BRILL

Amphibia-Reptilia (2024) DOI:10.1163/15685381-bja10189

brill.com/amre

Variability in personalities at sex, population, and taxon-levels in two European lacertid lizards

Roberto Sacchi[1,*], Dario Cominetti[1], Stefano Scali[2], Marco A.L. Zuffi[3], Marco Mangiacotti[1]

1 - Department of Earth and Environmental Sciences, University of Pavia, Via Taramelli 24, 27100 Pavia, Italy
2 - Museo di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy
3 - Museo di Storia Naturale dell'Università di Pisa, 56011 Calci (PI), Italy
*Corresponding author; e-mail: roberto.sacchi@unipv.it
ORCID iDs: Sacchi: 0000-0002-6199-0074; Scali: 0000-0002-4318-751X; Zuffi: 0000-0003-1710-9929; Mangiacotti: 0000-0001-7144-3851

Received 20 December 2023; final revision received 16 July 2024; accepted 17 July 2024;
published online 8 August 2024
Associate Editor: Miguel A. Carretero

Abstract. The variability in behavioural syndromes at different scale levels (e.g., within population or among species) is relevant in ecological and evolutionary patterns. It provides the basis on which natural selection can act to promote evolutionary processes. Additionally, behavioural syndromes can be seen as a form of pre-adaptation, favouring a species' ability to cope with novel selective pressures, establish in new habitats, enhancing population stability, and dealing with deseases and parasites. We assessed repeatability (two replicates for individual) for five behavioural traits (activity, boldness including components of exploration and escape, sociability, and foraging activity) and tested the occurrence of behavioural syndromes in both sexes of three taxa of lacertid lizards: two clades of the common wall lizard (*Podarcis muralis maculiventris* and *P. m. nigriventris*), and the Italian wall lizard (*Podarcis siculus*). All behavioural traits except sociability were repeatable in all the three taxa. Our findings clearly reveal the occurrence of a behavioural syndrome related to the propensity to move through and explore new enviroments, escape from predation risk, and successfully capture prey. We also provide empirical evidence for higher repeatability of behaviours in males compared to females, as well as differences in behavioural syndromes at the taxon-level. These results support the occurrence of personality in both common and Italian wall lizards, highlighting marked variability in personality across different scales. This variability could ultimately reflect the interaction between the specific needs inherent in both sexes within each species, and the environmental/competitive context in which these needs are fulfilled.

Keywords: behavioural syndromes, geographic variation, personality, repeatability, taxon and sex based variation.

Introduction

Individuals within populations commonly exhibit diverse behaviours, and when these differences persist consistently across time and contexts, they are often referred to as animal personality (Bell, Hankison and Laskowski, 2009; Boulton et al., 2014). This consistency in behavioural expression can extend to between-individual correlations across two or more functionally different behavioraltraits, resulting in what we call behavioural syndromes (Sih, Bell and Johnson, 2004; Sih and Bell, 2008). Despite the growing body of research documenting personality and behavioural syndromes across a wide range of animals (including vertebrates from fish to mammals, mollusks and artropods), the adaptive potential and importance of animal personalities in behavioural evolution is still debated (Wolf and Weissing, 2012). Indeed, behavioural consistency varies among individuals (Smith and Blumstein, 2008), and significantly impacts their fitness (Moiron, Laskowski and Niemelä, 2020) making it a crucial factor subject to selection and evolution.

Additionally, there is evidence that behavioural correlations can be quite unstable and

Published with license by Koninklijke Brill BV | DOI: 10.1163/15685381-bja10189
| ISSN: 0173-5373 (print) 1568-5381 (online)

easily formed or broken down over relatively short evolutionary time scales (Polverino et al., 2023). Sticklebacks (*Gasterosteus aculeatus*) experiencing high predation risk show a bold-aggressive behavioural syndrome, contrasting with individuals living under low predation risk (Bell and Sih, 2007). Behavioural traits such as activity, exploration, and boldness exhibit significant variation among populations at geographic scale in the delicate skink (*Lampropholis delicata*), suggesting that behavioural syndromes adapt to local environmental conditions (Michelangeli et al., 2019). Furthermore, in the delicate skink, a recent study analyzing the repeatability of behavioural traits over an extended time period yielded contrasting results: some traits (e.g., activity) remained consistent within individuals even after five months, while others (e.g., boldness and exploring) did not (Polverino et al., 2023). These findings collectively emphasize the importance of understanding how behavioural syndromes remain consistent across space and time in comprehending the evolutionary consequences of animal personalities (Michelangeli et al., 2019).

Variability in personality at geographic or temporal scale is relevant in ecological and evolutionary patterns because it forms the basis for trade-offs in individual resource investment, and serves as a platform for natural selection to promote evolutionary processes (Sih, Bell and Johnson, 2004; Wolf and Weissing, 2012). For example, bold and shy syndromes, combined with spatial or temporal variability in predation risk, may lead to the emergence of selective mechanisms (e.g., frequency dependent selection). These mechanisms allow certain species to adapt to predator occurrence, while those lacking such syndromes cannot (Sih, Kats and Maurer, 2003; Brodin, Johansson and Johanss, 2004). Simultaneously, these selective mechanisms can maintain behavioural syndromes in populations with varying frequencies and intensity, creating a spatio-temporal mosaic depending on the intensity of the selective pressure (Sinervo and Lively, 1996). The trade-off between obtaining food and avoiding predation correlates with the activity in the damselfly *Coenagrion hastulatum*, and the genetic regulation of activity levels explains why this species is abundant in aquatic systems both with and without potential predators (Brodin, Johansson and Johanss, 2004). Parallel results have been observed in the streamside salamander (*Ambystoma barbouri*) regarding correlations among activity, growth rates, and predation risk (Maurer and Sih, 1996; Sih, Kats and Maurer, 2003).

Looking at it from a different perspective, behavioural syndromes can be seen as a form of pre-adaptation, favouring a species' ability to cope with novel selective pressures, establish in new habitats, enhance population stability, and deal with deseases and parasites (Wolf and Weissing, 2012). This interpretation could help explain why some alien species become invasive much more rapidly and effectively than others. Indeed, highly exploratory individuals, along with those possessing personalities conducive to key factors affecting the invasion process, may dominate populations at the invasion front (Chapple, Simmonds and Wong, 2011; Wolf and Weissing, 2012).

Fewer studies have investigated how repeatability of behaviours differ between sexes (Nakagawa et al., 2007; Michelangeli, Chapple and Wong, 2016; Harrison, Noble and Jennions, 2022; Ruiz-Monachesi, Sommaro and Martínez, 2023), often focusing on a single behavioural trait. For instance, behavioural traits related to parental care exhibit greater repeatability in males than females in house sparrows (*Passer domesticus*) (Nakagawa et al., 2007). In contrast, limited sex-specific differences in behavioural sydromes were observed in skinks (Michelangeli, Chapple and Wong, 2016; Goulet et al., 2021).

All these considerations underscore the need for comparative studies that explore the variability of animal personality at various scales, from the intra-population level (i.e., between sexes or morph or age classes within population), to the among-population level (i.e., at a geographical scale within species) and up to the inter-specific levels (i.e., at an evolutionary scale). While such comparisons may not directly identify the determinants of behavioural syndromes or their patterns of evolution (Michelangeli et al., 2019), they are essential for establishing baseline information and formulating specific hypotheses regarding the evolution and maintenance of syndromes (Dingemanse and Wright, 2020).

Lizards, especially skinks, have been extensively used as model species in behavioural syndrome research. They show complex behavioural suites and, simultaneously, are relatively small and easy to keep in the laboratory for behavioural testing. In skinks (genera *Lampropholis* and *Eulamprurus*), behavioural syndromes have been already investigated for correlation with habitat (Moule et al., 2016; Michelangeli et al., 2018), dispersal and aggression (Chapple, Simmonds and Wong, 2011; Michelangeli et al., 2017), spatial learning (Carazo et al., 2014), sociality (Brand et al., 2022), geographic variation (Michelangeli et al., 2019), morphology (Michelangeli et al., 2020), life span (Polverino et al., 2023), sex related differences (Carazo et al., 2014; Michelangeli, Chapple and Wong, 2016; Goulet et al., 2021) as well as for potential bias in experimental design and analyzes (Michelangeli, Wong and Chapple, 2016). Much less work has been conducted on lacertid lizards, even if the number of published articles is rapidly increasing. Studies on behavioral syndromes in lacertid lizards include their relationship with habitat (Horváth et al., 2017; De Meester, Pafilis and Van Damme, 2022), density dependent selection and natal dispersal (Cote and Clobert, 2007; Le Galliard, Paquet and Mugabo, 2015), thermoregulation (Horváth et al., 2020), locomotor performance (Horváth et al., 2017, 2019), habituation to predators (Rodríguez-Prieto, Martín and Fernández-Juricic, 2011) or age (Bajer et al., 2015). Notably, comparative studies among species as well as analyses for sex specific effects among species are few for European Lacertidae (Wu et al., 2023), or have been done with a not fully appropriate statistical approach (Dingemanse and Wright, 2020).

In this study, we examine behavioural syndromes in three taxa of lacertid lizards, specifically two clades of the common wall lizard (*Podarcis muralis*) and the Italian wall lizard (*Podarcis siculus*). Notably, these two clades correspond to the *P. m. maculiventris* (synonym for *P. muralis brongniardii*) subspecies in the Southern Alps, and the *P. m. nigriventris* subspecies in the Central Italy (Yang et al., 2022). *P. muralis* is a medium-sized lacertid (50-70 mm in adult snout-vent length – SVL), occurring in many southwestern European countries (Sillero et al., 2014). It exhibits high ecological plasticity, allowing it to colonize various habitats, from urban areas to natural environments, including cultivated areas (Biaggini et al., 2011). In central Italy, *P. m. nigriventris* show exaggerated color ornaments, larger bodies and heads, and more aggressive, dominant behavior with respect to *P. m. maculiventris*, and all traits that are under sexual selection (Heathcote et al., 2016; MacGregor et al., 2017). *P. siculus*, also a medium-sized diurnal lizard (50-70 mm in SVL), is endemic to the Italian peninsula (Sillero et al., 2014). It occurs in a wide variety of habitats but prefers open habitats with tall vegetation and high insolation levels (Corti, Bologna and Capula, 2011). Furthemore, *P. siculus* has spread beyond its native range, Europe and US, potentially overlapping with and affecting other endangered species (Biaggini et al., 2011; Oskyrko et al., 2022; Zuffi et al., 2022). Specifically, our investigation focuses on whether there are sex specific differences in five behavioural traits (including activity, boldness, exploration, sociability, and prey capture), and whether the structure of behavioural syndromes, in term of repeatability and correlation among traits, differ between sexes and taxa.

Materials and methods

Lizard collection and housing

Between 21st and 30th May 2019, 14 adults lizards (common wall lizard SVL > 50 mm, Sacchi et al., 2017, Italian wall lizards SVL > 50 mm, Henle, 1988), 7 of each sex were collected by noosing for the three taxa: *P. m. maculiventris* were from the town of Pavia (Lombardy, Northern Italy, 45°11′N, 9°9′E, supplementary fig. S1), *P. m. nigriventris* were from the town of Calci (Tuscany, Central Italy, 43°43′N, 10°30′E, supplementary fig. S1), while Italian wall lizards were collected in the village of Castelnuovo Scrivia (Piedmont, Northern Italy, 44°58′N, 8°52′E, supplementary fig. S1). We individually housed lizards in 20 × 30 × 20 cm transparent plastic enclosures with a flat brick as a shelter/basking site and a small bowl of water. We chosed to collect seven males and seven females for each sites as a compromise between the number of individuals we could kept in the lab and the number of trials we were able to perform in a single day, when trying to keep constant the time between replicates of the same individual in the same activity (see experimental settings). We provided mealworms as food (one mealworm/day). The housing room was maintained between 15 and 30 °C (the natural temperature range for the season), and large windows provided natural daylight. An acclimation period of one week was given before starting trials, and we released all lizards at their capture sites following use in trials about three weeks after their capture date.

Experimental settings

Five behavioural trials were measured on each lizard, including activity, boldness in the two components of exploration and escaping, sociability and foraging activity, using standard methodologies described below (Le Galliard, Paquet and Mugabo, 2015; Michelangeli, Chapple and Wong, 2016). Tests have been repeated twice on all individuals, by the same researcher, at one-week interval. Behavioural assays were conducted within a constant temperature room (28 °C) in a predetermined order (to keep constant the time between the two trials), and each individual was tested only once a day. All experimental setups involved two identical opaque walled test arena (100 × 100 × 40 cm) with modifications specific to measuring each behavioural trait (see below). The arena floor was uniformely white to allow automatic tracking of the position of the lizards in video recordings (see below). Before starting the experiment, the focal lizard was heated under a infrared lamp (Reptiles-Planet.com 75 W) for 5 min to reach a normal activity temperature between 28 and 34 °C (Sannolo et al., 2014). Then, the lizard was gently transferred in the arena and acclimatized under an opaque cover for 5 minutes. The cover was then removed, and the movements of the lizard were recorded using a webcam (Microsoft LifeCam HD 3000) mounted on an easel, 60 cm above the arena, and connected to a laptop by a 3-m cable (Mangiacotti et al., 2019; Sacchi et al., 2021). Recording was managed by Free2X software v1.0.0.1, setting quality to 800 × 600 pixels and 15 frames/s. Recording duration was set to 15 min (13 500 frames), starting after the first movement of the lizard. At the end of the trial the body temperature was measured with a handheld infra-red thermometer (Lafayette TRP-39, sensitivity: 0.1 °C; precision: ±2%), and the lizard was moved into their own enclosure. We conducted all the experiments from 09.00 to 14.00 h in accordance with the more intense activity period of lizards. SVL of each lizard was measured prior to experiments to account for body size effects.

Activity (day 1). Activity levels are usually interpreted as the propensity to move in a novel environment (Michelangeli, Chapple and Wong, 2016; Michelangeli et al., 2019; Polverino et al., 2023). To measure activity, lizards were allowed to move freely in the experimental (empty) arena marked with 16 (4 × 4 cm) equal grid squares. Activity was scored based on the number of transitions between grid squares, assuming that greater number of transitions among grid squares represented higher activity levels.

Boldness (day 2 and 3). This trait is most often interpreted as the tendency to take risks, especially in novel situations and is usually measured in relation to anti-predatory behaviours or individual responses to novel cues (Rodríguez-Prieto, Martín and Fernández-Juricic, 2011; Carter et al., 2012; Carazo et al., 2014). However, there is not a single and consistent definition of boldness, and three main approaches have been used (i.e., response to a novel environment, to a novel object, and to predation risk), not necessarily comparable (Carter et al., 2013). Therefore, we assayed boldness by two ways, first we ran an anti-predatory trial (day 2) and then we ran an exploration trial (day 3). In the anti-predatory trial (escaping) we measured the refuge use by a lizard facing with a simulated attack by a human (Le Galliard, Paquet and Mugabo, 2015). The arena was equipped with a heat source on one side to provide a basking spot, and with a brick on the opposite side to provide a refuge. After the acclimation period, we simulated several consecutive attacks with a paintbrush (0.5 cm tick), softly touching the tail to force the lizard into the shelter. Then, we measured the time lizards spent before leaning out the refuge (only the head emerging from the shelter, but the body inside) and the time spent before emerging from the refuge (all the body out of the shelter). In the exploration trial we placed two opaque white plastic partitions in the arena dividing it into three equally sized compartments willing to form an S-path. The first arm of the S contained a refuge (a brick) in which the lizard was inserted and closed for the period of acclimation. Lizards could enter the second arm of the S by an opening such that they were no longer able to see the refuge once entered. The third arm of the S was identical to the second one, but oriented in the opposite direction. The total time lizards spent in the second and third arms of the arena was indicative of higher exploratory behaviour.

Sociability (day 4). We quantified sociability following a modified procedure from Cote and Clobert (2007) and Le Galliard et al. (2015). We measured the simultaneous choice between two heat sources providing a control basking spot and a basking spot with a mirror (15 × 15 cm) simulating the presence of a conspecific. We had previously shown that lizards perceive their own mirror image as a rival, and behave aggressively in response, sometimes even biting (Scali et al., 2019; Coladonato et al., 2020; Sacchi et al., 2021). Each basking spot was provided with a tile (15 × 15 cm) and the lizard could choose between basking with or without a conspecific. The time spent on the basking tiles was recorded after the acclimation time and the total time spent in the tile with the mirror minus the time on the control tile was used as relative sociability score.

Foraging activity (day 5). We measured foraging activity following a modified procedure from Michelangeli et al. (2016): after the acclimation period five crickets, of equal size, were dropped into the arena and we recorded how many crickets were eaten (N), the number of capture attempts (NTA), and the number of successfull attempts (NSA). Then we computed the overall foraging score FS (Michelangeli, Chapple and Wong, 2016) as follow: FS = (N/5)/(NTA/NSA).

Statistical analyses

We were interested to test whether differences in behaviour were consistent within individual, and to assess to what extent differences in behaviour depend on sex and taxa. To do this, we used random slope linear mixed models (LMM), one for each behavioural trait, to partition the variance between the fixed components, accounting for the variability in behaviour common to all individuals, and the random component including the individual identity, representing the portion of the behavioural variance proper to each individual. The repeatable part of this last variance corresponds to the individual personality (Dingemanse and Wright, 2020). The interaction sex × taxon entered the model as random slope, in order to estimate a random effect at individual level specific to males and females within each taxon. Consequently, the model estimated seven different variances, i.e., three among males within each taxon ($\sigma^2_{pmn:m}$, $\sigma^2_{pmm:m}$, and $\sigma^2_{sic:m}$), three among females within each taxon ($\sigma^2_{pmn:f}$, $\sigma^2_{pmm:f}$, and $\sigma^2_{sic:f}$) and the within individual variance (σ^2_{error}). All these three σ^2 allow the estimation of six intraclass correlation coefficients (ICCs) that can be used to assess the repeatability within individual (e.g., $\mathrm{ICC}_{sic:m} = \sigma^2_{sic:m}/(\sigma^2_{sic:m} + \sigma^2_{error})$), which corresponds to the individual personality specific for each sex in each taxon. The fixed component of the model included the SVL, the body temperature, the date (julian date referred to 1st April) and time of the day (hour after 8:00 a.m.) to account for seasonal and diurnal effects. All fixed effects were standardized to zero-mean and unit-variance. LMMs were fit in a Bayesian analytical framework available in the package STAN (https://mc-stan.org/), using flat normal priors ($\mu = 0$ and $\sigma = 100$) for intercept, coefficients, and standard deviations. For all models, Markov Chain Monte Carlo parameters were set as follows: number of independent chains = three; number of iterations = 750 000; burning = 50 000; thinning = 175. Convergence was checked, and results from the posterior distribution are reported as the half sample mode (HSM) (Bickel and Frühwirth, 2006) plus 95% (or 50%) highest density intervals (HDI_{95}; HDI_{50}) (Kruschke, 2010). Data preparation, model settings, call to STAN, and posterior elaborations were done in R 4.0 (R Core Team, 2022) using the package brms (Bürkner, 2017), modeest (Poncet, 2012), and HDInterval (Meredith and Kruschke, 2018).

We also tested for the occurrence of behavioural syndromes by estimating patterns of covariance between pairs of behavioural traits using the Bayesian mixed-effects multivariate models (Dingemanse and Wright, 2020; Polverino et al., 2023) implemented in the package MCMCglmm (Hadfield, 2010). In a first model, we included all the five behavioural traits as response matrix not considering sex and taxon, and always using the standardized (zero-mean and unit-variance) SVL, body temperature, date and time of the day as fixed component. Non-informative priors were used (expected variance V = diag (5); degree of belief nu = 1.002), and model was run for 750 000 iterations after a burn of 50 000 iterations, and thinned by 175 iterations. Model convergence was visually assessed by checking posterior density plots. Then, we computed the posterior distributions of the among-individual correlations among pairs of traits by dividing the corresponding covariance by the product of the square root of their variances (Houslay and Wilson, 2017).

Finally, we used the same model to look for possible associations between the behavioural syndrome and sex or taxa. Before being included in the response matrix, sex and taxon were transformed into dummy variables as it follows: sex was firstly converted in a 0/1 variable (0 for females and 1 for males), and susequently scaled to have zero-mean and unit-variance. therefore, any positive correlation indicates association with males, while negative with females. By the same way, the taxon was trasformed into two new 0/1 variables, one for *P. m. maculiventris* (1 for the taxon and 0 for the other two) and one for *P. m. nigriventris* (in which 1 is for the taxon and 0 for the other two), which have been scaled to zero-mean and unit-variance. Therefore, any positive correlation with these variables indicates association with the corresponding taxa, while negative correlations with both variables indicate association with *P. siculus*. These three new variables and the four behavioural traits involved in the syndrome (i.e., activity, the two components of boldness and foraging activity, see results) were assembled in the response matrix. The fixed and random components were the same as in the previous model, as well as all the settings for prior and number of iterations. As in the previous model, posterior distributions of the among-individual correlations among pairs of traits and with sex and taxa were computed by dividing the corresponding covariance by the product of the square root of their variances.

Results

When considering the overall response of sexes and species together, we found that activity, boldness, especially for the exploring component, and foraging activity were repeatable (table 1). By contrast, sociability had very low

Table 1. Output (half sample mode and high density intervals, HDI) of the random slope linear mixed-effect models for each of the five behavioural traits examined in this study, showing the fixed effects, the within-individual variance (σ^2_{error}), the between-individual variance estimated for each sex in the three taxa, and the corresponding repeatability (Intraclass correlation coefficient, ICC). β and σ^2 for foraging activity have been multiplied by 10^3.

Fixed effects	β (HDI$_{95}$)	Random slope	σ^2 (HDI$_{95}$)	ICC (HDI$_{95}$)
Activity				
SVL	8.75 (−8-24.53)	*P. m. maculiventris* females	217 (0-1360)	0.09 (0-0.44)
Temperature	−1.31 (−14.3-10.66)	*P. m. maculiventris* males	1295 (0-5415)	0.39 (0-0.75)
Date	27.4 (11.01-45.24)	*P. m. nigriventris* females	2753 (0-9918)	0.58 (0.09-0.89)
Hour	7.56 (−6.89-21.85)	*P. m. nigriventris* males	5533 (31-16 560)	0.73 (0.31-0.95)
		P. siculus females	1007 (0-4928)	0.33 (0-0.73)
		P. siculus males	2847 (4-10 592)	0.58 (0.15-0.91)
		Error (within-individual variance)	2023 (1270-2929)	–
Boldness (Escaping)				
SVL	−0.83 (−89.49-93.8)	*P. m. maculiventris* females	7251 (0-42 778)	0.04 (0-0.24)
Temperature	−15.84 (−103.16-68.58)	*P. m. maculiventris* males	29 760 (0-105 772)	0.16 (0-0.43)
Date	−8.48 (−17.32-0.22)	*P. m. nigriventris* females	33 608 (0-115 403)	0.17 (0-0.46)
Hour	−20.75 (−110.88-67.02)	*P. m. nigriventris* males	72 947 (544-203 500)	0.32 (0.03-0.62)
		P. siculus females	27 208 (1-101 804)	0.15 (0-0.43)
		P. siculus males	63 084 (196-188 980)	0.28 (0.02-0.58)
		Error (within-individual variance)	158 192 (103 285-225 504)	–
Boldness (Exploring)				
SVL	−0.34 (−1.12-0.41)	*P. m. maculiventris* females	0.74 (0-4.10)	0.12 (0-0.46)
Temperature	4.54 (3.84-5.21)	*P. m. maculiventris* males	8.65 (0.37-22.74)	0.62 (0.29-0.88)
Date	−0.81 (−1.59-0.04)	*P. m. nigriventris* females	2.95-14.48)	0.36 (0-0.75)
Hour	0.29 (−0.46-1.02)	*P. m. nigriventris* males	14.67 (1.54-40.31)	0.74 (0.43-0.94)
		P. siculus females	3.17 (0-14.84)	0.37 (0-0.75)
		P. siculus males	15.11 (1.02-40.44)	0.74 (0.44-0.93)
		Error (within-individual variance)	5.24 (3.35-7.59)	–
Sociability				
SVL	−35.12 (−140.91-75.58)	*P. m. maculiventris* females	3082 (0-24 624)	0.01 (0-0.08)
Temperature	114.49 (3.75-218.16)	*P. m. maculiventris* males	17 639 (1-76 920)	0.05 (0-0.21)
Date	−59.97 (−167.46-51.97)	*P. m. nigriventris* females	15 628 (1-69 457)	0.05 (0-0.19)
Hour	−8.18 (−114.17-104.37)	*P. m. nigriventris* males	40 931 (82-138 385)	0.12 (0-0.32)
		P. siculus females	18 284 (1-79 597)	0.06 (0-0.21)
		P. siculus males	45 237 (151-149 211)	0.13 (0-0.34)
		Error (within-individual variance)	306 723 (219 486-422 040)	–
Foraging activity				
SVL	7.79 (−22.11-36.15)	*P. m. maculiventris* females	1.670 (0-60.155)	0.22 (0-0.54)
Temperature	−17.69 (−38.42-4.11)	*P. m. maculiventris* males	6.948 (0-22.618)	0.54 (0.12-0.85)
Date	−47.11 (−74.36-18.61)	*P. m. nigriventris* females	5.688 (0-21.752)	0.49 (0.04-0.82)
Hour	−16.83 (−39.27-71.6)	*P. m. nigriventris* males	14.60 (0.62-44.63)	0.71 (0.32-0.95)
		P. siculus females	10.09 (0.15-31.44)	0.63 (0.24-0.91)
		P. siculus males	21.29 (1.63-58.49)	0.78 (0.46-0.95)
		Error (within-individual variance)	5.94 (3.33-8.88)	–

repeatabilities in all the six groups we considered in the analysis (table 1).

However, relevant differences emerged both between sexes within taxon, and among taxa within sex, in each of the four repeatable behavioural traits. Males had higher repeatability than females in all behavioural traits (table 1), as in the majority of cases the σ^2 of males was more than double that in females (fig. 1, supplementary table S1). In both sexes, the σ^2 of *P. m. nigriventris* exceeded, often more than double, the corresponding values of *P. m. maculiventris* (fig. 2, supplementary table S2), leading to systematically higher repeatability values (table 1). The σ^2 was not dissimilar between *P. m. nigriventris* and *P. siculus* (fig. 2, supplementary table S2), as well as the repeatabilities (table 1). Consequently, σ^2 and the corresponding ICC values were larger in *P. siculus* than *P. m. maculiventris* (table 1). Nonetheless, the differences between *P. m. nigriventris* and *P. siculus* with respect to *P. m. maculiventris* were much more evident in females than in males, in all behavioural traits (fig. 2, supplementary table S2).

Irrespective of sex and taxon, we found that the correlations between activity and the two components of the boldness were all positive (fig. 3, supplementary table S3). Furthermore, foraging activity also correlated with the two boldness related traits, but only weakly with activity (fig. 3, supplementary table S3). Altogether, these findings provided enough evidence for a behavioural syndrome involving these four traits. On the other hand, sociability did not correlate with any of the other behavioural traits (fig. 3, supplementary table S3).

When examining the four traits of the syndrome in relation to sex and taxa, we discovered a weak but clear association between the syndrome with males. Specifically, three out four of behavioural traits, especially foraging activity, were positively correlated with sex (fig. 4, supplementary table S4). *P. m. nigriventris* exhibited a strong association with activity, particularly related to the two components of boldness (fig. 4, supplementary table S4). However, a different pattern emerged for *P. m. maculiventris*, which was positively associated with activity but negatively associated with boldness in both components. Interestingly, *P. siculus* showed a negative association with activity. Notably, no relevant correlations between the syndrome and taxa were observed in terms of foraging behaviour.

Discussion

In this paper, we demonstrated the occurrence of marked personality traits in two species and two subspecies of European lacertides, which are widely distributed in Europe. Additionally, we documented clear differences in personality both among taxa and between males and females within taxon. Briefly, four out of the five behavioural traits we analyzed were repeatable in both subspecies of the common wall lizard (*P. m. maculiventris* and *P. m. nigriventris*) and *P. siculus*. Males consistently showed higher repeatability than females, reflecting their consistently higher variances in each behavioural trait compared to females. Overall, we can identify individuals that consistently show certain levels of mobility, boldness, and foraging effectiveness. The higher repeatability observed in males suggests that among individual differences, such as those between highly mobile and less mobile individuals, are more pronounced in males than in females. Conversely, we could argue that females' personalities are more homogeneous among themselves than in males.

Our results align with what is already known for other lizard taxa, particularly skinks, where personality is influenced by different factors such as sex, ontogeny, and environmental conditions (Carazo et al., 2014; Michelangeli, Chapple and Wong, 2016; Michelangeli et al., 2019; Brand et al., 2022). Thus, our data demonstrate that in lacertid lizards, the same behavioural activities related to how individuals move, explore the environment, and capture and manipulate prey form the basic elements upon which personalities develop. Actually, cues for the occurrence of personalities in lacertid lizards had already been identified in lacertids (Cote and Clobert, 2007; Le Galliard, Paquet and Mugabo, 2015; Horváth et al., 2017; De Meester, Pafilis and Van Damme,

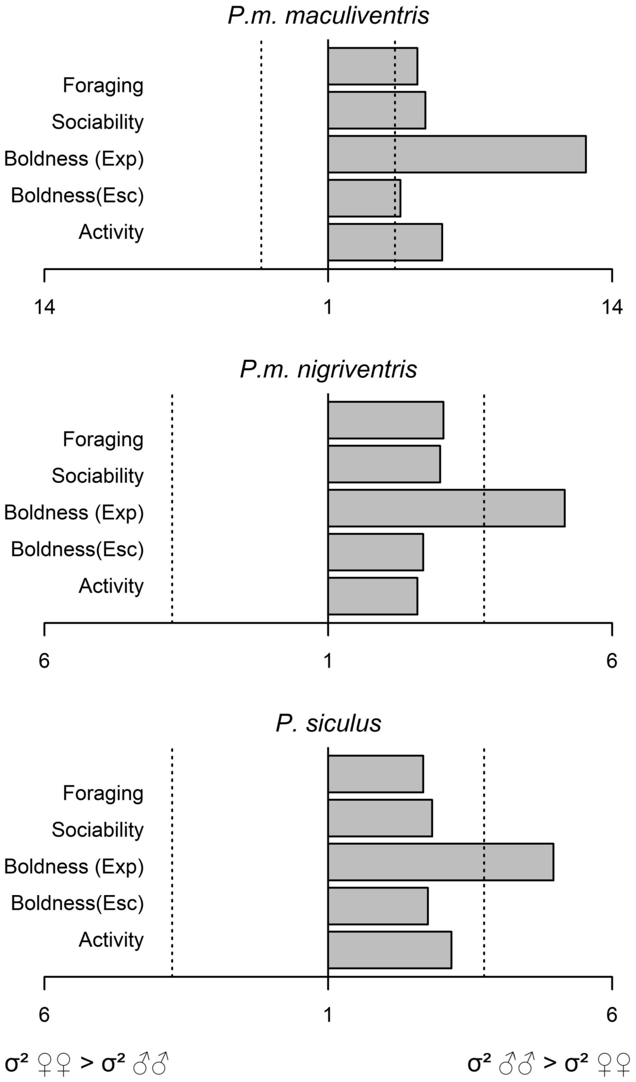

Figure 1. Ratios used to compare σ^2 between sexes as estimated by the LMM models for each taxon in the five behavioural traits analyzed in this study. Ratios are constructed by dividing the larger σ^2 by the smaller σ^2, so that the ratio tends to be greater when the σ^2 of one sex is larger than the other. The solid vertical line (i.e., ratio = 1) corresponds to equal σ^2 in both sexes; gray bars on the left are for larger σ^2 in females, whereas gray bars on the right are for larger σ^2 in males. The vertical dotted lines correspond to a probabilty higher than 70% that σ^2 in one sex is doubble the other (see supplementary table S1 for raw data).

2022). However, these cues have not yet been explored in *P. muralis* and *P. siculus*, nor in association with geographic or of specific sex variability.

However, the statistical approaches used in these studies were not always entirely appropriate (Dingemanse and Wright, 2020), particularly regarding associations with personality. In these cases, additional variables (e.g., sex and environmental variables) were included in LMMs as fixed effects rather than random effects. When examining associations with personality, adding variables (e.g., sex) as fixed effects in a random intercept LMM does not adequately account for differences in personality between males and females. Fixed effect consider the inherent difference between sexes shared by all individuals. Conversely, if we

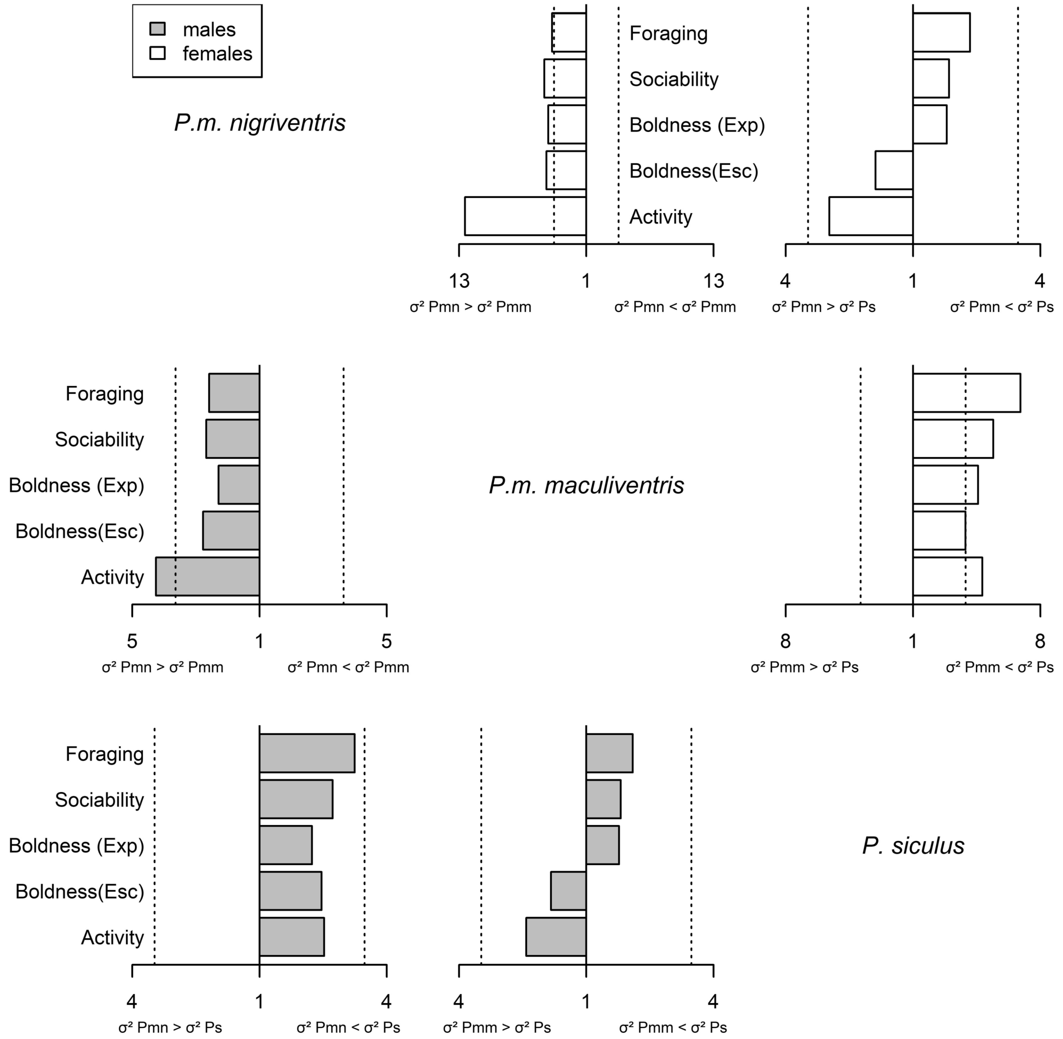

Figure 2. Ratios used to compare σ^2 between species within sex as estimated by the LMM models the five behavioural traits analyzed in this study. Ratios are constructed by dividing the larger σ^2 by the smaller σ^2, so that the ratio tends to be greater when the σ^2 of a species (within sex) is larger than the other. The solid vertical line (i.e., ratio = 1) corresponds to equal σ^2 in both species; gray bars on the left are for larger σ^2 in one species with respect the other and the opposite for gray bars on the right. The dotted lines correspond to a probabilty higher than 70% that the ratio exceeds 2 (see supplementary table S2 for raw data). Ratios between species for males are reported in the lower triangle and those for females are in the upper triangle.

want to investigate whether males and females exhibit different personalities, sex should interact with individual variation by including it as a random effects in a random slope LMM. This approach allow us to estimate sex-specific random effects and, consequently, sex-specific repeatabilities that can be directly compared. We applied this approach to common and Italian wall lizards, demostrating that sexes indeed exhibit different repeatability, resulting in distinct expressions of personality across the analysed behavioural traits.

Several explanations have been proposed to justify the occurrence of a geographic variability in animal personalities. These include responses to among-population variability of predation risk (Bell and Sih, 2007; Brydges, Heathcote and Braithwaite, 2008) and more

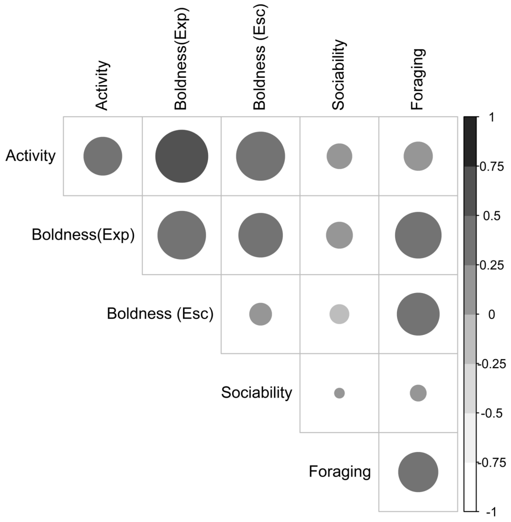

Figure 3. Correlogram between the five behavioural traits as estimated by the MCMCglmm: variances are on the diagonal, correlations in the upper triangle: the larger and darker the spot, the higher the value (see supplementary table S3 for details).

generally, local environmental conditions (Michelangeli et al., 2019). An alternative explanation interprets the geographical variability of personalities as a response to constraints imposed by intrinsic mechanisms, such as genes, physiology or hormones, at population-level (Martins and Bhat, 2014; Michelangeli et al., 2019). For example, zebrafish in Northern India exhibit boldness without aggression or aggression without boldness at population-level, and these associations are maintained by specific selective pressures (Martins and Bhat, 2014). In our study, we provide empirical evidence for the occurrence of a specific pressure that either contrains or promotes geographic variability in personalities at the population or taxon-level. Indeed, *P. m. nigriventris* from central Italy shows an exaggeration of characters, such as size, head size and bite force, that are under sexual selection in this species (Sacchi et al., 2009; While et al., 2015) and other *Podarcis* species (Olsson and Madsen, 1998; Whiting and Miles, 2019). This confers an advantage in male-male competition over *P. m. maculiventris* (While et al., 2015). Given that females do not discriminate between males of the two lineages, whereas males prefer females of their own lineage (Heathcote et al., 2016), genetic exchange with asymmetric introgression of *P. m. nigriventris* into *P. m. maculiventris* occurs in secondary contact zones (While et al., 2015; Yang et al., 2018). *P. m. nigriventris* in central Italy occurs in sympatry with *P. siculus*, which is a larger and more aggressive species (Corti, Bologna and Capula, 2011). Therefore, sympatry and syntopy with *P. siculus* might have led to a much more pronounced variability in personality in *P. m. nigriventris*, resulting in a more shy personality suitable for coexistence in the most advantageous habitats for *P. siculus*, and a more aggressive personality, suitable for coexistance in environments more similar to their own ecological needs. This increased variability in individual personalities would therefore have been advantageous in the secondary contact with the northern lineages, which have never experienced the competition with *P. siculus*. Consequently, the geographic differences emerged in the *P. muralis* could ultimately be due to the specific selective pressure experience by the two lineages in relation to coexistence (or lack thereof) with *P. siculus*.

A second relevant result of this study is the sex-specific effect on personalities in the three taxa. The occurrence and function of sex specific pattern in animal personality it is still debated (Harrison, Noble and Jennions, 2022). Indeed, sex specific behavioural syndromes have been documented for crustaceans (Chapman, Hegg and Ljungberg, 2013), spiders (Pruitt and Riechert, 2009), fish (Schuett and Dall, 2009), and birds (Fresneau, Kluen and Brommer, 2014), while not conclusive results have been obtained for lizards (Michelangeli, Chapple and Wong, 2016; Goulet et al., 2021). Some evidence, albeit limited, has been found for the delicate skinks, where females were more social and faster explorers than males (Michelangeli, Chapple and Wong, 2016). Conversely, no differences in activity, exploration and sociability between sexes were found in the

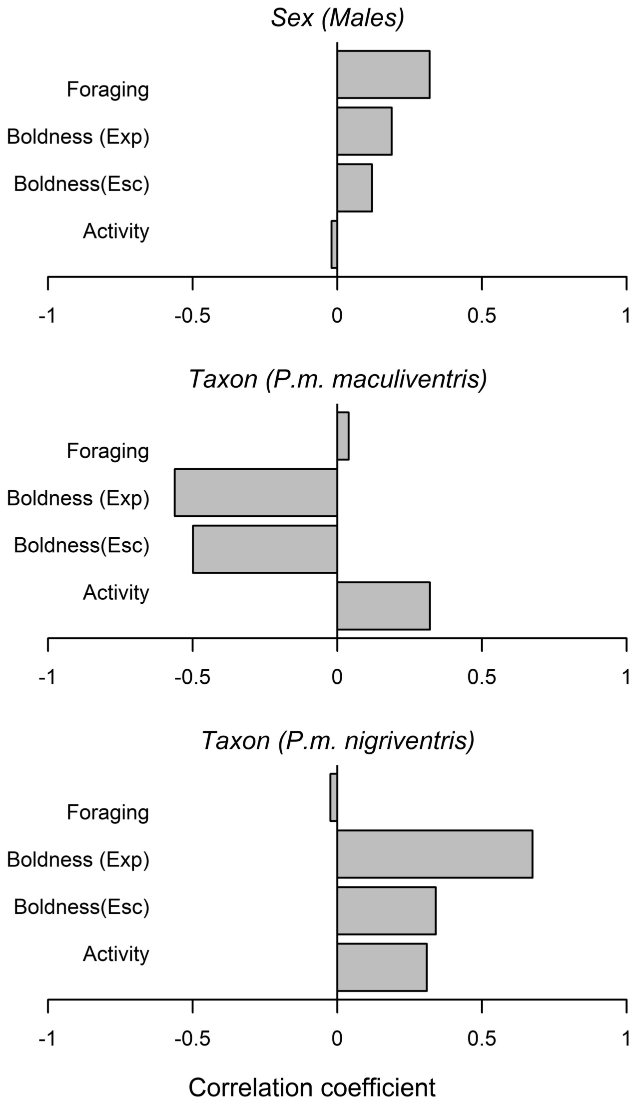

Figure 4. Correlations of the behavioural syndrome (involving four behavioural traits, see supplementary table S3) with sex and taxa as estimated by the MCMCglmm. Positive correlations for sex indicate associations of the syndrome with males (and negative correlations with females). Traits positively correlated with *P. m. maculiventris* and negatively correlated with *P. m. nigriventris* indicate associations of the syndrome with *P. m. maculiventris*. The opposite patterns indicate association of the syndeome with *P. m. nigriventris*. Negative correlations with both taxa indicate a positive association of the syndrome with *P. siculus* (and both positive a negative association).

Southern rainforest skink (Goulet et al., 2021). Lack of sex-based differences in personality among lizards is rather unexpected, considering that male and female adult lacertid lizards face distinct selection pressures, expecially in reproductive contexts. In this taxon, males commonly defend territories or resources essential for reproduction (Whiting and Miles, 2019) and often engage in active combat with each other (Sacchi et al., 2009). The levels of intrasexual competition are such that alternative, even markedly different, reproductive strategies frequently evolve (Sinervo and Lively, 1996). Therefore, a wide variability in behavioural traits related to mobility, propensity to explore novel environments, and responses to predators is expected in males of most lizard species (Samia et al., 2015). In contrast, female lacertid lizards allocate significant resources to egg production, which significantly constraints their ability to move and successfully escape predator attacks (Bauwens and Thoen, 1981; Sinervo and DeNardo, 1996). When individuals have a lot of future reproductive value at stake, selection is predicted to favour risk avoidance, thus promoting cautious movements and more fearful attitudes (Wolf, Van Doorn and Weissing, 2008). Therefore, the conditions for differences in male and females personalities are all present in lacertids, and our data demonstrate that these differences indeed occur. Regardless of species and subspecies, males consistently exhibit higher repeatability in each behavioural trait. The remarkable observation is that this "male syndrome" occurs in the three taxa without substantial variation, suggesting a link to intrinsic of being male features.

We did not find any support for the occurrence of personality in the fifth behavioural trait that we considered, namely sociability, across any of the taxa analized. Overall, all individuals performed similarly and did not discriminate between basking sites. However, the negative results we obtained here align with previous research that used the same experimental setup. For instance, sociability appears to be weakly repeatable in delicate skinks, but this repeatability is not observed within population (Michelangeli et al., 2019). In the case of common lizards, social personalities do exist, characterized by positive and negative reactions in response to conspecific density. However, these social behaviours are strongly context-dependent, specifically related to individual density (Cote and Clobert, 2007), and exhibit limited ontogenic consistency (i.e., they occur only during natal dispersal; Le Galliard, Paquet and Mugabo, 2015). The two species we used in our experiment are phylogenetically related and belong to the same main clade (Zheng and Wiens, 2016). Therefore, the lack of repeatability in sociability could be attributed to the use of individuals in an ontogenetic stage when the behavioural trait does not hold full adaptive significance.

Another significant finding from our data is the clear occurrence of a behavioural syndrome involving individual propensity to explore new environments, escape from and confront predation risks, and successfully capture highly mobile prey. It is essential to note that all these traits are correlated with each other, based on a partitioning of variances into the within-individual and among-individual components, which is the required approach to reveal authentic syndromes (Dingemanse and Wright, 2020). Another intriguing aspect of these behavioural correlations lies in the relationship between reponses to the two tests related to boldness. Indeed, boldness still remains an ill-defined trait, and alternative measurements may assess different aspects of the same personality trait (Carter et al., 2013). For istance, a lack of correlation among alternative measures of boldness has been reported in chickadees (*Poecile gambeli*; Fox et al., 2009), pumpkinseed sunfish (*Lepomis gibbosus*; Coleman and Wilson, 1998) and sticklebacks (*Gasterosteus aculeatus*; Dingemanse et al., 2007). On the other hand, comparing the performances of the same individuals in different tests designed to measure the same personality trait is the main method for test validation. This approach allows researchers to be confident about the specific aspect of personality they are truly measuring (Burns, 2008). Here we found a strong correlation between responses to a novel environment and responses to predation risk within the same individual – both of which are common procedures used to assess boldness. Furthermore, this correlation was consistent among taxa. Therefore, we are confident that these two types of tests effectively capture certain overlap in the personality traits putatively measured by each behavioural test and correlated in the behavioural syndrome. This is a pervasive problem in animal personality research, increasing the risk for all researchers of diagnosing a behavioural syndrome upon finding correlations between two or more personality traits, when in reality the tests employed captured the same personality trait in different contexts (Carter et al., 2013). Disentangling activity apart from exploring is crucial, as they are two different temperaments in an animal. The first pertains to the propensity to move within a given area, regardless of whether it is familiar or unfamiliar. The second relates to the propensity to explore a new area (and consequently take predation risk), directly linked with boldness. There are significant areas of overlapping when planning specific tests to measure these two aspects. For instance, the total area explored by the focal individual in the empty arena during the activity test (day 1) can be interpreted both as a measure of activity and as a measure of exploration. The number of transitions among grid squares does not depend on the total area explored or the familiarity/unfamiliarity of the crossed area. Consequently, it is not affected by boldness. Hence, we believe that the correlation between activity and boldness (in the two forms we measured) reflects an authentic syndrome of lizards rather than the same personality trait in different contexts. Boldness and activity behaviour are important traits in lizards, as they can affect fitness through factors such as the propensity to disperse and competition for territories (Cote, Dreiss and Clobert, 2008; Rodríguez-Prieto, Martín and Fernández-Juricic, 2010). Different propensity to move or explore (i.e., homing) and distinct strategies in territorial defense have actually been detected, for example, in the common wall lizard (Scali et al., 2013, 2021). So, the behavioural syndrome we detected in this analysis might be related to and influenced by how lizards disperse and interact in the competition for resources and mates.

A final outcome of this research is the correlation, albeit weak, of the syndrome with males, supporting the results we obtained in the univariate analyses of each single trait. We also found that the syndrome correlates with taxa, notably with *P. m. nigriventris* (with three out of the four traits involved in the syndrome), confirming the latter to be a more active and bold lineage compared to the other one (*P. m. maculivetris*). The emergence of an overall activity-exploration syndrome, involving the ability to manipulate prey, and the correlation with males and taxa supports the hypothesis that such a trait depends on some constraints intrinsic to sexes and taxa. Additionally, the variability observed in this study could ultimately reflect the interaction between the specific needs inherent in both sexes within each species, and the environmental/competitive context in which these needs are fulfilled. In this scenario, the emergence of different behavioural syndromes in various contexts might reflect the action of selection in promoting and maintaining those combinations of behaviours that, from time to time, maximizes individual fitness.

In this study, we did not take into account the importance of the temporal dimension in the maintenance of behavioural syndromes, which has recently been highlighted (Polverino et al., 2023). We expect that by increasing the number of populations and extending the time frame for analyzing the repeatability of behaviours, new data may emerge to understand how the correlations detected in this study remain stable within taxon, and how much the spatial and temporal variability of the competition between *P. muralis* and *P. siculus* in the areas of sympatry and syntopy contributes to the creation and maintenance of behavioural syndromes.

In conclusion, we demonstrated the occurrence of marked personality in both common and Italian wall lizards, and revealed a marked variability of personality at sex, population, and taxon level. These results provide basic knowledge to understand how selection can promote and maintain combinations of behaviours that maximize individual fitness in lizards.

Acknowledgements. The study was performed in accordance with the European and Italian laws on animal use in scientific research, and all the protocols have been authorized by Italian Environmental Ministry (Aut. Prot.

PNM/000685 22/11/2018, valid for the three years 2019-2021). We would like to thank Alan Jioele Coladonato, Thomas Dadda, Mara Battaiola, Carlotta Pasquariello, Simone Buratti, Cristian Matellini for the help during fieldwork. The authors declared no competing interests.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.26346922

References

Bajer, K., Horváth, G., Molnár, O., Török, J., Garamszegi, L.Z., Herczeg, G. (2015): European green lizard (*Lacerta viridis*) personalities: Linking behavioural types to ecologically relevant traits at different ontogenetic stages. Behav. Processes **111**: 67-74.

Bauwens, B.Y.D., Thoen, C. (1981): Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. **50**: 733-743.

Bell, A.M., Hankison, S.J., Laskowski, K.L. (2009): The repeatability of behaviour: a meta-analysis. Anim. Behav. **77**: 771-783.

Bell, A.M., Sih, A. (2007): Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol. Lett. **10**: 828-834.

Biaggini, M., Bombi, P., Capula, M., Corti, C. (2011): *Podarcis muralis* (Laurenti, 1768). In: Fauna d'Italia, p. 391-401. Corti, C., Capula, M., Luiselli, L., Razzetti, E., Eds, Calderini, Bologna.

Bickel, D.R., Frühwirth, R. (2006): On a fast, robust estimator of the mode: Comparisons to other robust estimators with applications. Comput. Stat. Data Anal. **50**: 3500-3530.

Boulton, K., Grimmer, A.J., Rosenthal, G.G., Walling, C.A., Wilson, A.J. (2014): How stable are personalities? A multivariate view of behavioural variation over long and short timescales in the sheepshead swordtail, *Xiphophorus birchmanni*. Behav. Ecol. Sociobiol. **68**: 791-803.

Brand, J.A., Naimo, A.C., Michelangeli, M., Martin, J.M., Sih, A., Wong, B.B.M., Chapple, D.G. (2022): Social context mediates the expression of a personality trait in a gregarious lizard. Oecologia **200**: 359-369.

Brodin, T., Johansson, F. (2004): Conflicting selection pressures on the growth/predation-risk trade-off in a damselfly. Ecology **85**: 2927-2932.

Brydges, N.M., Heathcote, R.J.P., Braithwaite, V.A. (2008): Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. Anim. Behav. **75**: 935-942.

Bürkner, P.C. (2017): brms: An R package for Bayesian multilevel models using Stan. J. Stat. Softw. **80**: 1-28.

Burns, J.G. (2008): The validity of three tests of temperament in guppies (*Poecilia reticulata*). J. Comp. Psychol. **122**: 344-356.

Carazo, P., Noble, D.W.A., Chandrasoma, D., Whiting, M.J. (2014): Sex and boldness explain individual differences in spatial learning in a lizard. Proc. R. Soc. B Biol. Sci. **281**: 20133275.

Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlishaw, G., Heinsohn, R. (2013): Animal personality: What are behavioural ecologists measuring? Biol. Rev. **88**: 465-475.

Carter, A.J., Marshall, H.H., Heinsohn, R., Cowlishaw, G. (2012): How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. Anim. Behav. **84**: 603-609.

Chapman, B.B., Hegg, A., Ljungberg, P. (2013): Sex and the syndrome: Individual and population consistency in behaviour in rock pool prawn *Palaemon elegans*. PLOS ONE **8**: 1-7.

Chapple, D.G., Simmonds, S.M., Wong, B.B.M. (2011): Know when to run, know when to hide: Can behavioral differences explain the divergent invasion success of two sympatric lizards? Ecol. Evol. **1**: 278-289.

Coladonato, A.J., Mangiacotti, M., Scali, S., Zuffi, M.A.L., Pasquariello, C., Matellini, C., Buratti, S., Battaiola, M., Sacchi, R. (2020): Morph-specific seasonal variation of aggressive behaviour in a polymorphic lizard species. PeerJ **8**: e10268.

Coleman, K., Wilson, D.S. (1998): Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. Anim. Behav. **56**: 927-936.

Corti, C., Bologna, M.A., Capula, M. (2011): Podarcis siculus (Rafinesque-Schmaltz, 1810). In: Fauna d'Italia, Reptilia, p. 406-417. Corti, C., Capula, M., Luiselli, L., Razzetti, E., Sindaco, R., Eds, Calderini, Bologna.

Cote, J., Clobert, J. (2007): Social personalities influence natal dispersal in a lizard. Proc. R. Soc. B Biol. Sci. **274**: 383-390.

Cote, J., Dreiss, A., Clobert, J. (2008): Social personality trait and fitness. Proc. R. Soc. B Biol. Sci. **275**: 2851-2858.

Dingemanse, N.J., Wright, J. (2020): Criteria for acceptable studies of animal personality and behavioural syndromes. Ethology **126**: 865-869.

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. J. Anim. Ecol. **76**: 1128-1138.

Fox, R.A., Ladage, L.D., Roth, T.C., Pravosudov, V.V. (2009): Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. Anim. Behav. **77**: 1441-1448.

Fresneau, N., Kluen, E., Brommer, J.E. (2014): A sex-specific behavioral syndrome in a wild passerine. Behav. Ecol. **25**: 359-367.

Galliard, J.F. Le, Paquet, M., Mugabo, M. (2015): An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. J. Evol. Biol. **28**: 1144-1155.

Goulet, C.T., Hart, W., Phillips, B.L., Llewelyn, J., Wong, B.B.M., Chapple, D.G. (2021): No behavioral syndromes or sex-specific personality differences in the southern rainforest sunskink (*Lampropholis similis*). Ethology **127**: 102-108.

Hadfield, J.D. (2010): MCMC methods for Multi-response generalized linear mixed models: The MCMCglmm R package. J. Stat. Softw. **33**: 1-22.

Harrison, L.M., Noble, D.W.A., Jennions, M.D. (2022): A meta-analysis of sex differences in animal personality no evidence for the greater male variability hypothesis. Biol. Rev. **97**: 679-707.

Heathcote, R.J.P., While, G.M., Macgregor, H.E.A., Sciberras, J., Leroy, C., D'Ettorre, P., Uller, T. (2016): Male behaviour drives assortative reproduction during the initial stage of secondary contact. J. Evol. Biol. **29**: 1003-1015.

Henle, K. (1988): Dynamics and ecology of three Yugoslavian populations of the Italian wall lizard (*Podarcis sicula campestris* De Betta) (Reptilia: Lacertidae). Zool. Anz. **220**: 33-48.

Horváth, G., Jiménez-Robles, O., Martín, J., López, P., la Riva, I. De, Herczeg, G. (2020): Linking behavioral thermoregulation, boldness, and individual state in male Carpetan rock lizards. Ecol. Evol. **10**: 10230-10241.

Horváth, G., Mészáros, B., Urszán, T.J., Bajer, K., Molnár, O., Garamszegi, L.Z., Herczeg, G. (2017): Environment-dependence of behavioural consistency in adult male European green lizards (*Lacerta viridis*). PLOS ONE **12**: 1-17.

Horváth, G., Rodríguez-Ruiz, G., Martín, J., López, P., Herczeg, G. (2019): Maternal diet affects juvenile Carpetan rock lizard performance and personality. Ecol. Evol. **9**: 14476-14488.

Houslay, T.M., Wilson, A.J. (2017): Avoiding the misuse of BLUP in behavioural ecology. Behav. Ecol. **28**: 948-952.

Kruschke, J.K. (2010): Bayesian data analysis. Wiley Interdiscip. Rev. Cogn. Sci. **1**: 658-676.

MacGregor, H.E.A., Lewandowsky, R.A.M., D'Ettorre, P., Leroy, C., Davies, N.W., While, G.M., Uller, T. (2017): Chemical communication, sexual selection, and introgression in wall lizards. Evolution **71**: 2327-2343.

Mangiacotti, M., Gaggiani, S., Coladonato, A.J., Scali, S., Zuffi, M.A.L., Sacchi, R. (2019): First experimental evidence that proteins from femoral glands convey identity-related information in a lizard. Acta Ethol. **22**: 57-65.

Martins, E.P., Bhat, A. (2014): Population-level personalities in zebrafish: Aggression-boldness across but not within populations. Behav. Ecol. **25**: 368-373.

Maurer, E.F., Sih, A. (1996): Ephemeral habitats and variation in behavior and life history: Comparisons of sibling salamander species. Oikos **76**: 337.

Meester, G. De, Pafilis, P., Damme, R. Van (2022): Bold and bright: shy and supple? The effect of habitat type on personality-cognition covariance in the Aegean wall lizard (*Podarcis erhardii*). Anim. Cogn. **25**: 745-767.

Meredith, M., Kruschke, J.K. (2018): HDInterval: Highest (Posterior) Density Intervals. Available at: https://cran.r-project.org/web/packages/HDInterval/index.html.

Michelangeli, M., Chapple, D.G., Goulet, C.T., Bertram, M.G., Wong, B.B.M. (2019): Behavioral syndromes vary among geographically distinct populations in a reptile. Behav. Ecol. **30**: 393-401.

Michelangeli, M., Chapple, D.G., Wong, B.B.M. (2016): Are behavioural syndromes sex specific? Personality in a widespread lizard species. Behav. Ecol. Sociobiol. **70**: 1911-1919.

Michelangeli, M., Goulet, C.T., Kang, H.S., Wong, B.B.M., Chapple, D.G. (2018): Integrating thermal physiology within a syndrome: Locomotion, personality and habitat selection in an ectotherm. Funct. Ecol. **32**: 970-981.

Michelangeli, M., Melki-Wegner, B., Laskowski, K., Wong, B.B.M., Chapple, D.G. (2020): Impacts of caudal autotomy on personality. Anim. Behav. **162**: 67-78.

Michelangeli, M., Smith, C.R., Wong, B.B.M., Chapple, D.G. (2017): Aggression mediates dispersal tendency in an invasive lizard. Anim. Behav. **133**: 29-34.

Michelangeli, M., Wong, B.B.M., Chapple, D.G. (2016): It's a trap: sampling bias due to animal personality is not always inevitable. Behav. Ecol. **27**: 62-67.

Moiron, M., Laskowski, K.L., Niemelä, P.T. (2020): Individual differences in behaviour explain variation in survival: A meta-analysis. Ecol. Lett. **23**: 399-408.

Moule, H., Michelangeli, M., Thompson, M.B., Chapple, D.G. (2016): The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity-exploratory behavioural syndrome. J. Zool. **298**: 103-111.

Nakagawa, S., Gillespie, D.O.S., Hatchwell, B.J., Burke, T. (2007): Predictable males and unpredictable females: Sex difference in repeatability of parental care in a wild bird population. J. Evol. Biol. **20**: 1674-1681.

Olsson, M., Madsen, T. (1998): Sexual selection and sperm competition in reptiles. In: Sperm Competition and Sexual Selection, p. 504-570. Birkhead, T.R., Møller, A.P., Eds, Academic Press, London.

Oskyrko, O., Sreelatha, L.B., Hanke, G.F., Deichsel, G., Carretero, M.A. (2022): Origin of introduced Italian wall lizards, *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Squamata: Lacertidae), in North America. BioInvasions Rec. **11**: 1095-1106.

Polverino, G., Buchholz, K.M., Goulet, C.T., Michelangeli, M., Chapple, D.G. (2023): Temporal repeatability of behaviour in a lizard: implications for behavioural syndrome studies. Evol. Ecol. **37**: 401-418.

Poncet, P. (2012): modeest: Mode estimation.

Pruitt, J.N., Riechert, S.E. (2009): Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. Anim. Behav. **78**: 175-181.

R Core Team (2022): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rodríguez-Prieto, I., Martín, J., Fernández-Juricic, E. (2010): Habituation to low-risk predators improves body condition in lizards. Behav. Ecol. Sociobiol. **64**: 1937-1945.

Rodríguez-Prieto, I., Martín, J., Fernández-Juricic, E. (2011): Individual variation in behavioural plasticity: Direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. Proc. R. Soc. B Biol. Sci. **278**: 266-273.

Ruiz-Monachesi, M.R., Sommaro, L.V., Martínez, J.J. (2023): Personality differences between sexes are present in a peaceful lizard, but not in an aggressive one: a chemical communication trial in two Liolaemus species. Can. J. Zool. **12**: 1-12.

Sacchi, R., Coladonato, A.J., Battaiola, M., Pasquariello, C., Buratti, S., Matellini, C., Mangiacotti, M., Scali, S., Zuffi, M.A.L.A.L. (2021): Subjective resource value affects aggressive behavior independently of resource-holding-potential and color morphs in male common wall lizard. J. Ethol. **39**: 179-189.

Sacchi, R., Mangiacotti, M., Scali, S., Ghitti, M., Zuffi, M.A.L. (2017): Effects of colour morph and temperature on immunity in males and females of the common wall lizard. Evol. Biol. **44**: 496-504.

Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M., Galeotti, P. (2009): Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome. Aggress. Behav. **35**: 274-283.

Samia, D.S.M., Møller, A.P., Blumstein, D.T., Stankowich, T., Cooper, W.E. (2015): Sex differences in lizard escape decisions vary with latitude, but not sexual dimorphism. Proc. R. Soc. B Biol. Sci. **282**: 1-7.

Sannolo, M., Mangiacotti, M., Sacchi, R., Scali, S. (2014): Keeping a cool mind: head-body temperature differences in the common wall lizard. J. Zool. **293**: 71-79.

Scali, S., Mangiacotti, M., Sacchi, R., Coladonato, A.J., Falaschi, M., Saviano, L., Rampoldi, M.G., Crozi, M., Perotti, C., Zucca, F., Gozzo, E., Zuffi, M.A.L. (2021): Close encounters of the three morphs: Does color affect aggression in a polymorphic lizard? Aggress. Behav. **47**: 430-438.

Scali, S., Sacchi, R., Azzusi, M., Daverio, S., Oppedisano, T., Mangiacotti, M. (2013): Homeward bound: Factors affecting homing ability in a polymorphic lizard. J. Zool. **289**: 196-203.

Scali, S., Sacchi, R., Falaschi, M., Coladonato, A.J., Pozzi, S., Zuffi, M.A.L., Mangiacotti, M. (2019): Mirrored images but not silicone models trigger aggressive responses in male common wall lizards. Acta Herpetol. **14**: 35-41.

Schuett, W., Dall, S.R.X. (2009): Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. Anim. Behav. **77**: 1041-1050.

Sih, A., Bell, A.M. (2008): Insight for behavioral ecology from behavioral syndromes. Adv. Study Behav. **38**: 227-281.

Sih, A., Bell, A.M., Johnson, J.C. (2004): Behavioral syndromes: An ecological and evolutionary overview. Trends Ecol. Evol. **19**: 372-378.

Sih, A., Kats, L.B., Maurer, E.F. (2003): Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. Anim. Behav. **65**: 29-44.

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.A., Isailović, J.C., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., Pous, P. De, Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., Vences, M. (2014): Updated distribution and biogeography of amphibians and reptiles of Europe. Amphib. Reptil. **35**: 1-31.

Sinervo, B.R., DeNardo, D.F. (1996): Costs of reproduction in the wild: Path analysis of natural selection and experimental tests of causation. Evolution **50**: 1299-1313.

Sinervo, B.R., Lively, C.M. (1996): The rock-paper-scissors game and the evolution of alternative male strategies. Nature **380**: 240-243.

Smith, B.R., Blumstein, D.T. (2008): Fitness consequences of personality: A meta-analysis. Behav. Ecol. **19**: 448-455.

While, G.M., Michaelides, S.N., Heathcote, R.J.P., Macgregor, H.E.A., Zajac, N., Beninde, J., Carazo, P., Pérez i de Lanuza, G., Sacchi, R., Zuffi, M.A.L., Horváthová, T., Fresnillo, B., Schulte, U., Veith, M., Hochkirch, A., Uller, T. (2015): Sexual selection drives asymmetric introgression in wall lizards. Ecol. Lett. **18**: 1366-1375.

Whiting, M.J., Miles, D.B. (2019): Behavioral ecology of aggressive behavior in lizards. In: Behavior of Lizards: Evolutionary and Mechanistic Perspectives, p. 289-319. Bels, V., Russell, A.P., Eds, CRC Press, Boca Raton.

Wolf, M., Doorn, G.S. Van, Weissing, F.J. (2008): Evolutionary emergence of responsive and unresponsive personalities. Proc. Natl. Acad. Sci. U. S. A. **105**: 15825-15830.

Wolf, M., Weissing, F.J. (2012): Animal personalities: Consequences for ecology and evolution. Trends Ecol. Evol. **27**: 452-461.

Wu, Q., Rutschmann, A., Miles, D.B., Richard, M., Clobert, J. (2023): Sex- and state-dependent covariation of risk-averse and escape behavior in a widespread lizard. Ecol. Evol. **13**: e10723.

Yang, W., Feiner, N., Salvi, D., Laakkonen, H., Jablonski, D., Pinho, C., Carretero, M.A., Sacchi, R., Zuffi, M.A.L., Scali, S., Plavos, K., Pafilis, P., Poulakakis, N., Lymberakis, P., Jandzik, D., Schulte, U., Aubret, F., Badiane, A., Lanuza, G.P. i. de, Abalos, J., While, G.M., Uller, T. (2022): Population genomics of wall lLizards reflects the dynamic history of the Mediterranean Basin. Mol. Biol. Evol. **39**: 1-13.

Yang, W., While, G.M., Laakkonen, H., Sacchi, R., Zuffi, M.A.L., Scali, S., Salvi, D., Uller, T. (2018): Genomic evidence for asymmetric introgression by sexual selection in the common wall lizard. Mol. Ecol. **27**: 4213-4224.

Zheng, Y., Wiens, J.J. (2016): Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Mol. Phylogenet. Evol. **94**: 537-547.

Zuffi, M.A.L., Coladonato, A.J., Lombardo, G., Torroni, A., Boschetti, M., Scali, S., Mangiacotti, M., Sacchi, R. (2022): The Italian wall lizard, *Podarcis siculus campestris*, unexpected presence on Gorgona Island (Tuscan Archipelago). Acta Herpetol. **17**: 135-145.