Bite and seek: bite force and exploratory behaviour of the lizard *Podarcis siculus* across its non-native range in the north-eastern United States

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Understanding how animals succeed in novel environments is critical to predicting the outcomes of species introductions under global change. Variation in exploratory behaviour—the willingness to investigate unfamiliar environments—has potential to influence species' invasion success. The Italian wall lizard, *Podarcis siculus*, is native to southern Europe and has been introduced across Europe and North America. To compare the exploratory behaviour and bite force of individuals from three non-native populations in the United States, we conducted a laboratory experiment involving wild-caught lizards from New York City, Philadelphia, and Boston. We tested a series of hypotheses concerning the predictions that: (1) exploratory behaviour would be greatest in the most recently established population and (2) bite force—associated with competitive ability—would be greatest in the densest populations. Across populations, exploratory behaviour increased significantly with body size. Contrary to our first prediction, exploratory behaviour was not significantly greater in more recently established populations. Consistent with our second prediction, however, lizards from the low-density Philadelphia population exhibited weaker bites. Results suggest that contemporary behavioural variation reflects differences in local ecological conditions, such as resource abundance, population density, and size structure rather than establishment history. Our findings highlight the need for further research into behavioural and performance drivers of lizard invasion success.

ADDITIONAL KEYWORDS: bite force – exploratory behaviour – invasion biology – Lacertidae – non-native species.

INTRODUCTION

By displacing native species and degrading local habitats, biological invasions threaten biodiversity, with costly implications for ecosystems and humans alike (Simberloff *et al*., 2013). Despite an eruption of research since the mid-1980s into the causes, impacts, and management of invasions, anthropogenic drivers such as global trade and climate change have intensified biological invasions worldwide (Seebens *et al*., 2018; Essl *et al*., 2020). Better indicators of invasion success from initial transport and introduction to final establishment and spread are needed (Blackburn *et al*., 2011), and animal behaviour is a key contributor

to invasion success (Holway & Suarez, 1999; Chapple *et al*., 2012). Exploratory behaviour—the willingness to seek out novel environments and resources—is expected to be particularly important for species whose transport, establishment, and spread depend upon the prompt acquisition of information about the distribution of food, shelter, and refuges in unfamiliar settings (Chapple *et al*., 2011; Miller *et al*., 2017). As a result, exploratory boldness is widely predicted to correlate positively with invasion success and evidence of this pattern has been found in fish (Rehage & Sih 2004), lizards (Chapple *et al*., 2011), and rodents (Russell *et al*., 2010).

Past studies have made links between exploratory behaviour and the invasion success of lizards. For example, Chapple *et al*. (2011) experimentally compared the exploratory behaviour of two congeneric skink species within their sympatric native range, one

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with a high invasive tendency and the other without. The invasive species was better able to find basking sites within novel environments, indicating enhanced exploratory behaviour relative to its non-invasive counterpart. Two recent studies involving Italian wall lizards (*Podarcis siculus*) reached similar conclusions: (1) individuals from a recently introduced population located food more efficiently in a maze than did lizards from two congeneric populations native to nearby regions (Limnios *et al.*, 2021); (2) individuals from an introduced population showed greater exploratory behaviour, boldness, and neophilia than in a sympatric congener (Damas-Moreira *et al.*, 2019). It remains to be determined whether variation in morphological characteristics and associated performance measures are associated with exploratory behaviour and invasion success in these lizards.

Lizard bite force is an ecologically important performance measure that varies substantially among species (Herrel *et al.*, 2004). The maximum force with which a lizard can bite dictates the array of foods it can consume (Herrel *et al.*, 2004). Strong bite force enables lizards to expand their diet to include tougher plant material and harder-bodied prey, a potentially key adaptation to novel environments (Herrel *et al.*, 2004, Sagonas *et al.*, 2014). Biting is also an aggressive behaviour in lizards, with stronger-biting lizards more often winning fights (Huyghe *et al.*, 2005; Lappin & Husak, 2005; Husak *et al.*, 2006). In areas of high population density and/or limited resources, lizards compete for food, mates, and territory (Diego-Rasilla & Pérez-Mellado, 2000; Vervust *et al.*, 2009). Thus, bite force is an indicator of the intensity of intrasexual or intraspecific competition (Vervust *et al.*, 2009; Donihue *et al.*, 2016). Because bite force is a biomechanical trait associated with both diet and intraspecific competition, it may influence the success of introduced lizard populations.

Our study focused on the Italian wall lizard, *Podarcis siculus*. A population was introduced to the United States in the 1960s, first as pets in New York City, where they were rapidly established as escapees (Gossweiler, 1975). Since then, populations have established in cities across the north-eastern United States (Mendyk & Adragna, 2014), including near Philadelphia in 2008 (Burke, 2010) and Boston in 2016 (Donihue, 2017). The Philadelphia population was established intentionally as a pest control experiment (Burke, 2010), but the Boston population was established without known human assistance but perhaps following dispersal along railroad corridors (Mendyk & Adragna, 2014; Donihue *et al.*, 2015). Understanding the role of exploratory behaviour in their establishment could lend new insight into their dispersal and potential invasiveness; we will use the term 'non-native' to describe species that occur outside their recognized historic range and 'invasive' when a non-native species causes biological, social, or economic harm (Schlaepfer *et al.*, 2011).

We investigated exploratory behaviours and bite force using wild-caught adult lizards from three populations—New York City, Philadelphia, and Boston—in a laboratory experiment. Based on the theorized connection between exploratory behaviour and introduction recency, we hypothesized that: (1) a greater proportion of lizards from Boston and Philadelphia would elect to explore the unfamiliar arena than from the initial introduction site in New York City. Moreover, among individuals that chose to explore, (2) the Boston and Philadelphia lizards would begin to do so faster than New York City lizards, (3) Boston and Philadelphia lizards would walk a greater distance while exploring the arena than New York City lizards, and (4) Boston and Philadelphia lizards would spend more time exploring the arena than New York City lizards. In addition, we hypothesized that (5) the propensity to explore and the extent of exploration would be significantly correlated with body size, such that larger lizards are more likely to leave their shelter and explore for a longer time and distance than smaller lizards. In terms of a competitive edge, we predicted (6) bite force would be greatest among New York City lizards, where population density is highest, and least among Philadelphia lizards, where density is lowest. Finally, we hypothesized that, (7) at similar body sizes, harder-biting individuals would exit the shelter sooner than weaker-biting individuals. These analyses contribute to a growing body of research into how animal behaviour, morphology and performance affect biological invasions.

MATERIAL AND METHODS

STUDY SPECIES

Italian wall lizards are small, heliothermic, ground-dwelling lacertids [adult snout-to-vent length (SVL) between 55 and 90 mm; Fig. 1D] that inhabit grassland, scrub, dry open woodland, and rocks in areas of varying human activity (Corti & Lo Cascio, 2002; Blazevic *et al.*, 2020). They are scansorial, proximal-intensive foragers (Anderson, 2007) with a generalist diet of invertebrates and plants (Herrel et al., 2008; Corti & Lo Cascio, 2002). Males are larger than females, having a longer tail and bulkier head, and reach sexual maturity after 1 year, in contrast to females, which mature in 1 to 2 years (Blazevic *et al.*, 2020). Populations occur naturally on the Italian Peninsula and Adriatic Coast (Corti & Lo Cascio, 2002), and have been introduced to Spain, Portugal, France, Turkey, and the United States (Kolbe *et al.*, 2012).

Figure 1. Overview of study populations. Panels show (A) a photo of the Boston (BOS) site in a community garden (42.3 °N, -71.1 °W), (B) a photo of the New York City (NYC) site in Mount Zion Cemetery of Queens (40.7 °N, -73.9 °W), (C) a map of all populations, (D) a photo of the study species, and (E) a photo of the Philadelphia (PHL) site in an office park at Mount Laurel Township, New Jersey (40.0 °N, -74.9 °W). Photos by Colin Donihue.

CAPTURE AND HOUSING

Lizards were collected near major urban centres that contained vegetated habitats (Fig. 1): the New York City (NYC) site is a grassy cemetery; the Philadelphia (PHL) site is an office park with large buildings surrounded by grass and planted bushes; the Boston (BOS) site is a community garden with native and non-native plant species. Based on relative sighting-to-capture ratios at consistent effort by the same researcher (C. Donihue), population density was highest in New York City (~4:1), intermediate in Boston (~3:1), and lowest in Philadelphia (~3:2). A total of 64 lizards were captured using a pole-snare technique, resulting in initial laboratory populations of ten females and 12 males from New York City (collected 27 September 2021), 11 females and 11 males from Philadelphia (collected 26 September 2021), and ten females and ten males from Boston (collected 6 October 2021) with permissions from the New York Department of Environmental Conservation, the New Jersey Division of Fish and Wildlife, Wildlife Permits Unit, and the Massachusetts Division of Fisheries and Wildlife. When the animal colony arrived at Brown University, a unique identification bead tag was sewn to the top of each lizard's tail for individual identification throughout the experiments (Galdino et al., 2014). Two lizards—a male and a female from the same population—were housed in each cage, and cages were maintained at 70 °F (21 °C). Artificial vegetation and a 15 × 15-cm cardboard shelter with a small circular cut-out in one face for entry and exit were placed atop astroturf cage lining in each cage to provide shelter and enrichment. Water and mealworms

(*Tenebrio molitor*) were provided to the lizards *ad libitum* throughout their time in captivity. All animal housing and experimental methods were approved by the Brown University Institutional Animal Care and Use Committee (IACUC: 20-05-0004).

EXPLORATORY BEHAVIOUR

Exploratory arenas were built from a 121 × 121 × 30-cm box with opaque foam walls and floor and an open top (Fig. 2). The box was divided to form two arenas of 121 × 59.5 × 30-cm, and the opaque walls prevented the lizards from seeing beyond their respective arena. A 15 × 15-cm cardboard shelter of the same design used in primary housing was placed inside each arena, facing the centre and approximately 13 cm from the shorter wall. A fabric flap was placed over the shelter opening to prevent exiting during adjustment periods. To begin each trial, one lizard was placed inside the shelter with the fabric flap lowered for a 5-min adjustment period, which allowed the lizard to recover from handling-induced stress before exploration; adjustment periods of similar arena-based behavioural experiments are often 2–10 min (Chapple et al., 2011; Lapiedra et al., 2016; Blazevic et al., 2020). After the adjustment period, behavioural observations began by lifting the flap with a drawstring and allowing the lizard to view and enter the arena. Researchers were not visible to the lizards, sitting still and silent behind the arena wall. Consistent with similar studies (Lapiedra et al., 2016), each lizard was allowed 10 min to exit the shelter and an additional 10 min to explore the arena if it exited the shelter. To avoid disturbances,
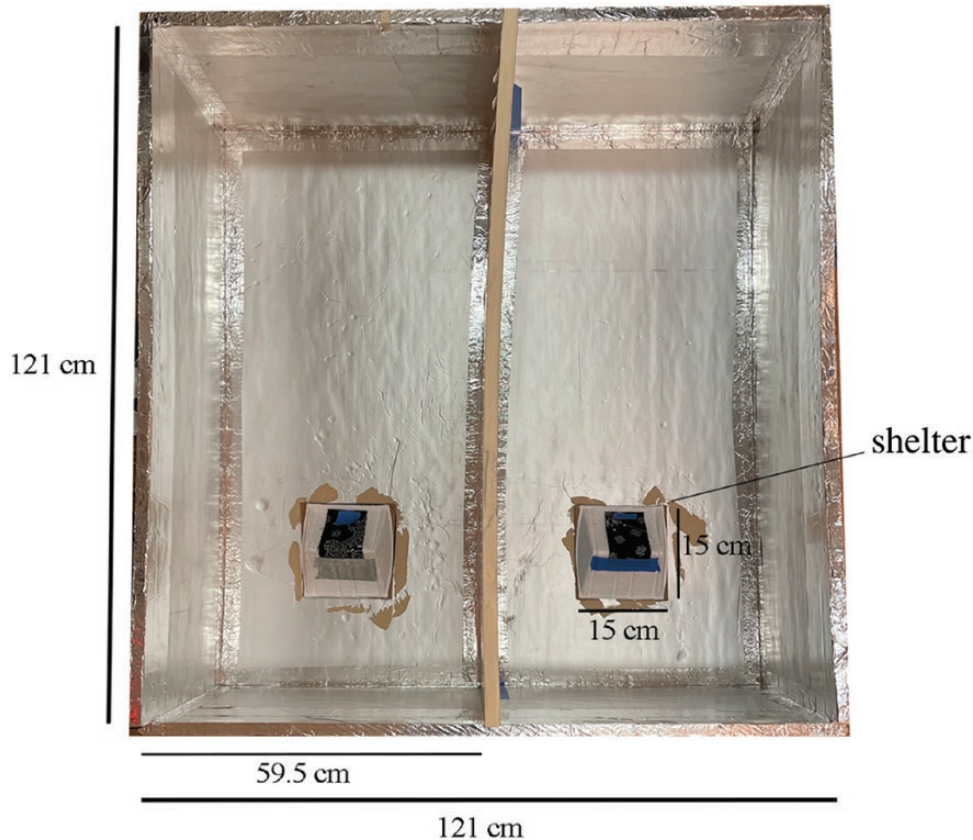
Figure 2. Two exploratory arenas nested within the experimental box. Cardboard shelters were provided and fabric flaps over the openings enabled us to ensure a 5-min adjustment period.

lizards were not removed from the arena until both individuals in concurrent trials completed their full allotment of time. A single digital video camera (Sony HDRPJ260V; 1920 × 1080 pixels; 50 Hz) was mounted on a tripod behind the arena wall farthest from the shelters, angled downward to record all timed activities in both arenas. With these recordings, we were able to extract behavioural data for all individuals for each time interval.

We measured four responses in each trial: (1) whether the individual exited the shelter in the 10-min window; (2) the time elapsed before the individual exited the shelter once the flap was lifted; (3) the total distance the individual travelled within the larger arena after beginning to explore; and (4) the proportion of time the individual spent exploring the arena, as opposed to resting inside or on top of the shelter after its initial exit. The variable of time elapsed before exiting was divided into two stages: the time for an individual to poke its head through the opening and the time for its hind legs to exit the shelter. All trials occurred within 72 days of collection, between 14 October 2021 and 6 December 2021. All three populations were tested concurrently to avoid

any bias arising from duration of captivity; we found no significant correlation between date of capture and date of behavioural trial for any behavioural metrics. The same observer (T. Patti) scored and analysed all behaviour videos to maintain consistency. Example videos are provided to demonstrate the experimental set-up and how we scored high, moderate, and low exploratory behaviours (Supporting Information, Videos S1–S3).

MORPHOLOGICAL MEASUREMENTS

After the arrival of the lizard colony, we measured a suite of morphological features on each lizard. Using digital calipers (Mitutoyo 500-752), we measured SVL, head length (snout tip to rear of parietal scale), head height (measured at parietal scale), head width (at the head's widest point, including soft tissue), and jaw length (between tip of lower jaw to jugal).

BITE FORCE

Maximum bite force of each captive lizard was measured using a bite force meter consisting of

two metal biting plates connected to a Kistler force transducer (Herrel *et al.*, 1999; Donihue *et al.*, 2016). The lizards were removed from their cages where they were thermoregulating *ad libitum* and were allowed to bite on the meter in three repeated trials (total handling time less than 1 min); the maximum force exerted among those three trials was used in our analysis (Donihue *et al.*, 2016).

STATISTICAL ANALYSIS

All analyses were conducted in R v.3.6.0 (R Core Team, 2019). We evaluated a series of generalized linear models using the 'glmer' function in the 'lme4' R package (Bates *et al.*, 2015) and investigated the significance of the factors using a Type III Analysis of Variance in the 'car' package (Fox & Weisberg, 2019). Relationships between each behavioural response variable, population source, sex, and body size (SVL) were analysed through the initial inclusion of interaction terms among all explanatory variables and subsequent simplification to only significant terms. For bite force, SVL was included in the model since strong bites are associated with large body size in similar species (Verwaijen *et al.*, 2002, Donihue *et al.*, 2016). Because our time-based response variables spanned multiple orders of magnitude (e.g., elapsed time before exploring range: 2–599 s) and were right-skewed, we $\log_{10}$-transformed them before analysis.

RESULTS

HYPOTHESIS 1: LIZARDS FROM RECENTLY ESTABLISHED POPULATIONS ARE MORE LIKELY TO EXPLORE

Partially consistent with our first hypothesis, the proportion of lizards that left the shelter to explore the arena differed significantly among populations (Fig. 3). We found a significant population × sex interaction in the probability of exiting the shelter [Logistic Regression (LR) X^2 = 6.4; d.f. = 2; P = 0.041; Fig. 3]. Among females, the source population had little influence over its probability of exiting the shelter within 10 min (LR X^2 = 0.1; d.f. = 2; P = 0.981). Thirteen females exited the shelter (42%): four out of ten from Boston, four out of nine from New York City and five out of 12 from Philadelphia. In contrast, source population had a strong, significant effect on the probability that a male would exit the shelter (LR X^2 = 11.1; d.f. = 2; P = 0.004). Surprisingly, Philadelphia males exhibited the lowest probability of exploring, whereas Boston and New York City males did not differ significantly ($|z|$ = 1.4; d.f. = 27; P = 0.171). Fourteen males exited the shelter (47%): eight out of ten from Boston, five out of ten from New York City,
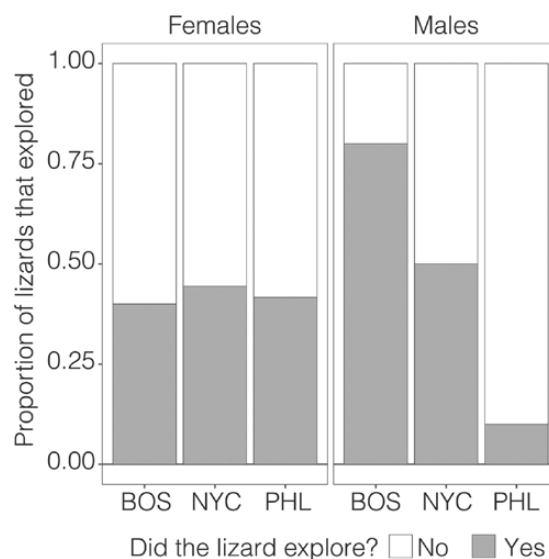

Figure 3. The proportion of lizards that exited the shelter within the 10-min observation window according to population and sex. Exit rates were similar for females from each population, but there was an eight-fold difference in exit rate for males from different populations.

and one out of ten from Philadelphia. The difference in exit rate between Boston males and Philadelphia males was significant ($|z|$ = 2.7, d.f. = 27; P = 0.007), whereas the difference between New York City and Philadelphia was marginally significant ($|z|$ = 1.8, d.f. = 18; P = 0.074).

HYPOTHESIS 2: LIZARDS FROM MORE RECENTLY ESTABLISHED POPULATIONS BEGIN TO EXPLORE SOONER

We found a significant population × sex interaction in the elapsed time before lizards poked their head through the shelter opening and surveyed the arena ($F_{2,26}$ = 4.8; P = 0.017; Fig. 4A). Tested individually, however, neither source population ($F_{2,29}$ = 0.7; P = 0.494) nor sex ($F_{1,30}$ = 0.8; P = 0.384) had a statistically significant effect on the timing of head exit. In further contrast to hypothesis 2, the time to fully exit the shelter did not differ significantly among populations ($F_{2,24}$ = 1.4; P = 0.273) or sexes ($F_{1,25}$ = 0.1; P = 0.756), nor was there a significant population × sex interaction ($F_{2,21}$ = 1.8; P = 0.197). Among females, exit times were similar: the four Boston females that exited took on average 243 ± 160 s to do so, the four New York City females took 224 ± 103 s, and the five Philadelphia females took 237 ± 109 s. Meanwhile, male exit times differed to a greater, though not significant, extent: the eight Boston males that exited averaged 353 ± 233 s, the five New York City males took 204 ± 266 s, and the lone Philadelphia male to
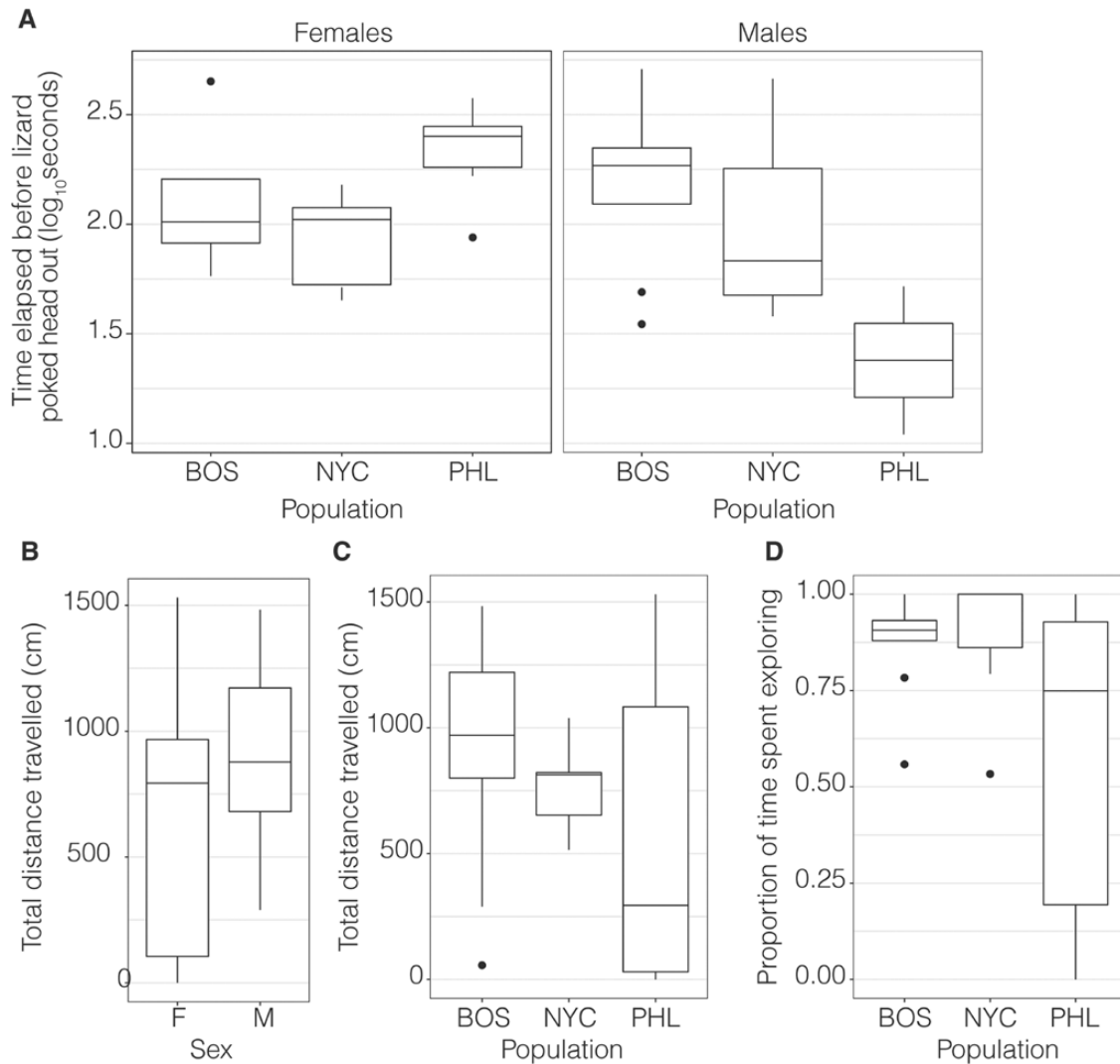
Figure 4. The effects of sex and population on exploratory behaviours. (A) There was a significant population × sex interaction in the time lizards took to poke their heads out of the shelter. We found significant differences in the distance travelled while exploring across both (B) sex and (C) population. (D) On average, New York City lizards spent the most time exploring and Philadelphia lizards explored the least, regardless of sex.

exit the shelter took 63 s. The comparison remained non-significant when just testing the Boston and New York City males.

HYPOTHESIS 3: LIZARDS FROM RECENTLY ESTABLISHED POPULATIONS TRAVEL FARTHER WHILE EXPLORING

Differences in the distance that lizards travelled after leaving the shelter contrasted with our third hypothesis. There was not a significant population × sex interaction in distance travelled ($F_{2,21}$ = 1.5; P = 0.239), but males travelled significantly farther than females ($F_{1,25}$ = 4.5; P = 0.043; Fig. 4B). Across all populations, males travelled an average of 920 cm, whereas females travelled an average of 646 cm. We

also found a significant difference among populations ($F_{2,24}$ = 4.7; P = 0.019; Fig. 4C), with Boston lizards travelling an average of 937 cm, New York City lizards travelling an average of 766 cm, and Philadelphia lizards travelling an average of only 568 cm.

HYPOTHESIS 4: LIZARDS FROM MORE RECENTLY ESTABLISHED POPULATIONS SPEND MORE TIME EXPLORING

Populations differed in the amount of time spent exploring, but lizards from Boston, a more recently founded population, did not spend more time exploring than those from New York City. The proportion of time spent exploring differed significantly among populations ($F_{2,24}$ = 4.0; P = 0.033; Fig. 4D), but there

was not a significant difference according to sex ($F_{1,25}$ = 0.9; P = 0.348) or the population × sex interaction ($F_{2,21}$ = 2.5; P = 0.109). Lizards from New York City spent the most time exploring (91%; 544 ± 95 out of 600 s provided), followed by Boston (88%; 529 ± 69 s), though this difference was not statistically significant ($|t|$ = 0.2, d.f. = 23; P = 0.825). Philadelphia lizards explored the least (58%; 350 ± 271 s), which was significantly less time compared to Boston ($|t|$ = 2.3; d.f. = 23; P = 0.031) but not New York City ($|t|$ = 1.5; d.f. = 12; P = 0.152). Males explored for 87% of the time (520 ± 89 s) and females explored for 77% (461 ± 218), including the one male from Philadelphia that explored, and this sex-based difference remained significant when comparing only Boston and New York City.

HYPOTHESIS 5: LARGER LIZARDS EXHIBIT GREATER EXPLORATORY BEHAVIOUR

Body size was predictive for some exploratory behaviours, but not all. Larger lizards poked their heads out significantly earlier than smaller lizards ($F_{1,28}$ = 7.6; P = 0.010; Fig. 5A) and explored over greater distances ($F_{1,23}$ = 9.8; P = 0.005; Fig. 5B). This effect was consistent for both sexes as there was not a significant sex × SVL interaction for any metric (head-out: $F_{1,26}$ = 0.9; P = 0.363; body-out: $F_{1,21}$ = 2.1; P = 0.160; distance travelled: $F_{1,21}$ = 1.8; P = 0.194). Larger lizards were quicker to peek out of the shelter but not significantly more likely to exit (LR X^2 = 0.1; d.f. = 1; P = 0.780) and did not spend significantly more time exploring ($F_{1,23}$ = 2.2; P = 0.152). That larger lizards covered more distance than smaller lizards in a similar amount of time indicates that they moved with greater speed.

HYPOTHESIS 6: LIZARDS FROM DENSER POPULATIONS HAVE STRONGER BITES

Although there was not a significant population × sex × SVL interaction ($F_{2,47}$ = 0.04; P = 0.957), each variable had a significant independent effect on bite force. Consistent with previous studies, larger lizards had significantly stronger bites ($F_{1,54}$ = 53.8; P < 0.001), and males had stronger bites when controlling for differences in body size ($F_{1,54}$ = 25.5; P < 0.001; Fig. 6). Male lizards averaged 13.9 ± 4.8 N of bite force and females averaged 8.2 ± 3.5 N. After accounting for bite force differences in sex and size, we found that bite force also differed significantly among populations ($F_{2,54}$ = 13.8; P < 0.001). Boston lizards displayed a mean bite force of 12.8 ± 5.5 N, New York City lizards 12.6 ± 3.7 N, and Philadelphia lizards 7.9 ± 4.4 N. Boston and New York City lizards did not differ significantly in bite force ($|t|$ = 0.6; d.f. = 54; P = 0.566), though Philadelphia lizards had significantly weaker bites than both Boston ($|t|$ = 4.9; d.f. = 54; P < 0.001) and New York City ($|t|$ = 5.6250; d.f. = 35; P < 0.001).

HYPOTHESIS 7: HARDER-BITING LIZARDS EXHIBIT GREATER EXPLORATORY BEHAVIOUR

Although we found that body size affected exploratory behaviour, we did not find a correlation between bite force and the likelihood of exploration (LR X^2 = 1.4; d.f. = 1; P = 0.233). We also did not find a significant correlation between bite force and the time elapsed before poking the head out ($F_{1,28}$ = 1.0; P = 0.319) or exiting the shelter ($F_{1,23}$ = 0.3; P = 0.614). Finally, bite force was not significantly correlated with distance
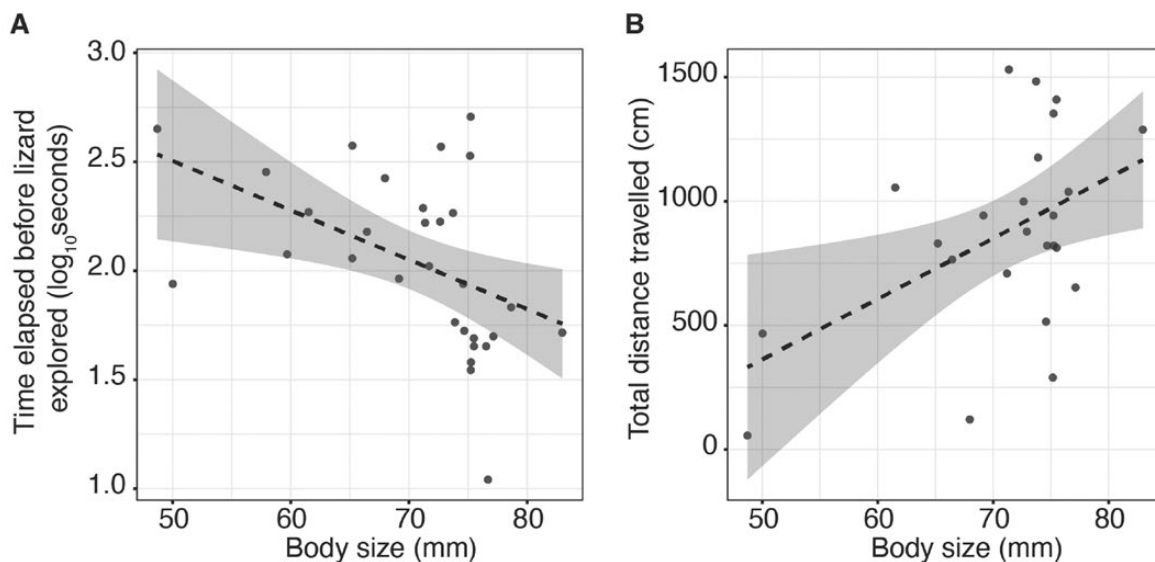

Figure 5. Body size was a significant predictor of two exploratory behaviours. Larger lizards (A) peeked out of their shelter after less time than smaller lizards and (B) travelled a significantly greater distance than smaller lizards.

travelled ($F_{1,22}$ = 0.001; P = 0.975) or proportion of time exploring ($F_{1,22}$ = 0.5; P = 0.480).

DISCUSSION

We found statistically significant differences in exploratory behaviours across the three non-native populations and between the sexes of the Italian wall lizards, but little evidence for an influence of the recency of population establishment. Whereas several previous studies have found heightened exploratory behaviour among invasive lizard populations (Chapple *et al.*, 2011; Limnios *et al.*, 2021), local differences in the ecology, evolution, and natural history of non-native *P. siculus* populations might better explain their behavioural variation. Knowledge of local variation in body size distributions, population density, and functional traits such as bite force that are associated with competitive ability and/or resource acquisition may help reconcile the disconnect between expectations about exploratory behaviour and establishment history.

Data from the Philadelphia population exemplified the disconnect between exploratory behaviour and population recency. Although exploratory behaviour is a requirement for range expansion (Chapple *et al.*, 2011; Miller *et al.*, 2017), Philadelphia lizards consistently explored less than their Boston and New York City counterparts, which was unexpected given the relative recency of population establishment.

Philadelphia females behaved comparably to Boston and New York City females in terms of shelter exit rate, but males exited significantly less often (only one Philadelphia male exited). After exiting, Philadelphia lizards also spent comparably less time exploring and covered less distance. That Philadelphia lizards would be so disinclined to explore suggests local ecological variables might modulate population-specific differences in behaviour. For example, proximity to the heated office buildings at the Philadelphia site might disincentivize establishment of large territories or exploration beyond these built refuges. This contrast highlights how context from *in situ* observations might guide the design and interpretation of behaviour experiments.

Further contradicting the expectation of a link between exploration and population recency, lizards from Boston and New York City explored in similar ways. Greater exploration was expected for the Boston population, which was discovered only in 2016 (Donihue, 2017), compared to the New York City population that was founded in 1966 (Gossweiler, 1975). Again, local environmental context might explain the differences: New York City offered perhaps the most homogeneous resource distribution in a grassy cemetery, which might have incentivized range expansion as the grassy matrix and gravestones provide both the foraging and basking sites that provide a mating advantage while avoiding the risk of resource depletion (Mendyk & Adragna, 2014). Better understanding of the current and historical trends
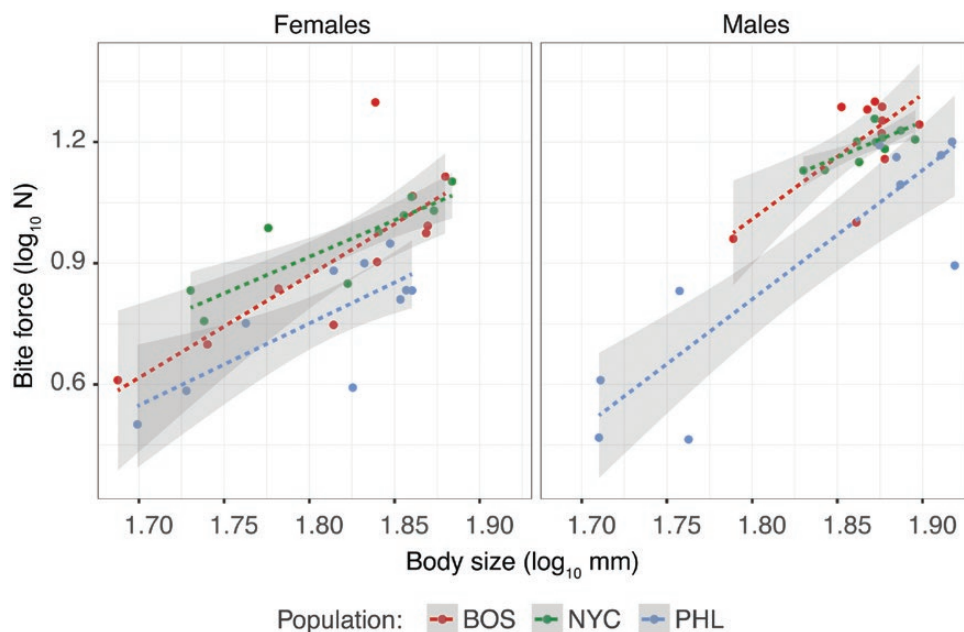

Figure 6. Bite force scaled positively with body size (i.e. SVL) across lizards from Boston, New York City, and Philadelphia. Boston and New York City lizards consistently bit harder than lizards from Philadelphia. Bite force positively correlated with body size. Males showed significantly greater bite force than females. Although the allometry of bite force increase was steeper for males than females, the bite force × sex interaction was not statistically significant.

in each population's size and geographical extent would lend additional insight into the relationships between resource availability and distribution, individual territory size, and exploratory behaviour.

As with the introduction of any non-native species, initial establishment processes might have failed or stalled for these Italian wall lizard populations, complicating inferences about the chronology and predictability of ecological and/or genetic change (Thurman *et al.*, 2023). For example, the Philadelphia population was first reported in 2008, but an anonymous source claimed to have started the population in 1984 (Burke, 2010). Selection pressures in human-built environments change quickly (Lambert & Donihue, 2020), so whether the Philadelphia population is closer to 15 or 35 years old, sufficient time has passed for selection on behavioural traits favoured during initial establishment to be relaxed (Lapiedra *et al.*, 2018). More recently, selection in response to novel trophic interactions—either avoiding predators (Lapiedra *et al.*, 2018; Donihue *et al.*, 2022) or acquiring prey (Pringle *et al.*, 2019)—could have a stronger influence on any given behavioural trait. A single behavioural trait is unlikely to be selected as the ideal response to every situation: though boldness may facilitate exploration, it can also thwart establishment by raising risks associated with predation (Huang *et al.*, 2012; Burns *et al.*, 2016) or human detection and intervention during transport (Chapple *et al.*, 2011). Yet behavioural syndromes, representing suites of correlated behaviours, can yield insight into the types of situations that exert strong selective pressures on populations (Sih *et al.*, 2004). For example, a correlation between exploratory behaviour and aggression (Rehage & Sih, 2004), which together aid potential invaders in transportation, dispersal and displacement of native species, might constitute an 'invasion syndrome' (Chapple *et al.*, 2012). These correlations can generate behavioural trade-offs whereby the costs of predation exposure might exceed the benefits of resource acquisition or interspecific dominance at different stages of the invasion process or different localities along an invasion front.

Body size was positively correlated with both bite force and some key exploratory behaviours, though we found no direct correlation between bite force and exploratory behaviours, perhaps reflecting the presence of an invasion syndrome in non-native populations of *P. siculus*. Specifically, larger lizards poked their heads out of the shelter faster and travelled significantly farther, matching results in other lizards (Chen *et al.*, 2019), as well as those of snakes (Maillet *et al.*, 2015; Mayer *et al.*, 2016). The correlation between body size and exploration might confer reduced predation risk or better competitive ability to larger individuals, emboldening them to engage in risky behaviour. Bite force also is an important indicator of competitive ability (Huyghe *et al.*, 2005; Husak *et al.*, 2006) and variation in bite force is often attributed to one of two causes: dietary differences, whereby increased bite force enables individuals to consume tough plant material and hard-bodied prey (Sagonas *et al.*, 2014), or intraspecific competition that selects for strong bites (Donihue *et al.*, 2016). Indeed, bite force generally increases with population density in *Podarcis* spp. (Vervust *et al.*, 2009; Donihue *et al.*, 2016), but is not often correlated with exploratory behaviour (contrary to hypothesis 7) in lizards (Herrel *et al.*, 2009; Chen *et al.*, 2019). In our study, males had stronger bites than females, as has been reported for similar species (Lappin *et al.*, 2006; Sagonas *et al.*, 2014), and this can be attributed to sexual selection since bite force predicts male mating success (Huyghe *et al.*, 2005; Husak *et al.*, 2006). Thus, as populations establish and increase in density, a high population density might incentivize behavioural syndromes that include boldness—not as a direct reflection of the establishment process but as a consequence of increases in population density that dilute predation risk (Roberts, 1996) and/or increase intraspecific competition (Drakeley *et al.*, 2015; Chejanovski *et al.*, 2017). Our results lend preliminary insight into spatiotemporal patterns of boldness in *P. siculus* populations across the north-eastern United States and comparisons across a broader gradient of population densities would help elucidate any generalizable relationships between population density, establishment recency, and exploratory behaviors.

CONCLUSION

We compared exploratory behaviours of three non-native populations of *P. siculus* and found that they exhibited substantial variation in exploratory behaviour and competitive ability. We found evidence contrary to our hypotheses concerning a theoretical link between exploratory behaviour and the recency of population establishment. Behavioural variation was better understood in light of contemporary population density and resource distributions than interpreted as a historical indicator of the ability to hide in cargo or otherwise expand their range. The influence of local environmental variation on behaviour highlights how non-native lizard populations may vary in their adaptations and behavioural responses through space and time along an invasion front.

ACKNOWLEDGEMENTS

DATA AVAILABILITY

All coded behavioural data are available in the Supporting Information (Table S1).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website.

Table S1. An archive of the datasheet used for analyses of bite force and exploratory behaviour.
Video S1. Example of low exploratory activity.
Video S2. Example of moderate exploratory activity.
Video S3. Example high exploratory activity.