Ants and antlions: The impact of ecology, coevolution and learning on an insect predator-prey relationship

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ABSTRACT

A behavioural ecological approach to the relationship between pit-digging larval antlions and their common prey, ants, provides yet another example of how the specific ecological niche that species inhabit imposes selection pressures leading to unique behavioural adaptations. Antlions rely on multiple strategies to capture prey with a minimal expenditure of energy and extraordinary efficiency while ants employ several different strategies for avoiding capture, including rescue of trapped nestmates. Importantly, both ants and antlions rely heavily on their capacity for learning, a tool that sometimes is overlooked in predator-prey relationships, leading to the implicit assumption that behavioural adaptations are the result of fixed, hard-wired responses. Nonetheless, like hard-wired responses, learned behaviour, too, is uniquely adapted to the ecological niche, a reminder that the expression of associative learning is species-specific. Beyond the study of ants and antlions, per se, this particular predator-prey relationship reveals the important role that the capacity to learn plays in coevolutionary arms races.

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1. Introduction

A behavioural ecological approach to behaviour, such as the one I describe here in the study of ants and antlions, is an attempt to understand how a species' ecology shapes its behaviour. One of the earliest demonstrations of this fruitful approach are Tinbergen's (1963) and Cullen's (1957) studies of black-headed gulls and their cliff-dwelling relatives, kittiwakes. Ground-nesting gulls build shallow, loosely constructed nests; because gull nests are easy prey for both aerial and ground predators, chicks are well camouflaged and their parents engage in frequent mobbing behaviour to protect them. In addition, parent gulls remove egg shells and defecate away from the nest, lest the white inner shell and faeces betray the nest location. Gull chicks leave the nest within a few days but run for cover when their parents sound an alarm. The behaviour of kittiwakes, on the other hand, reflects very different selection pressures. The pencil-thin cliff edges on which kittiwake parents build their nests not only force them to build deep cup-shaped nests with a solid mud foundation, but also force chicks to remain nestbound until they are able to fly. Cliff-nesting kittiwakes do not bother to remove egg shells from the nest and defecate just over the rim of

the nest, revealing the nest location. Although the nests are easy to spot, even from afar, the sheer cliffs offer full protection from ground predators, and aerial predators are mostly dissuaded from approaching as they can be detected from a great distance by thousands of simultaneously nesting colony members. Thus, mobbing is rare in kittiwakes. Finally, whereas gull chicks run to their parents to be fed as soon as they arrive anywhere on the territory sounding the feeding call, kittiwake chicks wait until their parents alight on the nest (McLannahan, 1973).

Two more recent examples of the way in which a species' ecology shapes behaviour, one in birds and another in mammals, reveal the important role of learning and memory. One of these is the now-35-year-old study of food-caching passerine birds in both the tit family, Paridae, and crow family, Corvidae. Marsh tits, because of their small size and, thus, their inability to compete for many of the same food resources with their close relatives, the larger great tits, quickly snatch seeds at the same time that great tits remain feeding at the food source (Cowie et al., 1981; Sherry et al., 1981). Marsh tits then fly away at some distance to store individual seeds in hundreds of locations that they are able to remember for several hours, a strategy shared by another close relative, chickadees (Sherry, 1985; see a review by Sherry, this volume). Another food-storing bird, the pinyon jay, faces a somewhat different challenge, namely the need to store food for over-winter survival and reproduction, which takes place during January and February when food, mostly pinyon seeds, are no longer available (Balda and Kamil, 1989). Research

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on the proximate mechanisms of food-storing birds' remarkable memory reveals that, compared to other passerines, food storing birds possess a larger hippocampus, an important spatial memory centre in the brain (Krebs et al., 1989; Sherry and Vaccarino, 1989).

The highly productive ways in which neuroscientific approaches have expanded the study of food-storing birds also have led to a deeper understanding of prairie voles' (*Microtus ochrogaster*) and meadow voles' (*M. pennsylvanicus*) behavioural ecology, species that possess very different social structures. Prairie voles have a monogamous mating system in which males (as well as females) have only one mate during a given breeding season, and in which males guard their mates and help take care of their young. Meadow voles, on the other hand, are highly polygynous; both males and females have multiple partners and only females take care of the young. These differences in social structure mirror profound differences in their endocrine systems (McGuire and Novak, 1984; Oliveras and Novak, 1986; Lim et al., 2004). Monogamous male prairie voles possess a much higher concentration of vasopressin receptors in a particular brain structure called the ventral pallidum than do polygynous male meadow voles, a difference that subsequent research has shown to be responsible for prairie vole males' monogamous attachment to their mates as well as their highly prosocial behaviour toward their young (Donaldson and Young, 2008).

Yet another difference between prairie and meadow voles is that, unlike the male prairie voles that stay near their mates, polygynous male meadow voles are forced to search for mates over the females' widely dispersed territories. Recent studies of these polygynous male voles (Ferkin et al., 2008), reveal that meadow vole males have the remarkable capacity to keep track of where they have encountered particular females, what each of their receptive states was at the time of that original encounter and, finally, where to find that particular female when, in the future, she would be expected to be receptive, thus displaying what is called episodic-like (or, "what-where-when") memory. Whether monogamous prairie vole males also possess the capacity for episodic-like memory is not known, although one might predict that they don't keep track of their single mate's cycle of receptivity.

These examples, and many more that form the rich, diverse field of behavioural ecology (Davies et al., 2012), demonstrate the deeper, broader understanding of animal behaviour that comes from a comparative study of a species' ecology. This approach is one that my collaborator, Elise Nowbahari, our students, and I have tried to mount in the study of predatory antlions and one of their common prey, sand-dwelling ants. Here I will describe our collaborative work – an attempt to study the coevolutionary arms race in which these species exert selection pressures on one another, resulting in a continually evolving series of adaptations and counteradaptations in which antlions capture prey more efficiently and ants evade capture more effectively. Equally important, we have endeavoured to identify the role that the capacity to learn plays in this predator-prey arms race.

2. Ants and antlions, an insect model of coevolution

2.1. Antlions (Myrmelondidae spp.)

Antlions, the larvae of a winged adult insect, are sit-and-wait predators that depend on prey coming to them instead of searching for prey as most animals do. Although some antlion species conceal themselves under leaves and other surface debris, waiting to ambush prey that wander nearby – making these species technically sit-and-pursue predators (Devetak et al., 2012; Loria et al., 2008) – other species, namely pit-digging antlions, are thought to be the most sedentary of insect sit-and-wait predators (Mansell,

1996, 1999): Once they have found a suitable location in the sandy soils these species inhabit, they spiral backwards, tossing sand with their head and mandibles as they dig deeper, creating the conical-shaped pits that form their predatory traps (Lucas, 1982, 1989; Mansell, 1996). Once their pits are formed – and moving only to occasionally repair their pits or, in extreme circumstances, to relocate – antlions wait motionless at the vertex, sometimes for months at a time, for prey to fall inside (Fig. 1).

2.1.1. Antlion pits, a unique predatory strategy

Antlion pits, the slopes of which are dictated by the particular composition of the sand in which they live (Klokočovnik et al., 2012), are a model of efficiency. Whenever a small arthropod accidentally wanders over the edge of an antlion's funnel-shaped pit trap, it quickly loses its footing on the pit's loose sandy walls and plunges to the vertex, where the predator's mandibles are ready and waiting for nearly instantaneous capture (Lucas, 1982, 1989; Mansell, 1996). If prey wander close to the pit edge but somehow miss the pit trap, antlions often will close their long, slightly inward-facing mandibles and use them like broad shovels to bombard prey with loose sand, a tactic thought to disorient the prey, increasing the likelihood that prey stumble inside (Devetak, 2014; Devetak et al., 2007; Guillette et al., 2009; Mencinger-Vračko and Devetak, 2008).

2.1.2. Learning in antlions

In addition to antlions' ability to exploit the efficient structural properties of their pits (Fertin and Casas, 2006; Griffiths, 1986; Lucas, 1982, 1989), research in my lab has shown that antlions' predatory toolkit features yet another tactic, namely the ability to anticipate prey (Guillette et al., 2009; Hollis et al., 2011). In three separate experiments, Guillette et al. (2009) presented antlions with a vibrational signal paired with the arrival of prey in their pit. The signal was meant to simulate the kinds of sand disturbances that antlions might detect whenever prey wander nearby. Although animals receiving these paired presentations of cue and food did not respond to the cue initially, they soon began to move their head and mandibles, readying themselves for prey arrival (Experiment 1). Animals in a control group that received random presentations of the cue relative to prey arrival remained unresponsive to the cue. The ability to anticipate prey arrival in experimental group antlions enabled them to extract prey contents faster (i.e., *extraction rate*, Experiments 2 & 3) and to extract a greater percentage of prey mass per unit time (i.e., *extraction efficiency rate*, Experiment 2), compared to control group antlions.

In those experiments (Guillette et al., 2009), the increase in experimental group antlions' ability to extract prey contents more efficiently was reflected in dramatic increases in the size of their pits, which is highly dependent on antlion size (e.g., Day and Zalucki, 2000; Griffiths, 1986; Mansell, 1996; Guillette et al., 2009). Such increases in pit (and antlion) size provide several advantages: Larger pits capture larger prey, which only larger antlions are able to handle but which is energetically more profitable for them. In addition, larger pits have higher encounter rates with prey (Griffiths, 1980). Indeed, increases even as small as 2 mm in pit diameter translate into as much as a 10% increase in capture success (Griffiths, 1980).

Yet another benefit of increased prey extraction was the decrease in antlions' latency to moult from second instar larvae – the second developmental phase of the larva in which they must shed their exoskeleton to accommodate increased growth – to the last, third instar of their larval stage (Guillette et al., 2009, Experiment 3). In another experiment (Hollis et al., 2011), this time with third instar larvae, the last instar before antlions pupate to become reproductive adults, we showed that the ability to anticipate prey enabled antlions in the experimental group to grow

Fig. 1. Pit-digging antlions (*Myrmeleon* sp.). A larval antlion exposed on the sand surface (top left), and in the process of burying itself under the sand (top right). Bottom: Funnel-shaped antlion pits in fine sand; the winding furrows on the right side of the photograph are the characteristic tracks made by antlions as they search for a suitable pit location. Photography by Cheryl McGraw. Adapted from Hollis et al. (2011).

faster, as indexed by larger pits, and pupate sooner than control group antlions. Both of these developmental shifts, namely decreases in the latency to moult and to pupate, are important to antlions' reproductive success: Not only do these shifts permit antlions to reach the adult stage, and thus reproduce, sooner, but also they enable antlions to escape the larval stage more quickly, a stage in which they are especially vulnerable as prey themselves.

More recent research on learning in antlions (Kuszewska et al., 2016) suggests that they are able to use learned cues in even more complex tasks than my colleagues and I were able to demonstrate. Antlions discriminated between cues associated with prey of different sizes, reducing energetic costs by ignoring smaller prey in favour of larger, more energetically profitable prey. In addition, antlions learned to associate a vibrational cue with the loss of their prey, responding by burying their victims under the sand more often and more rapidly than did individuals with no opportunities to form such associations.

Antlions are but one of an extraordinary – and continually growing – number of insect species that possess the capacity for associative learning. Although this ability to respond to learned cues increases fitness in ways that might appear similar across species – by, for example, helping individuals to secure food, locate hosts and avoid predation (see reviews in Hollis and Guillette, 2011, 2015) – the way in which associative learning is employed demonstrates the uniquely adaptive role it plays in enhancing individuals' ability to exploit a particular ecological niche. That is, for insects (and vertebrates, of course) that search actively for food or hosts, learned cues guide them to those resources in ways that are something akin to the use of classic search images (Hollis, 1982, 1989; Reid and Shettleworth, 1992). For pit-digging antlions, however, learning takes a very different form, one that is adapted

to a sedentary sit-and-wait predatory strategy: Instead of using signals to guide them to food, as in all other insect species thus far reported in the literature (Hollis and Guillette, 2015), antlions remain completely motionless, thus saving energy, in response to all signals for prey arrival except those in the immediate vicinity of their pits. Although one might be tempted to assume that antlions simply can't detect signals at a distance, the data suggest otherwise: Although antlions outwardly appeared to ignore signals that were not nearby, their digestive systems somehow were using those same cues, near as well as far, to prepare for prey extraction (Guillette et al., 2009). That is, no matter how far away the cue was in our experiments, antlions receiving paired presentations of cue and prey delivery benefitted in terms of the efficiency with which they were able to extract prey contents.

2.2. Sand-dwelling ants

2.2.1. Rescue behaviour

Ant species that inhabit the same kinds of sandy soils as antlions face a wide range of dangers specific to their environment, for example the danger of their nests collapsing under the heavy feet of roaming vertebrates (Hollis and Nowbahari, 2013) as well as the danger of antlion capture. In experiments designed to assess these particular threats, that is when ants become trapped under collapsing sand and debris, or captured by nearby antlions, several species of sand-dwelling ants exhibited the remarkable ability to respond to trapped nestmates with efficient, precisely tuned rescue behaviour (Czechowski et al., 2002; Hollis and Nowbahari, 2013; Nowbahari et al., 2016a,b, 2012, 2009). Detecting their nestmate's call-for-help by means of a specific chemical signal (Nowbahari et al., 2016a,b), one of many ant *pheromones*, rescuers rushed to

Fig. 2. Rescue behavior in *Cataglyphis cursor* ants. The to-be-rescued victim (lower right) has been tied by a nylon thread snare to a piece of filter paper and partially buried in the sand. A rescuer (center) can be seen biting at the snare holding the nestmate in place. The rescuer already has uncovered the victim by digging away the sand and transporting it away from the victim, thus exposing part of the filter paper (i.e., the white area just above the victim's abdomen). Photograph by Paul Devienne. Adapted from Nowbahari et al. (2009). Videos of rescue behaviour are freely available from "Supporting Information" at this site: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0006573.

the victim, quickly identified her as a nestmate, then picked up and carried away the sand that partially covered her, tugged and pulled on her legs, and repeatedly bit at the thread snare that tied the victim securely to a piece of filter paper (Fig. 2). More recent work suggests that this rescue behaviour, far from being a mere collection of random acts, follows a highly organized sequence that reflects both goal-directedness and flexibility (see Duhoo, Durand, Hollis & Nowbahari, this volume).

Several observations from these experiments are particularly important to the study of coevolutionary selection pressures and reveal the ways in which the behavioural ecology of the ant species under study – both rescuer and non-rescuer alike – shapes their behaviour. Across two of the studies, one in the laboratory (Nowbahari et al., 2009) and another in the field (Hollis and Nowbahari, 2013), three different species of ants, *Cataglyphis cursor*, *C. floricola* and *Lasius grandis*, rescued only nestmates, delivering no aid whatsoever to any other ants, even ants from the same species that inhabited neighbouring colonies. All three of these species shared the habitat with pit-digging antlions. Indeed, *C. floricola* feeds on the petals of a particular shrub (hence its species name), a shrub whose overhanging branches protect antlion pits from rain damage. Two other ant species, namely *Messor barbarous* and *M. marocanus*, nesting in the same relative vicinity but which inhabit much more compact, hard soils – soils whose composition prohibit antlions from constructing pit traps – did not engage in rescue behaviour. In addition to the difference in soils that these species inhabit, rescuer and non-rescuer species also differ in their means of foraging for food. All of the non-rescuer species in these experiments form long trails to food, trails that, importantly, are formed by successful foragers only on the return trip to the nest (Cerdan, 1989; Hölldobler and Wilson, 2009), insuring the trails' validity and preventing recruits from encountering antlion pits en route, even if the scouts wander far afield in search of food. All of the rescuer species, on the other hand, forage individually and, thus, are more at risk of becoming trapped in antlions' pits (Hollis and Nowbahari, 2013).

Interestingly, however, even the non-rescuer species appeared able to perform the various behavioural components of rescue behaviour, even if those components were rarely, if ever, performed and never appeared in the same organized, coherent pattern characteristic of rescuer species. In the case of *M. marocanus*, digging

behaviour, a common component of rescue in which rescuers remove sand covering the victim before attempting to pull her free, was used instead to displace their nestmate victim from the nest area: Foragers dug around the victim and the filter paper to which the victim was attached, and then carried the paper-plus-victim away from the nest entrance to the colony "garbage site" where other debris already had been deposited.

A study of two North American ant species permitted further examination of the importance of potential antlion predation in ants' predisposition to exhibit rescue behaviour (Taylor et al., 2013). One species, *Tetramorium* sp. E[1], occasionally inhabits the same sandy soils as antlions, while another species, *Prenolepis imparis*, the common honey ant, does not. The results of these tests, conducted in the field, were as predicted. Honey ants, not at risk of capture by antlions, ignored trapped nestmates. *Tetramorium* ants, on the other hand, responded to victims with exactly the same rescue behaviour patterns – digging, pulling, sand displacement and snare biting – as observed in previous tests with other rescuer species. In addition, *Tetramorium* ants offered a deeper appreciation of the role of relatedness in whether ants would engage in rescue behavior. Other rescuer species responded only to nestmate victims, acting with aggression toward neighbouring ants of the same species. However, because *Tetramorium* ants are unicolonial, meaning that they form very large – and kin-related – networks of interconnected nests (Steiner et al., 2003; Helanterä et al., 2009), tests of rescue behaviour with neighbouring colonies were predicted to resemble tests with ants from the same nest. This prediction, too, was corroborated: *Tetramorium* ants were just as likely to engage in rescue behaviour with foragers from other colonies as they were with their own nestmates.

A final observation of *Tetramorium* rescuers demonstrates the capacity of ants to adjust their behaviour to meet the specific requirements demanded by each rescue situation. When *Tetramorium* ants were brought into the laboratory and tested in a semi-natural situation, namely a nestmate caught in an antlion's pit trap, they fine-tuned their rescue strategy: Digging, a common behaviour amongst all rescuer species, *Tetramorium* included, but a response that would have put the rescuer at risk by causing the antlion's pit walls to collapse, was avoided altogether; instead, rescuers anchored their back legs well behind the pit edge and reached down into the trap to pull on their nestmates' legs. And, in the same way that rescuers in the filter-paper-and-snare tests somehow were able to recognize what was holding their nestmate in place, responding to this threat by closely approaching the victim and biting the snare, *Tetramorium* rescuers that encountered a victim captured by an antlion instead backed up, pointed their abdominal stingers at the antlion and attempted to sting the predator (Taylor et al., 2013).

Thus far, rescue behaviour in ants has been observed only in response to pit-digging antlions. However, this predator is not the only one to feed on ants. Photographs of *Formica pratensis*, a close relative of several other rescuer species belonging to the genus *Formica* (Czechowski et al., 2002), show it retrieving a nestmate trapped in an agelenid funnel spider web (Kupryjanowicz & Włodarczyk, personal communication). Although further research currently is underway by the researchers to document this single observation, it is probably safe to assume that rescue as an antipredator strategy extends beyond the single threat of antlions.

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[1] Formerly called Tetramorium caespitum, the taxonomy of this species, the common pavement ant, remains under investigation and is temporarily labelled *Tetramorium* sp. E.

Fig. 3. A typical antlion pit field. Antlions often build pits close together, sometimes up to a hundred or more, within a few centimetres of one another. As is evident in this photograph, pits differ enormously in size, shape, slope, and nearby landmarks. Photograph courtesy of Alexander Wild.

2.2.2. Learning in ants

Remarkable as rescue behaviour is in its precision and effectiveness, it is limited as an antipredator strategy because it requires another ant to be nearby, to detect the victim's call-for-help, and to intervene before the antlion protects its capture by pulling the victim under the sand, a behaviour termed *submergence* (Napolitano, 1998; see also Topoff, 1977). The sheer limitations of rescue might hint that it is not likely to be the only antipredator strategy in the evolutionary arms race between predator and prey (Hollis et al., 2015). Indeed, one might ask if ants were able to learn to avoid antlion pits if, somehow, they were successful in escaping capture by an antlion. This question is exactly the one that my coauthors and I recently attempted to answer and, although the data are not yet fully analysed, those experiments suggest that ants are indeed capable of learning to avoid subsequent encounters with antlions. Importantly, we discovered not only that pit avoidance was a learned antipredator strategy, but also that an ant's memory of the pit was sufficiently general to insure that it avoided other pits, very often nearby (Fig. 3), that differed substantially from the one in which it had escaped.

These recent experiments suggest that ants' antipredator toolkit contains both learned and hard-wired responses, as does, clearly, the behavioural arsenal of predatory antlions. Although it is relatively easy to understand how ants' and antlions' particular arms race might have shaped hardwired behaviour in both species, learned behaviour does not respond to coevolutionary selection pressures in exactly the same way (even if modern approaches to evolution postulate that evolutionary processes and simple learning processes are formally equivalent, e.g., Watson and Szathmáry, 2016). That is, particular learned responses, acquired by an individual during its lifetime, cannot in themselves be inherited by one's offspring. So, how can learned behaviour affect coevolutionary processes? In the next section, I describe coevolution and arms races in more detail and then attempt to address the role of learning in coevolution (see also Hollis et al., 2015).

3. Coevolution

Coevolutionary changes can be either mutualistic, when both entities benefit reciprocally from cooperative adaptations, or antagonistic, when the fitness interests of the participant lineages oppose each other, for example host versus parasite, or predator versus prey (Edmunds, 1974; Dawkins and Krebs, 1979). In antagonistic relationships, coevolved changes often continue to exert selection pressures over evolutionary time, resulting in what Dawkins and Krebs (1979) called *evolutionary arms races*: Just as the conflict between two warring countries often results in an unremitting build-up in weaponry, the evolutionary cycle of adaptations and counteradaptations produces a never-ending escalation of reciprocal changes between opponents (Dawkins and Krebs, 1979). But a build-up in weaponry is not always a countermeasure in response to a specific opponent. Likewise, what simply looks like a "close match" between opponents, for example between ants and antlions, is not necessarily the result of coevolution; much harder evidence is required (Thompson, 1994; Janzen, 1980). With this caveat in mind, a close look at one of the best-studied examples of an arms race, between rough-skinned newts and predatory garter snakes (Brodie and Brodie, 1990, 1991, 1999; Hanifin et al., 1999; Feldman et al., 2009, 2010) will serve here not only to illustrate the extraordinary lengths to which these arms races can reach, but also to demonstrate the hard scientific criteria and careful experimentation needed to establish that coevolution has taken place.

3.1. A road map for the study of antagonistic coevolution

The arms race between rough skinned newts and predatory garter snakes has been the subject of intense experimental scrutiny for over 50 years (Brodie, 1968). What began, according to local legend, as an investigation of the death of three hunters in Oregon during the 1950s,[2] Brodie's initial study of the newt found in their coffee pot eventually revealed that newts are capable of producing tetrodotoxin (TTX), which they sequester in skin glands, making this virulent neurotoxin immediately available to predators (or the hunters' coffee). TTX binds to motor nerve cell sodium channels, the effect of which is to block the conduction of nerve impulses, causing respiratory paralysis among other ill effects. However, some common garter snakes have evolved a mechanism – basically a modified sodium channel – that prevents TTX binding, protecting the snakes. In areas where snakes and newts co-reside, and, most importantly, only in these areas, reciprocal adaptations and counteradaptations have resulted in snakes that have become tolerant of incredibly high levels of TTX – consumption of one newt can kill an adult human but these small garter snakes can eat five or more – and newts that produce ever more potent levels of the toxin, far more than is necessary to disarm any of their other potential predators. To show that coevolution is responsible for these changes,

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[2] A highly entertaining, and at the same time scientifically accurate, description of the arms race between newts and garter snakes has been created by Becky Williams and her colleagues (the *Understanding Evolution* team) for students at the University of California, Berkeley. The website can be found here: http://evolution.berkeley.edu/evolibrary/article/0_0_0/biowarfare_01.

Brodie, his son, and their colleagues (Brodie and Brodie, 1990, 1991, 1999; Feldman et al., 2009, 2010; Hanifin et al., 1999), needed to demonstrate that natural selection operated on both newt toxicity *and* snake resistance, that is, *both* traits (a) showed variation; (b) were heritable; and, (c) provided selection advantages. Each of these three criteria, critical to all studies of evolutionary arms races, have been rigorously tested and amply demonstrated. As such, the study of rough-skinned newts and garter snakes provides a helpful roadmap for explorations of predator-prey arms races, our own study included.

Concerning the possible coevolution of hard-wired behavior, the variation in ant rescue across multiple species, tuned as it seems to be to the presence of predators, is encouraging. However, this difference between species could have resulted from two very different evolutionary paths, either that rescue behaviour has been lost in species without high antlion predation or that rescue has evolved in groups exposed to those selection pressures. Our observation that even non-rescuer species appear capable of performing at least some of the rescue behaviour patterns, however, hints that rescue behaviour is an evolutionary old characteristic of ants that has, indeed, responded to selection pressures. That is, rescue might have evolved in a very distant ancestor of extant ant species but has been maintained only as a well-integrated pattern of behaviour in some species (or some populations) as the result of their particular ecology, namely the soils they inhabit and the presence of pit-digging antlions and, perhaps, other predators. Although Nowbahari and I are in the process of gathering additional data, some preliminary tests of rescue behaviour with *basal* species of ants, namely species that are close to the root of the phylogenetic tree, does indeed support this phylogenetic hypothesis.

3.2. Learning and coevolution

As mentioned earlier in this paper, attempting to study the role of learning in coevolution is less straightforward than assessing the role of hard-wired behavior. Acquired responses are not inherited by offspring, although they certainly can alter DNA and, thus, might be subject to *epigenetic* effects, namely changes in organisms produced by external or environmental factors that switch genes on and off. Nonetheless, the *capacity* for learning – its underlying morphology and circuitry – is, indeed, heritable (Mery and Kawecki, 2002, 2004) and this capacity provides a solution to the puzzle of how learning can contribute to coevolutionary processes. That is, because the capacity to learn has been shown over and over again to increase fitness (e.g., Hollis, 1982; Dugatkin, 2014), environments that favour similar learned behavior in both parents and their offspring will reliably support those learned responses, even as the eliciting stimuli themselves may differ. For example, although the particular arthropods that wander near antlion pits may differ from one generation to the next, the ability to associate a vibrational cue with prey arrival increases fitness and this capacity for associative learning is what is inherited, even if the particular learned cues (e.g., the movement-produced vibrational patterns of prey) differ from one generation to the next. In this way, then, the ability to learn is subject to coevolutionary selection pressures. Yet another way in which learning may play a role in coevolution is via a gradual transformation of the previously learned response into one that is hard-wired, an idea that has come to be known as the *Baldwin Effect* (Baldwin, 1896). Such a transformation is predicted to occur whenever selection pressures on learned responses – to learn the response faster, for example, or earlier in one's development – favour hard-wired behavior (Dennett, 2003). But whether or not a learned response eventually becomes hard-wired, that response plays a key role in an animal's reproductive success and, thus, in the coevolutionary process.

One example of the role that learning might play, an example that might be especially useful in examining coevolutionary pressures on antlions, is their ability to discriminate between the different vibrational signatures of the many arthropods on which they prey. Because some prey, like stinging ants, not only are better able to avoid capture by antlions than others, but also have the capacity to inflict injury, antlions would do well to differentiate between the approach of these different prey types and prepare themselves to counter whatever antipredator strategies those prey possess. Several studies hint that they do: The vibrational patterns produced by different crawling insects and received by antlions are indeed different (Devetak et al., 2007), as might be expected; furthermore, antlions respond more frequently to the vibrations produced by some prey, non-stinging mealworms for example, than to those equipped with better antipredator tactics (Devetak, 2014; Mencinger-Vračko and Devetak, 2008). Although it seems unlikely that antlions would have evolved hard-wired responses to all the prey types that they possibly could encounter, nonetheless, it remains to be demonstrated experimentally that the ability to prepare for particular prey, especially dangerous prey like stinging ants, is learned rather than hard-wired. And, if learning is involved in prey discrimination, we also might expect to see differences across populations of antlions, both within and between species, in their inclination to form some associations more quickly than others, a phenomenon called *preparedness* or *belongingness*, which has been demonstrated in both vertebrates (Shettleworth, 2010) and invertebrates (Walker et al., 1989). In antlions, for example, groups that come into frequent contact with stinging prey may be quicker to learn that prey's vibrational signature than groups whose ancestors never have been exposed to that prey, suggesting coevolutionary processes at work.

Some species of ants pose yet another risk for which antlions might be able to prepare via learning, namely the arrival of rescuers. Given that antlions can detect vibrational patterns signalling the approach of prey, the especially intense and multidirectional vibrations produced by multiple approaching ants could be used as a signal that rescue is imminent. Our study of rescue behaviour in *Tetramorium* ants (Taylor et al., 2013), as well as studies of *Formica* ant rescuers by Czechowski and his colleagues (Czechowski et al., 2002), demonstrates that rescue is particularly dangerous for antlions and they would do well either to protect themselves in some way, perhaps by abandoning the prey and digging down into the sand, as they do when threatened, or by pulling themselves and their prey under the sand more quickly. Here, too, the role of coevolution could be explored by examining species and population differences; following the newt and garter snake example, such experiments would need to demonstrate (a) variation in the behaviour between groups; (b) heritability of these differences; and, (c) selection advantages for a particular behaviour.

4. Concluding remarks

Much additional research is necessary if we are to apply strict tests of coevolution to our study of ants and antlions, tests that require we assess the degree to which behavior in *both* predator and prey exhibit perfectly matched, reciprocal changes (Janzen, 1980; Thompson, 1994). Nonetheless, this model offers several advantages: The study of ants, a literature spanning over a century, offers both the foundation and increasingly more sophisticated tools for questions involving ants' genetics, development and evolution. More importantly, perhaps, because the capacity for learning in both species is well known, this particular model provides a way to assess the interplay between hard-wired and learned behavior in an antagonistic arms race between a predator and its prey.

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