

## Experimental Assessment of Turtle Predation on Larval Anurans

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The effect of predation by large non-gape-limited vertebrates on the survivorship and size distribution of larvae of four anuran species was assessed using two syntopic freshwater turtle species, *Emys orbicularis* and *Mauremys leprosa*. Predator species and predator sex within species were used as treatments in replicated, factorial experiments for predation trials on tadpoles of *Bufo calamita*, *Hyla meridionalis*, *Rana perezi*, and *Pelobates cultripes*. Tadpole consumption rates were significantly higher for the carnivorous *E. orbicularis* than for *M. leprosa*. *Rana perezi* tadpoles were the least consumed, whereas *P. cultripes* and *H. meridionalis* had the lowest survivorship rates, being relatively easier to catch than *R. perezi*. Significant size selection occurred for larger tadpoles of *P. cultripes*, whereas predation upon *R. perezi* tended to concentrate on the smaller size classes. The results point to an overall tendency of turtles to predate upon large tadpoles, yet the outcome of size selection by large vertebrates may depend on phenotypic traits that enhance the escape potential of tadpoles. *Mauremys leprosa* had a high rejection rate of tadpoles, suggesting a higher sensitivity to unpalatability as compared to *E. orbicularis*, especially with relation to *R. perezi*. The results indicate that the effect of unpalatability as a predation deterrent may vary even among taxonomically close predator species.

PREDATION is considered by various authors to be the main biotic factor structuring larval anuran communities (Smith, 1983; Wilbur et al., 1983; Toft, 1985). Both vertebrate and invertebrate predators may affect tadpole assemblage structures by influencing habitat use and activity patterns (Werner, 1991; Kupferberg, 1998; Schmidt and Amézquita, 2001), constraining the outcome of competition scenarios (Zaret and Paine, 1973; Morin, 1983) and ultimately limiting the distribution and relative abundance of tadpole species (Gascon, 1992; Skelly, 1997; Azevedo-Ramos et al., 1999).

Body size is a primary determinant of tadpole survivorship in predator-prey interactions. It follows from a large number of studies that invertebrate predators of tadpoles are size-limited, and many vertebrate predators (other tadpoles, fish, salamanders) are gape-limited, causing consumption rates to decrease with increasing tadpole size (Caldwell et al., 1980; Formanowicz, 1986; Richards and Bull, 1990). Otherwise, intra- and interspecific differences in tadpole mobility and activity levels may also strongly affect predation success, generally favoring the survival of less active and fast sprinting species (Woodward, 1983; Chovanec, 1992; Skelly, 1994).

The effect of large vertebrate predators on tadpoles is much less known (but see Crump and Vaira, 1991; Devito et al., 1998; Rödel, 1999). Nonetheless, large vertebrate predators are thought to be capable of total eradication of tadpole populations from a pond, thus de-

termining the distribution pattern of tadpoles in the landscape (Heyer et al., 1975). Because both the total abundance of predators and the abundance of vertebrate predators increases with pond size and permanence (Wellborn et al., 1996; Pearman, 1995), more vulnerable tadpole species are probably limited to smaller, ephemeral, relatively predator-free ponds (Morin, 1983; Woodward, 1983). Yet the relative safety of ephemeral habitats in relation to predation applies to water-bound organisms such as fish, which are important predators in permanent water bodies (Wellborn et al., 1996; Goodsell and Kats, 1999) but may not be effective in relation to animals that can move among ponds (e.g., birds, snakes, turtles) and predate upon tadpole populations even in very small, ephemeral pools (Newman, 1987).

In this study, we aimed to experimentally test the effect of predation by two large and mobile vertebrates on different larval anuran species. In aquatic habitats of southwestern Spain, the freshwater turtles *Emys orbicularis* and *Mauremys leprosa* are among the most common potential large vertebrate predators of tadpoles. Both species are similar in body size and may be locally abundant in permanent and temporary ponds. Turtles frequently move among ponds (Keller, 1997), potentially posing a threat to tadpole populations even in small, ephemeral ponds, where fish and other water-bound predators are absent. Peak densities of many tadpole species coincide with the main activity season of turtles in spring (Díaz-Paniagua, 1988; Keller, 1997).

This is also the egg-production phase of turtles (Keller, 1997), therefore a period when females are especially active and have high energetic requirements.

Both turtle species consume animal matter, although *M. leprosa* feeds largely on plants, whereas *E. orbicularis* is an almost strict carnivore and insectivore (Keller and Busack, 2001). Dietary analysis failed to identify tadpole remains in turtle fecal samples (C. Keller and J. L. Garcia-Mudarra, unpubl. data) but turtles of both species were observed to consume tadpoles caught in traps, indicating that both species potentially exploit tadpoles as a food resource.

Besides being capable of high prey consumption rates and of frequently moving among water bodies, turtles are not size- or gape-limited to predate upon larger tadpole size classes (Rödel, 1999; Kupferberg, 1998). On the premise of optimal foraging theory (Krebs, 1978), as long as the energetic requirements for capture and handling prey are not limiting, large predators are expected to select large prey, as was reported for an avian predator of tadpoles (Crump and Vaira, 1991). In addition to size, tadpole habit and activity patterns influence prey selection by large vertebrates, favoring the consumption of slow swimming, highly active tadpoles (Lawler, 1989; Rödel, 1999). Tadpole unpalatability has been suggested as one of the primary factors that decrease predation risk by fish (Kruse and Francis, 1977; Formanowicz and Brodie, 1982). Yet the reported effects of tadpole palatability on vertebrates are variable. Tadpoles from different species of *Rana*, *Bufo*, and *Hyla*, which are generally palatable to invertebrates (Formanowicz and Brodie, 1982, Azevedo-Ramos and Magnusson, 1999) were unpalatable to fish in tropical environments and humans (Wassersug, 1973; Azevedo-Ramos and Magnusson, 1999), but were heavily preyed upon by mosquito fish (Goodsell and Kats, 1999). Also, embryos of *Bufo calamita* were left intact by some *Triturus* newts (Denton and Beebe, 1991) but were palatable to predatory tadpoles (Heyer et al., 1975; Tejedo, 1991).

The relative predatory impact of both turtle species on anuran tadpoles was assessed experimentally, using larvae of four anuran species common in southwestern Spain as prey: *B. calamita*, *Hyla meridionalis*, *Rana perezi*, and *Pelobates cultripipes*. These tadpole species differ in their relative size, microhabitat use, sprint performance, and likely, unpalatability (Barbadillo et al., 1999, Salvador and Garcia-Paris, 2001). Experiments were designed to test (1) whether turtle species, and turtle sex within species, dif-

fered from one another in predatory impact on the different anuran species; (2) whether large predators should select larger tadpoles from any sample offered, according to the optimal foraging postulate; and (3) whether any of the tadpoles is unpalatable to turtles.

#### MATERIALS AND METHODS

Tadpoles were captured by dipnetting in temporary ponds in April 1999. All *B. calamita* and *P. cultripipes* and most *H. meridionalis* and *R. perezi* came from Sierra Morena and Sierras Subbéticas; a small sample of *H. meridionalis* and *R. perezi* came from Doñana National Park (all sites in southwestern Spain). The four tadpole species occur at the three capture sites, whereas turtles are common in Doñana N.P. but rare or absent at the other sites. Thus, we assumed that the possible confounding effect of differential previous exposure to predators, which can affect tadpole behavioral responses and morphology (Semlitsch and Reyer, 1992; Griffiths et al., 1998; Van Buskirk, 2002), was negligible in our experiments. Tadpoles were taken to the experimental site, an outdoor facility located some 100 km away from the trapping sites. Tadpoles were kept separated by species in plastic containers until the day of the experiment and were fed Rabbit Chow every other day.

Turtles were trapped using baited fyke nets in eight different ponds within Doñana N.P., ranging from ponds that dry each summer to those that are permanent for several years. Pond size varied from 0.02–18.0 ha surface area. Both species occur in four of the ponds, whereas the three smallest and most ephemeral ones are inhabited exclusively by *E. orbicularis* (Keller, 1997). At least one of the anuran species used in this study bred in each of the ponds (Table 1). Turtles used in each predation trial were trapped two to seven days prior to the day of the experiment. Within species, only adults of similar body size were employed. Body size did not differ between the sexes but differed significantly between species, owing to *M. leprosa* being larger than *E. orbicularis* (average straight carapace length: *M. leprosa* =  $174 \pm 12.0$  mm;  $n = 30$ ; *E. orbicularis* =  $149.1 \pm 6.0$  mm;  $n = 31$ ). Turtles were transported to the experimental site within three days of capture, kept in outdoor plastic pools of 150 cm diameter and 50 cm depth, filled with approximately 200 liters of outdoors-aged well water (30 cm water column), and fed fish and crayfish when captive periods exceeded two days.

TABLE 1. HYDRIC REGIME (HR), SURFACE AREA, RELATIVE ABUNDANCE OF *Emys orbicularis* AND *Mauremys leprosa* (AVERAGE NUMBER OF INDIVIDUALS CAPTURED PER TRAP AND TRAPPING-DAY DURING APRIL TO MAY 1991–1999) AND PRESENCE OF TADPOLES OF *Pelobates cultripes*, *Rana perezi*, *Hyla meridionalis*, AND *Bufo calamita* IN THE PONDS OF ORIGIN OF TURTLES USED IN THIS STUDY. P = permanent, SP = semipermanent, E = ephemeral. Tadpoles were trapped or sighted on one or more occasions from 1991–1999 (J. Román and H. Lefèvre [pers. comm.] and C. Keller and I. Gómez-Mestre [pers. obs.]).

HR	Area (ha)	<i>M. lep.</i>	<i>E. orb.</i>	<i>P. cul.</i>	<i>R. per.</i>	<i>H. mer.</i>	<i>B. cal.</i>
P	18.0	3.7	0.4		X		
P	3.5	6.0	3.3	X	X	X	
P	2.6	1.0	0.3	X	X	X	
SP	1.5	1.0	1.9	X			
E	0.3	0	1.1	X		X	
E	0.2	0	2.3			X	X
E	0.02	0	2.8		X	X	
E	0.02	0	0.6	X		X	X

*Experimental procedures.*—Each experiment was designed to compare the differential survivorship of one larval anuran species when exposed to predation by each of the two turtle species. Turtle sex was introduced as a factor within the main experimental factor, predator species. Therefore a 2 (*E. orbicularis*/*M. leprosa*) × 2 (male/female) factorial experiment was set for each prey species, using the previously described plastic pools as experimental units. The experiment was replicated four times in a four-block randomized design, where each block contained all treatments, spatially randomized. All tadpoles employed in the experiments were in the stages of early hind-limb development (roughly between stages 26 and 37 Gosner [Gosner, 1960]). We assumed that within species palatability of all tadpoles was similar, since changes in palatability have been reported only toward the metamorphic stages (Formanowicz and Brodie, 1982). Each turtle was used only once in the experiments to avoid pseudoreplication. Exceptions were made for two *M. leprosa* males, which were used in two trials each, because only 14 males were captured, and one *E. orbicularis* female used twice in substitution of another female, which was found to have an amputated forelimb. Repeated use of a turtle was always with a different prey species. Turtles were starved for 48 h prior to the predation trial. Because both tadpoles and turtles are capable of chemosensory detection of predators (Petranka et al., 1987; Jackson, 1990; Laurila et al., 1998) and thus probably of prey, the water was renewed in the containers between experiments, to avoid possible behavioral responses to the chemical cues either of predators or prey in subsequent trials.

Experiments were carried out on four differ-

ent days (one day for each potential prey species) between 14 April and 19 May 1999. Because activity levels of both turtles and tadpoles are influenced by ambient temperature, we minimized environmental variation by starting all trials when the water temperature in the containers had reached 21–22 C (starting time ranged from 1130 to 1530, depending on weather conditions). Water temperature at the end of the experiments varied from 21.5–24 C. In each trial, one of 16 turtles (four of each sex per species) was introduced into one of 16 pools (described above) 2 h prior to the beginning of the experiment, to allow for acclimatization of turtles to the experimental conditions before the addition of tadpoles. Tadpoles were exposed to turtles for 4 h. After removing the turtles, all surviving tadpoles were counted and measured. Tadpoles that were killed and not consumed were also recorded. All turtles showed normal feeding and basking behavior after the experiments.

To make the experiments comparable and to avoid satiation effects caused by differences in species-specific prey sizes, the number of tadpoles from each species offered to the turtles was adjusted to fit approximately the same value of wet biomass. To assess average species-specific values of individual wet biomass, we weighed a sample of tadpoles from each species (blotted dry on filter-paper) to the nearest 0.1 mg. Because of limitation in tadpole availability we achieved only 30% biomass equivalence for *H. meridionalis*. Tadpole sample sizes offered were 315 *B. calamita*, 14 *H. meridionalis*, 20 *R. perezi*, and 18 *P. cultripes*.

Response variables were tadpole survivorship rate (the proportion of tadpoles from the initial sample that survived the exposure to one tur-

TABLE 2. AVERAGE SURVIVORSHIP AND REJECTION RATES OF FOUR TADPOLE SPECIES (*Bufo calamita*, *Hyla meridionalis*, *Rana perezi*, AND *Pelobates cultripes*) IN PREDATION TRIALS BY FRESHWATER TURTLES *Emys orbicularis* AND *Mauremys leprosa*. Values are arithmetic means followed by the range, in parentheses. Chi-square estimates and p-values for tests examining differences between turtle species are also provided.

Prey species	<i>E. orbicularis</i>	<i>M. leprosa</i>	$\chi^2$	P
Survivorship rate				
<i>B. calamita</i>	0.54 (0.00–0.99)	0.93 (0.89–1.00)	6.50	0.0108
<i>H. meridionalis</i>	0.06 (0.00–0.29)	0.54 (0.07–0.93)	10.15	0.0014
<i>R. perezi</i>	0.65 (0.00–1.00)	0.89 (0.70–1.00)	2.99	0.0837
<i>P. cultripes</i>	0.00 (—)	0.53 (0.00–0.83)	62.43	<0.0001
Rejection rate				
<i>B. calamita</i>	0	0	—	—
<i>H. meridionalis</i>	0.009 (0–0.07)	0.15 (0–1)	8.55	0.0035
<i>R. perezi</i>	0.008 (0–0.05)	0.10 (0.50–1)	72.13	<0.0001
<i>P. cultripes</i>	0	0.15 (0–0.82)	14.88	0.0001

tle), consumption rate (proportion of tadpoles from the initial sample that were killed and consumed by one turtle), and rejection rate (the proportion of tadpoles killed by one turtle that were expelled and left uneaten). The rejection rate was assumed to be indicative of unpalatability.

Prey size selection was assessed by measuring the total body length of subsamples of at least 60 tadpoles from the initial species pools and comparing the initial body length distribution with that of the pooled survivors per treatment using generalized linear models (GLM). We measured total body length to the nearest millimeter by placing live tadpoles into a water-filled Petri dish placed on graph paper. We measured all surviving *H. meridionalis* and *P. cultripes* and random samples of 120 *B. calamita* and 60 *R. perezi*, which had higher numbers of survivors.

The fractional nature of the data (a proportion of the initial sample of available prey) required the adjustment of the error distribution to a binomial instead of a normal probability distribution. Contrast analyses were designed for planned comparisons between predator species (main effect) and predator sex within species (secondary effect). The experimental block was held as a random factor but, since its effect was always nonsignificant, it was removed from the final models. Analyses were carried out with the GENMOD procedure of SAS version 8.00, which allows the use of nonnormal error distribution of the data and also provides likelihood ratios instead of the sums of squares of the GLM procedure.

## RESULTS

*Effect of predator species and sex.*—*Emys orbicularis* was a more efficient predator than *M. leprosa* in

all cases, causing significant decreases in survivorship rates of *B. calamita*, *H. meridionalis*, and *P. cultripes* (Table 2). *Emys orbicularis* consistently eliminated all *P. cultripes* in all trials but had a more variable behavior with the other species. The lower survivorship of *B. calamita* exposed to *E. orbicularis* was caused by three turtles that predated upon 90–100% of the tadpole sample, all remaining tadpole survivorship rates varying from 0.57–0.99. Likewise the lower survivorship of *R. perezi* exposed to *E. orbicularis* was caused by two individuals that consumed 100% of tadpoles, the remaining survivorship rates (0.70–1.00) being similar to those obtained for *M. leprosa*. No differences were observed in tadpole survivorship when comparing males and females within predator species, except for a significantly lower survivorship of *P. cultripes* exposed to female *M. leprosa* ( $\chi_1^2 = 7.15$ ,  $P = 0.0075$ ).

*Evidence for size selection.*—*Pelobates cultripes* surviving exposure to *M. leprosa* were significantly smaller ( $F_{1,9} = 71.09$ ,  $P < 0.0001$ ), while *R. perezi* exposed to *E. orbicularis* were significantly larger ( $F_{1,8} = 6.04$ ,  $P = 0.039$ ) than tadpoles from the initial pool (Fig. 1). No evidence for size selection was observed for *B. calamita* and *H. meridionalis*, nor for *R. perezi* exposed to *M. leprosa*.

*Evidence for tadpole unpalatability.*—With the exception of *B. calamita*, significant differences were observed in rejection rates between turtle species (Table 2, Fig. 2), whereas rejection rates were < 1% in all cases for *E. orbicularis*, *M. leprosa* rejected, on average, from 50% to almost 90% of tadpoles killed. As a consequence, consumption rates differed more between predator species than tadpole survivorship rates. Notably, all *R. perezi* tadpoles killed were rejected by *M.*

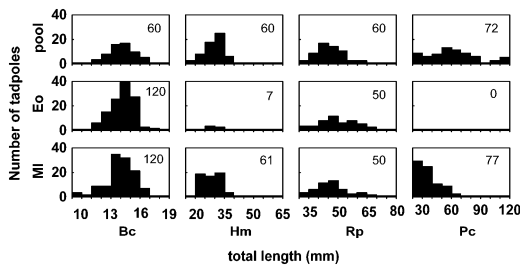


Fig. 1. Size distribution of tadpoles sampled from the initial pool (pool) and surviving predation trials by freshwater turtles *Mauremys leprosa* (Ml) and *Emys orbicularis* (Eo). Bc = *Bufo calamita*; Hm = *Hyla meridionalis*; Rp = *Rana perezi*; Pc = *Pelobates cultripes*. Numbers above histograms indicate sample size. Histograms for *B. calamita* survivors are truncated at  $n = 40$ .

*leprosa* except for two females that swallowed one tadpole each. For *H. meridionalis* and *P. cultripes* individual rejection responses of *M. leprosa* were more variable, ranging from 100% rejection to nearly 100% consumption of the predated tadpoles.

#### DISCUSSION

*Effect of predator species and sex.*—*Emys orbicularis* was a more efficient predator than *M. leprosa* in all cases. *Emys orbicularis* is an almost exclusive consumer of animal prey in Doñana, whereas *M. leprosa* feeds predominantly on plants (Keller and Busack, 2001). Direct observations in the experimental pools also indicated that, although *E. orbicularis* made frequent capture attempts, *M. leprosa* tended to ignore tadpoles more often.

In nature, nearly 30% of live animal biomass ingested by *E. orbicularis* is composed of small invertebrates, whereas *M. leprosa* favors crayfish and fish as animal prey (C. Keller and J. L. Garcia-Mudarra, unpubl. data). The habit of capturing small animals may explain why *E. orbicularis* was a more efficient consumer of smaller tadpoles like *B. calamita*.

Lower survivorship rates of *P. cultripes* (the largest tadpole species tested) when exposed to female *M. leprosa* as compared to males, seemed to indicate that females favored larger, probably energetically more rewarding prey, which may be caused by females being in the demanding egg-producing phase. Consumption rates of all tadpole species for female *E. orbicularis* (also in egg-maturing phase) were higher than those of female *M. leprosa*, but, unlike male *M. leprosa*, male *E. orbicularis* were as voracious as females.

The intraspecific individual variability in

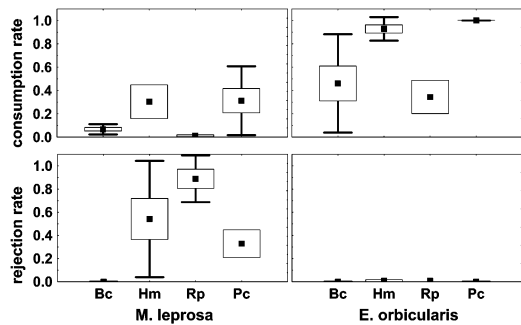


Fig. 2. Species specific relative frequencies of consumed and rejected tadpoles in predation trials by freshwater turtles *Mauremys leprosa* and *Emys orbicularis*. Points indicate the arithmetic mean, boxes  $\pm$  SE, and bars  $\pm$  SD. Bc = *Bufo calamita*; Hm = *Hyla meridionalis*; Rp = *Rana perezi*; Pc = *Pelobates cultripes*.

predatory efficiency of turtles observed in our experiments is likely to reflect differential foraging strategies or abilities. This might be related to distinct habits of microhabitat use, to individual differences in reaction time and sprint capacity or even different sensitivity to unpalatability (as suggested by the variance in rejection rates of *Hyla* and *Pelobates* tadpoles by *M. leprosa*). Studies concerning foraging habits of vertebrate species in the wild are traditionally standardized on the population level and usually overlook individual variation. However, individual variation in foraging strategies may cause considerable fitness differences among individuals (Grant and Grant, 1996; Annett and Pierotti, 1999; Fedriani and Kohn, 2001) and may, in turn, differentially affect prey fitness at the local scale.

*Evidence for size selection.*—*Pelobates cultripes* was predated upon frequently and consumed more frequently. The complete eradication of all *P. cultripes* by *E. orbicularis*, and the selection of larger tadpoles by *M. leprosa* both indicate that turtles tended to favor the capture of larger prey, in agreement with predictions of optimal foraging theory. In contrast with our predictions, however, *R. perezi* (the second largest prey species in body size), was the least consumed. Moreover, *E. orbicularis* predated more heavily on smaller *R. perezi* tadpoles. *Pelobates* tadpoles of the same length as *Rana* are bulkier, whereas *Rana* has a more streamlined profile and more powerful tail muscles, higher speed and greater maneuverability, which makes them less susceptible to predation than *Bufo* and *Hyla* (Chovanec, 1992; Richardson, 2001). Likewise, successful escapes of other tadpole species were related more to burst speed and maneuverability than

to stamina (Feder, 1983). Frustrated predation attempts of *E. orbicularis* on *R. perezi* occurred when tadpoles outmaneuvered the turtle, performing fast and short strokes in a direction other than the persecution line. Thus, the capture of *R. perezi* tadpoles probably has a higher energetic cost to turtles compared to slower species, and the enhancement of the escape performance associated with an increase in body size probably outbalances the benefits obtained from capturing larger prey. The higher predation rates upon *H. meridionalis* tadpoles in comparison with *R. perezi* were likely a consequence of the resemblance between the *Hyla* and *Pelobates* morphotypes as well as of the lower amount of *Hyla* biomass offered to turtles.

*Evidence for unpalatability.*—Besides being difficult to catch, all but two *R. perezi* tadpoles killed by *M. leprosa* were rejected. The same reaction was observed for *Ambystoma* newts predating upon *Rana sphenocephala* (Morin, 1983). These observations indicate that *Rana* tadpoles may be unpalatable to some vertebrates. Yet the fact that practically all *R. perezi* captured by *E. orbicularis* were readily consumed suggests that tadpole palatability may vary even among taxonomically close predator species, which was also observed by Banks and Beebee (1988) for predation of *B. calamita* and *Bufo bufo* tadpoles by three *Triturus* species. These observations suggest that the defensive value of producing substances aimed at distastefulness in terms of tadpole fitness may be highly dependent on the local composition of the predator guild at different ponds.

Contrary to expectations based on reports of unpalatability of *Bufo* embryos and tadpoles to vertebrate predators (Heyer et al., 1975; Denton and Beebee, 1991; Azevedo-Ramos and Magnusson, 1999) unpalatability seemed to be no deterrent to predation of *B. calamita* by *E. orbicularis* and *M. leprosa*, judged by the absence of rejected tadpoles. *Bufo calamita* have weaker axial musculature and are slower swimmers than comparable sized *Rana* tadpoles (Wassersug and Hoff, 1985), and their aggregation behavior and tendency to continuous activity makes them particularly vulnerable to visually oriented predators (Wassersug, 1973; Heyer et al., 1975; Chovanec, 1992). Thus higher evasiveness is unlikely to have been the cause of *Bufo* experiencing lower predation by turtles than either *Hyla* or *Pelobates*. Possibly the small size of *B. calamita* tadpoles, which was below the minimum sizes of all other tadpole species tested, made them less attractive to most turtles.

The 100% predation rates observed for *B. cal-*

*amita* by some *E. orbicularis*, however, indicate that individual *E. orbicularis* may be highly efficient predators of *B. calamita* in its usual breeding pools, which bear a closer resemblance with the experimental pools than most other amphibian breeding habitats. The adaptive advantage attributed to the use of very small ephemeral ponds as breeding sites by anurans is the reduction of predation pressure on larvae by aquatic predators (Woodward, 1983; Roth and Jackson, 1987; Pearman, 1995). In the present context, the robustness of this hypotheses deserves to be tested with relation to large vertebrate predators that are not bound to water, which have a much higher potential for consumption and for which the crowding and higher exposure of tadpoles in small pools may act as a facilitator of predation success. Newman (1987) found indirect evidence of turtles acting as total eradication agents of tadpole populations in small desert pools.

Although the biological significance of our results in natural conditions will be mediated by other factors, like availability and abundance of other food resources for turtles, habitat complexity, and the previous experience of tadpoles with predators, the evidence produced favors the notion that the impact of both turtle species—especially *E. orbicularis*—on tadpole populations is substantial. Our results suggest that turtles are generally keen on larger tadpoles, either because they are easier to see when they move, or because they represent a higher energy reward per unit of effort (as for *P. cultripes*) and, otherwise, that limitations like visual accuracy and sprint speed or maneuverability may impose prey size limitations even to predators that are not gape-size limited. Moreover, tadpole traits widely accepted as defensive strategies against vertebrate predators, like unpalatability, may vary in efficiency among predators of the same guild. Therefore, the presence of turtles in anuran breeding areas should not be overlooked in studies concerned with the conservation and ecological dynamics of tadpole assemblages.

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