

# An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia

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Rapid environmental change due to human activities has increased rates of extinction, but some species may be able to adapt rapidly enough to deal with such changes. Our studies of feeding behaviour and physiological resistance to toxins reveal surprisingly rapid adaptive responses in Australian black snakes (*Pseudechis porphyriacus*) following the invasion of a lethally toxic prey item, the cane toad (*Bufo marinus*). Snakes from toad-exposed localities showed increased resistance to toad toxin and a decreased preference for toads as prey. Separate laboratory experiments suggest that these changes are not attributable to learning (we were unable to teach naive snakes to avoid toxic prey) or to acquired resistance (repeated sub-lethal doses did not enhance resistance). These results strongly suggest that black snake behaviour and physiology have evolved in response to the presence of toads, and have done so rapidly. Toads were brought to Australia in 1935, so these evolved responses have occurred in fewer than 23 snake generations.

**Keywords:** coevolution; conservation; contemporary evolution; predator–prey

## 1. INTRODUCTION

The current biodiversity crisis and high species extinction rate are consequences of rapid environmental change, mediated by human activities (Ehrlich 1995). Overharvesting, invasive species and altered climate are all examples of significant environmental change. Because such changes are usually directional, we can expect non-random impact on species affected by a specific change. Therefore, many of the environmental changes mediated by humans exert strong selection on affected species and it is increasingly apparent that evolutionary responses to strong selection can occur rapidly, on time scales traditionally thought of as ‘ecological’ (Thompson 1998; Hendry & Kinnison 1999; Stockwell *et al.* 2003).

Understanding which species are likely to adapt to a given change provides valuable information for the setting of conservation priorities. Additionally, some categories of environmental change may facilitate adaptive responses by impacted species. In short, understanding the potential for evolution to affect anthropogenic impacts allows us to further refine conservation priorities and strategies (Ashley *et al.* 2003; Carroll *et al.* 2005; Schlaepfer *et al.* 2005).

Invasive species are a major concern to conservationists (Mack *et al.* 2000). They are second only to climate change in terms of ubiquity and have been implicated in the extinctions of numerous native species (e.g. Elton 1958; Fritts & Rodda 1998; Ogutu-Ohwayo 1999). From an evolutionary perspective, invasive species often represent an instantaneous and strong change in the selective environment. So what is the possibility that native species

can adapt to an invader? Here, we examine the possibility of an adaptive response by an Australian snake to the invasion of a toxic prey item, the cane toad.

Toads were introduced into Australia in 1935 (Lever 2001). They are highly toxic; the principal toxins (Bufodienolides) are highly cardiotoxic and unique to toads (Chen & Kovarikova 1967). Australia has no native species of bufonids (Lutz 1971; Cogger 2000). Hence, the arrival of toads presented a highly toxic potential prey item to a naive predator fauna. Australian snakes, in particular, have faced massive impacts in the presence of toads. More than 49 species of snake have the potential to be impacted and almost all of these are poorly equipped to survive a likely dose of toad toxin (Phillips *et al.* 2003). The arrival of toads thus potentially imposed selection on at least three traits: physiological resistance to toad toxin, prey preference (the tendency to eat toads) and the morphology of impacted snake species (relatively small-headed snakes are less likely to be capable of consuming a toxic dose: Phillips & Shine 2006). Our previous work (Phillips & Shine 2004) examined changes in morphology; this work focuses on prey preference and toxin resistance, traits that have previously been shown to be important in snakes handling dangerous toxic prey (e.g. Brodie & Brodie 1990; Arnold 1992; Williams *et al.* 2003).

One native species facing a high impact from toads is the red-bellied black snake (*Pseudechis porphyriacus*). These relatively large elapids feed primarily on frogs and have very low resistance to toad toxin (Phillips *et al.* 2003). Anecdotal reports indicate massive declines in black snake populations following the arrival of toads (Rayward 1974; Covacevich & Archer 1975; Fearn 2003; Phillips & Fitzgerald 2004). The current distribution of the black snake includes areas of sympatry and allopatry with toads. Here, we compare toad-naive and toad-exposed populations of black snakes to examine the possibility that these

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The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2006.3479> or via <http://www.journals.royalsoc.ac.uk>.

snakes display an adaptive response to the presence of toads. To do this, we first determine whether there are differences between populations that we could define, *a priori*, as adaptive. Second, we investigate plasticity in changed traits, to investigate whether observed changes are the result of plasticity or evolution.

## 2. MATERIAL AND METHODS

### (a) *Comparing toad-exposed and toad-naive populations*

#### (i) *Prey preference*

Twelve black snakes were collected from each of the following categories: (i) populations exposed to toads for 40–60 years (Childers and Agnes Waters, Qld; separated by 120 km), and (ii) toad-naive snakes from two populations; one immediately adjacent to the expanding toad front (Casino, NSW) and one approximately 570 km from the front (Macquarie Marshes, NSW). Exposed and naive populations were separated by a minimum straight-line distance (Childers–Casino) of 410 km (see electronic supplementary material). Black snakes are relatively sedentary (Shine 1987), so gene flow between our sampled populations is likely to be low. After a minimum of three weeks in captivity, each snake was offered a frog (*Limnodonastes peronii*—a widespread species, sympatric with snakes at all collection localities) and a toad in random order, 3 days apart. Prey items were offered to the snakes freshly killed, to eliminate behavioural differences between the preys and so that we could remove the parotoid glands from the toads; not doing so probably would have resulted in the death of snakes during the course of the experiment. In each case the snakes were left undisturbed for 24 h, after which we recorded whether the prey item had been eaten. Differences in numbers of prey consumed between toad-exposed and toad-naive localities were compared using Fisher's exact test.

#### (ii) *Toxin resistance*

Thirteen snakes from toad-exposed localities (between Agnes Waters and Casino) and 28 from toad-naive localities (between Casino and Macquarie Marshes; see electronic supplementary material) were tested for resistance to toad toxin. These snakes included 15 tested previously for prey preference (five from toad-exposed areas and 10 from toad-naive areas) and additional animals collected from a range of localities within each category. Toad-exposed snakes came from a range of populations representing exposure times of 5–60 years.

Resistance to toad toxin was assayed in a manner identical to that reported in Phillips *et al.* (2003), using the same toxin extract. Toad toxin was obtained from the skins of freshly killed cane toads collected from the Lismore area (northern NSW). A single extraction of toad toxin was made for the entire study to remove among-toad variance in toxicity and accurately control dosing. The resistance of individual snakes to toad toxin was assayed using the decrement in swimming speed following a dose of toxin (methodology modified from Brodie & Brodie (1990)). Snakes were swum around a 2.4 m circular swimming pool and their times to traverse each quarter of the pool were recorded. A total of eight speeds were recorded for each swimming trial and two trials were run (an hour apart) pre- and post-dose. The average of the fastest

speeds from each swimming trial was used to compare locomotor performance pre- and post-dosing. A large percentage reduction (%redn) in swimming speed indicates a lower resistance to toxin than a smaller reduction in swimming speed. Each snake was given a dose of 80 µg of toad skin per gram of body mass (a dose previously calculated to be non-lethal, but provide measurable reductions in speed; Phillips *et al.* 2003). Dosing was achieved with a feeding tube attached to a syringe or calibrated micropipette, inserted into the snake's stomach to a depth of 30% of its snout–vent length.

Differences in %redn were compared between exposed and naive populations using a *t*-test. Additionally, we examined the relationship between %redn and exposure time in toad-exposed populations by simple linear regression.

### (b) *Learning and acquired resistance experiments*

Observed differences in resistance and prey preference could either be acquired during a snake's lifetime or be the result of changes in gene frequency due to adaptive evolution. Following the observation of differences between exposed and naive populations, we exposed captive snakes to toad toxins to evaluate the possibility of either a learnt response or acquired resistance in naive black snakes.

#### (i) *Learning*

Sixteen snakes were collected from toad-naive areas (see electronic supplementary material). Snakes were kept in captivity for a month before the learning trial commenced. Each snake was offered each of two prey types three times, in random order. We used laboratory mice and a lizard (*Eulamprus tympanum*, Scincidae; an allopatric and hence novel species to all our snakes) as our two prey types. Prey items were offered to the snakes dead; the snakes were left undisturbed with this prey for 24 h, after which we recorded whether or not the prey item had been eaten. Successive feedings were 4 days apart. Following these six feeding events, a prey item was introduced that contained a high, but sub-lethal dose of toad toxin (120 µg of toad skin per gram of body mass, 65% of LD<sub>50</sub>: a dose that reduces a snake's locomotor ability by more than 50% for more than 24 h). Eight snakes received a toxin-laced lizard and eight snakes received a toxin-laced mouse. Following the consumption of this prey item, we repeated the previous feeding schedule, recording the number of prey consumed. At the conclusion of the trials we counted the number of prey items of each type that were consumed before and after the dose of toxin and used repeated measure ANOVA to assess differences in these scores.

#### (ii) *Acquired resistance*

Twenty snakes (including those used in the learning trials) were assessed for the possibility of acquired resistance (see electronic supplementary material). Every 5 days, we administered either a dose of toxin or a dose of water to each snake. This was repeated four times so that half the snakes received four doses of toxin and half received four doses of water. Dosing method was identical to that described for the assessment of differences in resistance to toxin between exposed and naive populations (dosing rate: 60 µg per gram of body weight, dose = 32% of the LD<sub>50</sub>). Four weeks after the last dose, all snakes were assessed for

resistance to toxin in a manner identical to that used to compare exposed and naive populations. Following the calculation of %redn scores, we compared the toxin and control groups and also compared all snakes in this experiment with snakes assessed for resistance from naive localities using ANOVA (%redn scores were non-normally distributed in this instance and thus were arcsine transformed). This allowed us to test whether repeated doses of toxin increase resistance and also whether a single dose of toxin (16 snakes had received at least one dose of toxin in the learning experiment) could increase resistance.

### 3. RESULTS

#### (a) Comparing toad-exposed and toad-naive populations

##### (i) Prey preference

All the snakes, from each exposure category, ate the frog that was offered to them (figure 1). Exactly half (i.e. six) of the snakes from toad-naive populations consumed a toad whereas no toads were consumed by snakes from toad-exposed populations—a statistically significant difference ( $\chi^2_1 = 5.6$ ,  $p = 0.014$ ; figure 1).

##### (ii) Toxin resistance

A significant difference between exposed and naive populations was detected, with naive populations exhibiting higher %redn and thus, lower resistance to toad toxin (two tailed  $t$ -test, equal variances:  $t = 3.259$ , d.f. = 39,  $p = 0.002$ ; figure 2). Additionally, %redn scores decreased (and hence the level of resistance increased) with exposure time (i.e. duration of sympatry between snakes and toads:  $F_{1,12} = 10.18$ ,  $p = 0.009$ ; figure 3).

#### (b) Learning and acquired resistance experiments

##### (i) Learning

To compare numbers of prey eaten before and after the administration of toxin required a repeated measures ANOVA with prey type and toxin/control (treatment) as orthogonal factors and number of prey eaten (before and after administration of the treatment) as the dependent variables. This analysis revealed that snakes fed a toxic prey item showed no inclination to avoid the prey item in further feeding opportunities ( $F_{1,27} = 0.007$ ,  $p = 0.93$ ; figure 4). This effect was independent of prey type (interaction,  $F_{1,26} = 0.1678$ ,  $p = 0.69$ ) and suggests that a black snake surviving an encounter with a toad is unlikely to avoid toads in the future.

##### (ii) Acquired resistance

Four doses of toxin over the period of a month did not induce a significant change in the level of resistance exhibited by snakes when compared with a control group ( $F_{1,18} = 3.94$ ,  $p = 0.06$ ; figure 5). Indeed, mean %redn in swimming speed was (albeit non-significantly) higher in the toxin-exposed group (42%) than the control group (24%). That is, snakes given several doses of toad toxin tended to exhibit lower rather than higher resistance to toxin. Because most of the snakes involved in this experiment had previously been exposed to a single dose of toxin during the learning experiment, it is possible that this single dose changed their resistance. To assess this possibility we compared the resistance of all the snakes in

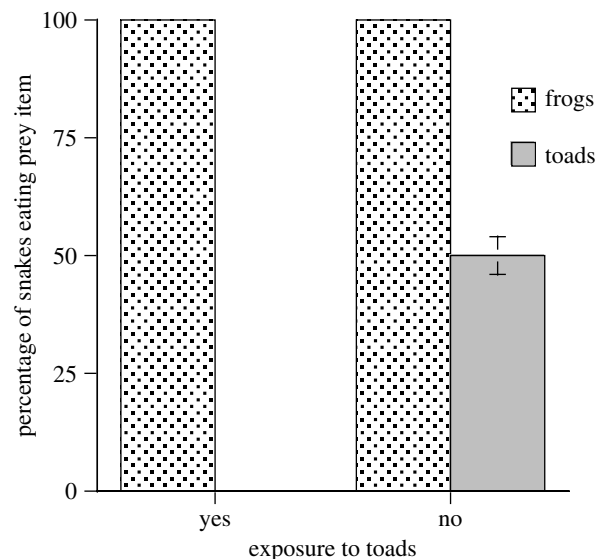


Figure 1. The percentage of black snakes from toad-exposed and toad-naive populations willing to eat a toad or a frog. No snake from a toad-exposed locality would consume a toad. Error bars represent a standard error.

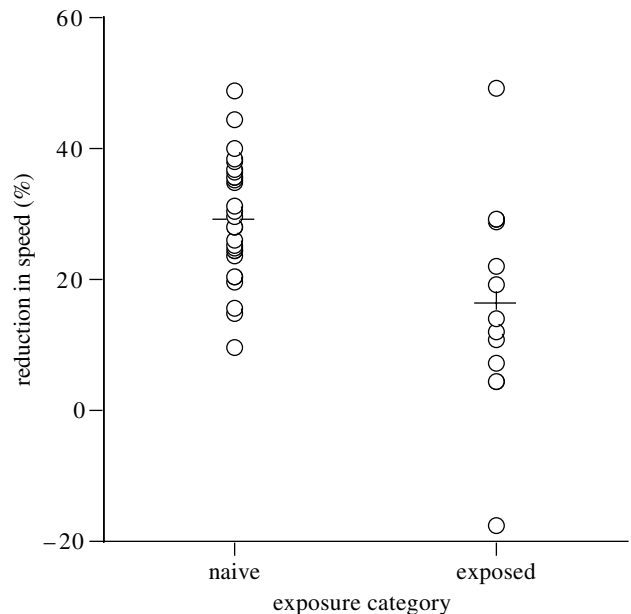


Figure 2. Resistance to toad toxin in toad-exposed and toad-naive populations. A large percentage reduction in speed indicates low resistance to toxin. Hence, snakes from toad-exposed populations exhibited higher resistance to toad toxin.

this experiment ( $n = 20$ , mean %redn = 33) to the resistance of all snakes previously tested from naive populations ( $n = 28$ , mean %redn = 29). ANOVA revealed no significant difference in %redn between these two samples ( $F_{1,47} = 0.03$ ,  $p = 0.87$ ).

### 4. DISCUSSION

Our results show differences between black snakes from toad-exposed versus toad-naive populations both in their physiological resistance to toad toxin and in their willingness to eat toads. Importantly, both of these differences are in an adaptive direction; that is, we see an increased resistance to toxin and lowered preference for consuming toads in toad-exposed populations. These changes could

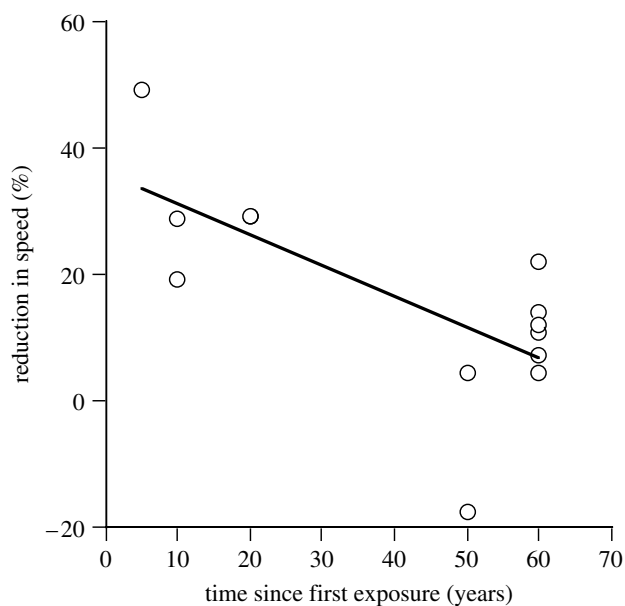


Figure 3. Resistance to toad toxin as a function of the time a snake population has been exposed to toads. A large percentage represents a low resistance. Hence, the snakes' resistance to toad toxin increases with increasing exposure time.

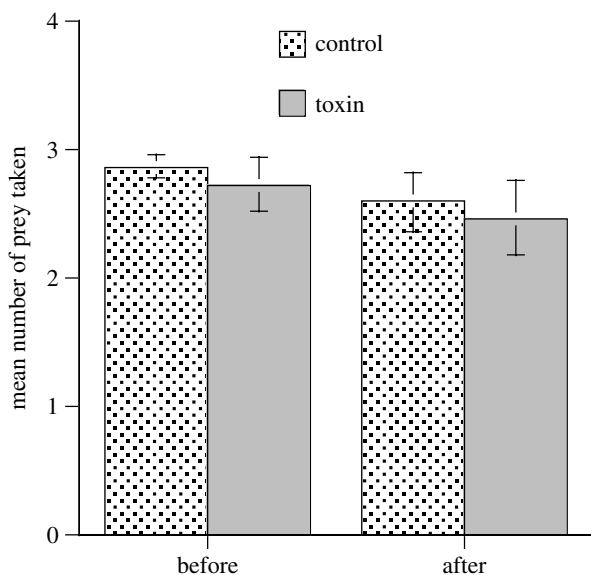


Figure 4. Can snakes learn to avoid toxic prey? Histograms show the number of prey taken by black snakes before and after exposure to a toxic prey item. Two prey types were used, only one of which was laced with toxin for each snake (see §2).

be evidence of either plasticity (a change acquired within an individual snake's lifetime) or strong selection imposed by toads (with or without a response to that selection). To discriminate between these possibilities, we attempted to elicit acquired responses in toad-naïve captive snakes. However, we found no evidence that black snakes can learn to avoid a toxic prey item, nor that they can acquire physiological resistance to toad toxin. Our inability to elicit acquired responses in either of these two traits suggests that the differences observed between toad-exposed and toad-naïve populations are due to selection rather than phenotypic plasticity.

This interpretation of strong selection also depends, to some extent, on the degree to which our acquired

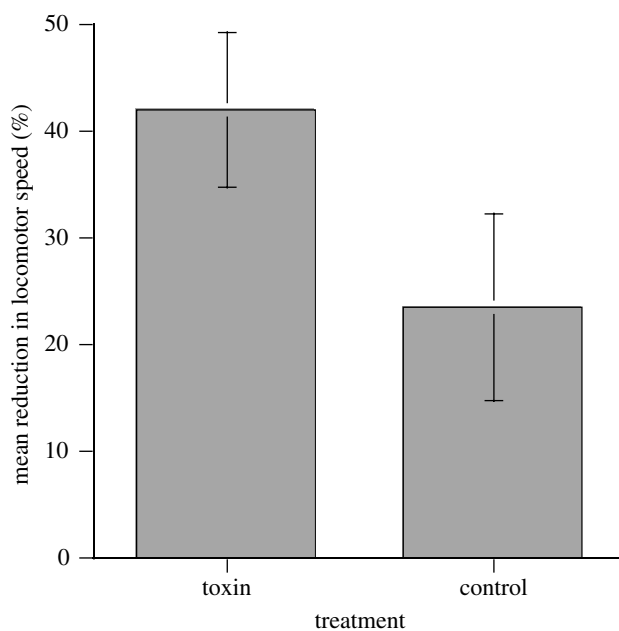


Figure 5. The effect of repeated doses of toxin on toxin resistance. A large percentage represents a low resistance. Hence, repeated doses of toxin tend to decrease a snake's resistance (albeit, non-significantly). Error bars represent a single standard error.

resistance and learning experiments mimic reality (i.e. have we given the snakes a realistic opportunity to express plasticity?). In designing these experiments we operated under the premise that most black snakes will be unlikely to survive even a single encounter with a large toad (Phillips *et al.* 2003; W. Seabrook & M. Fitzgerald 1996, unpublished work; R. Shine 2003, unpublished work). Any black snake that eats a large toad is likely to die. The window of sub-lethal toxin effect is relatively narrow (Phillips *et al.* 2003), such that few toads will be large enough to cause illness but small enough to be non-lethal. Because it is unlikely, therefore, that an individual snake will have several chances to learn avoidance, our learning experiment was based on a single noxious encounter. The fact that black snakes did not learn to avoid the toxic prey is surprising in that Burghardt *et al.* (1973) and Terrick *et al.* (1995) elicited learnt aversion in garter snakes (*Thamnophis*) after a single toxic encounter. Garter snakes are often sympatric with dangerously toxic newts and may have evolved this response to toxic prey (Brodie & Brodie 1999). In contrast, black snakes are not known to be sympatric with any naturally occurring, dangerously toxic prey and thus may have been under little or no selection to learn avoidance. It remains possible, however, that some cue specific to toads could increase a snake's tendency to learn avoidance (much as aposematic coloration appears to enhance learned avoidance in gartersnakes: Terrick *et al.* 1995). If this is the case, learning could occur but our experiment would not elicit it. Given that Australian snakes have no evolutionary history with toads or their toxins, and that toads are not aposematically coloured, it seems unlikely that a toad-specific cue would increase learning ability. Hence, given the apparent inability of naïve black snakes to learn avoidance despite a near-lethal encounter, the observation of strong differences in prey preference between toad-naïve and toad-exposed populations implies the impact of selection.

While most snakes probably experience only a single chance with a large toad, it is possible that they will consume several small toads with minimal ill effect and acquire an increased level of resistance through an immune or other physiological response. The acquired resistance experiment thus exposed snakes to four sub-lethal doses. One month after these dosings, toxin-exposed snakes were no better equipped to deal with toad toxin. Again, this result suggests that the differences between exposed and naive populations are the result of selection.

Given that we have selection, has there been an evolutionary response? Our data on toxin resistance suggest a steady increase in toxin resistance with time since exposure (figure 3), a pattern consistent with a response to selection. The data on prey preference, however, contained no variation within exposed populations (no toad-exposed snakes ate a toad) and so we are unable to infer a gradual shift in this trait. So, for prey preference at least, the possibility remains that exposed populations could be undergoing selection every generation, without response. Such a situation would require either zero heritability for prey preference or strong genetic constraints on prey preference because of genetic correlations with other traits (Merila *et al.* 2001; Blows & Hoffmann 2005). We consider these conditions unlikely for two reasons. First, prey preference has a highly heritable basis in garter snakes (Arnold 1981, 1992) and so it seems likely that this trait will also have high heritability in black snakes. Certainly, our naive snakes exhibited variability in their tendency to eat toads (only half of the naive snakes consumed a toad; figure 1), suggesting variance at this trait. Second, toads represent a very strong and completely novel selective force on black snake populations. The most general explanation for a true lack of heritability in large populations, even in multivariate trait space, is that selection has already used up most of the available variance (Fisher 1930; Gustafsson 1986; Merila & Sheldon 2000; Blows & Hoffmann 2005). The arrival of toads, however, probably represents a radical shift in selection pressure, such that equilibrational selection pressures are likely to be swamped by the new effect. Selection will be operating in a wholly new direction and any deviation from equilibrational selection is more likely to have some heritable variance with which to work.

It is important to note, however, that the shift in prey preference indicates either a congenital disposition to avoid toads or an evolved ability to learn from a single noxious encounter. The heritability of learning ability has never been measured in snakes and we detected little variation in this trait in naive populations of black snakes (although our sample sizes were small). Further work exploring the basis of the change in prey preference would be enlightening.

In light of the prey preference results (no snake from toad-exposed areas consumed a toad), it superficially seems paradoxical that we also detected evidence of selection on toxin resistance. This difference may be the result of historically strong selection when toads first arrived and toad-avoidance had yet to become fixed (or nearly fixed) in the population. Alternatively, if the prey preference result reflects an evolved ability to learn avoidance of toxic prey, there may be ongoing selection on toxin resistance. A third possibility is that spatial and temporal variation in relative prey abundances and/or levels of snake preadaptation might also lead to concurrent evolution in resistance and prey preference

(Brodie & Brodie 1999; Gomulkiewicz *et al.* 2000). Clearly, we cannot discriminate between these possibilities here and future work will be necessary.

In fact, systems such as this—where a novel species strongly interacts with a native—promise to be particularly useful for examining the formation of coevolutionary interactions and geographical mosaics (Gomulkiewicz *et al.* 2000; Brodie *et al.* 2002). For example, our recent work documents a reduction in the relative head size of black snakes (and hence their ability to eat large prey items) as a consequence of exposure to toads (Phillips & Shine 2004). Thus it appears that black snakes show adaptive change at multiple traits in response to the presence of toads. Given that the generation time of black snakes is approximately 3 years (Shine 1978) and that toads have only been present in Australia for 67 years prior to our study, these adaptive changes have occurred remarkably quickly (in fewer than 23 generations). Furthermore, toads have now been shown to exhibit directional change in traits that mediate their toxicity to snakes. Both toad body size and relative toxicity appear to be decreasing as a consequence of time since colonization (Phillips & Shine 2005). Therefore, while snakes appear to be becoming better equipped to deal with toads, toads are independently becoming less dangerous to snakes. In total, these results emphasize that it is critical to consider the potential for adaptation when predicting the long-term impact of environmental change (Stockwell & Ashley 2004). Our results also highlight the value of invasive species systems for understanding the genesis of coevolution (e.g. Brockhurst *et al.* 2003; Forde *et al.* 2004).

The current study demonstrates an adaptive response by a native species to an impact of conservation concern from an invasive. Invasive species are already on a growing list of environmental changes to which adaptive response has been demonstrated (Stockwell *et al.* 2003). The challenge remains to determine which classes of environmental change encourage adaptation rather than extinction, and which species are likely to mount adaptive responses. Answering these questions will give us a truly long-term perspective with which to prioritise conservation efforts.

This study would not have been possible without the assistance of many people in the collection of snakes (a difficult undertaking in toad-exposed areas). Foremost among these is Ian Jenkins with additional help from Eric Bateman, Julie Dickson, David Fouche, Richard Ghamroui, Jeff Hayter, Andrew Hugall, Ray Jones, Michael Kearney, Amanda Lane, Clare Morrison, Adnan Moussalli, Luke Shoo, Devi Stuart-Fox, Eric Vanderduys and Michael Wall. Steve Phillips and Jai Thomas assisted with husbandry and maintenance. The manuscript was improved by comments from E. D. Brodie and two anonymous reviewers. Funding was provided by grants from the Australian Research Council (to R.S.), The Royal Zoological Society of NSW, The Royal Linnean Society of NSW and the Norman Wettenhall Foundation (to B.L.P.).

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