Does geographical isolation influence group recognition and social preference in an invasive lizard?

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Abstract

The formation of aggregations is fundamental to animal organization and has been shown to confer an evolutionary advantage. Conspecific attraction often prompts the formation of social groups yet not all individuals are equally attracted to others of their own species. The decision to aggregate with or avoid a particular individual is based upon class-specific signals that serve to differentiate among members and non-members. Given that signal divergence may be driven by local adaptation, disjunct populations could potentially have evolved distinct recognition systems adapted to their own ecological conditions. Several studies have shown that individuals of a species are capable of discriminating between such classes as sex, mate, kin, and familiar. Yet research exploring conspecific attraction between populations is lacking. Invasive species offer a unique opportunity to determine the consequences of geographic isolation on recognition systems and social preferences, as these genetically distinct native-range source populations have the potential to undergo secondary contact within the invaded region. To this end, we used an invasive lizard species, the delicate skink (*Lampropholis delicata*), to investigate conspecific recognition and attraction among individuals from two identified source populations that vary both genetically and morphologically. Our results of the dichotomous choice tests indicate that *L. delicata* did not differ in the level of social attraction expressed towards individuals from either population. It is unclear whether these findings are due to an inability to discriminate between local and foreign lizards using visual cues or instead that attraction is not based upon an individual's population origin but rather some other factor such as thermoregulatory requirements. Understanding the role that conspecific attraction plays in the invasion process will enable us to better predict the impacts of biological invasions. Future studies should consider using other sensory modalities and investigate the physiological benefit of grouping.

Introduction

The formation of animal aggregations is taxonomically widespread and is fundamental to animal organization (Lancaster, Wilson & Espinoza, 2006). Groups can be comprised of multiple species or involve only a single species. Both types of group compositions can confer an evolutionary advantage, but conspecific aggregations, in particular, have been shown to afford a number of fitness benefits (McBride, 1964; Billingham *et al.*, 2010; Pizzatto *et al.*, 2016). For instance, grouping with conspecifics can improve reproductive success as it facilitates finding potential mates (Billingham *et al.*, 2010). It can also function as an anti-predatory strategy through the effects of predator dilution and group vigilance (Lanham & Bull, 2004; Pizzatto *et al.*, 2016). What's more, conspecific aggregation may also have the benefit of enhanced resource acquisition and thermoregulation (Stamps, 1988; Gruber *et al.*, 2017). Individuals may be attracted to the presence of conspecifics as they

can serve as cues to the location of food and quality habitat as well as mitigate physiological stressors imposed by the abiotic environment (Khan, Richardson & Tattersall, 2010; Pizzatto *et al.*, 2016; Gruber *et al.*, 2017).

However, grouping with conspecifics is not only dictated by ecological or physiological factors, other drivers may also be at play. This is indicated by observing the fine-scale patterns of conspecific aggregations which suggest that not all individuals are equally attracted to others of their own species (Ward *et al.*, 2009). Instead, individuals have the capacity to discriminate between subsets and this ability, in turn, mediates their choice of group mates. Such choices may be based upon population (local or foreign), sex (male or female), mate (mate or non-mate), offspring (own or other), kin (kin or non-kin) or familiarity (familiar or stranger) (Boal, 2006). Individuals must, therefore, be recognizable as belonging to one of these particular classes and this depends upon the transmission and reception of signalling information (i.e. phenotypic cues) (McBride,

1964; Billingham *et al.*, 2010). Visual (Head, Keogh & Doughty, 2005; Fenner & Bull, 2010; Kozak, Cirino & Ptacek, 2008; New *et al.*, 2012), auditory (Hauber & Sherman, 2001) or olfactory (Gabirot *et al.*, 2010; Labra, 2011; MacGregor *et al.*, 2017) sensory modalities are used in determining whether a receiver is attracted to or repelled by a signaller.

Much evidence does suggest that animals are indeed capable of discriminating between members of these classes by utilizing highly evolved recognition systems (Ord & Stamps, 2009; Labra, 2011; Pizzatto *et al.*, 2016; Iglesias-Carrasco *et al.*, 2017) and that a selective response towards these class-specific signals provides a high fitness value (Goth, 2004; Mateo, 2004; Campbell & Hauber, 2009; Ord & Stamps, 2009). In having recognition systems that are inherent to each class, identification errors are less likely to occur, reducing the potential of agonism or wasted reproductive investment by way of nonviable or infertile hybrid offspring (Mateo, 2004; Ord & Stamps, 2009; Labra, 2011).

Several studies have shown that individuals of a species are capable of discriminating between such classes as sex, mate, kin and familiar. Yet research exploring conspecific attraction between populations is lacking. It has been suggested that signal divergence may be driven by local adaptation to varying selective regimes (Seddon, 2005; Gruber *et al.*, 2017). Variation in the signalling environment could result in morphological and/or behavioural differentiation among populations which serve as visual cues during the recognition process.

Disjunct populations could, therefore, have evolved distinct recognition systems adapted to their own local conditions to maximize the transmission and reception of visual cues (Leal & Fleishman, 2004).

Of the relatively few studies investigating the discriminatory capacities and social preferences among different populations within species, they suggest that recognition systems for this class have evolved. Individuals were found to have the capacity of discriminating between foreign and local members (Rivault & Cloarec, 1998; Rupp & Woolhouse, 1999; Searcy *et al.*, 2002; Wong, Keogh & Jennions, 2004; Labra, 2011; Lin *et al.*, 2016; Iglesias-Carrasco *et al.*, 2017). For instance, when exposed to a two-choice experiment involving playback of local and foreign echolocation stimuli, greater horseshoe bats (*Rhinolophus ferrumequinum*) responded more rapidly and spent a greater amount of time aggregating in local compartments (Lin *et al.*, 2016). Among perch (*Perca fluviatilis*), individuals discriminated between populations using odour and chose to shoal on the side of the fluvarium having the odour of their own population (Behrmann-Godel, Gerlach & Eckmann, 2006). Among these studies, social preference was more often towards those of the same population as a way of improving mating opportunities and predator avoidance.

However, other, albeit limited, evidence indicates that preferential treatment (i.e. attraction) can instead be towards individuals from foreign populations. This pattern of group association seems to follow the model of optimal outbreeding where mate choice involves the selection of those having some level of genetic distance (Billingham *et al.*, 2010). Among Australian wood-boring cockroaches (*Panesthia australis*), for example, individuals were most likely to group with those

from a geographically distant population rather than their own local population (Billingham *et al.*, 2010). It was suggested that, in having low dispersal abilities, the restricted gene flow within this species prompts group association with genetically dissimilar cockroaches as a means of inbreeding avoidance.

Unravelling the mechanisms that underlie the evolution of recognition systems between populations and their effects on conspecific attraction is particularly important for determining how signalling cues shape social interactions in the context of biological invasions. It has been suggested that the invasion process may impose selection on social behaviour that plays a role in recognition signals resulting in divergence between different source populations as well as between long-colonized individuals and new arrivals (Carvalho *et al.*, 2013). Moreover, differences in the local environment between the source and invaded ranges could lead to geographical variation in signalling response systems. On the other hand, given that invasions have been found to result from repeated introductions of only a small number of individuals who are often from different source populations, having the ability to recognize both local as well as foreign conspecifics as potential mates would increase reproductive opportunity, thereby, allowing the problems arising from founder effects and genetic bottlenecks to be overcome (Chapple *et al.*, 2013). Under this premise, it would be expected, then, that the recognition systems of invaders would need to remain unchanged or that individuals would not exhibit strong social attraction on the basis of population origin. However, this has rarely been explored (but see Gruber *et al.*, 2017).

Invasive species, therefore, offer a unique opportunity to determine the consequences of geographic isolation on recognition systems and social attraction, as these genetically distinct native-range source populations have the potential to become in contact with one another within the invaded region. To this end, we used an invasive lizard species, the delicate skink (*Lampropholis delicata*), to investigate social attraction among individuals from geographically disjunct populations. The delicate skink is a gregarious species that is commonly found basking with conspecifics (ca. 2-10 individuals) under natural conditions (Chapple *et al.*, 2011a; Chapple, Simmonds & Wong, 2011b; Michelangeli *et al.*, 2017). They are native to eastern Australia but has since expanded its range through unintentional, multi-source introductions into Hawaii, New Zealand, and Lord Howe Island (Chapple *et al.*, 2013; Tingley *et al.*, 2016). The introduced populations have been shown to originate from five genetically distinct source regions (Brisbane, Tenterfield, Border Ranges, Yamba-Coffs Harbour, and Sydney) within the native range that are estimated to have been geographically isolated from each other for approximately two million years (Chapple *et al.*, 2011a,2011ba,b, 2013). High levels of genetic admixture (involving all five native-range source regions) within the introduced Lord Howe Island populations indicate that individuals from distinct populations are indeed coming into contact and interbreeding (Chapple *et al.*, 2013; Moule *et al.*, 2015). However, the mechanisms mediating the social interactions within the invaded regions have yet to be resolved. It can be surmised that visual cues are likely important in class recognition (i.e. population and sex) for this

species given that it exhibits geographic variation in the presence of a lateral stripe, body size, body shape, as well as skin reflectance, and it also shows sexual dimorphism in body proportions (Forsman & Shine, 1995a,b). Brisbane lizards are larger, have longer interlimb length and have a higher frequency of the lateral stripe. Indeed, the use of visual stimuli in terms of body colouration and behavioural displays is also well demonstrated in other skink species (Nicoletto, 1985; Langkilde, Schwarzkopf & Alford, 2003; Head *et al.*, 2005; New *et al.*, 2012; Abramjan *et al.*, 2015), including congenerics (*L. coggeri*: Scott *et al.*, 2015; and *L. guichenotti*: Shine and Torr).

We, therefore, examined the social preferences of delicate skinks from two identified native-range source regions using dichotomous choice tests to determine if previously isolated populations are indeed capable of distinguishing between each other based on visual cues and whether they show differential attraction for local or foreign conspecifics. Alternatively, it may be that group formation in this species is merely a behavioural response towards modulating physiological functionality and is therefore attracted to similar microclimates. By investigating group recognition within this species, not only will the resultant information contribute to our understanding of social behaviour but it will also serve to further our knowledge into the role that conspecific attraction plays in the invasion process.

Materials and methods

Animal collection and husbandry

A total of 60 adult (SVL > 35 mm) male delicate skinks were collected from two genetically distinct native-range source locations Lane Cove National Park, Sydney, Australia (33°47′17.754″ S, 151°08′43.968″ E; *n* = 30) and suburban Brisbane (27°27′8.863″ S, mimic152°59′32.338″ E; *n* = 30). Each individual was marked with a unique Visible Implant Elastomer (Northwest Marine Technology) colour code beneath the limbs which is not visible without the use of an ultraviolet light torch. Lizards were transported back to Monash University (Clayton, Victoria, Australia) where they were maintained at 22°C with a 14 h light: 10 h dark cycle (06:00–20:00 h). Given this species is known to aggregate into groups in the wild, individuals from each population were housed separately in groups of six to mimic natural social conditions as well as prevent interactions with individuals from other populations.

Social behaviour experiments

Prior to the onset of the experiments, lizards were either assigned to the focal group (Sydney = 23; Brisbane = 24) or stimulus group (Sydney = 7; Brisbane = 6). Each focal lizard was exposed to three dichotomous choice experiments (treatment 1, treatment 2 and treatment 3) to evaluate social attraction using visual cues. The experimental order and time of day tested (between 8:00 and 17:00) was block-randomized to account for potential confounding effects. All lizards were

fasted for 24 h prior to testing as digestion has been shown to affect behaviour (van Berkum *et al.*, 1989). Experiments were conducted in the same temperature-controlled room (22°C) in which they were housed.

Social attraction was assessed using the methods described in Michelangeli *et al.* (2017). Briefly, a focal lizard was placed in an experimental arena (55 cm length × 32 cm wide × 24 cm height) divided into three equal zones: two basking zones and an intermediate neutral zone. Black lines delineated the boundaries of each zone. Both basking zones were comprised of a basking site (heat lamp suspended above a ceramic tile) divided in half by a clear Perspex™ partition that ran the length of the test arena. In one basking zone, three unfamiliar stimulus lizards were placed behind the partition as to prevent direct interaction with the focal lizard while still enabling lizards to visually assess each other. On the opposite end of the arena was the second basking zone having the identical set-up. However, depending upon the treatment, this zone either contained three unfamiliar stimulus lizards or was left empty thereby serving as asocial choice. The neutral zone separated both basking zones and was considered a 'no choice' zone.

At the onset of each trial, the focal lizard was placed under a clear plastic cup in the centre of the neutral zone and allowed to acclimate for 10 minutes. Following acclimation, the cup was removed, and the lizard was allowed to move freely for 20 min. Each trial was filmed from a JVC Everio GZ-E100 video recorder suspended above the arena. All equipment was cleaned with soapy water between trials to prevent scent contamination amongst trials. Videos were downloaded for later playback and data analysis (JWatcher™: Blumstein, Evans & Daniels, 2006). The amount of time in seconds spent basking either alone or with conspecifics from either population was used to evaluate social preferences and served as a criterion of population recognition. Lizards were considered to be within a basking zone when all four limbs had crossed into the zone.

For each of the dichotomous tests, the source population from which the stimulus lizards originated from varied. In treatment 1, stimulus lizards from the same (local) population as the focal lizard were placed behind the partition in one basking zone while the other had no stimulus lizards and considered an asocial zone. Focal lizards were sourced from different housing containers than stimulus lizards so as to account for any potential bias on the basis of familiarity. For treatment 2, stimulus lizards from the genetically different (foreign) population were placed behind the partition in one basking zone while the other had no stimulus lizards and considered an asocial zone. Finally, for treatment 3, each basking zone contained stimulus lizards with one zone having lizards from the same population as the focal lizard while the other zone contained lizards from the different population.

Statistical analyses

Statistical analyses were completed using RStudio (Version 0.99.891; R Studio Team, 2015). The strength of attraction among members of the same or different population, as

indicated by the amount of time spent in either basking zone, served as the criterion for grouping preference. Only the time within either of the basking zones was included in the analyses while the time in the 'no choice' neutral zone was excluded. Within-population variation in basking site choice for each of the treatments was assessed using a paired *t*-test. Differences in selection between populations were assessed using a Welch's two-sample *t*-test.

Results

Within-population comparisons indicated that lizards from both Brisbane and Sydney showed little variation in the level of social attraction (Table 1). Brisbane lizards did not differ in the amount of time allocated to basking alone or grouping with lizards from the local population or foreign population. Sydney lizards, on the other hand, chose to bask alone to a greater degree than basking with conspecifics from the foreign population ($t = 4.16$, $P < 0.001$; Table 1). When considering the grouping behaviour between populations, variation was observed only when lizards were given the option to either bask with conspecifics from either the foreign population or alone ($t = -3.93$, $P < 0.001$; $t = 2.37$, $P = 0.02$; respectively; Table 2 and Fig. 1). For this treatment, Sydney lizards had greater attraction towards the foreign population, preferentially selected grouping with lizards from Brisbane. Time basking in all other contexts was the same between Sydney and Brisbane populations.

Discussion

In evaluating the social attraction and recognition capacity among two geographically isolated populations (Sydney and Brisbane) of *L. delicata*, our dichotomous choice tests showed that lizards did not vary in their grouping preferences. Instead, Brisbane lizards were neither preferentially attracted to, nor repelled by, lizards of either population. Sydney lizards, by contrast, exhibited a higher level of attraction towards foreign

lizards but only when given the choice to bask either with Brisbane lizards or alone.

Overall, our findings contrast previous work evidencing attraction at the population level. These studies demonstrated that individuals did have the capacity to recognize individuals as being either foreign or local (Labra, 2011; Macedonia *et al.*, 2013; Scott *et al.*, 2015; Lin *et al.*, 2016; Pizzatto *et al.*, 2016; Iglesias-Carrasco *et al.*, 2017). Preference was typically for those that were local rather than foreign as it promoted greater levels of foraging efficiency, predator defence and/or reproductive success (Billingham *et al.*, 2010; Pizzatto *et al.*, 2016). However, there are examples where attraction was higher towards foreign individuals (Houde & Hankes, 1997; Billingham *et al.*, 2010), which was observed among the Sydney lizards in our study. Although, for this preference to be considered robust, we would have expected that Sydney lizards would have been disproportionately attracted to Brisbane lizards when provided the choice between individuals from either their local or foreign population, which was not the case.

Three primary factors could have led to a lack of population attraction being observed in *L. delicata*. Firstly, it could be due to an inability to discriminate between foreign and local lizards. Similar ecological conditions across populations of *L. delicata* could have prevented divergence in this species' recognition system. Local adaptation has often been thought to arise through plasticity in phenotypic signals which respond to variation in selective regimes (Seddon, 2005; Iglesias-Carrasco *et al.*, 2017). Changes within the signalling environment prompt shifts in phenotypic traits that are used as cues, such as morphological, behavioural or auditory cues, in order for efficient transmission and detection of signalling information. Selection for the evolution of recognition systems is demonstrated in male anoles (*Anolis cristatellus*), where dewlap colouration varies as a function of the distinct light intensity and spectral quality of their respective habitat (Leal & Fleishman, 2004). Perhaps, then, similarity in habitat variables that influence signalling between *L. delicata* individuals has served

Table 1 Within-population variation in time allocation towards basking by delicate skinks from two genetically distinct populations (Sydney and Brisbane) across three dichotomous choice tests. All lizards were exposed to each treatment once (total trials per treatment = 47). Treatments varied in the option for the focal lizard to bask with three conspecifics from a foreign population, three conspecifics from a local population or alone. Significant values are in bold

Focal population	Treatment	N	Basking option	Mean time allocated (m)	t	P-value
Sydney	1	23	Foreign	8.34 ± 1.42	1.16	**<0.001***
			Alone	16.31 ± 1.07		
	2	23	Local	10.90 ± 1.35	1.64	0.12
			Alone	15.45 ± 1.46		
	3	23	Local	13.14 ± 1.46	0.74	0.47
			Foreign	11.30 ± 1.48		
Brisbane	1	24	Foreign	14.34 ± 1.09	−1.05	0.31
			Alone	12.33 ± 0.90		
	2	24	Local	12.82 ± 0.96	0.76	0.45
			Alone	14.30 ± 1.08		
	3	24	Local	12.07 ± 0.80	−1.57	0.13
			Foreign	14.40 ± 0.75		

Table 2 Between-population variation in time allocation in basking by delicate skinks from two genetically distinct populations (Sydney and Brisbane) across three dichotomous choice tests. Each treatment varied in the basking options available. The Foreign option enabled the focal lizard to bask with three conspecifics from a foreign population. The Local option allowed grouping with three lizards from the same population. Alone had no stimulus lizards. All lizards were exposed to each treatment once resulting in a total of 47 trials per treatment. Significant values are in bold

Treatment	N	Basking option	Mean difference (m)	t	P-value
1	47	Foreign	−6.00 ± 1.53	−3.93	**<0.001***
		Alone	3.98 ± 1.68	2.37	**0.02**
2	47	Local	−1.93 ± 1.65	−1.16	0.25
		Alone	1.14 ± 1.82	0.63	0.53
3	47	Local	1.07 ± 1.66	0.65	0.52
		Foreign	−3.10 ± 1.66	−1.87	0.07

to maintain consistency in cues that would otherwise be used to discriminate between local and foreign lizards.

Furthermore, it has also been suggested that recognition systems evolve in order to minimize the occurrence of hybridization between species or genetically distinct populations of a species. But given that populations of *L. delicata* have not undergone reproductive isolation, as indicated by high levels of genetic admixture within invaded regions, the recognition systems of Brisbane and Sydney lizards may not have diverged as a result of this. Without variation in signalling information
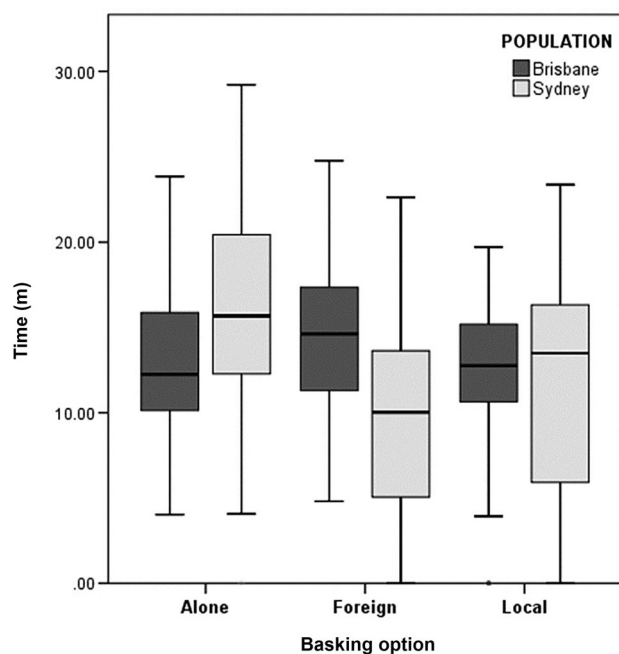

Figure 1 Social preferences of *Lampropholis delicata* from the two genetically distinct populations of Sydney and Brisbane. Time allocation towards each basking option served as the criterion of attraction.

between populations, lizards may not have the ability to distinguish between local and foreign individuals at all.

The second factor which may have led to a lack of observable social preferences may have arisen from the cue type used in our study. Even in having the ability to recognize individuals as belonging to this class, the use of visual rather than olfactory cues may have prevented lizards from being able to distinguish local from foreign members. Morphological and behavioural traits may not have provided sufficient signals to base a decision on. Here, focal and stimulus lizards were separated by a plastic barrier, which may have made chemosensory cues unperceivable. Chemical signals have indeed been purported to be an important component of the recognition system among reptiles (Bull *et al.*, 2001; Font & Desfilis, 2002; Labra, 2011; MacGregor *et al.*, 2017). The reliance of chemical information was demonstrated in a study involving a congeneric of *L. delicata*, *L. coggeri* (Scott *et al.*, 2015), which indicated that individuals preferentially mated with lizards from the same population. Although, visual information was also used during mate choice trials suggesting that these cues also played an important role in the discrimination process. Nevertheless, there is geographical variation in morphological characteristics among populations of *L. delicata* in terms of body proportions and the presence of a lateral stripe (Forsman & Shine, 1995a,b; Miller *et al.*, 2017). Colour variation usually correlates to differences in ultraviolet reflectance patterns, and these are used for intra-specific signalling in a variety of taxa, including lizards (Fleishman, Loew & Leal, 1993; Marshall & LeBas, 2001; Macedonia *et al.*, 2000; Blomberg, Owens & Stuart-Fox, 2001). It is likely, then, that the different spectral characteristics of *L. delicata* individuals from Sydney and Brisbane may afford the necessary visual cues needed for population recognition, making chemical information less necessary for discrimination in this species. Moreover, the importance of vision as a sensory cue among species of skinks has been widely evidenced (Head *et al.*, 2005; Fenner & Bull, 2010; New & Bull, 2011; New *et al.*, 2012). Future studies should, however, employ chemical cues to further investigate social attraction among populations of this species to determine if cue type does influence recognition capabilities.

Finally, the third explanation of a lack of differential attraction in our study could be that population origin does not influence grouping behaviour in *L. delicata*, irrespective of recognition capacity. Factors other than class membership could instead be more important in driving aggregation dynamics in this species. For example, group formation may be an anti-predatory strategy where shared vigilance would act to increase predator detection and greater numbers of potential prey would increase an individual's chance of survival through dilutionary effects. This would hold true no matter what the composition of the group is as long as the group members shared a common set of predators. This is not only demonstrated in other taxa (birds: Metcalfe, 1984; primates: Heymann & Buchanan-Smith, 2000) but it is also evidenced by the fact that *L. delicata* is commonly observed basking with both conspecifics and morphologically similar congenerics in the wild (Chapple *et al.*, 2011a,b).

Previous work has also suggested that grouping could be driven by thermoregulatory requirements or to reduce evaporative water loss, and thus serve a physiological purpose rather than a social benefit *per se* (Lancaster *et al.*, 2006; Khan *et al.*, 2010). In the case of ectotherms, they are especially vulnerable to the physiological effects of the abiotic environment. By being in close physical contact with others in a group would enable body temperatures to be elevated and maintained within an optimal range. Desiccation could also be modulated, particularly when grouping within retreat sites, as the surface area-to-volume ratio of the group is dramatically reduced (Lancaster *et al.*, 2006). These physiological benefits have been demonstrated in other lizard species (*Pogona vitticeps*: Khan *et al.*, 2010; *Coleonyx variegatus*: Lancaster *et al.*, 2006). Authors suggested that individuals may be prompted to aggregate due to a mutual attraction to similar microclimates. In other words, the presence of conspecifics served as visual cues indicating the location of quality thermal and humidity environments.

Regardless of whether recognition systems have yet to evolve or if grouping is merely uninfluenced by population origin, the lack of social preference among populations of *L. delicata* observed in this study certainly could have considerable implications within the context of this species' invasibility. Specifically, the willingness to form mixed social groups may act in promoting the occurrence of hybridization, as seen on Lord Howe Island. Within this introduced range, high levels of admixture may have contributed to the rapid spread of lizards throughout the southern portion of the island as increased genetic variation is thought to, at times, mitigate founder effects and genetic bottlenecks thereby bolstering population growth and spread (Chapple *et al.*, 2013). Clearly, determining the social preferences of invasive species would help increase our understanding of the drivers of biological invasions.

Conclusions

Understanding conspecific attraction within the context of secondary contact is of fundamental importance to our understanding of social behaviour and its role in biological invasions. Our results show that *L. delicata* expressed no social preference towards individuals from either population. Whether these findings are due to an inability to discriminate between local and foreign lizards or instead that attraction is not based on an individual's population origin could not be deciphered from our experimental set-up. Future work should focus on using chemical cues as well as comparisons with lizards from the introduced range to further tease apart the underlying mechanisms driving group formation in this species. Investigating the physiological benefit of grouping as an alternative driver of attraction should also be considered. Such information could provide greater insight into how conspecific attraction and the evolution of recognition systems influence biological invasions.

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Compliance with Ethical Standards

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