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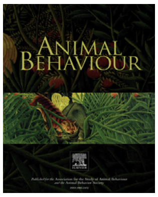

Attracting unwanted attention: generalization of behavioural adaptation to an invasive predator carries costs

Christopher J. Thawley [a, b, c, *], Tracy Langkilde [a, b, c, 1]

[a] *Department of Biology, The Pennsylvania State University, State College, PA, U.S.A.*
[b] *Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, State College, PA, U.S.A.*
[c] *The Center for Brain, Behavior and Cognition, The Pennsylvania State University, State College, PA, U.S.A.*

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Behavioural responses of animals to environmental cues are often governed by general 'rules of thumb'. Animals that face novel conditions as a result of global environmental change may alter these behavioural rules to persist. However, adaptation of generalized rules to novel pressures may cause a species to be maladapted to original conditions (e.g. predators) that remain in its environment. Invasive red imported fire ants, *Solenopsis invicta*, are novel predators of eastern fence lizards, *Sceloporus undulatus*. Lizards from fire ant-invaded sites break crypsis to flee from fire ants at higher frequencies than fire ant-naïve lizards. This shift promotes survival of attacks by these invasive ants but could result in attacks by native visual predators. Generalization of this increase in antipredator behaviour to native species could further increase this cost. We tested whether lizards' increased propensity to flee from fire ants is generalized to native ants and a predatory bird. We found that increased behavioural responsiveness to fire ants was generalized to two native ants but not to a perceived avian predator. We also found that lizards from populations invaded by fire ants had higher prevalence of injuries in the field, likely indicating greater attempted predation. We propose that generalized anti-ant behaviour may improve survival in the presence of fire ants but increase attacks by native visual predators. This study suggests that generalized rules can be maladaptive under novel conditions and highlights the challenges of assessing the costs and benefits of adaptations to rapid environmental change.

The complex suites of behaviours used by many organisms are often a product of both specific and general underlying rules. For example, individuals can use behavioural rules to decide to treat as a potential mate or predator anything that smells, tastes, appears or behaves in a specific way (Frid & Dill, 2002; Jennions & Petrie, 1997). General rules may allow responses to generic cues such as looming shapes (Carlile, Peters, & Evans, 2006) or objects of a particular colour, texture (Gwynne & Rentz, 1983) or size (Arak, 1983; Marco, Kiesecker, Chivers, & Blaustein, 1998). Precise rules may require a particular combination of multiple, specific cues to elicit a behavioural response (Hankison & Morris, 2003).

Behavioural rules are generally only as complex as required to be adaptive within an environment (Schlaepfer, Runge, & Sherman, 2002), and general rules may evolve more quickly and easily than complex ones (Orr, 2000). While relying on specific rules reduces the risk of making errors, general rules for behaviour are valuable as they allow for responses to many different environmental cues and obviate the costs of discriminating specific cues (Carthey & Banks, 2014; Sih, 2013). These rules are strategies that work on aggregate over multiple iterations in diverse or uncertain situations (Lima & Dill, 1990), and their use may lead to more predictable outcomes in variable environments (Heiner, 1983).

However, reliance on general rules can incur costs as the chances of responding inappropriately to cues are higher than if rules are more specific. For example, males with indiscriminate mate choice could waste time and energy, and lose mating opportunities, by attempting to mate with unsuitable partners or objects (e.g. anurans mating with dead or heterospecific individuals, or shoes; Meshaka, 1996), and parents caring for any offspring they encounter could bear the costs of raising unrelated individuals (e.g. hosts of nest parasites; Payne, 1998).

The fitness consequences of generalized behavioural responses are a focus of much recent research and theory, especially in the context of rapid environmental change (Carthey & Banks, 2014; Schlaepfer, Sherman, Blossey, & Runge, 2005; Sih, 2013). Novel or

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[*] Correspondence and present address: C. J. Thawley, Department of Biological Sciences, 120 Flagg Road, University of Rhode Island, Kingston, RI 02881, U.S.A.
E-mail address: cthawley@gmail.com (C. J. Thawley).
[1] *E-mail address:* tll30@psu.edu (T. Langkilde).

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rapidly changing selective regimes can result in maladaptation or evolutionary traps (Crespi, 2000; Schlaepfer, Sherman, & Runge, 2010), including in response to environmental change (Bradley St Clair & Howe, 2007; Kerby & Post, 2013; Sinervo et al., 2010). Indeed, general rules of behaviour can be especially costly when the environment changes and organisms apply these rules in the wrong context. For example, an organism could suffer reduced fitness by attempting to mate with an invasive species (Gröning & Hochkirch, 2008) or man-made object that fulfils their general rules for mate identification (Gwynne & Rentz, 1983). Generalized responses to novel predators and prey can also reduce survival. For instance, generalist predators preying upon toxic invasive cane toads, *Rhinella marina*, can be poisoned (Shine, 2010), and New Zealand mudsnails react to invasive crayfish by burrowing, an ineffective defence against these novel predators (Sih, 2013). Accelerating global environmental change provides an excellent opportunity to examine the costs and benefits of generalized behaviours, especially in the case of adaptive responses to the novel conditions (Carthey & Banks, 2014; Sinervo et al., 2010).

To determine fully the consequences of behavioural adaptations to novel selective pressures, we need to understand (1) how behaviour changes in response to novel environmental conditions, (2) whether behavioural changes are specific to novel environmental conditions (e.g. to an introduced predator only), or generalized to similar stimuli (e.g. to other ecologically similar species) or even more broadly (e.g. to all potential predators), and (3) whether behavioural changes are beneficial or costly (e.g. cause decreased survival or wasted time and energy), as might be expected if changes in behaviour are generalized across multiple situations/species.

Antipredator behaviour is an excellent system with which to address these issues. These behaviours are expected to be under strong selection in many situations including the introduction of novel predators (Abrams, 2000). For example, native tadpoles (*Rana aurora*) that are naïve to invasive predatory bullfrogs (*Lithobates catesbeiana*) suffer high mortality (Kiesecker & Blaustein, 1997). However, tadpoles from populations that have been exposed to this novel selection have adapted in less than 60 years by reducing activity levels to avoid predation (Kiesecker & Blaustein, 1997).

Even when successful, antipredator behaviour is known to carry a variety of costs, including higher energy usage, lower foraging rates/opportunities and reduced ability to defend territories (Lima & Dill, 1990; Martín, Luque-Larena, & Lopez, 2009). If adaptations to novel predators alter general antipredator behavioural rules, applying these rules to interactions with native predators may incur these costs and lower fitness. When a trade-off between the costs and benefits of novel behaviour is not optimally balanced, maladaptation, potentially as an ecological or evolutionary trap, may occur (Schlaepfer et al., 2002, 2005; Sih, 2013).

Here, we use a system involving change in antipredator behaviour of native eastern fence lizards, *Sceloporus undulatus*, in response to invasive, predatory red imported fire ants, *Solenopsis invicta* (hereafter fire ants) to address the three issues highlighted above.

(1) Behavioural change. Antipredator behaviour of eastern fence lizards has changed in response to invasion by fire ants: fence lizard populations largely switch from relying on crypsis (an adaptive response to predominantly visual predators; Martín et al., 2009) to flight during encounters with these predatory invaders (Langkilde, 2009a).
(2) Specificity of change. In this study, we use staged encounters to test whether this shift in behavioural response to fire ants is generalized to two native ant species that are prey for fence lizards, and to a native avian predator, revealing the specificity of this behavioural adaptation.
(3) Costs of change. We also look for evidence of greater prevalence of injuries in lizards from populations showing increased responsiveness to fire ants, a potential fitness cost of this behavioural change.

METHODS

Study System

Fire ants are native to South America and were introduced to Mobile, Alabama, U.S.A., in the southeastern Unites States in the 1930s (Tschinkel, 2006). This species has since spread throughout the southeastern United States where it overlaps with the range of the eastern fence lizard (Conant & Collins, 1998). While fence lizards and fire ants both favour disturbed, edge habitats (Langkilde, 2009b) and interact frequently in natural environments (Freidenfelds, Robbins, & Langkilde, 2012), fence lizards do not change their habitat use in the presence of fire ants (Langkilde, 2009b). Fire ants recruit in high numbers to potential prey, including small vertebrates (Allen, Demarais, & Lutz, 1994; Wojcik et al., 2001), and as few as 12 attacking ants can paralyse and kill an adult fence lizard (Langkilde, 2009a). Ants make up a significant portion of the diet of fence lizards (DeMarco, Drenner, & Ferguson, 1985; Mobley, 1998), and lizards can be envenomed when consuming fire ants (Langkilde & Freidenfelds, 2010), which become the numerically dominant ant within invaded areas (Epperson & Allen, 2010; Vinson, 1994).

Fence lizards have adapted morphologically and behaviourally to invasive fire ants within 70 years (≈40 generations; Langkilde, 2009a). These lizards are well camouflaged and generally rely on crypsis to defend against visual predators including lizards, snakes and birds of prey (Cooper, Burghardt, & Brown, 2000; Jensen, Camp, Gibbons, & Elliott, 2008). While lizards from populations not yet invaded by fire ants (uninvaded sites) flee from ≈50% of fire ant attacks, lizards from populations invaded by fire ants for long periods (invaded sites) flee at a higher rate (≈85%; Langkilde, 2009a). These flee behaviours reduce contact with and envenomation by attacking fire ants (Freidenfelds et al., 2012).

Study Sites and Animals

We captured lizards from six study sites in the southeastern United States: (1) Solon Dixon Forestry Education Center, Escambia Co., Alabama (31.16°, −86.70°), (2) Geneva State Forest, Geneva Co., Alabama (31.12°, −86.17°), (3) Historic Blakeley State Park, Baldwin Co., Alabama (30.74°, −87.91°), (4) Saint Francis National Forest, Lee Co., Arkansas (34.71°, −90.73°), (5) Edgar Evins State Park, Dekalb Co., Tennessee (36.08°, −85.83°) and (6) Standing Stone State Park, Overton Co., Tennessee (36.47°, −85.42°) (all coordinates in WGS84). Sites 1, 2 and 3 were first invaded by fire ants approximately 74, 55 and 82 years ago, respectively, while sites 4, 5 and 6 have not been invaded by fire ants (Callcott & Collins, 1996). All sites are characterized by temperate mixed forests and abundant edge and disturbed habitats, where both fence lizards and fire ants are found at their highest densities (Langkilde, 2009b; T. Langkilde, personal observation). Only adult fence lizards were collected for behavioural trials, as juvenile lizards flee from fire ant attack at high rates regardless of population of origin (Langkilde, 2009a). Following capture, lizards were measured for mass (to the nearest 1 g) and snout–vent length (SVL, to the nearest 1 mm). They were housed in mixed-sex groups (3–4 lizards) in plastic enclosures