



# Aggression mediates dispersal tendency in an invasive lizard



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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 (Dingemanse & 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, & Dingemanse, 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; ; Dingemanse, 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, & Hargett, 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 gravidity (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.

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