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FEATURED STUDENT RESEARCH PAPER

Invasion of cane toads (*Rhinella marina*) affects the problem-solving performance of vulnerable predators (monitor lizards, *Varanus varius*)

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Abstract

Variation in morphological, genetic, or behavioural traits within and among native species can modify vulnerability to impacts from an invasive species. If an individual's vulnerability depends upon its cognitive performance, we may see adaptive shifts in cognitive traits post-invasion. Commonly, animals with enhanced cognitive abilities perform better in novel tasks, often by prioritising decision accuracy over decision speed. In eastern Australia, giant monitor lizards (*Varanus varius*) are fatally poisoned if they ingest invasive cane toads (*Rhinella marina*), but vulnerability is lower for individuals that carefully evaluate the novel prey type before swallowing it. To test if toad-imposed selection for neophobia and caution affected cognitive performance, we tested free-ranging monitors with a device that required lizards to manipulate the apparatus in order to obtain food. Success at accomplishing that task, and the speed of that success, was lower and slower in lizards from long-colonised sites than from uninvaded sites. Our results suggest that toad invasion has modified cognitive phenotypes within populations of this apex predator, a change that might have substantial effects on other species.

Significance statement

Many studies of the impacts of biological invasions focus on the numerical effect of an invader on the abundances of native taxa, neglecting other types of impacts. Colonising taxa can also impose selection on behavioural traits of native species, generating shifts in behaviour as native taxa adapt to intruders. Such shifts in behaviour are interesting not only in their own right but also because such shifts (especially in apex predators) may influence other taxa within food webs. Importantly, the nature and magnitude of such shifts may change over time post-invasion.

Keywords Prey acquisition task · Behavioural flexibility · *Bufo* · Reptile cognition

Introduction

Biological invasions can pose novel challenges for native taxa, exerting powerful selective forces on a wide range of behavioural as well as physiological and morphological traits (Strauss et al. 2006; Berthon 2015). For example, the arrival of a novel invasive predator may select for an ability of native prey to detect and avoid cues produced by that predator (Bourdeau et al. 2013), whereas the arrival of a novel invasive prey may select for an ability to detect and willingness to consume that prey type (Barber et al. 2008). Adaptive shifts in antipredator or foraging tactics by native species, in turn, may influence interactions of the affected species with other organisms within food webs (David et al. 2017). Such effects may be especially strong if the native taxon that is affected is an apex predator that imposes top-down regulation of smaller species (Doody et al. 2012). For example, increased or decreased neophobia of predators due to an invasive species might influence both feeding rates and prey selection (Nersesian et al. 2011). More generally, an invader may induce adaptive shifts in the cognitive skills and tactics of a predator (Caller and Brown 2013).

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One type of threat posed by an invasive species is that of lethal toxic ingestion, if the new arrival possesses chemical defences fatal to native predators lacking a history of sympatry (and hence, coevolution) with the invader or its relatives (Marshall et al. 2018). One intensively studied example of such an impact involves the continuing spread of cane toads (*Rhinella marina*) through Australia (Shine 2010; Tingley et al. 2017). The bufadienolide defensive chemicals of toads are fatal to predators that lack an evolutionary history of sympatry with these anurans (Shine 2010; Pinch et al. 2017). In Australia, the arrival of toads has caused dramatic population declines (sometimes > 90%) in populations of vulnerable predators such as quolls, crocodiles, snakes, and lizards (Letnic et al. 2008; Shine 2010). However, populations of some of the affected predators are buffered from that impact through taste aversion, whereby they refuse to consume toads as prey as a result of learning (O'Donnell et al. 2010) or adaptation (Phillips and Shine 2004). Importantly, that refusal to consume toads may be part of a broader suite of behavioural changes, whereby a wide range of stimuli elicit a more cautious predator approach than was previously the case. For example, exposure to toad larvae induced predatory fish to cease consuming the larvae of native anurans as well (Nelson et al. 2010), and exposure to metamorph toads induced carnivorous marsupials (planigales) to assess other prey types more carefully before launching an attack (Webb et al. 2008). Other predatory fish not only learned to avoid toxic toad larvae, but showed rapid evolution of aversion learning capacity, performing better in trials with novel aversive stimuli as well as with toads (Caller and Brown 2013).

Although learnt avoidance of prey is a common behavioural response to the arrival of a toxic invasive species, are other behavioural traits modified also? In the case of apex predators, does the arrival of a toxic invasive species alter attack strategies and/or cognitive skills? Lizards of the family Varanidae (monitor lizards, "goannas") are apex predators across much of Australia (Sutherland et al. 2011) and appear to have more advanced cognitive skills than do most other reptiles, with captive specimens rapidly learning complex tasks (e.g., Manrod et al. 2008; Cooper et al. 2019). Also, a single population of varanids may contain individuals with a wide variety of "personality" types that differ along continua such as boldness-shyness, activity levels and neophobia (Ward-Fear et al. 2018) that affect a variety of ecological traits including an individual's vulnerability to invasive toads (Ward-Fear et al. 2020). Hence, selection imposed by the toad invasion might alter the distribution of behavioural phenotypes, and hence ability to solve a standardised cognitive challenge.

Previous studies have identified a correlation between cognitive ability and improved performance in novel tasks in a range of taxa (Sol et al. 2005) including reptiles (Amiel et al. 2011; Szabo et al. 2020). Commonly, higher cognitive performance translates into an enhanced ability to solve novel problems. For varanid lizards at the toad invasion front, the challenge is to detect the novel invader when it is first encountered, determine that it is toxic, and respond appropriately by avoiding consuming it and all conspecifics on future encounters. If cognitive ability is linked to lizard survival following the invasion of cane toads, we would expect to see lizards that can detect and avoid cane toads persisting through time, while lizards lacking the cognitive capacity to discriminate and avoid the toxic prey item would be removed from the population.

To explore this possibility, we designed a novel testing apparatus to assess problem-solving skills in these giant lizards, and we monitored the interactions between lizards and this apparatus in a wide range of sites encompassing areas with and without invasive cane toads. We predicted that the arrival of cane toads would select for lizards that had higher cognitive ability, such that lizards in toad-present areas would be more likely to solve the puzzle, and would do so faster than lizards from areas without toads.

Methods

Study animals

Cane toads (*Rhinella marina*) are large bufonid anurans native to a wide area of South America (Zug and Zug 1979). Released in north eastern Australia in 1935 as a biological control, toads have now expanded their range across many tropical and subtropical areas of that continent (Urban et al. 2007). Many native predators are physiologically unable to deal with the toad's potent toxins (Phillips et al. 2003; Pinch et al. 2017), and experience high levels of mortality following the arrival of toads (Ujvari and Madsen 2009; Ward-Fear et al. 2016).

The lace monitor (*Varanus varius*) is one of the world's largest lizards (exceeding 200 cm total length, 14 kg mass (Weavers 1988), and is abundant in open woodland habitats along eastern Australia (Vincent and Wilson 1999; Cogger 2014). This semi-arboreal apex predator and scavenger has a generalist diet, including anurans (Vincent and Wilson 1999; Cogger 2014). Lace monitors actively hunt using a range of sensory stimuli to locate food items, and commonly forage by dexterously clawing at burrows, logs, or crevices to extract prey (De Lisle 1996). Lace monitors are capable of learning to avoid toxic prey after a single encounter (Jolly et al. 2016), and in populations with a long history of sympatry with toads, the monitors exhibit a strong avoidance response to the toxic anuran (Pettit et al. 2020).

Site descriptions

We tested lace monitors from 17 populations along the east coast of Australia between October 2017 and April 2018, and again in March 2020. Six of these sites are yet to be invaded by cane toads, while the eleven other sites had been invaded for between 1 and 80 years at the time of our experiments (Fig. 1). Collectively, these sites encompass the complete cane toad invasion chronosequence in Australia.

Chronology of the cane toad invasion

Extensive monitoring of the cane toads' recent southerly advance in New South Wales allows precise estimation of invasion chronology in southern sites (Jolly et al. 2015). We used ARCGIS (version 10.5) to establish the year in which toads earlier invaded sites in Queensland. Records of the occurrence of cane toads were retrieved from the Atlas of Living Australia database. A 20 km radial buffer zone was established around each site and the earliest occurrence record within each buffer zone was extracted to provide a conservative estimate of toad arrival.

Problem-solving trial

We measured lizard responses to a novel prey acquisition task focused on a trial apparatus (puzzle) consisting of a PVC tube (28 cm high, diameter 16 cm) with a 9 × 12 cm window on the side of the tube. A PVC cylindrical sleeve on the outside of this tube could be rotated freely in either direction. The sleeve had two windows of the same size as the tube but positioned 180° apart. One sleeve window was covered with wire mesh while the other was unobstructed (Fig. 2).

We placed 10 chicken necks (approx. 220 g) inside the tube and aligned the mesh-covered window of the outer sleeve with the open window of the tube. The mesh allowed visual and scent cues, but physical access to the bait could be achieved only by rotating the outer sleeve 180° to align the open sleeve window with the open tube window. A motion-sensing camera (Scoutguard SG560K) was trained on the puzzle to record goanna responses in a series of 1-minute videos.

We deployed one or three puzzles for 48–72 h at 17 sites (6 toad-absent and 11 toad-present). Over the course of the study we increased the number of puzzles deployed (spaced approximately 50 m apart) in an attempt to target multiple individuals in high-density areas. A trial was initiated when a lizard triggered the remote camera and approached to within 30 cm of

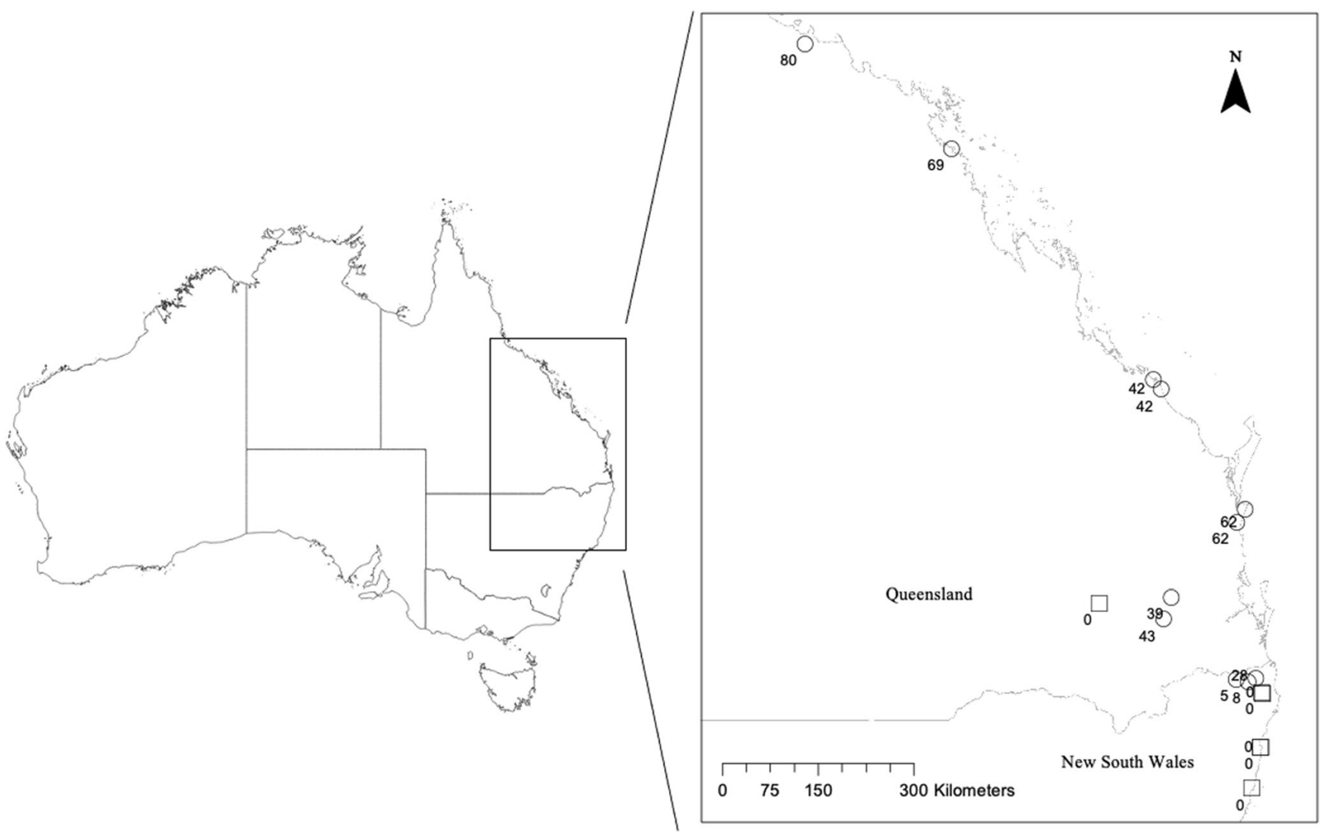

Fig. 1 Study sites in which we assessed the behaviour and cognition of lace monitors (*Varanus varius*) in areas with (circles) and without (squares) cane toads (*Rhinella marina*). Numbers represent the number of years for which cane toads have been present at each site

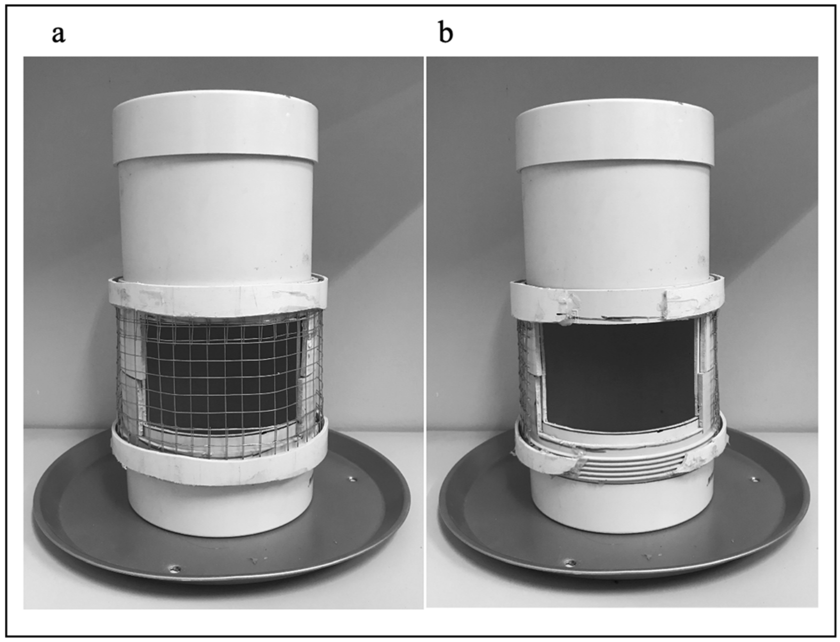

Fig. 2 Photos of the prey acquisition apparatus used in this study, showing the puzzle with the **a** outer sleeve in the closed position, and **b** with the outer sleeve rotated 180° in the solved position

the puzzle and concluded when 30 minutes had elapsed. As some lizards interacted with the puzzle sporadically (i.e., multiple short-duration visitations), we calculated the cumulative time that each lizard spent at puzzles for our measures of puzzle success. The puzzle was periodically checked (~ every three hours), and if solved it was refreshed with bait and reset.

We reviewed the videos to identify individual lizards (based on body size, patterning and tail condition), estimate the size of each animal (snout-vent length, SVL; measured to the nearest 50 mm), score if the problem was solved (yes/no), and record the time from initial engagement with the puzzle until it was solved. It was not possible to record data blind because our study involved focal animals in the field.

Analyses

We used generalised linear models (GLM) with a binomial distribution and logit link function to investigate if the number of years since toads invaded (continuous variable), the body size (SVL) of a lizard (continuous variable), and their interactions, predicted if a lizard could solve the puzzle. Years since toad invasion and lizard SVL were used as the predictor variables, with the outcome of the trial (solved or did not solve) as the response variable.

We used a GLM with a normal distribution and log link to test if the latency of lizards to solve the problem changed with the duration of toad invasion. Years since toad invasion, lizard body size, and their interaction were used as predictors, with the latency to solve the puzzle as the response variable.

All analyses were conducted in JMP Pro (v14.2). Where appropriate, Levene's test was used to test for equality of variances, while normality was assessed visually.

Results

Thirty individual lace monitors (16 from toad-free sites, and 14 from toad-present sites ranging from 5 to 62 years invaded) from 10 sites (5 uninvaded, 5 invaded) engaged with the puzzle. Of the 30 lizards that interacted with the puzzle, 16 successfully manipulated the puzzle and retrieved baits (see supplementary material for videos of lizards interacting with puzzles). Of these 16 animals, 14 succeeded on their first attempt. The proportion of lizards that successfully solved the puzzle declined with the number of years since toads invaded (GLM χ^2_1 = 6.05, P = 0.014; Fig. 3). There was a significant main effect of lizard body size (larger lizards had higher success rates; χ^2_1 = 5.12, P = 0.024), but the interaction

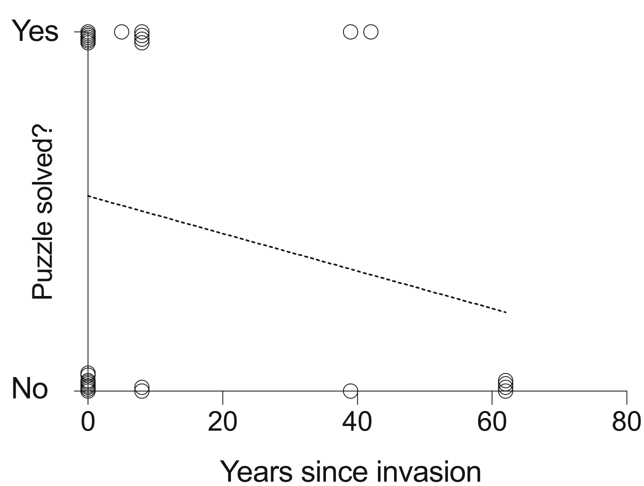

Fig. 3 The proportion of lace monitors (*Varanus varius*) that solved a novel prey acquisition task as a function of the number of years since the site was invaded by cane toads (*Rhinella marina*)

between years since toad invasion and body size was not significant ($\chi^2_1 = 0.80$, $P = 0.37$).

Three lizards successfully solved the puzzle within one minute, whereas the slowest lizard to solve the puzzle spent over 20 minutes to reach the bait. Among the 16 successful lizards, the time taken to complete the puzzle differed significantly with time since toad invasion (GLM $\chi^2_1 = 10.03$, $P = 0.0015$; Fig. 4) but was not affected significantly by lizard body size ($\chi^2_1 = 0.60$, $P = 0.81$), nor by the interaction between the number of years since toads invaded and body size ($\chi^2_1 = 1.28$, $P = 0.26$).

Discussion

Our study is one of the first to measure problem-solving ability of reptiles in a field context (but see; Storks and Leal 2020). Although field-based studies introduce many confounding factors (e.g., variable site-specific differences), they can also provide a more realistic study system by eliminating many of the artifacts, stresses and biases associated with laboratory studies. Our results indicated an effect of toad invasion on problem-solving success, but not in the direction that we had expected. In the rainbowfish studied by Caller and Brown (2013), sympatry with invasive cane toads was associated with an increase in the capacity for aversion learning. In strong contrast, the lizards that we studied exhibited a decline, not an increase in the ability to solve a novel problem. That decline was evident both in the proportion of lizards that solved the problem, and in the time taken to do so for the successful lizards.

The reduction in success rates of lizards interacting with our puzzle likely reflects intense selection on behavioural phenotypes as a consequence of cane toad invasion. The individual varanids most at risk of lethal toxic ingestion are large bold lizards that do not carefully assess prey items prior to ingestion

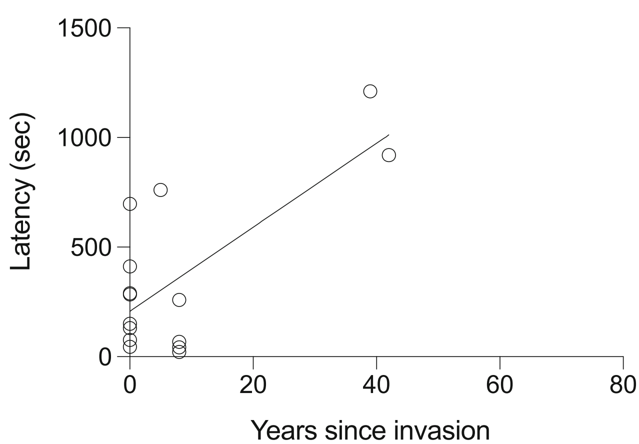

Fig. 4 The mean time required by lace monitors (*Varanus varius*) to solve a novel prey acquisition task as a function of time since invasion of the site by cane toads (*Rhinella marina*)

(Jolly et al. 2016; Ward-Fear et al. 2018). As these individuals are fatally poisoned, an increasing proportion of the varanid population post-invasion consists of smaller and shyer animals (as inferred from approach distances; Pettit et al. in press). Such animals may not be as willing to engage vigorously with the test apparatus as were their toad-vulnerable conspecifics. Thus, the primary driver of our results may not be that toad-sympatric varanids have weaker cognitive skills; instead, it may be that they adopt a more cautious approach. Such a shift would be consistent with the "pace of life" (POL) hypothesis, whereby selection has favoured individuals that are less bold, impulsive and risk-prone, and prioritise safety and eventual accuracy against the speed at which a task is completed (Réale et al. 2010). The shift we see thus may be in tactics rather than cognitive skills.

Regardless of the proximate mechanisms responsible for the shift that we have documented, such a change in foraging-associated behaviour of an apex predator may have substantial cascading effects on other species. Thus, for example, a population of shyer lizards may spend less time in exposed habitats (Carter et al. 2010), or may be less willing to attack novel prey types (Ward-Fear et al. 2018). Consequent shifts in the composition of the diet and the rate of feeding might affect smaller species in a variety of ways, and could either increase or decrease their numbers (Royauté and Pruitt 2015). More generally, a biological invasion can affect an ecosystem not simply by changing the numerical abundance of an apex predator, but also by modifying the ways in which those animals seek their food. In the system that we studied, the invasion of cane toads appears to have profoundly affected the behaviour of lace monitors (e.g., boldness, habitat use, engagement with a novel puzzle; (Pettit et al. in press; LP et al. unpubl. data), but with little overall effect on the abundance of the monitor species (LP et al. unpubl. data). As a result, a lack of numerical impact of an invader on a native taxon may not mean a lack of biologically significant effects.

Although our results are encouraging in respect to the feasibility of studying cognitive skills of free-living lizards, future studies could quantify problem-solving success on a wide variety of tasks, and do so repeatedly with the same individuals to explore the influence of learning (Szabo et al. 2018). Future work could also more carefully control issues such as ambient conditions (weather) and motivation (hunger), and explore additional questions such as the possibility of cultural learning (by observing conspecifics solving a problem; Kis et al. 2015).

Individuals with a higher capacity to learn, or those that make fast and accurate decisions, generally are thought to deal better with novel threats than do conspecifics exhibiting slow decision-making or inflexible behaviour (Amiel et al. 2011; Szabo et al. 2020). This may be true in dynamic contexts where decision speed is favoured over decision accuracy (e.g., where an animal must respond quickly to multiple threats in rapidly changing urban environments; Batabyal and Thaker 2019). However, slow-moving cane toads represent a different class of threat, where the advantages of decision accuracy (or being so inflexible as to avoid the threat altogether) may outweigh the benefits of making a rapid decision. In our system, we detected a significant decrease in the problem-solving performance of anurophagous lizards following toad invasion, suggesting that behavioural traits that facilitate problem-solving (at least on the task that we provided) reduce rather than enhance individual fitness when toads invade.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-02978-6.

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Author contribution LP designed the study, performed all fieldwork, conducted the statistical analyses, and drafted the manuscript. GWF designed the study and critically revised the manuscript. RS conceived and designed the study, and critically revised the manuscript. All authors gave final approval for publication.

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Data availability Data are available from the Figshare repository: 10.6084/m9.figshare.12863993.

Compliance with ethical standards

Ethics approval All procedures were approved by the University of Sydney ethics committee (approval 2017/1202) and were carried out in accordance with relevant guidelines and regulations under licence from state and federal wildlife agencies.

Conflict of interest The authors declare no competing interests.

References

Amiel JJ, Tingley R, Shine R (2011) Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. PLoS ONE 6:e18277

Barber NA, Marquis RJ, Tori WP (2008) Invasive prey impacts the abundance and distribution of native predators. Ecology 89:2678–2683

Batabyal A, Thaker M (2019) Lizards from suburban areas learn faster to stay safe. Biol Lett 15:20190009

Berthon K (2015) How do native species respond to invaders? Mechanistic and trait-based perspectives. Biol Invasions 17:2199–2211

Bourdeau PE, Pangle KL, Reed EM, Peacor SD (2013) Finely tuned response of native prey to an invasive predator in a freshwater system. Ecology 94:1449–1455

Caller G, Brown C (2013) Evolutionary responses to invasion: cane toad sympatric fish show enhanced avoidance learning. PLoS ONE 8: e54909

Carter AJ, Goldizen AW, Tromp SA (2010) Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. Behav Ecol 21:655–661

Cogger H (2014) Reptiles and amphibians of Australia. CSIRO publishing, Collingwood, Victoria

Cooper T, Liew A, Andrle G et al (2019) Latency in problem solving as evidence for learning in varanid and helodermatid lizards, with comments on foraging techniques. Copeia 107:78–84

David P, Thébault E, Anneville O, Duyck PF, Chapuis E, Loeuille N (2017) Impacts of invasive species on food webs. In: Bohan D, Dumbrell A, Massol F (eds) Networks of invasion: a synthesis of concepts. Academic Press, London, pp 1–60

De Lisle HF (1996) The natural history of monitor lizards. Krieger, Malabar, FL

Doody JS, Castellano CM, Rhind D, Green B (2012) Indirect facilitation of a native mesopredator by an invasive species: are cane toads reshaping tropical riparian communities? Biol Invasions 15:559–568

Jolly CJ, Shine R, Greenlees MJ (2015) The impact of invasive cane toads on native wildlife in southern Australia. Ecol Evol 5:3879–3894

Jolly CJ, Shine R, Greenlees MJ (2016) The impacts of a toxic invasive prey species (the cane toad, *Rhinella marina*) on a vulnerable predator (the lace monitor, *Varanus varius*). Biol Invasions 18:1499–1509

Kis A, Huber L, Wilkinson A (2015) Social learning by imitation in a reptile (*Pogona vitticeps*). Anim Cogn 18:325–331

Letnic M, Webb JK, Shine R (2008) Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. Biol Conserv 141:1773–1782

Manrod JD, Hartdegen R, Burghardt GM (2008) Rapid solving of a problem apparatus by juvenile black-throated monitor lizards (*Varanus albigularis albigularis*). Anim Cogn 11:267–273

Marshall BM, Casewell NR, Vences M, Glaw F, Andreone F, Rakotoarison A, Zancolli G, Woog F, Wuster W (2018) Widespread vulnerability of Malagasy predators to the toxins of an introduced toad. Curr Biol 28:R654–R655

Nelson DWM, Crossland MR, Shine R (2010) Behavioural responses of native predators to an invasive toxic prey species. Austral Ecol 36: 605–611

Nersesian CL, Banks PB, McArthur C (2011) Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. Behav Ecol Sociobiol 66:47–55

O'Donnell S, Webb JK, Shine R (2010) Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. J Appl Ecol 47:558–565

Pettit L, Ward-Fear G, Shine R (2020) To coexist with a toxic invader, choose your meals carefully. Sci Rep 10:21866

Pettit L, Ward-Fear G, Shine R (in press) Anthropogenically disturbed habitats contain bigger and bolder reptilian predators. Ecol Evol

Phillips BL, Brown GP, Shine R (2003) Assessing the potential impact of cane toads on Australian snakes. Conserv Biol 17:1738–1747

Phillips BL, Shine R (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. P Natl Acad Sci USA 101:17150–17155

Pinch K, Madsen T, Ujvari B (2017) No signs of Na+/K+-ATPase adaptations to an invasive exotic toxic prey in native squamate predators. Austral Ecol 42:929–933

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. Phil Trans R Soc B 365: 4051–4063

Royauté R, Pruitt JN (2015) Varying predator personalities generates contrasting prey communities in an agroecosystem. Ecology 96: 2902–2911

Shine R (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. Q Rev Biol 85:253–291

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. P Natl Acad Sci USA 102:5460–5465

Storks L, Leal M (2020) Thinking outside the box: problem-solving in free-living lizards. Behav Ecol Sociobiol 74:75

Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol Lett 9:357–374

Sutherland DR, Glen AS, de Tores PJ (2011) Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? Phil Trans R Soc B 278:641–648

Szabo B, Damas-Moreira I, Whiting MJ (2020) Can cognitive ability give invasive species the means to succeed? A review of the evidence. Front Ecol Evol 8:187

Szabo B, Noble DWA, Byrne RW, Tait DS, Whiting MJ (2018) Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility? Anim Behav 144: 17–26

Tingley R, Ward-Fear G, Schwarzkopf L, Greenlees MJ, Phillips BL, Brown G, Clulow S, Webb J, Capon R, Sheppard A (2017) New weapons in the Toad Toolkit: a review of methods to control and mitigate the biodiversity impacts of invasive cane toads (*Rhinella marina*). Q Rev Biol 92:123–149

Ujvari B, Madsen T (2009) Increased mortality of naive varanid lizards after the invasion of non-native can toads (*Bufo marinus*). Herpetol Conserv Biol 4:248–251

Urban MC, Phillips BL, Skelly DK, Shine R (2007) The cane toad's (*Chaunus [Bufo] marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. Phil Trans R Soc B 274:1413–1419

Vincent M, Wilson S (1999) Australian goannas. New Holland, Frenchs Forest, NSW

Ward-Fear G, Brown GP, Pearson DJ, West A, Rollins LA, Shine R (2018) The ecological and life history correlates of boldness in free-ranging lizards. Ecosphere 9:e02125

Ward-Fear G, Brown GP, Shine R (2020) Predators learning to avoid toxic prey: a study on individual variation among free-ranging lizards. Behaviour 157:1153–1172

Ward-Fear G, Pearson D, Brown G, Rangers B, Shine R (2016) Ecological immunization: in situ training of free-ranging predatory lizards reduces their vulnerability to invasive toxic prey. Biol Lett 12:20150863

Weavers BW (1988) Vital statistics of the lace monitor lizard (*Varanus varius*) in south-eastern Australia. Vic Nat 105:142–145

Webb JK, Brown GP, Child T, Greenlees MJ, Phillips BL, Shine R (2008) A native dasyurid predator (common planigale, *Planigale maculata*) rapidly learns to avoid a toxic invader. Austral Ecol 33: 821–829

Zug GR, Zug PB (1979) The marine toad, *Bufo marinus*: a natural history resume of native populations. Smithsonian Institution Press, Washington DC