



Repeated exposure and handling effects on the escape response of fence lizards to encounters with invasive fire ants

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Understanding the factors that influence escape responses can provide important insight into processes that permit coexistence between species. I tested whether learning shapes the expression and timing of escape behaviour of native lizards to invasive fire ants. Fence lizards survive encounters with fire ants by body twitching to remove stinging ants and fleeing the source of attack. I found that adult lizards from invaded sites body-twitched more frequently and fled sooner than did lizards from uninvaded sites, minimizing their exposure to envenomation. Juveniles' small size makes them more vulnerable to fire ants, and they fled rapidly from encounters, irrespective of their site of origin. A higher percentage of adult lizards body-twitched and fled, and they fled sooner, with repeated exposure to fire ants over 4 days, and lizards that had been repeatedly exposed to fire ants fled sooner than did control-conditioned lizards. These results suggest that adult lizards may learn to flee more rapidly after repeated encounters with fire ants. However, the percentage of lizards that performed this behaviour appeared to be driven by aspects of the testing procedure other than the presence of fire ants, as the percentage of lizards that fled or body-twitched in response to fire ants was not affected by prior fire ant conditioning. These results suggest that adult lizards cannot learn to show escape behaviour with repeated exposure to fire ants, but that they can optimize this behaviour by fleeing sooner. This study highlights the need to test alternative explanations rigorously for apparent learned behaviour.

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Differences in the expression of escape tactics between populations of a species can be associated with predation pressure (Ducey & Brodie 1991; Hedrick & Kortet 2006). These differences can be innate, suggesting a genetic shift due to selection for a particular response (Dalesman et al. 2006; Hedrick & Kortet 2006). This can be adaptive if individuals face consistently high predation risks within a population (Magurran 1999). However, threat levels in environments often vary and individuals can benefit from being able to flexibly adjust their responses (Dalesman et al. 2006), avoiding costs of unnecessarily adopting escape and avoidance behaviour (Skelly 1992; Persons et al. 2002). Escape behaviour can be modified through experience, as the information acquired during encounters can be used to predict and prepare an individual for future encounters with the same stimuli, resulting in an exaggeration or weakening of an individual's response (Peeke & Petrinovich 1984; Kummer 1995; Ohman & Mineka 2001). Learning to respond to stimuli is only possible if an individual lives through the encounter (a scenario that is relatively common in nature, even

during attempted predation events; Vermeij 1982). To have survival value the behavioural change must increase an individual's probability of escaping encounters with a threat or of avoiding future encounters (Wiedenmayer 2004). An animal's ability to learn can depend upon many factors, including the individual's physiological status (Overli et al. 2007), the nature of the stimulus (Suboski 1992; Terrick et al. 1995) and the individual's history of exposure (Huntingford & Wright 1992). Understanding the relative importance of these factors for shaping an escape response provides valuable insight into the evolution of species interactions, and has important consequences for species reintroductions and restocking programmes (Blumstein 2002; Vilhunen 2005) and for predicting the ability of native taxa to respond to novel introduced threats (Webb et al. 2008).

I examined factors affecting the escape response of native fence lizards, *Sceloporus undulatus*, to invasive fire ants, *Solenopsis invicta*. Native to South America, fire ants have invaded at least six countries and are predicted to spread globally (Morrison et al. 2004). They were introduced to the U.S.A. in the 1930s via Port Mobile, Alabama, and have since spread across 13 mainland states (Callcott & Collins 1996; Code of Federal Regulations 2008). Fire ants are generalist omnivores that use their venom to capture prey and defend their mound (Tschinkel 2006). Encounters between native

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species and foraging ants can occur tens of metres from the mound, but attacks on the mound itself are usually more intense, as ants recruit quickly to the attack (Markin et al. 1975; Langkilde 2009a). Fire ants swarm their victim and then sting synchronously and repeatedly (Holtcamp et al. 1997). Fire ant venom has a potent neuromuscular action (Blum et al. 1958) and can paralyse and kill native vertebrates (Allen et al. 2004). Envenomation does not instantaneously cause death, permitting animals to escape fire ant attack (Holtcamp et al. 1997; Langkilde 2009a).

Fence lizards are a medium-sized (average sizes: adults, 65 mm snout–vent length (SVL), 9.5 g; hatchlings 24 mm SVL, 0.5 g) species that lays between one and three clutches of eggs each summer. This lizard occupies open woodlots and forest edges from southeastern New York to central Florida, and west to eastern Kansas and Texas, U.S.A. (Conant & Collins 1998). These are habitats also frequented by fire ants (Langkilde 2009b), so encounters between these species are likely to occur regularly in nature (Langkilde 2009a). Fence lizards escape large predators by running short distances and then stopping, relying on their grey-brown mottled dorsal coloration to blend into the background (Cox et al. 2005, T. Langkilde, unpublished data). When attacked by fire ants, fence lizards can survive by removing attacking ants with vigorous body twitches and fleeing from the mound to prevent further recruitment (see video in Langkilde 2009a, Appendix F). This response depends on a population's historical exposure to fire ants: fence lizards from fire ant-invaded sites are more likely to respond to encounters with fire ants than are fence lizards from uninvaded locations (Langkilde 2009a).

In addition to causing mortality, venoms impose a wide range of sublethal consequences for prey (Richards & Parkinson 2000). Fire ant venom reduces growth rates of bobwhite quails, alligators and sea turtles (Giuliano et al. 1996; Allen et al. 1997; Krahe 2005). Fire ant venom has no detectable sublethal effects on locomotor performance or bite force of fence lizards, but it does result in significant cell lysis, and there is no evidence of increase venom tolerance of lizards following fire ant invasion (Boronow & Langkilde, 2010). While the presence or absence of an escape response will determine a fence lizard's chance of surviving a fire ant encounter, the frequency and latency of this response will affect the amount of venom an individual receives, and therefore the extent of any sublethal impact of envenomation. In the first part of this study, I use staged encounters to assess whether the frequency and latency of the response of fence lizards to fire ants differs depending on the invasion status of a site. In the second part of this study, I used free-operant-avoidance conditioning to test whether fence lizards can modify their behavioural response to fire ants through repeated exposure to this threat.

METHODS

Study Sites and Animals

For this study, I used animals from two sites, 540 km apart, that were matched for microhabitat but differed in fire ant invasion status (Langkilde 2009a). The 'invaded site' was first invaded by fire ants in the 1930s (Escambia County, AL, U.S.A.; 31°09'49"N, 86°42'10"W), and the 'uninvaded site' had not yet been invaded by fire ants (Lee County, AR, U.S.A.; 34°43'50"N, 90°42'18"W, approximately 100 km from the present fire ant invasion front in Arkansas; Code of Federal Regulations 2008). Although the use of sites in closer proximity to each other would minimize genetic differences between the populations, I chose these two sites to maximize the difference in exposure to fire ants over time. These sites were matched for habitat and elevation (Langkilde 2009a), and current evidence suggests that this lizard is relatively

undifferentiated across this range. Molecular markers show no fixed allelic difference between populations of *S. undulatus* across their range (Leaché & Reeder 2002; Miles et al. 2002), and coloration and scalation (previously used for subspecies designation; Smith et al. 1992) as well as morphology of museum specimens collected prior to invasion (Langkilde 2009a, unpublished data) do not vary between these sites.

I used both adult and juvenile lizards in this study. I captured adults directly from the field at each of the two sites using a hand-held noose. Juveniles were hatched from eggs that I obtained from females at these two sites and reared under common laboratory conditions until testing at between 5 and 23 days of age. Juveniles were housed at densities of five individuals per enclosure (30 × 20 × 25 cm, L × W × D). Enclosures were furnished with a water bowl, shelter and heat source, and lined with paper towelling. Lights were set to a 12:12 h light:dark cycle. Juveniles were provided water ad libitum and fed pinhead domestic crickets (*Acheta*) once per day, supplemented with calcium, vitamin and mineral powders once per week. Adults were housed four per enclosure (60 × 25 × 30 cm, L × W × D) under the same conditions. They were provided water ad libitum and were fed adult domestic crickets every third day, supplemented with nutrient powders once per week. Adults used in the learning trials were held in cloth bags (25 × 15 × 10 cm) between successive behavioural conditioning trials to minimize the stress associated with daily capture and rehousing (Langkilde & Shine 2006). Bags were held in insulated coolers maintained at 25 °C to prevent desiccation and overheating. Lizards were moved to enclosures for feeding and the opportunity to thermoregulate on the third day of trials. This regime conforms to the protocol approved for the transportation of reptiles set out in the Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research (ASIH 2004) and did not appear to negatively affect the lizards used in this study.

Behavioural Assays

I assayed the behavioural response of fence lizards to fire ants by staging encounters on natural fire ant mounds to ensure that the behaviour of both species was as natural as possible (as per Langkilde 2009a). I prevented the lizards from escaping during the trials by tethering them to a metal tent peg using a 1 m length of cotton tied loosely around their neck. The peg was anchored 40 cm from the mound. This tethering system did not interfere with the behaviour of the lizard during the trials and allowed them freedom to move up to 140 cm away from the mound. Immediately prior to each trial, my assistant or I lightly disturbed the surface of a mound with a stick. This encouraged enough ants to emerge from the mound to replicate naturally occurring, nonlethal levels of exposure to fire ants (6.35 ants/adult lizard, 95% CI = 5.76, 6.93; 2.04 ants/juvenile lizard, 95% CI = 1.83, 2.25; Langkilde 2009a; Boronow & Langkilde, 2010). Lizards were placed on the ground approximately 40 cm from the mound and encouraged to move onto the mound by tapping them on the tail. We used the cotton tether to guide the lizards and ensure that they came to a complete stop on the mound, after which the cotton was placed loosely on the ground. Lizards that did not remain stationary for at least 1 s before fleeing were repositioned back on the mound to ensure that their fleeing response was due to an external stimulus (e.g. fire ants) and not a consequence of their running onto the mound. Trials commenced when the first fire ant moved onto the stationary lizard, and ended as soon as a lizard fled from the mound or after 60 s for adults and 30 s for juveniles, if the lizard did not flee from the mound. During these trials, the behavioural response of the lizard was recorded. The temperature of the mound was measured between consecutive trial using an infrared thermometer so as not

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