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Responses of Australian wading birds to a novel toxic prey type, the invasive cane toad *Rhinella marina*

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Abstract The impact of invasive predators on native prey has attracted considerable scientific attention, whereas the reverse situation (invasive species being eaten by native predators) has been less frequently studied. Such interactions might affect invasion success; an invader that is readily consumed by native species may be less likely to flourish in its new range than one that is ignored by those taxa. Invasive cane toads (*Rhinella marina*) in Australia have fatally poisoned many native predators (e.g., marsupials, crocodiles, lizards) that attempt to ingest the toxic anurans, but birds are more resistant to toad toxins. We quantified prey preferences of four species of wading birds (Nankeen night heron, purple swamphen, pied heron, little egret) in the wild, by offering cane toads and alternative native prey items (total of 279 trays offered, 14 different combinations of prey types). All bird species tested preferred the native prey, avoiding both tadpole and metamorph cane toads. Avoidance of toads was strong enough to reduce foraging on native prey presented in combination with the toads, suggesting that the presence of cane toads could affect predator foraging tactics, and reduce the intensity of predation on native prey species found in association with toads.

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Introduction

Considerable research has focused on the effects of invasive predator species on native prey, but the related issue of how native predators affect invasive prey species has attracted less scientific attention (Carlsson et al. 2009). Also, most research in this area has focused on negative rather than positive impacts of invasive species (Pysek et al. 2008). As a result, we know relatively little about topics such as the consumption of invasive species by native predators (but see King et al. 2006; Caldow et al. 2007; Ward-Fear et al. 2010b). Clearly, such impacts have the potential to affect invasion success of the exotic taxon; an invader that is readily consumed by native species may be less likely to flourish in its new range than one which is ignored by those taxa (i.e. Colautti et al. 2004; deRivera et al. 2005; Gruner 2005; Jensen et al. 2007).

One case in which native predators of an invasive species have been intensively studied is the invasive cane toad (*Rhinella marina*) in Australia. The toad was introduced to Australia in 1935 to provide biological control of insect pests of commercial agriculture (Tyler 1999; Lever 2001). Native to South and Central America, this highly toxic anuran has spread to occupy more than 1 million square kilometers of tropical and subtropical Australia

(Lever 2001). The cane toad represents a new (but highly toxic) potential food source to native predators that consume anurans. Because Australia has no native bufonids (Lutz 1971; Cogger 2000), most native predators have no evolutionary history of exposure to the toads' distinctive bufadienolide toxins. Thus, the toad invasion has caused massive mortality of native predators that eat various anuran life-history stages, including native frog tadpoles (Crossland et al. 2008), crocodiles (Letnic et al. 2008), elapid snakes (Phillips et al. 2003; Phillips and Shine 2004), varanid lizards (Doody et al. 2006, 2009; Smith and Phillips 2006; Griffiths and McKay 2007); scincid lizards (Price-Rees et al. 2010) and marsupial quolls (Burnett 1997; Oakwood 2003). Other native predators have learned to avoid eating the toxic toads (e.g. fish—Nelson et al. 2010a, b; marsupial planigales—Webb et al. 2008; keelback snakes—Llewelyn et al. 2010a).

To date, the only native predators shown to actively consume toads are carnivorous ants (Ward-Fear et al. 2010a, b). Ants take only metamorph toads, and only during specific seasons and at specific locations, and hence are likely to have impacts only on a local scale (Ward-Fear et al. 2010b). Scavenging raptors (black kites (*Milvus migrans*) and whistling kites (*Haliastur sphenurus*)) eat road-killed toads, but only if no alternative food is available (Beckmann and Shine 2010). Additionally, anecdotal reports suggest that some native birds attack and consume live toads without ill effect (reviewed in Beckmann and Shine 2009). Thus, unlike many other frog-eating predators, Australian birds do not appear to have been strongly impacted by cane toad invasion. Rather than threatening population viability, cane toads may provide a novel food source for frog-eating birds (Beckmann and Shine 2009).

The bird species likely to be most significant as cane-toad predators would be wading birds (herons, egrets, ibis, rails), because these large predators overlap in habitat use with the vulnerable early life-history stages of cane toads (tadpoles and metamorphs, which possess relatively little toxin: Hayes et al. 2009). Indeed, there are several reports of wading birds consuming cane toads (see Beckmann and Shine 2009). Wading birds are abundant in the Northern Territory in tropical Australia, and their large body sizes, high feeding rates and mobility suggest that they might substantially affect cane toad numbers over broad areas. To assess if wading birds do indeed consume cane toads, we presented free-ranging foraging birds with cane toad tadpoles and metamorphs as well as alternative native prey items and measured consumption rates and prey type preferences.

Materials and methods

Field site and experimental design

Experiments were conducted at Fogg Dam Nature Reserve, Middle Point Village and Beatrice Hill Farm, approximately 60 km east of Darwin (131 02′ 48.19″ E; 12 34′ 14.81″S), Northern Territory, Australia in 2007 and 2008. We offered a variety of food items to free-ranging wading birds, in shallow white plastic trays (70 × 45 × 9 cm deep) placed in areas where wading birds had congregated to feed. All birds in our study would have been exposed to cane toads which arrived at our study site in 2004, 3 years prior to our study. Our target species all consume native anurans, as well as a diverse array of other prey types. Treatments varied with the species of bird targeted (see details below). We recorded numbers of birds foraging in the vicinity of the trays, and conducted observations to confirm that multiple individuals were feeding from the trays. A total of 20 food items were presented in each tray, either 20 of the same item, or in mixed groups (10 items each of two different types) to ensure that the birds encountered both types of food (see Table 1). All food items presented were standardized for size. Tray bottoms were covered with a thin layer of sand. For presentation of fish and tadpoles, trays were filled with water; for metamorphs and fruit, the sand in the trays was moistened. Due to seasonal availability of some food items, it was not possible to present each food item type in exactly equal numbers during each trial. To the extent possible, however, we aimed to have equal numbers of each food type presented daily.

Study species and species-specific experimental procedures

Nankeen night heron

At Fogg Dam Nature Reserve, 9 trays were placed along the dam wall where Nankeen night herons

Table 1 Bird species targeted, experiment locations and times, species-specific experimental treatments and sample sizes

Bird species	Location	Timing of trials	Treatments	Number of trays
Nankeen night heron	Fogg Dam Nature Reserve	Late wet season	(1) 20 toad metamorphs	5
		0,130–0,530 h	(2) 20 glass fish (*Ambassis macleayi*)	21
			(3) 20 toad tadpoles	15
			(4) 10 glass fish/10 toad tadpoles	20
Purple swamphen	Middle Point Village	Dry season	(1) 20 toad metamorphs	12
		Dawn–1,300 h	(2) 20 toad tadpoles	22
			(3) 20 pieces of fruit	13
			(4) 10 pieces of fruit/10 toad metamorphs	16
			(5) 10 pieces of fruit/10 toad tadpoles	12
Pied heron and little egret	Beatrice Hill Farm	Wet season	(1) 20 toad metamorphs	14
		Dawn–1,000 h	(2) 20 glass fish	16
			(3) 20 toad tadpoles	11
			(4) 20 *Litoria tornieri* tadpoles	11
			(5) 20 *Litoria rubella* tadpoles	12
			(6) 10 glass fish/10 toad tadpoles	25
			(7) 10 glass fish/10 *L. tornieri* tadpoles	13
			(8) 10 glass fish/10 *L. rubella* tadpoles	11
			(9) 10 toad tadpoles/10 *L. tornieri* tadpoles	11
			(10) 10 toad tadpoles/10 *L. rubella* tadpoles	10
			(11) 10 *L. tornieri* tadpoles/10 *L. rubella* tadpoles	9

(*Nycticorax caledonicus*) were foraging, and experiments were conducted over seven consecutive nights. On two days, one tray was empty due to the unavailability of one food item type. Trays were deployed at 0,130 h and collected at 0,530 h (before sunrise). Birds were observed using infra-red motion detector cameras and direct observation. This area receives human traffic at all hours of the day and night and therefore the birds are accustomed to human disturbance. Sample sizes for some food types were reduced by an earlier-than anticipated cessation of these trials because of the arrival of a large saltwater crocodile (*Crocodylus porosus*).

Purple swamphen

At Middle Point Village, we placed 10 trays in the yard of a house in the shade close to a (migratory) flock of purple swamphens (*Porphyrio porphyrio*) and experiments were conducted over eight consecutive days. On five days, one tray was empty due to the unavailability of one food item type. Trays were deployed just before dawn and collected at 1,300 h. Birds were observed using infra-red cameras and direct observation. The fruit (pawpaw) was cut into pieces the same size as the toad metamorphs. The swamphens were attracted to the area by edible fruit falling from trees (mango and pawpaw).

Pied heron, little egret

At Beatrice Hill Farm, we placed trays along a dam overflow just before dawn and collected them at 1,000 h. Experiments were conducted over 18 consecutive days, using 6 trays for the first 4 days, 5 trays for the last 4 days, and 10 trays on all other days. On one day, one tray was empty. As we had 11 different food combinations (see Table 1) but a maximum of 10 trays available, we randomly deleted treatment types from the presentation on a daily basis to match the number of trays available. Fish migrating upstream attracted pied herons (*Ardea picata*), little egrets (*Egretta garzetta*), intermediate egrets (*Ardea intermedia*), cattle egrets (*Ardea ibis*), great egrets (*Ardea alba*), and black-necked storks (*Ephippiorhynchus asiaticus*). Other birds in the area that may eat cane toad metamorphs and tadpoles included spur-winged plovers (*Vanellus miles*) and brolga (*Grus rubicundus*). Only pied herons and little egrets fed from the trays. Birds were observed from a distance of 150 m using binoculars (10 × 42) and a spotting scope (20 × 60). We recorded all bird species visiting the trays, and confirmed birds were capturing and consuming food items presented in the trays.

In addition to examining responses to cane toad tadpoles and metamorphs, we also examined whether predation on native frog tadpoles by pied heron and little egret was altered by the presence of cane toad tadpoles. Predators must often encounter toad tadpoles and native frog tadpoles in close proximity, because the invasive species overlaps strongly with many native frog taxa in terms of breeding sites and seasons (Crossland et al. 2008).

Statistical analysis

For these analyses, we used the raw binomial data and Proc GENMOD (SAS Institute 1998) with binomial error, the logit link function and Type 3 tests. Post-hoc tests were performed using the 'pdiff' option for all-pairwise comparisons of least-squares means and adjusting the critical p-value for the results by minimizing the false discovery rate (Verhoeven et al. 2005). For each group of predatory wading bird, we asked the following questions:

(a) How readily do birds consume toads, and is this feeding rate affected by the presence of alternative prey?
(b) Does the presence of cane toads affect the birds' rate of predation on alternative (native) prey types? and
(c) What are the relative rates of bird predation upon toads compared to other prey types?

Results

Night herons

Each night, more than 150 night herons were seen near our experimental trays, often foraging from them (and standing in them). The proportion of toads that were eaten in the presence or absence of alternate prey (fish) did not differ significantly among treatments ($\chi^2 = 0.58$, df = 2, $P = 0.75$, Fig. 1a). Night herons ate more fish when they were presented in trays of 20 fish, than when presented in trays of 10 fish and 10 toad tadpoles combined ($\chi^2 = 101.73$, df = 1, $P < 0.0001$, Fig. 1b). When presented with a single prey type, the proportion of food items eaten by night herons differed among treatments ($\chi^2 = 252.73$, df = 2, $P < 0.0001$, Fig. 1c). Post-hoc tests show the herons ate more fish than either toad metamorphs or toad tadpoles (both $P < 0.0001$; toad tadpoles vs. metamorphs, $P = 0.44$).

Purple swamphen

A flock of 30 purple swamphens visited the experimental trays every morning, and often fed from the experimental trays. The proportion of toads eaten by swamphens in the presence or absence of non-toad prey (fruit) differed among treatments ($\chi^2 = 18.39$, df = 3, $P = 0.0004$, Fig. 2a). Post-hoc tests show that swamphens ate more toad metamorphs when these were presented in combination with 10 pieces of fruit than any other treatment (all $P < 0.003$; all other treatments, $P > 0.1$). The proportion of fruit eaten by swamphens differed between treatments ($\chi^2 = 6.4$, df = 2, $P = 0.04$, Fig. 2b), with more fruit taken from fruit-only trays than from trays in which both fruit and tadpoles were presented (posthoc test, $P = 0.04$; all other treatments, $P > 0.05$). When presented with a single food type per tray, the proportion of all food items eaten by swamphens differed among treatments ($\chi^2 = 962.43$, df = 2, $P < 0.0001$, Fig. 2c). Overall, swamphens ate fruit more readily than they consumed either toad metamorphs or tadpoles (both $P < 0.0001$; toad tadpoles versus metamorphs, $P = 0.79$).

Pied heron, little egret

Despite many wading bird species foraging in the area, only pied herons and little egrets fed from the trays. A mixed-species flock of 16–25 pied herons and 8–16 little egrets fed from the trays. As both fed from the trays at the same time, we were unable to separate results from these two bird species. The proportion of fish eaten by the birds differed among treatments ($\chi^2 = 162.65$, df = 3, $P < 0.0001$, Fig. 3a). More fish were eaten when presented in

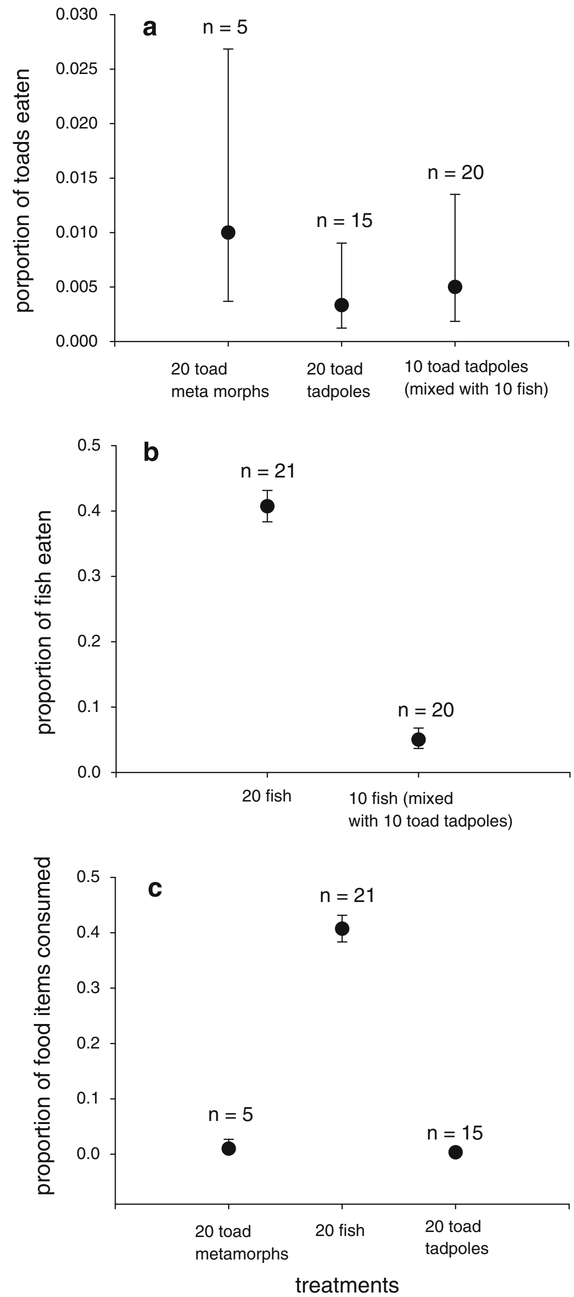

Fig. 1 The rates at which alternative prey types were eaten by night herons in our experimental trials. All *graphs* show back-transformed mean (± SE) proportions of available prey items that were consumed. *The upper panel* (**a**) shows predation on invasive cane toads, *the middle panel* (**b**) shows predation on native fish, and the *lower panel* (**c**) shows overall proportion of food items consumed by night herons. *Error bars* are present on all points, however in some instances they are obscured due to their small size

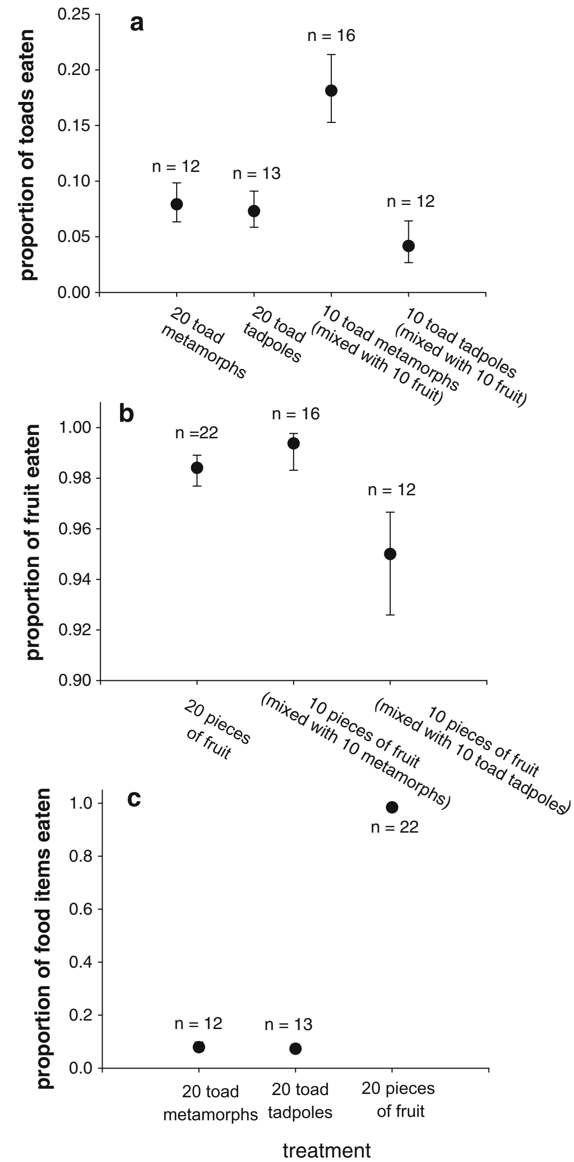

Fig. 2 The rates at which alternative prey types were eaten by purple swamphens in our experimental trials. All *graphs* show back-transformed mean (± SE) proportions of available prey items that were consumed. *The upper panel* (**a**) shows predation on invasive cane toads, *the middle panel* (**b**) shows consumption of fruit, and *the lower panel* (**c**) shows overall proportion of food items consumed by purple swamphens. *Error bars* are present on all points, however in some instances they are obscured due to their small size

trays with 20 fish, than when mixed with any other food item ($P < 0.0001$; mixed with toad vs. *L. tornieri* tadpoles, $P = 0.14$). Fewer fish were

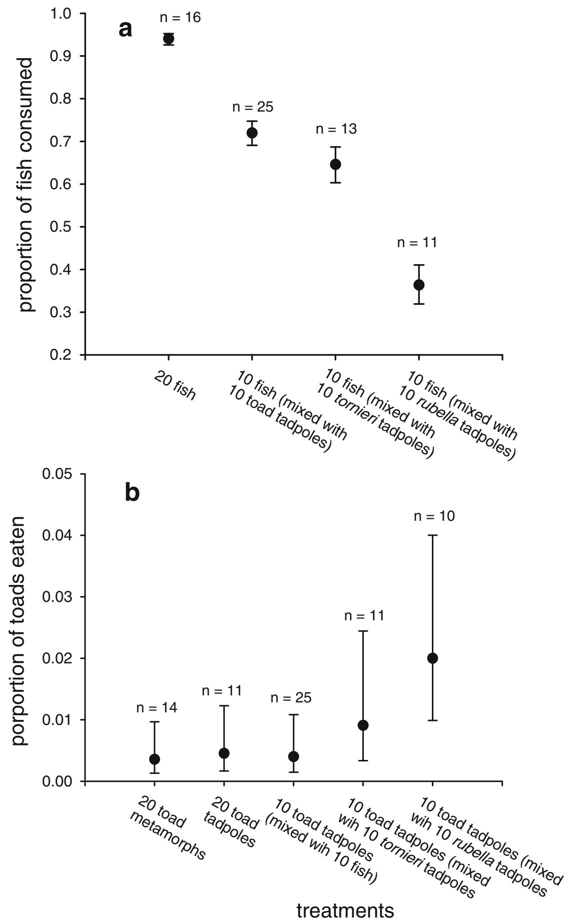

Fig. 3 The rates at which alternative prey types were eaten by pied herons and little egrets in our experimental trials. All *graphs* show back-transformed mean (± SE) proportions of available prey items that were consumed, under a range of experimental treatments that differed in the combination of potential prey types that were presented. *The upper panel* (**a**) shows predation on native fish, and *the lower panel* (**b**) shows predation on invasive cane toads

consumed when they were presented with 10 *L. rubella* tadpoles than in either of the other treatments (posthoc, $P < 0.0001$). The proportion of toads eaten did not differ among treatments regardless of the presence or absence of alternate prey types (fish or native tadpoles) ($\chi^2 = 2.78$, df = 4, $P = 0.59$, Fig. 3b). The proportion of *L. rubella* tadpoles eaten did not differ significantly among treatments ($\chi^2 = 7.19$, df = 3, $P = 0.07$, Fig. 4a). The proportion of *L. tornieri* tadpoles eaten by birds differed among treatments ($\chi^2 = 28.76$, df = 3, $P < 0.0001$, Fig. 4b). Birds ate more *L. tornieri* when these were presented in trays of 20 tadpoles than in all other treatments (all $P < 0.004$), but the proportion of *L. tornieri* eaten did not differ among all other trials (all $P > 0.7$). When presented with only one prey type per tray, the proportion of food items eaten by birds differed among treatments ($\chi^2 = 1010.06$, df = 4, $P < 0.0001$, Fig. 5), with more fish eaten than any other prey type (posthoc tests, all $P < 0.0001$; toad tadpoles vs. metamorphs, $P = 0.86$). Fewer toads (of both life-history stages) were consumed than were any other prey type (all $P < 0.002$), and more *L. tornieri* tadpoles were consumed than *L. rubella* ($P = 0.002$).

Discussion

Wading birds were reluctant to consume cane toads at any of the life-history stages that we tested. The birds readily consumed the alternative food items offered (except that pied herons and little egrets rarely ate native frog tadpoles) but all of the species that we tested - Nankeen night herons, purple swamphens, pied herons and little egrets—avoided both cane toad metamorphs and cane toad tadpoles. Likely, cane toads are unpalatable to wading birds, as they are to some other types of native predators, including fish (Crossland and Alford 1998; Crossland 2001; Nelson et al. 2010b), marsupials (Webb et al. 2008; Llewelyn et al. 2010b) and snakes (Llewelyn et al. 2010a). The only case of regular consumption of cane toads was by purple swamphens, in trays containing both toad metamorphs and fruit (rather than toads alone). This seems to reflect simple mistakes in prey selection, because swamphens clearly preferred fruit over toads.

The avoidance of cane toad tadpoles and metamorphs by wading birds was strong enough to affect the predators' consumption of other prey types, if these were offered at the same time as toads. Consistently, the proportion of available prey that was consumed was lower from trays that also contained toads. For example, night herons, pied herons and little egrets ate fewer fish from trays with both fish and toad tadpoles combined than from trays with only fish. Presumably, the birds' attempts to avoid ingesting the unpalatable toads interfered with their consumption of the simultaneously-offered palatable prey, and thus if a choice was available the birds tended to forage from trays that did not contain toads. The low consumption rates of native

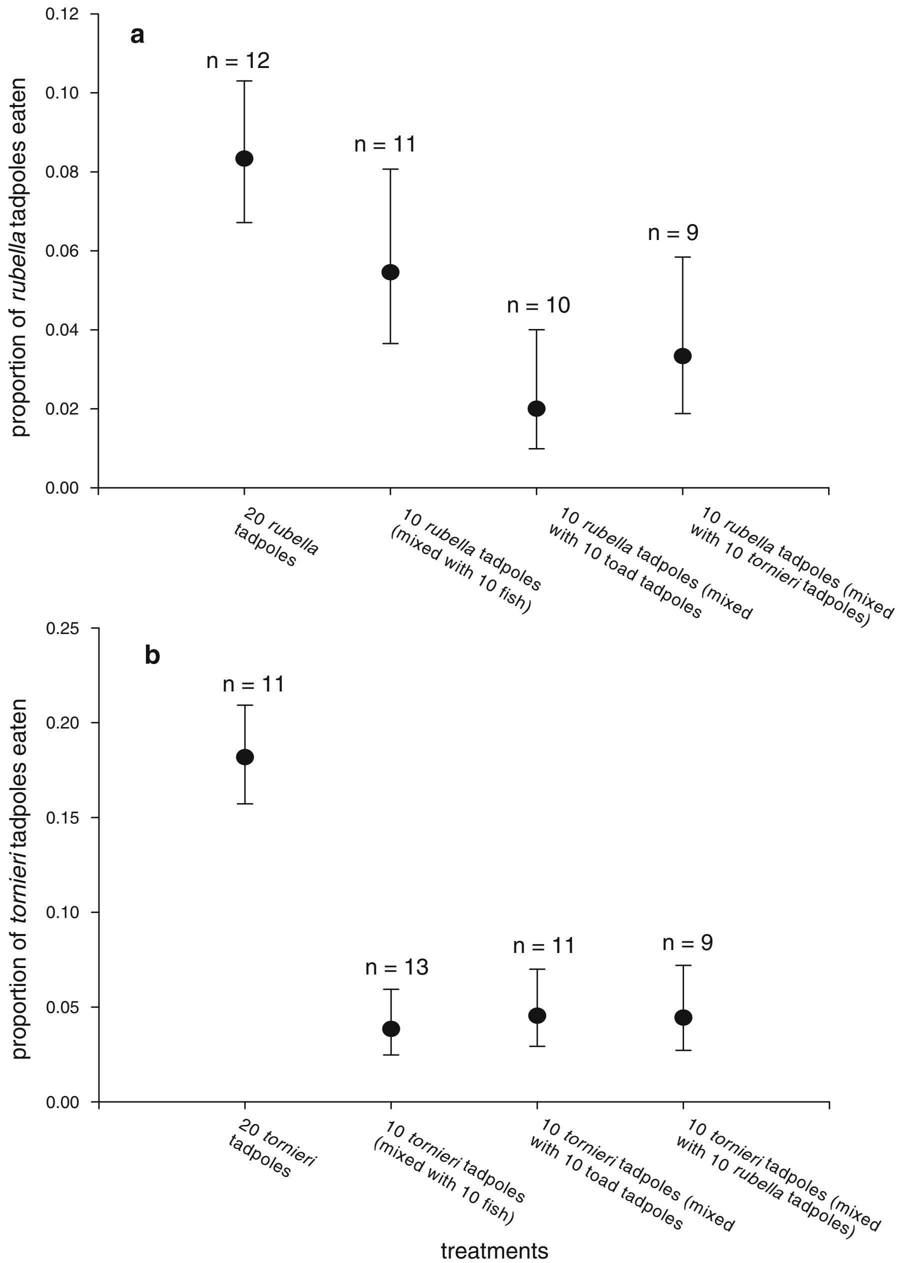

Fig. 4 The rates at which tadpoles of two species of native frogs (*Litoria rubella* and *L. tornieri*) were eaten by pied herons and little egrets in our experimental trials. All *graphs* show back-transformed mean (± SE) proportions of available prey items that were consumed, under a range of experimental treatments that differed in the combination of potential prey types that were presented. *The upper panel* (**a**) shows predation on *Litoria rubella*, and *the lower panel* (**b**) shows predation on *L. tornieri*

frog tadpoles by pied herons and little egrets also might reflect an indirect effect of toad presence. Encounters with toads induce some native predatory fish and mammals to ignore native tadpoles or frogs, presumably reflecting accidental mimicry of the toxic invader by native anurans (Webb et al. 2008; Nelson et al. 2010a). As fish readily consume *L. rubella* tadpoles (Nelson 2008, 2010a), these tadpoles are unlikely to be toxic to birds. There are few published records of the feeding habits of our target bird species (Beckmann and Shine 2009). Nankeen night herons eat both tadpoles and frogs (Barker and Vestjens 1989; Marchant and Higgins 1990). Purple swamphens, little egrets and pied herons all eat frogs (Marchant and Higgins 1990; Marchant and Higgins 1993; C. Beckmann pers. obs.), and probably eat tadpoles (given that many other species of herons and egrets in Australia eat tadpoles: reviewed by

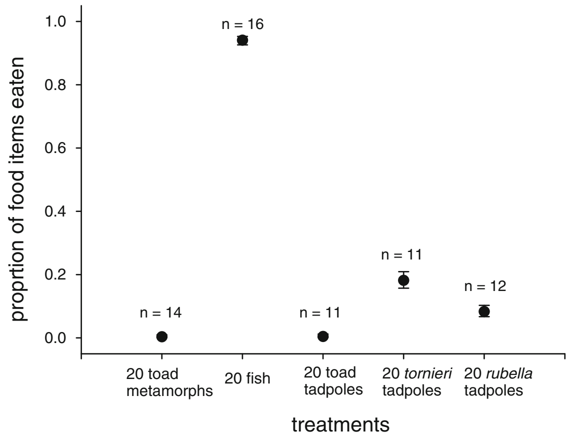

Fig. 5 Overall rates at which alternative prey types were eaten by pied herons and little egrets in our experimental trials. All *graphs* show back-transformed mean (± SE) proportions of available prey items that were consumed. *Error bars* are present on all points, however in some instances they are obscured due to their small size

Beckmann and Shine 2009). As toad tadpoles and metamorphs closely resemble native species, it is unlikely that birds would view them as novel prey and avoid them for this reason.

Toad tadpoles co-occur with tadpoles of *L. rubella* and *L. tornieri* in many temporary ponds in the study area (Crossland et al. 2008), and co-occur with glass fish in both temporary and permanent ponds in the study area (Crossland pers. obs.). Therefore at least some of the combinations of potential prey items in our experimental trays (simultaneously-presented toad tadpoles and frog tadpoles, and simultaneously-presented toad tadpoles and glass fish) are realistic simulations of naturally-occurring situations. Other combinations (such as fresh fruit and toad tadpoles) occur less frequently in nature. However, toad tadpoles can be found in a wide range of temporary and permanent water bodies in our study area, and throughout their range in Australia, so that potential predators often may encounter these tadpoles relatively close to other edible native items. Hence, a decreased rate of foraging on native species in the presence of toad tadpoles may well occur in nature (to the benefit of prey, and the detriment of predators); further work would be required to test this inference.

In combination, our data suggest that the arrival of cane toads has not generated a novel food supply for wading birds—they find the toads unpalatable—but may nonetheless have affected the foraging habits of these avian predators. Such interactions might have fitness consequences for the predators (if their predation rates on native prey are reduced, as suggested by our trials) as well as for the prey. If the presence of toad tadpoles or toad metamorphs increases rates of survival of native prey found in association with the tadpoles (as we suggest above), then we might expect natural selection to favour shifts in the times and places of activity of native tadpoles, such that they evolve to co-occur more frequently with tadpoles of the invasive cane toad. Given evidence of rapid evolutionary shifts both in toads and in some of the native species they affect (Phillips and Shine 2004, 2005), it would be of interest to examine schooling responses of native tadpoles in this way. Also, one intriguing result from our analyses was that the presence of (apparently palatable) native tadpoles, as well as (toxic) toad tadpoles, reduced the birds' rate of predation on fish (Fig. 3). Thus, mixed-species schooling responses may have been an effective antipredator tactic over much longer timescales, even in the absence of cane toads.

Overall, our data suggest that wading birds are not at risk of lethal toxic ingestion from consuming cane toads (unlike many other species of native predators in Australia: Shine 2010). No avian deaths due to toad ingestion have been recorded at water-bodies at our field site, further suggesting no lethal impact. However, the invasion of cane toads does not provide a novel food source for these birds, because they detect and avoid the toads. As a result, the invasion success of the cane toad is unlikely to have been suppressed by these avian predators. Similarly, native scavenging raptors (black and whistling kites) avoid toads as prey if alternative food items are available (Beckmann and Shine 2010). These scavengers, however, did increase their use of toads when alternate food sources were not readily available. The wading bird species we studied might consume toads in times of food shortage, but we have no data on this topic. Another gap in knowledge concerns other taxa of wading bird species, some of which have been recorded to eat toads (cattle egret *Ardea ibis*, Australian white ibis *Threskiornis moloucca*; reviewed in Beckmann and Shine 2009). Further research on these species, to assess their potential to consume toads, would be of great interest.

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