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Explora tory and Neophilic Behavior Explain Coexistence of Two Closely Related Lizard Species

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Abstract: Competition for resources in closely related species in coexistence is associated with divergence in behavioral traits, the mechanisms of which are still unclear. Italian (*Podarcis siculus*) and Dalmatian (*Podarcis melisellensis*) wall lizards have similar ecological traits and coexist in the Eastern Adriatic; however, *P. siculus* has invasive potential and is often larger in body size. To understand their mechanisms of coexistence, we investigated exploratory behavior, activity levels, neophilia, neophobia, and morphometrics associated with locomotion in lizards of both sexes and species from three syntopic wild populations (n = 240). Overall, *P. siculus* was more exploratory, active, and neophilic. Movement was likely not linked to morphology, as only one variable (number of moving segments) was linked with the larger body size of *P. siculus*. Males of both species were more neophilic and bigger than females in all measured morphological parameters. The reported behavioral differences could explain how these two very similar species share environments in sympatry and provide insight into species-specific traits that could explain *P. siculus* invasion success.

Key words: *Lacertidae*; Niche partitioning; Neophilia; *Podarcis*; Sympatry

The coexistence of phylogenetically proximate and morphologically similar animal species within the same geographical area (sympatry) presents ecological challenges, particularly regarding interspecific competition derived from overlapping resource requirements (Brown and Wilson 1956; Frey et al. 2017). Such competition could lead to evolutionary or plastic responses that result in phenotypic divergence between species, which may result in niche partitioning that fosters coexistence by allowing multiple trait combinations or ecological strategies to be viable within the same environment (Brown and Wilson 1956; Miller et al. 2024). Behavioral adaptations represent a key component of such strategies, frequently regulating competitive interactions to enable stable coexistence, prevent competitive exclusion, and foster dynamic ecological equilibria (Chesson 1994; Wong and Candolin 2015).

In sympatric communities, coexistence is often facilitated by behavioral divergence in traits like exploration (Morris and Palmer 2023), neophilia (Greenberg 2003), activity levels (Milles et al. 2020), and foraging strategies (Schlägel et al. 2020). These differences are regulated by critical trade-offs, including those between exploration and risk avoidance (Morris and Palmer 2023) and activity costs (Schlägel et al. 2020). Exploratory behavior could reveal subtle structuring, potentially through consistent, context-dependent differences in metrics like exploration intensity (along the active-search/sit-and-wait continuum) or differential responses to novelty (neophilia/neophobia) that influence resource use (Greenberg and Mettke-Hofmann 2001; Le Galliard et al. 2013; Schlägel et al. 2020; Szabo and Ringler 2023; Bhattacharjee et al. 2024).

Specifically, divergence in exploration (tendency to explore unfamiliar environments; Hughes 1997) and general activity levels (in nonrisky familiar environments; Greggor et al. 2015) shape niche partitioning by influencing foraging approaches, habitat selection, and dispersal in context-dependent ways (Kobler et al. 2009; Le Galliard et al. 2013; Schlägel et al. 2020; Bhattacharjee et al. 2024). This behavioral variation reflects different energy management strategies, ranging from more energy-conserving, lower-activity patterns to energetically costly, higher-activity patterns (Le Galliard et al. 2013; Schlägel et al. 2020). Thus, variation in exploration and activity represents a risk–return trade-off: bold explorers may obtain richer but unpredictable resources while facing higher predation risks, whereas less bold individuals tend to achieve more stable and safer returns (Patrick et al. 2017; Eccard et al. 2022; Siegal et al. 2022). For instance, a high exploration score could imply rapid assessment of the environment coupled with high levels of locomotion (Sih et al. 2004; Rodríguez-Prieto et al. 2011; Careau and Garland 2012). Alternatively, the same high exploration score could indicate a more thorough exploration strategy, where individuals simply spend more time actively moving to investigate the novel environment (Careau et al. 2009). Coexisting species can thus reduce competition by specializing toward different points along this activity-energy spectrum, thereby partitioning resources or adopting distinct energy management approaches (Kobler et al. 2009; Schlägel et al. 2020). In this context, the success of these divergent tactics depends on the environment: a cautious, low-exploration approach may enhance survival under conditions of elevated predation pressure, whereas highly exploratory behavior becomes advantageous when the rewards of rapid resource exploitation outweigh the risks. This illustrates how differing behavioral strategies can offer specific, context-dependent benefits (Prabh et al. 2023; Villa Martín et al. 2019; Stott et al. 2024).

Novelty modulates an individual's exploratory behavior, described by both neophobia (avoidance/hesitation toward novelty) and neophilia (attraction/interaction with novelty) (Greenberg and Mettke-Hofmann 2001; Bhattacharjee et al. 2024). Differences in these traits between species can drive divergence in diet breadth and use of novel microhabitats, influencing niche partitioning (Miller et al. 2025).

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Conceptually, neophilia and neophobia are best understood as distinct behavioral dimensions, potentially mediated by separate mechanisms reflecting the trade-off between discovery benefits and danger costs, rather than opposite ends of a single axis (Russell 1973). Neophobia, involving cognitive classification of stimuli as novel based on experience, is distinguished from general fearfulness or boldness (Greggor et al. 2015). Functionally, while high neophobia can constrain resource discovery through risk avoidance (Stöwe et al. 2006), neophilia promotes investigation, learning, and innovation (Greenberg 2003). Indeed, reduced neophobia is frequently linked to success in human-modified environments (Bhattacharjee et al. 2024). Because these reactions are highly context-dependent (influenced by internal state, experience, and setting; Szabo and Ringler 2023), experimentally isolating responses specifically to novelty requires careful methodological design, often involving novel stimuli presented within familiar environments (Greggor et al. 2015; Szabo and Ringler 2023). A reduction in object-neophobia, as reported in free-ranging dogs (*Canis familiaris*), can be an adaptive strategy to promote exploratory behavior, especially during foraging (Bhattacharjee et al. 2024).

In their native range in the Eastern Adriatic coast, Italian Wall Lizards *Podarcis siculus* (Rafinesque-Schmaltz 1810) are in sympatry with endemic Dalmatian Wall Lizards *Podarcis melisellensis* (Braun 1877; Arnold and Ovenden 2002; Jelić et al. 2012). This coexistence extends beyond broad geographic overlap to true syntopy, where populations share the exact same microhabitats. This proximate co-occurrence makes their coexistence particularly intriguing because, despite their evolutionary divergence (Podnar et al. 2004; Sherpa et al. 2023) and the broad geographic distribution of *P. siculus* (Panjković et al. 2021), both species demonstrate notable similarities in their ecological and morphological characteristics. They have similar body shapes and are active foragers on grassy terrains, olive groves, stone walls, and vineyards (Grbac and Bauwens 2001), hunt a diverse array of invertebrates, prefer body temperatures in the range of 32–36°C (Damme et al. 1990; Downes and Bauwens 2002), and exhibit strong territoriality (Downes and Bauwens 2004).

These similarities suggest that other mechanisms, such as resource differentiation, may have evolved to reduce direct competition (Schoener 1974). Behavioral characterization already revealed significant differences: *P. siculus* exhibits higher exploration and food intake but lower risk-taking tendencies compared to *P. melisellensis* (Glogoški et al. 2024). Moreover, research indicates that introduced *P. siculus* populations can adjust their competitive strategies, potentially displacing native species (Damas-Moreira et al. 2020), and laboratory studies suggest that direct behavioral interference could be a mechanism for competitive exclusion between *P. siculus* and *P. melisellensis* (Downes and Bauwens 2002). Beyond behavior, other subtle differences sustain the possibility of niche segregation: studies of noncoexisting (allopatric) island populations show dietary divergences, with *P. siculus* incorporating more plant matter and *P. melisellensis* consuming a greater diversity of invertebrate prey (Taverne et al. 2019). Additionally, *P. siculus* generally reaches a larger adult size and is known as an invasive species capable of utilizing urban environments, not typically associated with *P. melisellensis* (Huyghe et al. 2007; Damas-Moreira et al. 2024). Therefore, while the outcomes of niche partitioning—such as habitat preference (Grbac and Brnin 2006), competitive interactions (Downes and Bauwens 2002), and social interactions (Downes and Bauwens 2004)—are well-documented, the specific behavioral mechanisms driving these patterns remain unresolved. It is currently unknown whether these segregation patterns arise from inherent species-specific differences in exploration and neophobia or from plastic responses to immediate competitive pressure.

In our previous study on a single population, we determined behavioral differences (exploration, risk-taking, and food acquisition) in a sympatric native population of *P. siculus* and *P. melisellensis* (Glogoški et al. 2024). However, relying on a single population limits the generalization of these findings, leaving unresolved whether such behavioral divergences are consistent, species-specific mechanisms facilitating coexistence across their shared range or merely plastic, population-specific responses to local competitive intensity (Michelangeli et al. 2019). Geographic variation in behavioral traits and competitive abilities is common among sympatric species, making multipopulation assessments essential for identifying truly species-level mechanisms versus population-specific responses (Michelangeli et al. 2019; Syme et al. 2024; Brooker et al. 2025). Building upon that, this study investigated exploratory behavior, activity levels, neophilia, and neophobia across three different syntopic populations. We examined these behaviors in new and familiar environments, as well as in a familiar environment with a novel object, to provide a robust species-level comparison. Because behavioral phenotypes can show strong correlations with morphological traits (Travis and Reznick 2018), we also assessed the impact of morphological data (body and limb size) on behavioral differences. We hypothesized that inherent behavioral differences contribute to the coexistence of these two species by reflecting distinct ecological strategies. Given that *P. siculus* is a successful invasive species and frequently occupies urban environments, and our previous findings on a single population indicating higher exploration, we hypothesized that it would display higher activity, exploration, and neophilia, and lower neophobia compared to *P. melisellensis*.

Materials and Methods

Study System

On the Eastern Adriatic mainland, the lacertid lizards *P. siculus* and *P. melisellensis* exhibit both sympatric and allopatric distribution patterns. In areas of allopatry, these species demonstrate distinct microhabitat preferences: *P. siculus* typically occupies vegetated fields and coastal zones, while *P. melisellensis* is predominantly associated with hilly terrain characterized by limestone bedrock and macchia cover. Sympatry occurs in transition zones where these habitats integrate. Notably, within these sympatric regions, individuals of one species can be found within the preferred habitat of the other. Furthermore, specific microhabitats within sympatric zones, comprising a mosaic of lush grass, macchia, rocks, and stone walls, support syntopy. In such areas of syntopy, individuals of both species occur in close spatial and temporal proximity, observed basking meters apart or utilizing the same shrub within short time intervals. Given that syntopy between these species is observed across the Eastern Adriatic mainland, we examined specific syntopic populations within

broader sympatric areas to investigate the behavioral ecological mechanisms facilitating their coexistence.

Animals

Adult lizards of both *P. siculus* and *P. melisellensis* were caught by hand or by noose in the areas near Knin, Pag, and Sinj, Splitsko Dalmatinska County, Croatia, where both species naturally coexist in sympatry, and also in syntopy (for description of locations, see Supplemental Material, available online and Supplemental Figure S1). Lizards were captured during the late summer to early autumn period, spanning September to October, across two consecutive years (2020 and 2021). A total of 240 lizards were used in the study: 10 males and 10 females of each species at each location each year. Males were identified by their femoral pores and a swollen tail base (Brecko et al. 2008). Lizards whose sex was unclear (juveniles and subadults) were released and not included in our study. Once captured, lizards were transported to the Division of Animal Physiology at the University of Zagreb, Croatia. Each lizard was individually housed in a plastic terrarium (40 × 30 cm) with a heat bulb and UV lamp, peat substrate, and constant access to water and fed every other day with crickets (*Gryllus assimilis*), enriched with calcium and vitamins every other week. The terrariums simulated natural light cycles (12 h light, 12 h dark) and temperature conditions (22°C at night and 25°C during the day). After a month of acclimatization, tests were conducted for 4 wk. Testing order was randomized for species, sex, and location. Animals were divided into 3 groups of 32 and one group of 24 animals (equal number by species, sex, and location). The same procedure was followed in both study years. To minimize handling stress, we used plastic tubes for transferring the lizards to and from the experimental setup into the center of the arena (Glogoški et al. 2024). The lizards were gently encouraged to exit the tube in the center of the arena by rotating the tube. All tests were conducted between 9 and 17 h at a consistent temperature of 30°C (Downes and Bauwens 2004). At the end of behavioral testing, animals were sacrificed for other studies (Brižić et al. 2025; Šikić et al. 2025).

Behavioral Tests

Our behavioral tests were designed to quantify activity, exploratory behavior, and neophilic responses across three environmental contexts: a new environment (Context 1), a familiar environment (Context 2), and a familiar environment with a novel object as a measure of neophilia (Context 3). Our tests also allowed us to derive measures of neophobia by measuring behavioral changes between activity in an empty arena and with a novel object (Table 1).

Behaviors were evaluated using open field tests (Réale et al. 2007). Testing occurred in an empty, opaque Plexiglas test chamber (50 × 50 × 50 cm) with an open top and a camera mounted above that recorded all experiments. Animals were transferred from their terraria into the open field chamber via a plastic tube and gently coaxed to exit the tube (which was immediately removed). Trials lasted 15 min. At the end of each trial, the lizard was guided back into its tube and returned to its terrarium. Four experimental set-ups were used in parallel, and each test chamber was cleaned with 30% alcohol after each test to remove residual odors (Deacon and Rawlins 2006; Gould et al. 2009).

Testing spanned two consecutive days, consisting of four open field tests across the three environmental contexts. On the first day, individuals completed two consecutive trials: an initial exposure to a novel arena to assess baseline exploratory behavior (Context 1: new environment test), followed by a second trial essential for habituation to the testing environment for further assessment of activity and neophilia (not analyzed later). On the second day, lizards underwent two additional trials: a third exposure to the now-familiar arena to evaluate activity in a familiar context (Context 2: familiar environment test) and a fourth trial introducing a novel object (a small, knotted piece of powder-free rubber glove) centrally placed within the arena to assess neophilia (Context 3: novel object test). In the fourth trial, the lizard was placed in the center of the arena and allowed to acclimate for 5 min, after which the novel object was slowly placed at the center with clean forceps (in the same place each time, irrespective of the lizard's orientation). The recording began 5 s later, allowing for the lizard to calm. Each day, all the lizards in the group were tested. The order of the lizards for each experimental day was randomized using an online tool (https://www.randomizer.org). To maintain consistency and give the animals the same amount of time between tests in a day (4 h), the lizards entered the three different experiments in the same order.

To quantify different behavioral strategies that serve as proxies for search effort and energetic expenditure (Anderson 2007), distance moved, number of movement segments, and total time spent moving were scored (Table 1). Furthermore, the turning rate, or angular velocity, during movement was measured as an indicator of the intensity of local search; higher turning rates often signify focused searching within a specific area, such as immediately following resource discovery (Bell 1990). Video analysis was performed using Noldus Ethovision XT 15 software (Noldus Information Technology, Wageningen, The Netherlands), which automatically tracked and calculated several exploration variables from the recordings: absolute angular velocity, distance moved, number of moving segments, and movement duration (details in Table 1). Separately, behaviors related specifically to the novel object presented in the neophilia test (Context 3) were scored manually from the video playback. These included the latency to contact the novel object (s), measured as the time taken from the trial's start (placing of the tube in the arena) until the lizard's first physical touch of the object, and the frequency of contact with a novel object, which represented the total number of contacts initiated by the lizard. For scoring frequency, if continuous contact occurred, a new contact was tallied every 5 s. Neophobia was assessed by comparing Context 2 vs. Context 3 (De Meester et al. 2021) to quantify behavioral change between activity in the empty arena and with a novel object (log ratio change between contexts).

Morphological Measurements

Snout–vent length (SVL), interlimb length (ILL), and limb length (LL) were measured with digital calipers, and mass was measured with a digital scale (±0.1 g, Soehnle). To minimize stress before behavioral testing, measurements were taken after the end of testing. Limb-related parameters (ILL and LL) were measured on the right side of the lizard's body. Interlimb ratio was calculated as ILL divided by SVL. The hindlimb-to-forelimb ratio was calculated as hindlimb length divided by forelimb length. These ratios provide size-independent indices

TABLE 1.—Definitions of the variables scored from the videos of two species of sympatric wall lizards, *P. melisellensis* and *P. siculus*. These measures provide insights into the lizards' behavior across three different contexts: a new environment (Context 1), a familiar environment (Context 2), and a familiar environment with a novel object, as a measure of neophilia (Context 3). Neophobia was assessed by comparing Context 2 vs. Context 3 to quantify behavioral change between activity in the empty arena and with a novel object.

Type of behavior	Test environment	Variables scored from videos	Definition
Exploration	New	Distance moved (cm)	Total distance the animal moved during a trial.
		Movement duration (s)	Amount of time the animal spent moving during a trial.
Activity	Familiar	Number of moving segments	Number of times the animal started moving during a trial.
		Angular velocity (rad/s)	Rate of change in direction of the lizard's movement during a trial.
Neophilia	Familiar + novel object	Latency to contact the novel object (s)	Time from the start of the trial until the lizard first makes physical contact with the novel object.
		Frequency of contact with the novel object	Number of contacts with a novel object during a trial.
Neophobia	Derived metric	Distance moved (cm), movement duration (s), number of moving segments, angular velocity (rad/s)	Calculated as log (novel object environment/familiar environment) for each of these four behavioral variables.

of limb proportionality that are commonly used to assess ecomorphological and locomotor differentiation associated with habitat use (e.g., arboreal, ground-dwelling, or saxicolous environments; Kaliontzopoulou et al. 2010). The Scaled Mass Index (SMI), a measure of body condition, was calculated following Peig and Green (2009). Morphological comparisons across species, populations, and sexes are presented in Supplemental Material, Part B.

Statistical Analysis

All statistical analyses were performed using the R environment (v4.4.2; R Core Team 2024). Initial models (described below) incorporated species, sex, and location as fixed effects, including their interactions. Behavioral phenotypes can show strong correlations with morphological traits (Travis and Reznick 2018), such as body size, LL, and interlimb distance (Pough et al. 2016), warranting their inclusion in the main analysis. Additionally, accounting for sex-specific variation is essential, especially in sexually dimorphic species where such differences can be profound (Palanza and Parmigiani 2017). SVL was included to account for body size effects, and sampling year and time of testing (testing order) to account for potential temporal variation or habituation effects. Additional morphological indices (SMI, ILL ratio, hindlimb-to-forelimb ratio) were also assessed and retained as covariates if they significantly improved model fit (Likelihood Ratio Tests, LRT; $P < 0.05$).

A consistent model simplification approach was applied, systematically removing nonsignificant interaction terms ($P \geq 0.05$) via ANOVA and subsequently nonsignificant covariates ($P \geq 0.05$) via LRT. For each analysis type (Linear model [LM], Negative Binomial Generalized Linear Model [GLM], Accelerated Failure Time [AFT]), diagnostic checks were conducted to verify model assumptions (Zuur et al. 2010). To ensure reliable parameter estimates, final models were screened for multicollinearity using Variance Inflation Factors (VIF). Identification and treatment of potential outliers or influential cases are fully described in the code (see Data Availability).

Continuous exploration variables were analyzed using LMs: angular velocity, distance moved, number of moving segments, and movement duration. For LMs, we assessed assumptions using the Shapiro–Wilk test for normality, Levene's test for homogeneity of variance, and visual inspection of diagnostic plots (residuals vs. fitted, Q–Q plots, scale-location, and Cook's distance). Where violations occurred, Box–Cox transformations (Box and Cox 1964) were applied. Angular measurements were transformed across all trials ($\lambda = 0.2$), while other variables were transformed only where distributional assumptions were violated: distance in Trials 2 and 3 ($\lambda = 0.6$–0.7), duration in Trials 1 and 2 ($\lambda = 0.9$–1.2), and number of moving segments in Trial 1 ($\lambda = 1.2$). In all other instances, assumptions were met on the raw scale.

Contact frequency was analyzed using Negative Binomial GLMs. This GLM framework correctly handles the discrete, nonnegative nature of count data, and the Negative Binomial distribution specifically accommodates potential overdispersion common in ecological counts. For GLMs, overdispersion was assessed using three complementary approaches: the deviance-to-residual degrees of freedom ratio, Cameron and Trivedi's (1990) formal dispersion test, and comparison of quasi-Poisson dispersion parameters. Negative binomial models were used when overdispersion was detected (dispersion ratio > 1.5 or AER test $P < 0.05$). Zero-inflation was assessed by comparing standard models to zero-inflated equivalents using Vuong (1989). Final GLM diagnostics were verified using simulation-based residual diagnostics from the DHARMa package (Hartig 2022).

Time-to-event data (latency to first contact) were analyzed using AFT models. Survival analysis models like the AFT are well-suited for this data structure, as they appropriately handle censored observations and directly model the effect of covariates on the event timescale (Jahn-Eimermacher et al. 2011). The best-fitting parametric distribution was selected via AIC comparison, where models with ΔAIC >2 relative to the best model were considered to have substantially less support, and effects were interpreted using Acceleration Factors (Supplemental Table S5, available online). For AFT models, the best-fitting distribution (Weibull, log-normal, log-logistic, exponential) was determined via Akaike Information Criteria (AIC). Model assumptions were verified by examining Cox–Snell residuals for linearity against the cumulative hazard and by visually comparing Kaplan–Meier survival estimates against fitted parametric curves.

Neophobia (log [Context 3/Context 2]) was assessed using LMs on log ratios of exploration variables between novel object (Context 3) and familiar environment (Context 2) tests. This approach quantifies the proportional change in behavior relative to baseline activity, treating proportional increases and decreases symmetrically and satisfying normality assumptions

better than raw ratios or raw differences (Hedges et al. 1999; Curran-Everett 2013).

Finally, for significant effects involving the location factor or its interactions across the relevant models, post-hoc pairwise comparisons were conducted using estimated marginal means with Tukey adjustment. For all models, α was set at 0.05. Data and code are available at Mendeley Data (Gojak et al. 2025).

RESULTS

Our analysis examined four distinct aspects of lizard behavior: (1) initial exploration of a new environment, (2) general activity levels, (3) response to a novel object (neophilia), and (4) behavioral changes induced by the object's presence (neophobia). These behaviors were evaluated in three sequential contexts: a new environment, a familiar environment, and a familiar environment containing a novel object. The applied model simplification for behavioral variables resulted in models that did not include any interaction except species and location interaction for movement duration in the neophobia context. Our analyses revealed that neither the interlimb ratio nor the hindlimb-to-forelimb ratio improved model fit across any of the behavioral variables or contexts examined; hence, they were excluded from the final model. The influence of SVL or SMI is stated where it was found to be significant. For clarity, in the text, only significant P values will be shown; detailed results can be found in Supplemental Tables S1–S7 (available online) in the Supplemental Material.

In the new environment (Context 1: exploration), species differences substantially affected various exploratory variables. *Podarcis siculu*s exhibited a lower number of moving segments ($P < 0.001$), moved greater distances ($P < 0.001$), and demonstrated a higher angular velocity ($P < 0.001$) compared to *P. melisellensis* (Fig. 1). Furthermore, the influence of species on movement duration approached statistical significance ($P = 0.053$; Fig. 1c); this suggests a potential trend where *P. siculus* had longer movement durations than *P. melisellensis*, aligning with their higher activity observed in other metrics measured in this context. The location from which the lizards emanated also significantly influenced angular velocity ($P = 0.006$), movement duration ($P = 0.003$), and the number of moving segments ($P = 0.019$) but not distance moved (Supplemental Table S1). Post-hoc tests revealed that Sinj lizards had higher angular velocity than Knin lizards ($P = 0.02$), both Knin ($P < 0.001$) and Sinj ($P = 0.027$) lizards moved for a longer duration than Pag lizards, and Pag lizards exhibited a higher number of moving segments than Sinj lizards ($P = 0.046$; Supplemental Table S2). Body size (SVL) was also a significant predictor, positively associated with angular velocity ($P = 0.019$), distance moved ($P = 0.012$), and

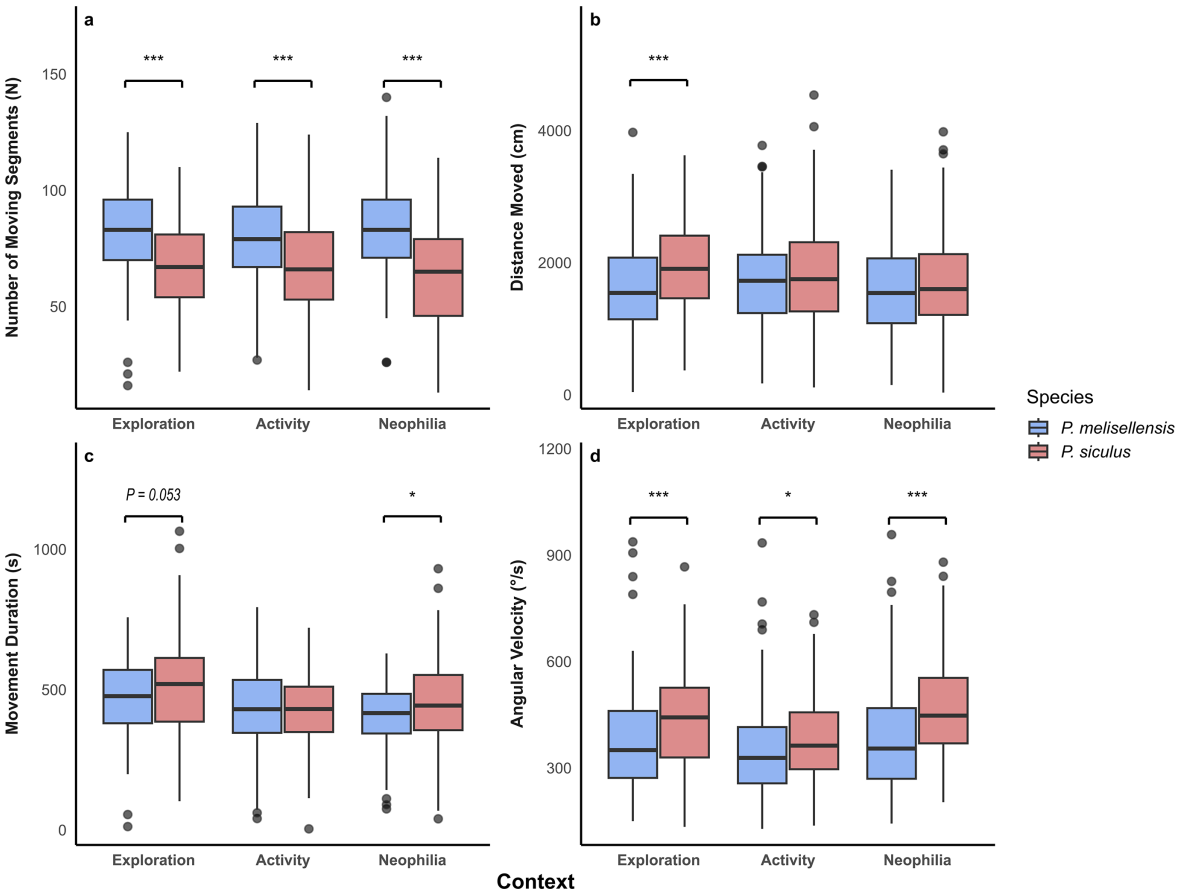

FIG. 1.—Comparison of movement-related traits between two species of wall lizards, *P. melisellensis* and *P. siculus,* across different contexts. (A) number of moving segments (N); (B) distance moved (cm); (C) movement duration (S); (D) angular velocity (rad/s). Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (points beyond the whiskers). Exploration = a new environment, Activity = a familiar environment, Neophilia = a familiar environment with a novel object. *$P < 0.05$, ***$P < 0.001$.

movement duration ($P = 0.003$). Sex did not significantly affect any measured variable in this context (Supplemental Table S1).

For the familiar environment (Context 2: activity), species differed for the number of moving segments (*P. melisellensis;* $P < 0.001$) and angular velocity (*P. siculus* higher; $P = 0.039$), but not for distance moved or movement duration (Fig. 1 and Supplemental Table S1). Location influenced angular velocity ($P = 0.041$), distance moved ($P = 0.048$), movement duration ($P = 0.008$), and the number of moving segments ($P = 0.001$; Supplemental Table S1). Post-hoc comparisons showed Sinj lizards had higher angular velocity than Knin ($P = 0.013$), Knin lizards moved greater distances than Pag ($P = 0.003$), Knin lizards had longer movement durations than both Pag ($P = 0.046$) and Sinj ($P = 0.002$); however, no significant differences were found in the number of moving segments (Supplemental Table S2). Sexes differed, with males showing higher angular velocities than females ($P = 0.016$). SVL was a significant predictor, negatively associated with the number of moving segments ($P = 0.022$; Supplemental Table S1).

In the familiar environment with a novel object (Context 3: neophilia), introducing a novel object showed strong effects. Species differed in the number of moving segments (*P. melisellensis* higher; $P < 0.001$), movement duration (*P. siculus* inferred longer; $P = 0.01$), and angular velocity (*P. siculus* higher; $P < 0.001$), but not for distance moved (Fig. 1; Supplemental Table S1). Sex was a significant predictor for angular velocity (males higher; $P = 0.002$). Location affected angular velocity ($P = 0.002$) and the number of moving segments ($P < 0.001$; Supplemental Table S1), with Sinj lizards showing higher angular velocity than Knin ($P = 0.012$) and Pag ($P = 0.035$), while Pag lizards had more segments than Sinj ($P = 0.002$; Supplemental Table S2). Morphological factors were context-specific: SVL negatively influenced the number of moving segments ($P = 0.012$), while SMI negatively affected angular velocity ($P = 0.029$; Supplemental Table S1).

For latency to first contact of the novel object, the log-logistic distribution was selected as best for the AFT model (Supplemental Table S4). Species differed in how they interacted with the novel object: *P. siculus* had a higher contact frequency ($P = 0.001$) and significantly shorter latency to first contact ($P = 0.048$) than *P. melisellensis* (Fig. 2; Supplemental Table S5). Location did not impact contact frequency or latency. Sex also influenced both variables: males exhibited higher contact frequency ($P = 0.004$) and shorter contact latency ($P = 0.049$) compared to females (Fig. 2; Supplemental Table S5).

Finally, neophobia, assessed by comparing Context 2 with Context 3 to quantify behavioral change between activity in the empty arena and with a novel object (log ratio change between contexts), revealed specific responses. The log ratio of movement duration was significant for species ($P = 0.008$), location ($P = 0.003$), and the species-by-location interaction ($P = 0.002$; Fig. 3; Supplemental Table S1). Post-hoc tests indicated *P. melisellensis* from Knin had a lower log ratio (greater reduction/less increase in movement duration) compared to several other groups (vs. PS Knin $P = 0.029$; vs. PM Pag $P = 0.018$; vs. PM Sinj $P = 0.029$; vs. PS Sinj $P = 0.018$), suggesting a stronger neophobic response for this group (Supplemental Table S3). The log ratio of angular velocity was significantly influenced only by species ($P = 0.012$), with *P. melisellensis* maintaining a lower velocity, suggesting a greater neophobic response. Our analysis found no differences in neophobia as related to the number of moving segments or the distance moved (Supplemental Table S1).

The year of sampling did not significantly influence the results. Time of testing showed only one specific significant effect: it influenced angular velocity in the new environment (Context 1, $P = 0.03$). Time of testing did not significantly affect the other behavioral variables measured within this context (distance moved, movement duration, number of moving segments), nor did it significantly influence any measured variables in the subsequent contexts (Supplemental Tables S1, S4). Sexes differed in all morphological traits, and species significantly differed in interlimb ratio and SMI (see Supplemental Table S6 and Figure S2, available online).

Discussion

Traits such as exploration and neophilia can shape ecological interactions and adaptations across species (Rodríguez-Prieto et al. 2011; Ward-Fear et al. 2018; Damas-Moreira et al. 2019). Overall, we found that *P. siculus* was more active, more explorative, more neophilic, and less neophobic compared to *P. melisellensis*. Additionally, we observed sexual dimorphism in both species in angular velocity in familiar and neophilic contexts, with males of both species being more neophilic than females. Differences in morphological traits further emphasize the distinction between larger *P. siculus* and smaller *P. melisellensis*. Previously, we studied lizards in the Sinj region and found that *P. siculus* showed higher exploratory and reduced risk-taking behavior and greater food consumption than *P. melisellensis* (Glogoški et al. 2024). To extend our results beyond a single population, here we compared three distinct populations of syntopic lizards and measured more variables to understand the following behaviors: activity, exploration, neophilia, and neophobia.

The observed behavioral differences likely facilitate niche partitioning and syntopic coexistence of *P. siculus* and *P. melisellensis*. Mettke-Hofmann et al. (2002) observed that across parrot species, neophobia and exploration varied depending on the species' diet, suggesting that these traits may influence resource use under competitive conditions. The elevated neophobia observed in *P. melisellensis* may suggest a more conservative strategy, as the exploration of novel stimuli can entail higher costs (Walsh et al. 2018). In parallel, the higher exploration and neophilia observed in *P. siculus* may facilitate a specific response to resource scarcity: while *P. melisellensis* maintains higher overall prey diversity across habitats, *P. siculus* shows the capacity to increase diet disparity (including plants) specifically when facing resource limitations on smaller islands (Taverne et al. 2019). This is supported by findings from Greggor et al. (2015) and Ferrari et al. (2015), who observed that animals with lower neophobia are more likely to utilize novel resources. Although neophilia can facilitate the exploration of alternative resources, it also puts animals at greater risk of predation (Tebbich and Teschke 2014). However, in our previous research on a single population (Glogoški et al. 2024), we found that *P. siculus* takes fewer risks, meaning it could be compensating with other behaviors for the negative aspects of increased neophilia. Furthermore, Moretti

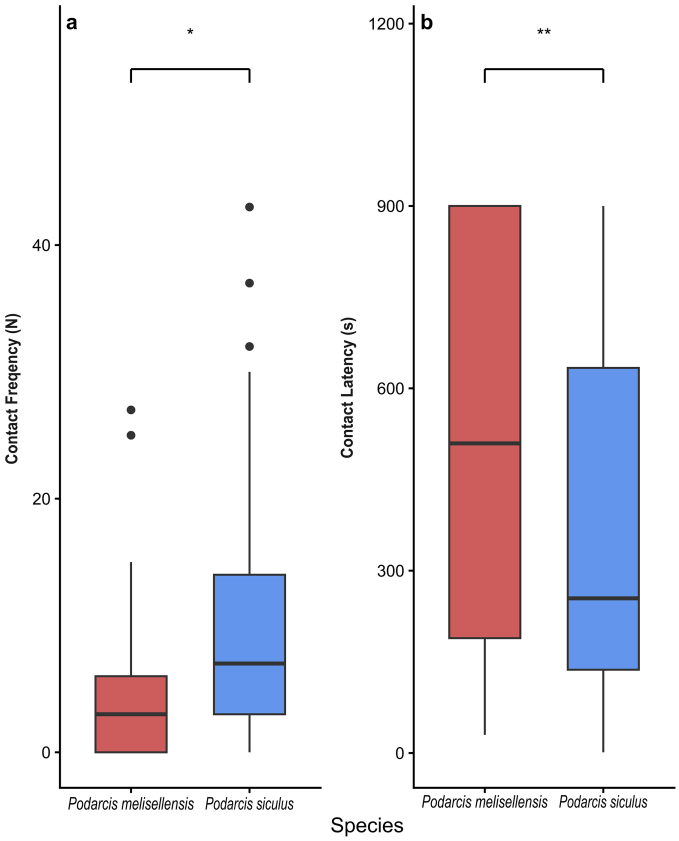

FIG. 2.—(A) Contact frequency (N) and (B) contact latency (S) in response to a novel object in two species of wall lizards, *P. melisellensis* (PM) and *P. siculus* (PS). Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and points beyond the whiskers. $*P < 0.05$, $**P < 0.01$.

et al. (2015) propose that variations in neophilia might enable species to exploit different aspects of a shared environment, thus facilitating sympatric coexistence. Reinforcing these observations, recent studies have specifically highlighted that introduced populations of *P. siculus* are more exploratory and neophilic than other native sympatric species like *Podarcis virescens* (Damas-Moreira et al. 2019), *Podarcis milensis*, and *Podarcis erhardii* (Limnios et al. 2022).

We can infer from their movement patterns that *P. siculus* and *P. melisellensis* exhibit differing foraging strategies linked to their behavioral profiles (Cooper 2005). *P. siculus*'s higher exploratory and neophilic behavior allows it to adopt a more active foraging strategy characterized by longer movement distances, fewer stops per unit time, and higher angular velocity compared to *P. melisellensis*. Consequently, this exploratory capacity likely facilitates the exploitation of diverse resources across a wider spatial range. High exploration could also imply rapid assessment of the environment coupled with high levels of locomotion, suggesting what is often termed a more proactive behavioral type (Sih et al. 2004; Rodríguez-Prieto et al. 2011; Careau and Garland 2012). This interpretation aligns with certain life history and risk-reward trade-off predictions, which propose positive correlations between activity, exploration, energetic expenditure, and locomotor performance (Le Galliard et al. 2013). Such active foraging may explain the distinct response pattern observed in *P. siculus*, where diet disparity increases on smaller, resource-limited islands—a negative correlation with island size contrasting with the positive correlation observed in *P. melisellensis* (Taverne et al. 2019). Indeed, *P. siculus* has been shown to often move more than other sympatric species, which may aid it in resource exploitation and competitive ability (Damas-Moreira et al. 2020; Limnios et al. 2022). This aligns with findings that widely foraging lacertids capture significantly more food relative to their maintenance needs. Conversely, the less active strategy of *P. melisellensis* likely conserves energy through reduced rates of movement (Sparrow and Newell 1998; McDuie et al. 2019). Consistent with the sit-and-wait foraging mode, this strategy is typically associated with the capture of mobile, active prey that bring themselves to the predator, rather than sedentary items that require energy-intensive searching (Donihue 2016). Such behavioral divergence in foraging strategies may facilitate syntopy through resource partitioning, thereby reducing niche overlap and enabling stable coexistence (Webber et al. 2020).

The observed differences in angular velocity between the sexes indicate differing strategies for males and females in familiar environments and when faced with a novel stimulus. Female lizards have been shown to have a higher capacity or attentiveness for processing visual signals, probably requiring a decreased rate of angle change during exploration (Nava et al. 2009). This finding supports the common concept that males engage in riskier behavior to enhance their reproductive success by encountering and securing more mates (Clark et al. 2016; Cooper 1999; Martín et al. 2003).

We observed differences between locations across different contexts in almost all exploratory variables, which suggests a strong influence of habitat characteristics on the exploratory behavior of lizards. The lack of significant species × location interaction indicates consistently distinct exploration strategies between species across three syntopic populations of *P. siculus* and *P. melisellensis*, highlighting their specialized adaptations to different ecological niches and also indicates stable behavioral strategies within each species. Similarly, stable exploratory behavior was also reported in two populations of Great-tailed Grackles (*Quiscalus mexicanus*) on the edge range and within the core range (Logan et al. 2023). Among the four exploratory behavior measures, only movement duration in neophobia had interaction between species and location, *P. melisellensis* from Knin differed from both other locations and from *P. siculus* in the same location, suggesting that certain aspects of exploratory behavior may be more sensitive to local environmental conditions than others.

The higher exploratory behavior observed in *P. siculus* suggests that, in this invasive species, elevated exploration may represent a preexisting trait that facilitates invasiveness rather than a characteristic selected during the invasion process. A similar phenomenon was also observed in gray squirrels (*Sciurus carolinensis*), showing heightened cognitive performance in both invasive and native populations (Chow et al. 2021). *Podarcis siculus* increased exploration could explain earlier documented instances when it outperformed other lizard species (Capula et al. 2002; Ribeiro and Sá-Sousa 2018), often leading to competitive exclusion. Notably, *P. siculus* led to the extinction of *P. melisellensis* on the small island of Pod Mrčaru following its experimental introduction (Herrel et al. 2008), and its dominance has also been

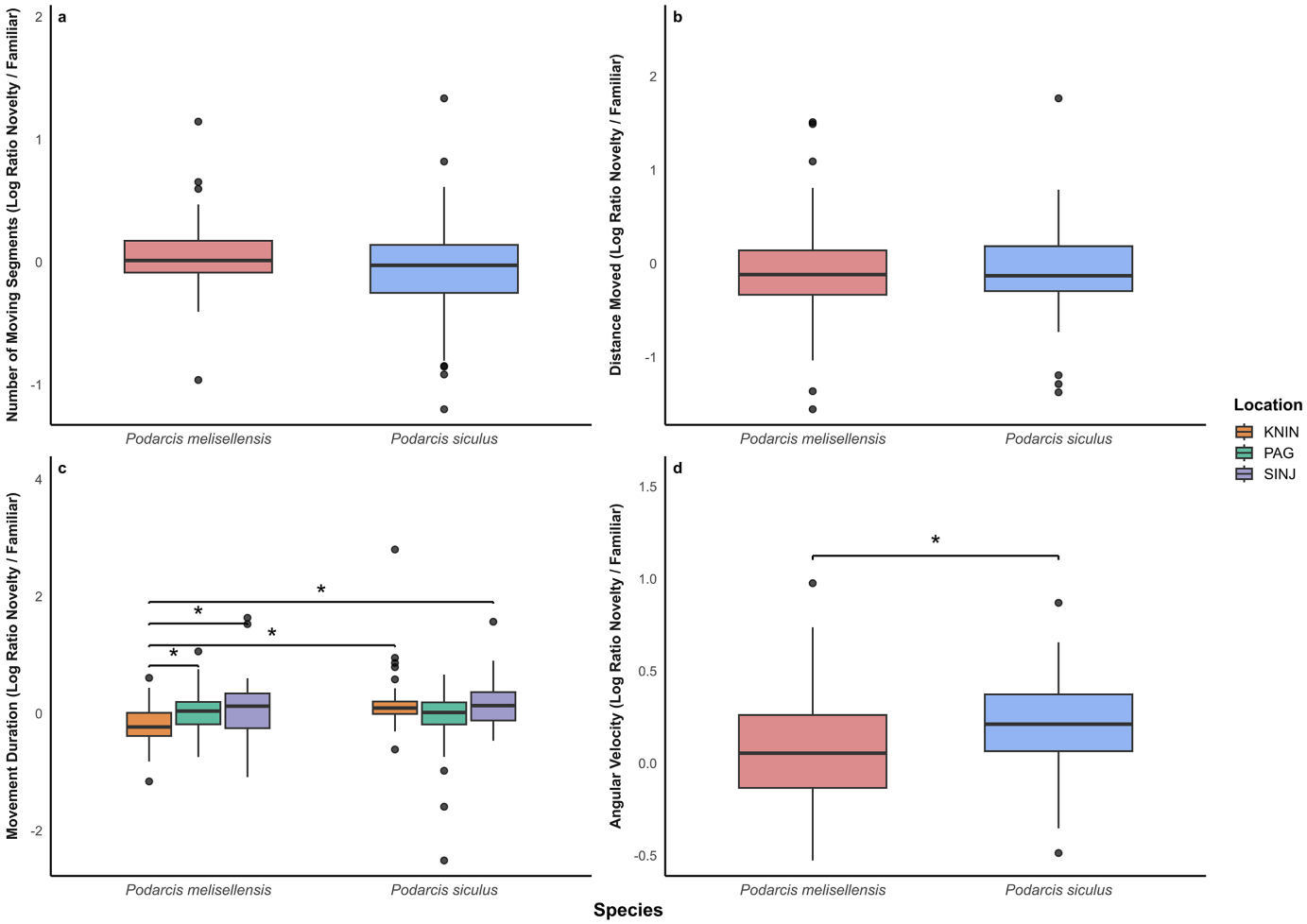

FIG. 3.—Comparison of neophobia between *P. melisellensis* and *P. siculus*. Neophobia was assessed by the change in behaviors expressed in the presence of a novel object relative to behaviors in a familiar environment but without a novel object (log ratios, see Table 1). Neophobic behaviors were: (A) number of moving segments (N); (B) distance moved (cm); (C) movement duration (S); (D) angular velocity (rad/s). A lower log ratio indicates a stronger neophobic response. For movement duration (C), species and location (Knin, Pag, and Sinj) comparisons are presented. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (points beyond the whiskers). *$P < 0.05$.

confirmed in a controlled laboratory setting (Downes and Bauwens 2002). These findings emphasize how behavioral traits influence interspecies interactions, potentially driving competitive outcomes and ecological dynamics.

The propensity of *P. siculus* for higher exploratory behavior, greater neophilia, and lower neophobia positions it well for adaptation to urbanized environments. This aligns with research by Sol et al. (2011) which indicates that species in highly urbanized areas, exhibiting less fear and more opportunistic foraging, are better at solving foraging tasks quickly. Additionally, similar trends are observed in other species such as possums (*Trichosurus vulpecula*; Wat et al. 2020), field mice (*Apodemus agrarius*; Dammhahn et al. 2020), and common voles (*Microtus arvalis*; Mazza et al. 2020), where more exploratory, bolder individuals are more frequently found in urban than rural areas.

Differences in morphology may also play a role in syntopic coexistence. Contrary to our initial hypothesis that behaviors connected to movement would be associated with morphology, we found limited association. The higher interlimb ratio in *P. siculus*, associated with active foraging (Vanhooydonck and Van Damme 2001), may explain the greater exploratory behavior observed here. Only one morphological variable (SMI) significantly influenced one behavioral variable—angular velocity; a lower SMI meant a higher angular velocity in both species. Since SMI is an indicator of the relative size of energy reserves, lower SMI may be explained as lower energy storage in animals that scan the environment more. Furthermore, *P. siculus*'s lower SMI might reflect higher energy expenditure from exploration (Peig and Green 2009), consistent with intermediate endurance measures (Vanhooydonck and Van Damme 2001). Future research on the energy expenditure of each species could connect behavior with the physiological adaptations underlying distinct ecological strategies.

The strength of these results lies in the comparison of a substantial sample of individuals of both sexes from two species when found in syntopy from three distinct locations. In parallel, the lack of direct ecological measurements (such as population density, predation risk, etc.) is a limitation of our current study and highlights the need for future research to include detailed ecological assessments. However, we would like to note that the recent research from Patti et al. (2023) on populations of *P. siculus* outside their native range did not find

an association between population density (a feature directly connected to environmental quality) and exploratory behavior.

Further studies would provide a more robust framework for understanding how different habitat conditions influence the behavior of sympatric species like *P. siculus* and *P. melisellensis*. The presented results establish behavioral differences in activity, exploration, neophilia, and neophobia in two native sympatric species, contributing to our understanding of this syntopic coexistence. Further research is needed to understand the factors that enable sympatry and how these behaviors are influenced at the molecular and physiological levels.

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DATA AVAILABILITY STATEMENT

Data and code are available at Mendeley Data: Gojak et al. (2025). DOI: http://doi.org/10.17632/xsw84zcy7k.1.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-24-00057.S1.

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