The behavioral ecology of cannibalism in cane toads (*Bufo marinus*)

Lígia Pizzatto · Richard Shine

Abstract Laboratory studies show that predatory cane toads (*Bufo marinus*) exhibit specialized toe-luring behavior that attracts smaller conspecifics, but field surveys of toad diet rarely record cannibalism. Our data resolve this paradox, showing that cannibalism is common under specific ecological conditions. In the wet–dry tropics of Australia, desiccation risk constrains recently metamorphosed toads to the edges of the natal pond. Juvenile toads large enough to consume their smaller conspecifics switch to a primarily cannibalistic diet (67% of prey biomass in stomachs of larger toads). Cannibalistic attack was triggered by prey movement, and (perhaps as an adaptive response to this threat) small (edible-sized) toads were virtually immobile at night (when cannibals were active). Smaller metamorphs were consumed more frequently than were larger conspecifics. The switch from insectivory to cannibalism reflects the high dry season densities of small conspecifics (in turn, due to desiccation-imposed constraints to dispersal) and the scarcity of alternative (insect) prey during dry weather. Our study pond (102 m in circumference) supported >400 juvenile toads, which consumed many metamorphs over the course of our study. Toads appear to be low-quality food items for other toads; in laboratory trials, juvenile toads that fed only on conspecifics grew less rapidly than those that ate an equivalent mass of insects. This effect was not due to parotoid gland toxins per se. Thus, cane toads switch to intensive cannibalism only when seasonal precipitation

regimes increase encounter rates between large and small toads, while simultaneously reducing the availability of alternative prey.

Keywords Anuran · Feeding habits · Growth rate · Intraspecific predation · Natural selection

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Introduction

"I do wish we could chat longer, but I'm having an old friend for dinner"—Dr. Hannibal Lecter, in "The Silence of the Lambs"

Cannibalism is widespread among living creatures (Fox 1975; Polis 1981), ranging from unicellular organisms (Claverys and Havarstein 2007) to humans (Shankman 1969). Eating conspecifics may enhance the cannibal's fitness via direct nutritional benefit (Fox 1975; Polis 1981; Ebensperger 1998; Manica 2002; Lourdais et al. 2005) or via less direct pathways (Polis 1981; Summers 1989; Forster 1992; Sasaki and Iwahashi 1995; Andrade 1996, 1998). In amphibians, cannibalism is common in early life history stages (Crump 1992; Rosen 2007). The larvae of some species exhibit discrete morphs that differ in feeding habits and associated trophic morphologies, with one morph acting as specialized cannibals (Collins and Holomuzki 1984; Crump 1992; Larson et al. 1999). Predation by tadpoles upon freshly laid eggs is so common as to be the norm rather than the exception (Crump 1992; Duellman and Trueb 1994; Alford 1999), and the most significant predators of tadpoles may be other amphibians (Duellman and Trueb 1994), perhaps facilitating conspecific predation. However, less is known about cannibalism in the terrestrial phase of the anuran life cycle (Crump 1992; Wiseman and

Bettaso 2007). Many frogs and toads are generalized feeders (Toft 1985) so that other anurans (including conspecifics) are likely to be consumed occasionally (Crump 1992; Alford 1999). Some frog species are specialized to prey upon other frogs (Duellman and Trueb 1994), and cannibalism may be more common in such taxa (see Scott and Aquino 2005 for evidence that conspecific predation may be rare in such an assemblage, although cannibalism was easily induced by experimental presentation of smaller conspecifics to foraging adults). Nonetheless, despite many anecdotal reports of cannibalism among non-larval anurans, we are not aware of any detailed analyses of this topic.

Recent work suggests a potential model system for such a study. One of the most intensively studied anurans worldwide is the cane toad *Bufo marinus*; for example, a recent 230-page book was devoted to reviewing published literature on this species (Lever 2001). Extensive dietary data (based on stomach contents of field-collected specimens) show that adult cane toads take a wide range of prey items but with a strong preponderance of small invertebrates (see Lever 2001 for a review). Such studies come from the native range of cane toads in South America (Zug and Zug 1979; Bayliss 1995) as well as countries to which the toad has been introduced (e.g., continental USA—Pack 1922; Hawaii—Illingworth 1941; Oliver and Shaw 1953; Puerto Rico—Box 1925; Dexter 1932; Fiji—Hinckley 1963; Papua New Guinea—Pippet 1975; Zug et al. 1975; Bailey 1976; Australia—Niven and Stewart 1982; Freeland et al. 1986; Greenlees et al. 2006). Hence, despite occasional reports of predation on vertebrates, including other frogs (Covacevich and Archer 1975; Quesnel 1986; Bayliss 1995; Caudell et al. 2000), and a single record of two juveniles being eaten by conspecifics (Zug et al. 1975), the cane toad at first sight seems an unlikely candidate for a study on cannibalism. However, recent detailed observations on captive cane toads revealed a complex, stereotyped toe-luring behavior that was performed primarily by medium-sized toads, was stimulated by the proximity of smaller (edible-sized) conspecifics, and elicited close approach by those smaller animals (Hagman and Shine 2008). Experimental manipulation of toe colors and movement frequencies showed that the lure was well-suited to attract smaller conspecifics and, hence, appears to be an adaptation for cannibalism (Hagman and Shine 2008). These results seem paradoxical in light of field reports that anurophagy is rare in cane toads (see above). One resolution of this paradox might be that cannibalism is indeed an important part of toad trophic ecology but only under specific ecological conditions.

In the course of field studies on cane toads near the invasion front in tropical Australia (Brown et al. 2006; Phillips et al. 2007), we identified a situation that might facilitate cannibalism. During the prolonged dry season (April to November), toads breed sporadically, but desiccation risk in the surrounding landscape constrains metamorph and small toads (but not adults—see "Discussion") to the moist margins of the natal pond (Child et al. 2008; see also Freeland and Kerin 1991; Cohen and Alford 1993, for studies in other areas). The consequent high densities of small metamorphs provide an opportunity for predation by larger juvenile conspecifics, especially because dry weather reduces the availability of alternative (invertebrate) prey (Child et al. 2008). We, thus, conducted detailed studies of one such pond, to ask:

(1) Do juvenile toads in this situation act as specialist cannibals?
(2) Could the risk of cannibalism explain why small metamorphs are active diurnally, unlike their older conspecifics which are nocturnally active?
(3) Does cannibalism substantially affect population demography or the growth rates of larger toads?

Materials and methods

Study species

The cane toad *B. marinus* (= tentatively allocated to *Chaunus marinus* by Frost et al. 2006) is a large [to 24-cm snout-urostyle length (SUL), 2.8 kg] terrestrial anuran native to South and Central America but widely translocated elsewhere in attempts to control insect pests affecting agricultural enterprises (Lever 2001). Cane toads were brought to Queensland in 1935 and are now abundant throughout most of tropical Australia (Urban et al. 2007). In the wet–dry tropics of the Northern Territory, toads breed sporadically over much of the year but with a peak in the late wet season and early dry season (March–June: R. Shine, unpublished data). Because a single clutch can contain >30,000 eggs, transforming metamorphs can attain high densities at water body margins during the dry season (Freeland and Kerin 1991; Cohen and Alford 1993; Child et al. 2008). Metamorph toads are primarily diurnal, whereas larger juveniles and adults are nocturnal (Freeland and Kerin 1991; Child et al. 2008; Pizzatto et al. 2008).

Study area

We worked at a circular pond (approximately 2 m deep; circumference 101.7 m) beside the Arnhem Highway, about 70 km east of Darwin (12°39′36.46″ S, 131°20′11.28″ E). The pond was lined by open muddy banks 10–60 cm wide, flanked on the edge by thick grass (Fig. 1a). In July 2007,

Fig. 1 In the mid-dry season (July), the margins of the natal pond (**a**) provide the only moist microhabitats within the nearby landscape. Hence, both newly metamorphosed cane toads and larger, older conspecific juvenile toads were concentrated on these pond margins (**b**). Juvenile toads readily seized metamorphs dangled in front of them (**c**), and dissection of juveniles revealed that cannibalism was frequent (**d**)
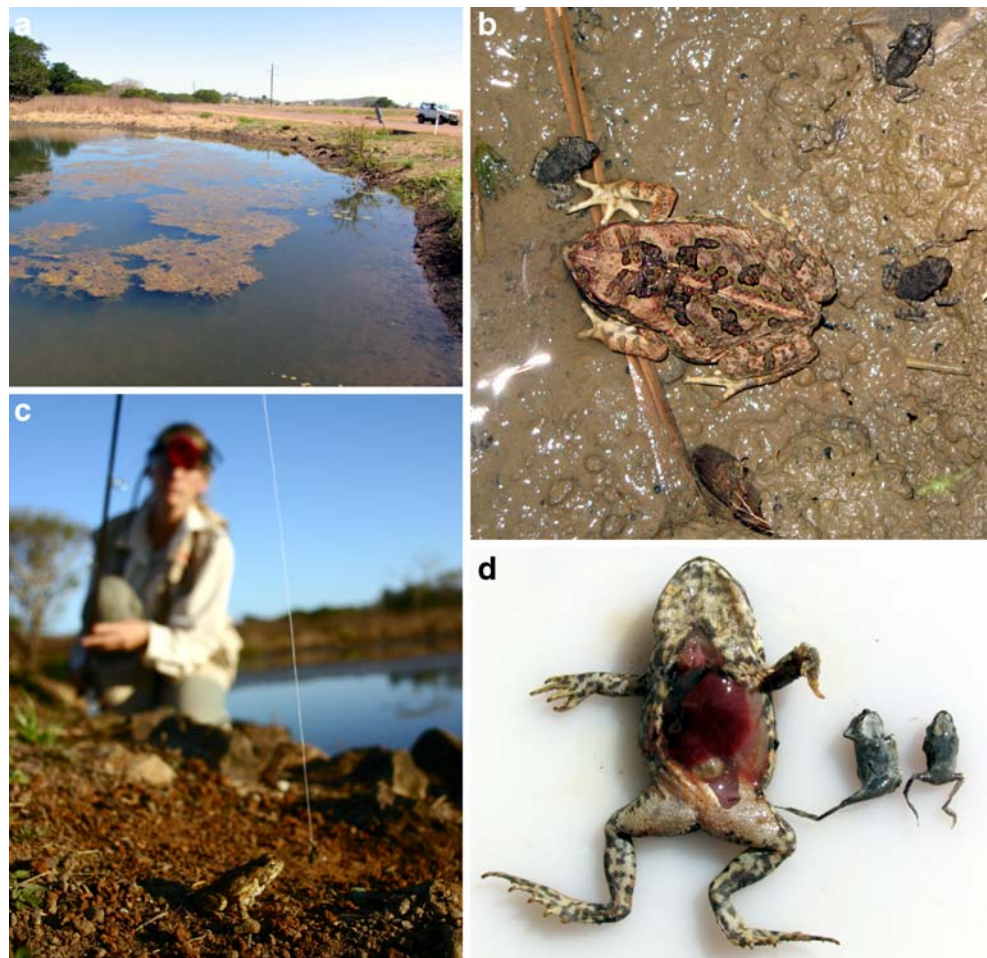
the pond contained many fishes (e.g. *Melatotaenia australis*, *Mogurnda mogurnda*, *Oxyeleotris lineolata*, *Glossamia aprion*, *Amniataba percoides*, *Megalopes cyprinoides*), anurans (*Litoria bicolor*, *Litoria dahlii*, *Litoria microbelos*, *Litoria nasuta*) and one saltwater crocodile (*Crocodylus porosus*). Cane toads bred in the pool on multiple occasions from the mid-wet season (first record of amplexus 13 December: M. Crossland, personal communication) through the early dry season (June) and tadpoles continued to metamorphose and emerge from the water during our studies in July. At this time, the toads around the pond fell unambiguously into three size classes: newly emerged metamorphs (<20 mm SUL), juveniles (20–70 mm), and adults (>70 mm), with no intermediate-sized animals. The muddy banks of the pond contained high densities of metamorphs (25 to 145 m^2, based on quadrat counts) whenever we checked, by day or night, whereas larger (juvenile and adult) toads were seen only at night (Fig. 1b). Juvenile toads were seen emerging in the early evening from holes under rocks and from grassy retreats.

Dietary habits and estimating densities of cannibals and their prey

The massive numbers of metamorphs emerging from the pond, and the prolonged period over which they did so, precluded direct enumeration. However, we estimated (1) the relative numbers of small metamorphs and juvenile toads in 18 quadrats along the bank (each 100×20 cm) and (2) the total number of toads in the juvenile size class. To assess the latter variable, the larger (juvenile) animals were repeatedly sampled (with removal) on 33 nights over a 5-week period from 12 June to 22 July 2007. A random subsample of 41 of these animals was euthanized within an hour of collection (first anesthetized by immersion in tricaine methanesulfonate [MS222] then killed by freezing) and dissected to score their stomach contents. The remaining 378 juvenile toads (i.e., those not euthanized immediately after capture) were kept for use in other experiments. We also took random samples of metamorphs on two of those nights, to quantify body size distributions.

Spontaneous activity and response to disturbance

To quantify nocturnal–diurnal shifts in behavior of meta-morph toads, we haphazardly selected the first individual we saw when we carefully approached the pond edge (to within 1 m of the water) and scored whether or not they moved over a 2-min period. To assess their response to a predation threat, we touched each metamorph on the back with a twig and recorded whether the animal remained immobile or moved away. These experiments were run during the day (1600 to 1700 hours) and night (2000 to 2100 hours) on consecutive days.

Cues for cannibalistic attack

Would immobility protect metamorph toads from cannibal-istic attack? It is well known that prey movement can elicit a feeding response by toads (e.g., Buxbaum-Conradi and Ewert 1999), but prey odor, without movement, can also elicit feeding (Dole et al. 1981; Roth and Wiggers 1983). Indeed, cane toads are renowned for taking nonmoving prey such as dog food (Lever 2001). Ten metamorph toads (collected as part of the random sampling to document metamorph size distributions: see above) were anesthetized by immersion in tricaine methanesulfonate and then killed by freezing. We then thawed these animals and used them as lures to investigate feeding responses of larger toads (Fig. 1c). Metamorphs were suspended on cotton thread from fishing rods for these trials, and all observations were made in the field under red light and for 2-min periods. Trials were conducted from 1930 to 2130 hours. We manipulated two variables: metamorph body size ("small" = 11–12.5 mm; "large" = 14–16 mm) and movement ("immobile" = metamorph deposited on substratum 1 cm in front of the snout of a juvenile toad; "moving" = metamorph moved about similarly to natural activity in front of the larger toad). Treatments were applied in random order, and we scored whether or not each juvenile toad seized the metamorph. All juvenile toads were then collected and euthanized as above.

Effects of cannibalism on growth rates

We investigated the influence of cannibalism on predator growth by keeping juvenile toads (1.2–3.77 g) individually in plastic containers (15×10×7 cm) lined with wet sand and with ad libitum access to water in a shaded outdoor area (and, thus, exposed to natural air temperatures and photoperiod). All containers included a cardboard shelter attached to the side of the container to provide refuge. Twelve juvenile toads were fed on smaller metamorph toads only (maintained during the trials in containers identical to those used for larger toads, but in groups of

20 per container; fed on tiny crickets), and 15 were fed on crickets only. The juvenile toads were allowed to feed ad libitum by introducing metamorphs or crickets to each cage at night and removing uneaten animals the following morning (which were then returned to their home cages). Metamorphs do not feed at night (Pizzatto et al. 2008) so no prey items for this size class were added during these nocturnal trials. All prey items provided to the juvenile toads (i.e., crickets or metamorph toads) were preweighed (to 0.01 g). Juvenile toads were weighed at the outset of the study, fed for 12 days and then reweighed. All animals (juveniles and surviving metamorphs) were then euthanized as above. Because this experiment provided a surprising result (see below), we repeated it to compare growth rates of juvenile toads fed either on crickets (as above) or on crickets painted with the parotoid gland secretions of toads. We obtained the toxin by manually squeezing the parotoid glands of recently killed adult toads, to provide several times more toxin per cricket (approximately 0.01 g) than is found within the parotoid glands of a metamorph toad. We fed 14 juvenile toads (5.3–12.5 g) on crickets and 12 toads on crickets painted with toad toxin.

Results

Stomach contents analysis

Of seven large adult toads (>95 mm SUL, 70 g) collected at the pond, five had empty stomachs, one contained an ant, and one a beetle. Of the 124 juvenile toads that we dissected, 29 had empty stomachs (chi-square test testing null hypothesis of equal % empty stomachs adults vs. juveniles, $\chi^2=5.67$, $df=1$, $P<0.02$). The 95 juveniles with food contained a total of 443 prey items, of which 69 (15.5%) were metamorph toads (Fig. 1d). Although a minority numerically, these metamorphs constituted two thirds of the total biomass of prey recorded in stomachs of juvenile toads (13.08 of 19.44 g). Non-anuran prey items were invertebrates, mostly ants (186 items, 1.72 g), beetles (115 items, 1.69 g), and hemipterans (35 items, 2.22 g), plus a few arachnids (5, 0.19 g), orthopterans (2, 0.47 g), and dipterans (2, 0.07 g). The body size of a juvenile toad was not significantly correlated with that of its prey (linear regression using mean prey size per predator, $n=41$ predators, $r=0.15$, $P=0.35$ for prey SUL; $n=39$, $r=0.20$, $P=0.23$ for prey mass). The metamorphs consumed by juvenile toads were smaller on average than those in the random samples of surviving metamorphs in terms of body length [analysis of variance (ANOVA): SUL, $F_{1,821}=8.29$, $P=0.004$; Fig. 2] but not body mass (ANOVA: $F_{1,821}=0.67$, $P=0.42$). This minor bias was probably due to reduced vulnerability of the (infrequent) larger metamorphs (Fig. 2).
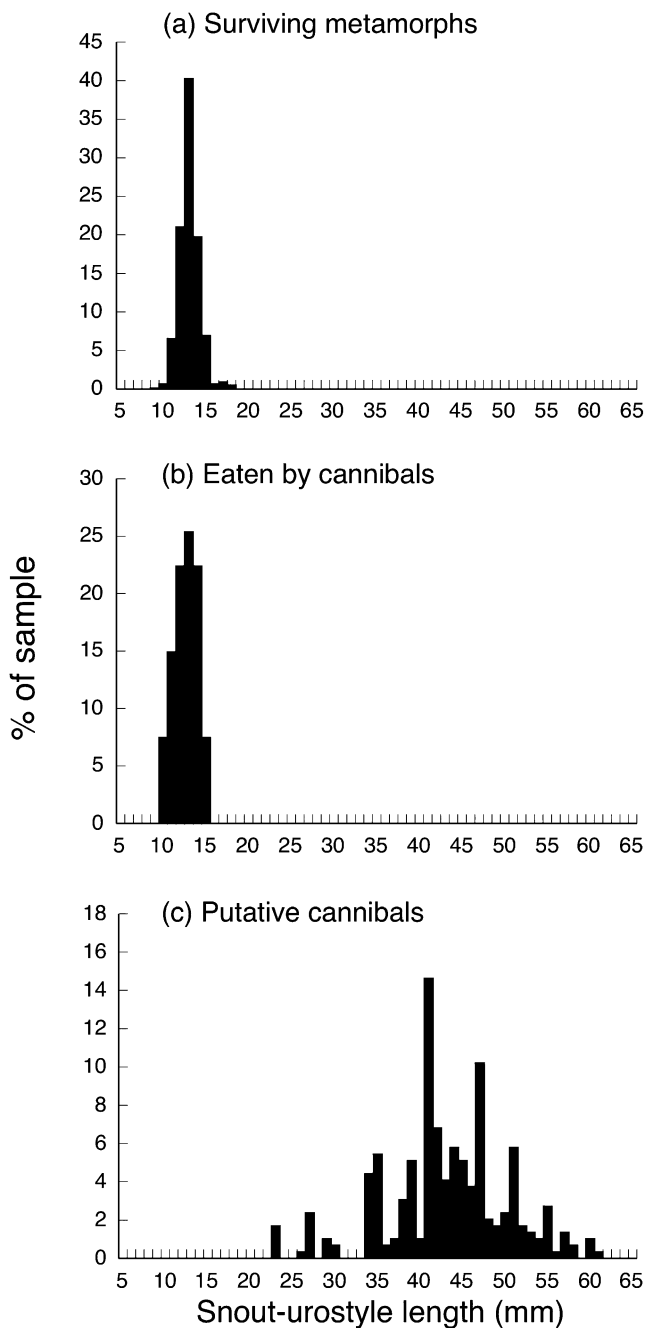
Fig. 2 Body sizes of recently emerged metamorph cane toads and of the larger juvenile conspecifics that preyed upon them. The upper graph (**a**) shows the frequency distribution of body sizes of the sample of 780 surviving metamorph toads; the middle graph (**b**) shows the sizes of 67 metamorph toads found in the stomachs of cannibalistic conspecifics; and the lower graph (**c**) shows the body sizes of 124 juvenile (putative cannibal) toads. Note the different scales on axes for metamorph versus juvenile toads

Most of the prey items that we identified were freshly ingested; metamorph toads in the stomachs of juveniles are barely recognizable 24 h after ingestion (L. Pizzatto, unpublished data). We saw three cases of cannibalism in progress (smaller toads in the mouths of larger conspecifics) during our nocturnal surveys, so most identifiable anuran prey items in stomachs probably were consumed in the few hours prior to our surveys.

Densities of cannibals and their prey

Our quadrat counts conducted within 2 h of dusk revealed average densities of 54.2 (SD=32.50, range 25 to 145) metamorph toads and 2.9 (SD=3.45) juvenile toads per square meter, respectively (see Fig. 1b). Because metamorphs (mean mass 0.23 g) were about 20 times as common as their larger conspecifics (mean mass 7.8 g), the total standing-crop biomass of the two groups was fairly similar. Mean metamorph densities did not differ significantly between quadrats that contained or did not contain cannibalistic juvenile toads (ANOVA: $F_{1,17}=2.23$, $P=0.15$). Although we never found more than 49 juvenile toads on any single night, new individuals kept appearing to replace the ones we had removed; in total, we collected and removed a total of 419 juveniles and seven adults from the pond margins over 33 nights, and doubtlessly failed to find many others.

Spontaneous activity and response to disturbance

When observed during daylight hours, 81% of metamorphs (34 of 42) changed their locations during the 2-min observation period. At night, spontaneous activity was seen in only 14% of animals (chi-square test: 6 of 42; comparing day vs. night, $\chi^2=33.08$, $df=1$, $P<0.0001$). When touched with a twig during daylight hours, 59% of metamorphs moved away, compared to 12% at night (chi-square test: 33 of 56 vs. 7 of 60; $\chi^2=26.58$, $df=1$, $P<0.0001$).

Cues for cannibalistic attack

Juvenile toads never attacked immobile metamorphs, but seized 45% of moving "lures" (chi-square test: 0 of 15 vs. 17 of 38; $\chi^2=7.97$, $df=1$, $P<0.005$). The size of the metamorph used as a "lure" did not influence the predators' responses (chi-square test: attacks in eight of 19 trials with "small" lure, nine of 19 trials with "large" lure; $\chi^2=0.00$, $df=1$, $P>0.99$).

Effects of cannibalism on growth rates

In the first experiment, both groups of juvenile toads increased significantly in mean body mass over the trial period (comparing initial vs. final mass with paired t-tests; cannibals, $t=0.86$, $df=11$, $P<0.0001$; insectivores, $t=1.83$, $df=14$, $P<0.0001$). The toads that fed on conspecifics grew less rapidly than those that ate an equivalent mass of

crickets, however [analysis of covariance (ANCOVA) with prey mass ingested as the covariate, mass gain as the dependent variable: slopes homogeneous so interaction term deleted; main effect of diet, $F_{1,24}=9.80$, $P<0.005$; see Fig. 3]. When we repeated the trials to compare growth rates of toads that were fed crickets with or without parotoid gland secretions, growth rates were unaffected by toxin addition (ANCOVA with prey mass ingested as the covariate, mass gain as the dependent variable: slopes homogeneous so interaction term deleted, main effect of diet, $F_{1,23}=0.54$, $P=0.47$).

Discussion

Extensive published analyses of dietary habits show that adult cane toads feed primarily on invertebrate prey, typically small ants, termites, and beetles (Zug et al. 1975; Zug and Zug 1979; Bayliss 1995; Lever 2001). This conclusion is consistent with our limited data on adult toads from the study pond, as well as extensive information from nearby study sites (Greenlees et al. 2006; M. Greenlees, unpublished data). Recently emerged metamorph toads also feed exclusively on tiny invertebrates (Child 2007; T. Child, unpublished data). In striking contrast, however, our data show that intermediate-sized (juvenile) toads function as specialist cannibals under some circumstances, with about two thirds of their prey biomass consisting of

Fig. 3 Growth increments of captive cane toads over a 12-day period as a function of their diet. Twelve toads were fed entirely on juvenile conspecifics, whereas 15 were given crickets. In both cases, food was provided ad libitum; toads grew more rapidly on crickets than on a cannibalistic diet

smaller toads. The population that we studied is an invasive one, and we know relatively little about the ecological parameters of natural populations of cane toads (Zug and Zug 1979). However, the climate of our study area is broadly similar to that over much of the toad's natural range (Lever 2001); hence, many of the same constraints and opportunities are likely to occur. Many ecological aspects of cannibalism in cane toads also display strong analogies with cannibalism in other animal species, as discussed below.

First, body size plays a major role. Cannibalism appears to be characteristic of juvenile cane toads, rather than adults or metamorphs. Similar size-specificity of cannibalism is widespread. Although typically the cannibals are the largest individuals in the population (see Fox 1975; Polis 1981; Crump 1992), as in bullfrogs (Korschgen and Moyle 1955; Bury and Wheian 1984; Schwalbe and Rosen 1988; Stuart 1993; Rogers 1996), a greater incidence of cannibalistic behavior in intermediate-sized individuals has been reported for some fishes, dragonfly larvae, and parasitoid insect larvae (see Polis 1981) as well as the cane toad (present study); and there is one record of a young-of-the-year *Rana pipens berlandieri* with a conspecific in its mouth (Kirn 1949). Similarly, the victims of cannibals are a nonrandom subset of the population, typically the smallest and/or weakest animals (see Polis 1981; Crump 1992). In our cane toad population, the individuals that were eaten were smaller, on average, than the survivors of the same cohort; indeed, many of the animals consumed likely had emerged from the water only recently. Although it is clear that other life history stages of cane toads also engage in cannibalism (e.g., tadpoles eat eggs, and large adults consume smaller conspecifics: Zug et al. 1975; Lever 2001; M. Crossland, personal communication), predation of juvenile animals upon recent metamorphs is the most common such interaction. Why are these particular age or size groups involved? The likely explanations are that:

(1) Newly metamorphosed anurans have limited locomotor abilities and may be especially vulnerable to predation at this time (Wassersug and Sperry 1977; Huey 1980). In at least four species of spadefoot toads (genera *Scaphiopus* and *Spea*) and in the treefrog *Osteopilus septentrionalis*, younger conspecifics cannibalize transforming individuals (Bragg 1964; Crump 1986, 1992; Alford 1999);

(2) These small animals occur at high densities and are accessible because they do not hide in refuges at night when larger conspecifics are active; and

(3) Desiccation risk restricts these two groups (metamorphs and juveniles) to pond margins during the dry season, whereas larger adult toads can disperse into food-rich areas further from water (Freeland and Kerin 1991; Cohen and Alford 1993; Child et al. 2008).
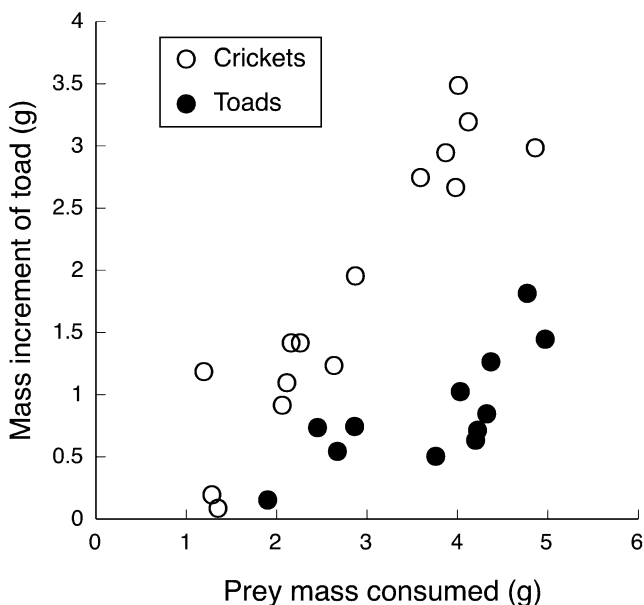
Hence, encounter rates between adult toads and smaller (edible-sized) conspecifics will be much lower than between metamorphs and juveniles; adult toads were rarely seen during our study and those at the pond appeared to be there for rehydration or breeding rather than for feeding (based on their mostly empty stomachs).

The dynamics of cannibalism in cane toads likely depend upon seasonal schedules of precipitation and, thus, toad recruitment and dispersal. The cannibals in our study were toads that had emerged from this same (isolated) waterbody a few months previously, from clutches laid earlier in the wet season (based on growth rates measured in toads at a nearby site: G. P. Brown, personal communication), thus cannibals and metamorphs are unlikely to be siblings. Hence, the prolonged breeding season of toads is critical in that it generates sufficient disparity in ages (and, thus, body sizes) of small toads around a waterbody to enable some individuals to grow large enough to consume others. If breeding was highly synchronized, or if metamorph toads could disperse from the waterbody margins soon after they emerged from the water, cannibalism would be less common; explosive (synchronous) breeding decreases intraspecific predation in *Rana sylvatica* (Petranka and Thomas 1995). Cane toad metamorphs do indeed disperse soon after emergence during the wet season, when the risk of desiccation is virtually eliminated by frequent rain and luxuriant vegetation cover (Child et al. 2008). Thus, the high incidence of cannibalism may be a direct result of the extreme seasonality in precipitation in the wet–dry tropics, coupled with the extended breeding seasonality of cane toads in this area. A similarly central role of reproductive timing is seen in other cases of cannibalism: for example, early-hatching beetles search for, and eat, later-deposited eggs and younger larvae (Kaddou 1960; Brown 1972) and poison-arrow frog tadpoles (*Dendrobates ventrimaculatus*) cannibalize eggs laid later in the wet season (Poelman and Dicke 2006) and, thus, as in *B. marinus*, the cannibals are the early-hatching animals. The incidence of cannibalism also depends on specific conditions in spadefoot tadpoles and larval salamanders. Cannibal morphs of tiger salamanders grow faster than non-cannibals and are more likely to develop in temporary ponds than in permanent ponds (Pfennig 1997). In spadefoot tadpoles, older individuals sometimes are consumed by younger ones (Bragg 1964). Two-legged and four-legged tadpoles usually do not attack conspecifics (even younger ones) in metamorphic aggregations; however, they will promptly attack and eat newly emerged toadlets that fail to leave the water (Bragg 1964).

The incidence of cannibalism (proportion of the diet composed of conspecifics) often varies seasonally (Bulkley 1970; Chevalier 1973; Forney 1974), as it does in cane toads. The proximate mechanisms generating seasonal variation in the incidence of cannibalism vary among species but often may involve seasonal concentration of individuals around specific biotic or abiotic resources (as occurs with toads). High population densities are a strong correlate of cannibalism (see Fox 1975; Polis 1981; Collins and Cheek 1983; Crump 1992), presumably because higher densities provide more opportunities for encounters between conspecifics. Experimental studies show that encounter rates influence the frequency of cannibalism in a range of taxa (Thibault 1974; Fox 1975; Polis 1981). Seasonal depression of alternative food supplies (Fox 1975; Polis 1981; Collins and Cheek 1983), especially of higher quality food (Babbitt and Meshaka 2000), also may militate towards cannibalism and may play a major role in cane toads. Invertebrate biomass falls dramatically with drier cooler conditions at the onset of the dry season, with a concomitant decrease in food intake and body condition of cane toads (G. P. Brown, personal communication). Because the increasingly arid landscape prevents dispersal, the end result is a concentration of increasingly hungry juvenile toads with only one abundant food source: smaller conspecifics.

In some amphibian species, cannibalistic habits typify only a proportion of each cohort, with morphological and behavioral correlates related to the ingestion of conspecifics (reviewed by Polis and Myers 1985; Crump 1992). In some other amphibians, however, all or nearly all individuals take conspecifics as prey (e.g., *Ambystoma tigrinum*: Rose and Armentrout 1976; Lannoo and Bachmann 1984; Holomuzki 1986); thus, conspecifics can comprise a high proportion of prey taken by an entire cohort (e.g., in the frogs *Rana esculenta* and *Rana ridibunda*, conspecific tadpoles and smaller individuals comprise up to 20% of prey volume for adults; Dushin 1975). Most or all juvenile cane toads appear to function as cannibals. We can confidently score willingness to consume conspecifics for the 38 juvenile toads that we tested with "lures" of dead metamorphs. Of these animals, 18 attacked the "lure" and nine of the remainder contained freshly ingested toads in their stomachs. Thus, at least 27 of 38 juvenile toads (71%) acted as cannibals if given the opportunity; we suspect that this would have been true for all individuals if testing were repeated. In our experience, virtually all captive cane toads readily consume smaller conspecifics (L. Pizzatto and R. Shine, personal observation).

In some amphibians, the high incidence of cannibalism among larvae constitutes a major threat to siblings and may have favored the evolution of kin discrimination (Pfennig 1999). For example, spadefoot tadpoles and larval tiger salamanders prefer to consume nonkin conspecifics (Pfennig 1997; Pfennig et al. 1994), and the presence of siblings suppresses the development of cannibalistic morphs (Pfennig and Collins 1993; Pfennig and Frankino 1997). In our

system, cannibal cane toads and their prey differ considerably in size (and, thus, cohort identity); thus, the system is unlikely to create a selective force for kin recognition (Pfennig 1999). However, the high incidence of cannibalism may have imposed significant selection on the behaviors of both potential cannibals and potential victims. For example, toe-luring is most commonly exhibited by medium-sized toads (the same size group identified as cannibals in the present study) and functions to attract edible-sized conspecifics (Hagman and Shine 2008). Similarly, the behavioral traits of metamorph toads may reduce their vulnerability to predation. Most obviously, times of activity differ ontogenetically: all size classes of cane toads except the smallest animals are exclusively nocturnal (Freeland and Kerin 1991). Metamorphs at our study site were virtually immobile at night, even if touched, whereas they were active by day. This response was driven by light levels not temperatures because metamorph toads were similarly immobile if placed under low illumination levels at high temperatures (Pizzatto et al. 2008). Our experimental trials demonstrated that immobility offers an effective defense against predatory conspecifics (as expected from the movement-activated visual systems of toads; Buxbaum-Conradi and Ewert 1999). Ontogenetic shifts from diurnal to nocturnal habits are seen in many species of toads (Bragg 1940; Bragg and Weese 1950; Cunningham 1962; Sievert and Sievert 2005) and may reflect an adaptation to avoid cannibalism in many or all of these taxa.

Cannibalism can have significant consequences at the population level also (Fox 1975; Polis 1980). In extreme cases, cannibalism may eliminate a large proportion of offspring (>90% of chicks and eggs of crows; Yom-Tov 1974) or entire cohorts (see Fox 1975; Polis 1981). Even very low rates of cannibalism can have significant effects on a population (Chevalier 1973). We lack data on the numbers of metamorphs emerging at our study pond, but cannibalism at our study pond may be common enough to significantly influence metamorph survival. We recorded an average of 12 juvenile toads active per night; if each of these animals took a single metamorph per night (as is likely; we sampled early in the evening, so metamorphs caught later in the night were not included in our stomach contents data), then about 12 metamorphs would be consumed each night, or 360 each month, and >1,440 over the critical period in the early to mid-dry season. This predation is imposed on the survivors of density-dependent mortality processes that occur earlier in the life history (Cohen and Alford 1993). The end result may be to reduce total effective recruitment of cane toads from the natal pond (if predation kills animals that would otherwise have survived to disperse in the subsequent wet season) or to increase recruitment (if the death of already-doomed smaller metamorphs enhances survival prospects of a small

number of larger, older animals). Given widespread concerns about the ecological impact of cane toads in Australia (Phillips and Shine 2005), the degree of density-dependence in mortality rates warrants further study.

An intriguing consequence of one size class preying upon a different size class is that juvenile toads obtain nutrients that ultimately are derived from sources (parental investment in egg yolk and tiny invertebrates consumed by metamorphs) from which they would otherwise be unable to extract any benefit. In that sense, cannibalism may enable a population to persist by expanding the range of food sources that it can acquire (the "Life Boat Strategy"; Polis 1980, 1981). If juveniles take many emerging metamorphs, the end result at a population level would be a functional increase in offspring size—and given the very small size of bufonid metamorphs (Cohen and Alford 1993), such an increase might well be favored under circumstances of high desiccation risk (Child et al. 2008). Cannibalism also enhances the survival advantages of reproducing early in the season because it is progeny from these early clutches that grow large enough to function as cannibals later in the season (for similar examples, see Anhold 1994; Kinoshita 1998; Matsushima and Kawata 2005). Several authors have speculated that cannibalism also may benefit the predator by reducing the density of competitors, but this issue is inapplicable to cane toads. The size disparity between cannibals and their prey results in a major divergence in the size of dietary items (mean lengths 1.3 vs. 12.9 mm; Child 2007; T. Child, unpublished data); thus, removing small metamorphs is unlikely to enhance feeding opportunities for larger toads. Lastly, cannibalism might affect population demography by facilitating the spread of parasites (Gajdusek and Alpers 1972; Matuschka and Bannert 1989; Pfennig et al. 1998; Macneil et al. 2003). Some Australian populations of cane toads are heavily parasitized by nematode lungworms (Barton 1998) that can be transferred by direct ingestion (Baker 1979; Smyth and Smyth 1980), and this possibility merits further study because of its potential relevance to toad control (Kelehear 2007).

Lastly, cannibalism can confer an energetic and nutritional benefit to the cannibal, such that cannibals grow faster than their non-cannibal kin (Lannoo et al. 1989; Crump 1992; Wildy et al. 1998). However, our data paint a cautionary picture in this respect. The biomass of ingested prey may be a poor guide to nutritional value in cane toads because a given biomass of metamorphs supported less bodily growth of the predator than did the same mass of insects (crickets). Cannibalism does allow a juvenile toad to grow but not to grow as rapidly as if it had access to invertebrate prey. Similarly, low growth rates from consumption of toads (compared to frogs) have been reported also for snakes that eat these anurans (Llewelyn et al.

2008). This result suggests that cane toads constitute poor-quality food. The most obvious explanation would involve the powerful toxins that they possess, but our second growth-rate experiment suggests instead that the most important factor may be nutritional content rather than costs of detoxifying parotoid secretions. Further work is needed to clarify this puzzling result.

In summary, cannibalism in cane toads is readily interpretable in the light of this species' ecology within the wet–dry tropics. The seasonality of precipitation regimes—and, thus, of the degree of aggregation of metamorphs, the rates of encounter between metamorphs and juvenile toads, and the availability of alternative (insect) prey—ultimately may drive the incidence and timing of cannibalism in this population. Thus, for example, surveys during the wet season show no large juvenile toads remaining near waterbodies; metamorph toads disperse soon after emerging and rarely return to the natal pond (Child et al. 2008). Cane toads appear to rely on cannibalism only under circumstances where smaller conspecifics offer abundant feeding opportunities, and where alternative preys are difficult to find.

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