



## Creatures of habit: similar but more repeatable behaviours in insular compared with mainland lizards

Ioanna Gavriilidi <sup>a, b, \*</sup> , Simon Baeckens <sup>c, a</sup> , Panayiotis Pafilis <sup>b, d</sup> ,  
Raoul Van Damme <sup>a</sup> 

<sup>a</sup> Functional Morphology Lab, Department of Biology, University of Antwerp, Antwerp, Belgium

<sup>b</sup> Section of Zoology and Marine Biology, Department of Biology, National and Kapodistrian University of Athens, Athens, Greece

<sup>c</sup> Earth and Life Institute, UCLouvain, Louvain-la-Neuve, Belgium

<sup>d</sup> Museum of Zoology, National and Kapodistrian University of Athens, Athens, Greece

### ARTICLE INFO

#### Article history:

Received 30 April 2025

Initial acceptance 16 June 2025

Final acceptance 24 November 2025

Available online xxx

MS. number: 25-00274R

#### Keywords:

aggression  
behaviour  
cognition  
evolution  
islands  
lizard  
personality  
*Podarcis erhardii*

Island habitats often differ markedly from those on the mainland in many biotic and abiotic factors. Typically, they harbour fewer predator, competitor and prey species and resources tend to be scarcer or more variable. In response, many island dwelling species have evolved a series of morphological, physiological and life-history adaptations, collectively referred to as 'island syndrome'. Although morphological and life-history island-induced trait shifts are particularly well documented, the effects of insularity on behaviour have attracted much less attention. In this study, we examined the effects of insularity on two putatively interrelated behavioural domains: cognition and personality. We compared cognitive and personality-related traits of Aegean wall lizards, *Podarcis erhardii*, from several mainland, island and small islet populations. We anticipated that the ecological peculiarities of insular environments would induce convergent changes in the behaviour of island lizards. However, we found few clear or consistent shifts in cognitive or personality trait means that were linked to insularity. One notable exception was the discernible decrease in the aggressiveness of insular lizards compared with their mainland counterparts, suggesting that high population densities on islands alter the economics of territorial defence. However, we observed recurrent differences in behavioural variation: insular lizards exhibited higher repeatability (higher among- and lower within-individual variation) in their behavioural traits (predominantly aggressiveness, risk-taking and sociability). This suggests increased behavioural specialization and reduced flexibility in insular populations compared with mainland populations. Our findings highlight the complexity of behavioural evolution in insular systems and suggest that, unlike morphological and life-history traits, behavioural responses to insularity may be more variable and nuanced than previously assumed.

© 2026 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Islands often differ markedly from the mainland in a variety of biotic and abiotic factors. Owing to their smaller size and distinct boundaries, they typically support fewer predator, competitor and prey species (Losos & Ricklefs, 2009; MacArthur & Wilson, 1967). Consequently, insular animal populations often reach much higher densities than conspecific populations on the mainland (Buckley & Jetz, 2007; Case et al., 1979; MacArthur et al., 1972). However, resource availability on islands tends to be lower or more variable (Blanco et al., 2014; Janzen, 1973; but see Sale & Arnould, 2013). Therefore, in response to the peculiarities of insular conditions,

many insular populations have evolved a number of morphological, physiological and life-history adaptations, collectively known as 'island syndrome' (Adler & Levins, 1994; Baeckens & Van Damme, 2020 and references therein). Indeed, a steadily increasing body of evidence documents how a wide array of insular species have different body dimensions, occupy wider trophic niches, lose their locomotor abilities and exhibit reduced fecundity and longer lifespan compared with their mainland relatives (reviewed in Adler & Levins, 1994; Baeckens & Van Damme, 2020; Jezierski, Smith, & Clegg, 2024; Lomolino et al., 2013; Losos & Ricklefs, 2009).

However, despite extensive research into morphological and life history island-induced trait shifts, the effects of insularity on behaviour remain largely unexplored (Gavriilidi et al., 2022). One notable exception is the documented phenomenon of 'island

\* Corresponding author.

E-mail address: [ioanna.gavriilidi@uantwerpen.be](mailto:ioanna.gavriilidi@uantwerpen.be) (I. Gavriilidi).

tameness', whereby insular prey species often fail to recognize or respond adequately to predators (Cooper Jr, Pyron, & Garland, 2014; Darwin, 1839). However, other behavioural domains, including cognition (sensu Dukas, 2004; Shettleworth, 2009) and personality (sensu Dall et al., 2004; 'broad-sense definition', Réale et al., 2010), have received very little attention. This is unfortunate because cognitive functions and personality traits have important effects on the way animals negotiate their socio-ecological environments (Dunbar & Shultz, 2007; Jolly, 1966; Mettke-Hofmann, 2014; Parker & Gibson, 1977; Réale et al., 2007; Sih & Del Giudice, 2012; Sih et al., 2004; Sol, 2009; Wolf & Weissing, 2012; Wooster et al., 2024). For example, there are certain personality traits that may reduce individuals' risk of predation and increase their competitive ability, reproductive success and probability of survival (e.g. Cole & Quinn, 2011; Cote et al., 2008; Sinn et al., 2006; Smith & Blumstein, 2008). In some animals, superior cognition has been associated with greater foraging efficiency (e.g. González-Gómez et al., 2011), enhanced body condition (e.g. Huebner et al., 2018), higher survival rates (reviewed in Rochais et al., 2022), increased reproductive output (e.g. White et al., 2022) and invasion success (reviewed in Szabo et al., 2020), indicating selection advantages for superior cognition.

However, there is a high energy cost of developing and maintaining the nervous tissues that form the substrate for cognitive functions (Aiello & Wheeler, 1995; Isler & van Schaik, 2009; Laughlin et al., 1998). Depending on the spatiotemporal context, personality traits may also be disadvantageous and bear fitness costs (Dingemans et al., 2004; Smith & Blumstein, 2008). However, natural selection can be expected to bestow animals with the correct amount of cognitive power and type of behaviours to survive in their specific environments.

Aspects of behavioural phenotypes are often interrelated (Dougherty & Guillette, 2018; Goulet et al., 2018; Sih & Del Giudice, 2012); as such, personality and cognitive traits may experience a shared evolutionary fate on islands. For example, behavioural traits (e.g. aggression, boldness, exploration, sociability and neophobia) are often found to covary, giving rise to behavioural syndromes (reviews in Conrad et al., 2011; Sih et al., 2004). In many species, these traits have also been linked to cognitive performance (e.g. birds: Guillette et al., 2009; fish: Lucon-Xiccato & Bisazza, 2017; mammals: Mazza et al., 2018, Shultz & Dunbar, 2022; reptiles: Carazo et al., 2014), albeit in varied ways (Dougherty & Guillette, 2018). A small number of these behavioural traits have also been considered as potential components of the island syndrome (e.g. aggression, Adler & Levins, 1994; risk sensitivity, Cooper Jr et al., 2014); as such, insular conditions may impose indirect selection on cognitive traits by affecting the associated behavioural traits and vice versa.

Although there is a lack of empirical evidence, it is plausible that cognitive and personality differences between mainland and island populations exist and may arise through multiple pathways (Gavriilidi et al., 2022). If cognitive abilities have an influence on an individual's capacity to colonize new or challenging environments (Amiel et al., 2011; Sol et al., 2005), such as islands, then insular populations may already differ from their mainland counterparts owing to a selective filtering process that reduces the range of behavioural phenotypes found in island populations. Once a population is established, the unique ecological pressures could drive developmental, phenotypically plastic or genetic changes in individual's cognition that, depending on the peculiarities of the island system, either favour or constrain cognitive abilities. Potentially, poor or erratic food availability (e.g. on small islands) may select against the allocation of energy into expensive neuronal tissue, thus favouring individuals with smaller brains and lower cognitive capacity (Heldstab et al., 2022; van Woerden et al.,

2010). The reduction in predation and interspecific competition may likewise reduce selection for performant brains (Kotrschal et al., 2015; Reichert & Quinn, 2017; but see Stankowich & Romero, 2017), leading to cognitive decline on islands. Increased inbreeding, a common feature of small-island populations (Frankham, 1998; Sherpa et al., 2024), may further diminish cognitive abilities (Gavriilidi & Van Linden, 2024). However, higher population densities may drive selection towards larger brains capable of coping with increased social complexity (following the assumption that higher densities increase social complexity; Hemelrijk, 2017). Furthermore, in insular environments, animals often face challenging situations and must exploit novel or more diverse food sources; this is hypothesized to promote the evolution of larger brains and more well-developed cognitive skills (Sayol et al., 2018). Any directional selection on islands could further reduce behavioural variation among insular animals. Therefore, despite the potential cognitive divergence between mainland and island populations, comparative studies remain underutilized as a framework for testing cognitive evolution.

Similarly, certain personality types may influence individuals' movement, activity and dispersal tendencies, thereby increasing their chances of establishing in new habitats or surviving in challenging habitats (Chapple et al., 2012; Spiegel, Leu, Bull, & Sih, 2017), such as islands. Once a population is established, the same ecological pressures (limited or erratic food availability, relaxed predation and increased population density) that act on cognition may also favour specific personality types. For example, a poor nutritional environment (i.e. low protein intake) resulted in less aggressive phenotypes in southern field crickets that were less active during courting (*Gryllus bimaculatus*; Han & Dingemans, 2017), whereas high-predation regimes selected against risk-taking behaviour in salmonid fishes (Biro et al., 2004). Moreover, these ecological pressures may influence not only the average levels of personality traits but also their correlations (i.e. behavioural syndromes). Indeed, populations of three-spined sticklebacks, *Gasterosteus aculeatus*, exposed to high predation exhibited a behavioural syndrome, characterized by correlated aggressiveness, activity and exploration, which was weakened or absent in populations experiencing lower predation pressure (Dingemans et al., 2007).

In this study, we investigated the effects of insularity on a suite of cognitive and personality-related traits in Aegean wall lizards, *Podarcis erhardii*, by comparing mainland and insular populations. We hypothesized that mainland and island lizard populations would differ in their average cognitive performance and personality traits, as well as the correlations between these traits, and that these differences would be pronounced in smaller, more isolated islets, as the populations would experience the largest ecological shift relative to mainland and larger islands (Whittaker & Fernández-Palacios, 2007).

## METHODS

### *Study Species and System*

*Podarcis erhardii* is a diurnal, ground-dwelling lacertid that has an adult snout-vent-length (SVL) of up to 75 mm (Valakos et al., 2008). Native to the Balkans, it inhabits a variety of semi-open environments from rocky islets with xeric vegetation to continental mountaintops (Valakos et al., 2008). Owing to the gradual fragmentation of its range since the Miocene, *P. erhardii* now includes more than 60 small, isolated, island populations that have undergone substantial morphological and genetic differentiation (Hurston et al., 2009; Poulakakis et al., 2003).

In the summers of 2021, 2022 and 2023, we caught a total of 219 adult lizards (males:  $N = 191$ , mean SVL = 64.38 mm,

range = (54.71, 80.21), females:  $N = 28$ , mean SVL = 63.91 mm, range = (52.74, 79.14) from two mainland ( $N = 67$ ; Parnitha and Evia), two large island ( $N = 36$ ; Naxos: 430 km<sup>2</sup>; Anafi: 40 km<sup>2</sup>) and five small islet populations ( $N = 116$ ; Parthenos, Fidoussa, Aspronissi, Glaronissi and Megalo Fteno; <1 km<sup>2</sup>; Fig. 1). To minimize interference with female pregnancies, we aimed to study males only. However, in some populations, it was necessary to include females to increase the sample size (Table S1 in supplementary material). Lizards were sampled from dense shrublands with scattered trees on the mainland, whereas those from insular populations were captured in rocky habitats, including stone walls, dominated by phrygana vegetation. Mainland and insular wall lizard populations likely experience very different ecological conditions owing to differences in predation pressure (smaller predator communities on islands) and intraspecific competition (higher densities on islands) (Brock et al., 2015; Foufopoulos et al., 2023; Pafilis et al., 2009; Table S1 in supplementary material).

The lizards were housed individually in plastic terraria (57 × 39 × 42 cm) with opaque walls, containing a sandy substrate, enrichment material (small stones and clay shelters) and water bowls. A 65 W bulb, suspended above each terrarium, provided light and heat between 0800 and 1800 hours. The lizards had ad libitum access to fresh water and were fed one mealworm (*Tenebrio molitor*) dusted with multivitamin powder each day. Before the experiments were started, all lizards were permitted a 2-day acclimation period in their home terrarium. All experimental procedures were conducted within a brief captivity period no longer than one month, after which the lizards were returned in good health to their original capture sites.

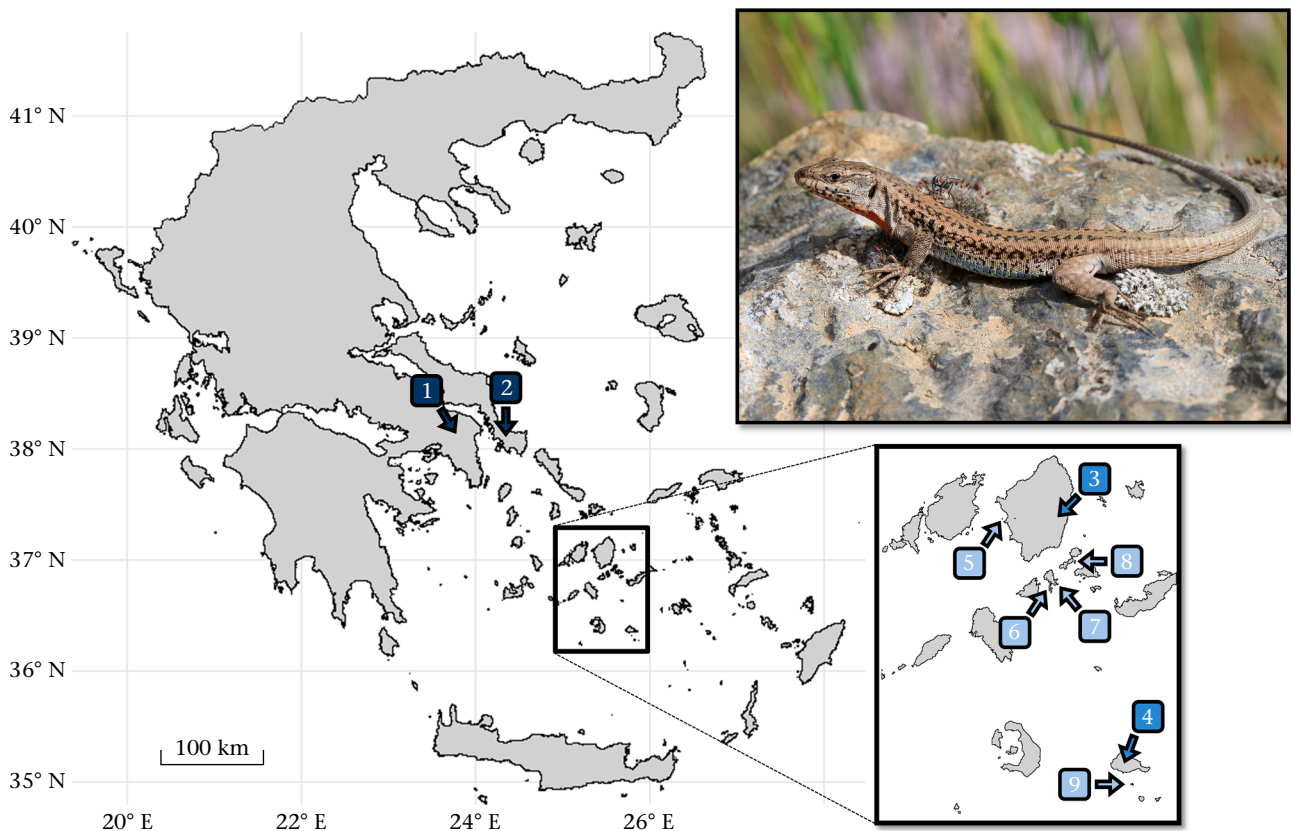
## Experimental Procedures

We assessed the behavioural traits of the lizards using various experimental settings under controlled conditions; specifically, we measured five personality-related behaviours (aggressiveness, risk-taking, exploratory behaviour, neophobia and sociability) and four cognitive traits (spatial and reversal learning, inhibitory control and problem-solving ability). Most traits were assessed between 0900 and 1800 hours, when lizards are most active. Prior to testing, the lizards were allowed to thermoregulate freely in their home enclosures for at least one hour, to ensure their body temperatures were within the preferred range. Heat bulbs were left on throughout the experiments to maintain the optimal thermal conditions. To minimize external disturbances, the researcher was not present in the room during most experimental trials. All trials were recorded on video, and lizard behaviours were quantified using Solomon Coder software (Péter, 2017; RRID:SCR\_016041). To reduce stress from unnecessary handling, all experiments were conducted in the lizards' home terraria. To standardize experimental procedures across populations, lizards were tested in a consistent sequential order.

## Personality-Related Assays

### Aggressiveness

Aggressiveness was estimated by scoring the lizards' behaviour in response to their mirror image (similar to Scali et al., 2019). At the start of each trial, water bowls and food were removed from the home terrarium and a mirror (38 cm × 30 cm) was introduced



**Figure 1.** Sites of origin of the lizards studied. Mainland Greece (dark blue): 1. Mountain Parnitha, Attica, 2. Mountain Ochi, Evia, Aegean archipelago, islands (medium blue): 3. Naxos, 4. Anafi and smaller islets (light blue): 5. Parthenos, 6. Fidoussa, 7. Aspronissi, 8. Glaronissi, 9. Megalo Fteno. An image of the Aegean wall lizard, the study species, is displayed in the top right corner (photo credit: Lefteris Stavarakas).

against one of its walls. Behaviour was recorded for the 10 min immediately after the mirror was introduced. Each lizard was tested three times, with one trial on each of 3 consecutive days. For each trial, the side of the terrarium in which the mirror was placed was randomly selected and we recorded the number of biting attempts directed at the mirror image.

#### *Risk-taking*

Risk-taking was assessed in an antipredator context (Carter et al., 2012) and quantified as the latency to emerge from a shelter after a simulated predator attack (Carazo et al., 2014; Damas-Moreira et al., 2019). Each individual was tested once per day for 3 consecutive days. In each trial, the lizards were gently chased into a cardboard shelter (9 cm long and 4 cm high) by tapping their tail with a paintbrush. We then recorded the time taken for the lizard to peek their head out of the shelter; lizards that did not peek their head out of the shelter within 10 min were assigned the maximum score of 600 s.

#### *Exploratory behaviour*

Exploratory behaviour was measured by scoring the lizards' behaviour in a novel environment (Carter et al., 2012; Damas-Moreira et al., 2019). We temporarily removed the lizards from their home terraria, cleared their terraria and replaced the substrate with white sand. Then, we placed new shelters made of cardboard cups (9 × 4 cm) in each corner of the terrarium (four in total). Individual lizards were then placed back in the centre of their terrarium, underneath a transparent cover. After 2 min, the transparent cover was removed to allow the lizards to explore the terrarium freely, and their behaviour was recorded for 4 min. The time spent moving was recorded and assessed as a proxy of exploratory behaviour.

#### *Neophobia*

Neophobia was evaluated by observing changes in the lizards' foraging behaviour when a novel object (brightly coloured and artificial) was placed near a familiar food source (De Meester et al., 2022; Greenberg, 1983). We performed three neophobia trials, one on each of 3 consecutive days. Neophobia trials followed the same procedure as the inhibitory trials (see below, cognitive tests), with the exception that a novel object (a red toy car, two yellow glow sticks or a colourful clothespin, selected in a random order) was placed next to the Petri dish at the start of each trial. For each trial, we recorded the feeding latency as the time it took the lizard to touch the Petri dish after the mealworm and the novel object were introduced. Individuals that did not touch the Petri dish within 15 min were assigned the maximum latency (900 s). In each trial, we calculated individuals' neophobia score based on the normalized relative change ((−100%, +100%)) in their feeding latency when the novel object was present compared with the 'control' average feeding latency during inhibitory control (De Meester et al., 2022; Guido et al., 2017).

#### *Sociability*

Sociability was assessed as attraction towards the odour of conspecifics (Cote & Clobert, 2007; Léna et al., 2000) and was assessed for 10 consecutive days. Thirty minutes before the lights were switched off for the night, two identical shelters made of white clay were introduced into each lizard's home terrarium, placed in a random position each time to avoid any side biases. One shelter was sprayed with a solution of water containing faeces and shredded skin of several same-sex conspecifics from the same population; the other was sprayed with pure water (to standardize for humidity levels). We checked the shelters shortly after the lights were switched off in the evening and shortly before they

were switched on again the next morning (similar to Léna et al., 2000). A score of '1' was assigned if the lizards chose to hide under the scented shelter and '0' if they chose to hide under the shelter sprayed only with water.

#### *Cognitive Tasks*

##### *Spatial and reversal learning*

The lizards' spatial learning abilities were assessed using a spatial memory task during which lizards needed to learn the location of a safe hiding spot (similar to Font, 2019). Identical shelters (made of cardboard cups; 9 × 4 cm) were placed in each of the four corners of the lizards' home terraria (four in total). One shelter was randomly assigned as 'safe' for each lizard. Visual cues in (stickers) and around (wooden poles) each terrarium were provided to help lizards' orientation. Prior to the experiment, lizards were allowed 24 hours to acclimate to the shelters. Before the beginning of each trial, we removed water bowls and enrichment material from the terraria. At the beginning of a trial, each lizard was placed in the centre of the terrarium underneath a transparent cover for 2 min. After this familiarization period, the cover was lifted and the lizard was chased by gently tapping the base of its tail with a paintbrush. Chasing stopped when the lizard entered the correct ('safe') shelter or after 120 s if the lizard did not enter the safe shelter (after which the lizard was gently directed towards the assigned safe shelter). When the lizard made a wrong decision (i.e. entered an unsafe shelter), the unsafe refuge was lifted and the chasing continued. Each individual was tested four times per day, with at least 1 h in between trials, for 6 consecutive days. For each trial, we recorded the number of errors (i.e. number of times a lizard visited an unsafe shelter) and a successful score was given if the lizard's first choice was the safe shelter. Individuals were considered to have learnt the task if they were successful in four out of five consecutive trials (a robust learning criterion tested by an exact binomial test,  $P < 0.05$ ).

Immediately thereafter, lizards that successfully completed the learning criterion (i.e. had learnt the location of the safe shelter), were tested for reversal-learning capacity. In this reversal-learning test, the safe shelter became unsafe, and another, previously unsafe shelter became the safe shelter. Lizards were considered to have successfully reversed the learned information if they were successful in four out of five consecutive trials (binomial test,  $P < 0.05$ ). Lizards' reversal-learning ability was determined from the number of correct trials and the average number of errors during the reversal-learning trials.

##### *Inhibitory control*

The lizards' ability to exercise inhibitory control (Diamond, 2013) was tested with a detour task (Kabadayi, Bobrowicz, & Osvath, 2017) during which they had to surmount a transparent barrier to reach the prey. This required the suppression of their natural (but here, ineffective) behaviour of attacking their prey in a straight line. Lizards were tested for their ability to eat from a transparent Petri dish fixed on top of a wooden platform (10 × 10 × 1.5 cm) (similar to De Meester et al., 2022). To standardize motivation and avoid satiation, lizards were fed exactly one mealworm per day. Before each trial, we removed the water bowls and enrichment material from the lizards' home terraria and introduced the wooden platform with the Petri dish. After a 2 min familiarization period, a mealworm (0.10–0.20 g) was placed in the Petri dish, and the lizards were permitted 15 min to find and consume it. Each lizard was tested once per day for 5 consecutive days, although a second attempt was provided in case the lizard did not eat the mealworm during the first trial. For each trial, we recorded the lizards' feeding latency (i.e. the time it took lizards to

touch the Petri dish after the mealworm was introduced). We also noted the 'solving time', defined here as the time elapsed between the lizard first making contact with the Petri dish and grabbing the mealworm. Lizards that failed to overcome the barrier within the assigned 15 min were assigned the maximum time of 900 s. Individual performance in inhibition was determined by averaging the solving time in all valid trials (i.e. when the lizard touched the Petri dish; range of valid trials per individual = (2,10)).

#### *Problem-solving: lid removal task*

The problem-solving ability of the lizards was judged by their performance in a lid-removal task (De Meester et al., 2022; Leal & Powell, 2012). In this task, lizards had to remove an opaque plastic disc (6 cm in diameter) that was placed on top of a Petri dish fixed on a wooden platform (the same platform they were trained to eat from during the inhibitory control) to gain access to a mealworm (similar to De Meester et al., 2022). Similar to the inhibitory control task, lizards were fed one only worm per day to standardize motivation. A lizard successfully completed the task if it displaced the disc (e.g. by lifting or pushing it) and then immediately grabbed the prey. Lizards were tested three times and the number of times they solved the task (0, 1, 2 or 3) as well as the solving time (i.e. time between the lizard's first contact with the Petri dish and grabbing the prey) were recorded.

#### *Ethical Note*

This research was conducted under all necessary permits issued by the Greek Ministry of Environment (Permit numbers 2021: ΥΠΕΝ/ΔΔΔ/28501/968; 2022: ΥΠΕΝ/ΔΔΔ/12534/504; 2023: 64014653ΠΙ8-ΒΒΞ) and was approved by the Ethical Committee of the University of Antwerp (ECD-dossier 2022-09). We made all necessary adjustments to our protocols to minimize the stress of all animals involved in the experiments. Animals were caught by noosing, a technique commonly used for wall lizards, which minimizes handling time and stress. During experiments, disturbance and animal handling were minimized. Handling was performed by trained researchers (FELASA category C) in accordance with Finnish, Belgian and EU regulations governing the use of animals in research. The study also adhered to the ASAB/ABS Guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2023). All experiments were conducted in the lizards' home terraria, which provided ample space, enrichment material, opportunities for thermoregulation, food and ad libitum access to water. Although the use of a paintbrush to chase lizards during spatial and reversal learning may cause minor discomfort, the procedure is brief, does not inflict injuries and has been previously employed in numerous studies. Upon the completion of the experiments, all lizards were returned in good health to their original capture locations.

#### *Statistical Analysis*

All analyses were performed using R (version 4.4.2; R Core Team, 2024). To maximize the statistical power, we pooled data across the three sampling years, as preliminary analyses confirmed the absence of a significant year-effect. Given the absence of significant sex-related effects and the low number of females sampled, we also combined data from both sexes.

#### *Personality-Related Assays*

To examine the effect of insularity (mainland, island or islet) on aggression, risk-taking, exploratory behaviour, neophobia and sociability we used a series of Bayesian mixed effect models (BMMs)

with default weakly informative priors ('brms' package; Bürkner, 2017; chains = 4, iter = 4000, adapt\_delta = 0.99). In all models, scaled SVL was included as a fixed covariate, and individual ID nested within population was incorporated as a random effect. Exploratory behaviour values were square-root-transformed to improve model performance. In the case of risk-taking behaviour (measured as the time taken to peek out of a shelter), we included a binary censoring indicator (0: observed latencies, 1: right-censored observations at the maximum latency) to account for censoring (i.e. individuals that did not emerge within the observation window). The distribution family for each model was chosen based on the nature of the data and the performance of each model (aggression: negative binomial, risk-taking: lognormal, exploratory behaviour and neophobia: Gaussian, sociability: Bernoulli). Overall predictor effects were extracted directly from the model's summary, and the proportions of total variance attributable to among-individual (i.e. repeatability) and among-population differences were calculated using the variance components from each model (Dingemans & Dochtermann, 2013; Royauté & Dochtermann, 2021). We were unable to test the repeatability of exploratory behaviour as it was assessed in a single trial; as such, ID was not included in the model. Consequently, we could not determine whether exploratory behaviour could be considered a personality trait. Trait means were compared across insularity levels by estimating marginal means ('emmeans' package; Lenth, 2024). To compare behavioural variance components (i.e. among- and within-individual variance) across insularity levels, we re-fitted the same model for each behavioural trait, but included group-specific random effects allowing both among-individual and within-individual variance to differ by insularity (wherever applicable). For each variance component comparison across insularity levels, we calculated the posterior probability of a difference (Royauté & Dochtermann, 2021).

#### *Cognitive Assays*

Similar to the procedure used for personality-related assays, we used a series of BMMs with default weakly informative priors ('brms' package; Bürkner, 2017; chains=4, iter=4000, adapt\_delta=0.999) to assess whether insularity influenced performance in the spatial and reversal learning, inhibitory control and problem-solving tasks. For the spatial and reversal learning we used only the number of correct trials as response variables, as there was a strong correlation with the average number of errors in each case (spatial: Spearman's  $\rho = -0.84$ ,  $P < 0.005$ ; reversal: Spearman's  $\rho = -0.69$ ,  $P < 0.005$ ). Reversal learning was tested only for the subset of lizards that achieved the spatial learning criterion ( $N = 89$ ). For the inhibitory-control test, we used the average solving time (log-transformed) as the response variable. For the model investigating the effects of insularity on problem solving, we used a three-level factor to categorize how many times an individual lizard solved the lid removal task (0: never, 1: once, 2: twice or more) as the response variable. In all models, we included scaled SVL as a covariate and population as random effect. In each case, the distribution family was chosen based on the nature of the data and the model performance (spatial and reversal learning and inhibitory control: Gaussian, problem-solving: cumulative with 'probit' link). For all BMMs, overall predictor effects were extracted directly from the model summary and variance components were partitioned based on posterior draws from each model (Dingemans & Dochtermann, 2013; Royauté & Dochtermann, 2021). Comparisons across insularity levels were performed by estimating marginal means ('emmeans' package; Lenth, 2024). To compare cognitive trait variances across insularity levels, we re-fitted the same models and allowed the residual

variance to vary by insularity. For each variance comparison across insularity levels, we calculated the posterior probability of a difference (Royauté & Dochtermann, 2021).

### General Behavioural Profiles and Phenotypic Correlations

We employed a multivariate Bayesian mixed-effects modelling approach to investigate the differences in behavioural profiles among lizards from mainland, island and islet populations. All nine behavioural traits considered (aggressiveness, risk-taking, exploratory behaviour, sociability, neophobia, spatial learning, reversal learning, inhibitory control and problem solving) were included in a joint multivariate model ('brms' package; Bürkner, 2017). For aggressiveness, risk-taking and neophobia, we used the average across the three trials as the response variables; for sociability, we used the sum of all daily scores (i.e. 20 observations). To ensure normality, aggressiveness averages, risk-taking averages, and inhibitory control latencies were log transformed, whereas exploratory behaviour values were square-rooted. To align all behavioural traits on a comparable scale, all response variables were standardized (mean = 0, SD = 1) before entering the model. Subsequently, each trait was modelled as a function of insularity (mainland, island and islet), with a random intercept for population to account for the hierarchical structure of the data. Problem solving, an ordinal outcome, was modelled using a cumulative probit link. We used posterior means and 95% CrI to assess insularity effects across traits.

We then examined the phenotypic correlation structure of behavioural traits of lizards from mainland and insular origin. However, given the nature of our data (collected in sequential order with a varying number of repeated trials per trait) we were unable to decompose raw phenotypic correlations into among- and within-individual components (Dingemans & Dochtermann, 2013). Instead, we calculated Spearman rank correlation matrices ('Hmisc' package; Harrell Jr, 2024) based on the individual raw mean values of each behavioural trait separately for mainland, island and islet lizards, as well as for each individual population. To increase the sample size, we excluded reversal learning as only a subset of lizards were assayed. To statistically examine similarities between insularity- and population-level correlation matrices, we conducted a series of Mantel tests (999 permutations) using the 'vegan' package (Oksanen et al., 2024), applying the Benjamini–Hochberg correction for multiple comparisons.

## RESULTS

### Personality-Related Assays

The results of BMMs testing for the effects of insularity on each personality-related trait are summarized in Table 1 and Table S2 (supplementary material). Overall, insularity explained only a small proportion of the total variance (Fig. S1; supplementary material) and had few consistent effects on most personality-related traits, with the exception of aggression. Individual repeatability varied across behavioural traits and was generally higher in insular lizards than in mainland lizards (Table S2; Fig. 2), although statistical support for some traits, particularly neophobia, was weak.

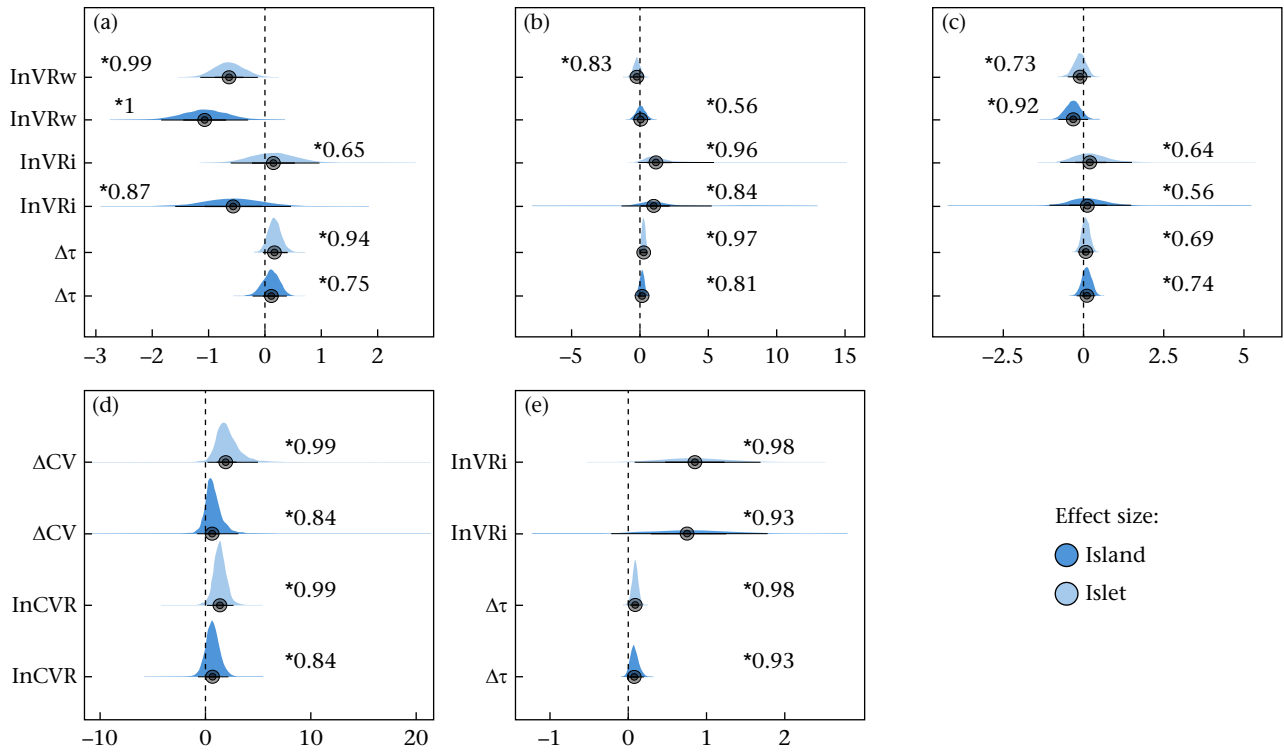
Mainland lizards exhibited higher aggression ( $\beta = 1.03$ , posterior SD = 0.46, 95% CrI = (0.17, 2.01)) than island lizards ( $\beta = -0.97$ , posterior SD = 0.67, 95% CrI = (-2.36, 0.30)) and, especially, islet lizards ( $\beta = -1.19$ , posterior SD = 0.56, 95% CrI = (-2.38, -0.14)) (Table 1; Fig. 3). The number of biting attempts increased somewhat with lizard body size ( $\beta = 0.26$ , posterior SD = 0.16, 95% CrI = (-0.06, 0.58)). Variability in aggressiveness (measured as the

**Table 1** Summary output of Bayesian mixed-effects models examining the effects of insularity (Island or Islet vs Mainland) and scaled body size (SVL) on behavioural traits

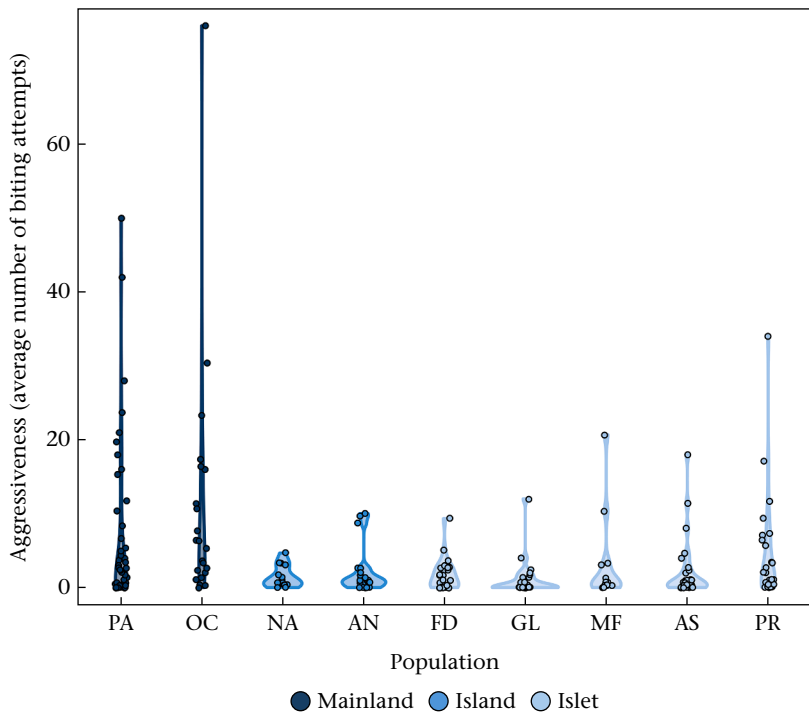
Trait	Island $\beta$ , SD, (95 % CrI)	Islet $\beta$ , SD, (95 % CrI)	SVL $\beta$ , SD, (95 % CrI)	Population variance (%), (95 % CrI)	Individual variance (%), (95 % CrI)	Variability across insularity levels
Aggressiveness	-0.97, 0.67, (-2.36, 0.3)	-1.19, 0.56, (-2.38, -0.14)	0.26, 0.16, (-0.06, 0.58)	2.7, (0.01, 12.8)	24.8, (12.7, 35.7)	CV <sub>M</sub> : 0.79, (0.24, 1.82) CV <sub>I</sub> : 1.53, (0.49, 3.76) CV <sub>V</sub> : 2.84, (1.34, 5.68) V <sub>M</sub> : 2.87, (2.04, 4.04) V <sub>I</sub> : 3.80, (2.43, 6.03) V <sub>V</sub> : 3.27, (2.47, 4.36) V <sub>M</sub> : 9.99, (7.08, 14.1) <sup>1</sup> V <sub>I</sub> : 3.04, (1.85, 4.93) <sup>1</sup> V <sub>V</sub> : 3.64, (2.78, 4.75) <sup>1</sup>
Risk-taking	0.27, 1.11, (-1.95, 2.58)	0.23, 0.93, (-1.61, 2.12)	0.06, 0.13, (-0.2, 0.33)	13.1, (2.53, 43.6)	12.9, (4.59, 24.5)	V <sub>M</sub> : 1921, (1452, 2556) V <sub>I</sub> : 1613, (1180, 2264) V <sub>V</sub> : 1862, (1569, 2215) V <sub>M</sub> : 3.58, (3.42, 3.82) V <sub>I</sub> : 3.92, (3.57, 4.52) V <sub>V</sub> : 3.95, (3.72, 4.25)
Exploratory behaviour	-0.29, 0.81, (-1.89, 1.33)	-1.13, 0.67, (-2.49, 0.3)	-0.17, 0.2, (-0.58, 0.22)	5.62, (0.02, 24.9)	NA	
Neophobia	-10.1, 13.9, (-37.27, 18.4)	5.91, 11.69, (-17.04, 29.9)	-2.15, 2.89, (-7.75, 3.62)	5.89, (0.12, 22.4)	32.5, (22.1, 42.6)	
Sociability	0.02, 0.27, (-0.53, 0.56)	-0.19, 0.22, (-0.65, 0.25)	-0.16, 0.07, (-0.31, -0.02)	0.75, (0, 4.5)	11.3, (8.43, 14.6)	

For each trait, Bayesian posterior estimates of the mean ( $\beta$ ) and standard deviation (SD) for each insularity level and for body size (scaled SVL) are reported, along with the associated 95 % credible interval (95 % CrI). The proportions of total variance attributable to populations and to individuals (i.e. individual repeatability) are presented as percentages (%) with the 95 % CrI, based on posterior predictions from the models. Posterior means of total individual-level variance, along with the 95 % CrI, are shown for each insularity group (mainland: V<sub>M</sub>; island: V<sub>I</sub>; islet: V<sub>V</sub>). For aggression, the coefficient of variation (CV) is reported instead of variance owing to differences in trait means.

<sup>1</sup> Posterior mean residual variances and 95 % credible intervals.



**Figure 2.** Effect sizes of variance differences in island (dark blue) and islet (light blue) lizards relative to mainland populations (dashed baseline) for (a,d) aggressiveness, (b) risk-taking, (c) neophobia and (e) sociability. Panels (a, b, c) show effect sizes of repeatability differences ( $\Delta\tau$ ), as well as log variance ratios of among-individual (InVRi) and within-individual (InVRw) variances. Panel (d) presents the effect sizes of differences in the coefficient of variation ( $\Delta CV$ ) and log ratios of the coefficient of variation (InCVR) in aggressiveness to account for differences in trait means across insularity levels. Panel (e) shows effect sizes of repeatability differences ( $\Delta\tau$ ) and log variance ratios of among-individual (InVRi) variances, as residual variance is fixed at  $\pi^2/3$  in models with the Bernoulli distribution. Numbers with asterisks (\*) indicate the posterior probabilities of a difference. For traits in which variance could not be partitioned into within- and between-individual components, effect sizes of residual variance differences are presented in Fig. S2 of the supplementary material.



**Figure 3.** Violin plots of lizards' average number of biting attempts towards their mirror image (considered a proxy of aggressiveness) by population (PA: Mountain Parnitha, OC: Mountain Ochi, NA: Naxos, AN: Anafi, FD: Fidoussa, GL: Glaronissi, MF: Megalo Fteno, AS: Aspronissi, PR: Parthenos) and coloured by insularity levels (mainland: dark blue, islands: medium blue, islets: light blue). Points represent raw values.

coefficient of variation; CV) was higher among insular lizards (islet: CV = 2.84, 95% CrI = (1.34, 5.68); island: CV = 1.53, 95% CrI = (0.49, 3.76)) than among mainland lizards (CV = 0.79, 95% CrI = (0.24, 1.82)) (Fig. 2).

### Cognitive Assays

The results for each cognitive trait are summarized in Table 2 and variance partitioning from BMMs is shown in Table S3 and Fig. S1 of the supplementary material. Other than the few exceptions detailed below, there was very little evidence for consistent effects of insularity on cognitive traits. The presence or direction of residual variance differences across insularity levels was trait specific (Table 2; Fig. S2).

A larger proportion of island lizards (64%) reached the spatial-learning criterion compared with their islet (42%;  $\chi^2_1 = 4.33$ ,  $P = 0.04$ ) and mainland (42%;  $\chi^2_1 = 3.52$ ,  $P = 0.06$ ) conspecifics. Similarly, a larger proportion of insular lizards (island: 52%; islet: 49%) achieved the reversal-learning criterion than their mainland conspecifics (29%); however, this difference was not statistically significant ( $\chi^2_2 = 2.41$ ,  $P = 0.30$ ). Otherwise, insularity did not influence spatial or reversal learning performance (Table 2).

In the inhibitory control task, mainland lizards ( $\beta = 1.93$ , posterior SD = 0.10, 95% CrI = (1.74, 2.15)) performed only marginally better (i.e. had shorter solving times) than islet lizards ( $\beta = 0.23$ , posterior SD = 0.13, 95% CrI = (-0.04, 0.47)) but not compared with island lizards ( $\beta = 0.08$ , posterior SD = 0.16, 95% CrI = (-0.25, 0.39); Table 2). Inhibitory control performance improved as body size increased ( $\beta = -0.12$ , posterior SD = 0.04, 95% CrI = (-0.21, -0.03)).

### General Behavioural Profiles and Phenotypic Correlations

In line with the above univariate analyses, multivariate Bayesian mixed-effects modelling did not reveal any consistent behavioural differentiations among mainland, island and islet lizards (Fig. S3; supplementary material). The magnitude of population-level variation differed across behavioural traits (range of SDs of population intercept: (0.23, 0.61); Table S4). Full model outputs from the multivariate Bayesian analysis are available in the supplementary material (Table S4).

Behavioural correlation matrices were only similar between island and islet lizards (Mantel's  $r = 0.47$ ,  $P = 0.02$ ), with no statistically significant similarities found with the mainland (mainland versus island: Mantel's  $r = -0.03$ ,  $P = 0.58$ ; mainland vs islet: Mantel's  $r = 0.29$ ,  $P = 0.11$ ). Overall, we found very few statistically significant correlations among behavioural traits (Fig. 4; Fig. S4,

supplementary material). Population pairwise comparisons revealed very little similarity, indicating that, independent of origin, populations largely differed in their behavioural correlation structures (Fig. S4; Table S5, supplementary material).

### DISCUSSION

Although we hypothesized that insular populations would diverge from their mainland counterparts in consistent and deterministic ways, our results suggest the reality is more nuanced. We expected that the particularities of island environments would lead to consistent, predictable shifts in behavioural trait means; however, this was observed only for aggressiveness, which decreased as insularity increased. Instead, we observed recurrent differences in the structure of variation for most behavioural traits (aggressiveness, risk-taking, neophobia and sociability): within-individual variance was generally lower and among-individual variance was generally higher in insular populations than in mainland populations. These findings suggest that individuals living on islands, and especially on islets, exhibit more repeatable behaviours or less behavioural flexibility, than individuals from the mainland. The variation on cognitive behavioural was more complex: residual variance was generally lower in islet populations, whereas island populations did not differ significantly from the mainland. Below, we consider possible reasons for the lack of effects of insularity on the average values and discuss possible drivers for the observed changes in variance composition.

#### *Insular Lizards are More Docile than Their Mainland Counterparts, but Otherwise Similar*

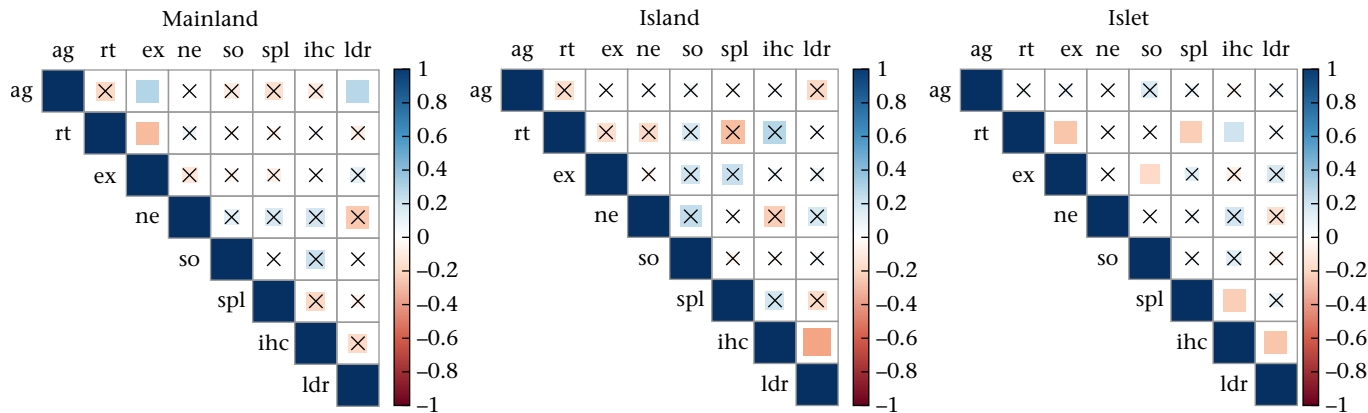
A reduction in aggressiveness is considered one of the manifestations of the 'island syndrome' (Adler & Levins, 1994). However, somewhat surprisingly, there have been few direct comparisons of aggression levels in mainland and insular animals (reviewed in Gavriilidi et al., 2022). Most of the supporting evidence is provided in insular rodent populations (Adler & Levins, 1994; Jette et al., 2020). In lizards, the picture is rather less clear; some studies report increased aggression on islands (e.g. in the Italian wall lizard, *Podarcis siculus*: Raia et al., 2010; and clouded anoles, *Anolis nebulosus*: Siliceo-Cantero et al., 2017) but other studies show opposite pattern (e.g. Agassiz's anole, *A. agassizi*: Rand et al., 1975; and chuckwalla, *Sauromalus spp*: Case, 1978, 1982; see Stamps & Buechner, 1985 for an early review).

Several hypotheses propose why insularity selects for lower levels of aggression. The resource hypothesis holds that the high

**Table 2**  
Summary output of Bayesian mixed effect models examining the effect of insularity (Island or Islet vs Mainland) and body size (SVL) on each cognitive trait

Trait	Island $\beta$ , SD, (95 % CrI)	Islet $\beta$ , SD, (95 % CrI)	SVL $\beta$ , SD, (95 % CrI)	Population variance (%), (95 % CrI)	Variability across insularity levels
Spatial learning	1.93, 2.08, (-2.24, 6.10)	0.64, 1.73, (-2.93, 4.21)	-0.36, 0.37, (-1.07, 0.36)	13.4, (0.87, 39.7)	$V_M$ : 19.8, (14.1, 27.9) $V_I$ : 21.1, (13.1, 33.9) $V_i$ : 16.4, (12.7, 21.3)
Reversal learning	3.20, 2.12, (-1.01, 7.41)	1.86, 1.82, (-1.66, 5.57)	0.49, 0.51, (-0.51, 1.48)	10.5, (0.05, 39.1)	$V_M$ : 11.7, (5.63, 24) $V_I$ : 26.7, (14.6, 47.9) $V_i$ : 12.2 (8.18, 18.3)
Inhibitory control	0.08, 0.16, (-0.25, 0.39)	0.23, 0.13, (-0.04, 0.47)	-0.12, 0.04, (-0.21, -0.03)	3.05, (0, 16.5)	$V_M$ : 0.35, (0.24, 0.49) $V_I$ : 0.35, (0.22, 0.57) $V_i$ : 0.24 (0.19, 0.31)
Problem solving	0.06, 0.35, (-0.64, 0.71)	-0.24, 0.29, (-0.81, 0.3)	0.14, 0.1, (-0.06, 0.33)	3.62 (0, 20.5)	NA

For each cognitive trait, Bayesian posterior estimates of the mean ( $\beta$ ) and standard deviation (SD) for each insularity level and for body size (scaled SVL) are reported, along with the associated 95 % credible interval (95 % CrI). The proportions of total variance attributable to populations are presented as percentages (%) along with the 95 % CrI. Mean posterior residual variances and the associated 95 % CrI are shown for each insularity group (mainland:  $V_M$ ; island:  $V_I$ ; islet:  $V_i$ ).



**Figure 4.** Spearman's correlation matrices of personality-related and cognitive traits (ag: aggression, rt: risk-taking, ex: exploratory behaviour, ne: neophobia, so: sociability, spl: spatial learning, ihc: inhibitory control, ldr: problem solving) of mainland, island and islet lizards. The square size indicates the magnitude of the correlation coefficients and the square colour and intensity represent, respectively, the direction and strength of the correlation (shades of blue: positive correlations, shades of red: negative correlations). Nonsignificant correlations ( $P \geq 0.05$ ) are indicated with a cross.

density of resources on islands renders territorial behaviour and the accompanying aggressiveness unnecessary (Stamps & Buechner, 1985). Resources may be denser on islands than on the mainland owing to the paucity of competitor species (Buckley & Jetz, 2007). The defence hypothesis argues that animals on islands may abandon or reduce territoriality because of increased defence costs (Stamps & Buechner, 1985). High population densities, especially large numbers of territorial intruders and claimants, may render territorial defence uneconomical. There is a third hypothesis that reduced mortality schedules and selection for reduced dispersal on islands may increase familiarity among neighbours, also reducing the requirement for aggressiveness (Adler & Levins, 1994). Unfortunately, in the absence of detailed island–mainland comparisons of resource densities, territoriality and home range overlap in *P. erhardii*, it is impossible to distinguish among these hypotheses. Detailed observations on the social organization of lizards are required to understand why aggression scores were consistently lower for insular individuals than their mainland conspecifics in our study.

Unexpectedly, aggressiveness was the only examined trait with means that differed between insular and mainland populations. We propose the following explanations of why behavioural and cognitive traits would be affected by insularity. First, the ecological conditions may be not sufficiently different between our insular and mainland sites to result in phenotypical divergence. Low trophic resource density and reduced mortality due to predation relaxation are often assumed to be key drivers of change in insular phenotypes; however, (1) insular populations may switch to alternative food types, potentially offsetting the expected limitations in nutrient supply (e.g. marine subsidy: Pafilis et al., 2011; Sale & Arnould, 2013; plant material: Van Damme, 1999) and (2) predation relaxation may be counterbalanced by increased cannibalism (Cooper Jr, Dimopoulos, & Pafilis, 2015). In addition, as our mainland populations were confined to mountaintops, they may represent 'ecological islands' (Dawson et al., 2016; but see Itescu, 2019) and experience partly similar (or rather analogous) biological conditions to that of insular populations. However, as many of the behavioural and cognitive traits considered here appear sensitive to animals' social environments (e.g. Sachser et al., 2013), and density on islets is generally higher than on the mainland, we consider the first explanation, that ecological conditions may not be sufficiently different between our insular and mainland sites to result in phenotypical divergence, to be questionable.

Second, insular and mainland lizards may exhibit similar behaviour and have similar cognitive abilities, but for different reasons. The average expression of many traits constitutes a compromise that balances the effects of several drivers of selection acting upon simultaneously upon a trait. If two antagonistic drivers change to a similar degree, the resulting behavioural compromise may remain unchanged. For example, although nutrient shortage on islands (Blanco et al., 2014) may disfavour investment in performant brains (Aiello & Wheeler, 1995), density compensation (MacArthur et al., 1972) may lead to increased social complexity that promotes enhanced cognition (Speechley et al., 2024). Ultimately, in both types of sites, this would produce lizards with a similar cognitive capacity. Similar trade-offs may influence other aspects of behaviour, leading to convergence of insular and mainland behavioural phenotypes.

Finally, evolution on islands may be highly unpredictable, with traits changing in one direction on one island and in another direction on a different island. This could occur if stochastic events (such as founder effects and subsequent genetic drift) are important (Foster, 2013; Foster, 1999r study, the population of origin accounted for a considerable amount of variation in risk-taking and spatial learning, much greater than insularity, suggesting that each population may have followed its own trajectory for these traits. Naturally, a similar pattern of geographical variation, but no insularity effect, could arise if all islands individually represent distinctive selective environments. Several studies question the generality of island rules or syndromes (e.g. Meiri et al., 2008), with an increasing appreciation of the variability in socio-ecological factors within mainland and insular locations. However, as population accounted for only a very small proportion of the total variance for the other behavioural traits considered here, it is unlikely that differential selective pressures among islands can explain the lack of significant behavioural differences between mainland and island lizards.

#### *Insular Lizards Exhibit More Repeatable Behaviour Than the Mainland Lizards*

Although, with the exception of aggressiveness, behavioural trait means remained similar among mainland and insular lizards, scores for many behavioural traits were more consistent and repeatable for the latter (higher among- and lower within-individual variation). In essence, this means that, compared with mainland lizards, insular lizards behave in a more individually

consistent way: namely each individual shows a stable behavioural pattern with less behavioural flexibility. Reduced residual variance in exploratory behaviour and most cognitive traits (i.e. the rest of the behavioural traits without repeated assessments) may also indicate a decline in behavioural flexibility, particularly on islets. One notable exception was reversal learning; however, this may be an artefact of the small sample size analysed for this trait. However, without detailed partitioning into within- and among- individual components, these results remain inconclusive.

Intraindividual variance, the degree to which an individual's actions or performance varies across situations and time, may have an (epi)genetic basis (reviewed by [Dochtermann et al., 2019](#); [Ledón-Rettig, Richards, & Martin, 2013](#)) or result from exposure to divergent environments (now or during development) (e.g. [Carere et al., 2010](#); [Dall et al., 2004](#); [Dingemans & Wolf, 2010](#); [Stamps & Groothuis, 2010](#)). Furthermore, idiosyncratic differences (e.g. in body size, internal state or experience) may further reinforce consistent behavioural variation within a population ([Bergmüller & Taborsky, 2010](#); [Dall et al., 2004](#)). Accordingly, geographical variation in intraindividual and interindividual variance (just as in average expression) is expected when populations occur in different environments or have experienced different histories of selection and genetic drift. For example, there is geographical variation in the repeatability of the exploratory behaviour of rufous-collared sparrows (*Zonotrichia capensis*), although their average exploratory behaviour does not differ among populations ([van Dongen et al., 2010](#)).

Therefore, we must consider why insular *P. erhardii* lizards display more consistent behaviour than their mainland conspecifics. Several mechanisms fuelled by insularization may lead to genetic or plastic and developmental changes in behavioural consistency.

First, a dispersal filter might favour individuals with consistent behaviour (i.e. high repeatability). However, it is difficult to imagine how this could occur without there being an effect on the average trait value. For example, an individual that is consistently more explorative and risk-prone (high repeatability) will be more likely to disperse to islands than an individual with only occasional exploration and risk-prone tendencies (low repeatability). However, if certain behavioural types are more likely to colonize or become isolated (as is likely the case in our insular system) we would also expect a directional shift in mean behavioural expression, which we do not observe. Moreover, dispersal filters have been found to favour behavioural flexibility. For example, in delicate skinks (*Lampropholis delicata*), island colonization may have acted as a selective filter that promotes risk-prone behavioural types and enhances behavioural plasticity. This manifested as concurrent shifts in the average levels of exploratory behaviour, boldness and activity, and a substantial decrease in among-individual variation and repeatability for these traits ([Chapple et al., 2022](#)).

Stochastic events (e.g. bottlenecks, founder effects and genetic drift) could also produce peculiar insular phenotypes, but it is not likely that this would happen in a consistent way on all islands. Under this scenario, we would expect higher intraindividual variation on some islands or islets, and lower variation in others, which would obscure any general insularity effects after population-level differences are accounted for. Alternatively, stochastic events and isolation may increase the likelihood of inbreeding in insular populations ([Frankham, 1998](#)). If personality traits are highly heritable and/or influenced by condition-dependent traits that are affected by inbreeding, this may result in greater behavioural consistency on islands. However, inbreeding would likely also affect mean values of behavioural (e.g. [Müller & Jušauskas, 2018](#)) and cognitive (reviewed in

[Gavriilidi & Van Linden, 2024](#)) traits in inbred and outbred individuals. Moreover, there is little evidence of personality differences between inbred and outbred individuals (e.g. Japanese quail, *Coturnix japonica*; [Beccardi et al., 2024](#); guppies, *Poecilia reticulata*; [Herdegen-Radwan, 2019](#)), making inbreeding also an unlikely explanation for our findings.

The third possibility is that behavioural flexibility is adaptive on the mainland, but not on islands. As mainland habitats tend to be more structurally complex and socio-ecologically more variable than island habitats, mainland lizards must deal with a greater variety of predators, competitors and prey. In such heterogeneous and dynamic environments, behavioural flexibility can be an asset ([Mery & Burns, 2010](#)). For example, the complex territorial dynamics of the mainland may impose strong selection for greater behavioural flexibility. Indeed, urban great tits, *Parus major*, showed greater territorial aggression and lower individual behavioural repeatability (personality) compared with their rural conspecifics, and these traits were deemed essential for successfully holding urban territories ([Hardman & Dalesman, 2018](#)).

Conversely, on islands, relaxed territoriality and higher population densities may favour stable yet diverse behavioural strategies that are maintained, for example, by frequency-dependent selection ([Bergmüller & Taborsky, 2010](#); [Dall et al., 2004](#)). Frequency-dependent selection has been invoked to explain the coexistence of mixed fighting strategies, alternative mating tactics, and even personalities within populations ([Wolf & Weissing, 2010](#)). One example is the European earwig, *Forficula auricularia*: in insular populations, dominant and subordinate male morphs, which differ in their fighting ability, coexist, whereas mainland populations are mostly monomorphic. This pattern is attributed to high population densities on islands, which alter the relative fitness benefits of each morph ([Tomkins & Brown, 2004](#)). Similarly, increased density and reduced predation may promote niche specialization, such that individuals occupy only a subset of their population's socio-ecological niche ([Araújo et al., 2011](#); [Bergmüller & Taborsky, 2010](#); [Bolnick et al., 2003](#)), further increasing consistent among-individual behavioural variation on islands. In addition, selection may act against superfluous behavioural flexibility, because the underlying neural structures and sensory machinery are costly to develop and maintain ([Dukas, 1999](#); [Mery & Burns, 2010](#)). If insular lizards face nutritional constraints ([Blanco et al., 2014](#)), they may also simply lack the resources to support such plasticity. Alternatively, resource limitation within dense island populations may lead to pronounced differences in individuals' state (e.g. growth and body condition) resulting from differences in their competitive abilities. Because behaviour can be state dependent, consistent individual differences in state may lead to stable among-individual behavioural variation, and, consequently, the coexistence of different personality types within a single population ([Dingemans & Wolf, 2010](#); [Wolf & Weissing, 2010](#)).

#### *Behavioural Correlations on Islands*

In recent years, the notion that behavioural traits covary among individuals has garnered much interest; both proximal (e.g. [Bell, 2005](#); [Ketterson & Nolan, 1999](#)) and evolutionary ([Bell, 2005](#); [Cheverud, 1996](#)) pathways have been proposed to explain the phenomenon.

In this study, there was very little evidence that personality or cognitive traits formed behavioural syndromes. However, without decomposing raw phenotypic correlations into between- and within-individual components ([Dingemans & Dochtermann, 2013](#)), our results remaining inconclusive. Overall, the strength and direction of behavioural correlations varied across lizard origins and populations. This population-level variability suggests

that behavioural syndromes, if present, are not fixed and may be shaped by local ecological or evolutionary contexts; moreover, different selective pressures across populations may lead to the decoupling of behavioural traits. Alternatively, stochastic processes such as genetic drift, especially in small or isolated populations, may weaken any consistent trait associations.

### Conclusion

Although insular and mainland *P. erhardii* lizards did not differ in average behavioural expression, with the exception of aggressiveness, insular individuals exhibited greater behavioural repeatability and reduced flexibility (i.e. higher among- and lower within-individual variation). Further investigation is required to determine whether these differences reflect genetic divergence or are shaped by developmental plasticity. If genetically based, the reduced behavioural flexibility of insular lizards (particularly islet lizards) may limit their capacity to cope with rapid environmental change, which raises important conservation concerns. As animal personalities can shape evolutionary potential and modify population resilience to environmental change (Wolf & Weissing, 2012), an understanding of the underlying mechanisms is crucial for informing conservation strategies that can preserve particularly vulnerable insular populations. We strongly encourage researchers to assess the variation in such traits under more natural conditions, and to establish their relevance for fitness in insular and mainland environments.

### Author Contributions

**Ioanna Gavriilidi:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Simon Baeckens:** Writing – review & editing, Supervision, Conceptualization. **Panayiotis Pafilis:** Writing – review & editing, Supervision. **Raoul Van Damme:** Writing – review & editing, Supervision, Methodology, Conceptualization.

### Data Availability

The data that support the findings of this study are openly available in Figshare: <https://doi.org/10.6084/m9.figshare.28855997>

### Declaration of Interest

The authors have no conflicts of interest to declare.

### Acknowledgments

This research would not have been possible without the financial support by the Research Foundation – Flanders (FWO) (IG:1105122N, 1105124N; SB:1218822N). The study fieldwork was funded by two FWO travel grants (IDs: V422322N, V423623N) and one travel grant from the Royal Belgian Zoological Society; all were awarded to IG. The authors would like to thank Jan Scholliers, Jorrit Mertens, and Aris Deimezis-Tsikoutas for their help during the fieldwork, as well as Elina Trafali, Stef Jans, Emilie Zimmer, Lucas Van Passel, and Clara Vinyeta-Cortada for their assistance with experiments. We extend our heartfelt thanks to Scar for his unwavering support during fieldwork and for all the interesting conversations, as his companionship made every challenge more enjoyable.

### Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2026.123493>.

### References

- Adler, G. H., & Levins, R. (1994). The island syndrome in rodent populations. *Quarterly Review of Biology*, 69(4), 473–490. <https://doi.org/10.1086/418744>
- Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36(2), 199–221. <https://doi.org/10.1086/204350>
- Amiel, J. J., Tingley, R., & Shine, R. (2011). Smart moves: Effects of relative brain size on establishment success of invasive amphibians and reptiles. *PLoS One*, 6(4), Article e18277. <https://doi.org/10.1371/journal.pone.0018277>
- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14(9), 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- ASAB Ethical Committee/ABS Animal Care Committee. (2023). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Animal Behaviour*, 195, 1–XI. <https://doi.org/10.1016/j.anbehav.2022.09.006>
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Baeckens, S., & Van Damme, R. (2020). The island syndrome. *Current Biology*, 30(8), R338–R339. <https://doi.org/10.1016/j.cub.2020.03.029>
- Beccardi, M., Moiron, M., Salmón, P., Tschirren, B., & Vedder, O. (2024). Does inbreeding affect personality traits? An experimental study in a precocial bird. *Behavioral Ecology and Sociobiology*, 78(12), 123. <https://doi.org/10.1007/s00265-024-03524-w>
- Bell, A. M. (2005). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18(2), 464–473. <https://doi.org/10.1111/j.1420-9101.2004.00817.x>
- Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9), 504–511. <https://doi.org/10.1016/j.tree.2010.06.012>
- Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1554), 2233–2237. <https://doi.org/10.1098/rspb.2004.2861>
- Blanco, G., Laiolo, P., & Fargallo, J. A. (2014). Linking environmental stress, feeding-shifts and the 'island syndrome': A nutritional challenge hypothesis. *Population Ecology*, 56(1), 203–216. <https://doi.org/10.1007/s10144-013-0404-3>
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161(1), 1–28. <https://doi.org/10.1086/343878>
- Brock, K. M., Bednekoff, P. A., Pafilis, P., & Foutopoulou, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? *Evolution*, 69(1), 216–231. <https://doi.org/10.1111/evo.12555>
- Buckley, L. B., & Jetz, W. (2007). Insularity and the determinants of lizard population density. *Ecology Letters*, 10(6), 481–489. <https://doi.org/10.1111/j.1461-0248.2007.01042.x>
- Carazo, P., Noble, D. W. A., Chandrasoma, D., & Whiting, M. J. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 281(1782), Article 20133275. <https://doi.org/10.1098/rspb.2013.3275>
- Carere, C., Caramaschi, D., & Fawcett, T. W. (2010). Covariation between personalities and individual differences in coping with stress: Converging evidence and hypotheses. *Current Zoology*, 56(6), 728–740. <https://doi.org/10.1093/czoolo/56.6.728>
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, 84(3), 603–609. <https://doi.org/10.1016/j.anbehav.2012.06.015>
- Case, T. J. (1978). A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, 59(1), 1–18. <https://doi.org/10.2307/1936628>
- Case, T. J. (1982). Ecology and evolution of the insular gigantic chuckawallas, *Sauromalus hispidus* and *Sauromalus varius*. In G. M. Burghardt, & A. S. Rand (Eds.), *Iguanas of the world: Their behavior, ecology, and conservation* (pp. 184–212). Noyes Publications.
- Case, T. J., Gilpin, M. E., & Diamond, J. M. (1979). Overexploitation, interference competition, and excess density compensation in insular faunas. *American Naturalist*, 113(6), 843–854. <https://doi.org/10.1086/283440>
- Chapple, D. G., Naimo, A. C., Brand, J. A., Michelangeli, M., Martin, J. M., Goulet, C. T., Brunton, D. H., Sih, A., & Wong, B. B. M. (2022). Biological invasions as a selective filter driving behavioral divergence. *Nature Communications*, 13(1), 5996. <https://doi.org/10.1038/s41467-022-33755-2>

- Chapple, D. G., Simmonds, S. M., & Wong, B. B. M. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution*, 27(1), 57–64. <https://doi.org/10.1016/j.tree.2011.09.010>
- Cheverud, J. M. (1996). Developmental integration and the evolution of pleiotropy. *American Zoologist*, 36(1), 44–50. <https://doi.org/10.1093/icb/36.1.44>
- Cole, E. F., & Quinn, J. L. (2011). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 279(1731), 1168–1175. <https://doi.org/10.1098/rspb.2011.1539>
- Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B., & Sih, A. (2011). Behavioural syndromes in fishes: A review with implications for ecology and fisheries management. *Journal of Fish Biology*, 78(2), 395–435. <https://doi.org/10.1111/j.1095-8649.2010.02874.x>
- Cooper Jr, W. E., Dimopoulos, I., & Pafilis, P. (2015). Sex, age, and population density affect aggressive behaviors in island lizards promoting cannibalism. *Ethology*, 121(3), 260–269. <https://doi.org/10.1111/eth.12335>
- Cooper Jr, W. E., Pyron, R. A., & Garland, J. T. (2014). Island tameness: Living on islands reduces flight initiation distance. *Proceedings of the Royal Society B: Biological Sciences*, 281(1777), Article 20133019. <https://doi.org/10.1098/rspb.2013.3019>
- Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 383–390. <https://doi.org/10.1098/rspb.2006.3734>
- Cote, J., Dreiss, A., & Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences*, 275(1653), 2851–2858. <https://doi.org/10.1098/rspb.2008.0783>
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>
- Damas-Moreira, I., Riley, J. L., Harris, D. J., & Whiting, M. J. (2019). Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. *Animal Behaviour*, 151, 195–202. <https://doi.org/10.1016/j.anbehav.2019.03.008>
- Darwin, C. (1839). *Journal of researches into the geology and natural history of the various countries visited by H. M. S. Beagle, under the command of Captain Fitzroy, R. N. from 1832–1836*. Henry Colburn.
- Dawson, M. N., Algar, A. C., Heaney, L. R., & Stuart, Y. E. (2016). The evolutionary biogeography of islands, lakes, and mountaintops. In R. Gillespie (Ed.), *The encyclopedia of evolutionary biology* (pp. 203–210). Academic Press. <https://doi.org/10.1016/B978-0-12-800049-6.00112-8>
- De Meester, G., Pafilis, P., & Van Damme, R. (2022). Bold and bright: Shy and supple? The effect of habitat type on personality–cognition covariance in the Aegean wall lizard (*Podarcis erhardii*). *Animal Cognition*, 25(4), 745–767. <https://doi.org/10.1007/s10071-021-01587-0>
- Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, 64(1), 135–168. <https://doi.org/10.1146/annurev-psych-113011-143750>
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1541), 847–852. <https://doi.org/10.1098/rspb.2004.2680>
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54. <https://doi.org/10.1111/1365-2656.12013>
- Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3947–3958. <https://doi.org/10.1098/rstb.2010.0221>
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, 76(6), 1128–1138. <https://doi.org/10.1111/j.1365-2656.2007.01284.x>
- Dochtermann, N. A., Schwab, T., Anderson Bernal, M., Dalos, J., & Royauté, R. (2019). The heritability of behavior: A meta-analysis. *Journal of Heredity*, 110(4), 403–410. <https://doi.org/10.1093/jhered/esz023>
- Dougherty, L. R., & Guillelte, L. M. (2018). Linking personality and cognition: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1756), Article 20170282. <https://doi.org/10.1098/rstb.2017.0282>
- Dukas, R. (1999). Costs of memory: Ideas and predictions. *Journal of Theoretical Biology*, 197(1), 41–50. <https://doi.org/10.1006/jtbi.1998.0856>
- Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 347–374. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130152>
- Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, 317(5843), 1344–1347. <https://doi.org/10.1126/science.1145463>
- Font, E. (2019). Rapid learning of a spatial memory task in a lacertid lizard (*Podarcis liolepis*). *Behavioural Processes*, 169, Article 103963. <https://doi.org/10.1016/j.beproc.2019.103963>
- Foster, S. A. (1999). The geography of behaviour: An evolutionary perspective. *Trends in Ecology & Evolution*, 14(5), 190–195. [https://doi.org/10.1016/S0169-5347\(98\)01577-8](https://doi.org/10.1016/S0169-5347(98)01577-8)
- Foster, S. A. (2013). Evolutionary insights from behavioural geography: Plasticity, evolution, and responses to rapid environmental change. *Evolutionary Ecology Research*, 15(6), 705–731.
- Foufopoulos, J., Zhao, Y., Brock, K. M., Pafilis, P., & Valakos, E. D. (2023). Predation risk, and not shelter or food availability, as the main determinant of reproduction investment in island lizards. *Animals*, 13(23), 3689. <https://doi.org/10.3390/ani13233689>
- Frankham, R. (1998). Inbreeding and extinction: Island populations. *Conservation Biology*, 12(3), 665–675. <https://doi.org/10.1111/j.1523-1739.1998.96456.x>
- Gavriilidi, I., De Meester, G., Van Damme, R., & Baeckens, S. (2022). How to behave when marooned: The behavioural component of the island syndrome remains underexplored. *Biology Letters*, 18(4), Article 20220030. <https://doi.org/10.1098/rsbl.2022.0030>
- Gavriilidi, I., & Van Linden, L. (2024). Inbreeding and cognition in wild populations: A relationship that remains unnoticed. *Oikos*, 2024(9), Article e10674. <https://doi.org/10.1111/oik.10674>
- González-Gómez, P. L., Vásquez, R. A., & Bozinovic, F. (2011). Flexibility of foraging behavior in hummingbirds: The role of energy constraints and cognitive abilities. *Auk*, 128(1), 36–42. <https://doi.org/10.1525/auk.2011.10024>
- Goulet, C. T., Michelangeli, M., Chung, M., Riley, J. L., Wong, B. B. M., Thompson, M. B., & Chapple, D. G. (2018). Evaluating cognition and thermal physiology as components of the pace-of-life syndrome. *Evolutionary Ecology*, 32(5), 469–488. <https://doi.org/10.1007/s10682-018-9948-1>
- Greenberg, R. (1983). The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *American Naturalist*, 122(4), 444–453. <https://doi.org/10.1086/284148>
- Guido, J. M., Biondi, L. M., Vasallo, A. I., & Muzio, R. N. (2017). Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, *Milvago chimango*. *Animal Cognition*, 20(4), 591–602. <https://doi.org/10.1007/s10071-017-1083-9>
- Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes*, 82(3), 265–270. <https://doi.org/10.1016/j.beproc.2009.07.005>
- Han, C. S., & Dingemanse, N. J. (2017). You are what you eat: Diet shapes body composition, personality and behavioural stability. *BMC Evolutionary Biology*, 17(1), 8. <https://doi.org/10.1186/s12862-016-0852-4>
- Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs among urban and rural great tits (*Parus major*). *Scientific Reports*, 8(1), 5042. <https://doi.org/10.1038/s41598-018-23463-7>
- Harrell Jr, F. E. (2024). Hmisc: Harrell Miscellaneous. *R package version 5.2-0*. <https://cran.r-project.org/package=Hmisc>
- Heldstab, S. A., Isler, K., Graber, S. M., Schuppli, C., & van Schaik, C. P. (2022). The economics of brain size evolution in vertebrates. *Current Biology*, 32(12), R697–R708. <https://doi.org/10.1016/j.cub.2022.04.096>
- Hemelrijk, C. (2017). Simulating complexity of animal social behaviour. In B. Edmonds, & R. Meyer (Eds.), *Simulating Social Complexity. Understanding Complex Systems* (pp. 633–670). Springer International Publishing. [https://doi.org/10.1007/978-3-319-66948-9\\_24](https://doi.org/10.1007/978-3-319-66948-9_24)
- Herdegen-Radwan, M. (2019). Does inbreeding affect personality traits? *Ecology and Evolution*, 9(19), 10929–10937. <https://doi.org/10.1002/ece3.5487>
- Huebner, F., Fichtel, C., & Kappeler, P. M. (2018). Linking cognition with fitness in a wild primate: Fitness correlates of problem-solving performance and spatial learning ability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1756), Article 20170295. <https://doi.org/10.1098/rstb.2017.0295>
- Hurston, H., Voith, L., Bonanno, J., Foufopoulos, J., Pafilis, P., Valakos, E., & Anthony, N. (2009). Effects of fragmentation on genetic diversity in island populations of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Reptilia). *Molecular Phylogenetics and Evolution*, 52(2), 395–405. <https://doi.org/10.1016/j.jmpev.2009.03.028>
- Isler, K., & van Schaik, C. P. (2009). The expensive brain: A framework for explaining evolutionary changes in brain size. *Journal of Human Evolution*, 57(4), 392–400. <https://doi.org/10.1016/j.jhev.2009.04.009>
- Itescu, Y. (2019). Are island-like systems biologically similar to islands? A review of the evidence. *Ecography*, 42(7), 1298–1314. <https://doi.org/10.1111/ecog.03951>
- Janzen, D. H. (1973). Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, 54(3), 687–708. <https://doi.org/10.2307/1935359>
- Jeziarski, M. T., Smith, W. J., & Clegg, S. M. (2024). The island syndrome in birds. *Journal of Biogeography*, 51(9), 1607–1622. <https://doi.org/10.1111/jbi.14720>
- Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, 153(3735), 501–506. <https://doi.org/10.1126/science.153.3735.501>
- Juette, T., Garant, D., Jameson, J. W., & Réale, D. (2020). The island syndrome hypothesis is only partially validated in two rodent species in an inland–island system. *Oikos*, 129(11), 1739–1751. <https://doi.org/10.1111/oik.07249>
- Kabadayi, C., Bobrowicz, K., & Osvath, M. (2017). The detour paradigm in animal cognition. *Animal Cognition*, 21(1), 21–35. <https://doi.org/10.1007/s10071-017-1152-0>
- Ketterson, E. D., & Nolan, V. (1999). Adaptation, exaptation, and constraint: A hormonal perspective. *American Naturalist*, 154(S1), S4–S25. <https://doi.org/10.1086/303280>
- Kotrschal, A., Buechel, S. D., Zala, S. M., Corral-Lopez, A., Penn, D. J., & Kolm, N. (2015). Brain size affects female but not male survival under predation threat. *Ecology Letters*, 18(7), 646–652. <https://doi.org/10.1111/ele.12441>
- Léna, J. P., De Fraipont, M., & Clobert, J. (2000). Affinity towards maternal odour and offspring dispersal in the common lizard. *Ecology Letters*, 3(4), 300–308. <https://doi.org/10.1046/j.1461-0248.2000.00155.x>
- Laughlin, S. B., de Ruyter van Steveninck, R. R., & Anderson, J. C. (1998). The metabolic cost of neural information. *Nature Neuroscience*, 1(1), 36–41. <https://doi.org/10.1038/236>

- Leal, M., & Powell, B. J. (2012). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters*, 8(1), 28–30. <https://doi.org/10.1098/rsbl.2011.0480>
- Ledón-Rettig, C. C., Richards, C. L., & Martin, L. B. (2013). Epigenetics for behavioral ecologists. *Behavioral Ecology*, 24(2), 311–324. <https://doi.org/10.1093/beheco/ars145>
- Lenth, R. V. (2024). *emmeans: Estimated Marginal Means, aka Least-Squares Means (R package version 1.10.5)*. <https://cran.r-project.org/package=emmeans>.
- Lomolino, M. V., van der Geer, A. A., Lyras, G. A., Palombo, M. R., Sax, D. F., & Rozzi, R. (2013). Of mice and mammoths: Generality and antiquity of the island rule. *Journal of Biogeography*, 40(8), 1427–1439. <https://doi.org/10.1111/jbi.12096>
- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457(7231), 830–836. <https://doi.org/10.1038/nature07893>
- Lucon-Xiccato, T., & Bisazza, A. (2017). Individual differences in cognition among teleost fishes. *Behavioural Processes*, 141, 184–195. <https://doi.org/10.1016/j.beproc.2017.01.015>
- Müller, T., & Juškauskas, A. (2018). Inbreeding affects personality and fitness of a leaf beetle. *Animal Behaviour*, 138, 29–37. <https://doi.org/10.1016/j.anbehav.2018.02.002>
- MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, 53(2), 330–342. <https://doi.org/10.2307/1934090>
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
- Mazza, V., Eccard, J. A., Zaccaroni, M., Jacob, J., & Dammhahn, M. (2018). The fast and the flexible: Cognitive style drives individual variation in cognition in a small mammal. *Animal Behaviour*, 137, 119–132. <https://doi.org/10.1016/j.anbehav.2018.01.011>
- Meiri, S., Cooper, N., & Purvis, A. (2008). The island rule: Made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, 275(1631), 141–148. <https://doi.org/10.1098/rspb.2007.1056>
- Mery, F., & Burns, J. G. (2010). Behavioural plasticity: An interaction between evolution and experience. *Evolutionary Ecology*, 24(3), 571–583. <https://doi.org/10.1007/s10682-009-9336-y>
- Mettke-Hofmann, C. (2014). Cognitive ecology: Ecological factors, life-styles, and cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 5(3), 345–360. <https://doi.org/10.1002/wics.1289>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., & Szocs, E. (2024). *vegan: Community ecology package (R package version 2.6–8)*. <https://cran.r-project.org/package=vegan>.
- Péter, A. (2017). *Solomon Coder (Version Beta: 17.03.22): A simple solution for behaviour coding*. <https://solomoncoder.com/>.
- Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P., & Valakos, E. D. (2009). Tail shedding in island lizards [acertidae, reptilia]: Decline of antipredator defenses in relaxed predation environments. *Evolution*, 63(5), 1262–1278. <https://doi.org/10.1111/j.1558-5646.2009.00635.x>
- Pafilis, P., Foufopoulos, J., Sagonas, K., Runemark, A., Svensson, E., & Valakos, E. D. (2011). Reproductive biology of insular reptiles: Marine subsidies modulate expression of the “island syndrome”. *Copeia*, 2011(4), 545–552. <https://doi.org/10.1643/CE-10-041>
- Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, 6(7), 623–641. [https://doi.org/10.1016/S0047-2484\(77\)80135-8](https://doi.org/10.1016/S0047-2484(77)80135-8)
- Poulakakis, N., Lymberakis, P., Antoniou, A., Chalkia, D., Zouros, E., Mylonas, M., & Valakos, E. (2003). Molecular phylogeny and biogeography of the wall-lizard *Podarcis erhardii* (Squamata: Lacertidae). *Molecular Phylogenetics and Evolution*, 28(1), 38–46. [https://doi.org/10.1016/S1055-7903\(03\)00037-X](https://doi.org/10.1016/S1055-7903(03)00037-X)
- R Core Team. (2024). *R: A Language and Environment for Statistical Computing (R version 4.4.2)*. R Foundation for Statistical Computing. <https://www.r-project.org/>.
- Réale, D., Dingemans, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3937–3946. <https://doi.org/10.1098/rstb.2010.0222>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemans, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Raia, P., Guarino, F. M., Turano, M., Polese, G., Ripa, D., Carotenuto, F., Monti, D. M., Cardi, M., & Fulgione, D. (2010). The blue lizard spandrel and the island syndrome. *BMC Evolutionary Biology*, 10, 289. <https://doi.org/10.1186/1471-2148-10-289>
- Rand, A. S., Gorman, G. C., & Rand, W. M. (1975). Natural history, behavior, and ecology of *Anolis agassizi*. In J. B. Graham (Ed.), *The Biological investigation of Malpelo Island, Colombia* (pp. 27–38). City of Washington: Smithsonian Institution Press. In Smithsonian Contributions to Zoology, 176.
- Reichert, M. S., & Quinn, J. L. (2017). Cognition in contests: Mechanisms, ecology, and evolution. *Trends in Ecology & Evolution*, 32(10), 773–785. <https://doi.org/10.1016/j.tree.2017.07.003>
- Rochais, C., Rymer, T. L., & Pillay, N. (2022). Challenges in linking cognition and survival: A review. *Frontiers in Ecology and Evolution*, 10, Article 729546. <https://doi.org/10.3389/fevo.2022.729546>
- Royauté, R., & Dochtermann, N. A. (2021). Comparing ecological and evolutionary variability within datasets. *Behavioral Ecology and Sociobiology*, 75(9), 127. <https://doi.org/10.1007/s00265-021-03068-3>
- Sachser, N., Kaiser, S., & Hennessy, M. B. (2013). Behavioural profiles are shaped by social experience: When, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618), Article 20120344. <https://doi.org/10.1098/rstb.2012.0344>
- Sale, M. G., & Arnould, J. P. Y. (2013). Inflated population density of island Antechinus: A case of allochthonous marine inputs leading to increased food availability? *Australian Journal of Zoology*, 60(5), 343–351. <https://doi.org/10.1071/ZO12073>
- Sayol, F., Downing, P. A., Iwaniuk, A. N., Maspons, J., & Sol, D. (2018). Predictable evolution towards larger brains in birds colonizing oceanic islands. *Nature Communications*, 9(1), 2820. <https://doi.org/10.1038/s41467-018-05280-8>
- Scali, S., Sacchi, R., Falaschi, M., Coladonato, A., Pozzi, S., Zuffi, M., & Mangiacotti, M. (2019). Mirrored images but not silicone models trigger aggressive responses in male Common wall lizards. *Acta Herpetologica*, 14(1), 35–41. [https://doi.org/10.13128/Acta\\_Herpetol-24651](https://doi.org/10.13128/Acta_Herpetol-24651)
- Sherpa, S., Salvi, D., Silva-Rocha, I., Capblancq, T., Paris, J. R., Carretero, M. A., & Ficetola, G. F. (2024). Reconstructing the complex colonisation histories of lizards across Mediterranean archipelagos. *Journal of Biogeography*, 51(2), 157–172. <https://doi.org/10.1111/jbi.14739>
- Shettleworth, S. J. (2009). *Cognition, evolution, and behavior*. Oxford University Press.
- Shultz, S., & Dunbar, R. I. M. (2022). Socioecological complexity in primate groups and its cognitive correlates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1860), Article 20210296. <https://doi.org/10.1098/rstb.2021.0296>
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1603), 2762–2772. <https://doi.org/10.1098/rstb.2012.0216>
- Siliceo-Cantero, H. H., Zúñiga-Vega, J. J., Renton, K., & Garcia, A. (2017). Assessing the relative importance of intraspecific and interspecific interactions on the ecology of *Anolis nebulosus* lizards from an island vs. a mainland population. *Herpetological Conservation and Biology*, 12(3), 673–682.
- Sinn, D. L., Apiolaza, L. A., & Moltchanivskiy, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, 19(5), 1437–1447. <https://doi.org/10.1111/j.1420-9101.2006.01136.x>
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, 19(2), 448–455. <https://doi.org/10.1093/beheco/arm144>
- Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, 5(1), 130–133. <https://doi.org/10.1098/rsbl.2008.0621>
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, 102(15), 5460–5465. <https://doi.org/10.1073/pnas.0408145102>
- Speechley, E. M., Ashton, B. J., Foo, Y. Z., Simmons, L. W., & Ridley, A. R. (2024). Meta-analyses reveal support for the social intelligence hypothesis. *Biological Reviews*, 99(5), 1889–1908. <https://doi.org/10.1111/brv.13103>
- Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1), 3–18. <https://doi.org/10.1111/ele.12708>
- Stamps, J. A., & Buechner, M. (1985). The territorial defense hypothesis and the ecology of insular vertebrates. *Quarterly Review of Biology*, 60(2), 155–181. <https://doi.org/10.1086/414314>
- Stamps, J. A., & Groothuis, T. G. G. (2010). Developmental perspectives on personality: Implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4029–4041. <https://doi.org/10.1098/rstb.2010.0218>
- Stankovich, T., & Romero, A. N. (2017). The correlated evolution of antipredator defenses and brain size in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 284(1846), Article 20161857. <https://doi.org/10.1098/rspb.2016.1857>
- Szabo, B., Damas-Moreira, I., & Whiting, M. J. (2020). Can cognitive ability give invasive species the means to succeed? A review of the evidence. *Frontiers in Ecology and Evolution*, 8, Article 530130. <https://doi.org/10.3389/fevo.2020.00187>
- Tomkins, J. L., & Brown, G. S. (2004). Population density drives the local evolution of a threshold dimorphism. *Nature*, 431(7012), 1099–1103. <https://doi.org/10.1038/nature02918>
- Valakos, E. D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., & Foufopoulos, J. (2008). *The amphibians and reptiles of Greece* (Edition Chimaira).

- Van Damme, R. (1999). Evolution of herbivory in lacertid lizards: Effects of insularity and body size. *Journal of Herpetology*, 33(4), 663–674. <https://doi.org/10.2307/1565584>
- van Dongen, W. F. D., Maldonado, K., Sabat, P., & Vásquez, R. A. (2010). Geographic variation in the repeatability of a personality trait. *Behavioral Ecology*, 21(6), 1243–1250. <https://doi.org/10.1093/beheco/arq145>
- Van Woerden, J. T., Van Schaik, C. P., & Isler, K. (2010). Effects of seasonality on brain size evolution: Evidence from strepsirrhine primates. *American Naturalist*, 176(6), 758–767. <https://doi.org/10.1086/657045>
- White, D. J., Arthur, J., Davies, H. B., & Guigueno, M. F. (2022). Cognition and reproductive success in cowbirds. *Learning & Behavior*, 50(1), 178–188. <https://doi.org/10.3758/s13420-021-00506-0>
- Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation*. Oxford University Press.
- Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3959–3968. <https://doi.org/10.1098/rstb.2010.0215>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>
- Wooster, E. I. F., Gaynor, K. M., Carthey, A. J. R., Wallach, A. D., Stanton, L. A., Ramp, D., & Lundgren, E. J. (2024). Animal cognition and culture mediate predator-prey interactions. *Trends in Ecology & Evolution*, 39(1), 52–64. <https://doi.org/10.1016/j.tree.2023.09.012>