Response behaviour of native lizards and invading wall lizard to interspecific scent: implications for invasion success

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The human-assisted movement of species beyond their native range facilitates novel interactions between invaders and native species that can determine whether an introduced species becomes invasive and the nature of any consequences for native communities. Avoiding costly interactions through recognition and avoidance can be compromised by the naïvety of native species to novel invaders and vice versa. We tested this hypothesis using the common wall lizard, *Podarcis muralis*, and the native lizard species with which it may now interact in Britain (common lizard, *Zootoca vivipara*, sand lizard, *Lacerta agilis*) and on Vancouver Island (northern alligator lizard, *Elgaria coerulea*) by exploring species' responses (tongue flicks, avoidance behaviour) to heterospecific scent cues in controlled experiments. The tongue flick response of *P. muralis* depended on the different species' scent, with significantly more tongue flicks directed to *E. coerulea* scent than the other species and the control. This recognition did not result in any other behavioural response in *P. muralis* (i.e. attraction, aggression, avoidance). *Lacerta agilis* showed a strong recognition response to *P. muralis* scent, with more tongue flicks occurring close to the treatment stimuli than the control and aggressive behaviour directed towards the scent source. Conversely, *Z. vivipara* spent less time near *P. muralis* scent cues than the control but its tongue flick rate was higher towards this scent in this reduced time, consistent with an avoidance response. There was no evidence of *E. coerulea* recognition of *P. muralis* scent in terms of tongue flicks or time spent near the stimuli, although the native species did show a preference for *P. muralis*-scented refuges. Our results suggest a variable response of native species to the scent of *P. muralis*, from an avoidance response by *Z. vivipara* that mirrors patterns of exclusion observed in the field to direct aggression observed in *L. agilis* and an ambiguous reaction from *E. coerulea* which may reflect a diminished response to a cue with a low associated cost. These results have significant implications for the invasive success and potential impacts of introduced *P. muralis* populations on native lizards.

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Competition within and among species arises through overlap in utilization of limited resources, and plays an important role in determining species' distributions and abundance (Case & Gilpin, 1974; Schoener, 1983). The outcomes of conflict arising from this competition are often asymmetrical, commonly driven by factors such as contestant body size, residency and prior experience (Chen & Hsu, 2016; Chock, Shier, & Grether, 2018; Schoener, 1974). In time, contests (both direct behavioural interference and exploitative competition for limited resources) can lead to niche segregation,

character displacement and exclusion of inferior competitors from optimal habitat (Heltai, Saly, Kovacs, & Kiss, 2015; Losos, 2000; Peiman & Robinson, 2010). The human-assisted movement of species beyond their native range can force novel competitive (and predation/prey) interactions between invaders and native species. Furthermore, behavioural traits indicative of successful invaders (i.e. high levels of boldness and aggression) can give a competitive advantage in such encounters (Chapple, Simmonds, & Wong, 2012; Damas-Moreira, Riley, Harris, & Whiting, 2019; Downes & Bauwens, 2002), with the potential to cause niche shifts and drastic declines or local extinctions of native species (Brzezinski, Chibowski, Gornia, Gorecki, & Zalewski, 2018; Cadi & Joly, 2003; Doody et al., 2009; Dorrestein, Todd, Westcott, Martin, &

Welbergen, 2019; Hernandez-Brito, Carrete, Ibanez, Juste, & Tella, 2018). Understanding how species may interact when faced with novel competitors is therefore an important part of assessing the invasion potential of non-native species introductions and their impacts on native communities.

Conflict between species is a hierarchical process, beginning with contact and ending with physical interactions. However, mediating these physical interactions is a variety of behavioural decisions that can influence the severity of the outcome for one or both organisms (Langkilde, Lance, & Shine, 2005). Individuals might detect but choose not to interact with one another, such as if one individual perceives the other to be dominant (Brazill-Boast, 2013). Individuals might also engage in ritualized display behaviours that reduce the need for physical altercation by giving further information about the likely outcome (Baeckens, Driessens, Huyghe, Vanhooydonck, & Van Damme, 2018; Edwards & Lailvaux, 2012; Reichert & Gerhardt, 2014). When native species encounter novel non-native species, this system of recognition might be compromised by the lack of evolutionary history between the two taxa. Without such recognition, naïve/native species' responses may be suboptimal during encounters that leave them particularly vulnerable to pressures from introduced species (prey naïvety hypothesis; Sih et al., 2010; Ehlman, Trimmer, & Sih, 2019). Avoidance of costly encounters therefore requires accurate recognition of potential threats through sensory discrimination, followed by an appropriately gauged response that weights the relative costs of the threat. As stated by the threat sensitivity hypothesis, individuals should respond more strongly to cues associated with higher risks/costs (e.g. trade-off between avoidance of threat and reduced foraging time), but less strongly to cues with lower associated threat (Amo, Lopez, & Martin, 2005, 2007; Cisterne, Vanderduys, Pike, & Schwarzkopf, 2014; Payne, Tillberg, & Suarez, 2004).

Chemosensory cues are an important source of information on which to base judgement of likely costs of encounters and a suitable response. They can reliably allow forewarning of the immediate or recent presence of predators, and in certain circumstances they may be the only cues available (Kats & Dill, 1998). Indeed, the majority of examples of behavioural response (or lack thereof) of natives to chemical cues of novel species come from predator–prey systems (Cisterne et al., 2014; Hoffmann, McGarrity, & Johnson, 2018; Stanbury & Briskie, 2015). For example, the foraging behaviour of two native Australian lizards was compromised when individuals were exposed to scents of both native and invasive mammalian predators (Webster et al., 2018), suggesting prey naïvety is not the rule in native/non-native systems. The reverse situation, of invasive species' response to cues from novel predators, has also received attention, as in the avoidance response of the Asian house gecko, *Hemidactylus frenatus*, to some native predatory snake cues (Cornelis, Nordberg, & Schwarzkopf, 2019). There is less known, however, about behavioural responses to novel scent cues outside of predator–prey systems. It is reasonable to suspect that the presence of an introduced competitor species might have an effect similar to that of a novel predator, and therefore native species might learn to avoid cues from invasive species if these cues were previously associated with an encounter that incurred a cost (Ferrari, Crane, Brown, & Chivers, 2015). Examples come from Spanish terrapins', *Mauremys leprosa*, avoidance of water pools when chemical stimuli of the invasive red-eared slider, *Trichemys scripta*, is detected (Polo-Cavia, Lopez, & Martin, 2009), and honey bee, *Apis mellifera*, avoidance of flowers occupied by invasive Argentine ants, *Linepithema humile* (Sidhu & Rankin, 2016). Responses may, however, be more ambiguous, such as the preference of both the endemic Barbados leaf-toed gecko, *Phyllodactylus pulcher*, and an invasive house gecko, *Hemidactylus mabouia*, for

refuges conditioned with the scent of the other species (Williams, Pernetta, & Horrocks, 2016).

Chemoreception is highly developed in squamate reptiles (Cooper, 1994; Mason & Parker, 2010; Schwenk, 1993) and has an important function in social interactions with conspecifics (i.e. mate selection, Martin & Lopez, 2000, 2014; Pellitteri-Rosa et al., 2014; kin recognition, O'Connor & Shine, 2006; Pernetta, Reading, & Allen, 2009; Muellman, Da Cunha, & Montgomery, 2018; territorial behaviour, Lopez & Martin, 2002; Carazo, Font, & Desfilis, 2008; Font, Barbosa, Sampedro, & Carazo, 2012; Mangiacotti et al., 2019) and foraging (Baeckens, Huyghe, Palme, & Van Damme, 2017; Cooper, 1994; Wall & Shine, 2009). Recognition of chemical cues is also fundamental to formulating antipredator responses in squamates, as demonstrated by avoidance of refuges bearing only the scent of predators (Amo, Lopez, & Martin, 2006; Kats & Dill, 1998; Lopez & Martin, 2001; Ortega, Mencia, & Perez-Mellado, 2018). The ability of lizards to also discriminate between closely related sympatric species through pheromones has been demonstrated by the selective sexual behaviour and ethological isolation between *Eumeces* skinks (Cooper & Vitt, 1986), *Liolaemus* lizards (Labra, 2011) and lacertid lizards in the genus *Podarcis* (Barbosa, Desfilis, Carretero, & Font, 2005; Barbosa, Font, Desfilis, & Carretero, 2006).

Podarcis muralis is a small oviparous lizard native to southern and central Europe and northwestern Asia Minor, with an expanding introduced range in northern Europe and North America (Bertram, 2004; Hedeen & Hedeen, 1999; Kwiat & Gist, 1987; Michaelides, While, Zajac, & Uller, 2015; Schulte, Veith, Mingo, Modica, & Hochkirch, 2013). Being highly territorial, introduced *Podarcis* spp. populations pose a potential competitive (and predatory) threat to ecologically similar native species (Boag, 1973; Heym, Deichsel, Hochkirch, Vieth, & Schulte, 2013). On Vancouver Island, British Columbia, Canada, *P. muralis* is rapidly expanding its range into the habitat of the island's only native lizard, the northern alligator lizard, *Elgaria coerulea* (Engelstoft, Robinson, Fraser, & Hanke, 2020). In Britain, *P. muralis* has been introduced to habitat of the native common lizard, *Zootoca vivipara*, and in some areas has encroached upon habitat of the nationally rare sand lizard, *Lacerta agilis* (Mole, 2010; Woodfine et al., 2017). To date, there is little knowledge of the effects of introduced *P. muralis* populations on native lizard communities, although field observations suggest *P. muralis* is able to suppress or replace *L. agilis* (Kühnis & Schmocker, 2008; Schulte, Thiesmeier, Mayer, & Schweiger, 2008; but see ; Heym et al., 2013), *Z. vivipara* (Münch, 2001; Mole, 2010; R. Williams, personal observation) and *E. coerulea* (Engelstoft et al., 2020) where *P. muralis* has become abundant, especially in disturbed habitats.

With a view to exploring the possible indirect competitive interaction between *P. muralis* and native lizards, our objective in this study was to examine experimentally the scent recognition and behavioural response of non-native *P. muralis* individuals to scent cues of native lizard species within its introduced range in Britain (*L. agilis*, *Z. vivipara*) and on Vancouver Island (*E. coerulea*), and vice versa. Based on the naïvety and threat sensitivity hypotheses, we predicted differences in behavioural responses dependent on the associated cost incurred through interspecific interactions and/or the degree to which chemical cues used for interspecific communication might be similar among phylogenetically related species. In the context of our model system, we therefore predicted the taxonomic distance separating *P. muralis* and native *E. coerulea*, combined with the recent shift into sympatry (i.e. *P. muralis* was introduced in 1967, but recent rapid range expansion has increased potential for contact with *E. coerulea*), would lead to no scent recognition, whereas, despite being a relatively recent introduction to Britain (Foster, 2015), the closer phylogenetic relatedness and

substantial sympatry in continental Europe between *P. muralis* and the lacertids *L. agilis* and *Z. vivipara* (Sillero et al., 2014) would produce differences in behavioural response to scent cues.

METHODS

Animal Collection, Husbandry and Welfare

All wild-caught animals (see below for species' sampling locations and methods) were sexed based on the presence of hemipenes in males (Schulte, 2008), health screened and checked for external parasites before being taken into captivity.

All lizards were transported to the study facilities in plastic vivaria (20 × 12 cm and 16 cm high) with natural substrate and refuge objects obtained at the capture site. Lizard species were housed separately in large plastic vivaria (70 × 30 and 50 cm high), with water supplied ad libitum and provision for basking, a thermal gradient (18—28 °C) and shelter. Live food was offered every other day in the form of third-instar crickets, mealworms and waxworms. Light and heat were provided by incandescent (40 W) bulbs placed above each vivarium to provide a 14:10 h light:dark cycle; vivaria were moved outside during the day if weather conditions allowed. All lizards were marked dorsally with an identifying number in nontoxic marker and were given a 5-day acclimatization period to allow habituation to the general disturbances and handling prior to the experimental trials beginning.

Podarcis muralis

All *P. muralis* were caught by hand or noosing. Twenty-one adult males (snout—vent length >45 mm) with origins in the Emilian Apennines, Italy (Deichsel & Schweiger, 2004) were collected from the introduced population around the Prospect lake area (48.30°N, -123.25°E) and Fairfield district of Victoria, BC (48.24°N, -123.20°E). Nineteen adult male *P. muralis* of Venetian origin (Michaelides et al., 2015) were collected from an introduced population at West Worthing, Sussex, U.K. (50.48°N, 0.22°W). All *P. muralis* were euthanized as per approved ethical guidelines (see Ethical Note) following behavioural testing and retained for future research.

Zootoca vivipara

All *Z. vivipara* (11 females, seven males) were caught as part of active mitigation translocations at two sites: High Wycombe, Buckinghamshire, U.K. (51.61°N,−0.71°E) and West Malling, Kent, U.K. (51.28°N, 0.32°E) between 1 and 5 August 2018. *Podarcis muralis* is absent at both sites. Individuals were caught by hand under artificial refuges. These lizards were retained in captivity for 10 days for inclusion in the scent recognition experiments and subsequently released to the respective translocation receptor sites.

Lacerta agilis argus

Owing to the conservation status of *L. agilis* in Britain and necessary restriction on use of wild-caught animals, we used its most closely related subspecies *L. a. argus* (Andres, Franke, Bleidorn, Bernhard, & Schlegel, 2014). Five juveniles (three females, two males, born in August 2017) were acquired from captive stock in March 2018. These individuals were reared as a group in captivity and had reached adult size by August 2018. They were retained in a private collection after this study.

Elgaria coerulea

Elgaria coerulea (10 females, seven males) were collected, either by hand under natural refuges or by noose, from Kingzett Lake quarry (48.67°N, -123.63°E) and Mt Douglas (48.49°N, -123.34°E) on Vancouver Island in early July 2018. These lizards were retained in captivity for 10 days for inclusion in the scent recognition experiments after which they were returned to the point of capture. *Podarcis muralis* was absent at both sites in 2018.

Scent Recognition Experimental Procedure

The methodology for experimental trials of scent recognition was adapted from several chemosensory studies involving *Podarcis* spp. (Barbosa et al., 2005; Bertram, 2004; Font et al., 2012) and from pilot trials conducted in June 2017. Experimental trials were conducted on Vancouver Island, BC, between 10 and 20 July 2018, and in England between 15 and 21 August 2018. Trials were conducted between 0900 and 1700 h to coincide with the lizards' period of daily activity. The experimental enclosure was a clear plastic storage container (70 × 30 cm and 15 cm high) with opaque back and sides. Two textured, nonabsorbent, washable liners were used as floor coverings which were alternated between trials. The centre line of the enclosure was marked on each liner to delineate treatment halves for observation and analysis. Two small refuges (10 × 10 cm and 2 cm high) with a single entrance (3 cm long, 1 cm high) were created using slate and plastic building blocks and were placed against the side wall of each end of the enclosure (Fig. 1). A 60 W spot bulb was suspended directly overhead the experimental enclosure casting uniform heat (18 °C) and light throughout.

Treatment was randomly assigned to each half of the enclosure before each trial using a random number generator. Four swabs were placed in each half of the arena: one in each corner of the arena, one at the entrance to, and one on top of, each refuge (Fig. 1). For the control treatment, swabs were dipped in deionized water. We did not use a pungency control because in many previous studies, including those specifically dealing with *P. muralis* and *E. coerulea*, it has already been well established that these lizards have highly developed olfaction and can discriminate the scent of congeners, predators and prey from biologically irrelevant scents (Cooper, 1990; Cooper & Perez-Mellado, 2002; Gabirot, Castilla, Lopez, & Martin, 2010). Scent treatment was obtained according to established protocol from similar studies by first dipping swabs in deionized water and then gently rubbing the swab over the body of the scent donor making sure to swab femoral pores and cloacal regions, since these are the body areas most frequently and intensely investigated by tongue flicking during social encounters (Cooper & Perez-Mellado, 2002; Lopez, Martin, & Cuadrado, 2002). Scent donors were always males randomly selected from the relevant test population.

Test subjects were introduced to the experimental enclosure underneath a transparent container (15 × 10 cm and 10 cm high) placed on the central line of the enclosure. Once the lizard showed relaxed movement behaviour the container was gently removed,
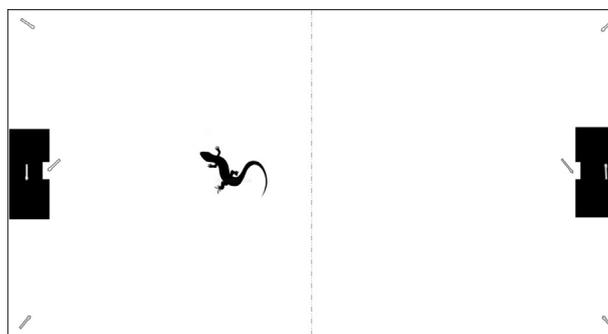

Figure 1. Diagram of the enclosure used for controlled experiments of scent recognition between *Podarcis muralis*, *Zootoca vivipara*, *Lacerta a. argus* and *Elgaria coerulea*. Scent/control swabs are depicted in the four corners of the enclosure and at the entrance to, and on top of, the refuges.

and on the first tongue flick from the subject a 10 min timer was started on the video camera recording the trial. Subsequent tongue flicks were tallied according to the treatment side in which they occurred. After the 10 min trial, test subjects were returned to the housing vivaria and were only used in one trial a day. Fresh swabs were used for each trial, and the liner, experimental enclosure and refuges thoroughly washed with warm water and wiped with alcohol to eliminate residual chemical traces before air drying prior to next use. Only British *P. muralis* took part in multiple trials (i.e. each was tested against *Z. vivipara* and *L. a. argus*). All other lizards were only involved in one trial, with no replicates, to avoid habituation to scent cues.

Cowlog 2.0 software was used to retrospectively analyse video recordings and quantify time spent between the enclosure halves (Hanninen & Pastell, 2009). We limited behaviour classifications to either the time spent in each half or the time spent exhibiting escape behaviour in each half of the enclosure. We defined escape behaviour as time spent standing in an upright position against the wall of the enclosure performing scratching movements with the forelegs. During escape behaviour the lizards were not engaged in tongue flicking or assessing their surroundings. The duration of escape behaviour in each half was thus subtracted from the total time spent in the half enabling quantification of only exploratory or stationary behaviour. Where variation in the time spent between treatment halves was observed we tested the rate of tongue flicks occurring in each half. We also recorded the number of times individuals fully entered (entire body under a refuge) either control or treatment refuges.

Ethical Note

Capture, husbandry, humane euthanasia of *P. muralis* and experimental procedure were carried out under licence from Natural England 2016-21938-SPM-NNR and approved by the ethics committee of BC Ministry of Forests, Lands and Natural Resource Operations and Rural Development (NA18-288615). All *P. muralis* were euthanized (by pithing and decapitation) following anaesthesia with 25% benzocaine gel via oral administration and stored in 90% ethanol after the experimental trials for further study. Currently accepted best practice for euthanasia of small lizards involves either straight blunt force trauma to the cranium, decapitation and/or pithing without prior anaesthesia (Leary, 2013). Recent discussions within the research community have recommended the efficiency of benzocaine as a general anaesthetic for small reptiles and amphibians. As such, its use prior to existing methods exceeds protocols previously considered humane for dispatching small lizards.

Data Analysis

All analyses were performed in R version 3.4.2 (R Core Team, 2017).

Podarcis muralis *response to scent of native species*

We tested two key hypotheses concerning the response of *P. muralis* to native species. First, we tested whether there was a difference in the response between the three native species using generalized linear models (GLM) with binomial errors. Response variables were the number of tongue flicks and the time spent exploring in treatment and control halves. We used the D^2 value (percentage deviance explained) to evaluate model fit, calculated as 1- deviance/null deviance. Post hoc Tukey tests via the 'glht' function in the package 'multcomp' (Hothorn, Bretz, & Westfall, 2008) were then applied to explore pairwise differences between species. Second, we tested whether there was evidence of scent

recognition or avoidance behaviour by *P. muralis* of each species individually. For each of the native species, we compared scent recognition (counts of tongue flicks in control versus treatment halves) and avoidance behaviour (time spent in each treatment half) by *P. muralis* using individual paired *t* tests. As all *P. muralis* individuals were male, sex was not included as a predictor in any models.

Native species' response to P. muralis

For native species' responses, we first tested whether there was a difference in the responses by the different native species to *P. muralis*. Since both male and female animals were used, we ran individual GLMs with binomial errors to determine the effects of sex on the response variables (ratios of number of tongue flicks and time spent exploring in treatment and control halves). Second, we tested for evidence of scent recognition and avoidance behaviour towards *P. muralis* scent using paired *t* tests for each native species to compare behaviours in the control and treatment halves of the enclosure (as above).

RESULTS

P. muralis *Response to Native Species*

There was a significant difference in the response of *P. muralis* towards the three native species in terms of ratio of tongue flicks in each treatment half (Table 1).

Post hoc Tukey's HSD tests showed that *P. muralis* responded with more tongue flicks to the *E. coerulea* treatment compared to both *Z. vivipara* and *L. a. agilis* treatments. There was no difference in the *P. muralis* tongue flick response towards *Z. vivipara* and *L. a. argus* ($z = -1.18$, $P = 0.46$). Analysis of the *P. muralis* discriminatory response (tongue flicks) to control and treatment scents showed a significantly greater response to *E. coerulea* scent versus the control (paired *t* test: $t_{20} = 2.63$, $P = 0.01$), no difference in response towards *Z. vivipara* scent versus the control ($t_{18} = 0.14$, $P = 0.88$) and no difference between *L. a. argus* scent versus the control ($t_{14} = 1.20$, $P = 0.24$; Fig. 2a).

There was also a significant difference in the response of *P. muralis* towards the other three species in terms of the ratio of time spent exploring each treatment half (Table 1). Post hoc Tukey's HSD tests showed that *P. muralis* spent significantly more time in the *Z. vivipara* treatment half of the arena than it did *E. coerulea* ($z = 10.65$, $P < 0.001$) and *L. a. argus* ($z = -7.46$, $P < 0.001$) treatments. There was no difference in the time spent by *P. muralis* near *E. coerulea* and *L. a. argus* treatments ($z = 2.28$, $P = 0.05$). Analysis of the aversion response (time spent near stimuli) of *P. muralis* to

Table 1
Binomial GLM results for *P. muralis* behavioural responses (ratio of tongue flicks towards scent versus control, ratio of time spent exploring in treatment versus control halves) towards scent of native lizard species *E. coerulea*, *L. agilis* and *Z. vivipara* (predictors)

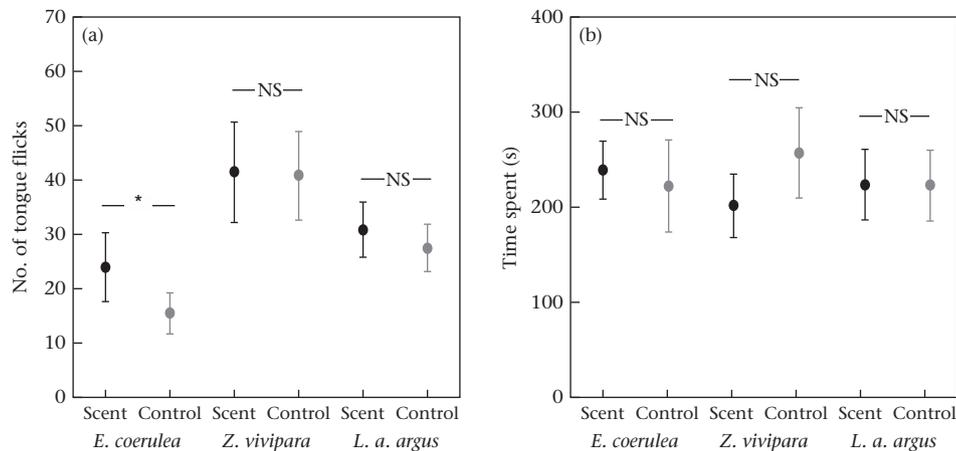|	Estimate	SE	Z	P
Tongue flicks				
E. coerulea	0.436	0.071	6.137	<0.001
L. agilis	-0.319	0.098	-3.253	<0.001
Z. vivipara	-0.420	0.087	-4.812	<0.001
D^2	0.126			
Time spent exploring				
E. coerulea	0.074	0.020	3.640	<0.001
L. agilis	-0.072	0.031	-2.282	0.02
Z. vivipara	-0.316	0.029	-10.655	<0.001
D^2	0.030			

D^2: percentage deviance explained.

Figure 2. Responses by *Podarcis muralis* towards scent cues from the native *Elgaria coerulea*, *Lacerta agilis argus* and *Zootoca vivipara* versus control stimuli. (a) Number of tongue flicks (mean ± SE) and (b) time spent (mean ± SE) near the scent stimulus. *$P < 0.05$.

treatment scents, however, showed no significant difference between time spent in the scent versus the control halves across groups (*E. coerulea*: $t_{20} = 0.36$, $P = 0.71$; *Z. vivipara*: $t_{18} = -1.23$, $P = 0.23$; *L. a. argus*: $t_{14} = 0.01$, $P = 0.99$; Fig. 2b).

Native Species' Responses to P. muralis

Sex had a significant effect only on the time spent by *L. a. argus* and *E. coerulea* in the treatment halves (Table 2). However, owing to small sample sizes (*E. coerulea* male:female = 7:10, *L. a. argus* 2:3, *Z. vivipara* 7:11), the pattern of response being similar between the sexes and our interest being primarily with species' response, we pooled the data across sexes for analysis.

Only *L. a. argus* showed a significant recognition response to *P. muralis* scent, with a mean ± SE = 103 ± 28.0 tongue flicks in the treatment end of the enclosure with *P. muralis* scent and 42 ± 8.0 tongue flicks in the control end ($t_4 = 2.99$, $P = 0.04$). There was no significant difference in the mean number of tongue flicks between *P. muralis* scent and control ends of the enclosure for *Z. vivipara* (40.2 ± 6.1 scent versus 46.1 ± 8.6 control; $t_{17} = -1.08$, $P = 0.29$) or *E. coerulea* (16.2 ± 2.4 scent versus 16.9 ± 3.9 control; $t_{16} = -0.23$, $P = 0.81$; Fig. 3a).

Neither group showed a significant aversion/attraction response to *P. muralis* scent as indicated by the time spent in each treatment

half. Although *L. a. argus* spent longer on average (66%) in the scented half than in the control ($t_4 = 1.93$, $P = 0.12$), that time can be attributed to four instances of direct attack (biting) of a scented swab. Conversely, *Z. vivipara* spent less time on average (38%) in the scent treatment half ($t_{17} = -1.88$, $P = 0.07$). Despite less time being spent in the scent treatment half, the rate of tongue flicks by *Z. vivipara* was greater in this half (mean ± SE = 0.24 ± 0.13) than in the control (0.16 ± 0.12; $t_{17} = 2.10$, $P = 0.05$). The average time spent in each treatment half was relatively even for *E. coerulea* (55% scented; $t_{16} = 1.22$, $P = 0.23$; Fig. 3b).

Refuge Use

Only *E. coerulea* used the scented refuge more often than the control refuge, whereas *L. a. argus* did not use either refuge. In all other experiments the control refuge received more visits than the scented refuge. The difference in visits between control and treatment refuge was greatest in the response of *Z. vivipara* to *P. muralis*, with four and nine visits, respectively (Fig. 4).

DISCUSSION

The results of this study highlight the potential for varied recognition and behavioural responses towards chemical cues within a native/non-native species model. In accordance with the study hypothesis, the results provide evidence of differing responses with taxonomic distance that are demonstrative of naïvety to scent cues of novel competitors and threat sensitivity between more closely related species.

P. muralis/E. coerulea Interaction

The responses of *P. muralis* and *E. coerulea* to each other's scent in our experiments complement the results of the only other behavioural study on interaction between these two species (Bertram, 2004). The previous study also found *P. muralis* scent to have no detectable effect on the behaviour of *E. coerulea*. The lack of discriminatory response of *E. coerulea* in the two studies suggests that the species is either unable to detect the odour of *P. muralis*, despite the highly developed chemosensory abilities of the species (Cooper, 1990), or does not respond behaviourally to the stimulus. Possible explanations for the observed lack of *E. coerulea* response is that, besides four snake species, there are no other terrestrial native reptile species occurring in sympatry with *E. coerulea* on

Table 2
Binomial GLM results for the effects of sex on the behavioural responses (ratio of tongue flicks towards scent versus control, ratio of time spent exploring in treatment versus control halves) of *E. coerulea*, *L. agilis* and *Z. vivipara* towards scent of *P. muralis*

		Estimate	SE	Z	P	D²
Tongue flicks						
E. coerulea	♀	-0.059	0.108	-0.544	0.587	0.003
	♂	0.059	0.171	0.344	0.731	
L. agilis	♀	0.969	0.110	8.777	<0.001	0.154
	♂	-0.164	0.164	-0.999	0.318	
Z. vivipara	♀	-0.149	0.068	-2.180	0.029	0.000
	♂	0.024	0.102	0.243	0.808	
Time spent exploring						
E. coerulea	♀	0.393	0.032	11.999	<0.001	0.007
	♂	-0.171	0.048	-3.545	<0.001	
L. agilis	♀	0.911	0.053	17.170	< 0.001	0.146
	♂	-0.589	0.081	-7.219	<0.001	
Z. vivipara	♀	-0.429	0.025	-17.120	<0.001	0.000
	♂	-0.053	0.045	-1.181	0.238	

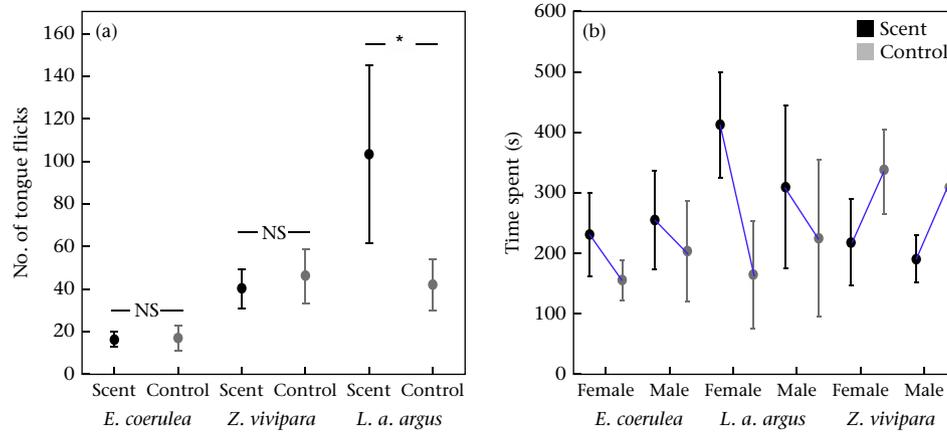D²: percentage deviance explained.

Figure 3. Responses of native lizards *Elgaria coerulea*, *Lacerta agilis argus* and *Zootoca vivipara* to scent cues of non-native *Podarcis muralis* versus control stimuli. (a) Number of tongue flicks (mean ± SE) and (b) time spent (mean ± SE), by sex, near the scent stimulus. *P < 0.05.
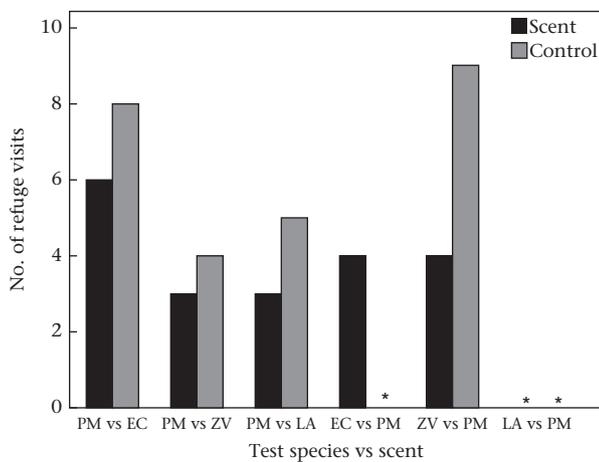

Figure 4. Number of visits to scent treatment and control refuges by *Elgaria coerulea* (EC), *Lacerta agilis argus* (LA), *Zootoca vivipara* (ZV) and *Podarcis muralis* (PM) individuals in the laboratory. Initials beneath bars denote species pairings, such that the first of each pair is the focal species and the second is the scent treatment (e.g. PM vs EC is *P. muralis* exposed to *E. coerulea* scent). An asterisk indicates zero.

Vancouver Island (Gregory & Campbell, 1984; Matsuda, Green, & Gregory, 2006), and therefore a complete naïvety of *E. coerulea* to scent of a phylogenetically distant lacertid lizard species is not unexpected. Similarly, a response is not to be expected if chemoreception is limited to foraging and intraspecific communication in this species. Our observations of *E. coerulea* readily using scented *P. muralis* refuges, seemingly in preference to unscented ones, do, however, warrant further investigation into the species' ability to recognize the scent of *P. muralis,* and support the hypothesis that the physical presence of *P. muralis*, not its scent alone, may deter *E. coerulea* from cohabiting refuges with the non-native (Bertram, 2004). If chemosensory recognition were influencing selection for the *P. muralis*-scented refuges, this could indicate that in the absence of visual cues and any previous negative experience, the scented refuge was perceived to be safe in an otherwise novel and unfamiliar environment. A similar outcome has been observed in refuge selection trials involving a native and an invasive gecko, where both species preferred a refuge previously occupied by the other (Williams et al., 2016). Identification with common compounds in species' scents may have driven refuge choice in such cases (Garcia-Roa, Cabido, Lopez, & Martin, 2016; Martin & Lopez, 2014; Mason & Parker, 2010), or there may be a benefit in using

heterospecific cues as a measure of refuge quality (Parejo, Danchin, & Avilés, 2004).

Naïvety was not symmetrical in this pairing, however, and the discrimination and heightened response of *P. muralis* towards the scent of *E. coerulea,* above that shown towards the scent of the other species in our experiment, is unexpected considering the taxonomic distance between the two. There are numerous examples across lizard species, including *Podarcis* spp., of an ability to discriminate between closely related species based on chemical cues alone (Barbosa et al., 2006; Cooper & Perez-Mellado, 2002; Cooper & Vitt, 1986; Gabirot et al., 2010; Labra, 2011). There is, however, little evidence for scent recognition of more taxonomically distant species outside predator/prey systems (e.g. snake predator/lizard prey interactions; Amo, Lopez, & Martin, 2004; Cabido, Gonzalo, Galan, Martin, & Lopez, 2004; Labra & Hoare, 2015; Zagar, Bitenc, Vrezec, & Carretero, 2015; Ortega et al., 2018). For example, *Blanus cinereus*, a fossorial amphisbaenian, reacted strongly to scent stimuli of sympatric snake and centipede predators, yet showed no difference in reaction towards a water control and an innocuous, sympatric skink (Lopez & Martin, 2001). Male *Podarcis hispanica* are capable of discriminating conspecific scent from that of *Psammodromus algirus*; however, no variation in tongue flick response between an odourless control and *P. algirus* scent suggests a lack of behavioural response towards, or inability to detect, the latter (Gomez, Font, & Desfilis, 1993). Regardless of the context in which *P. muralis* explored the scent of *E. coerulea* (i.e. inquisitiveness towards a novel or biologically relevant scent) the fact that this discrimination of scent did not elicit a behavioural response in *P. muralis* (e.g. attraction, avoidance or aggression) suggests that the stimuli (alone) may have been regarded as benign. A lack of behavioural response having distinguished the odour is to be expected if fitness costs associated with avoidance behaviour outweigh those of any naturally occurring direct interaction, such as limited agonistic behaviour between the two species (Langkilde et al., 2005). This response of *P. muralis* can also be interpreted as a heightened boldness and willingness to explore unfamiliar stimuli (neophilia), coupled with high levels of behavioural plasticity to mediate the response. Such facilitative traits may be common among species that become invasive (Damas-Moreira et al., 2019) and may be fundamental to the expansion of the species' range on an intercontinental scale. These results and reasoning are in keeping with observations of a greater propensity for *P. muralis* to make the first approach in controlled direct encounters with *E. coerulea*, but ultimate lack of aggression arising between the two (Bertram, 2004).

P. muralis/L. agilis/Z. vivipara *Interaction*

In light of the recognition of *E. coerulea* scent by *P. muralis*, the lack of similar response towards the more closely related lacertids *L. a. argus* and *Z. vivipara* strongly suggests a diminished response by *P. muralis* rather than an inability to detect their chemical cues. This lack of response could indicate that *P. muralis* has no evolved or learned aversion to the stimuli (at least in the absence of other cues), in accordance with the threat sensitivity hypothesis. A threat-sensitive response is apparent in the different antipredator responses of *P. muralis* in relation to visual and scent cues (Amo et al., 2006). Conversely, the responses of *Z. vivipara* and *L. a. argus* to scent cues of *P. muralis* appear to have been based on a threat-sensitive perception of potential for a costly encounter, eliciting definitive avoidance and aggressive behaviour in *Z. vivipara* and *L. a. argus*, respectively.

If the aggressive reaction of *L. a. argus* represents an innate antagonistic response to *P. muralis* then an appropriate reciprocal behaviour might be expected in the reverse treatment. More likely, however, is that the sensory naïvety of the captive-born *L. agilis* individuals used in our study led to misinterpretation of the novel scent of the swabs as a potential prey item. Similar attacks on swabs have been observed in experiments specifically testing lizard discrimination of prey odours (Cooper, 1990, 1991, 1992). These results must therefore be considered with caution without further tests (e.g. including visual cues and recognition tests between *L. agilis* and *Z. vivipara*).

Taken on its own, there is a certain amount of ambiguity in the tongue flick response of *Z. vivipara* towards *P. muralis*. The greater amount of time spent in the control half (although not statistically significant), paired with more than twice the number of visits to the control refuge and an increased rate of exploratory tongue flicking in the scented half, is, however, indicative of an aversion response by *Z. vivipara* towards the non-native scent cues. This is in keeping with field observations of population declines and displacement of *Z. vivipara* in areas where introduced *P. muralis* are thriving (Mole, 2010; R. Williams, personal observation). Avoidance behaviour elicited by indirect cues alone has obvious advantages to mediating potential fitness costs arising from direct encounters, particularly when the costs of avoidance are low (Langkilde et al., 2005).

Overall, our results suggest that non-native *P. muralis* are unlikely to alter their behaviour in response to indirect chemical cues from native lizards with which they may potentially compete. Continued range expansion of non-native populations and greater overlap with native species' ranges is therefore likely to increase the incidence of direct interaction and possible aggressive encounters that may have fitness costs for native lizards (and *P. muralis*). In the case of *Z. vivipara*, an aversion response to indirect cues from *P. muralis* may mitigate the chance of direct encounters but ultimately lead to displacement of the native from previously occupied areas. Conversely, interactions between *P. muralis* and *E. coerulea* and *L. agilis* have potential to be more direct, the outcomes of which are likely to be context dependent and further research is needed to determine the nature and outcome of interactions when resources are limited (i.e. refuge, basking spot). Juveniles of all the species tested here are vulnerable to predation from larger adult lizards, and therefore further experiments on juveniles may also reveal ontogenetic differences in responses.

These results highlight how responses to indirect cues might act to shape the competitive interaction between invading and native species, interactions that will ultimately determine invasion success and the impact on native communities.

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