



Aggression mediates dispersal tendency in an invasive lizard



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ARTICLE INFO

Article history:

Received 22 February 2017
Initial acceptance 24 April 2017
Final acceptance 31 July 2017

MS. number: 17-00177R

Keywords:

animal personality
behavioural syndrome
competition
dispersal
invasive species
range expansion
reptile

Personality-dependent dispersal is a key ecological and evolutionary process that is likely to facilitate the successful movement and colonization/invasion success of species. This dispersal syndrome suggests that dispersers should possess a suite of behavioural tendencies that differ from those of nondispersers, thus influencing the composition of populations in the new range and, ultimately, colonization success. However, dispersal is also often condition dependent, and is probably mediated by the interaction between an individual's personality and environmental and social factors such as competition. Accordingly, we investigated whether dispersal tendency was linked to an activity, exploration and social syndrome and/or aggression in a reptile, the delicate skink, *Lampropholis delicata*, which has had a successful invasion history via accidental introductions. Contrary to our prediction, we found that dispersal was not related to activity, exploration or social personality traits. Instead, dispersal tendency was associated with aggression: the most aggressive individuals dispersed further and faster than less aggressive individuals. The presence of aggression-dependent dispersal could be due to either (1) dispersers generally being more aggressive than nondispersers or (2) aggressive individuals forcing nonaggressive individuals into hiding, thus impinging on the ability of subordinates to disperse regardless of their personality. Our study highlights the need to consider the ecological context when examining personality-dependent dispersal and suggests that aggression and the social environment can play an important role in dispersal decisions.

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Dispersal is a key ecological and evolutionary process governing how individuals, populations and species respond and adapt to changing environments (Chaine & Clobert, 2015). For example, dispersal is the mechanism that allows individuals to move away from degraded habitats and/or expand their range to colonize new areas (Bestion, Clobert, & Cote, 2015; Clobert, Galliard, Cote, Meylan, & Massot, 2009). However, dispersers are not a random subset of the population, but instead typically consist of individuals that have a certain suite of morphological, physiological and behavioural characteristics that differ from those of nondispersers (sensu a dispersal syndrome: Clobert et al., 2009). As a result, phenotype-dependent dispersal should ultimately lead to structurally assorted populations in the new range that are composed of individuals with a certain phenotypic repertoire (e.g. a founder effect: Brodin, Lind, Wiberg, & Johansson, 2013), and this is expected to have strong implications for colonization success and population persistence (Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

Personality-dependent dispersal is a recently documented dispersal syndrome that links dispersal tendency to other, functionally unrelated, repeatable, behavioural tendencies (sensu animal personality traits: Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Sih, Bell, & Johnson, 2004). These behaviours are likely to complement a high dispersal propensity and an ability to disperse long distances in order to facilitate the successful movement and colonization of new habitat patches, including the invasion of novel environments (Chapple, Simmonds, & Wong, 2012; Cote, Clobert, et al., 2010). For example, dispersal tendency is correlated with sociability in invasive mosquitofish, *Gambusia affinis*, whereby asocial individuals consistently disperse further than their social counterparts (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010). However, dispersal is also often condition dependent and, thus, is probably mediated by the interaction between an individual's personality and the ecological context, such as the level of predation risk, population density or habitat quality (Calsbeek, 2009; Clobert et al., 2009; Cote & Clobert, 2007; Le Galliard, Rémy, Ims & Lambin, 2012; Mossop, Moran, Chapple, & Wong, 2017). For instance, social-dependent dispersal in mosquitofish was nonexistent when predation pressure was high (Cote, Fogarty, Tymen, Sih, & Brodin, 2013). Similarly, dispersal in common lizards, *Lacerta*

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vivipara, is influenced by population density: social individuals tend to disperse when population densities are low whereas asocial individuals tend to disperse when population densities are high (Cote & Clobert, 2007). Moreover, while not regularly considered in studies of personality-dependent dispersal, social cues may also interact with personality to shape dispersal decisions (discussed in Wey, Spiegel, Montiglio, & Mabry, 2015). In this regard, dispersal tendency may be contingent not only upon an individual's behavioural profile, but also on the personality of the individuals it encounters and interacts with (Dingemans & Araya-Ajoy, 2015). The presence of aggressive individuals, for example, has been shown to alter the behaviour of surrounding individuals, either by eliciting more aggression from those individuals or limiting the activity of those that are attempting to avoid costly competitive interactions (McGlothlin, Moore, Wolf & Brodie, 2010; Santostefano, Wilson, Araya-Ajoy, & Dingemans, 2016).

In the current study, we examined links between personality and dispersal in the presence of conspecifics, using a lizard model species, the delicate skink, *Lampropholis delicata*. The delicate skink is a small lizard (adult snout–vent length [SVL] 34–51 mm) that has had a successful invasion history via accidental introductions. Accidental introductions rely more heavily on passive human-mediated dispersal, both before and after introduction, than deliberate introductions (Chapple et al., 2012; Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). However, active dispersal is also likely to be an important mechanism driving these invasions (e.g. invasive land snails; Aubry, Labaune, Magnin, Roche, & Kiss, 2006), and personality could play a role in both active and passive dispersal. For example, being extremely explorative may lead to an increased chance of being ensnared within a transport vector and passively moved to a new location (Chapple et al., 2012). Indeed, it has been suggested that the delicate skink has used both active and passive dispersal mechanisms to successfully spread and establish populations in Hawaii, New Zealand and Lord Howe Island (Chapple, Reardon & Peace, 2016; Chapple, Simmonds, & Wong, 2011; Chapple, Whitaker, Chapple, Miller & Thompson, 2013), making it an ideal model species to investigate personality-dependent dispersal. Furthermore, within the native range of this species, a behavioural syndrome between activity, exploration and sociability has been found in both sexes (Michelangeli, Chapple, & Wong, 2016; Michelangeli, Wong, & Chapple, 2016). We hypothesized that this syndrome could be linked to dispersal for two reasons. First, activity, exploration and sociability are behavioural traits that have previously been linked to dispersal in other species (e.g. Cote, Fogarty, et al., 2010; Cote & Clobert, 2007; ; Dingemans, Both, Van Noordwijk, Rutten, & Drent, 2003; Fraser, Gilliam, Daley, Le, & Skalski, 2001; Hoset et al., 2011). Second, such personality-dependent dispersal could have benefits for invasion, as active, explorative and social skinks should be more likely to relocate and find mates in low population densities that are often associated with accidental introduction events (Chapple et al., 2012). However, because the delicate skink is a group-living species, we also predicted that the social environment could play an important role in mediating an individual's decision to disperse, because the behavioural responses of individuals can often be modulated via their social interactions with counterparts (Aguillon & Duckworth, 2015; Dochtermann, Jenkins, Swartz, & Hargrett, 2012).

METHODS

Animal Collection and Husbandry

Seventy-one skinks were collected from Sydney, NSW, Australia (33°47'S, 151°08'E) in October 2014, using hand capture and

mealworm fishing trapping methods. These trapping methods were used as they have previously been shown not to retain any personality-biased sampling (Michelangeli, Wong, et al., 2016). Only adult (SVL > 34 mm), full-tailed (SVL > tail length) male lizards were collected to avoid the confounding influence of tail loss (Cromie & Chapple, 2012) and gravity (Shine, 2003) on behaviour.

Skinks were transported back to animal housing facilities where, on arrival, they were given a minimally invasive unique permanent identification code using different colour combinations of Visual Implant Elastomer (Northwest Marine Technology, Shaw Island, WA, U.S.A.). Skinks were housed in groups of five in plastic containers (300 × 230 mm and 370 mm high) within a temperature-controlled room (kept at 22–23 °C). On one end of each housing container, a basking area was created using a heat lamp over a terracotta basking tile. This provided a thermal gradient in the housing container (22–32 °C), that allowed thermoregulation from 0800 to 1700 hours. Small plastic pots and newspaper were added to provide shelter. UV lighting was placed above the containers, and was activated from 0800 to 1800 hours. Room lighting was provided between 0700 and 2000 hours daily. Skinks were fed a diet of crickets, *Acheta domesticus*, dusted in a vitamin supplement (Rep-tivite), three times a week, and water was made available *ad libitum*.

Behavioural Measurements

We conducted a series of behavioural assays to examine whether there is personality-dependent dispersal in the delicate skink. Assays were carried out in a fixed order (presented below) where assays that could have the greatest influence on behaviour were carried out last to reduce potential carryover effects (Bell, 2012). We performed each behavioural assay on each individual twice, 2 weeks apart, to examine short-term repeatability and reduce the effects arising from potential developmental changes within individuals (Bell, Hankison, & Laskowski, 2009).

Trials were recorded using JVC Everio GZ-E100 video cameras. After each trial, the footage was downloaded to a computer for later playback (using JWatcher: Blumstein, Evans, & Daniels, 2006) and data analysis. All equipment was thoroughly washed between trials with hot water and scentless dishwashing detergent to prevent scent contamination among trials. Since *Lampropholis* skinks are known to modify their behaviours following large meals (Shine, 2003), we ensured that lizards were not fed in the 24 h prior to each behavioural assay. Assays were conducted in temperature-controlled rooms at 23 °C.

Activity and exploration

To measure activity levels, skinks were allowed to roam freely in an opaque-walled test arena (550 × 320 mm and 240 mm high) marked with 20 equal grid squares. This assay is commonly used to test general activity in personality research (Cromie & Chapple, 2012; Michelangeli, Wong, et al., 2016; Michelangeli, Chapple, et al., 2016; Moule, Michelangeli, Thompson, & Chapple, 2016). Skinks were allowed to acclimatize under transparent containers for 10 min prior to the trial. The level of activity of skinks was scored based on the number of transitions an individual made between grid squares over 20 min (see Appendix Fig. A1 for a more detailed description of the test arena set-up). Because we have previously found that activity is strongly correlated with exploratory behaviour in delicate skinks from Sydney (Goulet, Thompson, Michelangeli, Wong & Chapple, in press; Michelangeli, Wong, et al., 2016; Michelangeli, Chapple, et al., 2016; Moule et al., 2016), we considered the behavioural measurements taken from this assay to be an accurate proxy for testing activity and exploration.

Sociability

We conducted a dichotomous choice experiment to measure the social behaviour of skinks. Delicate skinks are often observed either basking in small groups (ca. 2–10 individuals) or alone in the wild (Chapple et al., 2011). Thus, we offered individual lizards a choice between basking with a group of conspecifics and basking alone (sensu Michelangeli, Wong, et al., 2016; Michelangeli, Chapple, et al., 2016). This was achieved by splitting an opaque-walled test arena (550 × 320 mm and 240 mm high) into three zones: social, asocial and neutral. Both the social and asocial zones comprised a basking site that was divided in half by a clear Perspex partition that ran the length of the test arena. In the social zone, three stimulus lizards were placed behind the partition, whereas the asocial zone was left bare (see Appendix Fig. A2 for a more detailed description of the test arena set-up). Focal lizards could see, but not physically interact with, the stimulus lizards, which were individuals that were unfamiliar to the focal lizard (i.e. they were not housed together) and were caught during the collecting trip in October but were not used for any other behavioural assay. No focal lizards were used as stimuli. Following a 10 min acclimation period, we recorded the amount of time focal individuals spent basking in the social zone (i.e. with conspecifics) over 20 min.

Dispersal and aggression

To examine an individual's dispersal and aggressive tendencies, we observed its behaviour within an artificial environment created in large polyethylene terrariums (diameter: 130 cm; height: 65 cm; see Fig. 1). Each terrarium was separated into four equal-sized compartments by polyethylene barriers. Within each compartment were identical microhabitats consisting of a stand of plastic grass tussock (22 cm high) surrounded by mulch, two rocks and a sand substrate. Above each compartment was a 40 W heating lamp. Compartment 1 (C1) was connected to compartment 2 (C2), C2 to

compartment 3 (C3) and C3 to compartment 4 (C4). These compartments were connected to each other by funnel-shaped tunnels that had a 3 cm opening at the entrance but narrowed to a 0.5 cm exit. Tunnels were designed this way to allow skinks to disperse to each compartment, but also to reduce the likelihood that they would attempt to return to the compartment from which they had just dispersed. Only two trials had to be excluded because skinks had dispersed backwards.

Lizards were tested in groups of four and individuals were randomly assigned to their test group. We chose to test individuals within groups because this more closely reflects environmental conditions whereby delicate skinks are often observed inhabiting patches in densities of 2–10 individuals (Chapple, Reardon, et al., 2016, pp. 341–359; M. Michelangeli, & D. G. Chapple, personal observations). As each group started in C1, the furthest compartment to which an individual could disperse was C4. After a 1-day acclimation period, tunnels were opened and skinks were allowed to disperse for 8 h. During this period, we recorded the following measurements for each individual: time of first dispersal event (i.e. time taken for an individual to disperse from C1 to C2), dispersal distance (the furthest compartment to which an individual dispersed), whether an individual never dispersed, number of aggressive interactions and number of interactions 'won'. An aggressive interaction involved two individuals attempting to bite each other. An individual was considered to have 'won' this interaction if the counterpart retreated (i.e. attempted to run away). As the behavioural metrics associated with dispersal (time of first dispersal event, dispersal distance, if an individual never dispersed) and aggression (number of aggressive interactions and number of interactions 'won') were strongly correlated, respectively, we ran separate principal component analyses (PCAs) to reduce these variables into single standardized variables (which we henceforth refer to as dispersal tendency and aggression score).

Ethical Note

Research was conducted in accordance with appropriate collection and research permits (New South Wales: SL101600; Victoria: 1006866) and was approved by the Monash University animal welfare committee (BSCI/2014/26).

Statistical Analysis

Data were analysed in the statistical program R (R Development Core Team, 2014). Statistical significance was assigned at $\alpha = 0.05$. Repeatability of behaviours was calculated using variance components derived from generalized linear mixed-effects models (GLMM, 'lme4' package: Bates, Maechler, Bolker & Walker, 2014) with skink ID as a random factor. Repeatability is calculated by dividing the between-individual variance by the total phenotypic variance (between-individual variance + within-individual variance). Confidence intervals were calculated using parametric bootstrapping following methods described by Nakagawa and Schielzeth (2010). We also ran Spearman rank correlations to test consistency between trials.

Associations between variables were examined using Spearman rank correlation tests. Tests were run separately for both Trial 1 and Trial 2. To account for multiple comparisons, we applied a conservative Bonferroni correction to all *P* values (critical $\alpha = 0.008$). We also used linear mixed-effects models with Gaussian error distributions to examine the relationship between dispersal tendency, the behavioural traits (i.e. activity, sociability and aggression score)

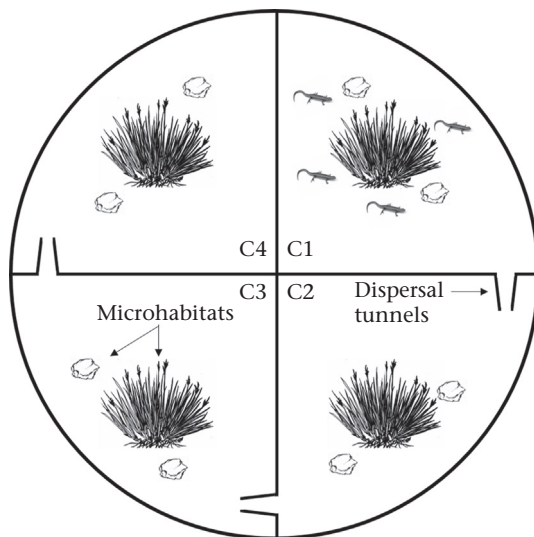


Figure 1. Diagrammatical representation of dispersal assay. An artificial environment was created in large polyethylene terrariums (diameter: 130 cm; height: 65 cm). Each terrarium was separated into four equal-sized compartments (C1–C4) by polyethylene barriers. Within each compartment were identical microhabitats consisting of a stand of plastic grass tussock (22 cm high) surrounded by mulch, two rocks and a sand substrate. Above each compartment was a 40 W heating lamp. C1 was connected to C2, C2 to C3 and C3 to C4 by dispersal tunnels that had a 3 cm opening at the entrance but narrowed to a 0.5 cm exit. Skinks began trials in C1 and were tested in random groups of four.

and SVL. Skink ID and test group were random factors. Skink ID was a random factor to account for repeated measures, whereas test group was a random factor to account for the variance caused by group composition (i.e. the individuals within each test group) during the dispersal assay. Models were simplified using backward elimination of nonsignificant terms.

RESULTS

All behaviours were significantly repeatable and consistent between trials, except for sociability (Table 1). Dispersal tendency and aggression score were positively correlated in both trials (Trial 1: $r_S = 0.46$, $P < 0.001$; Trial 2: $r_S = 0.54$, $P < 0.001$), but dispersal tendency was not correlated with either activity (Trial 1: $r_S = -0.01$, $P = 0.98$; Trial 2: $r_S = -0.05$, $P = 0.65$) or sociability (Trial 1: $r_S = -0.03$, $P = 0.82$; Trial 2: $r_S = -0.17$, $P = 0.15$). Aggression score was not correlated with either activity (Trial 1: $r_S = 0.09$, $P = 0.47$; Trial 2: $r_S = 0.03$, $P = 0.79$) or sociability (Trial 1: $r_S = 0.05$, $P = 0.69$; Trial 2: $r_S = -0.12$, $P = 0.32$) and activity and sociability were also not correlated in either trial (Trial 1: $r_S = -0.04$, $P = 0.77$; Trial 2: $r_S = -0.01$, $P = 0.96$). Furthermore, aggression score was the only significant fixed term related to dispersal tendency whereas activity–exploration, sociability and SVL had no effect (Table 2). This suggests the presence of an aggression-dependent dispersal syndrome, as individuals that were involved in more aggressive interactions and that ‘won’ these interactions dispersed further and faster than less aggressive individuals (Fig. 2).

DISCUSSION

Contrary to our prediction, dispersal was not related to activity, exploration or sociability in the delicate skink. However, we did find that individuals that were more aggressive dispersed

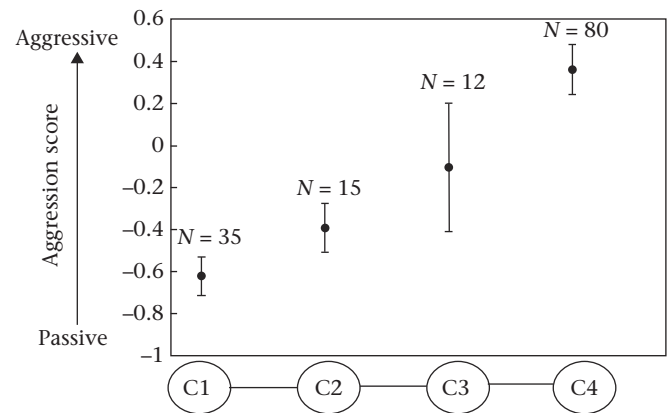


Figure 2. Association between mean \pm SE aggression score and dispersal distance. Dispersal distance refers to the furthest compartment (C1, C2, C3 or C4) to which a lizard dispersed during the trial. ‘N’ refers to the total number of individuals that were found in each compartment across both trials (total $N = 142$).

further and faster than individuals that were less aggressive, suggesting the presence of aggression-dependent dispersal in the delicate skink. There are two possible reasons why we found aggression-dependent dispersal: either (1) dispersers are generally more aggressive than nondispersers or (2) aggressive individuals forced nonaggressive individuals into hiding, thus impinging on the ability of subordinates to disperse regardless of their personality. Indeed, we are unable to disentangle from our results which of these two factors is driving dispersal. However, in either case, our results still suggest that aggression plays an important role in mediating the tendency to disperse in the delicate skink and is one of a few studies to highlight the importance of the social environment when investigating dispersal mechanisms.

Aggression is often an advantageous behavioural trait at the front of an invasion or range expansion, because it can allow the spreading species to outcompete the native biodiversity for resources and habitats. Evidence for aggression-dependent dispersal has been found in other species and has been shown to aid in range expansion and invasion (Duckworth & Badyaev, 2007; Pintor, Sih, & Kerby, 2009). For example, aggression-dependent dispersal in western bluebirds, *Sialia mexicana*, allows aggressive individuals to lead range expansion and displace native birds from their nesting sites. This displacement of native birds at the expansion front provides an opportunity for less aggressive western bluebirds to eventually disperse and colonize the now unoccupied habitat leading to the establishment of a new population (Duckworth & Badyaev, 2007). The role aggression has played in the invasion success of the delicate skink has never previously been explored. However, a combination of aggression-dependent dispersal and the ability to reach high population densities may contribute to our understanding of the mechanisms that have allowed the delicate skink to seemingly displace native skink species in both New Zealand and Hawaii and become the dominant species in their invaded range (Chapple, Miller, Kraus, & Thompson, 2013; Chapple, Knechtmans, Kikillus & van Winkel, 2016).

It is possible that dispersal in our study was driven by an interaction between the social context and an individual’s personality, rather than just how aggressive an individual was. Nonaggressive individuals may not have dispersed as regularly as aggressive individuals because they were attempting to avoid interactions with conspecifics and thus the competitive

Table 1
Repeatability with confidence intervals (CIs) of behavioural traits

Behavioural trait	N	Var _A	Var _W	Repeatability (CIs)	r_S	P
Activity–exploration	71	0.744	0.261	0.740 (0.614, 0.829)	0.739	<0.001
Sociability	71	0.179	0.823	0.178 (0, 0.393)	0.196	0.102
Aggression	71	0.438	0.565	0.437 (0.229, 0.607)	0.366	0.002
Dispersal tendency	71	0.341	0.661	0.341 (0.119, 0.530)	0.310	0.009

Number of cases (N), variance components (Var_A: between-individual variance; Var_W: within-individual variance) and Spearman correlation estimate. Statistical significance is assigned at $\alpha = 0.05$.

Table 2
Outcome from mixed-effects linear models of dispersal tendency in relation to behavioural traits and snout–vent length (SVL)

	N	Δ AIC	χ^2	P
Fixed effects				
Activity–exploration	71	+1.35	0.648	0.421
Sociability	71	+1.98	0.012	0.889
Aggression score	71	-26.16	28.155	<0.001
SVL	71	+1.87	0.132	0.716
Random effects				
Test group		+0.36	2.358	0.125
Skink ID		-2.78	4.774	0.029

Random effects include test group and Skink ID. Δ AIC values refer to differences in the Akaike’s information criterion when specific fixed and random factors were included versus excluded from the reduced model.

environment was mediating their dispersal decisions. Competition has often been found to regulate dispersal decisions, but, typically, it is the subordinates that are forced to disperse by dominant, more aggressive individuals (Calsbeek, 2009; Cote, Clobert, et al., 2010). On the other hand, very few studies have documented aggressive individuals being more dispersive, but those that have were a response of aggressive individuals to either high population density (Myers & Krebs, 1971), range expansion (Duckworth & Badyaev, 2007) or competition from kin (Aguillon & Duckworth, 2015). Furthermore, aggression is often linked to intolerance (or asocial behaviours) towards conspecifics, and asocial individuals are typically shown to disperse more than social individuals (Cote, Fogarty, Brodin, Weinersmith, & Sih, 2011; Cote, Fogarty, et al., 2010), particularly in response to high population densities (Cote & Clobert, 2007; Duckworth & Badyaev, 2007; Cote et al., 2011). However, in our study, sociability was not correlated with either aggression or dispersal tendency, suggesting that dispersers, even though they were more aggressive, were as social towards conspecifics as nondispersers.

In this study, an individual's dispersal distance was limited by the size of the dispersal arena and the experimental period. In the wild or in an invasion context, such spatial or temporal limitations would not be present. However, we still believe our dispersal assay appropriately addressed our aim: to assess the possible behavioural mechanisms driving variation in dispersal tendencies in the delicate skink. We found that dispersal tendency was a repeatable trait, suggesting that skinks that never dispersed and skinks that dispersed to the furthest compartment did so in both trials. This appears to be two distinct dispersal decisions (i.e. to leave or not to leave: see Fig. 1), and that some individuals are more likely to begin the process of transience relative to other individuals.

In conclusion, we found evidence of aggression-dependent dispersal in the delicate skink. Specifically, skinks that were consistently more aggressive towards counterparts dispersed further than individuals that were less aggressive. Dispersal tendency was not related to activity, exploratory or social behavioural traits, but this may be because these personalities were mitigated by the competitive environment. It is possible that if we had tested each lizard's dispersal tendency individually rather than in groups, we may have found that dispersal was linked to these personality traits. However, individuals rarely encounter situations where conspecifics are not present, particularly in social species that live in relatively high densities like the delicate skink. To summarize, this study is one of the few that empirically highlights the need to consider the ecological context when examining personality-dependent dispersal and suggests that aggression and the social environment can play an important role in dispersal decisions.

COMPETING INTERESTS

We have no competing interests.

AUTHORS' CONTRIBUTIONS

M.M. carried out fieldwork, laboratory experiments and data analysis, contributed to the design of the study and drafting of the manuscript. B.B.M. and D.G.C. contributed to the design of the study and drafting of the manuscript. All authors gave final approval for publication.

Acknowledgments

We thank C. Goulet and E. Drummond for assistance with animal housing and care and three anonymous referees for their constructive feedback. This research was funded by the Ecological Society of Australia (grant to M.M.), and an Australian Research Council Discovery Project Grant (DPI170100684; grant to D.G.C. and B.B.M.W.).

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APPENDIX

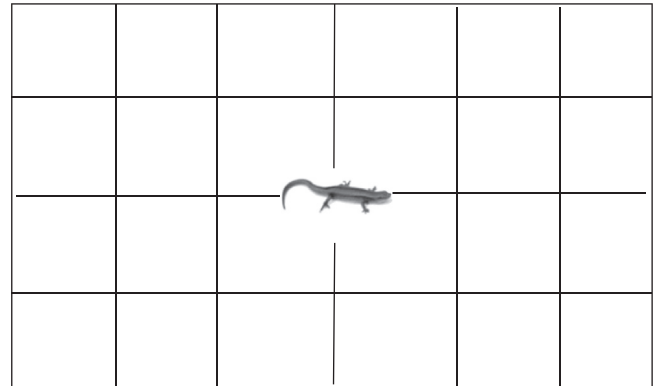


Figure A1. Diagrammatic representation of the activity-exploration test. The experimental arena (550 × 320 mm and 240 mm high) was split into 20 equal-sized grid squares. The level of activity-exploration of skinks was scored based on the number of transitions an individual made between grid squares over 20 min.

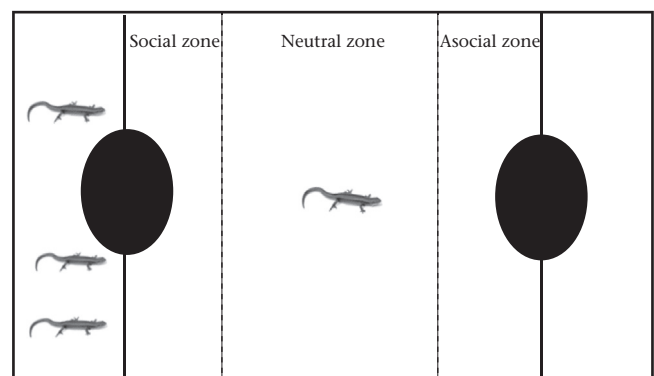


Figure A2. Diagrammatic representation of the sociability test. The experimental arena was split into three zones: social, asocial and neutral. A black marker pen was used to draw five 11 cm segments along the length of the experimental arena to create the three zones. A basking site, positioned under a 40 W heating lamp, was placed at the end of each arena, on the inner edge of the exterior segments. Each basking site was divided in half by a clear Perspex partition (11 cm high), which ran the width of the arena. Three stimulus lizards were placed within the peripheral sections, enabling focal lizards to see, but not physically interact, with them. The two adjoining segments were designated as either the 'social zone' (next to the stimulus lizards) or the 'asocial zone' (no lizards) and the central one was considered a 'no choice' or neutral zone. The temperature underneath the heat lamps (ca. 35 °C) was substantially higher than the ambient temperature (ca. 20 °C), prompting the lizards to use the basking sites.