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Learning with lacertids: studying the link between ecology and cognition within a comparative framework.

Running title: Lacertid cognition

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Author contributions

This study was conceived by GDM, PP, ES and RVD. Data was collected by LVL, GDM, JT, TZ, DS, AS and multiple other contributors (see acknowledgments). Statistical analyses were performed by LVL. Drafts were written by LVL, GDM, and RVD, with all authors contributing to the final version of this manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

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Data accessibility statement

Data is stored at the University of Antwerp and will be deposited at Figshare (link to collection: https://figshare.com/s/a6dd93361f6045968ad3) upon acceptance.

Abstract

Cognition is an essential tool for animals to deal with environmental challenges. Nonetheless, the ecological forces driving the evolution of cognition throughout the animal kingdom remain enigmatic. 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 tested 13 species of lacertid lizards (Reptilia: Lacertidae) using a battery of cognitive tests measuring inhibitory control, problem-solving, and spatial and reversal learning. Next, we tested the relationship between species' performance and a) resource availability (temperature and precipitation), habitat complexity (NDVI) and habitat variability (seasonality) in their natural habitat, and b) their life-history (size at hatching and maturity, clutch size and frequency). Although species differed markedly in their cognitive abilities, such variation was mostly unrelated to their ecology and life-history. Yet, species living in more variable environments exhibited lower behavioural flexibility, likely due to energetic constrains in such habitats. Our standardised protocols provide opportunities for

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collaborative research, allowing increased sample sizes and replication, essential for moving forward in the field of comparative cognition. Follow-up studies could include more detailed measures of habitat structure and look at other potential selective drivers such as predation.

Keywords: Cognition – Lacertidae – Comparative cognition – Cognitive Buffer Hypothesis – Expensive Brain Hypothesis – Learning

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 and 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 (increased behavioural flexibility; Sol, 2009) and costs (developmental, maintenance, and operational costs of neural tissue: Isler and van Schaik, 2006b; Kotrschal et al., 2019; Mink et al., 1981) of cognition, resulting in differential selection (Striedter, 2005). However, which exact environmental forces drive the evolution of cognition remains heavily debated (Henke-von der Malsburg et al., 2020; Holekamp and Benson-Amram, 2017; Mettke-Hofmann, 2014; van Horik and Emery, 2011).

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). Another hypothesis, the Ecological Intelligence Hypothesis (EIH) instead focuses on the non-social challenges that animals face: acquiring resources, evading predators, responding to climatological uncertainty,

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etc. (Henke-von der Malsburg et al., 2020; Parker and Gibson, 1977; Sol et al., 2005a). The SIH has been (partially) successful in explaining cognitive variability among species that clearly vary in sociality, such as primates (e.g., Dunbar and Shultz, 2017; but see 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 non-social ecological challenges shape the cognitive phenotypes of animals (Henke-von der Malsburg et al., 2020; Mettke-Hofmann, 2014).

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 enhanced cognitive performance (i.e., how fast and accurate animals learn or solve new tasks), especially in the spatial cognition domain (Lefebvre and Sol, 2008; Safi and Dechmann, 2005; Shumway, 2008; Sol, 2009). Evidence for this idea is mixed, with some studies finding a clear relationship between habitat complexity and cognitive performance (e.g., in bats: Clarin et al., 2013; in fish: Shumway, 2008; White and Brown, 2015) or relative brain size as proxy thereof (e.g., in bats: Safi and Dechmann, 2005; in fish: Shumway, 2008), and others failing to find such relationship between cognitive performance and habitat complexity (e.g., in mice: Mackay and Pillay, 2017) or brain size and habitat complexity (e.g., in reptiles: De Meester et al., 2019; Powell and Leal, 2014; in amphibians: Liao et al., 2015).

Another 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 (Fristoe et al., 2017; Sol, 2009) 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 performance 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

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has been found, for example, across populations of chickadees (Freas et al., 2012; Roth et al., 2010b) and chimpanzees (Kalan et al., 2020), and among bird species with brain size as a proxy of cognitive performance (Fristoe et al., 2017; Sayol et al., 2018; Schuck-Paim et al., 2008; Sol et al., 2005a). However, this effect can go either way. 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 and van Schaik, 2006b; Kotrschal et al., 2019). Animals in highly variable environments may not be able to do so, 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 and Wheeler, 1995) has found empirical support in, for example, frogs (Luo et al., 2017) and strepsirrhine primates (van Woerden et al., 2010). Likewise, animals in environments with permanent low resource availability (limited rainfall, low temperatures) are also expected to economize on expensive neural tissue.

Another school of thought has tried to link brain size and cognitive performance to life-history pace (e.g., brain size and life-history: González-Lagos et al., 2010; Pagel and Harvey, 1988; Sol et al., 2016; Street et al., 2017; e.g., cognitive performance and life-history: 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 and van Schaik, 2006a; Isler and 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 increase longevity (Deaner et al., 2003; González-Lagos et al., 2010; Rushton, 2004; Sol, 2009), further contributing to a slow pace of life. Support for these ideas is also mixed. Several studies have found that large brains are indeed linked to a slow pace of life (e.g., in Euarchontoglires but not other mammals: DeCasien et al., 2018; in mammals: Isler and van Schaik, 2009; in birds: Jiménez-ortega et al., 2020), but other found quite the opposite (e.g., in killifishes: Eckerström-Liedholm et al., 2021; computer simulations: Liedtke and Fromhage, 2019).

A fair number of studies have tested the above ideas by comparing the cognitive performance of species inhabiting contrasting environments (see e.g. review in Henke-von der Malsburg et al., 2020),

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but a number of issues complicate the interpretation of their 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 and Chaine, 2016; Healy and Rowe, 2007; Roth et al., 2010b). Brain size, whether absolute or relative, may be a poor predictor of cognitive performance in general (Cauchoix and 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 and 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 and Dicke, 2005) or tailored per species (Bitterman, 1975; Chittka et al., 2012; Shettleworth, 2010). Cognitive tests should be carefully standardised 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 problem-solving in 39 carnivore species (Benson-Amram et al., 2016), a study on habituation in 13 pit vipers (Krochmal et al., 2018), a study on associative learning in 16 bee species (Collado et al., 2021), and a study on inhibitory control across 36 mammal and bird species (MacLean et al., 2014). Low taxon sampling hampers the identification of environmental drivers of among-species variation in cognitive performance; 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 standardisation of cognitive protocols across species. Lacertid species do vary in life-history traits

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(maturation, clutch size, hatchling size; Bauwens, 1999; Bauwens and Díaz-Uriarte, 1997). 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). Information about each species and its origin is provided in the Supplementary Material & Methods (Study animals and Table S3). The animals were housed at the facilities of the University of Antwerp or associated universities (Supplementary Table S1), 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 S1. 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 De Meester et al. (2022), 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).

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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. The timing of cognitive tests varied slightly among species (Supplementary Table S1) 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. Testing started minimally two hours after the heat bulbs had been turned on, to allow the lizards sufficient time to reach preferred body temperatures. 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 S2). 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. To confirm that the inter-observer reliability was high, the trainer re-scored videos (N = 30 – 80) taken by other observers and compared the results. 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 (Bjorklund and Harnishfeger, 1995; Cookson, 1962; Diamond, 2013) and is considered a crucial aspect of behavioural flexibility (Diamond, 2013; Griffin et al., 2016; Szabo et al., 2020a). Animals may need

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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 (Cookson, 1962; Diamond, 2013; Gavriilidi et al., 2022; Kabadayi et al., 2018; Storks and Leal, 2020; Szabo et al., 2020b). At the start of an inhibitory trial, a lizard was introduced into a terrarium with blinded walls 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 and Leal, 2020; Szabo et al., 2020a). 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 (i.e., catching the mealworm) (Gomes et al., 2020), or until they had completed ten valid trials (i.e., attempted to catch the mealworm). 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, as to get an indication of their ability to spontaneously exhibit inhibitory control (the trials were averaged rather than taking the first trial to minimise the effects of neophobia or other external factors influencing their behaviour). To score whether lizards were capable of learning inhibitory control, we noted whether individuals reached the learning criterion within 10 trials or not (Y/N) ($CRIT_{IC}$).

Lid-removal

The ability to develop new behaviours and/or use pre-existing behaviours in new contexts can help animals to survive in unfamiliar and fluctuating environments, e.g., by gaining access to novel or

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difficult resources more efficiently (Griffin et al., 2016). We assessed our lizards' problem-solving skills by measuring their performance in a lid-removal task (De Meester et al., 2021; Gavriilidi et al., 2022; Leal and Powell, 2012; Noble et al., 2014). 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 and 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.

Escape box

The escape box assay (De Meester et al., 2022; 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., 1999; 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 (De Meester et al., 2022; Kis et al., 2015; Siviter et al., 2017). 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.

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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 (Font, 2019; Martin et al., 2003; Noble et al., 2012; Paulissen, 2008). 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 and 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 and 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 (Carazo et al., 2014; Dayananda and Webb, 2017; De Meester et al., 2022; De Meester et al., 2021; Font, 2019; Gavriilidi et al., 2022; Noble et al., 2012)

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 in a random orientation. 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

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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). 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 (De Meester et al., 2021; Gavriilidi et al., 2022; Noble et al., 2014; Vardi et al., 2020). 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) (Carazo et al., 2014; De Meester et al., 2021; Noble et al., 2014). 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.

Reversal learning assays typically switch the reward contingency either after animals have been trained until a certain level of success or after a fixed number of trials. We opted for the latter approach as a way to standardise task experience and the opportunity to learn across individuals and species (see e.g., van Horik et al., 2018; van Horik et al., 2019, Boussard et al., 2019; Aljadeff & Lotem, 2021). In addition, it is not necessarily guaranteed that reaching an identical 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” (i.e., indicative of high cognitive flexibility) when they succeeded in both the spatial and reversal learning task ($CRIT_{SLRL}$) (Noble et al., 2012). 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.

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Environmental variables and life history characteristics

Environmental quality

We used the Normalized Difference Vegetation Index (NDVI) as a proxy for the lushness of the lizards' habitat. In line with previous studies, we assumed that visually restricted and more three-dimensional (i.e., lusher and greener) habitats are structurally more complex , as animals living here will need to process and store more environmental information, while filtering out relevant cues from irrelevant background noise (Safi and Dechmann, 2005; Powell and Leal, 2014; Calisi et al., 2017; Steck and Snell-Rood, 2018). 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 (Fernandez-Tizon et al., 2020; Roiz et al., 2015; Sweet et al., 2015). It can thus 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 S3.1). 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, Boisvenue and Running, 2006; Ortega et al., 2014) and arthropod abundance (i.e., resource availability) (Dunham, 1978; Kizito et al., 2017; Lessard et al., 2011; Spiller and Schoener, 1995; Stamps and Tanaka, 1981), 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 and Porter, 1996).

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From the CRU-TS 4.03 dataset (Harris et al., 2014) downscaled with WorldClim 2.1 (Fick and 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 S3.1) 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 (Linvill, 2019; Monteith and Unsworth, 1990) 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.

Temporal complexity

It has been argued that the variability, rather than the average condition of the environment could play a role in the evolution of cognition (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 (De Meester et al., 2021; Kalan et al., 2020). 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

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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 and 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 S3.2): SVL at hatchling stage and maturity as indicators of developmental time (larger individuals have a longer development time) (Adolph and 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 S5.2) (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

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variable was continuous (e.g., average solving time), we used a Gaussian error structure, with a weakly informative inverse γ-distribution prior ($V = 1$; $\mu = 0.002$) 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 ($V = 1$; $\mu = 0.002$). 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 ($V = 1$; $\mu = 0.002$) 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 $\mu = 2$) and parameter-expanded priors (e.g., $V = 1$; $\mu = 1$; $\alpha\mu = 0$; $\alpha V = 1000$). The use of the different types of priors is indicated in the results (Table S6-8).

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 complexity: 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 S6-8).

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 under 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

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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).

Results

Descriptive statistics for the cognitive performance per species and per test is shown in Figure 2 and summarized in Supplementary Information Table S4. The climate and life-history variables per species are shown in Table S5.

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 S5).

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 S5).

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 S5).

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Inhibitory control

Across all species, 76 % of test subjects succeeded in reaching the ($CRIT_{IC}$) 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 S4). Average solving time (ST_{IC}) during successful trials was 120.79 (± SD: 128.56) 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% ([0.00, 88.87]) and 17% (CI: [0.00, 50.35]) 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, 0.125]; $\lambda = 0.010$ [0.000, 0.034]).

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 S6). 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, -0.04], pMCMC < 0.05) and solved the task slower (ST_{IC}~CV_{NDVI}: 23.94 [6.85, 41.03], pMCMC < 0.05) (Figure 3). Males also tended solve the task faster than females (-77.56 [-162.93, 7.46], pMCMC = 0.08). None of the life-history variables were associated with inhibitory control performance (pMCMC > 0.22) (Table S8).

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 S4). Across species, the average solving time ST_{LR} was 290 (± 267) s. Individual *Takydromus sexlineatus* performed worst, (ST_{LR} = 384.23 ± 316.68 s), with individuals of *Z. vivipara* solving the problem approximately 3 times faster (ST_{LR} = 126.94 ± 142.60 s; Figure 2). Among-species differences explained 19% ([0.00,

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66.17]) of the variation observed in SR_{LR} and 8% ([0.00, 31.60]) in ST_{LR}. Both SR_{LR} and ST_{LR} had a weak phylogenetic signal ($\lambda = 0.018$ [0.00, 0.057]; $\lambda = 0.003$ [0.00, 0.012]).

None of the aspects of the physical environment of the lizards were associated with solving time (pMCMC > 0.30). However, across species, larger lizards tended to remove the lid more often than smaller ones (SR_{LR}~SVL: 0.03 [-0.00, 0.07], pMCMC = 0.07) (Table S6). 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}: 11.16 [-0.25, 22.84], pMCMC = 0.06) and succeeded less often (SR_{LR}~CV_{NDVI}: -0.18 [-0.43, 0.03], pMCMC = 0.07) (Table S7). None of the life-history variables correlated with lid removal performance (all pMCMC > 0.47) (Table S8).

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 550.11 (± 401.16) 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% (± 45) across all species, from 0% in individuals from *T. lepidus* and *P. ionicus* to 91% (± 21) in *D. oxycephala*. Among-species variation is 13% ([0.00, 55.71]) for ST_{ESC} and 53% ([18.59, 85.86]) for SR_{ESC}. The phylogenetic signal was weak for ST_{ESC} ($\lambda = 0.018$ [0.00, 0.051]), but moderate for SR_{ESC} ($\lambda = 0.145$ [0.024, 0.304]).

Larger individuals escaped slower (ST_{ESC}~ SVL: 8.17 [0.62, 15.41], pMCMC < 0.05) (Table S6). No other variables predicted escape time or success rate (pMCMC > 0.10) (Table S6-8).

Spatial cognition

Of all the specimens tested, 42% reached the spatial learning criterion ($CRIT_{SL}$). These animals required on average 8.23 (± 3.21) 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 5% ([0.01,

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21.82]) of the variation in CRIT_{SL} and 7% ([0.24, 21.96]) in LS_{SL}. The phylogenetic signal of LS_{SL} was weak ($\lambda = 0.008$ [0.001,0.018]), as was the one for CRIT_{SL} ($\lambda = 0.004$ [0.000, 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: 0.16 [0.07, 0.26], pMCMC < 0.05), and were marginally less successful in reaching the learning criterion (CRIT_{SL}~ Safe side: -0.57 [-1.20, 0.04], pMCMC = 0.07). Male lizards tended to learn slower (LS_{SL}~Sex: 0.11 [-0.01, 0.24], pMCMC = 0.09). None of environmental or life-history variables were associated with LS_{SL} and CRIT_{SL} (pMCMC > 0.22) (Table S6-8).

In the reversal learning task, 43% of the individuals successfully reached the learning criterion (CRIT_{RL}), needing on average 8.35 (± 2.92) 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 S4). *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, 26.16]) of the variation in CRIT_{SL} and 7% ([0.29, 23.03]) in LS_{SL}. The phylogenetic signals for LS_{RL} and CRIT_{RL} were $\lambda = 0.009$ ([0.002, 0.021]) and $\lambda = 0.004$ ([0.0001, 0.0140]), respectively.

Precipitation, temperature, NDVI, and the seasonality in the latter two variables did not predict LS_{RL} or CRIT_{RL} (pMCMC > 0.16) (Table S6-7). However, lizards originating from environments with low precipitation seasonality tended to be more likely to reach the learning criterion (CV_{PREC} ~ CRIT_{RL}: -0.02 [-0.04, 0.00], pMCMC = 0.09) (Table S7). 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 [0.03, 0.22], pMCMC < 0.05) and were less likely to reach the criterion (-0.89 [-1.54, -0.22], pMCMC < 0.05). None of the life-history characteristics correlated with performance in the reversal learning task (pMCMC > 0.42) (Table S8).

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Across all specimens measured, only 11% of lizards reached the learning criteria of both spatial and reversal learning tasks. Among-species variation accounts for 41% ([0.00, 92.24]) of the total variation in $\mathrm{CRIT}_{\mathrm{SLRL}}$ and for 47% ([5.05, 89.65]) 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 ($\lambda = 0.033$ [0.000, 0.144]; $\lambda = 0.095$ [0.003, 0.250]). Environmental quality did not predict performance in the spatial cognition tasks (pMCMC > 0.25). The same result was found for life-history characteristics (pMCMC > 0.24) (Table S8). Lizards from areas with high seasonality in precipitation were less likely demonstrate flexible learning ($\mathrm{CRIT}_{\mathrm{SLRL}}{\sim}\mathrm{CV}_{\mathrm{NDVI}}$: -7.84 [-18.03, 0.66], pMCMC < 0.05; Figure 4).

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; Mettke-Hofmann, 2014. Safi and Dechmann, 2005). Our data, however, lend no support to this idea, as none of the cognitive variables was related to habitat complexity (as outlined by precipitation and NDVI). This agrees with previous research on reptiles, revealing that relative brain size (and the assumed concomitant cognitive skills, but see

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Cauchoix and Chaine, 2016) does not correlate with habitat complexity across species (De Meester et al., 2019; Powell & Leal, 2014). 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). 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 and 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 and 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. Although successfully used in previous studies (Lassau et al., 2005; Miranda et al., 2018), NDVI is probably but a crude proxy of habitat complexity; it 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. We should also note that we did not test the effect of NDVI directly, as this proxy was highly correlated with precipitation which was included in the models instead. Nonetheless, it is safe to assume that more rainfall will result in greener, denser and thus more complex vegetation (Lassau et al., 2005).

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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 (Brust et al., 2014; Mink et al., 1981; Munch et al., 2018). Alternatively, behavioural flexibility 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; Kalan et al., 2020; Sol, 2009). 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 and problem-solving, while species exposed to more seasonal precipitation regimes tended to have reduced reversal learning abilities and cognitive flexibility. Inhibitory control, problem-solving, and reversal learning are all considered indicators of behavioural flexibility (Szabo et al., 2020a; Szabo et al., 2019b; Tebbich and Teschke, 2014; 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 (Luo et al., 2017; Van Woerden et al., 2010). Additionally, if the environment becomes too

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variable, animals may never learn faster than their surroundings change, rendering higher cognition ultimately pointless (Niemela et al., 2013).

Interestingly, our results seem to be in line with two previous studies on reptiles. Aegean wall lizards (*P. erhardii*) from an island exposed to higher seasonal variation in resource availability show worse reversal learning compared to conspecifics from a more stable mainland population (De Meester et al., 2021). Squamate reptiles from Neotropical ecosystems, which are both richer in terms of resources and supposedly climatically more stable (Foley et al., 1996; Pamela Delarue et al., 2015; Whitton et al., 2012; but see Jetz and Rubenstein, 2011), have relatively larger brains than relatives from temperate regions (De Meester et al., 2019). On the other hand, sleepy lizards (*Tiliqua rugosa asper*) from unpredictable arid environments show greater cognitive flexibility compared to blue-tongue skinks (*T. scincoides scincoides*) from milder habitats (Szabo and Whiting, 2020). Nonetheless, there seems to be a general pattern that reptiles deviate from many other taxa in which there is often improved tool use, problem-solving and reversal learning in more seasonal environments (chimpanzees: Kalan et al., 2020; black-capped chickadees: Roth et al., 2010b; woodpecker finches: Tebbich and Teschke, 2014). We see two potential explanations for why these studies have yielded such deviating results.

Firstly, it has been argued that seasonality has a differential impact on brain size and cognition in poikilothermic and homeothermic animals, as for ectotherms, with their low whole-body metabolism, maintaining the same amount of brain mass would be relatively more costly compared to endotherms (Tsuboi et al., 2015; Luo et al., 2017). Thus energetic constrains associated with fluctuating resource availabilities will be a much more restrictive factor in the evolution of cognition within ectotherms than in endotherms. However, this hypothesis seems unlikely, given that other studies have reported positive associations between behavioural flexibility and seasonality in ectotherm animals (Szabo and Whiting, 2020) and vice versa, negative associations in endotherm taxa (great tits: Hermer et al., 2018; mountain chickadees: Tello-Ramos et al., 2018). The endo- versus ectotherm dichotomy is nonetheless an interesting avenue to explore in future studies.

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Secondly, these inconsistent results could be due to variation in how exactly animals deal with environmental variability. Most lacertid lizards simply cease activity during adverse environmental conditions (e.g. cold winters or heat peaks in summers). As such, they will likely not face the challenges associated with the changing environment, and would thus not need improved behavioural flexibility. In a similar vein, hibernating mammals or migrating birds, who also 'evade' environmental changes, also often possess relatively smaller brains (Heldstab et al, 2018; Sol et al., 2005b; Vincze, 2016). Studies correlating cognition and environmental conditions should be careful to also consider possible (non-cognitive strategies) through which some animals may avoid or mitigate the negative effects of unfavourable settings (Fristoe and Botero, 2019).

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. In other species, inhibitory control, problem-solving, and reversal learning are often associated with higher rates of adult neurogenesis (Audet et al., 2018; Burghardt et al., 2012; Guitar and Sherry, 2018; Kalm et al., 2013; Swan et al., 2014; Zhang et al., 2012). If this is also true for lizards, this might explain why these cognitive abilities are more strongly selected against when resources are scarce. However, the functions of adult neurogenesis in reptiles should be further investigated to confirm this. 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 (X et al., 2022). 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 (Audet and Lefebvre, 2017; Griffin and Guez, 2014). 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

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sometimes found to be less vulnerable to predation (Bajer et al., 2015; Blomberg and Shine, 2000; 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 easier 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 conjunction 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 and 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 (DeCasien et al., 2018; Isler and van Schaik, 2006a; Isler and van Schaik, 2006b; Isler and van Schaik, 2009; 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

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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 and 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 (Roitberg et al., 2015; Sorci et al., 1996) 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 possible 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 and Braithwaite, 2005; Burns and 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; De Meester et al., 2021; Szabo et al., 2019b; visual pattern bias: Paulissen,

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2021), age (e.g., Noble et al., 2014), personality (e.g., Goulet et al ., 2018), developmental conditions (e.g., Amiel et al., 2014; Amiel and Shine, 2012; Munch et al., 2018), microhabitat (Rodrigues and Kohlsdorf, 2019) and sex (e.g., this study; Carazo et al., 2014), and can vary across populations of the same species (e.g., Batabyal and 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.

Some of the variation within species could be explained by sex-differences. Males were slightly faster in solving the inhibitory control test, but slower in learning the spatial task. Currently, the link between cognition and sex in lizards has received little attention (Carazo et al., 2014; De Meester and Baeckens, 2021; Szabo et al., 2019c). Sex-differences in (spatial) cognition are generally expected due to differences in reproductive strategies between males and females (Araya-Salas et al., 2018; Carazo et al., 2014; Ecuyer-Dab and Robert, 2004; Gaulin and FitzGerald, 1986; Jones et al., 2003; Szabo et al., 2019c). Previous studies have predicted and reported both higher and lower inhibitory control in males (Brandão et al., 2019). However, it is generally predicted that males should possess superior spatial learning compared to females (Carazo et al., 2014; Szabo et al., 2019c). This is the opposite of what we found in our lacertid lizards. One possible explanation could be that female lizards may rely more on spatial memory in an antipredator context compared to males. Females are often assumed to be more vulnerable to predation due to their reduced mobility while gravid (Shine, 1980) and would thus more strongly benefit of learning the location of nearby shelter. Likewise, female spatial cognition may be more finetuned at a smaller spatial scale (finding nearby shelter) while males may require stronger spatial skills over a larger scale due to their need to defend territories and locate females (Ecuyer-Dab and Robert, 2004). Nevertheless, the reported sex-differences only present statistical trends. Hence we propose that a more elaborate experiment, in which we consistently sample both sexes across multiple species, both on a small- and larger spatial scale, while collecting data on their territorial behaviour, sex-dependent dispersal, and home range sizes, is needed to confirm and understand potential sex-differences in lacertid cognition.

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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 more desert and tropical species, for example. 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 and Brown, 2014; White and 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 simplicity, 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 to 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 and Baeckens, 2021; Szabo et al., 2022).

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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 (Krasheninnikova et al., 2020; MacLean et al., 2012; Shaw and Schmelz, 2017). 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., 2021), 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 and Baeckens, 2021; Szabo et al., 2021). Their broad ecological and taxonomic diversity (Vitt and 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. This is also evident in our study, as we found that lacertids are capable of inhibitory control, problem-solving, spatial and reversal learning, and most interestingly, we found an unexpected, but evident, link between the ecology of the species and their cognitive performance: species from more variable environments exhibit lower behavioural flexibility. 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

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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.

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 *L. viridis* and *P. ionicus* were given by the Ethical Committee of the University of Sarajevo (file ID: 01/01-1099/2-2021) and Greek Ministry of Environmnent and Energy (permit nr. 7M7T4653Π8-ΠA5) respectively. Additional ethical clearance was provided by the Dienst Dierenwelzijn (Vlaamse Overheid) for the use of wild-caught individuals of *D. oxycephala* and *P. siculus* (DWZ/KF/20/1.15/41), and *P. muralis* and *Z. vivipara* (DWZ/EV/19/1.15/4). Field permits to capture wild-caught animals were obtained for *D. oxycephala, P. siculus* and*, P. 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.: 7ZΠP4653Π8-E76 and 7M7T4653Π8-ΠA5), *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.

Data accessibility statement

Data is stored at the University of Antwerp and archived at Figshare (link to collection: https://figshare.com/s/a6dd93361f6045968ad3).

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Tables

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 Supplementary Materials and Methods.

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 ionicus	14	11 ♂, 3 ♀	60.9 ± 8.81	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
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

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Figure legends

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 (Table S2).

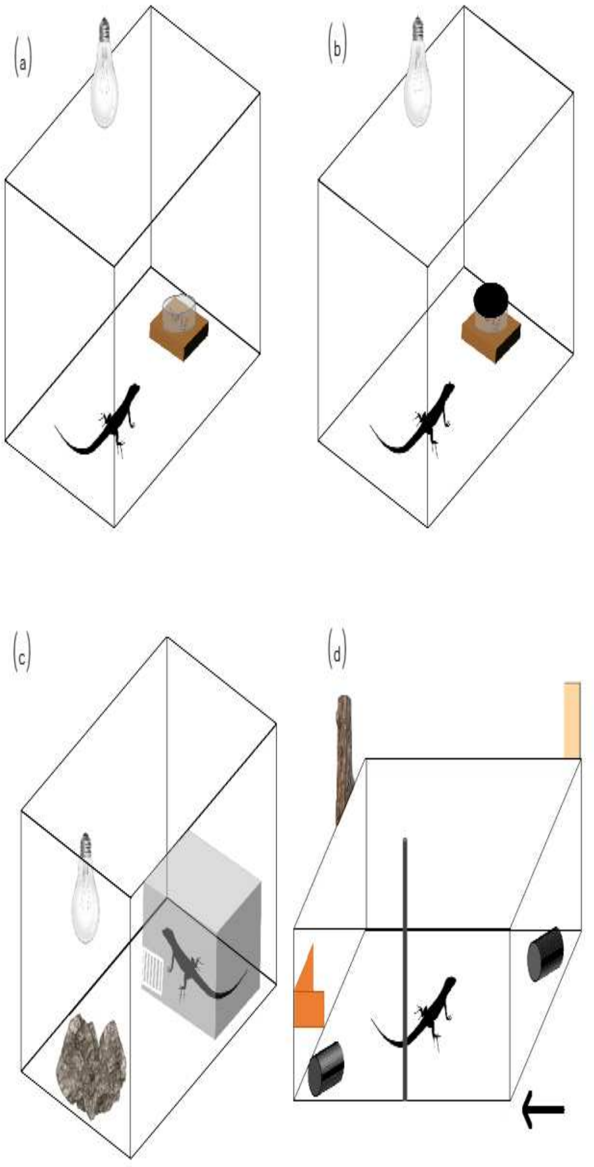

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Figure 2: Overview of the results (mean + standard error) of the cognitive tests. See also Table S4 for detailed results. Performance success increases along the x-axis. Photo credits: *Podarcis melisellensis*: BB; *Podarcis ionicus*: AB; *Podarcis erhardii*: SR; *Podarcis siculus*: LVL; *Podarcis muralis*: GDM; *Timon lepidus*: Pixabay; *Lacerta viridis*: AZ; *Takydromus sexlineatus*: GDM; *Dalmatolacerta oxycephala*: LVL; *Zootoca vivipara*: GDM; *Eremias brenchleyi*: GDM; *Acanthodactylus pardalis*: LVL; *Gastropholis prasina*: LVL.

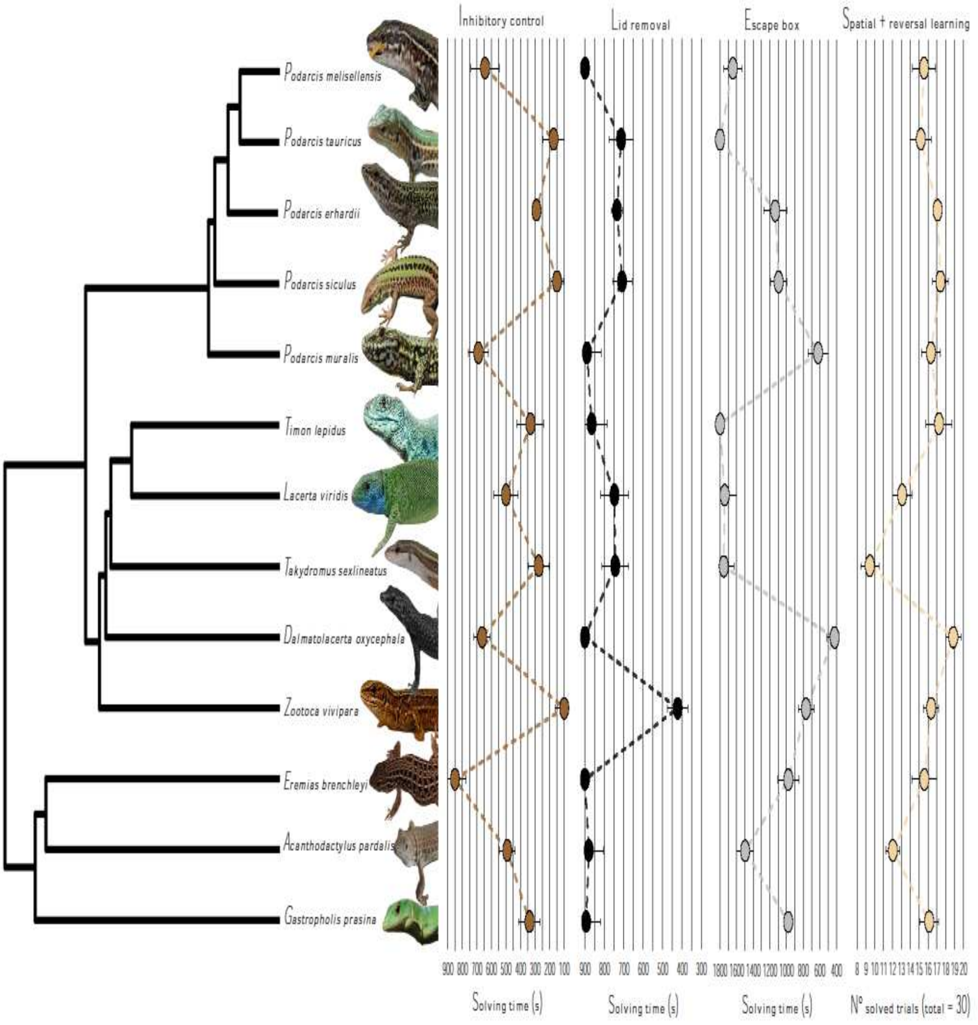

Figure 3: (a) Solving time during the inhibitory control task (s) vs. habitat variability (CV_{NDVI} in %). Each dot represents a species. Error bars represent standard errors. Species from environments with a

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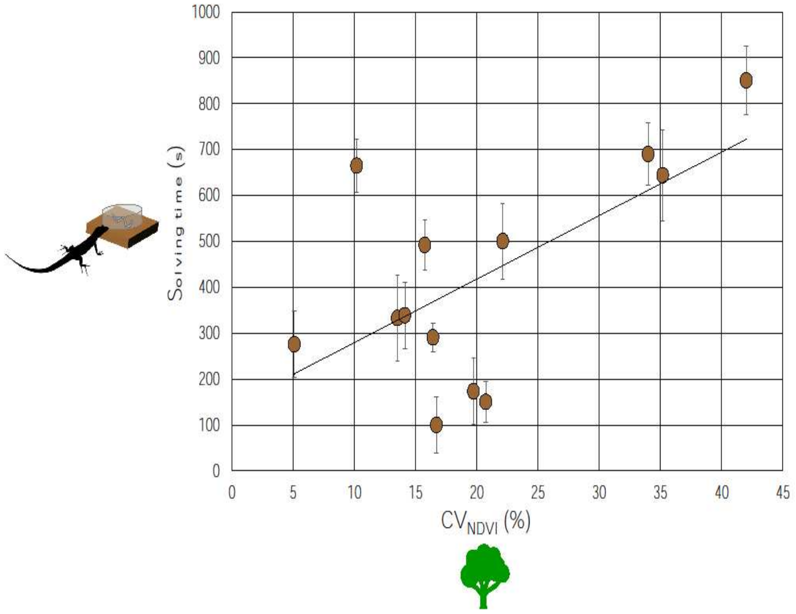
high seasonality in NDVI solved the task slower (MCMCglmm results - posterior mean [95% confidence interval]: 23.94 [6.85, 41.03], pMCMC < 0.05). (b) Mean CV_{NDVI} (%) of successful individuals (reaching the criterion of solving three in four consecutive trials) vs. the non-successful individuals. Each dot represents a species. Species from environments with a high seasonality in NDVI were less successful (MCMCglmm results: -0.24 [-0.45, -0.04], pMCMC < 0.05).

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



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

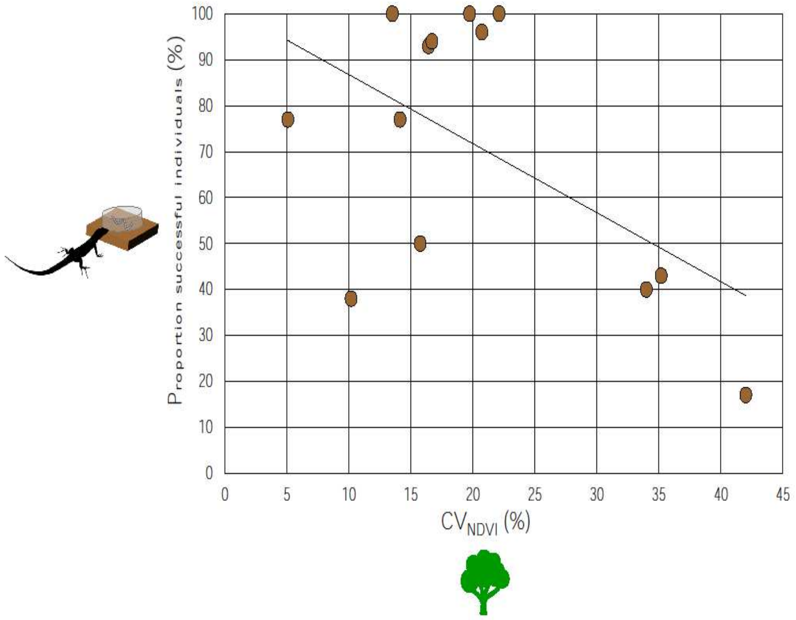


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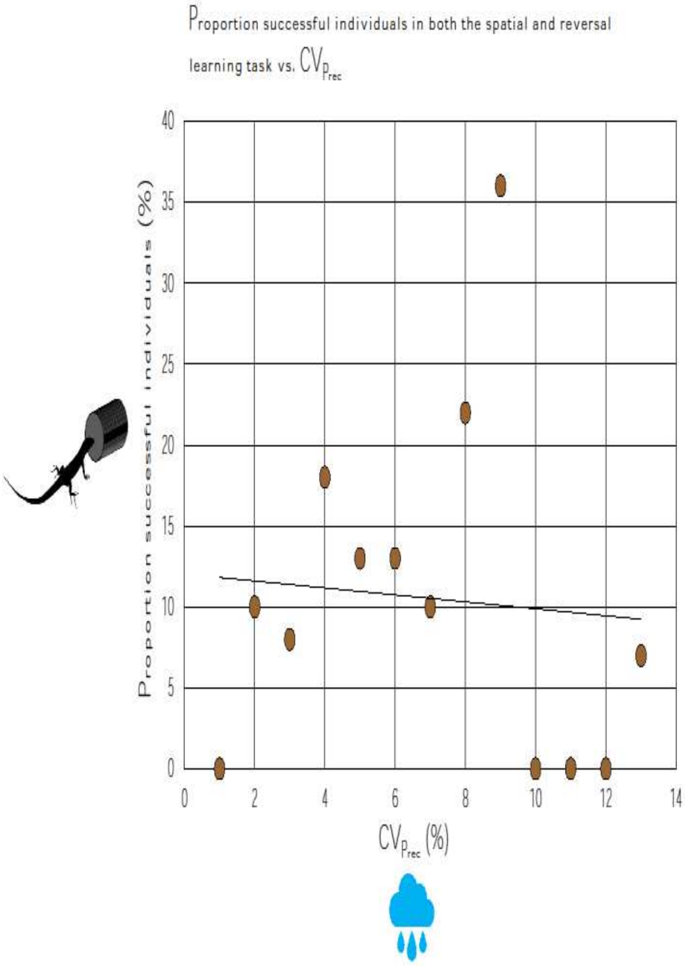
Figure 4: Proportion of individuals succeeding on both the spatial and reversal learning task vs. habitat variability (CV_{PREC} in %). Each dot represents a species. Species from environments with a high seasonality in precipitation were less likely to exhibit flexible learning (i.e., learning during the spatial phase and relearning during the reversal) (MCMCglmm results - posterior mean [95% confidence interval]: -7.84 [-18.03, 0.66], pMCMC < 0.05).



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