Fatal attraction: adaptations to prey on native frogs imperil snakes after invasion of toxic toads

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Adaptations that enhance fitness in one situation can become liabilities if circumstances change. In tropical Australia, native snake species are vulnerable to the invasion of toxic cane toads. Death adders (*Acanthophis praelongus*) are ambush foragers that (i) attract vertebrate prey by caudal luring and (ii) handle anuran prey by killing the frog then waiting until the frog's chemical defences degrade before ingesting it. These tactics render death adders vulnerable to toxic cane toads (*Bufo marinus*), because toads elicit caudal luring more effectively than do native frogs, and are more readily attracted to the lure. Moreover, the strategy of delaying ingestion of a toad after the strike does not prevent fatal poisoning, because toad toxins (unlike those of native frogs) do not degrade shortly after the prey dies. In our laboratory and field trials, half of the death adders died after ingesting a toad, showing that the specialized predatory behaviours death adders use to capture and process prey render them vulnerable to this novel prey type. The toads' strong response to caudal luring also renders them less fit than native anurans (which largely ignored the lure): all toads bitten by adders died. Together, these results illustrate the dissonance in behavioural adaptations that can arise following the arrival of invasive species, and reveal the strong selection that occurs when mutually naive species first interact.

Keywords: *Acanthophis praelongus*; ambush predator; *Bufo marinus*; Elapidae; foraging mode; invasive species

1. INTRODUCTION

Organisms become adapted via natural selection for traits that enhance an individual's performance in its natural environment (Williams 1966). But adaptations that have accumulated because they enhanced fitness in previous generations may lose their fitness advantage if conditions (and thus, selective optima) change (Schlaepfer *et al.* 2002; Robertson & Hutto 2006). Environmental shifts enforced by humans often happen quickly, so traits that previously enhanced fitness may be rapidly rendered maladaptive. For example, grassland birds that normally nest in habitats with low vegetation may choose to nest in pasture, but then face high nestling mortality due to mechanical harvesting of hay prior to fledging (Best 1986). In this example, the suite of habitat-selection behaviours that now reduce fitness was termed an 'ecological trap', enforced by the mismatch between historically adapted behavioural rules (Darwinian algorithms) and the current selective environment (Schlaepfer *et al.* 2002, 2005). Such mismatches may be common, as in hatchling sea turtles moving towards the lights of suburbia rather than the light horizon of the open ocean (Witherington 1997). One widespread reason for previously beneficial adaptations to reduce rather than enhance fitness involves invasive species. For example, female pierid butterflies readily oviposit on an introduced plant species on which their larvae are unable to survive (Porter 1994).

The most striking examples of how adaptations suddenly may disfavour an organism involve complex morphologies and behaviours that switch instantaneously from enhancing to reducing fitness due to a sudden change in the organism's environment—such as the arrival of an invasive species. Our studies in tropical Australia reveal exactly this situation. A snake species exhibits complex behavioural and morphological adaptations for catching and handling native prey; but the same traits that facilitate successful predation on native prey have increased the vulnerability of these snakes to a newly arrived (and highly toxic) prey species (the cane toad, *Bufo marinus*). Similarly, cane toads, naive to the predator, exhibit behavioural responses that render them more vulnerable to adder predation than are native prey species.

2. MATERIAL AND METHODS

(a) Study species

Floodplain death adders (*Acanthophis praelongus hawkei*; Wuster *et al.* 2005) are large (up to 750 mm, 486 g), heavy-bodied venomous elapid snakes that are abundant in the wet-dry tropics of northern Australia (Wuster *et al.* 2005). Unlike most Australian elapid snakes, death adders are ambush foragers, waiting in camouflaged sites and attracting prey items close enough for capture by undulating their tail tip (figure 1). Presumably reflecting selection on its effectiveness in attracting potential prey, the tail tip is distinctively coloured and shaped (Cogger 1992; figure 1). The lure's efficacy in prey attraction has been confirmed in laboratory trials with artificial lures as well as with live snakes (Hagman *et al.* 2008). Stomach-content analysis of field-caught snakes shows that death adders feed mostly on

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0192> or via <http://rspb.royalsocietypublishing.org>.

Figure 1. Sequential still photographs from a video sequence showing caudal luring by a death adder (*Acanthophis praelongus*) in response to the proximity of a cane toad (*B. marinus*). Note tail movement, and modified morphology of the tail tip.

frogs and lizards, but occasionally take birds and mammals (Webb *et al.* 2005).

In 2003, our study site on the Adelaide River floodplain 60 km east of Darwin (12°39' S, 131°19' E) was invaded by cane toads (*B. marinus*), highly toxic anurans that were brought to Australia in 1935 and have since spread across much of the tropics (Lever 2001; Urban *et al.* 2007; Phillips *et al.* 2008). Although Australia has a diverse anuran fauna, it has no native bufonids (i.e. toads) and thus many Australian predators are unable to survive exposure to even small doses of the toads' toxic bufadienolides (Phillips *et al.* 2003). Death adders are highly sensitive to the toxin (Phillips *et al.* 2003), and anecdotal reports suggest that *Acanthophis* populations have declined dramatically coincident with cane toad invasion (Shine *et al.* 2006).

(i) Stimuli eliciting caudal luring

We captured death adders and cane toads from the Adelaide River floodplain and quantified a range of their behavioural characteristics in the laboratory. We placed adders in individual plastic boxes (400 × 300 mm floor area) lined with paper, and provided water *ad libitum*. A week after capture, at dusk we added a single prey item, either a native frog *Limnodynastes convexiusculus*, *Litoria dahlii*, *Litoria nasuta*, or a cane toad. To minimize the risk of fatal poisoning, we reduced toxin content of the toads prior to the trial by surgically ablating the parotoid gland. We videotaped the encounter, and examined the video to score whether or not the adder displayed caudal luring.

(ii) Responses to caudal luring

From the same video recordings, we also scored whether or not the potential prey item approached the luring snake.

To further clarify responses elicited by the caudal lure, we conducted additional trials with an artificial lure (the severed tail of a road-killed death adder, connected to a machine that moved it in a 'natural' fashion to mimic the rates and

distances of movement by the tail tip during luring by captive snakes). The machine was modified from one used to mimic toe-waving (prey-luring) behaviour by cane toads (see Hagman & Shine (2008) for details). A 12 V engine rotated (on a vertical axis) a circular plate of aluminium to which we affixed a flat metallic arm (10 × 150 mm) holding the tail of a death adder. The motion of the aluminium plate moved the 'lure' in a fashion closely resembling that of a real snake (the tip of the artificial lure moved 8–10 mm from side to side at a rate of 4.5 sideways movements s⁻¹, well within the range of tail-luring bouts videotaped from captive snakes; Hagman *et al.* 2008). The tail protruded through a hole on the floor at one end of a plastic bin (60 × 45 × 50 cm) housing either a frog or a toad. We videotaped the trial to score whether or not the anuran attacked the lure. Tails removed from freshly killed snakes remained supple and hence usable for a few days post-mortem; in total, we used 12 tails during our experiments. Prior to analysis, data were ln-transformed to achieve normality and variance homogeneity.

(iii) Prey handling by snakes

We also scored prey-handling behaviour after the prey was killed. Floodplain death adders handle different prey species in highly stereotyped ways: adders that kill non-toxic frogs, e.g. *L. nasuta*, swallow them immediately, whereas adders that kill toxic frogs (possessing glue or poisons), e.g. *L. convexiusculus* and *L. dahlii*, delay ingestion until the threat has abated (i.e. the glue and toxin both break down rapidly after prey death, eventually permitting safe ingestion; Phillips & Shine 2007). Thus, we scored the duration of elapsed time between the snake striking the prey and attempting to eat it. The dataset for frogs in the present paper is the same as that used by Phillips & Shine (2007) but with the addition of (concurrently run) trials on cane toads. To determine whether adders handled toads differently from some or all native frogs, we conducted a discriminant function analysis of prey-handling traits (time the prey was

held, whether or not the snake gaped and whether or not the snake finished ingestion), then looked at *a posteriori* misclassification rates. That is, we asked the programme to identify distinctive attributes of prey handling for each of the four anuran species involved, then *a posteriori* we asked it to classify the most probable anuran taxon involved in each ingestion episode, based on the behaviours that we scored. This procedure allowed us to quantify the number of toads that were handled differently from any of the frog species, as well as the numbers of toads that were handled as if they were one of the three common frogs.

(iv) *Impact of toad invasion on death adder survival*

To determine whether these staged laboratory encounters also occurred in the field, we radio-tracked death adders at our study site shortly after toads arrived in the area (during the summers of 2004–2005 and 2005–2006). The death adders we tracked included those used in our filming trials as well as additional animals that had been offered toads but, for logistical reasons, were not filmed. Because these animals had already been exposed to toads in the laboratory, they represent the survivors from laboratory-based encounters and were, presumably, less likely to be killed in the field. During radio-tracking, each snake was located daily. If a snake was found dead, the area within 2 m of the snake was carefully searched for a dead toad and the snake was autopsied.

(b) *Ethical note*

This study resulted in the deaths of several animals during predator–prey encounters in captivity, a situation requiring careful ethical cost–benefit analysis. That analysis was conducted by us, and approved by the relevant animal ethics authority (University of Sydney Animal Ethics Committee). The work was part of a larger conservation-based research programme, of which this behavioural work was a key component in the development of a management strategy for reducing the ecological impact of invasive cane toads (i.e. not simply ‘pure’ research). For example, the behavioural work allowed us to quantify immediate impact (which is necessary for legislative recognition of threatening processes), as well as assess the probable long-term effect of toads on populations of native predators (which is critical for robust conservation planning). The proportion of a given predator species that will attack, eat and die from toads in a natural setting is the keystone of the work. There was no realistic alternative to real, staged encounters, but sample sizes were kept to a minimum within the requirement for valid scientific inference. We also incorporated procedures to mitigate risk to the study animals, such as squeezing/ablating toxin from toads to reduce risk to adders, and using small (less toxic) toads as prey items. Anurans typically die very rapidly following adder bite (less than 2 min, although the snakes thereafter delay ingestion for variable periods), so that suffering following snakebite was brief. Frogs and toads were only used for a single trial, and if uneaten were released unharmed the following day.

3. RESULTS

(a) *Results from all trials*

We conducted 76 trials with live death adders and anurans, and 720 trials with the artificial caudal lure. Each snake or anuran was used in only a single trial,

Figure 2. Comparisons among three species of native frogs and invasive cane toads (*B. marinus*), in terms of (a) the rates at which exposure to these taxa stimulated caudal luring by death adders (*A. praelongus*); and (b) the rates at which these anurans approached an artificial lure (a death adder tail attached to a machine that caused it to move in a fashion resembling caudal luring).

to avoid pseudoreplication, but we used each artificial lure in an average of 60 trials.

(i) *Stimuli eliciting caudal luring*

Previous work shows that small death adders tend to caudal lure more readily than larger snakes. In our trials, adder body size did not vary significantly between animals exposed to the different prey types ($F_{3,78}=1.96$, $p=0.12$), so systematic differences in snake body size between prey treatments do not drive the differences we observe here. Overall, death adders were far more likely to caudal lure in response to cane toads than to native frogs (in total, 12 out of 29 tests with toads (41%), versus 7 out of 47 with native frogs (15%); logistic regression with ‘frog versus toad’ as the factor, and luring as the response variable: likelihood ratio test, $\chi^2_1=6.57$, $p=0.01$). One native frog species (*L. dahlia*) elicited similar response levels as did cane toads (7 out of 14 trials=50%; including only these two species, $\chi^2_1=0.28$, $p=0.59$) whereas luring was never elicited by two other anuran species that are frequently eaten by death adders (Webb et al. 2005): *L. nasuta* (0 out of 16 trials) and *L. convexiusculus* (0 out of 17 trials; see figure 2; pairwise comparisons against responses to other species, all $p<0.001$). The occurrence of luring was not affected by prey size relative to predator size (logistic regression with prey species and relative prey mass as independent

variables, effect of prey species $\chi^2_3=22.72$, $p<0.0001$; effect of relative prey mass, $\chi^2_1<0.13$, $p=0.71$).

(ii) Responses to caudal luring

In trials with live snakes, toads approached the caudal lure in 11 out of 12 trials (83%), whereas native frogs never did so. Statistical analysis confirms that toads responded significantly more frequently than did frogs ($\chi^2_1=31.61$, $p<0.0001$; see figure 2).

The same bias was evident in trials with the artificial lure: toads approached the lure in 32 per cent of trials (93 out of 288) whereas frogs approached in only 0.5 per cent of cases (2 out of 144 trials with *L. nasuta*; 0 out of 144 trials with *L. dahlii*, 0 out of 144 trials with *L. convexiusculus* (comparing frogs versus toads, $\chi^2_1=173.87$, $p<0.0001$; figure 2). A prey's interest in the artificial lure did not change as the tail aged, confirming the value of using a real snake tail in our experiments. As in trials using live snakes, an anuran's body size did not influence its response to the artificial lure (looking only at data from toads, $\chi^2_1=1.74$, $p=0.19$). Toads of the entire range of body sizes tested approached the lure (range 2.6–233.0 g; 31–131.5 mm snout–urostyle length), and 11 toads actually seized the lure and tried to ingest it. Those 11 animals were smaller, on average, than the 82 toads that approached the lure but did not seize it (means of 52.8 versus 82.8 mm snout–urostyle length; $F_{1,91}=7.91$, $p<0.007$).

(iii) Prey handling by snakes

As previously reported by Phillips & Shine (2007), death adders swallowed the non-toxic *L. nasuta* immediately after striking, but waited an average of 10 min post-strike before ingesting the moderately toxic *L. convexiusculus*, and even longer (mean=42 min) before ingesting *L. dahlii*, the most toxic of the three species. The discriminant function accurately classified 74 per cent (32 out of 43) of prey-handling trials involving frogs to the 'correct' species, and of the 11 misclassified encounters, only one was classified as a toad. Responses to cane toads (tested prior to toad arrival at our study site, thus novel to these adders), however, were more varied. Based on *a posteriori* classification rates, only 46 per cent of adders treated toads uniquely, and this was driven primarily by these snakes not completing ingestion: two snakes treated the toads as if they were the non-toxic *L. nasuta* (2 out of 28=7%), five toads as if they were the 'sticky' *L. convexiusculus* (i.e. delayed ingestion for approx. 10 min: 5 out of 28=18%) and eight as if they were the toxic *L. dahlii* (i.e. waited approx. 40 min prior to ingestion: 8 out of 28=29%). Snakes that handled toads as if they were native frogs were more likely to die than snakes that treated toads as different from native frogs (contingency table: $\chi^2_1=3.83$, $p=0.05$).

Delaying ingestion, however, did not enhance snake survival rates, because toad toxins (unlike those of these native frogs) do not degrade shortly after the prey dies (Phillips & Shine 2007). Of the 28 snakes that interacted with toads, 15 completed ingestion. Among these 15 animals, 5 (33%) died following ingestion. Delay time prior to ingestion varied widely (ranging from 3 to 46 min post-strike) but did not affect the snake's probability of survival (logistic regression: $\chi^2_1=0.12$,

$p=0.73$). By comparison, no adders died following the ingestion of native prey.

(iv) Impact of toad invasion on death adder survival

A total of 54 snakes were radio-tracked for a total of 2608 days (average radio-tracking period per snake was 48 days). Of the 54 radio-tracked snakes, 22 per cent (12 out of 54) died after attacking a toad in the field. Causation was obvious in all cases: eight snakes had toads in their stomachs, and the remaining four had dead toads either in their mouth or within 1 m of their body. The remaining 42 snakes either survived to the end of the radio-tracking period ($n=19$) were lost (failed transmitter=14; moved out of study area=6), or were eaten by monitor lizards ($n=3$). Clearly, some of the 'survivors' may later have attacked a toad and died, and thus our estimates of impact are conservative.

4. DISCUSSION

Death adders are at great risk following the invasion of cane toads: overall, approximately half of the snakes that ingested toads during our studies died as a result. This vulnerability was evident even in the laboratory, where we used toads with reduced toxin content. In our radio-telemetry studies, many of the telemetered snakes died after attempting to eat toads. Our data on behavioural responses identify a major contributor to that vulnerability. The foraging tactics of death adders place them at heightened risk of poisoning by invasive cane toads.

The specialized modes of prey attraction and prey handling exhibited by death adders presumably have worked well for millions of years. Although luring did not attract native frogs in our study, it works well with scincid lizards (Hagman *et al.* 2008). However, those traits reduce rather than enhance fitness of death adders when toxic cane toads arrive. First, the visual stimulus provided by toxic cane toads elicits luring by the snakes, far more than does the visual stimulus from native anurans. Second, caudal luring attracts toads, and does so more effectively than it attracts natural prey. Third, the tactic of delaying ingestion to permit toxin breakdown does not protect adders against the highly stable bufadienolides of the invading species.

On an evolutionary time scale, the arrival of toads has rapidly changed the selective value of these traits. Death adders were abundant on these tropical floodplains prior to toad invasion (Gow 1976), presumably due in some degree to the advantages conferred by caudal luring and facultatively delayed ingestion. Adders thereby have been able to feed on agile prey items that are difficult to capture via active pursuit; and the tactic of delayed ingestion post-strike allows death adders to exploit frog species too toxic to be consumed by other snakes (Madsen & Shine 1994; Phillips & Shine 2007). The arrival of cane toads, however, has placed a large penalty on both of these traits resulting in an ecological trap. Reliance on caudal luring is likely to result in snakes encountering toads rather than native anurans. Similarly, the simpler tactic of rejecting toxic prey soon after the strike may facilitate predator survival relative to the more specialized mode exhibited by adders, of ingestion following delay—because, unlike the toxins of native frogs (Phillips & Shine 2007), those of cane toads remain functional for long after the anuran's

death (Lever 2001). Interestingly, some of the adders that we examined did, in fact, reject toads as prey (albeit often after a lengthy period of repeated tasting), and rejection of the prey was associated with improved survival in the laboratory. Thus, upon the arrival of toads, there appears to be an advantage to the basic strategy of simple rejection following strike: snakes that can recognize toads as unpalatable prey and quickly reject them should be selectively favoured in this new environment.

One of our more perplexing results is that toads elicited more luring from adders than did native frogs. Why did this happen? The answer may lie in the movement patterns of toads, which often walk fairly continuously rather than hop intermittently. Native frogs are typically immobile, then move large distances in a single leap. Thus, the movement pattern of toads is probably more similar to that of lizards (which consistently elicit high rates of luring from adders; Hagman *et al.* 2008), than that of native frogs. Toads also grow larger than native frogs, perhaps providing a stronger visual stimulus—but in our trials, the frogs offered as prey averaged larger body sizes than the toads. Thus, the disparity between rates of caudal luring elicited by toads versus frogs may be even greater in the field, where toads average larger body size than do native frogs. Rates of encounter between death adders and toads also will be increased by overlap between the two species in habitat use and seasonal activity patterns as cane toads continue to spread across Australia. Many native anurans are arboreal, and most are active only during the brief wet season, whereas toads are terrestrial and remain active throughout the long dry season (Freeland & Kerin 1988; Child *et al.* 2008). Death adders continue to feed throughout this period (Webb *et al.* 2005) and thus, for much of the year the most abundant anurans encountered by death adders will be cane toads.

Why did cane toads respond more strongly to caudal luring than did native frogs? The lure presumably elicits a generalized response to the movement of an elongate, invertebrate-resembling object. Both frogs and toads feed on small invertebrates (Freeland & Kerin 1988; Greenlees *et al.* 2006) but it is likely that native frogs have coevolved with death adders and so may be able to discriminate between adder lures and actual prey items. Toads, on the other hand, have not had this opportunity for co-adaptation. In fact, responses of juvenile toads to a moving stimulus are strong enough to have favoured the evolution of specialized toe-waving behaviour in large (cannibalistic) cane toads that attract smaller conspecifics within striking range (Hagman & Shine 2008). Indeed, the movement pattern of the tail in many caudal-luring bouts that we filmed in captive death adders was almost identical to that seen in the pedal lure of toe-waving cane toads: that is, 4.5–5 displacement cycles s^{-1} , covering an arc of approximately 10 mm (Hagman & Shine 2008). This pattern was maximally effective in attracting small toads (Hagman & Shine 2008), suggesting that death adder luring provides a stimulus ideally suited to attracting cane toads.

Overall, both the characteristic movement patterns of toads, which attract the attention of their predators, along with their susceptibility to caudal luring, are examples of the same phenomenon seen in death adders: behaviours that become maladaptive in a new context. Is it possible that cane toads are maladapted to Australia

in ways that could quickly reduce their numbers? We suspect that their toxicity will trump any behavioural maladaptiveness that they might have, so that their survival in this area may not be 'threatened'. Regardless, it is an interesting example of how a mix of evolved traits can interact to determine a species' fitness in a new/ changing environment.

Does the death adder's specialized behaviour for handling prey after the strike also contribute to their vulnerability to toads? Most elapid snakes simply seize and retain prey items, whereas the death adders in our study area use this method only for non-toxic native frogs (Phillips & Shine 2007). Death adders, however, bite-and-release frogs with chemical defences (glue or toxin) and then delay ingestion, allowing the chemical defence to degrade (Phillips & Shine 2007). In such a system, a snake may proceed to ingest the item even if toxins are detected, because the time delay between prey death and toxicity in natural prey has favoured that tactic. In fact, we observed exactly this behaviour in more than half of our filmed adders. However, the long-term stability of bufadienolides (Lever 2001) makes this a dangerous behaviour relative to the simpler alternative (as seen in other elapid snakes in the area) of simply releasing, and not attempting to ingest, a toxic frog (Phillips & Shine 2007). Nonetheless, the fact that many adders eventually rejected toads suggests variance in prey-ingestion traits, either of plastic or genetic origin. This variance will clearly mediate the long-term impact of toads on death adders, either by allowing rapid evolution to proceed, or by providing the ability for individual adders to learn to avoid toads.

In summary, death adders use specialized behaviours that work well in one context but are detrimental in a new context: the presence of toxic cane toads. Cane toads also exhibit behavioural responses that work in one context, but not in a new context: the presence of a caudal-luring predator. In the field, death adders now frequently encounter a stimulus that elicits luring; luring frequently attracts toads; and ingesting a toad (even if that ingestion is delayed until long after prey death) almost certainly results in death. Toads also encounter a stimulus that encourages their approach, but approaching a death adder is fatal. The end result is a mismatch between the foraging tactics of both predator and prey and components of their respective fitness. This behavioural dissonance between predator and prey exerts a strong ecological impact on death adders. More generally, the form of this complex effect reflects the critical importance of predator foraging tactics in rendering a species vulnerable to anthropogenically induced environmental changes.

Permits for the research were provided by the Northern Territory Parks and Wildlife Service, and all research procedures were approved by the Animal Ethics Committee of the University of Sydney, Australia.

We thank Michelle Gray and Sam Ruggeri for technical assistance; Matt Greenlees, Greg Brown, Thomas Madsen and Bea Ujvari for assistance with the collection of death adders; and David Nelson and Georgia Ward-Fear for collecting frogs. Brodie Wilson, Chris Gregory and Matt Greenlees assisted with animal husbandry and radio-tracking. The Australian Research Council funded our work.

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