.0002, 1.16]	-
Population	9990	0.15 [0.000, 0.67]	-
Units	-	-	-
Fixed effect			
Intercept	9990	2.18 [-1.14, 5.50]	0.18
SVL hatchling	10691	2.04 [-3.77, 7.84]	0.44
SVL maturity	9990	-2.79 [-11.35, 5.67]	0.47
Clutch size	9990	0.47 [-1.52, 2.42]	0.58
Clutch frequency	9990	-0.41 [-1.44, 0.57]	0.37
Sex - juvenile	10321	0.049 [-3.07, 3.47]	0.98
Sex - male	9067	0.24 [-0.65, 1.12]	0.59
SVL	9990	-0.022 [-0.055, 0.010]	0.18
Safe side - right	**9989**	**-1.02 [-1.71, -0.30]**	**0.005**

Supplementary Table S3.10. (Continued)

SPATIAL + REVERSAL LEARNING

1. ***SR$_{SLRL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.0012 [0.0001, 0.0033]	-
Species	9990	0.014 [0.0002, 0.050]	-
Population	9990	0.0034 [0.0002, 0.011]	-
Units	9365	0.0019 [0.0002, 0.0050]	-
Fixed effect			
Intercept	**9990**	**3.04 [2.41, 3.67]**	**<1e-04**
SVL hatchling	9200	0.97 [-0.31, 2.33]	0.12
SVL maturity	9990	-0.68 [-2.57, 1.23]	0.43
Clutch size	9990	0.16 [-0.29, 0.59]	0.40
Clutch frequency	9990	-0.11 [-0.33, 0.091]	0.25
Sex - juvenile	9522	0.27 [-0.11, 0.69]	0.17
Sex - male	9912	-0.013 [-0.098, 0.082]	0.77
SVL	9469	-0.002 [-0.0052, 0.0016]	0.33

2. ***CRIT$_{SLRL}$***

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	491.8 [9.12, 1787]	-
Species	9990	838.5 [11.1, 2334]	-
Population	9596	1460 [11.01, 3679]	-
Units	7836	202533 [13423, 451122]	

Supplementary Table S3.10. (Continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	9598	80.01 [-637.27, 829.51]	0.81
SVL hatchling	9150	200.90 [-900.21, 1404.47]	0.72
SVL maturity	9699	841.73 [-858.81, 2550.70]	0.28
Clutch size	9990	-58.61 [-44454, 271.44]	0.73
Clutch frequency	9878	-112.29 [-333.47, 91.55]	0.25
Sex – juvenile	-	-	-
Sex – male	-	-	-
SVL	8914	-5.94 [-15.43, 1.75]	0.12

Supplementary Table S3.11. MCMCglmm results for the reversal learning models containing only data from individuals that passed the 5/6 -criterion during the spatial learning phase. Significant p-values (pMCMC) and non-overlap of the 95% CI with zero are indicated in bold, as are trends close to significance. Sex was removed in multiple models due to complete separation of the data. The results reported here are those of the models with the priors leading to sample sizes > 1000 and autocorrelations < 0.1. These priors are either weakly informative inverse γ-distribution (V = 1; μ = 0.002), fixed to one (V = 1; fix = 1), informative (V = 100 and μ = 2), or parameter-expanded (V = 1; μ = 1; αμ = 0; αV = 1000), as indicated in the table. ST = solving time, CRIT = whether an animal reached the learning criterion (Y/N), SR = success rate, LS = learning speed (see main text for a more detailed explanation of all tests and cognitive traits).

REVERSAL LEARNING – ENVIRONMENTAL QUALITY

1. LS_{RL}

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9632	0.0009 [0.0001, 0.0022]	-
Species	9990	0.0093 [0.0001, 0.0343]	-
Population	9990	0.0047 [0.0002, 0.0155]	-
Units	9990	0.0052 [0.0002, 0.0166]	-
Fixed effect			
Intercept	**10271**	**3.071 [2.060, 4.057]**	**< 0.0001**
Average temperature	9990	-0.020 [-0.061, 0.021]	0.308
Precipitation	**9990**	**-0.004 [-0.009, 0.004]**	**0.08**
Sex – juvenile	9990	-0.285 [-0.943, 0.408]	0.38
Sex – male	9990	-0.048 [-0.189, 0.086]	0.50
SVL	9473	0.002 [-0.003, 0.0067]	0.48
Safe side – right	9064	0.12 [-0.057, 0.242]	0.27

Supplementary Table S3.11. (continued)

2. ***CRIT***$_{RL}$

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	3966	49.47 [9.901, 119.3]	-
Species	9694	197.2 [10.38, 641.9]	-
Population	9990	130.2 [13.2, 371.3]	-
Units	-	-	-
Fixed effect			
Intercept	5306	-113.44 [-338.833, 90.154]	0.27
Average temperature	6917	2.436 [-6.162, 10.573]	0.55
Precipitation	3204	0.907 [-0.257, 2.286]	0.11
Sex – juvenile	9527	15.867 [-92.557, 127.283]	0.76
Sex – male	9990	3.552 [-4.658, 12.298]	0.41
SVL	9990	-0.278 [-0.674, 0.114]	0.15
Safe side – right	**9990**	**-11.373 [-19.841, -2.323]**	**0.009**

REVERSAL LEARNING – ENVIRONMENTAL VARIABILITY

1. ***LS***$_{RL}$

Non-informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.071 [0.0001, 0.255]	-
Species	10539	1.283 [0.0002, 6.128]	-
Population	9990	0.424 [0.0002, 2.186]	-
Units	9990	12.9 [9.195, 16.97]	-

Supplementary Table S3.11. (continued)

Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	**9990**	**7.885 [0.234, 15.732]**	**0.053**
Seasonality temperature	9990	0.039 [-0.062, 0.138]	0.42
Seasonality Precipitation	9626	0.027 [-0.034, 0.085]	0.31
Seasonality NDVI	9990	0.008 [-0.227, 0.226]	0.94
Sex – juvenile	10425	-2.085 [-9.012, 4.683]	0.54
Sex – male	9990	-0.505 [-2.158, 1.350]	0.56
SVL	9990	0.016 [-0.040, 0.0724]	0.58
Safe side – right	9990	1.241 [-0.629, 3.002]	0.0

2. ***CRIT$_{RL}$***

Parameter expanded priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9635	1478 [0.000, 5257]	-
Species	10315	8342 [0.000. 38090]	-
Population	9990	9802 [0.000, 45019]	-
Units	9701	158745 [28214, 336599]	-
Fixed effect			
Intercept	**9645**	**-1321.79 [-67.28, 2829.12]**	**0.031**
Seasonality temperature	9990	-4.730 [-23.190, 13.032]	0.59
Seasonality Precipitation	**9389**	**-8.613 [-21.098, 1.995]**	**0.075**
Seasonality NDVI	**9990**	**-27.386 [-67.717, 8.377]**	**0.099**
Sex – juvenile	9990	-1.925 [-937.437, 1047.122]	0.99
Sex – male	10319	104.142 [-155.654, 415.194]	0.44
SVL	9990	-5.599 [-17.321, 4.510]	0.27
Safe side – right	**9990**	**-260.025 [-554.765, -19.970]**	**0.049**

Supplementary Table S3.11. (continued)

REVERSAL LEARNING – LIFE HISTORY

1. ***LS$_{RL}$***

Informative priors

	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	9990	0.003 [0.0001,0.0076]	-
Species	9990	0.036 [0.0002, 0.132]	-
Population	9990	0.007 [0.0002, 0.0233]	-
Units	990	0.006 [0.0002, 0.0179]	-
Fixed effect			
Intercept	**9990**	**2.670 [1.718, 3.736]**	**0.002**
SVL hatchling	9990	0.690 [-1.279, 2.887]	0.45
SVL maturity	9990	-0.602 [-3.565, 2.173]	0.61
Clutch size	9990	0.155 [-0.478, 0.891]	0.60
Clutch frequency	9699	-0.073 [-0.401, 0.266]	0.63
Sex – juvenile	9990	-0.231 [-1.260, 0.789]	0.60
Sex – male	9554	-0.037 [-0.187; 0.110]	0.63
SVL	9641	0.001 [-0.004, 0.007]	0.68
Safe side – right	9990	0.083 [-0.077, 0.242]	0.31

2. ***CRIT$_{RL}$***

Informative priors

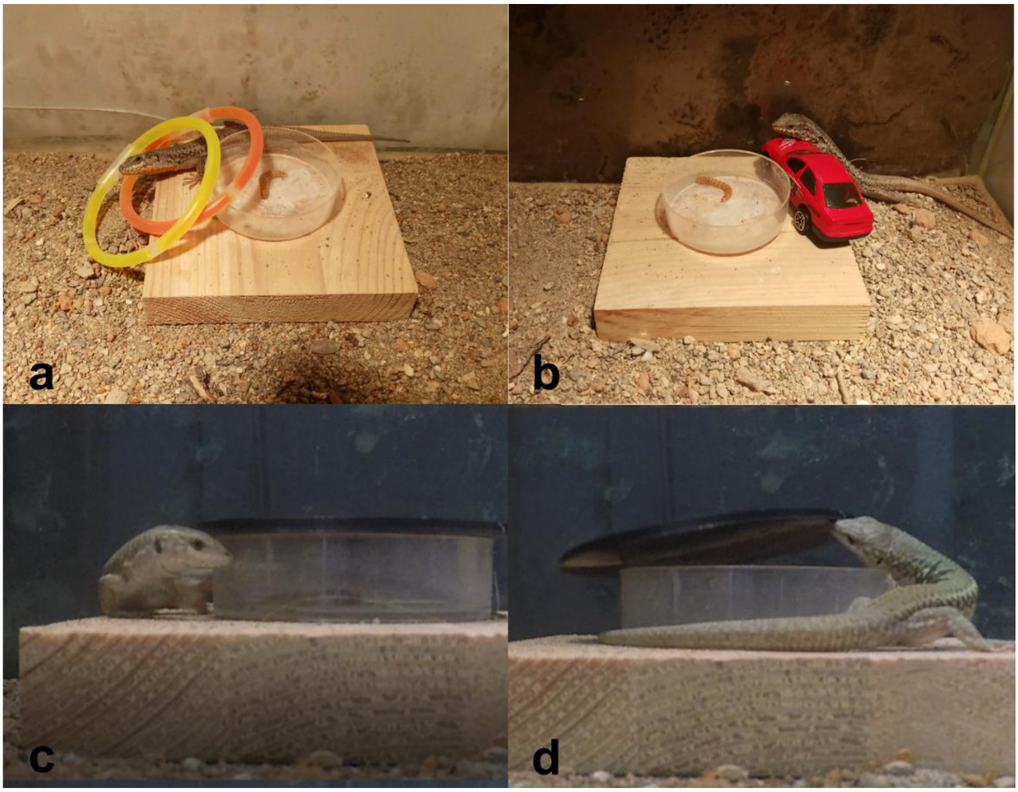
	Effective sample size	Posterior mean [95% CI]	pMCMC
Random effect			
Phylogeny	10765	100.4 [74.91, 129.6]	-
Species	9990	101.9 [75.1, 132.1]	-
Population	8926	101.7 [74.91, 130.9]	-
Units	10160	114.7 [83.6, 151.4]	-

Supplementary Table S3.11. (continued)

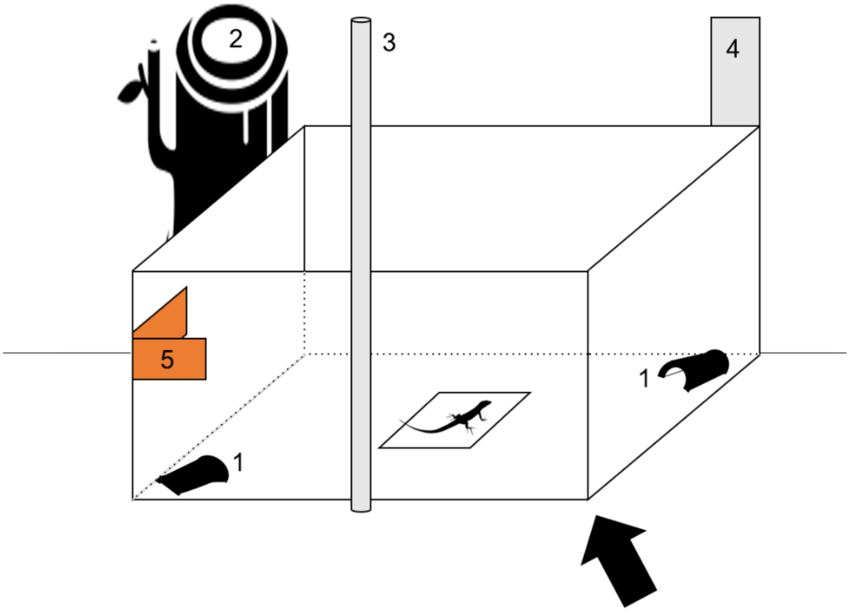
Fixed effect	Effective sample size	Posterior mean [95% CI]	pMCMC
Intercept	**9286**	**4.062 [-161.092, 189.760]**	**0.98**
SVL hatchling	7144	-131.907 [-529.681, 260.373]	0.53
SVL maturity	9112	57.259 [-392.626, 505.102]	0.80
Clutch size	7064	-45.677 [-158.324, 69.313]	0.43
Clutch frequency	6582	-2.149 [-0.67.521, 61.399]	0.96
Sex – juvenile	8877	-18.699 [-171.215, 141.849]	0.81
Sex – male	9990	5.888 [-3.497; 15.969]	0.23
SVL	9990	-0.314 [-0.778, 0.125]	0.15
Safe side – right	**9990**	**-11.687 [-21.769, -2.342]**	**0.015**

APPENDIX CHAPTER 4

CHAPTER 4: SUPPLEMENTARY METHODS



Supplementary Figure S4.4. Set-up during the neophobia and problem-solving assays. The novel objects used during the neophobia tests were a) a pair of yellow and orange glow sticks and b) a red toy car. During the problem-solving task, lizards needed to remove the lid from a transparent petri dish in order to access a prey (c-d). See main text for more details regarding the protocol. Photo credits: A. Sfendouraki-Basakarou (a-b) & G. De Meester (c-d).



Supplementary Figure S4.5. Set-up during the spatial / reversal learning experiments. Lizards had to learn the location of a safe refuge (1) within an arena (60 x 60 x 30 cm). Walls of the arena were blinded, but the following distal cues were provided in order to allow navigation and orientation: a tree trunk (2), an iron rod (3) and piece of cardboard (4). One side of the arena was always placed against a wall, which could serve as an additional distal cue. Inside the arena, a piece of orange paper (5) was taped into one of the corners to serve as a local cue. The position of the distal and local cues, as well as the location of the arena, was consistent across all trials. The black arrow indicates the position of the observer, which was fixed throughout the entire experiment and thus also served as a cue for orientation. See main text for more details regarding the protocol.

APPENDIX CHAPTER 5

CHAPTER 5: SUPPLEMENTARY RESULTS

Supplementary Table S5.1. Average (± SE) scores for the cognition and personality tests, by habitat type and by sex. In some cases, sample size within a cognitive test varies depending on the measured variable (see main text).

Test	Complex	Simple	Female	Male
	PERSONALITY			
Neophobia	N = 66	N = 72	N = 66	N = 72
Attack latency control (s)	123 ± 9	103 ± 8	123 ± 10	103 ± 8
Relative neophobia (%)	19.3 ± 17.4	55.3 ± 29.4	29.7 ± 22.6	45.7 ± 26.4
Exploration	N = 65	N = 71	N = 69	N = 67
PC1	-0.17 ± 0.15	0.16 ± 0.13	0.09 ± 0.15	-0.08 ± 0.13
PC2	-0.25 ± 0.12	0.23 ± 0.12	0.10 ± 0.12	-0.10 ± 0.13
Aggression	N = 35	N = 34	/	/
Aggression score	2.87 ± 1.18	1.42 ± 0.68	/	/
	COGNITION			
Lid Removal	N = 65 – 66	N = 70 – 71	N = 67	N = 68 - 70
Lid Removal Score	0.49 ± 0.10	0.69 ± 0.10	0.55 ± 0.10	0.63 ± 0.10
Solving time (s)	777 ± 28	742 ± 30	777 ± 27	742 ± 31
Escape Box	N = 64 – 61	N = 68 – 61	N = 65 - 61	N = 67 - 61
Escape probability	75 %	80.9 %	83.1 %	73.1 %
Escape time (s)	932 ± 82	811 ± 79	760 ± 75	984 ± 84
Spatial Learning	N = 62	N = 67	N = 65	N = 64
Proportion learner	64.5 %	47.8 %	56.9 %	54.7 %
Number of errors	0.69 ± 0.04	0.81 ± 0.04	0.77 ± 0.04	0.73 ± 0.04
Reversal Learning	N = 62	N = 67	N = 65	N = 64
Proportion learner	40.3 %	52.2 %	43.1 %	50.0 %
Number of errors	0.95 ± 0.04	0.85 ± 0.04	0.94 ± 0.04	0.87 ± 0.04
Flexible learners	12. 9%	10.4 %	10.8 %	12.5 %
Flexibility scores	0.82 ± 0.03	0.83 ± 0.03	0.86 ± 0.04	0.80 ± 0.03

Supplementary Table S5.2. Outcome of the (G)LMMs testing the effect of habitat complexity and other variables on cognition and personality, for the models in which population was not included as random factor. Statistical significant differences are indicated as follows: '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$ (see also main text).

Response	Predictor	F/Wald-stats	P
Relative neophobia (log)	Habitat	$F_{1,130} = 0.47$	0.49
	Sex	$F_{1,130} = 0.79$	0.38
	Year	$F_{1,130} = 0.00$	0.95
	Tail status	$F_{1,130} = 0.75$	0.39
	SVL	$F_{1,130} = 2.18$	0.14
	Habitat*Year	$F_{1,129} = 1.54$	0.22
	Sex*Year	$F_{1,128} = 1.37$	0.24
	SVL*Year	$F_{1,127} = 1.51$	0.22
LR Score	Habitat	$\chi^2_1 = 1.09$	0.30
	Sex	$\chi^2_1 = 0.10$	0.75
	Year	$\chi^2_1 = 4.84$	**0.03***
	Tail status	$\chi^2_1 = 0.00$	0.95
	SVL	$\chi^2_1 = 0.01$	0.93
	Habitat*Year	$\chi^2_1 = 0.04$	0.84
	Sex*Year	$\chi^2_1 = 0.15$	0.85
	SVL*Year	NA	NA
LR time (cox-proportional hazard model)	Habitat	$\chi^2_1 = 2.57$	0.11
	Sex	$\chi^2_1 = 1.42$	0.23
	Year	$\chi^2_1 = 3.40$	0.07°
	Tail status	$\chi^2_1 = 0.22$	0.64
	SVL	$\chi^2_1 = 0.17$	0.68
	Habitat*Year	$\chi^2_1 = 0.02$	0.88
	Sex*Year	$\chi^2_1 = 0.20$	0.66
	SVL*Year	$\chi^2_1 = 0.10$	0.75
Exploration PC1 (box-cox: $\lambda = 1.3$)	Habitat	$F_{1,130} = 2.26$	0.14
	Sex	$F_{1,130} = 0.52$	0.47
	Year	$F_{1,130} = 2.68$	0.10
	Tail status	$F_{1,130} = 0.54$	0.46
	SVL	$F_{1,130} = 0.32$	0.58
	Habitat*Year	$F_{1,129} = 0.56$	0.45
	Sex*Year	$F_{1,128} = 0.16$	0.69
	SVL*Year	$F_{1,127} = 0.03$	0.87
Exploration PC2	Habitat	$F_{1,130} = 3.39$	0.07°
	Sex	$F_{1,130} = 2.26$	0.14
	Year	$F_{1,130} = 7.79$	**<0.01****
	Tail status	$F_{1,130} = 13.59$	**<0.001*****
	SVL	$F_{1,130} = 3.69$	0.06°
	Habitat*Year	$F_{1,129} = 2.88$	0.09°
	Sex*Year	$F_{1,128} = 1.15$	0.29
	SVL*Year	$F_{1,127} = 0.03$	0.86

Supplementary Table S5.2. (continued)

Response	Predictor	F/Wald-stats	P
Aggression	Habitat	$\chi^2_1 = 0.89$	0.35
	Year	$\chi^2_1 = 1.43$	0.23
	Tail status	$\chi^2_1 = 1.93$	0.17
	SVL	$\chi^2_1 = 0.18$	0.67
	Nr of previous trails	$\chi^2_1 = 2.48$	0.12
	Habitat*Year	$\chi^2_1 = 0.72$	0.40
	SVL*Year	$\chi^2_1 = 0.04$	0.83
ESC Success (Y/N)	Habitat	$\chi^2_1 = 0.12$	0.73
	Sex	$\chi^2_1 = 2.19$	0.14
	Year	$\chi^2_1 = 0.96$	0.33
	Tail status	$\chi^2_1 = 7.21$	**<0.01****
	SVL	$\chi^2_1 = 0.24$	0.63
	Habitat*Year	$\chi^2_1 = 0.84$	0.36
	Sex*Year	$\chi^2_1 = 0.20$	0.65
	SVL*Year	$\chi^2_1 = 0.61$	0.43
ESC Time (box-cox: λ = 0.3)	Habitat	$F_{1,116} = 0.50$	0.48
	Sex	$F_{1,116} = 3.90$	0.05°
	Year	$F_{1,1} = 0.13$	0.79
	Tail status	$F_{1,116} = 3.90$	**0.03***
	SVL	$F_{1,88} = 0.03$	0.86
	Habitat*Year	$F_{1,113} = 0.10$	0.75
	Sex*Year	$F_{1,114} = 1.10$	0.30
	SVL*Year	$F_{1,115} = 1.57$	0.21
SL Success (Y/N)	**Habitat**	$\chi^2_1 = 5.17$	**0.02***
	Safe side	$\chi^2_1 = 39.49$	**<0.001*****
	Sex	$\chi^2_1 = 0.66$	0.42
	Year	$\chi^2_1 = 0.98$	0.32
	SVL	$\chi^2_1 = 0.90$	0.34
	Habitat*Year	$\chi^2_1 = 2.91$	0.09°
	Sex*Year	$\chi^2_1 = 0.02$	0.88
	SVL*Year	$\chi^2_1 = 0.09$	0.76
SL Errors	Habitat	$\chi^2_1 = 1.67$	0.20
	Safe side	$\chi^2_1 = 276.80$	**<0.001*****
	Trail	$\chi^2_1 = 8.16$	**<0.01****
	Year	$\chi^2_1 = 6.61$	**0.01***
	Habitat*Year	$\chi^2_1 = 0.02$	0.90
	Trail*Year	$\chi^2_1 = 0.12$	0.73
	Habitat*Trail	$\chi^2_1 = 0.22$	0.64
	Safe side * Trail	$\chi^2_1 = 0.53$	0.47

Supplementary Table S5.2. (continued)

Response	Predictor	F/Wald-stats	P
RL Success (Y/N)	Habitat	χ^2_1 = 2.41	0.12
	Safe side	χ^2_1 = 40.40	**<0.001*** **
	Sex	χ^2_1 = 0.21	0.65
	Year	χ^2_1 = 0.83	0.36
	Tail status	χ^2_1 = 0.05	0.82
	SVL	χ^2_1 = 4.08	**0.04***
	Habitat*Year	χ^2_1 = 1.87	0.17
	Sex*Year	χ^2_1 = 0.25	0.62
	SVL*Year	χ^2_1 = 0.25	0.61
	Safe side * Habitat	χ^2_1 = 0.02	0.88
RL Errors	Habitat	χ^2_1 = 1.04	0.31
	Safe side	χ^2_1 = 223.55	**<0.001*** **
	Trail	χ^2_1 = 10.64	**<0.001*** **
	Year	χ^2_1 = 0.36	0.55
	Habitat*Year	χ^2_1 = 4.00	**0.05***
	Trail*Year	χ^2_1 = 3.20	0.07°
	Habitat*Trail	χ^2_1 = 0.53	0.47
	Safe side * Trail	χ^2_1 = 0.78	0.38
Flexible learner (Y/N)	Habitat	χ^2_1 = 2.24	0.13
	Safe side	χ^2_1 = 0.93	0.34
	Sex	χ^2_1 = 0.02	0.89
	Year	χ^2_1 = 1.03	0.31
	Tail status	χ^2_1 = 3.85	**0.05***
	SVL	χ^2_1 = 0.94	0.33
	Habitat*Year	χ^2_1 = 3.85	**0.05***
	Sex*Year	χ^2_1 = 0.17	0.68
	SVL*Year	χ^2_1 = 1.67	0.20
	Safe side * Habitat	χ^2_1 = 3.10	0.08°

Supplementary Table S5.3. Outcome of the (G)LMMs testing the relationship between personality traits, between cognitive traits, and between personality and cognition. Standardized regression slopes + SE are given. Statistical significant differences are indicated as follows: '°' p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001 (see also main text).

Association	Predictor	Regression slope	F/Wald-stats	P
	BEHAVIOURAL SYNDROME			
NEO ~ EXP PC1	Exp PC1	0.07 ± 0.10	$F_{1,112} = 0.61$	0.44
	Habitat		$F_{1,2} = 0.00$	1.00
	Year		$F_{1,111} = 0.00$	0.94
	Exp PC1*Habitat		$F_{1,111} = 0.53$	0.47
	Exp PC1*Year		$F_{1,111} = 0.03$	0.87
	Exp PC1*Habitat*Year		$F_{1,108} = 3.08$	0.08°
	2018			
	Exp PC1	0.08 ± 0.15	$F_{1,44} = 0.32$	0.58
	Habitat		$F_{1,2} = 0.22$	0.68
	Exp PC1*Habitat		$F_{1,43} = 0.62$	0.44
	2019			
	Exp PC1	0.07 ± 0.12	$F_{1,63} = 0.29$	0.59
	Habitat		$F_{1,3} = 0.23$	0.67
	Exp PC1*Habitat		$F_{1,62} = 2.94$	0.09°
		C: -0.09 ± 0.15	t = -0.61	0.54
		S: 0.34 ± 0.20	t = 1.70	0.10°
NEO ~ EXP PC2	Exp PC2	0.08 ± 0.10	$F_{1,112} = 0.69$	0.41
	Habitat		$F_{1,3} = 0.00$	0.95
	Year		$F_{1,111} = 0.00$	0.96
	Exp PC2*Habitat		$F_{1,110} = 1.30$	0.26
	Exp PC2*Year		$F_{1,110} = 0.02$	0.89
	Exp PC2*Habitat*Year		$F_{1,103} = 0.61$	0.44
NEO ~ AGG	Aggression	0.10 ± 0.14	$F_{1,55} = 0.52$	0.48
	Habitat		$F_{1,2} = 0.11$	0.77
	Year		$F_{1,55} = 0.68$	0.41
	Aggression*Habitat		$F_{1,50} = 0.01$	0.93
	Aggression*Year		$F_{1,53} = 1.01$	0.32
	Agg*Habitat*Year		$F_{1,51} = 0.07$	0.79
EXP PC1 ~ AGG	Aggression	0.09 ± 0.14	$F_{1,55} = 0.40$	0.53
	Habitat		$F_{1,2} = 0.98$	0.41
	Year		$F_{1,55} = 0.90$	0.35
	Aggression*Habitat		$F_{1,50} = 0.09$	0.77
	Aggression*Year		$F_{1,54} = 0.92$	0.34
	Agg*Habitat*Year		$F_{1,51} = 0.17$	0.68

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
EXP PC 2^1~ AGG	Aggression	-0.18 ± 0.14	$F_{1,55}$ = 1.73	0.19
	Habitat		$F_{1,2}$ = 0.00	0.96
^{1}log-transformed	Year		$F_{1,55}$ = 0.00	0.98
	Aggression*Habitat		$F_{1,51}$ = 2.55	0.12
	Aggression*Year		$F_{1,53}$ = 0.00	0.96
	Aggression*Habitat*Year		$F_{1,51}$ = 3.21	0.08°
	<u>2018</u>			
	Aggression	-0.17 ± 0.22	$F_{1,20}$ = 3.36	0.08°
	Habitat		$F_{1,2}$ = 2.17	0.29
	Aggression*Habitat		$F_{1,20}$ = 4.20	0.05°
		C: 0.06 ± 0.23	t = 0.25	0.81
		S: -1.02 ± 0.47	t = -2.15	0.05°
	<u>2019</u>			
	Aggression	-0.22 ± 0.19	$F_{1,31}$ = 1.43	0.24
	Habitat		$F_{1,3}$ = 1.24	0.36
	Aggression*Habitat		$F_{1,29}$ = 0.21	0.65
	COGNITIVE SYNDROME			
LR (Y/N) ~ ESC*	ESC		χ^2_1 = 2.46	0.12
	Habitat		χ^2_1 = 0.91	0.34
*box-cox transformed	**Year**		χ^2_1 = 4.76	**0.03***
	ESC*Habitat		χ^2_1 = 1.14	0.29
	ESC*Year		χ^2_1 = 5.21	**0.02***
	ESC*Habitat*Year		χ^2_1 = 3.90	**0.05***
	<u>2018</u>			
	ESC	*0.72 ± 0.43*	χ^2_1 = 2.76	0.10°
	Habitat		χ^2_1 = 0.14	0.71
	ESC*Habitat		χ^2_1 = 1.16	0.28
	<u>2019</u>			
	ESC		χ^2_1 = 1.12	0.29
	Habitat		χ^2_1 = 0.96	0.33
	ESC*Habitat		χ^2_1 = 4.58	**0.03***
		C: -1.03 ± 0.53	z = -1.92	0.06°
		S: 0.41 ± 0.38	z = 1.06	0.29
LR (Y/N) ~ SL SCORE^1	SL	-0.05 ± 0.22	χ^2_1 = 0.05	0.83
	Habitat		χ^2_1 = 0.82	0.36
	Year		χ^2_1 = 2.88	0.09°
^{1}log-transformed	SL*Habitat		χ^2_1 = 0.74	0.39
	SL*Year		χ^2_1 = 1.46	0.23
	SL*Habitat*Year		χ^2_1 = 0.24	0.63
LR (Y/N) ~ RL SCORE^1	RL	0.25 ± 0.22	χ^2_1 = 1.37	0.24
	Habitat		χ^2_1 = 0.62	0.43
	Year		χ^2_1 = 2.86	0.09°
^{1}log-transformed	RL*Habitat		χ^2_1 = 0.01	0.91
	RL*Year		χ^2_1 = 0.00	0.92
	RL*Habitat*Year		χ^2_1 = 0.00	0.97

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
LR (Y/N) ~ FLEX SCORE^1	Flex	0.22 ± 0.22	$\chi^2_1 = 0.99$	0.32
	Habitat		$\chi^2_1 = 0.90$	0.34
	Year		$\chi^2_1 = 3.15$	0.08°
^{1}log-transformed	Flex*Habitat		$\chi^2_1 = 0.55$	0.46
	Flex*Year		$\chi^2_1 = 0.53$	0.47
	Flex*Habitat*Year		$\chi^2_1 = 0.04$	0.83
ESC* ~ SL SCORE^1	SL		$F_{1,110} = 0.30$	0.59
	Habitat		$F_{1,3} = 0.89$	0.42
*box-cox transformed	Year		$F_{1,112} = 0.01$	0.91
^{1}log-transformed	SL*Habitat		$F_{1,109} = 0.05$	0.82
	SL*Year		$F_{1,111} = 5.13$	**0.03***
		18: -0.26± 0.14	t = -1.83	0.07°
		19: 0.16 ± 0.12	t = 1.35	0.18
	SL*Habitat*Year		$F_{1,108} = 0.07$	0.79
ESC* ~ RL SCORE^1	RL	0.05 ± 0.09	$F_{1,112} = 0.33$	0.56
	Habitat		$F_{1,3} = 1.01$	0.40
*box-cox transformed	Year		$F_{1,113} = 0.00$	0.98
^{1}log-transformed	RL*Habitat		$F_{1,111} = 0.96$	0.33
	RL*Year		$F_{1,110} = 0.08$	0.78
	RL*Habitat*Year		$F_{1,108} = 0.14$	0.71
ESC* ~ FLEX SCORE^1	Flex	-0.05 ± 0.09	$F_{1,112} = 0.28$	0.60
	Habitat		$F_{1,3} = 1.01$	0.40
*box-cox transformed	Year		$F_{1,113} = 0.00$	0.96
^{1}log-transformed	Flex*Habitat		$F_{1,110} = 0.07$	0.79
	Flex*Year		$F_{1,110} = 2.43$	0.12
	Flex*Habitat*Year		$F_{1,107} = 0.04$	0.85
RL SCORE^1 ~ SL SCORE^1	**SL**	**-0.23 ± 0.09**	$F_{1,113} = 6.02$	**0.02***
	Habitat		$F_{1,3} = 0.07$	0.81
	Year		$F_{1,111} = 4.59$	0.03*
^{1}log-transformed	SL*Habitat		$F_{1,112} = 0.45$	0.50
	SL*Year		$F_{1,111} = 0.04$	0.83
	SL*Habitat*Year		$F_{1,109} = 0.28$	0.60
FLEX SCORE^1 ~ SL SCORE^1	**SL**	**0.46 ± 0.08**	$F_{1,113} = 29.98$	**<0.001*** **
	Habitat		$F_{1,3} = 0.15$	0.73
^{1}log-transformed	Year		$F_{1,111} = 1.59$	0.21
	SL*Habitat		$F_{1,111} = 0.00$	0.98
	SL*Year		$F_{1,112} = 0.25$	0.62
	SL*Habitat*Year		$F_{1,109} = 0.22$	0.64

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
FLEX SCORE^1 ~ RL SCORE^1	RL	**0.62 ± 0.07**	$F_{1,112} = 70.25$	**<0.001*****
	Habitat		$F_{1,3} = 0.60$	0.50
	Year		$F_{1,113} = 0.71$	0.40
^{1}log-transformed	RL*Habitat		$F_{1,109} = 0.01$	0.91
	RL*Year		$F_{1,111} = 0.73$	0.39
	RL*Habitat*Year		$F_{1,108} = 0.00$	0.97
	PERSONALITY – COGNITION			
LR (Y/N) ~ NEO	Neo		$\chi^2_1 = 2.24$	0.13
	Habitat		$\chi^2_1 = 0.76$	0.38
	Year		$\chi^2_1 = 1.84$	0.18
	Neo*Habitat		$\chi^2_1 = 2.87$	0.09°
	Neo*Year		$\chi^2_1 = 3.06$	0.08°
	Neo*Habitat*Year		$\chi^2_1 = 4.80$	**0.03***
	2018			
	Neo	-0.09 ± 0.38	$\chi^2_1 = 0.06$	0.81
	Habitat		$\chi^2_1 = 0.39$	0.54
	Neo*Habitat		$\chi^2_1 = 2.87$	0.09°
		C: -1.25 ± 0.83	z = -1.50	0.13
		S: 0.42 ± 0.53	z = 0.80	0.42
	2019			
	Neo	-0.15 ± 0.27	$\chi^2_1 = 0.31$	0.58
	Habitat		$\chi^2_1 = 0.53$	0.47
	Neo*Habitat		$\chi^2_1 = 2.15$	0.14
LR (Y/N) ~ EXP PC1	Exp PC1		$\chi^2_1 = 2.29$	0.13
	Habitat		$\chi^2_1 = 0.89$	0.35
	Year		$\chi^2_1 = 0.95$	0.33
	Exp PC1*Habitat		$\chi^2_1 = 3.22$	0.07°
	Exp PC1*Year		$\chi^2_1 = 6.63$	**0.01***
	Exp PC1*Habitat*Year		$\chi^2_1 = 5.67$	**0.02***
	2018	-0.09 ± 0.39	$\chi^2_1 = 0.05$	0.82
	Exp PC1		$\chi^2_1 = 0.44$	0.50
	Habitat		$\chi^2_1 = 3.23$	0.07°
	Exp PC1*Habitat	C: -1.18 ± 0.78	z = -1.51	0.13
		S: 0.55 ± 0.57	z = 0.98	0.33
	2019			
	Exp PC1	**0.67 ± 0.33**	$\chi^2_1 = 4.16$	**0.04***
	Habitat		$\chi^2_1 = 0.48$	0.49
	Exp PC1*Habitat		$\chi^2_1 = 2.45$	0.12

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
LR (Y/N) ~ EXP PC2	Exp PC2	0.00 ± 0.23	$\chi^2_1 = 0.00$	1.00
	Habitat		$\chi^2_1 = 0.86$	0.35
	Year		$\chi^2_1 = 2.86$	0.09°
	Exp PC1*Habitat		$\chi^2_1 = 1.43$	0.23
	Exp PC2*Year		$\chi^2_1 = 2.04$	0.15
	Exp PC2*Habitat*Year		$\chi^2_1 = 0.47$	0.49
LR (Y/N) ~ AGG	Aggression	-0.25 ± 0.31	$\chi^2_1 = 0.66$	0.42
	Habitat		$\chi^2_1 = 0.17$	0.68
	Year		$\chi^2_1 = 1.95$	0.16
	Aggression*Habitat		$\chi^2_1 = 0.09$	0.77
	Aggression*Year		$\chi^2_1 = 0.90$	0.34
	Aggression*Habitat*Year		$\chi^2_1 = 2.14$	0.14
ESC* ~ NEO *box-cox transformed	Neo	0.06 ± 0.09	$F_{1,111} = 0.37$	0.54
	Habitat		$F_{1,3} = 1.00$	0.40
	Year		$F_{1,113} = 0.00$	0.99
	Habitat*Neo		$F_{1,110} = 0.42$	0.52
	Year*Neo		$F_{1,110} = 0.16$	0.69
	Neo*Habitat*Year		$F_{1,109} = 0.40$	0.53
ESC* ~ EXP PC1 *box-cox transformed	Exp PC1	0.01 ± 0.09	$F_{1,111} = 0.00$	0.95
	Habitat		$F_{1,3} = 1.04$	0.39
	Year		$F_{1,113} = 0.00$	0.99
	Exp PC1*Habitat		$F_{1,110} = 1.45$	0.23
	Exp PC1*Year		$F_{1,109} = 0.14$	0.71
	Exp PC1*Habitat*Year		$F_{1,107} = 2.50$	0.12
ESC* ~ EXP PC2 *box-cox transformed	Exp PC2	0.03 ± 0.09	$F_{1,111} = 0.08$	0.78
	Habitat		$F_{1,3} = 0.98$	0.40
	Year		$F_{1,113} = 0.00$	0.98
	Exp PC2*Habitat		$F_{1,110} = 1.23$	0.27
	Exp PC2*Year		$F_{1,110} = 0.95$	0.33
	Exp PC2*Habitat*Year		$F_{1,108} = 0.83$	0.36
ESC[1] ~ AGG [1]log-transformed	Aggression	-0.02 ± 0.14	$F_{1,55} = 0.02$	0.88
	Habitat		$F_{1,2} = 2.75$	0.22
	Year		$F_{1,55} = 0.68$	0.41
	Aggression*Habitat		$F_{1,52} = 0.05$	0.83
	Aggression*Year		$F_{1,54} = 0.78$	0.38
	Aggression*Habitat*Year		$F_{1,51} = 3.54$	0.07°
	2018			
	Aggression	-0.17 ± 0.22	$F_{1,22} = 0.57$	0.46
	Habitat		$F_{1,2} = 1.46$	0.35
	Aggression*Habitat		$F_{1,20} = 1.83$	0.19
	2019			
	Aggression	0.10 ± 0.18	$F_{1,31} = 0.30$	0.59
	Habitat		$F_{1,3} = 0.94$	0.41
	Aggression*Habitat		$F_{1,30} = 0.89$	0.35

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
SL SCORE[1] ~ NEO	Neo	-0.06 ± 0.09	$F_{1,113} = 0.44$	0.51
	Habitat		$F_{1,2} = 1.76$	0.30
[1]log-transformed	Year		$F_{1,111} = 0.06$	0.80
	Habitat*Neo		$F_{1,111} = 0.01$	0.94
	Year*Neo		$F_{1,109} = 0.23$	0.63
	Neo*Habitat*Year		$F_{1,107} = 0.78$	0.38
SL SCORE[1] ~ EXP PC1	Exp PC1		$F_{1,112} = 0.62$	0.43
	Habitat		$F_{1,2} = 1.58$	0.31
	Year		$F_{1,111} = 0.11$	0.75
[1]log-transformed	Exp PC1*Habitat		$F_{1,110} = 0.39$	0.53
	Exp PC1*Year		$F_{1,111} = 1.48$	0.23
	Exp PC1*Habitat*Year		$F_{1,108} = 3.33$	0.07°
	<u>2018</u>			
	Exp PC1	-0.22 ± 0.15	$F_{1,45} = 2.04$	0.16
	Habitat		$F_{1,2} = 0.16$	0.73
	Exp PC1*Habitat		$F_{1,44} = 0.75$	0.39
	<u>2019</u>		<u>2019</u>	
	Exp PC1		$F_{1,63} = 0.11$	0.74
	Habitat		$F_{1,3} = 1.45$	0.32
	Exp PC1*Habitat		$F_{1,62} = 3.03$	0.09°
		C: 0.20 ± 0.15	t = 1.33	0.19
		S: -0.23 ± 0.20	t = -1.17	0.24
SL SCORE[1] ~ EXP PC2	Exp PC2	0.02 ± 0.09	$F_{1,112} = 0.00$	0.99
	Habitat		$F_{1,3} = 1.71$	0.30
	Year		$F_{1,111} = 0.06$	0.80
[1]log-transformed	Exp PC2*Habitat		$F_{1,110} = 3.01$	0.09°
		C: -0.21 ±0.15	t = -1.37	0.17
		S: 0.13 ± 0.12	t = 1.06	0.29
	Exp PC2*Year		$F_{1,110} =$	0.96
	Exp PC2*Habitat*Year		0.00	0.98
			$F_{1,103} = 0.00$	
SL SCORE[1] ~ AGG	Aggression	0.07 ± 0.13	$F_{1,55} = 0.01$	0.91
	Habitat		$F_{1,2} = 0.60$	0.51
[1]log-transformed	Year		$F_{1,55} = 0.46$	0.50
	Aggression*Habitat		$F_{1,50} = 0.86$	0.36
	Aggression*Year		$F_{1,54} = 2.71$	0.11
	Aggression*Habitat*Year		$F_{1,51} = 0.97$	0.33

Supplementary Table S5.3. (continued).

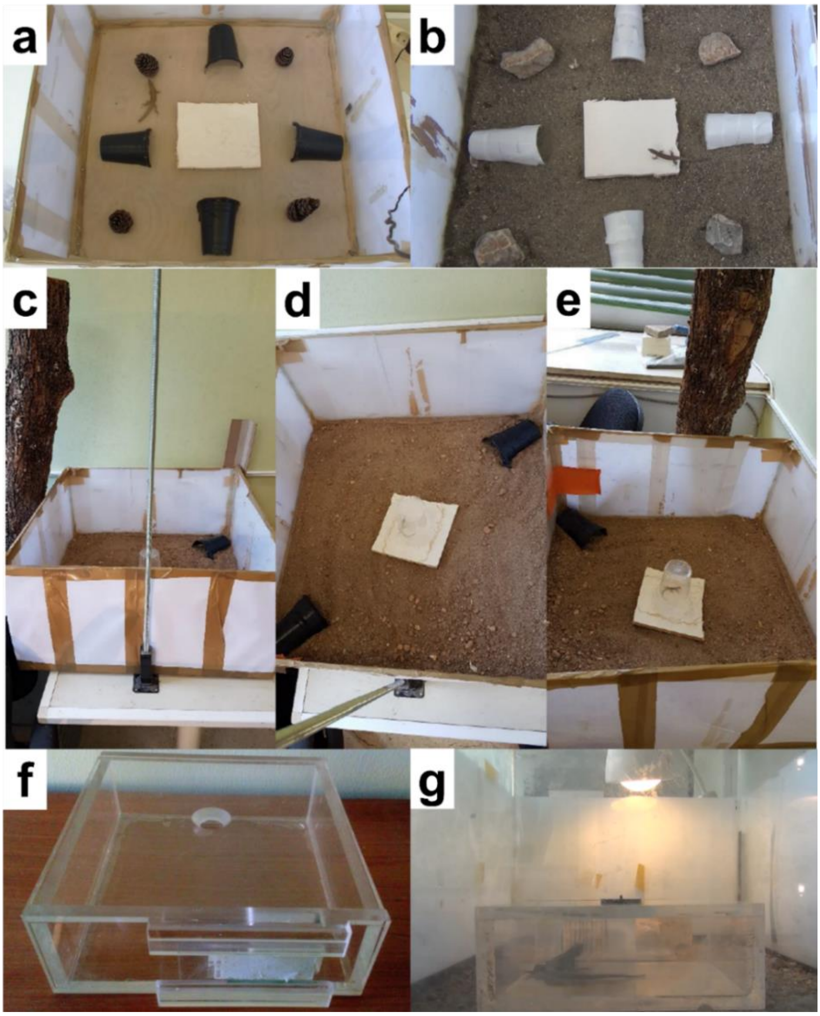
Association	Predictor	Regression slope	F/Wald-stats	P
RL SCORE^1 ~	Neo	0.03 ± 0.09	$F_{1,113} = 0.09$	0.76
NEO	Habitat		$F_{1,2} = 0.77$	0.46
	Year		$F_{1,111} = 0.05$	0.82
^{1}log-transformed	Habitat*Neo		$F_{1,111} = 0.44$	0.51
	Year*Neo		$F_{1,109} = 0.89$	0.35
	Neo*Habitat*Year		$F_{1,107} = 1.83$	0.18
RL SCORE^1 ~	Exp PC1		$F_{1,111} = 1.22$	0.27
EXP PC1	Habitat		$F_{1,2} = 0.62$	0.50
	Year		$F_{1,110} = 0.05$	0.83
^{1}log-transformed	**Exp PC1*Habitat**		$F_{1,111} = 4.98$	**0.03***
		C: -0.10 ± 0.13	t = -0.82	0.41
		S: 0.31 ± 0.14	t = 2.28	**0.02***
	Exp PC1 *Year		$F_{1,110} = 0.71$	0.40
	Exp PC1*Habitat*Year		$F_{1,108} = 1.44$	0.23
RL SCORE^1 ~	Exp PC2		$F_{1,111} = 2.41$	0.12
EXP PC2	Habitat		$F_{1,3} = 1.15$	0.37
	Year		$F_{1,111} = 0.04$	0.84
^{1}log-transformed	**Exp PC2*Habitat**		$F_{1,110} = 6.40$	**0.01***
		C: 0.09 ± 0.15	t = 0.62	0.54
		S: -0.38 ± 0.12	t = -3.29	**<0.01****
	Exp PC2*Year		$F_{1,111} = 0.00$	0.97
	Exp PC2*Habitat*Year		$F_{1,103} = 2.42$	0.12
RL SCORE^1 ~	Aggression	0.13 ± 0.13	$F_{1,55} = 0.72$	0.40
AGG	Habitat		$F_{1,2} = 0.91$	0.43
	Year		$F_{1,55} = 0.02$	0.88
^{1}log-transformed	Aggression*Habitat		$F_{1,50} = 0.09$	0.77
	Aggression*Year		$F_{1,54} = 0.31$	0.58
	Aggression*Habitat*Year		$F_{1,51} = 0.07$	0.79
FLEX SCORE^1 ~	Neo	0.00 ± 0.09	$F_{1,113} = 0.00$	0.99
NEO	Habitat		$F_{1,2} = 0.07$	0.81
	Year		$F_{1,111} = 1.01$	0.32
^{1}log-transformed	Habitat*Neo		$F_{1,109} = 0.01$	0.91
	Year*Neo		$F_{1,107} = 0.02$	0.89
	Neo*Habitat*Year		$F_{1,107} = 0.80$	0.37
FLEX SCORE^1 ~	Exp PC1	-0.07 ± 0.10	$F_{1,112} = 0.52$	0.47
EXP PC1	Habitat		$F_{1,2} = 0.04$	0.85
	Year		$F_{1,111} = 0.87$	0.35
^{1}log-transformed	Exp PC1*Habitat		$F_{1,111} = 1.51$	0.22
	Exp PC1 *Year		$F_{1,110} = 1.59$	0.21
	Exp PC1*Habitat*Year		$F_{1,108} = 0.68$	0.41

Supplementary Table S5.3. (continued).

Association	Predictor	Regression slope	F/Wald-stats	P
FLEX SCORE[1] ~ EXP PC2	Exp PC2	*-0.18 ± 0.09*	$F_{1,112} = 3.65$	0.06°
	Habitat		$F_{1,3} = 0.00$	0.97
	Year		$F_{1,111} = 1.25$	0.27
[1]log-transformed	Exp PC2*Habitat		$F_{1,110} = 0.21$	0.65
	Exp PC2 *Year		$F_{1,110} = 0.02$	0.89
	Exp PC2*Habitat*Year		$F_{1,103} = 0.16$	0.69
FLEX SCORE[1] ~ AGG	Aggression	-0.02 ± 0.14	$F_{1,55} = 0.03$	0.87
	Habitat		$F_{1,3} = 0.04$	0.85
	Year		$F_{1,55} = 1.51$	0.22
[1]log-transformed	Aggression*Habitat		$F_{1,53} = 0.17$	0.68
	Aggression*Year		$F_{1,53} = 2.68$	0.11
	Aggression*Habitat*Year		$F_{1,50} = 1.50$	0.23

APPENDIX CHAPTER 6

CHAPTER 6: SUPPLEMENTARY METHODS



Supplementary Figure S6.1. Experimental set-ups used to measure personality and cognition within the Aegean wall lizards. a - b) arenas used to test spatial exploration. c – e) set-up for the spatial + reversal learning tasks. Both intra – (orange paper) and extra-maze cues are provided (e.g. iron rod, tree trunk, cardboard piece, wall) to allow navigation and orientation. f – g) escape box used to test problem-solving ability. See main text for more details regarding the experimental procedures.

Supplementary Figure S6.2. Two of the semi-natural enclosures in which lizards were housed from 2019 to 2020. Enclosures were characterized either by open, structural simple habitat (top) or structural complex, densely vegetated habitat (bottom).

CHAPTER 6: SUPPLEMENTARY RESULTS

Supplementary Table S6.1. Performance (mean ± SE) on the exploration test and cognitive tasks for lizards that were tested in both 2019 and 2020, given per original habitat and enclosure type. For the meaning of the exploration PCs, we refer to Table 1 (Chapter 6) in main text.

	Complex habitat		Simple habitat	
Enclosure	Complex	Simple	Complex	Simple
Exploration PC1	N = 13	N = 9	N = 13	N = 8
2019	1.20 ± 0.31	0.32 ± 0.38	1.25 ± 0.25	0.76 ± 0.23
2020	-0.14 ± 0.38	-0.58 ± 0.49	0.07 ± 0.31	-0.37 ± 0.37
Exploration PC2	N = 13	N = 9	N = 13	N = 8
2019	-0.18 ± 0.25	-0.21 ± 0.20	0.49 ± 0.23	0.59 ± 0.25
2020	0.19 ± 0.27	0.25 ± 0.25	0.55 ± 0.28	-0.02 ± 0.39
# Spatial Errors	N = 12	N = 9	N = 13	N = 8
2019	0.80 ± 0.20	0.79 ± 0.19	1.12 ± 0.23	1.03 ± 0.29
2020	0.58 ± 0.15	0.85 ± 0.29	0.97 ± 0.19	0.76 ± 0.23
# Reversal Errors	N = 12	N = 9	N = 13	N = 8
2019	1.0 ± 0.20	0.79 ± 0.26	0.61 ± 0.16	0.61 ± 0.18
2020	0.82 ± 0.18	1.13 ± 0.23	0.63 ± 0.15	0.79 ± 0.25
# Flexibility Errors	N = 12	N = 9	N = 13	N = 8
2019	0.90 ± 0.07	0.79 ± 0.09	0.85 ± 0.07	0.82 ± 0.11
2020	0.70 ± 0.06	0.99 ± 0.13	0.80 ± 0.05	0.78 ± 0.10
# Escaped from Box	N = 11	N = 9	N = 13	N = 8
2019	9	7	12	6
2020	11	8	11	8
Escape Time (s)	N = 11	N = 9	N = 13	N = 8
2019	885 ± 179	772 ± 243	717 ± 169	804 ± 228
2020	492 ± 93	767 ± 182	809 ± 150	546 ± 130

Supplementary Table S6.2. Performance (mean ± SE) on the exploration test and cognitive tasks for each age group. For the meaning of exploration PCs, we refer to Table 1 in main text.

Enclosure	Adults 2019	Intruders	Juveniles
Exploration PC1	N = 66	N = 21	N = 45
	0.91 ± 0.13	0.02 ± 0.22	-1.14 ± 0.17
Exploration PC2	N = 66	N = 21	N = 45
	0.19 ± 0.11	-0.00 ± 0.19	-0.54 ± 0.12
# Spatial Errors	N = 66	N = 21	N = 44
	0.82 ± 0.08	0.57 ± 0.07	0.55 ± 0.09
# Reversal Errors	N = 66	N = 21	N = 44
	0.85 ± 0.08	0.70 ± 0.10	0.53 ± 0.08
# Flexibility Errors	N = 66	N = 21	N = 44
	0.83 ± 0.03	0.64 ± 0.05	0.54 ± 0.04

Supplementary Table S6.3. Results of the post-hoc pairwise comparisons on the differences in exploration PC2 and RL scores between different age groups. Data was analysed using a MCMCglmm and pairwise comparisons were conducted using the ‘emmeans’ function in R (Lenth et al., 2019). For each pairwise comparison, the estimated difference + 95 % credible interval (CI, between brackets) is given. Bold indicates that the CI did not overlap with zero and the groups thus differed from each other.

Model	Predictor	Groups	Estimate + CI
Exploration PC2	Age	**Intruders - Adults ‘19**	**-0.548 [-0.893; -0.209]**
		Intruders – Adults ‘20	0.096 [-0.282; 0.450]
		Intruders – Juveniles	**0.590 [0.204; 0.972]**
		Adults ’19 – Adults ‘20	**0.642 [0.409; 0.858]**
		Adults ’19 – Juveniles	**1.135 [0.864; 1.423]**
		Adults ’20 – Juveniles	**0.494 [0.185; 0.783]**
RL Scores	Enclosure * Age	Intruders$_{\text{complex}}$ – Intruders$_{\text{simple}}$	-0.565[-1.966; 0.790]
		Intruders$_{\text{complex}}$ – Adults$_{\text{complex}}$ ‘19	-0.370 [-1.055; 0.293]
		Intruders$_{\text{complex}}$ – Adults$_{\text{simple}}$ ‘19	-0.188 [-1.131; 0.766]
		Intruders$_{\text{complex}}$ – Adults$_{\text{complex}}$ ‘20	-0.248 [-0.833; 0.328]
		Intruders$_{\text{complex}}$ – Adults$_{\text{simple}}$ ‘20	-0.692 [-1.609; 0.236]
		Intruders$_{\text{complex}}$ – Juveniles$_{\text{complex}}$	0.582 [-0.169; 1.370]
		Intruders$_{\text{complex}}$ – Juveniles$_{\text{simple}}$	0.494 [-0.529; 1.606]
		Intruders$_{\text{simple}}$ – Adults$_{\text{complex}}$ ‘19	0.200 [-1.138; 1.729]
		Intruders$_{\text{simple}}$ – Adults$_{\text{simple}}$ ‘19	0.373[-0.885; 1.581]
		Intruders$_{\text{simple}}$ – Adults$_{\text{complex}}$ ‘20	0.330 [-1.040; 1.680]
		Intruders$_{\text{simple}}$ – Adults$_{\text{simple}}$ ‘20	-0.124 [-1.251; 1.173]
		Intruders$_{\text{simple}}$ – Juveniles$_{\text{complex}}$	1.160 [-0.381; 2.612]
		Intruders$_{\text{simple}}$ – Juveniles$_{\text{simple}}$	1.066 [-0.252; 2.394]
		Adults$_{\text{complex}}$ ‘19– Adults$_{\text{simple}}$ ‘19	0.180 [-0.634; 0.977]
		Adults$_{\text{complex}}$ ‘19– Adults$_{\text{complex}}$ ‘20	0.126 [-0.401; 0.740]
		Adults$_{\text{complex}}$ ‘19– Adults$_{\text{simple}}$ ‘20	-0.319 [-1.304; 0.648]
		Adults$_{\text{complex}}$ ‘19– Juveniles$_{\text{complex}}$	**0.961 [0.266; 1.698]**
		Adults$_{\text{complex}}$ ‘19– Juveniles$_{\text{simple}}$	0.856 [-0.187; 1.947]
		Adults$_{\text{simple}}$ ‘19– Adults$_{\text{complex}}$ ‘20	-0.057 [-0.977; 0.865]
		Adults$_{\text{simple}}$ ‘19– Adults$_{\text{simple}}$ ‘20	-0.503 [-1.070; 0.173]
		Adults$_{\text{simple}}$ ‘19– Juveniles$_{\text{complex}}$	0.779 [-0.140; 1.861]
		Adults$_{\text{simple}}$ ‘19– Juveniles$_{\text{simple}}$	**0.692 [0.014; 1.449]**
		Adults$_{\text{complex}}$ ‘20– Adults$_{\text{simple}}$ ‘20	-0.438 [-1.348; 0.455]
		Adults$_{\text{complex}}$ ‘20– Juveniles$_{\text{complex}}$	**0.833 [0.095; 1.530]**
		Adults$_{\text{complex}}$ ‘20– Juveniles$_{\text{simple}}$	0.743 [-0.259; 1.840]
		Adults$_{\text{simple}}$ ‘20– Juveniles$_{\text{complex}}$	**1.271 [0.264; 2.437]**
		Adults$_{\text{simple}}$ ‘20– Juveniles$_{\text{simple}}$	**1.187 [0.355; 1.946]**
		Juveniles$_{\text{complex}}$ – Juveniles$_{\text{simple}}$	-0.088 [-1.076; 0.834]

Supplementary Table S6.4. Full model outcome of the GLMMs testing the performance of lizards over consecutive trials during the spatial and reversal learning task. If an interaction was non-significant, it was removed and main effects would be reported from an main-effect model only. Significance levels are indicated as follows: : '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

Response variable	Predictor	Wald-stats	P
Spatial learning	**Trial**	$\chi^2 = 11.970$, df =1	**<0.001 *** **
	Safe Side	$\chi^2 = 307.027$,df =1	**<0.001 *** **
	Group	$\chi^2 = 28.202$, df =3	**<0.001 *** **
	Trial * Group	$\chi^2 = 3.846$, df =3	0.279
	Trial * Safe side	$\chi^2 = 2.063$, df =1	0.151
Reversal learning	**Trial**	$\chi^2 = 24.311$, df =1	**< 0.001 *** **
	Safe Side	$\chi^2 = 6.001$,df =1	**0.014 ***
	Group	$\chi^2 = 10.395$, df =3	**0.015 ***
	Trial * Group	$\chi^2 = 10.387$, df =3	**0.016 ***
	Trial * Safe Side	$\chi^2 = 4.577$, df =1	**0.032 ***

Supplementary Table S6.5. Post-hoc multiple pairwise comparisons for the (G)LMMs, using Tukey's method with the 'emmeans' and 'emtrends' functions in R (Lenth et al., 2019). Significance levels are indicated as follows: : '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

Model	Predictor	Groups	Ratio + SE	Stats
Spatial learning (per trial)	Age group	Adult 20 – Adult 19	0.848 ± 0.104	z = -1.340, p = 0.537
		Adult 20 – Intruder	0.925 ± 0.151	z = -0.478, p = 0.964
		Adult 20 – Juvenile	1.669 ± 0.237	**z = 3.615, p = 0.002 *****
		Adult 19 – Intruder	1.090 ± 0.165	z = 0.572, p = 0.940
		Adult 19 – Juvenile	1.968 ± 0.256	**z = 5.204, p < 0.001 *****
		Intruder – Juvenile	1.805 ± 0.305	**z = 3.497, p = 0.003 *****
Reversal learning (per trial)	Age * trial	$\mathbf{slope}_{\mathbf{Adult\ 20}}$ **–** $\mathbf{slope}_{\mathbf{Adult\ 19}}$	-0.046 ± 0.017	**z = -2.767, p = 0.029 ***
		$\text{slope}_{\text{Adult 20}}$ – $\text{slopeI}_{\text{ntruder}}$	-0.037 ± 0.023	z = -1.619, p = 0.368
		$\text{slope}_{\text{Adult 20}}$ – $\text{slope}_{\text{Juvenile}}$	-0.003 ± 0.021	z = -0.146, p = 0.999
		$\text{slope}_{\text{Adult 19}}$ – $\text{slope}_{\text{Intruder}}$	0.009 ± 0.022	z = 0.418, p = 0.976
		$\text{slope}_{\text{Adult 19}}$ - $\text{slope}_{\text{Juvenile}}$	0.043 ± 0.019	z = 2.325, p = 0.092 °
		$\text{slope}_{\text{Intruder}}$ - $\text{slope}_{\text{Juvenile}}$	0.034 ± 0.024	z = 1.410, p = 0.493
RL Scores LTR	Enclosure * Year	Complex 19 – Simple 19	1.112 ± 0.057	t = 2.081, p = 0.277
		Complex 19 – Complex 20	1.029 ± 0.048	t = 0.614, p = 0.921
		Complex 19 – Simple 20	0.964 ± 0.055	t = -0.647, p = 0.911
		Simple 19 – Complex 20	0.926 ± 0.053	t = -1.344, p = 0.592
		Simple 19 – Simple 20	0.867 ± 0.047	t = -2.653, p = 0.151
		Complex 20 – Simple 20	0.936 ± 0.048	t = -1.293, p = 0.605

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APPENDIX CHAPTER 7

CHAPTER 7: SUPPLEMENTARY RESULTS

Supplementary Table S7.1. Model-averaged parameter estimates + standard error (between brackets) for adult survival after 11 – 12 months in the experimental enclosures. Estimates were obtained by conditional averaging of all (generalized mixed-effect) models within ≤ 2 ΔAICc units of the top model. Bold indicates statistical significance ($p < 0.05$), italic indicates a statistical trend ($p < 0.10$). NEO = neophobia, EXP = exploration, AGG = aggression, LR = lid-removal score, SL = spatial learning scores, RL = reversal learning scores, FLEX = learning flexibility (see main text, Chapter 7). ^{2} indicates a quadratic term. '-' indicates that the variable/interaction was not included in the top models, 'NA' indicates that the variable/interaction could not be included due to overfitting and/or convergence issues.

SURVIVAL	NEO	EXP	AGG	LR	SL	RL	FLEX
N	122	123	64	121	123	123	123
Top models	12	4	7	5	12	17	9
Intercept	**2.080** **(0.640)**	**2.627** **(0.655)**	**2.151** **(0.848)**	**2.599** **(0.655)**	**2.519** **(0.710)**	**2.209** **(0.618)**	2.013 (0.830)
Behaviour	0.255 (0.226)	**-0.931** **(0.400)**	*-1.898* *(1.070)*	LR_{OCC}: **-1.601** **(0.609)** LR_{CONS}: -0.457 (0.559)	0.858 (0.687)	-0.189 (0.375)	$\text{FLEX}_{\text{ONCE}}$: 0.972 (0.717) $\text{FLEX}_{\text{BOTH}}$: *1.909* *(1.083)*
Behaviour^2	0.182 (0.283)	-	-0.110 (0.578)	NA	-0.348 (0.210)	-0.116 (0.115)	NA
Enclosure (Simple)	**-1.229** **(0.598)**	**-1.378** **(0.485)**	**-1.978** **(0.828)**	**-1.372** **(0.676)**	**-1.555** **(0.596)**	**-1.311** **(0.465)**	**-1.419** **(0.592)**
Year (2019)	-0.731 (0.577)	-0.861 (0.519)	-0.761 (0.706)	-0.848 (0.645)	-0.704 (0.631)	-0.685 (0.499)	-0.868 (0.654)
Sex (M)	-0.549 (0.453)	-0.602 (0.478)	-	-0.487 (0.463)	-0.780 (0.569)	-0.671 (0.509)	-0.578 (0.455)

Supplementary Table S7.1. (Continued)

SURVIVAL	NEO	EXP	AGG	LR	SL	RL	FLEX
SVL	-	-0.154 (0.244)	-	-	-	-	-
B * E	-	-	**2.140** **(1.034)**	-	-0.601 (0.653)	-0.568 (0.516)	-
B * Y	-	**1.075** **(0.452)**	-	-	0.763 (0.534)	-	NA
B * S	-	-0.505 (0.425)	NA	-	*-1.086* *(0.611)*	-	NA
B^2 * E	-0.534 (0.339)	-	**1.080** **(0.524)**	NA	-	-	NA
B^2 * Y	-	-	NA	NA	0.719 (0.446)	-	NA
B^2 * S	-	NA	NA	NA	-	NA	NA
E * Y	1.009 (1.012)	NA	NA	0.851 (1.045)	1.124 (1.047)	NA	1.044 (1.014)
E* S	-	-	NA	-	0.710 (1.017)	-	-
Y * S	-	NA	NA	-	-	0.778 (0.954)	-

Supplementary Table S7.2. Model-averaged parameter estimates + standard error (between brackets) for adult growth rate (mm/day) after 11 – 12 months in the experimental enclosures. Growth rate was Box-Cox transformed for NEO, EXP and LR, everywhere else the estimates should be multiplied by 10^{-3}. Estimates were obtained by conditional averaging of all (linear mixed-effect) models within ≤ 2 ΔAICc units of the top model. Bold indicates statistical significance ($p < 0.05$), italic indicates a statistical trend ($p < 0.10$). NEO = neophobia, EXP = exploration, AGG = aggression, LR = lid-removal score, SL = spatial learning scores, RL = reversal learning scores, FLEX = learning flexibility (see main text, Chapter 7). ² indicates a quadratic term, '-'that the variable/interaction was not included in the top models and 'NA' that the variable/interaction could not be included due to overfitting and/or convergence issues.

GROWTH	NEO	EXP	AGG	LR	SL	RL	FLEX
N	80	81	39	80	81	81	81
Top models	3	3	3	3	2	5	2
Intercept	**-2.145 (0.015)**	**-2.148 (0.017)**	**10.200 (1.197)**	**-2.144 (0.015)**	**8.159 (0.937)**	**7.953 (1.007)**	**8.159 (0.937)**
Behaviour	0.008 (0.010)	-	-	LR_{OCC}: 0.026 (0.043) LR_{CONS}: -0.031 (0.033)	-	0.726 (0.732)	-
Behaviour²	-	0.005 (0.005)	0.823 (0.525)	NA	-	*0.751 (0.442)*	NA
Enclosure (Simple)	-	-	-	-	0.966 (1.142)	1.656 (1.467)	0.291 (0.767)
Year (2019)	-	-	1.798 (1.832)	-	-	-	-

Supplementary Table S7.2. (Continued)

GROWTH	NEO	EXP	AGG	LR	SL	RL	FLEX
Sex (M)	*0.035 (0.021)*	*0.036 (0.021)*	NA	0.024 (0.025)	**2.801 (1.149)**	**2.623 (1.158)**	**2.801 (1.149)**
SVL	**-0.062 (0.010)**	**-0.062 (0.010)**	**-4.309 (0.962)**	**-0.062 (0.010)**	**-4.048 (0.593)**	**-3.884 (0.594)**	**-4.048 (0.593)**
B * E	-	-	-	-	-	-	-
B * Y	-	-	-	-	-	-	-
B * S	-	-	NA	LR$_{OCC}$: 0.026 (0.063) **LR$_{CONS}$: 0.128 (0.049)**	-	**-2.819 (1.233)**	-
B^2 * E	-	-	-	NA	-	**-1.889 (0.779)**	NA
B^2 * Y	-	-	-	NA	-	-	NA
B^2 * S	-	-	NA	NA	-	NA	NA
E * Y	-	-	-	-	-	-	-
E* S	-	-	NA	-	-	-	-
Y * S	-	-	NA	-	-	-	-

Supplementary Table S7.3. Model-averaged parameter estimates + standard error (between brackets) for change in adult body condition after 11 – 12 months in the experimental enclosures. Body condition change was Box-Cox transformed, except in the LR and SL models. Estimates were obtained by conditional averaging of all (linear mixed-effect) models within ≤ 2 ΔAICc units of the top model. Bold indicates statistical significance ($p < 0.05$), italic indicates a statistical trend ($p < 0.10$). NEO = neophobia, EXP = exploration, AGG = aggression, LR = lid-removal score, SL = spatial learning score, RL = reversal learning score, FLEX = learning flexibility (see main text, Chapter 7). '-' indicates that the variable/interaction was not included in the top models, 'NA' indicates that the variable/interaction could not be included due to overfitting and/or convergence issues.

BODY CONDITON	NEO	EXP	AGG	LR	SL	RL	FLEX
N	86	87	42	86	87	87	87
Top models	3	8	2	4	6	8	2
Intercept	**-0.469 (0.029)**	**-0.435 (0.028)**	**-0.333 (0.017)**	-0.039 (0.029)	-0.042 (0.031)	**-0.444 (0.026)**	**-0.461 (0.022)**
Behaviour	-	-0.010 (0.010)	-	$\mathrm{LR}_{\mathrm{OCC}}$: -0.041 (0.052) $\mathrm{LR}_{\mathrm{CONS}}$: 0.060 (0.039)	0.019 (0.015)	-	-
Behaviour^2	-0.015 (0.010)	-0.016 (0.010)	-	NA	0.017 (0.012)	*-0.016 (0.009)*	NA
Enclosure (Simple)	*-0.068 (0.039)*	**-0.060 (0.029)**	*-0.044 (0.025)*	-0.051 (0.032)	-0.056 (0.035)	**-0.055 (0.027)**	*-0.044 (0.025)*
Year (2019)	-	-0.032 (0.026)	-	-	-	-	-
Sex (M)	**0.095 (0.025)**	**0.084 (0.022)**	NA	**0.113 (0.031)**	**0.116 (0.031)**	**0.078 (0.025)**	**0.087 (0.023)**
SVL	-	-	-	-	-	-	-

Supplementary Table S7.3. (Continued)

BODY CONDITON	NEO	EXP	AGG	LR	SL	RL	FLEX
B * E	-	-	-	-	-	-	-
B * Y	-	-	-	-	-	-	-
B * S	-	-	NA	-	-	-	-
B^2 * E	**0.047** **(0.022)**	*0.020* *(0.012)*	-	NA	-	0.026 (0.016)	NA
B^2 * Y	-	**0.023** **(0.011)**	-	NA	-	-	NA
B^2 * S	NA	-	NA	NA	-	0.023 (0.020)	NA
E * Y	NA	-	-	-	-	-	-
E * S	-	-	NA	-	-	-	-
Y * S	-	NA	NA	-	-	-	-

Supplementary Table S7.4. Model-averaged parameter estimates + standard error (between brackets) for adult reproductive success (number of offspring) in the experimental enclosures. Estimates were obtained by conditional averaging of all models within ≤ 2 ΔAICc units of the top model. Bold indicates statistical significance ($p < 0.05$), italic indicates a statistical trend ($p < 0.10$). NEO = neophobia, EXP = exploration, AGG = aggression, LR = lid-removal score, SL = spatial learning score, RL = reversal learning score, FLEX = learning flexibility (see main text, Chapter 7). ^{2} indicates a quadratic term, ‘-‘that the variable/interaction was not included in the top models and ‘NA’ that the variable/interaction could not be included due to overfitting and/or convergence issues. We used generalized mixed-effect models with a zero-inflated negative binomial distribution, hence why both the conditional and zero-inflated intercept are reported.

# OFFSPRING	NEO	EXP	AGG	LR	SL	RL	FLEX
N	90	91	45	90	91	91	91
Top models	7	4	6	4	3	5	3
Cond Intercept	**1.289 (0.226)**	**1.283 (0.216)**	**1.097 (0.264)**	**1.289 (0.218)**	**1.276 (0.222)**	**1.292 (0.213)**	**1.276 (0.222)**
ZI Intercept	**-1.702 (0.442)**	**-1.692 (0.426)**	**-1.569 (0.752)**	**-1.804 (0.466)**	**-1.696 (0.430)**	**-1.702 (0.437)**	**-1.696 (0.430)**
Behaviour	0.117 (0.084)	-0.080 (0.068)	-	LR_{OCC}: -0.518 (0.340) LR_{CONS}: 0.129 (0.195)	-	-0.021 (0.136)	-
Behaviour^2	-0.048 (0.056)	-	-0.117 (0.098)	NA	-	-	NA
Enclosure (Simple)	0.409 (0.281)	0.396 (0.282)	*0.501 (0.276)*	0.391 (0.287)	0.396 (0.282)	0.396 (0.282)	0.385 (0.282)
Year (2019)	**-0.449 (0.168)**	**-0.449 (0.165)**	**-0.427 (0.266)**	**-0.465 (0.167)**	**-0.454 (0.166)**	**-0.469 (0.169)**	**-0.454 (0.166)**

Supplementary Table S7.4. (Continued)

# OFFSPRING	NEO	EXP	AGG	LR	SL	RL	FLEX
Sex (M)	-	-	NA	-	-	-	-
SVL	**0.166** **(0.082)**	*0.158* *(0.080)*	*0.297* *(0.149)*	*0.157* *(0.081)*	*0.160* *(0.081)*	*0.159* *(0.085)*	*0.160* *(0.081)*
B * E	-	-	-	-	-	-	-
B * Y	-0.172 (0.152)	-	-	-	-	-0.320 (0.204)	-
B * S	-	-	NA	NA	-	-	-
B^2 * E	-	-	-	NA	-	-	NA
B^2 * Y	-	-	NA	NA	-	-	NA
B^2 * S	-	-	NA	NA	-	-	NA
E * Y	-	-	-	-	-	-	-
E* S	-	-	NA	-	-	-	-
Y * S	-	-	NA	-	-	-	-

Table S7.5. Model-averaged parameter estimates + standard error (between brackets) for juvenile fitness after 9 months in the experimental enclosures. Estimates were obtained by conditional averaging of all (generalized mixed-effect) models within ≤ 2 ΔAICc units of the top model. Growth rate and body condition change were Box Cox transformed. Bold indicates statistical significance ($p < 0.05$), italic indicates a statistical trend ($p < 0.10$). SL = spatial learning scores, RL = reversal learning scores, FLEX = learning flexibility (see main text, Chapter 7). ² indicates a quadratic term, '-' indicates that the variable/interaction was not included in the top models, 'NA' indicates that the variable/interaction could not be included due to overfitting and/or convergence issues.

	SURVIVAL		GROWTH RATE		BODY CONDITION	
	SL	RL	SL	RL	SL	RL
N	44	44	26	26	26	26
Top models	4	2	2	2	2	2
Intercept	1.808 (2.790)	0.602 (0.426)	**-1.409** **(0.010)**	**-1.409** **(0.010)**	**-0.407** **(0.030)**	**-0.430** **(0.025)**
Behaviour	4.380 (8.388)	-	-	-	-	-
Behaviour²	10.244 (6.174)	-	-	-	-0.037 (0.021)	0.027 (0.027)
Enclosure (Simple)	-3.303 (4.068)	-0.680 (0.637)	**-0.044** **(0.014)**	-0.044 (0.014)	-	-
SVL	-	-	-0.010 (0.007)	-0.010 (0.007)	-	-
B * E	*-17.829* *(10.131)*	-	-	-	-	-
B² * E	*-10.716* *(6.228)*	-	-	-	-	-

ACADEMIC CV

First author publications

De Meester, G., Pafilis, P., Vasilakis, G., & Van Damme, R. (2022). Exploration and spatial cognition show long-term repeatability but no heritability in the Aegean wall lizard — Anim. Behav. XX (Accepted 02/05/22).

De Meester, G., Pafilis, P., & Van Damme, R. (2022). Bold and bright – shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (*Podarcis erhardii*) — Anim. Cogn. XX (Published online 17/01/22).

De Meester, G. & Baeckens, S. (2021). Reinstating reptiles: from clueless creatures to esteemed models of cognitive biology — Behaviour 158, 1057-1076 (Editorial)

De Meester, G., Sfendouraki-Basakarou, A., Pafilis, P., & Van Damme, R. (2021). Dealing with the unexpected: the effect of environmental variability on behavioural flexibility in a Mediterranean lizard — Behaviour 158, 1193-1223.

De Meester, G., Šunje, E., Prinsen, E., Verbruggen, E., Van Damme, R. (2021). Toxin variation among salamander populations: discussing potential causes and future directions — Integr. Zool. 16, 336-353.

De Meester, G., Huyghe, K. & Van Damme, R. (2019). Brain size, ecology and sociality: a reptilian perspective — Biol. J. Linn. Soc. 126, 381-391.

De Meester, G., Lambreghts, Y., Briesen, B., Smeuninx, T., Tadić, Z., & Van Damme, R. (2018). Hunt or hide: How insularity and urbanization affect foraging decisions in lizards — Ethology 124, 227-235.

Co-authored publications

Gavriilidi, I., **De Meester, G.,** Van Damme, R., & Baeckens, S. (2022). How to behave when marooned: the behavioural component of the island syndrome remains underexplored — Biol. Lett. 18, 20220030.

Gavriilidi, I., Baeckens, S., **De Meester, G.,** Van Linden, L., & Van Damme, R. (2022). The gullible genius: fast learners fall for fake news — Behav. Ecol. Sociobiol. 76, 5.

Thys, B., Pinxten, R., Raap, T., **De Meester, G.,** Rivera-Gutierrez, H. F., & Eens, M. (2017). The female perspective of personality in a wild songbird: repeatable aggressiveness relates to exploration behaviour — Sci. Rep. 7, 765.

Conference talks

De Meester, G., Pafilis, P. & Van Damme, R. (2022, January). *Survival of the wittiest? Habitat-dependent fitness value of cognitive traits in lizards.* Oral presentation at the 2022 Virtual Meeting of the Society for Integrative and Comparative Biology (SICB+).

De Meester, G., Pafilis, P. & Van Damme, R. (2021, August). *Bold and bright – shy and supple? Elusive links between lizard personality and cognition.* Oral presentation at the 2021 Virtual Meeting of the Animal Behavior Society.

De Meester, G., Pafilis, P. & Van Damme, R. (2019, November*). Simple habitats, simple lizards? The effect of habitat complexity on spatial memory in a Mediterranean lizard*. Oral presentation at the 2019 Benelux Congress of Zoology, Groningen.

De Meester, G., Huyghe, K. & Van Damme, R. (2018, December). *Brain size, ecology and sociality: a reptilian perspective*. Oral presentation at the 2018 Benelux Congress of Zoology, Antwerp.

De Meester, G., Šunje, E., Prinsen, E., Verbruggen, E. & Van Damme, R. (2018, September). *Toxin variation in alpine salamander populations.* Oral presentation at the 2nd Balkan Herpetological Symposium, Poreč.

De Meester, G. & Van Damme R. (2018, June*). Learning with lizards: problem-solving skills in lacertids from different environments*. Oral presentation at the 2nd Symposium on Mediterranean Lizards, Tel Aviv.

Grants and awards

FWO Travel Grant: Travel grant for a long research stay abroad awarded by the Flemish Research Foundation (FWO). Received in 2019 and 2020.

RBZS Travel Grant: Travel grant for an international research stay awarded by the Royal Belgian Zoological Society (RBZS) in 2018.

Biology Research Day PhD Presentation Award: Award by the Department of Biology at the University of Antwerp for best PhD pitch presentation at the 2018 (internal) Biology Research Day

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"If you trust in yourself ... and believe in your dreams ... and follow your star ... you'll still get beaten by people who spent their time working hard and learning things and weren't so lazy."

- Terry Pratchett (2003)

Wist je dat hagedissen en doctoraatstudenten eigenlijk niet zoveel verschillen? Beiden zijn sterk afhankelijk van een warmtebron voor hun energie in de ochtend (de zon en een hete kop koffie respectievelijk), spenderen veel te veel tijd in de kelder van het D gebouw op Campus Drie Eiken en worden verondersteld een zekere mate van gedragsflexibiliteit te vertonen. Net zoals mijn hagedissen ben ik doorheen dit doctoraat geconfronteerd geweest met vele uitdagingen. Conferenties, meetings en studenten stelden mijn sociaal brein op de proef. Ik heb moeten navigeren doorheen allerhande complexe biotopen, zoals de Universiteit van Athene, en minstens even complexe R-scripts. Ik ben terechtgekomen in nieuwe habitaten (specifiek aan het geweldige Naxos ben ik mijn hart verloren) en heb moeten leren omgaan met onverwachte veranderingen in mijn omgeving en/of onderzoeksplannen (en niet alleen door een lukrake pandemie). Maar net zoals bij mijn hagedissen is het nog niet helemaal duidelijk of deze uitdagingen mijn cognitieve vaardigheden hebben aangescherpt, of juist teniet hebben gedaan.

En noch doctoraatstudenten noch hagedissen staan er persé alleen voor. Vandaag de dag weten we dat zelfs reptielen in staat zijn tot 'social learning'. En ik heb tijdens mijn doctoraat het voorrecht gehad om sociaal te leren van de besten:

Raoul, ik had me geen betere promotor kunnen wensen. Je bent een fantastische wetenschapper maar een nog betere mentor, en ik ben oprecht dankbaar dat je me zoveel hebt willen bijleren. Bedankt om in me te geloven vanaf het prille begin. Dit doctoraat begon als een taak voor een van jouw keuzevakken, maar jij zag er potentieel in en gaf me de kans om het verder uit te werken tot een volwaardige beursaanvraag. Zowel voor de aanvraag als de rest van mijn doctoraat gaf je me enorm veel vrijheid om zelf mijn onderzoeksvragen en experimenten en nevenprojectjes uit te bouwen, maar stuurde ook bij waar nodig en was altijd beschikbaar om me te helpen (zelfs tijdens het midden van de pandemie bleef je bereikbaar). Ik kan me niet veel andere promotoren inbeelden die zelf de handen uit de mouwen zouden steken om onder de hete Griekse zomerzon een stuk of tachtig metalen platen een steile helling op te sleuren. Raoul, één van je meest bewonderenswaardige eigenschappen is dat je als promotor werkelijk het beste wil voor je studenten. Je gaf me advies en kansen (stond je uitnodiging om een TEDx-speech te geven door aan mij, welke promotor doet zoiets?), en daar ben ik je ongelooflijk dankbaar voor. Het spijt me ook dat ik je het niet altijd even gemakkelijk heb gemaakt met mijn neiging om simpele zaken te hard te overdenken. Terwijl ik dit schrijf, voel ik me klaar om de volgende stap in de academische wereld te zetten, en jij bent degene die me op dit pad heeft geholpen. Eeuwig dankbaar hiervoor!

Panayiotis, this thesis would literally not have been possible without you. When we first started talking, I was still a master student, full of wild ideas and ambitions. And you made these wild ideas feasible. I cannot thank you enough for advising me during my grant application, even spontaneously offering me to write a recommendation letter, finding a field on Naxos for our enclosures and showing great hospitality for three consecutive years when I had the immense pleasure of staying and working at your lab. While writing this thesis in the final months, I often missed my research stays at your lab, and Greece in general. Panayiotis, you once jokingly called me the “pillar of your lab” because I was still doing experiments in the basement while the rest of the university was enjoying the Greek summer. But to be honest, I think it it’s the other way around. I am very happy to call you one of the very essential pillars of my PhD. Thank you so much for everything!

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Contrary to popular belief, a PhD is a team effort. I was lucky to meet and work with some absolutely brilliant and wonderful people. Many of these people contributed to the scientific aspects of my work, and have already been acknowledged in the respective research chapters (but I will repeat it here anyway, because they deserve it!). Many others, however, have provided me with friendship, yet unfortunately, emotional support is rarely acknowledged in scientific papers. So let’s do it here. I apologize in advance if I would forget anyone. My own social brain is extremely fallible.

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