Bold and bright : shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (Podarcis erhardii)

Reference:

De Meester Gilles, Pafilis Panayiotis, Van Damme Raoul.- Bold and bright : shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (Podarcis erhardii)
Animal cognition - ISSN 1435-9456 - Heidelberg, Springer heidelberg, 25(2022), p. 745-767
Full text (Publisher's DOI): https://doi.org/10.1007/S10071-021-01587-0
To cite this reference: https://hdl.handle.net/10067/1854490151162165141

Bold and bright – shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (*Podarcis erhardii*).

Gilles De Meester[1,2*], Panayiotis Pafilis[2] & Raoul Van Damme[1]

[1] Department of Biology, Functional Morphology Group, University of Antwerp, Wilrijk, Belgium.

[2] Department of Biology, Section of Zoology and Marine Biology, National & Kapodistrian University of Athens, Athens, Greece.

ACKNOWLEDGEMENTS

We would like to thank Kinsey Brock for her help with catching lizards, Colin Donihue & Menelia Vasilopoulou-Kampitsi for advice regarding fieldwork, Aris Deimezis and his students for help with care of the animals, and Chryssa Economou for assistance during the experiments. The research was funded by the Research Foundation – Flanders (FWO) through a PhD fellowship (grant ID: 1144118N) and a travel grant (ID: V416719N), and by the Royal Belgian Zoological Society via a travel grant (all to GDM).

---

[*] Corresponding author:

Gilles De Meester

Campus Drie Eiken, Building D – Room D.141

Universiteitsplein 1, 2610 Wilrijk, Belgium

email: Gilles.DeMeester@uantwerpen.be

telephone: +3232658916

ORCID ID: 0000-0001-7051-9957

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 behavioral associations were often habitat- but also year-dependent. In general, behavioral 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.

Keywords: cognition, animal personality, cognitive styles, behavioral syndromes, habitat complexity, *Podarcis*,

DECLARATIONS

Funding: The research was funded by the Research Foundation – Flanders (FWO) through a PhD fellowship (grant ID: 1144118N) and a travel grant (ID: V416719N), and by the Royal Belgian Zoological Society via a travel grant (all to GDM).

Conflicts of interest/Competing interests: The authors declare no conflicts of interest.

Availability of data and material: Data is included as supplementary material.

Code availability: R scripts used for analyzing data are available upon request.

Authors' contributions: All authors contributed to study conception and design. GDM collected and analyzed the data and wrote the first draft of the manuscript. All authors provided feedback on previous versions of the manuscript and approved the final version.

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.

Consent to participate: Not applicable.

Consent for publication Not applicable.

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 and Dechmann, 2005; Powell and Leal, 2014; Calisi et al., 2017) while filtering out vast quantities of irrelevant background data (Shumway, 2008; Steck and Snell-Rood, 2018). As a consequence, structured habitats are believed to select for superior spatial cognition (White and 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 and Verts, 1986; bats: Safi and 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 and Leal, 2014; three-spined sticklebacks: Ahmed et al., 2017; Squamata: De Meester et al., 2019; *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 behavioral 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 and Brown, 2014; 2015; Carbia and 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 and 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 and Del Giudice, 2012; Bensky et al., 2017; Dougherty and 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 behavioral flexibility: initial fast learners are deemed less capable of changing a behavioral 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 and Bell, 2020; Carib grackles: Ducatez et al., 2014; delicate skinks: Chung et al., 2017; common mynas: Lermite et al., 2017; carpenter ants: Udino et al., 2017; delicate skinks: Goulet et al., 2018; common waxbills: Gomes et al., 2020). A recent meta-analysis by Dougherty and 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 and Fromhage, 2019), 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 and Leal, 2014; White and 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 and 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., 2015). Its diet mostly consists of arthropods, but occasionally includes snails, eggs, fruits and even conspecifics (Adamopoulou et al., 1999; Brock et al., 2014; Donihue, 2016; Madden and Brock, 2018).

This study was conducted on Naxos, the largest island of the Greek Cyclades. Due to its relatively large size (429.8 km²), 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 (Fig. 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 Fig. 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 (Fig. 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.

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 and 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 and Teschke, 2014). Neophobia was measured using a standard procedure, by looking at how foraging behavior changes when a novel, conspicuously colored, and artificial object is introduced near a familiar food source (Greenberg, 1983; Candler and 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). 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 analyzed 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 behavior (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 and Bates, 2000; Martin and Réale, 2008).

Problem-solving: lid-removal task

Cognition allows individuals to solve new problems by inventing a new behavior or by expressing a familiar behavior in a novel context (Griffin and Guez, 2014). Problem-solving was tested using the classical lid-removal paradigm for lizards (Leal and 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). 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 analyzed using Cox proportional hazard models ('survival' and 'coxme' packages, Therneau & Lumley 2015; Therneau 2015) as these are better suited for right-censored data.

Exploratory behavior

The tendency to explore and sample novel environments is likely linked to how fast individuals solve new problems and learn new information (Sih and 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 center, and four identical objects (either pine cones or stones) were placed in between them. A lizard was placed in the center 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 behaviors: 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 center 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 center 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 behavior lizards received a score of '+1' and for each evasive behavior a '-1' (Table 1), which were then summed to calculate an individual's 'aggression score'.

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 analyze two trials for ten individuals. We tested both males and females, but because true fights between females were rare we only analyzed the data for male-male encounters.

Aggression scores were analyzed 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 analyzed 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 center 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). 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., 2019a) 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-behavioral 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. Guilette 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; Branch et al., 2019; Goulet et al., 2018). 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-behavioral syndrome, we ran a series of (G)LMMs for each pair of behavioral 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 analyzing 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.

RESULTS

Descriptive statistics for all cognitive and behavioral variables per habitat and per sex are presented in Supplementary Table S1. 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 behavioral parameters using equivalent models without population as random factor, and obtained largely identical results (Supplementary Table S2).

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) (Fig. 2).

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.

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 (Fig. 2).

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 (Fig. 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 $p > 0.05$, Fig. 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 (Fig. 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: $\chi^2_1 = 4.00$, $p = 0.05$).

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 (Fig. 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. 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 – behavioral syndromes

An overview of our results is given in Fig. 5 (see also Table S3 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 behavioral 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 Fig. 2).

Secondly, there was stronger evidence for the existence of a cognitive syndrome. Across years and habitats, spatial and reversal learning capacity were inversely related (Fig. 6a, $F_{1,113} = 6.02$, $p = 0.02$), and both measures correlated positively with flexibility scores (Fig. 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 $p > 0.10$).

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 (Fig. 6d, t = 2.28, $p = 0.02$), but, unexpectedly, so did lizards with low scores on exploration PC2 (Fig. 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 (Fig. 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 and Fromhage, 2019). Our results add to the general observation that individual animals, including lizards, exhibit consistent differences in aspects of their behavior. 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 and 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 and Brown, 2014, 2015), aerial (Clarin et al., 2013), fossorial (Costanzo et al., 2009) and terrestrial animals (our study, but see Mackay and 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 defense, 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 behavior in a natural setting, and how this changes with vegetation density. Perhaps lizards from dense habitats, like gobies (White and 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).

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., 2010; Tebbich and Teschke, 2014; Tello-Ramos et al., 2019; Szabo and Whiting, 2020), of which both problem-solving and reversal learning are believed to be strong indicators (Tebbich and 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., 2010; Szabo and 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 and 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. (2005) 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). 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 and Mushinsky, 1997; Mullin and 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 and Stamps, 1992; Johnson et al., 2010; Church and Grant, 2018). Interestingly, some lizard species seemingly adjust their territorial behavior to changes in habitat structure (Eason and Stamps, 1992; Calsbeek and 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 and 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).

Behavioral associations

As predicted, we found numerous behavioral 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 behavioral syndrome (among personality traits, *sensu* Sih et al., 2004) was only weakly supported. No correlations were found in lizards from complex habitats. Potentially, behavioral syndrome structure has dissolved in these populations as a consequence of more relaxed predation pressure (Sih et al., 2004; Bell and Sih, 2007; Brydges et al., 2008; Harris et al., 2011). But then again, evidence for a behavioral 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 behavioral 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 and 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. 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 behavioral flexibility (Tebbich and 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 and 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 and 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 and 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 behavior 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 behavioral associations were either independent of habitat or solely found in the simple environments. The behavioral associations exclusively found in simple habitats (e.g. Exploration PC2 – RL) may have arisen because specific environmental challenges in these populations select for specific behavioral combinations/strategies (Sih et al., 2004; Brydges et al., 2008; Sih and Del Giudice, 2012; Liedtke and Fromhage, 2019). Predation, for instance, is considered an important force shaping behavioral syndromes (Bell and Sih, 2007; Dingemanse et al., 2007; Harris et al., 2011) and potentially cognitive styles (Sih and Del Giudice, 2012; Liedtke and Fromhage, 2019). 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., 2010; Sih and 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., 2010; Sih and 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., 2015). 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 behavioral associations found. Nevertheless not all behavioral 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 behavioral development during early life (Clark et al., 2013; Amiel et al., 2014; Dayananda and Webb, 2017; Munch et al., 2018; Siviter et al., 2017a; Siviter et al., 2017b; Beltrán et al., 2020; Vardi et al., 2020). Environmental changes can also shift the adaptive value of particular behavioral combinations, and thus alter such associations via selection and behavioral plasticity (Bell and 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 behavioral 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., 2019b). 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., 2019b). 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 behavioral syndromes, and is thus likely to advance the field of cognitive ecology as well.

REFERENCES

Abalos J, Pérez i de Lanuza G, Carazo P, Font E, 2016. The role of male coloration in the outcome of staged contests in the European common wall lizard (*Podarcis muralis*). Behaviour 153:607-631. DOI: 10.1163/1568539X-00003366

Adamopoulou C, Valakos ED, Pafilis P, 1999. Summer diet of *Podarcis milensis, P. gaigeae* and *P. erhardii* (Sauria: Lacertidae). Bonn zool Beitr 48:275-282.

Ahmed NI, Thompson C, Bolnick DI, Stuart YE, 2017. Brain morphology of the threespine stickleback (*Gasterosteus aculeatus*) varies inconsistently with respect to habitat complexity: A test of the Clever Foraging Hypothesis. Ecol Evol 7:3372-3380. DOI: 10.1002/ece3.2918

Amiel JJ, Lindström T, Shine R, 2014. Egg incubation effects generate positive correlations between size, speed and learning ability in young lizards. Anim Cogn 17:337-347. DOI: 10.1007/s10071-013-0665-4

Aragón P, Meylan S, Clobert J, 2006. Dispersal status-dependent response to the social environment in the common lizard, *Lacerta vivipara*. Funct Ecol 20: 900-907. DOI: 10.1111/j.1365-2435.2006.01164.x

Audet J-N, Lefebvre L, 2017. What's flexible in behavioral flexibility? Behavioural Ecology 28:943-947. DOI: 10.1093/beheco/arx007

Audet JN, Ducatez S, Lefebvre L, 2015. The town bird and the country bird: problem-solving and immunocompetence vary with urbanization. Behav Ecol 0:1-8. DOI: 10.1093/beheco/arv201

Axelrod CJ, Laberge F, Robinson BW, 2018. Intraspecific brain size variation between coexisting sunfish ecotypes. Proc Royal Soc B 285. DOI: 10.1098/rspb.2018.1971

Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1-48. DOI: 10.18637/jss.v067.i01

Bebus SE, Small TW, Jones BC, Elderbrock EK, Schoech SJ, 2016. Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. Anim Beh 111:251-260. DOI: 10.1016/j.anbehav.2015.10.027

Bell AM, Sih A, 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10:828-834. DOI: 10.1111/j.1461-0248.2007.01081.x

Beltrán I, Loiseleur R, Durand V, Whiting MJ, 2020. Effects of early thermal environment on the behavior and learning of a lizard with bimodal reproduction. Behav Ecol Sociobiol 74. DOI: 10.1007/s00265-020-02849-6

Bensky MK, Bell AM, 2020. Predictors of individual variation in reversal learning performance in three-spined sticklebacks. Anim Cogn 23:925-938. DOI: 10.1007/s10071-020-01399-8

Bensky MK, Paitz R, Pereira L, Bell AM, 2017. Testing the predictions of coping styles theory in threespined sticklebacks. Behav Process 136:1-10. DOI: 10.1016/j.beproc.2016.12.011

Boogert NJ, Madden JR, Morand-Ferron J, Thornton A, 2018. Measuring and understanding individual differences in cognition. Philosophical Transactions of the Royal Society London B 373. DOI: 10.1098/rstb.2017.0280

Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Pravosudov VV, 2019. Smart is the new sexy: female mountain chickadees increase reproductive investment when mated to males with better spatial cognition. Ecol Lett 22:897-903. DOI: 1010.1111/ele.13249

Braun CA, Baird TA, York JR, 2018. Behavioural plasticity in physically variable microhabitats: a field test of potential adaptive consequences in male collared lizards (*Crotaphytus collaris*). Biol J Linn Soc 125:37-49. DOI: 10.1093/biolinnean/bly100/5061979

Brock K, Donihue CM, Pafilis P, 2014. New records of frugivory and ovophagy in *Podarcis* (Lacertidae) lizards from East Mediterranean Islands. North-West J Zool 10:223-225.

Brock KM, Bednekoff PA, Pafilis P, Foufopoulos J, 2015. Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? Evolution 69:216-231. DOI: 10.1111/evo.12555

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM, 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378-400. DOI: 10.32614/RJ-2017-066

Bruinjé AC, Coelho FEA, Paiva TMA, Costa GC, 2019. Aggression, color signaling, and performance of the male color morphs of a Brazilian lizard (*Tropidurus semitaeniatus*). Behav Ecol Sociobiol 73. DOI: 10.1007/s00265-019-2673-0

Brydges NM, Colegrave N, Heathcote RJP, Braithwaite VA, 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. J Anim Ecol 77:229-235. DOI: 10.1111/j.1365-2656.2008.01343.x

Budeau DA, Verts BJ, 1986. Relative brain size and structural complexity of habitats of chipmunks. J Mammal 67:579-581. DOI: 10.2307/1381291

Calisi RM, Chintamen S, Ennin E, Kriegsfeld L, Rosenblum EB, 2017. Neuroanatomical changes related to a changing environment in lesser earless lizards. J Herpetol 51:258-262. DOI: 10.1670/16-056

Calsbeek R, Sinervo B, 2002. An experimental test of the ideal despotic distribution. J Anim Ecol 71:513-523. DOI: 10.1046/j.1365-2656.2002.00619.x

Candler S, Bernal XE, 2014. Differences in neophobia between cane toads from introduced and native populations. Behav Ecol 26:97-104. DOI: 10.1093/beheco/aru162

Carazo P, Noble DW, Chandrasoma D, Whiting MJ, 2014. Sex and boldness explain individual differences in spatial learning in a lizard. Proc Royal Soc B 281:20133275. DOI: 10.1098/rspb.2013.3275

Carbia PS, Brown C, 2019. Environmental enrichment influences spatial learning ability in captive-reared intertidal gobies (*Bathygobius cocosensis*). Anim Cogn 22:89-98. DOI: 10.1007/s10071-018-1225-8

Cauchard L, Angers B, Boogert NJ, Lenarth M, Bize P, Doligez B, 2017. An experimental test of a causal link between problem-solving performance and reproductive success in wild great tits. Front Ecol Evol 5. DOI: 10.3389/fevo.2017.00107

Chung M, Goulet CT, Michelangeli M, Melki-Wegner B, Wong BBM, Chapple DG, 2017. Does personality influence learning? A case study in an invasive lizard. Oecologia 185:641-651. DOI: 10.1007/s00442-017-3975-4

Church KDW, Grant JWA, 2018. Does increasing habitat complexity favour particular personality types of juvenile Atlantic salmon, *Salmo salar*? Anim Beh 135:139-146. DOI: 10.1016/j.anbehav.2017.11.006

Clarin TM, Ruczynski I, Page RA, Siemers BM, 2013. Foraging ecology predicts learning performance in insectivorous bats. PLOS ONE 8:e64823. DOI: 10.1371/journal.pone.0064823

Clark BF, Amiel JJ, Shine R, Noble DWA, Whiting MJ, 2013. Colour discrimination and associative learning in hatchling lizards incubated at 'hot' and 'cold' temperatures. Behav Ecol Sociobiol 68:239-247. DOI: 10.1007/s00265-013-1639-x

Cooper T, Liew A, Andrle G, Cafritz E, Dallas H, Niesen T, Slater E, Stockert J, Vold T, Young M, Mendelson J, 2019. Latency in problem solving as evidence for learning in varanid and helodermatid lizards, with comments on foraging techniques. Copeia 107. DOI: 10.1643/CH-18-119

Costanzo MS, Bennett NC, Lutermann H, 2009. Spatial learning and memory in African mole-rats: the role of sociality and sex. Physiol Behav 96:128-134. DOI: 10.1016/j.physbeh.2008.09.008

Crane AL, Ferrari MCO, Rivera-Hernández IAE, Brown GE, Candolin U, 2019. Microhabitat complexity influences fear acquisition in fathead minnows. Behav Ecol 31:261-266. DOI: 10.1093/beheco/arz187

Croston R, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Parchman TL, Pravosudov VV, 2017. Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. Anim Beh 123:139-149. DOI: 10.1016/j.anbehav.2016.10.004

Dalesman S, 2018. Habitat and social context affect memory phenotype, exploration and covariance among these traits. Philosophical Transactions of the Royal Society London B 373. DOI: 10.1098/rstb.2017.0291

Dalesman S, Rendle A, Dall SR, 2015. Habitat stability, predation risk and 'memory syndromes'. Sci Rep 5:10538. DOI: 10.1038/srep10538

Damas-Moreira I, Riley JL, Harris DJ, Whiting MJ, 2019. Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. Anim Beh 151:195-202. DOI: 10.1016/j.anbehav.2019.03.008

Day LB, Crews D, Wilczynski W, 2001. Effects of medial and dorsal cortex lesions on spatial memory in lizards. Behav Brain Res 118:27-42. DOI: 10.1016/s0166-4328(00)00308-9.

Dayananda B, Webb JK, 2017. Incubation under climate warming affects learning ability and survival in hatchling lizards. Biol Lett 13. DOI: 10.1098/rsbl.2017.0002.

De Meester G, Huyghe K, Van Damme R, 2019. Brain size, ecology and sociality: a reptilian perspective. . Biol J Linn Soc 126:381-391. DOI: 10.1093/biolinnean/bly206/5297451

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:1-31. DOI:10.1163/1568539X-bja10088

DiMiceli C, Carroll M, Sohlberg R, Kim D, Kelly M, Townshend J, 2015. MOD44B MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250 SIN Grid V006. NASA EOSDIS Land Processes DAAC. DOI: 10.5067/MODIS/MOD44B.006.

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM, 2004. Fitness consequences of avian personalities in a fluctuating environment. Proc Royal Soc B 271:847-852. DOI 10.1098/rspb.2004.2680

Dingemanse NJ, Wright J, Kazem AJ, Thomas DK, Hickling R, Dawnay N, 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J Anim Ecol 76:1128-1138. DOI: 10.1111/j.1365-2656.2007.01284.x

Donihue CM, 2016. Aegean wall lizards switch foraging modes, diet, and morphology in a human-built environment. Ecol Evol 6:7433-7442. DOI: 10.1002/ece3.2501

Dougherty LR, Guillette LM, 2018. Linking personality and cognition: a meta-analysis. Philosophical Transactions of the Royal Society London B 373. DOI: 10.1098/rstb.2017.0282

Ducatez S, Audet JN, Lefebvre L, 2014. Problem-solving and learning in Carib grackles: individuals show a consistent speed–accuracy trade-off. Anim Cogn 18:485-496. DOI: 10.1007/s10071-014-0817-1 ·

Dukas R, 2004. Evolutionary biology of animal cognition. Annu Rev Ecol Evol Syst 35:347-374. DOI: 10.2307/annurev.ecolsys.35.112202.30000014

Eason PK, Stamps JA, 1992. The effect of visibility on territory size and shape. Behav Ecol 3:166-172.

Font E, 2019. Rapid learning of a spatial memory task in a lacertid lizard (*Podarcis liolepis*). Behav Process 169:103963. DOI: 10.1016/j.beproc.2019.103963

Garcia FAC, Moura RR, Ogawa CY, Zanette LRS, Silva JRF, Rezende CF, 2020. Never forget where you came from: Microhabitat of origin influences boldness and exploration in the hermit crab *Clibanarius symmetricus* (Diogenidae). J Exp Mar Biol Ecol 527. DOI: 10.1016/j.jembe.2020.151365

Godfrey-Smith P, 2002. Environmental complexity and the evolution of cognition. In: Sternberg R, Kaufman J, editors. The evolution of intelligence. Mahwah, New Jersey: Lawrence Erlbaum Associates London. p. 223-250.

Gomes ACR, Guerra S, Silva PA, Marques CI, Trigo S, Boogert NJ, Cardoso GC, 2020. Proactive common waxbills make fewer mistakes in a cognitive assay, the detour-reaching task. Behav Ecol Sociobiol 74:1-15. DOI: 10.1007/s00265-020-2809-2

Goulet CT, Michelangeli M, Chung M, Riley JL, Wong BBM, Thompson MB, Chapple DG, 2018. Evaluating cognition and thermal physiology as components of the pace-of-life syndrome. Evol Ecol 32:469-488. DOI: 10.1007/s10682-018-9948-1

Greenberg R, 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. Am Nat 122:444-453. DOI: 10.1086/284148

Griffin AS, Guez D, 2014. Innovation and problem solving: a review of common mechanisms. Behav Process 109 Pt B:121-134. DOI: 10.1016/j.beproc.2014.08.027

Griffin AS, Guez D, Lermite F, Patience M, 2013. Tracking changing environments: innovators are fast, but not flexible learners. PLOS ONE 8:e84907. DOI: 10.1371/journal.pone.0084907

Griffin AS, Guillette LM, Healy SD, 2015. Cognition and personality: an analysis of an emerging field. Trends Ecol Evol 30:207-214. DOI: 10.1016/j.tree.2015.01.012

Guido JM, Biondi LM, Vasallo AI, Muzio RN, 2017. Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, *Milvago chimango*. Anim Cogn 20:591-602. DOI: 10.1007/s10071-017-1083-9

Guillette LM, Reddon AR, Hurd PL, Sturdy CB, 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. Behav Process 82:265-270. DOI: :10.1016/j.beproc.2009.07.005

Harris S, Eroukhmanoff F, Green KK, Svensson EI, Pettersson LB, 2011. Changes in behavioural trait integration following rapid ecotype divergence in an aquatic isopod. J Evol Biol 24:1887-1896. DOI: 10.1111/j.1420-9101.2011.02322.x

Henderson CR, 1975. Best linear unbiased estimation and prediction under a selection model. Biometrics 31:423-447. DOI: 10.2307/2529430

Hendry AP, 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. J Hered 107:25-41. DOI: 10.1093/jhered/esv060

Henke-von der Malsburg J, Kappeler PM, Fichtel C, 2020. Linking ecology and cognition: does ecological specialisation predict cognitive test performance? Behav Ecol Sociobiol 74. DOI: 10.1007/s00265-020-02923-z

Janzen DH, 1973. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day and insularity. Ecology 54:687-708.

Johnson MA, Revell LJ, Losos JB, 2010. Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in Anolis lizards. Evolution 64:1151-1159. DOI: :10.1111/j.1558-5646.2009.00881.x

Johnson ZV, Moore EC, Wong RY, Godwin JR, Streelman JT, Roberts RB, 2020. Exploratory behaviour is associated with microhabitat and evolutionary radiation in Lake Malawi cichlids. Anim Beh 160:121-134. DOI: 10.1016/j.anbehav.2019.11.006

Keiser CN, Ingley SJ, Toscano BJ, Scharf I, Pruitt JN, 2018. Habitat complexity dampens selection on prey activity level. Ethology 124:25-32. DOI: 10.1111/eth.12700

King AJ, Furtbauer I, Mamuneas D, James C, Manica A, 2013. Sex-differences and temporal consistency in stickleback fish boldness. PLOS ONE 8:e81116. DOI: 10.1371/journal.pone.0081116

Kotrschal A, Buechel SD, Zala SM, Corral-Lopez A, Penn DJ, Kolm N, 2015. Brain size affects female but not male survival under predation threat. Ecol Lett 18:646-652. DOI: 10.1111/ele.12441

Le Cœur C, Thibault M, Pisanu B, Thibault S, Chapuis J-L, Baudry E, 2015. Temporally fluctuating selection on a personality trait in a wild rodent population. Behav Ecol 26:1285-1291. DOI: 10.1093/beheco/arv074

Leal M, Powell BJ, 2012. Behavioural flexibility and problem-solving in a tropical lizard. Biol Lett 8:28-30. DOI: 10.1098/rsbl.2011.0480

Lermite F, Peneaux C, Griffin AS, 2017. Personality and problem-solving in common mynas (*Acridotheres tristis*). Behav Process 134:87-94. DOI: 10.1016/j.beproc.2016.09.013

Liedtke J, Fromhage L, 2019. Modelling the evolution of cognitive styles. BMC Evol Biol 19:234. DOI: 10.1186/s12862-019-1565-2

López P, Aragón P, Martin J, 1998. Ibarian rock lizards (*Lacerta monticola cyreni*) assess conspecific information using composite signals from faecal pellets. Ethology 104:809-820. DOI: 10.1111/j.1439-0310.1998.tb00033.x

Lymberakis P, Pafilis P, Poulakakis N, Sotiropoulos K, Valakos ED, 2018. The Amphibians and Reptiles of the Aegean Sea. In: Sfenthourakis S, Pafilis P, Parmakelis A, Poulakakis N, Triantis KA, editors. Biogeography and Biodiversity of the Aegean In honour of Prof Moysis Mylonas Nicosia, Cyprus: Broken Hill Publishers Ltd. p. 169-189.

Mackay MK, Pillay N, 2017. Similarities in spatial cognition in sister species of the striped mouse *Rhabdomys* originating from different ecological contexts. Behaviour 154:1397-1420. DOI: 10.1163/1568539X-00003474

Madden I, Brock KM, 2018. An extreme record of cannibalism in *Podarcis erhardii mykonensis* (Reptilia: Lacertidae) from Siros island, Cyclades, Greece. Herpetol Notes 11:291-292.

Martin J, López P, Douglas ME, 2003. Changes in the escape responses of the lizard *Acanthodactylus erythrurus* under persistent predatory attacks. Copeia 2003:408-413. DOI: 10.1643/0045-8511(2003)003[0408:CITERO]2.0.CO;2

Martin JGA, Réale D, 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Anim Beh 75: 309-318. DOI: 10.1016/j.anbehav.2007.05.026

Mazza V, Eccard JA, Zaccaroni M, Jacob J, Dammhahn M, 2018. The fast and the flexible: cognitive style drives individual variation in cognition in a small mammal. Anim Beh 137:119-132. DOI: 10.1016/j.anbehav.2018.01.011

Mazza V, Jacob J, Dammhahn M, Zaccaroni M, Eccard JA, 2019. Individual variation in cognitive style reflects foraging and anti-predator strategies in a small mammal. Sci Rep 9:10157. DOI: 10.1038/s41598-019-46582-1

McEvoy J, While GM, Sinn DL, Carver S, Wapstra E, 2015. Behavioural syndromes and structural and temporal consistency of behavioural traits in a social lizard. J Zool 296:58-66. DOI: 10.1111/jzo.12217

Mettke-Hofmann C, 2014. Cognitive ecology: ecological factors, life-styles, and cognition. Wiley Interdiscip Rev Cogn Sci 5:345-360. DOI: 10.1002/wcs.1289

Mettke-Hofmann C, Winkler H, Leisler B, 2002. The significance of ecological factors for exploration and neophobia in parrots. Ethology 108:249-272. DOI: 10.1046/j.1439-0310.2002.00773.x

Michelangeli M, Chapple DG, Goulet CT, Bertram MG, Wong BBM, 2019. Behavioural syndromes vary among geographically distinct population. Behav Ecol 30: 393e401. DOI: 10.1093/beheco/ary178

Michelangeli M, Melki-Wegner B, Laskowski K, Wong BBM, Chapple DG, 2020. Impacts of caudal autotomy on personality. Anim Beh 162:67-78. DOI: 10.1016/j.anbehav.2020.02.001

Mullin SJ, Gutzke WHN, 1999. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). I. Influence of habitat structural complexity when searching for mammalian prey. Herpetologica 55:18-28.

Mullin SJ, Mushinsky HR, 1997. Use of experimental enclosures to examine foraging success in water snakes: A case study. J Herpetol 31. DOI: 10.2307/1565610

Munch KL, Noble DWA, Botterill-James T, Koolhof IS, Halliwell B, Wapstra E, While GM, 2018. Maternal effects impact decision-making in a viviparous lizard. Biol Lett 14. DOI: 10.1098/rsbl.2017.0556

Names G, Martin M, Badiane A, Le Galliard J-F, 2019. The relative importance of body size and UV coloration in influencing male-male competition in a lacertid lizard. Behav Ecol Sociobiol 73. DOI: 10.1007/s00265-019-2710-z

Noble DW, Carazo P, Whiting MJ, 2012. Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions. Biol Lett 8:946-948. DOI: 10.1098/rsbl.2012.0813

Odling-Smee LC, Boughman JW, Braithwaite VA, 2008. Sympatric species of threespine stickleback differ in their performance in a spatial learning task. Behav Ecol Sociobiol 62:1935-1945. DOI: 10.1007/s00265-008-0625-1

Overington SE, Cauchard L, Cote KA, Lefebvre L, 2011. Innovative foraging behaviour in birds: what characterizes an innovator? Behav Process 87:274-285. DOI: 10.1016/j.beproc.2011.06.002

Pafilis P, Foufopoulos J, Poulakakis N, Lymberakis P, Valakos ED, 2009. Tail shedding in island lizards [Lacertidae, Reptilia]: decline of antipredator defenses in relaxed predation environments. Evolution 63:1262-1278. DOI: /10.1111/j.1558-5646.2009.00635.x

Pafilis P, Herrel A, Kapsalas G, Vasilopoulou-Kampitsi M, Fabre A-C, Foufopoulos J, Donihue CM, 2019. Habitat shapes the thermoregulation of Mediterranean lizards introduced to replicate experimental islets. J Therm Biol 84:368-374. DOI: 10.1016/j.jtherbio.2019.07.032

Paulissen MA, 2008. Spatial learning in the little brown skink, *Scincella lateralis*: the importance of experience. Anim Beh 76:135-141. DOI: :10.1016/j.anbehav.2007.12.017

Pinheiro JC, Bates, DM, 2000. Mixed-effects models in S and S-PLUS, New York: Springer New York.

Powell BJ, Leal M, 2014. Brain organization and habitat complexity in *Anolis* lizards. Brain Behav Evol 84:8-18. DOI: 10.1159/000362197

Quadros ALS, Barros F, Blumstein DT, Meira VH, Nunes JACC, 2019. Structural complexity but not territory sizes influences flight initiation distance in a damselfish. Mar Biol 166. DOI: 10.1007/s00227-019-3508-2

Quinn JL, Cole EF, Reed TE, Morand-Ferron J, 2016. Environmental and genetic determinants of innovativeness in a natural population of birds. Philosophical Transactions of the Royal Society London B 371. DOI: 10.1098/rstb.2015.0184

R Team 2018. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Reale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO, 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society London B 365:4051-4063. DOI: 10.1098/rstb.2010.0208

Rodriguez-Prieto I, Martin J, Fernandez-Juricic E, 2011. Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. Proc Royal Soc B 278:266-273. DOI: 10.1098/rspb.2010.1194

Roth TC, LaDage LD, Pravosudov VV, 2010. Learning capabilities enhanced in harsh environments: a common garden approach. Proc Royal Soc B 277:3187-3193. DOI: 10.1098/rspb.2010.0630

Safi K, Dechmann DK, 2005. Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). Proc Royal Soc B 272:179-186. DOI: 10.1098/rspb.2004.2924

Shaw RC, Schmelz M, 2017. Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. Anim Cogn 20:1003-1018. DOI: 10.1007/s10071-017-1135-1

Shumway CA, 2008. Habitat complexity, brain, and behavior. Brain Behav Evol 72:123-134. DOI: 10.1159/000151472

Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372-378. DOI: 10.1016/j.tree.2004.04.009

Sih A, Del Giudice M, 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc Lond B Biol Sci 367:2762-2772. DOI: 10.1098/rstb.2012.0216

Siviter H, Charles Deeming D, Rosenberger J, Burman OH, Moszuti SA, Wilkinson A, 2017a. The impact of egg incubation temperature on the personality of oviparous reptiles. Anim Cogn 20:109-116. DOI: 10.1007/s10071-016-1030-1

Siviter H, Deeming DC, van Giezen MFT, Wilkinson A, 2017b. Incubation environment impacts the social cognition of adult lizards. R Soc Open Sci 4:170742. DOI: 10.1098/rsos.170742

Smaers J, Rothman R, Hudson D, Balanoff A, Beatty B, Dechmann D, de Vries D, Dunn J, Fleagle J, Gilbert C, 2021. The evolution of mammalian brain size. Science Advances 7:eabe2101. 10.1126/sciadv.abe2101

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L, 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci USA 102. DOI: 10.1073_pnas.0408145102

Sorato E, Zidar J, Garnham L, Wilson A, Lovlie H, 2018. Heritabilities and co-variation among cognitive traits in red junglefowl. Philosophical Transactions of the Royal Society London B 373. DOI: 10.1098/rstb.2017.0285.

Steck M, Snell-Rood EC, 2018. Specialization and accuracy of host-searching butterflies in complex and simple environments. Behav Ecol 29:486-495. DOI: 10.1093/beheco/ary001

Stoffel MA, Nakagawa S, Schielzeth H, Goslee S, 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol 8:1639-1644. DOI: 10.1111/2041-210X.12797

Storks L, Powell BJ, Leal M, 2020. Peeking inside the lizard brain: Neuron numbers in anolis and its implications for cognitive performance and vertebrate brain evolution. Integrative and Comparative Biology. DOI: 10.1093/icb/icaa129

Szabo B, Noble DW, Whiting MJ, 2019a. Context-specific response inhibition and differential impact of a learning bias in a lizard. Anim Cogn 22:317-329. DOI: 10.1007/s10071-019-01245-6

Szabo B, Whiting MJ, 2020. Do lizards have enhanced inhibition? A test in two species differing in ecology and sociobiology. Behav Process 172:104043. DOI: 10.1016/j.beproc.2020.104043

Szabo B, Whiting MJ, Noble DWA, 2019b. Sex-dependent discrimination learning in lizards: A meta-analysis. Behav Process 164:10-16. DOI: 10.1016/j.beproc.2019.04.002

Tebbich S, Stankewitz S, Teschke I, 2012. The relationship between foraging, learning abilities and neophobia in two species of Darwin’s finches. Ethology 118:135-146. DOI: 10.1111/j.1439-0310.2011.02001.x

Tebbich S, Taborsky M, Fessl B, Dvorak M, 2002. The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). Ecol Lett 5:656-664. DOI: 10.1046/j.1461-0248.2002.00370.x

Tebbich S, Teschke I, 2014. Coping with uncertainty: woodpecker finches (*Cactospiza pallida*) from an unpredictable habitat are more flexible than birds from a stable habitat. PLOS ONE 9:e91718. DOI: 10.1371/journal.pone.0091718

Tello-Ramos MC, Branch CL, Kozlovsky DY, Pitera AM, Pravosudov VV, 2019. Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. Anim Beh 147:129-136. DOI: 10.1016/j.anbehav.2018.02.019

Therneau TM, 2015. coxme: mixed effects Cox models. R package version 2.2-3.

Therneau TM, Lumley T, 2015. Package "survival". Survival analyses.

Udino E, Perez M, Carere C, d'Ettorre P, 2017. Active explorers show low learning performance in a social insect. Curr Zool 63:555-560. DOI: 10.1093/cz/zow101

Valakos ED, Pafilis P, Sotiropoulos K, Lymberakis P, Maragou P, Foufopoulos J, 2008. The Amphibians and Reptiles of Greece. Frankfurt am Main: Chimaira.

Vardi R, Goulet CT, Matthews G, Berger-Tal O, Wong BBM, Chapple DG, 2020. Spatial learning in captive and wild-born lizards: heritability and environmental effects. Behav Ecol Sociobiol 74. DOI: 10.1007/s00265-020-2805-6

Vicente NS, Halloy M, 2017. Interaction between visual and chemical cues in a *Liolaemus* lizard: a multimodal approach. Zoology 125:24-28. DOI: 10.1016/j.zool.2017.07.006

Vila Pouca C, Mitchell DJ, Lefèvre J, Vega-Trejo R, Kotrschal A, 2021. Early predation risk shapes adult learning and cognitive flexibility. Oikos 130: 1477-1486. DOI: 10.1111/oik.08481

White GE, Brown C, 2014. Cue choice and spatial learning ability are affected by habitat complexity in intertidal gobies. Behav Ecol 26:178-184. DOI: 1 0.1093/beheco/aru178

White GE, Brown C, 2015. Microhabitat use affects goby (Gobiidae) cue choice in spatial learning task. J Fish Biol 86:1305-1318. DOI: 10.1111/jfb.12638

Zidar J, Balogh A, Favati A, Jensen P, Leimar O, Sorato E, Lovlie H, 2018. The relationship between learning speed and personality is age- and task-dependent in red junglefowl. Behav Ecol Sociobiol 72:168. DOI: 10.1007/s00265-018-2579-2

FIGURE LEGENDS

Fig. 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).

Fig. 2 (Adjusted) repeatability of behavioral 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: $N_{\text{complex}} = 66$, $N_{\text{simple}} = 72$, exploration: $N_{\text{complex}} = 65$, $N_{\text{simple}} = 71$, aggression: $N_{\text{complex}} = 35$, $N_{\text{simple}} = 34$. Significance levels according to a likelihood-ratio test are indicated as follows: : '°' $p < 0.10$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

Fig. 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. $N_{\text{complex}} = 62$, $N_{\text{simple}} = 67$.

Fig. 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. $N_{\text{complex-left}} = 32$, $N_{\text{complex-right}} = 30$, $N_{\text{simple-left}} = 32$, $N_{\text{simple – right}} = 35$, $N_{\text{complex -18}} = 28$, $N_{\text{complex – 19}} = 34$, $N_{\text{simple – 18}} = 32$, $N_{\text{complex – 19}} = 35$.

Fig. 5 Overview of cognitive – behavioral 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 S3. Sample sizes were as follows: $N_{\text{complex}} = 57$ & $N_{\text{simple}} = 60$, 30 and 29 males respectively. Note that all regressions with aggression as predictor were solely performed using data of males.

Fig. 6 Associations between cognitive traits (a-c) and personality and cognition (d-f) 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 table S3.

TABLES

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

Behaviors		**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

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
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

Table 2. (continued)

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 **(box-cox: λ = 0.3)**	Habitat	$F_{1,3} = 0.35$	0.60
	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
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

Table 2. (continued)

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°

Table 3. Principal Component Analysis of the behaviors 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**	

SUPPLEMENTARY FILES

ESM_1. Supplementary results (three tables) (.docx file).

ESM_2. Overview of all behavioral data used for this study (.xlsx file).

Fig. 1

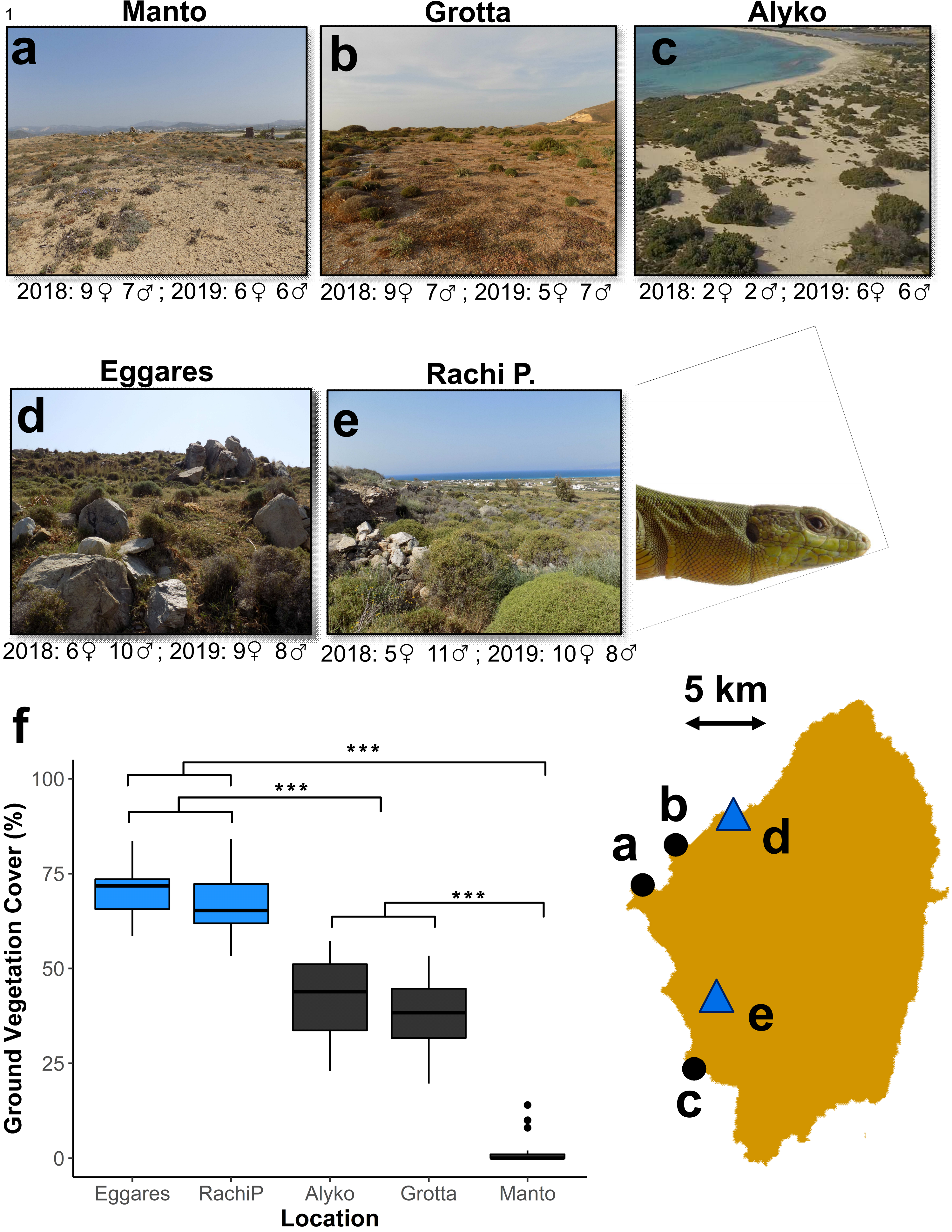
Manto
a
2018: 9♀ 7♂; 2019: 6♀ 6♂
Grotta
b
2018: 9♀ 7♂; 2019: 5♀ 7♂
Alyko
c
2018: 2♀ 2♂; 2019: 6♀ 6♂
Eggares
d
2018: 6♀ 10♂; 2019: 9♀ 8♂
Rachi P.
e
2018: 5♀ 11♂; 2019: 10♀ 8♂
f
***
***
***
100
75
50
25
0
Ground Vegetation Cover (%)
Eggares
RachiP
Alyko
Grotta
Manto
Location
5 km
a
b
c
d
e

Fig. 2 Revised

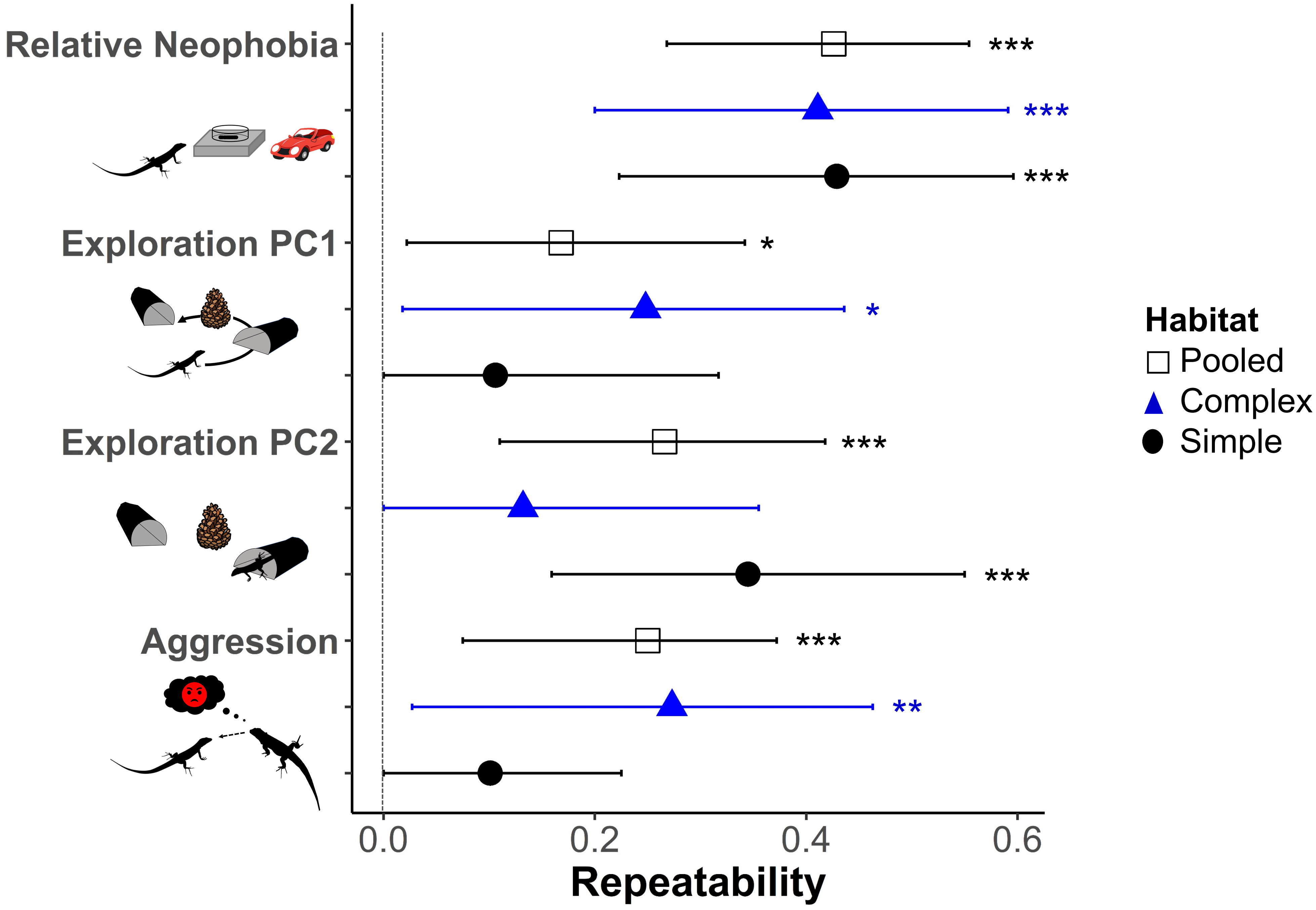

Fig. 3

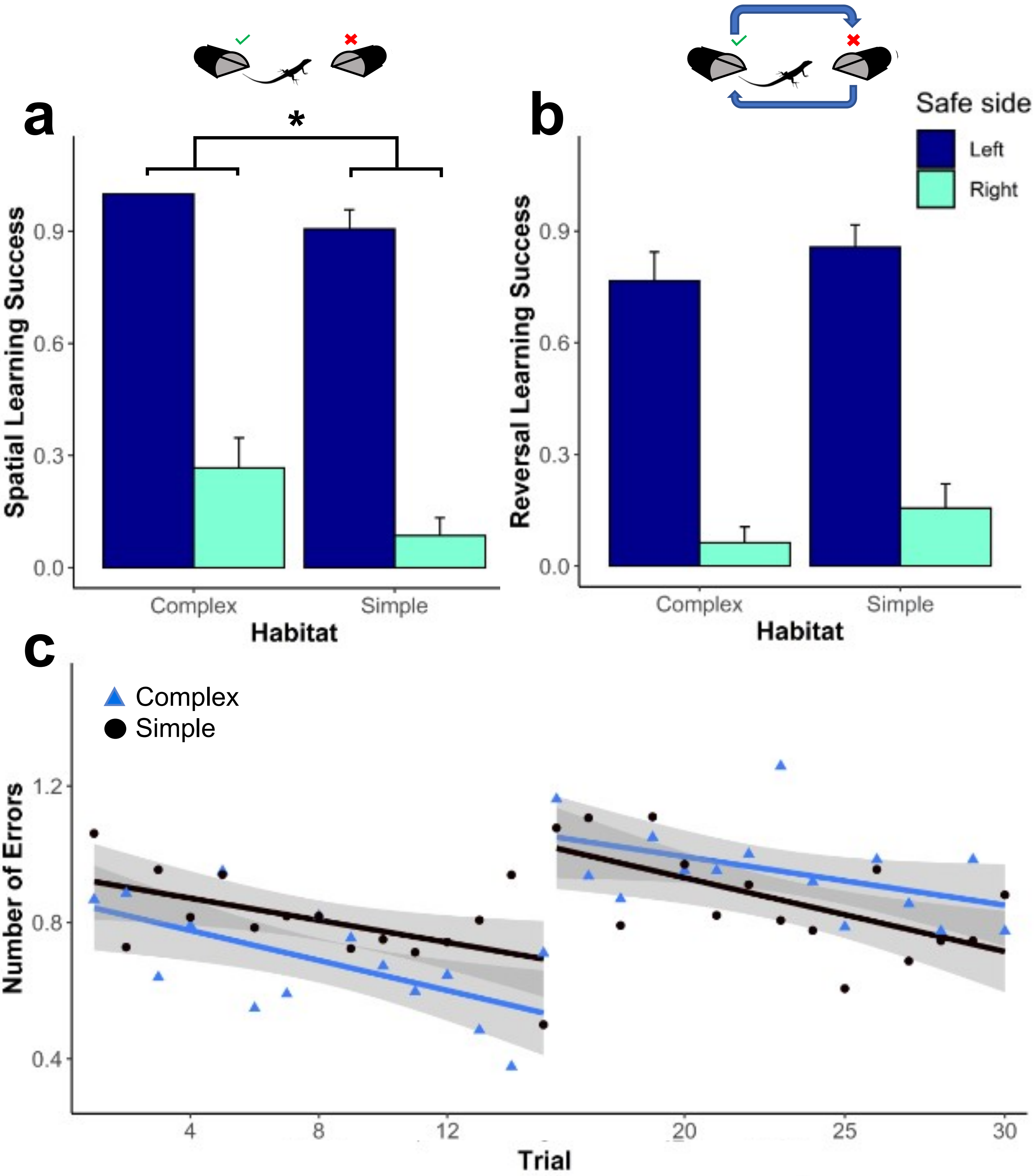
a
*
Spatial Learning Success
0.0
0.3
0.6
0.9
Complex
Simple
Habitat
b
Reversal Learning Success
0.0
0.3
0.6
0.9
Complex
Simple
Habitat
Safe side
Left
Right
c
Complex
Simple
Number of Errors
0.4
0.8
1.2
4
8
12
20
25
30
Trial

Fig. 4

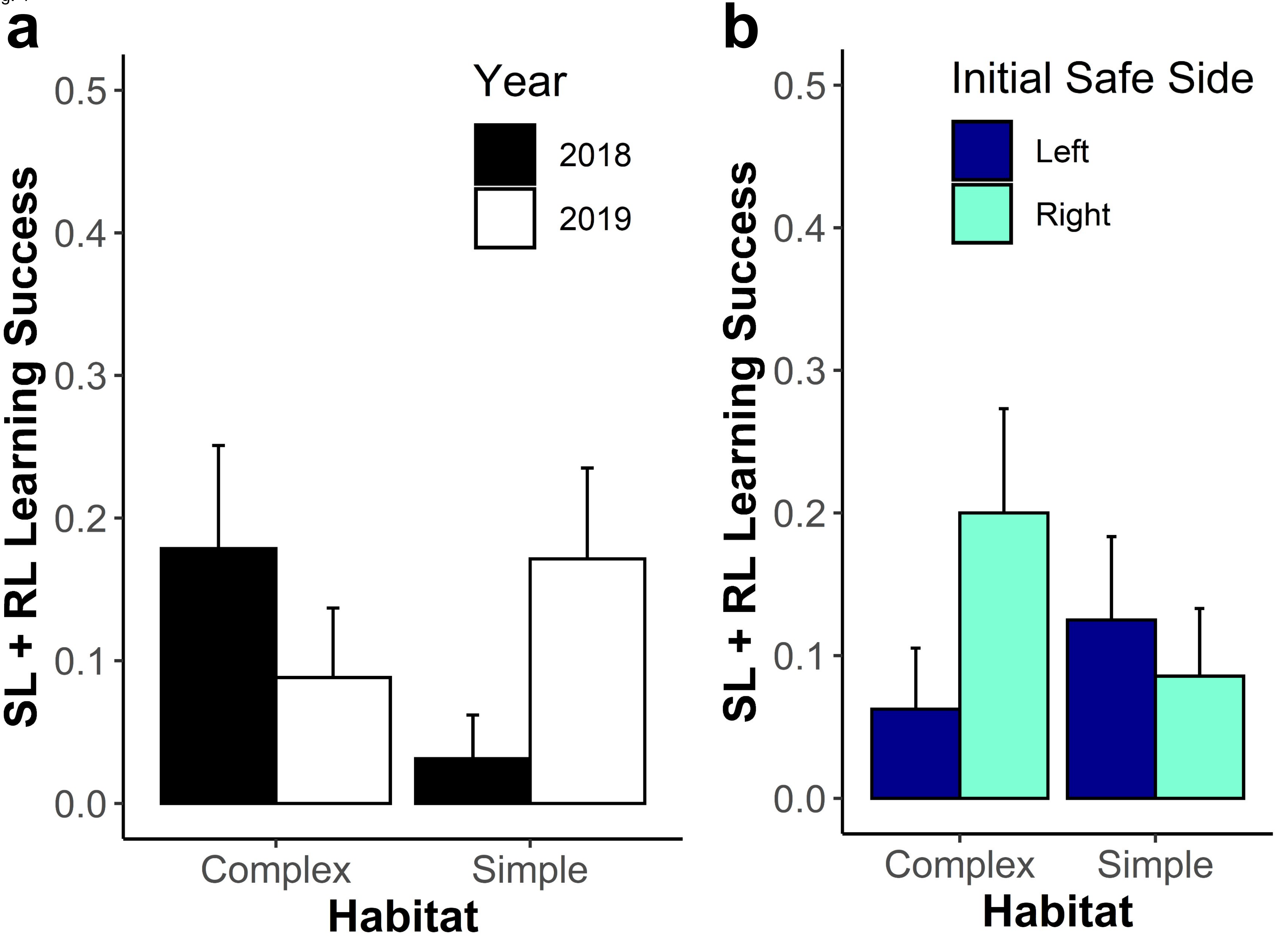
a
SL + RL Learning Success
0.5
0.4
0.3
0.2
0.1
0.0
Year
2018
2019
Complex
Simple
Habitat
b
SL + RL Learning Success
0.5
0.4
0.3
0.2
0.1
0.0
Initial Safe Side
Left
Right
Complex
Simple
Habitat

Fig. 5 Revised

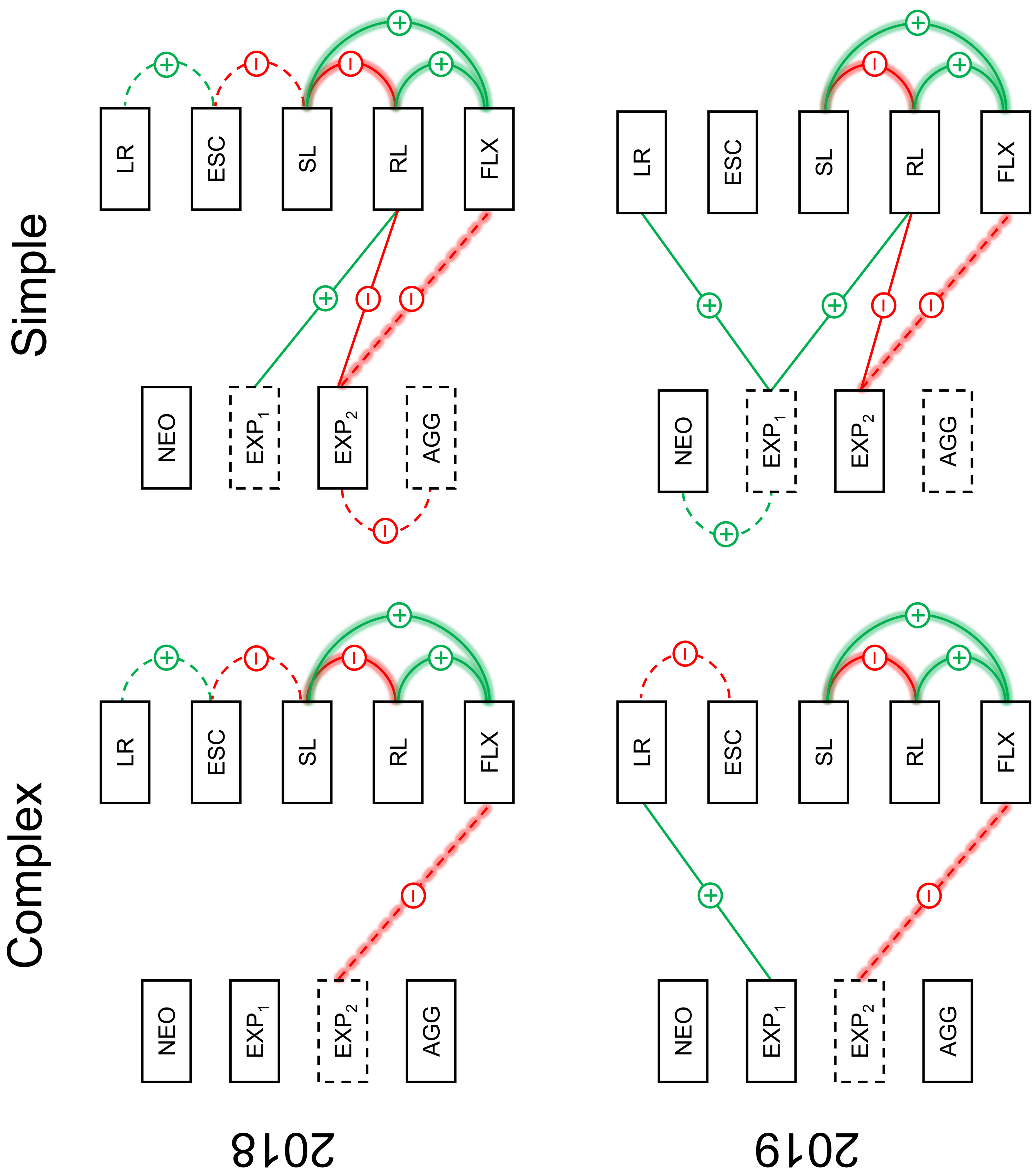

Fig. 6 Revised