

Larval interactions with an invasive species (the Cane Toad *Rhinella marina*) affect life-history traits in an Australian anuran (the Marbled Frog *Limnodynastes convexiusculus*)

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ABSTRACT

The viability of a metamorph anuran can be influenced by its body size and the time it has taken to complete larval development. In a laboratory experiment, we show that the presence of tadpoles of the invasive Cane Toad *Rhinella marina* causes tadpoles of a native frog (Marbled Frog *Limnodynastes convexiusculus*) to metamorphose later and at smaller sizes. These effects may render frog metamorphs more vulnerable to desiccation and predation, but render them less vulnerable to Cane Toads. Marbled Frogs prey upon other anurans, including the highly toxic Cane Toad metamorphs. Small, late-emerging metamorph frogs are unlikely to encounter metamorph toads small enough to ingest; and hence, are less likely to be fatally poisoned by consuming the toxic invader. Developing in the presence of larval Cane Toads thus increases the native taxon's ability to survive the presence of toads post-metamorphosis. Predicting the ecological impacts of an invasive species on native taxa with biphasic life histories (such as most anurans) thus requires information on interactions in both aquatic and terrestrial environments. The expression of phenotypic plasticity in one phase may influence fitness in a subsequent phase, in complex and non-intuitive ways.

Key words: Bufonidae, competition, Limnodynastidae, metamorphosis, phenotypic plasticity, *Bufo marinus*, tadpole

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Introduction

Understanding the mechanisms by which invasive species affect native taxa can help us to predict and mitigate such effects, but the challenge is formidable. Such impacts result from a diverse array of mechanisms, including predation, competition and pathogen transfer (Eastwood *et al.* 2007; Salo *et al.* 2007; Bohn *et al.* 2008), and often, a single invader can affect native taxa in more than one way (Kiesecker and Blaustein 1997; Boland 2004; Geiger *et al.* 2005). Adding to this complexity, invaders can induce shifts in behaviour or life-history traits in the native fauna (Blanchet *et al.* 2007; Greenlees *et al.* 2007; Hoare *et al.* 2007), so that impacts are mediated by such reaction norms (Strauss *et al.* 2006; Carroll 2007) and finally, mechanisms of impact, and the fitness consequences of interactions, may differ between life-history stages. For example, Cane Toads *Rhinella marina* are preyed upon by a native taxon (Meat Ants *Iridomyrmex reburrus*) during the metamorph phase, compete with Meat Ants during the sub-adult phase, and eat Meat Ants during the adult phase (Lever 2001; Greenlees *et al.* 2006; Pizzatto and Shine 2008; Ward-Fear *et al.* 2009). In species with multi-phasic life histories, such ontogenetic shifts in mechanisms and outcome of impact are most likely where ecological and morphological divergences between larvae and adults are profound (Wilbur and Collins 1973; Wilbur 1980).

We have studied a system that incorporates all of these complexities. The rapid spread of invasive Cane Toads *Rhinella marina* through tropical Australia has resulted in the deaths of many native predators through lethal ingestion of these toxic invaders (Griffiths and McKay 2007; Letnic *et al.* 2008; Phillips *et al.* 2010). Native anurans are frequent victims in this respect (Crossland *et al.* 2008; Crossland and Shine 2010). Cane Toads also produce large clutches of eggs in waterbodies used as breeding sites by native anurans, generating a range of interactions among larvae (Williamson 1999; Crossland 2000; Crossland *et al.* 2009). In light of recent studies showing that smaller body size enhances a metamorph frog's chances of surviving an interaction with a metamorph Cane Toad (Greenlees *et al.* 2010a), we conducted a simple experimental trial to determine whether the presence of toad tadpoles induce life-history shifts in native frogs in ways that might influence frog fitness in subsequent encounters with toads during the terrestrial phase of the life-history.

Methods

Study area and animals

We studied anurans on the Adelaide River floodplain in the Australian wet-dry tropics, 60 km east of Darwin (Northern Territory: 131°18'48.19" E, 12°34'14.81" S). The

climate is hot year-round (mean monthly maxima $>30^{\circ}\text{C}$ in all months), but $>75\%$ of the 1400 mm annual rainfall occurs in the monsoonal wet season (December–March: based on readings taken from Middle Point, less than 5 km from the study site; Bureau of Meteorology 2009). Most breeding by native anurans in this area occurs during the wet season (Tyler *et al.* 1983). Cane Toads and Marbled Frogs (*Limnodynastes convexiusculus*) often breed in the same ponds at the same time (Crossland *et al.* 2008).

Collection, husbandry and experimental design

We collected 10 clutches of Marbled Frog eggs from a temporary pond ($131^{\circ}18'46.74''\text{ E}$, $12^{\circ}34'15.33''\text{ S}$) on 27 February 2007, the morning after they were deposited. The clutches were taken to our research facility less than 5 km from the collection site, and all clutches hatched within three days. Frog eggs and tadpoles were housed in an open-sided shed, initially in plastic containers (38 cm long x 26 cm wide x 20 cm high). Tadpoles were reared on a diet of frozen lettuce provided *ad libitum*. Water was partially changed twice weekly. On 23 May 2007, 10 tadpoles at stage 25 of development (Gosner 1960) were randomly selected from each clutch, and a tadpole from each clutch was added to each of 10 bins (60 cm long x 40 cm wide x 40 cm high, filled to 5 cm below the rim; i.e. 10 tadpoles total per container). To half of these bins (randomly selected), we added 10 Cane Toad tadpoles between Gosner stages 26–30, collected from a pond 10 km away ($131^{\circ}18'57.07''\text{ E}$, $12^{\circ}38'24.72''\text{ S}$). We used mid-stage toad tadpoles to minimise toxic effects, in case any toad tadpoles died and were consumed by frog tadpoles (Hayes *et al.* 2009). All containers contained frozen lettuce *ad libitum* as food, and water was partially changed weekly. Over the course of the experiment, water temperature ranged from 26 to 30°C . We did not include additional treatments of different densities of frog tadpoles because our aim was to simulate effects of toad invasion; at least initially, these anurans add to total anuran biomass rather than replacing native taxa (Greenlees *et al.* 2006, 2007).

Measurements and statistical analysis

Once per week, tadpoles were checked for developmental progress. Any toad tadpoles that died or metamorphosed were replaced, so that there were constantly 10 toad tadpoles in treatment tubs. We did this because our focus was to investigate the effects of Cane Toad tadpoles on Marbled Frogs, and replacement of dead or metamorphosing toad tadpoles ensured standard densities in containers. We collected metamorphosing Marbled Frogs as they emerged from experimental containers, and measured mass within two days of tail resorption. To avoid pseudoreplication, we used means of each container for duration of larval period and mass at metamorphosis in our statistical analyses. We used multivariate analysis of variance (MANOVA) to test for differences between groups raised with, versus without toad tadpoles present (see Morin 1983; Alford 1989; Knight *et al.* 2009). Three dependent variables were used: proportion surviving to metamorphosis, duration of larval period and mass at metamorphosis. When MANOVA detected a significant difference between treatments, one-way ANOVAs were used to determine the effect of the various dependent variables.

Results

Toad tadpoles were replaced in treatment tubs at an average of 3.7 per container per week. There was no significant difference among treatment containers in the rate at which they were replaced (ANOVA: $F_{4,30} = 0.24$, $P = 0.92$). The presence of Cane Toad tadpoles affected the development and phenotype of metamorphosing Marbled Frogs (MANOVA: Wilks' Lambda = 0.163, $F_{3,6} = 10.26$, $P = 0.009$). Although survival rates of frog tadpoles were not affected by the presence of Cane Toad larvae (ANOVA: $F_{1,95} = 0.00$, $P = 1.00$; Fig. 1a), Marbled Frog larvae that were raised with toad larvae took about 25 days longer to metamorphose (a 10% increase in larval duration; ANOVA: $F_{1,95} = 13.87$, $P < 0.001$; Fig. 1b) and did so at smaller body sizes (15% smaller; ANOVA: $F_{1,95} = 5.60$, $P = 0.02$; Fig. 1c).

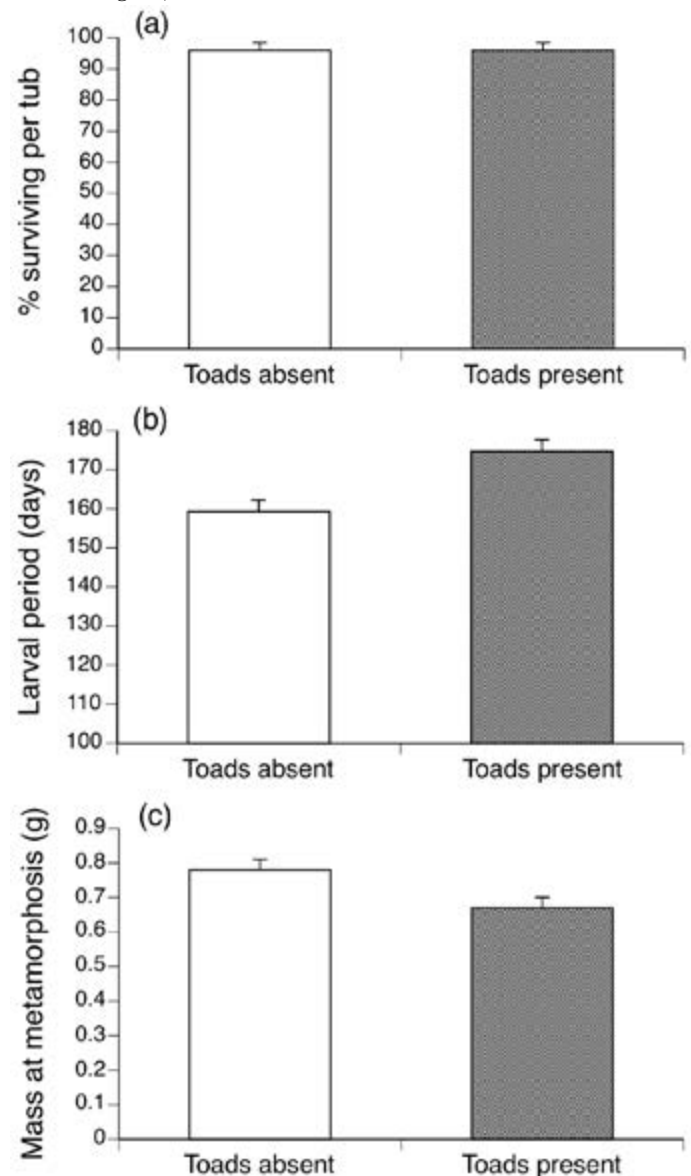


Figure 1. The effects on Marbled Frogs (*Limnodynastes convexiusculus*) of adding larvae of the invasive Cane Toad (*Rhinella marina*) to experimental containers. The presence of toad tadpoles did not affect the frog tadpole's survival rates (a), but delayed metamorphosis (b) and reduced body sizes at metamorphosis (c). Graphs show mean values per experimental enclosure, with standard errors.

Discussion

In combination with previous studies, our results reveal complex impacts of invasive Cane Toads on native frogs, with impacts of the presence of toad tadpoles during larval life inducing life-history shifts that have the potential to influence subsequent toxin-mediated interactions between terrestrial-phase frogs and toads.

An extensive literature indicates that anuran larvae are sensitive to competitive suppression by both conspecific and heterospecific tadpoles (e.g. Wilbur 1977; Katzmann *et al.* 2003; Richter-Boix *et al.* 2007), mediated not only by direct reduction in per-capita food availability (Steinwascher 1979; Dash and Hota 1980), but also via more subtle means such as response to chemical substances produced by developing larvae (Rose 1960; Licht 1967; Beebe 1991). A range of life-history shifts has been documented in response to such competitive forces, with the responses that we saw in Marbled Frogs (no change in tadpole survival, but production of small, late-emerging metamorphs) being a common outcome of larval competition between introduced and endemic larval anurans (Kupferberg 1997; Williamson 1999; Smith 2005; Knight *et al.* 2009).

Although we provided ad libitum food during the experiment, our results may have been due to subtle chemically-mediated effects as well as exploitative competition. Additionally, body sizes and developmental rates of Marbled Frog tadpoles may have been reduced by ingestion of Cane Toad toxins. During the experiment, Marbled Frog tadpoles occasionally 'nibbled' the tails of live Cane Toad tadpoles, and fed on the carcasses of dead toad tadpoles. Ingestion of toad tissue resulted in low rates of growth in snakes (Llewelyn *et al.* 2009) and in Cane Toads themselves (Pizzatto and Shine 2008). Predatory interactions between native frogs and toads can be influenced by additional factors including relative sizes of predator and prey, as well as environmental variables (Crossland and Shine 2010). Regardless of the exact mechanisms, our results clearly show that the presence of toads has significant effects on life-history traits of marbled frogs.

Both smaller size at metamorphosis, and an increase in the duration of the larval period, are generally thought to reduce metamorph viability (Berven and Gill 1983; Smith 1987). For example, Berven (1990) showed that smaller metamorphs had lower survival than larger conspecifics, and had lower fecundity as adults. Smaller metamorphs may be more vulnerable to desiccation (Child *et al.* 2009), predation (Ward-Fear *et al.* 2009), cannibalism (Pizzatto and Shine 2008) and parasite attack (Kelehear *et al.* 2009). Later emergence entails a greater risk of the ephemeral pond drying out, or the shrinking water levels exposing larvae to increased competition, predation and heat and water stress (Heyer *et al.* 1975; Wilbur 1980; Denver 1997).

If the presence of Cane Toad tadpoles in natural ponds generates small, late-emerging Marbled Frogs (as it did in our laboratory trials), the viability of metamorph frogs may be reduced by the mortality sources outlined above. However, another major source of mortality – vulnerability to fatal poisoning after ingesting a Cane Toad – may be reduced rather than increased. Frogs do die as a result of eating Cane Toads, with the danger being greatest for large metamorph frogs (because they can physically ingest a toad metamorph) and for early-emerging frog metamorphs, because they encounter very young – and hence, edible-sized – toad metamorphs (Greenlees *et al.* 2010a). Thus, emerging small and late (due to competition with Cane Toad tadpoles) means that a metamorph Marbled Frog likely will be only slightly larger than the Cane Toad metamorphs it encounters – and hence, is unlikely to attempt to eat one (Greenlees *et al.* 2010a). Smaller metamorph frogs also have more opportunity to learn not to eat toads (because they often seize toads, hold them briefly, then release them if they are too large to swallow). Such aversion learning enhances frog survival in subsequent encounters with edible-sized toads (Greenlees *et al.* 2010b).

Our results highlight how complex interactions can influence the impact of an invasive species. The presence of the invader during the larval phase induces phenotypically plastic changes to life-history traits (time and size at metamorphosis) that are likely to render the young anurans more vulnerable to some mortality sources, but less vulnerable to fatal poisoning by the toxic invader. In a somewhat analogous result, the addition of Cane Toad eggs (rather than larvae) can result in high rates of frog tadpole mortality (through fatal ingestion of toxins) but paradoxically, the resultant decrease in larval densities reduces competitive effects and results in increased rather than decreased size at metamorphosis (in the Ornate Burrowing Frog *Opisthodon ornatus*: Crossland *et al.* 2009). As in the present study, the overall impact of larval encounters thus is to change life-history traits in ways that increase mortality due to some sources, while decreasing vulnerability to other risks. Future work could focus on elucidating the specific mechanisms underlying these results and more usefully, explore the generality of such effects, conduct field studies to explore competitive effects in nature, and to directly measure the consequences of larval interactions for metamorph viability. More generally, the feedback mechanisms that link events in larval life to those in terrestrial life may determine the nature and magnitude of ecological impacts of invasive species – or other environmental changes – on taxa with multiphasic life histories.

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References

- Alford, R.A. 1989. Variation in predator phenology affects predator performance and prey community composition. *Ecology* 70: 206–219. <http://dx.doi.org/10.2307/1938427>
- Beebee, T.J.C. 1991. Purification of an agent causing growth inhibition in anuran larvae and its identification as a unicellular unpigmented alga. *Canadian Journal of Zoology* 69: 2146–2153. <http://dx.doi.org/10.1139/z91-300>
- Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71: 1599–1608. <http://dx.doi.org/10.2307/1938295>
- Berven, K.A. and Gill, D.E. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23: 85–97. <http://dx.doi.org/10.1093/icb/23.1.85>
- Blanchet, S., Loot, G., Grenouillet, G. and Brosse, S. 2007. Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. *Ecology of Freshwater Fish* 16: 133–143. <http://dx.doi.org/10.1111/j.1600-0633.2007.00205.x>
- Bohn, T., Amundsen, P.A. and Sparrow, A. 2008. Competitive exclusion after invasion? *Biological Invasions* 10: 359–368. <http://dx.doi.org/10.1007/s10530-007-9135-8>
- Boland, C.R.J. 2004. Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: observational and experimental evidence. *Biological Conservation* 120: 53–62. <http://dx.doi.org/10.1016/j.biocon.2004.01.025>
- Bureau of Meteorology. 2009. Climate records. <<http://www.bom.gov.au>> accessed 25 March 2009.
- Carroll, S.P. 2007. Natives adapting to invasive species: ecology, genes, and the sustainability of conservation. *Ecological Research* 22: 892–901. <http://dx.doi.org/10.1007/s11284-007-0352-5>
- Child, T., Phillips, B.L. and Shine, R. 2009. Does desiccation risk drive the distribution of juvenile cane toads (*Bufo marinus*) in tropical Australia? *Journal of Tropical Ecology* 25: 193–200. <http://dx.doi.org/10.1017/S0266467408005695>
- Crossland, M.R. 2000. Direct and indirect effects of the introduced toad *Bufo marinus* (Anura: Bufonidae) on populations of native anuran larvae in Australia. *Ecography* 23: 283–290. <http://dx.doi.org/10.1111/j.1600-0587.2000.tb00283.x>
- Crossland, M.R., Brown, G.P., Anstis, M., Shilton, C. and Shine, R. 2008. Mass mortality of native anuran tadpoles in tropical Australia due to the invasive cane toad (*Bufo marinus*). *Biological Conservation* 141: 2387–2394. <http://dx.doi.org/10.1016/j.biocon.2008.07.005>
- Crossland, M.R., Alford, R.A. and Shine, R. 2009. Impact of the invasive cane toad (*Bufo marinus*) on an Australian frog (*Opisthodon ornatus*) depends on reproductive timing. *Oecologia* 158: 625–632. <http://dx.doi.org/10.1007/s00442-008-1167-y>
- Crossland, M. and Shine, R. 2010. Vulnerability of an Australian anuran assemblage to the toxic eggs of the invasive cane toad (*Bufo marinus*). *Austral Ecology* 35: 197–204. <http://dx.doi.org/10.1111/j.1442-9993.2009.02027.x>
- Dash, M.C. and Hota, A.K. 1980. Density effects on the survival, growth rate, and metamorphosis of *Rana tigrina* tadpoles. *Ecology* 61: 1025–1028. <http://dx.doi.org/10.2307/1936818>
- Denver, R.J. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *American Zoologist* 37: 172–184. <http://dx.doi.org/10.1093/icb/37.2.172>
- Eastwood, M.M., Donahue, M.J. and Fowler, A.E. 2007. Reconstructing past biological invasions: niche shift in response to invasive predators and competitors. *Biological Invasions* 9: 397–407. <http://dx.doi.org/10.1007/s10530-006-9041-5>
- Geiger, W., Alcorlo, P., Batanas, A. and Montes, C. 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. *Biological Invasions* 7: 49–73. <http://dx.doi.org/10.1007/s10530-004-9635-8>
- Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183–190.
- Greenlees, M.J., Brown, G.P., Webb, J.K., Phillips, B.L. and Shine, R. 2006. Effects of an invasive anuran [the cane toad (*Bufo marinus*)] on the invertebrate fauna of a tropical Australian floodplain. *Animal Conservation* 9: 431–438. <http://dx.doi.org/10.1111/j.1469-1795.2006.00057.x>
- Greenlees, M.J., Brown, G.P., Webb, J.K., Phillips, B.L. and Shine, R. 2007. Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? *Austral Ecology* 32: 900–907. <http://dx.doi.org/10.1111/j.1442-9993.2007.01778.x>
- Greenlees, M.J., Phillips, B.L. and Shine, R. 2010a. An invasive species imposes selection on life-history traits of a native frog. *Biological Journal of the Linnean Society* 100: 329–336. <http://dx.doi.org/10.1111/j.1095-8312.2010.01432.x>
- Greenlees, M.J., Phillips, B.L. and Shine, R. 2010b. Adjusting to a toxic invader: native Australian frogs learn not to prey on cane toads. *Behavioral Ecology* 21: 966–971. <http://dx.doi.org/10.1093/beheco/arq095>
- Griffiths, A.D. and McKay, J.L. 2007. Cane toads reduce the abundance and site occupancy of Merten's water monitor (*Varanus mertensi*). *Wildlife Research* 34: 609–615. <http://dx.doi.org/10.1071/WR07024>
- Hayes, R.A., Crossland, M.R., Hagman, M., Capon, R.J. and Shine, R. 2009. Ontogenetic variation in the chemical defenses of cane toads (*Bufo marinus*): toxin profiles and effects on predators. *Journal of Chemical Ecology* 35: 391–399. <http://dx.doi.org/10.1007/s10886-009-9608-6>
- Heyer, W.R., McDiarmid, R.W. and Weigmann, D.L. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7: 100–111. <http://dx.doi.org/10.2307/2989753>
- Hoare, J.M., Pledger, S., Nelson, N.J. and Daugherty, C.H. 2007. Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biological Conservation* 136: 510–519. <http://dx.doi.org/10.1016/j.biocon.2006.12.022>
- Katzmann, S., Waringer-Loschenkohl, A. and Waringer, J.A. 2003. Effects of inter- and intra-specific competition on growth and development of *Bufo viridis* and *Bufo bufo* tadpoles. *Limnologia* 33: 122–130. [http://dx.doi.org/10.1016/S0075-9511\(03\)80041-5](http://dx.doi.org/10.1016/S0075-9511(03)80041-5)
- Kelehear, C., Webb, J.K. and Shine, R. 2009. *Rhabdias pseudosphaerocephala* infection in *Bufo marinus*: lung nematodes reduce viability of metamorph cane toads. *Parasitology* 136: 919–927. <http://dx.doi.org/10.1017/S0031182009006325>
- Kiesecker, J.M. and Blaustein, A.R. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology* 78: 1752–1760. <http://dx.doi.org/10.2307/2266098>

- Knight, C.M., Parris, M.J. and Gutzke, W.H.N. 2009.** Influence of priority effects and pond location on invaded larval amphibian communities. *Biological Invasions* **11**: 1033–1044. <http://dx.doi.org/10.1007/s10530-008-9314-2>
- Kupferberg, S.J. 1997.** Bullfrog (*Rana catesbiana*) invasion of a California river: the role of larval competition. *Ecology* **78**: 1736–1751. <http://dx.doi.org/10.2307/2266097>
- Letnic, M., Webb, J.K. and Shine, R. 2008.** Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biological Conservation* **141**: 1773–1782. <http://dx.doi.org/10.1016/j.biocon.2008.04.031>
- Lever, C. 2001.** *The Cane Toad. The History and Ecology of a Successful Colonist*. Westbury Academic Publishing, Otley, West Yorkshire.
- Licht, L.E. 1967.** Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. *Ecology* **48**: 736–745. <http://dx.doi.org/10.2307/1933731>
- Llewelyn, J.S., Phillips, B.L. and Shine, R. 2009.** Sublethal costs associated with the consumption of toxic prey by snakes. *Austral Ecology* **34**: 179–184. <http://dx.doi.org/10.1111/j.1442-9993.2008.01919.x>
- Morin, P.J. 1983.** Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* **53**: 119–138. <http://dx.doi.org/10.2307/1942491>
- Phillips, B.L., Greenlees, M.J., Brown, G.P. and Shine, R. 2010.** Predator behaviour and morphology mediates the impact of an invasive species: cane toads and death adders in Australia. *Animal Conservation* **13**: 53–59. <http://dx.doi.org/10.1111/j.1469-1795.2009.00295.x>
- Pizzatto, L. and Shine, R. 2008.** The behavioral ecology of cannibalism in cane toads (*Bufo marinus*). *Behavioral Ecology and Sociobiology* **63**: 123–133. <http://dx.doi.org/10.1007/s00265-008-0642-0>
- Richter-Boix, A., Llorente, G.A. and Montori, A. 2007.** Hierarchical competition in pond-breeding anuran larvae in a Mediterranean area. *Amphibia-Reptilia* **28**: 247–261. <http://dx.doi.org/10.1163/156853807780202549>
- Rose, S.M. 1960.** A feedback mechanism of growth control in tadpoles. *Ecology* **41**: 188–199. <http://dx.doi.org/10.2307/1931953>
- Salo, P., Korpimäki, E., Banks, P.B., Nordstrom, M. and Dickman, C.R. 2007.** Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B* **274**: 1237–1243. <http://dx.doi.org/10.1098/rspb.2006.0444>
- Smith, D.C. 1987.** Adult recruitment in chorus frogs: effects of size and date of metamorphosis. *Ecology* **68**: 344–350. <http://dx.doi.org/10.2307/1939265>
- Smith, K.G. 2005.** Effects of non-indigenous tadpoles on native tadpoles in Florida: evidence of competition. *Biological Conservation* **123**: 433–441. <http://dx.doi.org/10.1016/j.biocon.2005.01.005>
- Steinwascher, K. 1979.** Competitive interactions among tadpoles: responses to resource level. *Ecology* **60**: 1172–1183. <http://dx.doi.org/10.2307/1936965>
- Strauss, S.Y., Lau, J.A. and Carroll, S.P. 2006.** Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities. *Ecology Letters* **9**: 357–374. <http://dx.doi.org/10.1111/j.1461-0248.2005.00874.x>
- Tyler, M.J., Crook, G.A. and Davies, M. 1983.** Reproductive biology of the frogs of the Magela creek system, Northern Territory. *Records of the South Australian Museum* **18**: 415–440.
- Ward-Fear, G., Brown, G.P., Greenlees, M.J. and Shine, R. 2009.** Maladaptive traits in an invasive species: in Australia, cane toads are more vulnerable to predatory ants than are native frogs. *Functional Ecology* **23**: 559–568. <http://dx.doi.org/10.1111/j.1365-2435.2009.01556.x>
- Wilbur, H.M. 1977.** Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* **58**: 196–200. <http://dx.doi.org/10.2307/1935122>
- Wilbur, H.M. 1980.** Complex life-cycles. *Annual Review of Ecology and Systematics* **11**: 67–93. <http://dx.doi.org/10.1146/annurev.es.11.110180.000435>
- Wilbur, H.M. and Collins, J.P. 1973.** Ecological aspects of amphibian metamorphosis. *Science* **182**: 1305–1314. <http://dx.doi.org/10.1126/science.182.4119.1305>