



Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards

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To reduce the impact of biological invasions, we need to understand the behavioural mechanisms that enable some species to be successful invaders. Testing differences in behaviour between sympatric congeneric species with different invasive potential is an opportunity to study specific behavioural traits associated with invasion success. Using the invasive Italian wall lizard, *Podarcis sicula*, and a noninvasive congeneric, the green Iberian wall lizard, *Podarcis virescens*, which live in sympatry in a location that is novel for *P. sicula*, we tested their exploratory behaviour, neophobia and boldness: all traits that should promote invasion success. The invasive *P. sicula* was more exploratory, bold and neophilic than the sympatric native *P. virescens*. Native lizards had highly repeatable behaviour, whereas in *P. sicula* boldness was the only behavioural trait that was repeatable. The behavioural traits of the native species, but not the invasive species, were correlated. A lack of correlation between behavioural traits, as well as a lack of repeatability in two of the three behavioural traits, suggests higher levels of behavioural plasticity in *P. sicula*, which may also explain the success of this lizard during invasions. Our experiment highlights the potential importance of behavioural traits in invasions and provides insight into why *P. sicula* is such a successful invader.

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Biological invasions have enormous ecological and economic costs and are of great concern worldwide. To prevent or limit the impact of invasions, we need to better understand what makes some species successful, and others unsuccessful, invaders (Carere & Gherardi, 2013; Chapple, Simmonds, & Wong, 2012; Holway & Suarez, 1999). Recent work has begun focusing on how behavioural traits at the population and individual levels promote invasion success (Carere & Gherardi, 2013; Chapple et al., 2012; Holway & Suarez, 1999; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). In general, invasive species have been associated with higher levels of aggression (Downes & Bauwens, 2002; Weis, 2010), exploration and boldness (Chapple, Simmonds, & Wong, 2011; Monceau, Moreau, Poidatz, Bonnard, & Thiéry, 2015; Short & Petren, 2008) than noninvasive species. They may be more

likely to disperse (Rehage & Sih, 2004) and they may be more efficient at foraging (Pintor & Sih, 2009; Short & Petren, 2008). These behaviours are likely to promote the progress and success of a species during different stages of the invasion process (Chapple et al., 2012). For example, high levels of boldness and exploration can determine whether individuals leave their native range, enter a human transport vector and exit in a novel location (Chapple et al., 2011; 2012). Once in a new environment, the establishment of a species is often associated with higher levels of boldness and exploration (Chapple et al., 2012; Monceau et al., 2015; Short & Petren, 2008), and lower levels of neophobia (Candler & Bernal, 2015; Griffin, Guez, Federspiel, Diquelou, & Lermite, 2016). These traits could promote the exploitation of resources and also give invasive species an advantage over native ones. During establishment, higher aggression and foraging levels can also give invasive species a competitive advantage over native species, which may increase their establishment success (Downes & Bauwens, 2002; Weis, 2010). After establishment, the expansion of a population's range can depend on the individual's affinity for dispersal, its boldness and exploratory behaviour, aggression levels and sociability (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Gruber,

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Brown, Whiting, & Shine, 2017a; Michelangeli, Smith, Wong, & Chapple, 2017; Rehage & Sih, 2004).

An individual's personality (i.e. repeatable behaviours across time; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf & Weissing, 2012) can be correlated across contexts, forming a 'behavioural syndrome' (Chapple et al., 2012; Sih, Bell, Johnson, & Ziemba, 2004). For example, an individual that is bold in terms of its activity and use of habitat (e.g. active for long periods and/or uses more open habitat) may also be bold when confronted with a predator (e.g. flees late). If this correlation enhances a species' invasion success it is termed an 'invasion syndrome' (Chapple et al., 2012), and can determine the invasion success of a species (Cote et al., 2010; Dame & Petren, 2006; Michelangeli et al., 2017; Monceau et al., 2015; Pintor, Sih, & Kerby, 2009, 2008; Rehage & Sih, 2004). For example, the invasion success of the signal crayfish, *Pacifastacus leniusculus*, is because of a positive correlation between aggression and foraging activity (Pintor et al., 2009). The invasion success of the mosquitofish, *Gambusia affinis* (Cote et al., 2010), and Asian hornet, *Vespa velutina* (Monceau et al., 2015), can also be explained by a positive correlation between their boldness, activity and exploratory behaviour. Interestingly, the correlation found in invasive *V. velutina* was also found in the native *Vespa crabro* (with the invasive species exhibiting greater boldness, activity and exploration), yet the invasive species did not behave consistently while the native species did (Monceau et al., 2015). This suggests that invasive species might be more plastic in their behaviour than native species, which can be a significant advantage when dealing with new challenges and opportunities that arise from novel environments (Sih et al., 2012). The native species are likely to experience consistent selection pressure on behavioural traits, which promotes repeatability across time (Sih et al., 2012).

Behavioural differences between a successful invader and a congeneric native species can shed light on behaviour that promotes invasion success (Holway & Suarez, 1999; Rehage, Barnett, & Sih, 2005). If both congeneric species with different invasive potential are sympatric, then any environmental effects are minimized (as they live sympatrically), and there is an opportunity to better understand behavioural traits associated with invasion success. This comparison not only gives insight into why particular species are successful invaders, but also helps us understand any potential impacts on native species (Carere & Gherardi, 2013; Holway & Suarez, 1999; Phillips & Suarez, 2012). The Italian wall lizard, *Podarcis sicula*, is an invasive species native to the Italian Peninsula and the Adriatic coast but is established in several countries outside its native range (CABI, 2018; Carretero & Silva-Rocha, 2015). It spreads mainly through human transport vectors (Carretero & Silva-Rocha, 2015; Kraus, 2009; Silva-Rocha, Salvi, & Carretero, 2012; 2014), reaching high-density populations and affecting native lizards in new locations (Capula, 1993, 2002; Carretero & Silva-Rocha, 2015; Downes & Bauwens, 2002; Kraus, 2009). About 20 years ago, a population was accidentally introduced to Lisbon, Portugal, from Tuscany, Italy (González de la Vega, González-García, García-Pulido, & González-García, 2001; Silva-Rocha et al., 2012). This population lives in sympatry with the congeneric green Iberian wall lizard, *Podarcis virescens*, but not in syntopy (although they can be found as close as 50 m from each other; Ribeiro & Sá-Sousa, 2018). *Podarcis virescens* is a noninvasive lizard that can occur in transport hubs but has never been recorded in an established population outside its native range. These two congeneric species thus have different invasive potential and live under very similar environmental conditions (i.e. similar predation pressure, urbanization level, habitat, humidity, temperature and prey availability) which makes them a model system to study the role behaviour plays in facilitating invasion success.

We quantified three behaviours typically associated with a species' invasive potential, exploration, neophobia and boldness (Chapple et al., 2012; Griffin et al., 2016; Phillips & Suarez, 2012), and tested how they differed between the invasive *P. sicula* and the native *P. virescens*. We predicted that *P. sicula* would be more exploratory, bolder and less neophobic, given its potential to travel to new places, prosper there and displace native species (CABI, 2018). We also investigated the repeatability of the behavioural traits in each species. We expected *P. sicula* individuals to be less repeatable than *P. virescens* individuals in their behavioural traits, indicating more plasticity in the invasive species. Finally, we investigated whether behavioural traits were correlated within each species, to explore the existence of 'behavioural' and/or 'invasion' syndromes.

METHODS

Study Species and Captive Conditions

We collected 26 *P. sicula* and 29 *P. virescens* from the wild and assayed their behavioural traits. All lizards were adult males with complete or completely regenerated tails. To ensure all lizards were adults, we only collected lizards with femoral pores, and that were larger (snout–vent length, SVL) than the known minimum SVL at sexual maturity for these two species (male *P. sicula*: 55 mm, Capula, Luiselli, & Rugiero, 1993; male *P. virescens*: 40 mm, Geniez, Sá-Sousa, Guillaume, Cluchier, & Crochet, 2014). During capture, we also tried to control for lizard size as much as possible in order to reduce this factor as a potential confounding effect in our study: *P. sicula* ranged from 59.53 to 80.75 mm SVL (average SVL = 74.09 mm, SE = 1.09 mm) and *P. virescens* ranged from 47.87 to 61.05 mm SVL (average SVL = 55.54 mm, SE = 0.77 mm). We also weighed lizards (*P. sicula* = 8.96 ± 0.35 g and *P. virescens* = 3.64 ± 0.14 g), and measured tail size (*P. sicula* = 115.69 ± 4.63 mm and *P. virescens* = 86.97 ± 3.23 mm). We did not test females as the reproductive status of wild-caught females (whether gravid or not or recently postparturient) cannot be assessed with certainty, and the different hormones acting in each reproductive stage could greatly influence their behaviour. Male *Podarcis* spp. typically copulate from March to July, and testosterone levels tend to be synchronous within a locality and breeding season, reducing this problem in males of our model species (Carretero, 2006).

We collected all lizards (both species) during June (spring) from Parque das Nações, Lisbon, Portugal (38°45'41.7N, 9°5'43.8"W) on 2 different days, 2 weeks apart. We assigned these lizards to two separate groups (1 or 2) based on collection date. Lizards were transported to CIBIO-InBIO, at the University of Porto, and acclimatized to captivity for 2 weeks, while being fed every other day with three live mealworms. During the experimental period (2 days at a time), lizards were fed the day before trials commenced and at the end of the second day, after trials had finished (Fig. 1). This also helped with controlling individual variability in mass during experiments. Animals were kept in individual terraria (200 × 300 mm and 200 mm high) at 20–22 °C with constant access to water and a small brick shelter. The room had indirect natural light, as well as artificial lamps set for a photoperiod of 12 h (0800–2000). A 50 W heat cable beneath the enclosure created a thermal gradient.

Experimental Set-up

We separately measured exploration, neophobia and boldness. We quantified each lizard's exploratory behaviour within a novel environment containing four shelters (Fig. 1) by measuring its activity and exploration of the shelters. We measured neophobia as

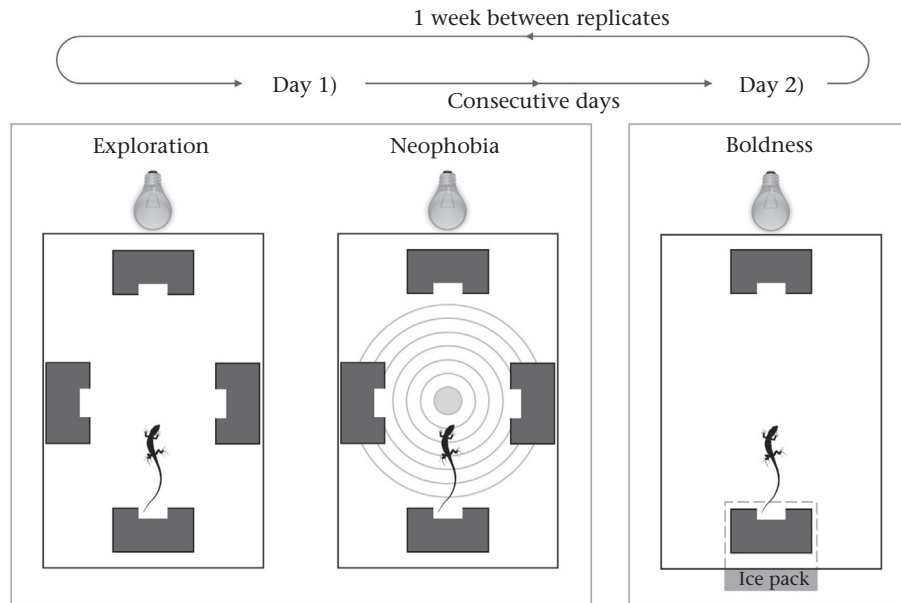


Figure 1. Diagram of the three behavioural trials, and their arena set-up, which were carried out on 2 consecutive days. Regardless of the trial, all arenas always had a 100 W halogen light bulb suspended on one side. Each trial was replicated three times per individual in the same sequence, 1 week apart. Day 1 refers to the first experimental day in each week during which we measured exploration and neophobia. The solid grey circle in the middle of the arena for the neophobia trial was where we placed the novel object. Day 2 refers to the second experimental day in which boldness was measured. All trials took 30 min.

the minimum distance a lizard would get to a novel object (Fig. 1); to measure this distance, we drew a black circle in the centre of the arena, and subsequent circles separated by 2 cm (all circles were drawn beneath the arena). Lastly, we quantified boldness as the amount of time the lizard would take to leave a suboptimal refuge (Fig. 1). All trials were conducted in an experimental arena (320 × 480 mm and 300 mm high); this was a clear plastic container covered with white paper on the outside. Each trial was carried out three times per individual and replicates were 1 week apart. We randomly allocated lizards to one of four different batches across the day (batch = 1, 2, 3 or 4), because the number of lizards that could fit in our experimental room was limited. We measured exploration and neophobia on the same day (day 1) and boldness on the following day (day 2; Fig. 1). At the beginning of each experimental day, lizards were removed from their enclosure and transferred to the centre of the experimental arena. After the neophobia and boldness tests (on different days), lizards were returned to their home enclosures.

Lizards always had access to shelters (black plastic containers: 80 × 120 mm and 50 mm high), with a small opening on one side (40 × 25 mm). We cleaned all cage materials with 96% ethanol between trials. All trials were remotely video-recorded with CCTV cameras.

Exploration

At the beginning of the exploration trial, each lizard was placed under a closed, opaque plastic shelter (circular, 100 mm diameter and 70 mm high) for 5 min, to acclimatize. The arena consisted of four shelters placed along the four sides of the enclosure with the opening facing the centre of the arena (e.g. Gruber et al., 2017a). The trial began when we remotely lifted the shelter using wire, so the lizard could not see the researcher, and lasted for 30 min. For each exploration trial ($N = 3$) we used a different substrate: first dark pine bark, then white sand and then soil. We scored four measures related to exploration: the time spent active (s), time in hiding (s), the frequency of entering the shelters (count) and the number of unique shelters visited during the trial (range 0–4; Table 1). We

used the program BORIS (Friard & Gamba, 2016) to measure the time lizards spent active and in hiding. To create one exploration score for analysis, we performed a principal component analysis (PCA) summarizing our four exploration measures using the princomp function (Jolliffe, 2002) in R version 3.4.2 (R Core Team, 2017). Because these variables have different scales, the PCA used a correlation matrix to standardize the data (Jolliffe, 2002). The first principal component (PC1) explained 52% of the variance in these four traits, and so we used PC1 in all statistical analyses as the exploration score. The time spent active, frequency of entering a shelter and the number of unique shelters visited negatively loaded on PC1, while the time spent hiding positively loaded on PC1 (Table 2). Therefore, as our exploration score decreased, lizards were more exploratory.

Neophobia

Once the exploration trial finished, we ushered the lizard into the closed refuge. We then placed a novel object in the centre of the arena (Fig. 1). After 5 min, we lifted the closed shelter using the same method as before. We recorded the lizard's behaviour for 30 min and later scored the minimum distance between the lizard and the novel object (e.g. White, Meekan, McCormick, & Ferrari, 2013) using the circles in the arena. If the lizard contacted the object, it was given a score of 0 cm (Table 1). For each replicate of the neophobia trial ($N = 3$) we used a different novel object presented in the order: white nonperfumed candles in foil, yellow cupcake paper and blue plastic clothes pegs. We chose these objects because lizards are unlikely to encounter them in the wild and because they look very different. In each replicate, the new object was placed on a novel substrate, because the preceding experiment was exploration, which required novelty in the arena. To control for a potential effect of this combination on the neophobia test, we always used the same combination, and in the same order, for all lizards. For the statistical analyses, we applied a rank transformation to our neophobia score to normalize the data (Riley, Noble, Byrne, & Whiting, 2017). As the neophobia score

Table 1
Behaviours scored in each trial

Trial	Behaviours scored from videos	Variables
Exploration	Activity: time (s) spent moving in the arena (0–1800 s) Hiding: time (s) spent inside a shelter (0–1800 s) Shelter frequency: number of times entered all shelters (0 to unlimited) Shelter number: number of shelters visited (0–4)	Exploratory score (PC1): more sedentary with values \uparrow more exploratory with values \downarrow
Neophobia	Minimum distance: the minimum distance (cm) a lizard would get to the new object during the trial (0–14 ⁺ cm)	Minimum distance (Rank transformed): more neophobic with values \uparrow more neophilic with values \downarrow
Boldness	Latency to leave shelter: time (s) to emerge from the cold shelter (0–1800 s)	Latency to leave shelter: shyer with values \uparrow bolder with values \downarrow

Behaviours were scored from remotely recorded videos of the exploration, neophobia and boldness trials. Explanations of each of the parameters we measured, as well as the response variables used in statistical analyses, and how we interpreted them, are listed.

decreases, it reflects more neophilic behaviour, because the lizard is closer to the novel object.

Boldness

For this trial, the experimental arena had white paper as a substrate, one shelter under the heat lamp to create a hot ('optimal') shelter and another at the opposite end of the enclosure (Fig. 1). An ice pack was placed under this shelter, to create a cold ('suboptimal') refuge (e.g. Riley et al., 2017). The mean substrate temperature inside each shelter was $T_{\text{hot}} = 30^{\circ}\text{C}$ and $T_{\text{cold}} = 9^{\circ}\text{C}$. We placed the lizard in the arena and, after 20 min, we started the boldness trial by lifting the hot refuge and, using a nitrile-gloved hand, we gently tapped the lizard repeatedly to scare it inside the cold shelter. Once inside the cold shelter, the hot shelter was placed back in the arena. We then recorded the lizard's behaviour for 30 min and scored boldness as the latency from when the lizard entered the cold shelter until it emerged (Table 1). We believe both species would be similarly impacted by the suboptimal refuge given both inhabit small refuges in the wild and have similar preferred temperatures (Carretero, 2015).

Ethical Note

We collected lizards from the wild using noosing, which is a standard method for catching many lizard species. A dental floss noose is attached to the end of a telescopic pole and dropped over the lizard's head, before lifting the lizard off the ground. We only collected lizards that appeared healthy and had complete tails. We endeavoured to keep stress to a minimum by only handling lizards when we needed to move them to experimental arenas and by keeping them individually, thereby avoiding any social conflict. We did have to gently tap lizards on the tail base during the boldness assay, but this only resulted in a short-term behavioural response and lizards quickly resumed normal behaviour after they were returned to their home enclosure. All lizards had access to shelter

and a heat source, even during behavioural trials. Also, all lizards ate food (mealworms) when it was offered. After the experiment, all *P. sicula* were euthanized by injection of sodium pentobarbital, as required by the Portuguese Institute for Conservation of Nature and Forests (ICNF) because they are an invasive species and all *P. virescens* were returned to their exact capture location. Our protocols and research were approved by the Macquarie University Animal Ethics Committee (ARA2017/004) and by the Portuguese ICNF (Licence 428/2017/CAPT).

Statistical Analysis

All analyses were performed in R version 3.4.2 (R Core Team, 2017). Prior to analyses we explored our data to ensure it fitted model assumptions using the protocol described in Zuur, Ieno, and Elphick (2010). During this process, we found significant differences in SVL ($R^2 = 0.789$, $\beta = -18.544 \pm 1.318$, $t_{1,53} = -14.070$, $P < 0.001$) and mass ($R^2 = 0.794$, $\beta = -5.285 \pm 0.373$, $t_{1,52} = -14.160$, $P < 0.001$) between species. We therefore did not include SVL or mass in our models, to ensure the assumption of no collinearity between variables was met. Data for this study are accessible at Figshare: <https://doi.org/10.6084/m9.figshare.7822100.v1>.

Differences between species

We examined exploration, neophobia and boldness separately, but used the same analyses. In each model, we tested whether the behavioural trait differed between species using a linear mixed-effects model (LMM, using the function lmer from the lme4 R package; Bates, Mächler, Bolker, & Walker, 2015). These models incorporated the fixed effects of species (*P. sicula* or *P. virescens*), the trial day (the day the trial occurred on, with 1 being the first experimental day), the experimental group (collection day 1 or 2) and the batch (1–4). We also initially tested for an interaction between the fixed effect of species and trial day, which was removed and the model rerun if the effect was nonsignificant. The continuous predictor variable trial day was z-transformed prior to analysis to standardize the variable and facilitate interpretation of interactions if present (Schielzeth, 2010). We also included each lizard's identity as a random effect (intercept only) in the model to control for dependencies in the data due to repeated behavioural trials on the same lizards. When we plotted our data (see Fig. 2), we set the fixed effect of batch to intercept level values because we were not interested in visualizing this effect (we chose group 2 for visualization purposes because it contained more individuals to ensure better estimation of variance components), and we did not include the variance from the random effect of lizard identity.

Table 2
Principal component analysis (PCA) to form an exploratory score

Exploratory behaviours	PC1 loadings
Activity	−0.5026
Hiding	0.2341
Shelter frequency	−0.5864
Shelter number	−0.5905

Exploratory behaviours were combined using a PCA to form an exploratory score ($N_{\text{sicula}} = 78$ and $N_{\text{virescens}} = 87$). The first principal component (PC1) explained 52% of the variation in these four behaviours and was used in statistical analysis as our exploratory score. Higher values of the PC1 reflect less exploratory lizards.

Repeatability of behavioural traits

We estimated the consistency of behavioural traits by calculating adjusted repeatability (R_{adj}) with 95% confidence intervals (CIs) for each behavioural trait (exploration, neophobia and boldness), for each species separately. We used the rpt function from the R package rptR with 1000 permutations and accounted for the same covariates used in our LMM models (Nakagawa & Schielzeth, 2010). To assess whether R_{adj} was significant, we visually examined whether the 95% CIs for each estimate included 0. We also compared differences in repeatability between species by visually examining overlap in 95% CIs.

Correlations between traits

We also investigated correlations between the behavioural traits for each species separately. This analysis was restricted by the sample size of our study, and we were unable to account for dependencies within our data (i.e. repeated measures of the same individuals) or additional explanatory variables (i.e. experimental group, batch, etc.) in this analysis. However, this analysis may afford

some insight into the correlations between behavioural traits in our study species. We calculated Spearman rank-order correlations between all behavioural traits using the function cor in the R package stats, and then used the function cocor.indep.groups from the R package cocor to test for significant differences between species in trait correlations using Fisher's z tests (Diedenhofen & Musch, 2015).

RESULTS

Behavioural Differences Between Species

Podarcis sicula were significantly more exploratory than *P. virescens* and became more exploratory as trials progressed, while *P. virescens* became less exploratory (Table 3, Fig. 2a). Neither group (collection day) nor batch significantly affected exploratory behaviour (Table 3).

In the neophobia trial, *P. sicula* got significantly closer to the novel object than *P. virescens* (Table 3, Fig. 2b) and was therefore more neophilic than *P. virescens*. We found no effect of trial day or group (collection day) on neophobia score, but we did find a significant effect of batch; batch 4 was significantly less neophobic than batch 1 (Table 3). We found substantial individual variation in the response to a novel object: some animals never made contact with the novel object and had long minimum distances, while others passed by the object, briefly touching it without paying much attention and some lizards explored the novel object through tongue flicking and even climbed onto it. During the neophobia trial, 21.8% ($N_{trials} = 19/87$; $N_{individuals} = 29$) of *P. virescens* and 37.2% ($N_{trials} = 29/78$; $N_{individuals} = 26$) of *P. sicula* explored the novel object.

During the boldness trials, latency to emerge from the cold shelter after being scared was significantly shorter for *P. sicula* than for *P. virescens* (Table 3, Fig. 2c). The model indicated a significant effect of batch, where batch 3 was significantly bolder than batch 1. There was no effect of group (collection day) or trial day (Table 3).

Repeatability of Behavioural Traits

Podarcis virescens was significantly repeatable in all three behavioural traits (Fig. 3), whereas *P. sicula* was significantly repeatable in their boldness (Fig. 3). The species were not significantly different from each other in the repeatability of behavioural traits (Fig. 3).

Correlations Between Traits

The behavioural traits measured in *P. virescens* were significantly correlated; individuals that exhibited more exploratory behaviour were also bolder and less neophobic (Table 4). We did not find any significant correlation between *P. sicula* behavioural traits (Table 4), and the difference between species' behavioural trait correlations were all nonsignificant (Table 4).

DISCUSSION

Overall, our predictions for the behavioural differences between an invasive and a native species were supported. The invasive species, *P. sicula*, was more exploratory, bolder and less neophobic than the native *P. virescens*. *Podarcis virescens* were highly repeatable in their behaviours, while only boldness of *P. sicula* was repeatable. In the native *P. virescens* there were correlations between all behavioural traits, with more exploratory individuals also being bolder and less neophobic. In contrast, there were no significant correlations between behavioural traits in *P. sicula*.

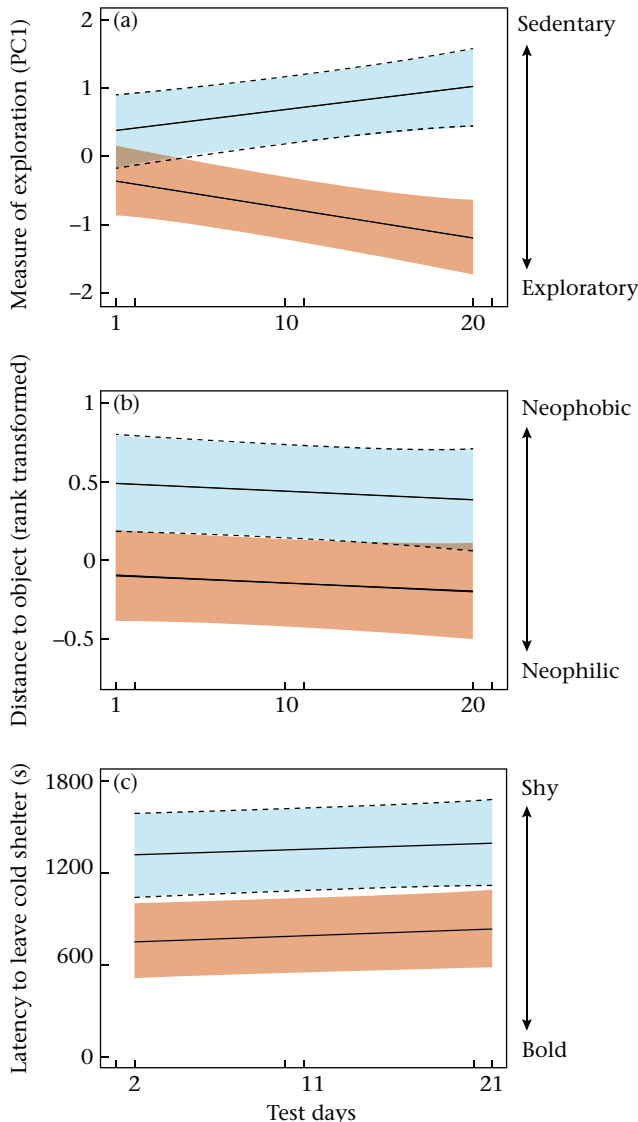


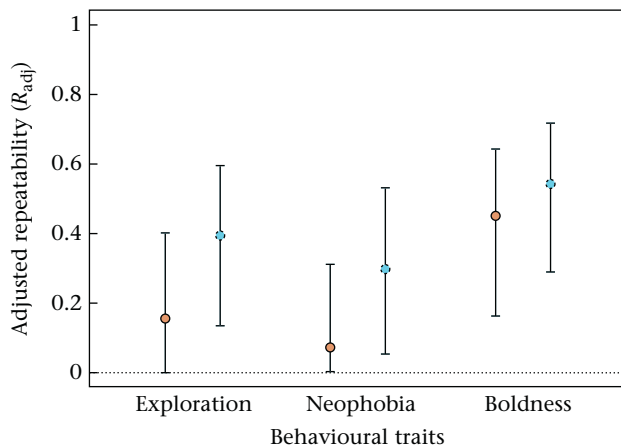
Figure 2. Behavioural differences between the invasive *P. sicula* (orange) and the native *P. virescens* (blue) for (a) exploration, (b) neophobia and (c) boldness. We plotted fitted lines predicted from our linear mixed-effect models with 95% confidence intervals (shaded polygon).

Table 3

Outcomes of the linear mixed-effects models for each behavioural trait: exploration, neophobia and boldness

	Exploration				Neophobia				Boldness			
	$N_{\text{obs}} = 165, N_{\text{ind}} = 55$				$N_{\text{obs}} = 165, N_{\text{ind}} = 55$				$N_{\text{obs}} = 165, N_{\text{ind}} = 55$			
	β	SE	t	P	β	SE	t	P	β	SE	t	P
Fixed effects												
Intercept	−1.089	0.298	−3.662	<0.001	−0.190	0.180	−1.054	0.292	650.455	172.600	3.769	<0.001
Species (<i>virescens</i> ; REF = <i>sicula</i>)	1.451	0.254	5.719	<0.001	0.582	0.151	3.858	<0.001	561.030	143.234	3.917	<0.001
Trial day	−0.337	0.121	−2.797	0.005	−0.042	0.054	−0.777	0.437	32.293	32.925	0.981	0.327
Group (2; REF = 1)	0.328	0.263	1.244	0.213	0.047	0.157	0.297	0.766	139.666	151.958	0.919	0.358
Batch (2; REF = 1)	0.135	0.219	0.613	0.540	−0.058	0.142	−0.407	0.684	−10.293	116.764	−0.088	0.930
Batch (3; REF = 1)	0.248	0.266	0.933	0.351	0.056	0.170	0.328	0.743	−245.284	124.279	−1.974	0.048
Batch (4; REF = 1)	0.212	0.256	0.827	0.409	−0.566	0.167	−3.399	0.001	−75.716	131.157	−0.577	0.564
Species*Trial day (<i>virescens</i> ; REF = <i>sicula</i>)	0.597	0.166	3.592	<0.001	—	—	—	—	—	—	—	—
Random effects												
Lizard identity	σ^2	SE			σ^2	SE			σ^2	SE		
Residual	0.470	0.053			0.139	0.029			207288.000	35.445		
	1.104	0.082			0.472	0.054			174750.500	32.541		

When the interaction effect was nonsignificant, which is indicated by '—', we reran the model without this effect. Significant results are in bold.

**Figure 3.** Adjusted repeatability (R_{adj}) and 95% confidence intervals of behavioural traits (exploration, neophobia and boldness) for the invasive *P. sicula* ($N_{\text{obs}} = 78$, $N_{\text{ind}} = 26$, orange circles) and the native *P. virescens* ($N_{\text{obs}} = 87$, $N_{\text{ind}} = 29$, blue circles). The dashed line represents 0.

Being bolder, more exploratory and neophilic probably enhances the ability of *P. sicula* to be successful during all aspects of the invasion process. For example, bolder and more exploratory behaviour may increase an invader's likelihood of entering a transport vector, and thereby colonize a new environment (Chapple et al., 2012; Griffin et al., 2016). These behaviours might have been similarly expressed and important for *P. sicula* when they were introduced 20 years ago, as these behavioural traits are likely to be heritable (Gruber, Brown, Whiting, & Shine, 2017b; Réale et al., 2007). We cannot exclude the possibility that selection might have acted on these behavioural traits during the invasion process,

leaving only the bolder, more exploratory and neophilic individuals. Nevertheless, the differences between traits we found in this study might favour the invasive species when it has to compete for food and habitat (by more easily finding and exploiting new resources, such as food and shelter sites), and increase its likelihood of interacting with other lizards (by being bolder for example), which can promote aggressive encounters with native species (Candler & Bernal, 2015; Gruber et al., 2017a; Rehage & Sih, 2004; Short & Petren, 2008; Sol, Timmermans, & Lefebvre, 2002). Indeed, the displacement of *P. virescens* from gardens inhabited by *P. sicula* (Ribeiro & Sá-Sousa, 2018), or of other *Podarcis* species native to other invaded sites, may be explained in part by higher levels of aggression in this species (Downes & Bauwens, 2002), which can result in competitive exclusion of native species (Nevo et al., 1972; Valdeón, Perera, Costa, Sampaio, & Carretero, 2010).

Podarcis virescens was consistent in all behavioural traits, while *P. sicula* was only consistent in their boldness. This was a similar result to a study of hymenopterans, where the native wasp *V. crabro* was repeatable for activity, boldness and exploration, but the invasive *V. velutina* was not (Monceau et al., 2015). The invasive *P. sicula* may benefit from being more plastic in its behaviour because invasive species in general have to respond to changing, novel environments (Griffin et al., 2016). *Podarcis sicula* is usually unintentionally transported to new locations (Carretero & Silva-Rocha, 2015) and very successful at adapting to new conditions (Herrel et al., 2008; Vervust, Grbac, & Van Damme, 2007). Its behavioural plasticity may thus partly explain this species' invasion success. Interestingly, *P. sicula* did exhibit repeatability in boldness, which potentially highlights the importance of boldness in all stages of the invasion process in this species. For example, bold individuals may also be more likely to be transported outside their native range because they are more likely to enter containers or vessels being prepared for transport (e.g. olive trees; Rivera,

Table 4

Spearman rank order correlations and 95% confidence intervals between behavioural traits for each species

	Exploration vs boldness	Boldness vs neophobia	Neophobia vs exploration
<i>P. sicula</i>	0.0793 (−0.1439, 0.3039)	0.1481 (−0.1023, 0.3676)	0.1917 (−0.0358, 0.4041)
<i>P. virescens</i>	0.2452 (0.0432, 0.4250)	0.3043 (0.1045, 0.4949)	0.3708 (0.1534, 0.5501)
Species comparison (Fisher's z test)	$z = 1.32, P = 0.185$	$z = 1.04, P = 0.299$	$z = 1.23, P = 0.219$

Significant results are in bold.

Arribas, Carranza, & Maluquer-Margalef, 2011; Silva-Rocha et al., 2012). After introduction in a novel location, bolder individuals may gain greater access to resources and do better in social interactions (Monceau et al., 2015; Pintor, Sih, & Bauer, 2008; Short & Petren, 2008). Moreover, *P. sicula* usually invades urbanized locations perhaps because they are in or near transport hubs (the introduced population in Lisbon inhabits city gardens), and boldness confers an advantage in urban environments because it can translate into higher foraging efficiency (Short & Petren, 2008).

Behavioural traits of *P. virescens* were correlated with more exploratory individuals also being bolder and less neophobic, which suggests a possible behavioural syndrome in this native species (Sih et al., 2004). However, the same was not true for *P. sicula*, for which we did not find any correlations between their behavioural traits. The correlations between behavioural traits we found in this study should be interpreted with caution, however, because we did not control for dependency among variables or additional sources of variation. It is also important to consider both within- and between-individual correlations in behavioural traits, to understand the selective forces acting on behavioural traits within a population and their evolutionary significance (Dingemanse & Wolf, 2013; Sih et al., 2012). Nevertheless, the lack of correlation between traits, allied with the overall inconsistency in *P. sicula*'s repeatability, may be advantageous during biological invasions. Variation in behavioural traits within a population increase the likelihood of success in fluctuating environments and novel habitats and allow for a population's persistence in novel environments (Dingemanse & Wolf, 2013; Sih et al., 2012). Likewise, correlations between behavioural traits constrain a population, because if selection acts on one trait, correlated behaviours are also likely to be affected (Sih et al., 2012).

In conclusion, we have shown that congeneric invasive and native lizard species differed in key behavioural traits, exploration, neophobia and boldness, that could promote the invasion success of *P. sicula*. These behavioural traits are likely to be important for the success of other introduced *P. sicula* populations given that these populations share the same long-range transport and establishment pattern (CABI, 2018; Carretero & Silva-Rocha, 2015). Increasingly, behavioural mechanisms are being appreciated as playing an important role in determining invasion success (Chapple et al., 2012). We also suggest that comparisons between closely related species that are variable in their invasive ability may provide important insights into the relationship between plasticity and personality and their relative roles in determining invasive success.

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