

THE INVASION ECOLOGY OF THE TOAD *BUFO MARINUS*: FROM SOUTH AMERICA TO AUSTRALIA

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Abstract. Mark–recapture studies indicate that *Bufo marinus* populations introduced into Australia tend to attain densities much higher than those reported in native habitats in South America. Moreover, its high rate of spread into northern Australia is raising concerns about the local fauna. The major ecological factors contributing to the observed differences in density are unknown. A population model based on empirical data from both continents was derived to explore the relationship between the life history parameters and population densities of this species, and to identify those parameters most likely to explain the differences in densities observed between continents. Model predictions seem consistent with the empirical data. The model predicted equilibrium densities in Australia one order of magnitude higher than those reported in South America. Moreover, a sensitivity analysis showed that adult equilibrium densities were much more sensitive to variations in adult survival than to variations in any of the other parameters at high densities. Coincidentally, it is adult survival for which the biggest differences between continents have been detected, suggesting that the higher toad densities reported in Australia are likely to be the result of higher adult survival in that continent. On the other hand, the high sensitivity of adult equilibrium densities to adult survival also has important implications for control of this species in Australia.

Key words: Australia; Brazil; *Bufo marinus*; population densities; population dynamics; species invasions; stage-structured model; Venezuela.

INTRODUCTION

Many species introductions into new geographic areas are well known for their devastating effect upon native fauna (Elton 1958, Usher 1986, Bright 1996). In many cases, the introduced species attain densities much higher than those observed in areas where they are native. For example, rodent populations are reported as “unusually” higher on islands where they have been recently introduced (Gliwicz 1980), the introduced European rabbit attained enormous densities in Australia and England, where it was regarded as a pest (Fenner 1983), and some commercial fish species have undergone “unexpected” demographic explosions upon introduction into Hawaii (Devick 1989, cited in Bunkley et al. 1994). Furthermore, many species introduced as control agents have unexpectedly become pests in their own right, e.g., cats, dogs, and mongooses, once introduced as control agents against rats in some islands (Seaman and Randall 1962, Dobson 1988).

A great deal of effort has been devoted to understanding the ecological changes brought about in native species following the introduction of a new species (Brockie et al. 1988, Pimm 1989, Simberloff 1995) and understanding which factors determine the probability

of success of an invading species (Crawley 1986, Newsome and Noble 1986, Usher 1988, Pimm 1989, Kareiva 1996). A traditional way of addressing the issue of which factors may control the abundance of animal and plant populations is to discriminate between bottom-up and top-down mechanisms (Begon et al. 1990). Herbivory, predation, and parasitism regulate populations from the top, whereas competition for food, space, light, nutrients, and resources, in general, are the fundamental bottom-up mechanisms. Accordingly, four hypotheses have been proposed to explain the demographic explosions of introduced species: (1) introduced species may exploit a resource not fully utilized by native species; (2) reproduction of the introduced species may be favored as a result of a decrease in inter- and/or intraspecific competition due to the availability of native prey that have not evolved effective antipredatory strategies; (3) predation pressure on the introduced species may be lower because predators cannot recognize this species as a potential prey; and (4) introduced species may have a depauperate pathogenic fauna because native pathogens were left behind in the process of introduction (Dobson 1988). All of these hypotheses stem from the fundamental idea that species evolve within ecosystems, and their removal from this evolutionary context may bring about important changes in their ecology.

The invasion and establishment of *Bufo marinus* in Australia is an interesting case study, because this spe-

Manuscript received 27 September 1996; revised 15 May 1997; accepted 14 July 1997; final version received 4 September 1997.

cies, introduced as a control agent into Northern Queensland in 1929, is today a subject of biological control itself. Having a diet predominantly composed of insects, *B. marinus* was thought to be a promising control agent against the gray-backed cane beetle *Deromolepida albohirtum* and the Frenchi beetle *Lepidiota frenchi*. Later, published work indicated that beetles are an important food item in the *B. marinus* diet in native habitats (Weber 1938, Zug and Zug 1979, Evans and Lampo 1996). Surprisingly, not only did *B. marinus* fail to control these pest beetles, but also it is currently believed to threaten some native Australian animal species (Covacevich and Archer 1970). Moreover, its potential geographical distribution makes vast wetland areas in Australia, such as Kakadu and Myall Lakes National Parks, highly sensitive "target areas" for *B. marinus* (Sutherest et al. 1995).

The urge to design control strategies against *B. marinus* in Australia has raised fundamental questions about its ecology in its native habitats and in those areas where it has been introduced, and about major ecological changes to which this species has been subjected upon its introduction into Australia. To address these questions and to devise control strategies against *B. marinus*, series of studies have been carried out in South America and Australia in the last decade (Freeland 1986, Freeland et al. 1986, Hearnden 1991, Cohen and Alford 1993, Bayliss 1994, Alford et al. 1995, Cohen and Alford 1996, Lampo and Bayliss 1996a, b, Lampo and Medialdea 1996, Schwarzkopf and Alford 1996). As a result, *B. marinus* is probably one of the few amphibians for which life history and population data are available from within and outside its natural range. A comparative analysis of some of these data has revealed differences between Australian and South American populations. The most notorious of these is that *B. marinus* tends to attain higher densities in Australia than in South America. Mark-recapture density estimates from 28 localities in Australia, 22 in Venezuela, and two in Brazil showed that average densities in Australia are one order of magnitude higher than in South America: ~20 adults/100 m of shoreline in South America (Lampo and Bayliss 1996a) vs. 1000–2000 adults in Australia (Alford et al. 1995). However, the major ecological factors contributing to these differences in densities are not clear.

Here, we (1) derive an age-structured population model that describes the life cycle of *B. marinus*, to explore the relationship between life history parameters and population densities; (2) summarize the available data relevant to the model; and (3) identify, by means of a sensitivity analysis, those parameters most likely to explain the differences in densities between continents. This analysis allows us to discuss how the three proposed hypotheses of demographic explosion of non-native species apply to the specific case of the introduction of *B. marinus* in Australia. Potential im-

plications for controlling population densities are briefly illustrated in light of our findings.

METHODS

Life cycle

Female *Bufo marinus* lay their eggs in water bodies. Within 2–4 d, these eggs hatch into tadpoles that feed and develop in unpredictable and potentially hostile aquatic environments. Tadpoles metamorphose 14–28 d later, depending on water temperature (Hearnden 1991, Bayliss 1994), and leave the water, moving inland toward terrestrial refuges to avoid dehydration and predation (Zug and Zug 1979, Cohen and Alford 1993, Bayliss 1994). Eggs hatched during the late dry season will become metamorphs before the late wet season, when food availability is higher and moisture stress is lower (Bayliss 1994). Juveniles invest most of their energy in growth (Bayliss 1994). Although *B. marinus* seem capable of reproducing during the first year (Alford et al. 1995), most seem to delay reproduction to the second year to take advantage of a second rapid growth period during the wet season (van Beurden 1980, Bayliss 1994). Once they become reproductive, growth slows down significantly (Zug and Zug 1979, van Beurden 1980). Because ovarian development is dependent upon the accumulation of fat tissues during the wet season (Vijayakumar et al. 1971, Jørgensen 1982, Jørgensen et al. 1986, Lampo and Medialdea 1996), it is unlikely that females reproduce more than once a year.

The model

Based on the available knowledge on the *B. marinus* life cycle, we derived a population model to explore the relationships among fecundity, stage-specific survival, and adult density. The model presented herein is the simplest time-based matrix population model that separates the adult reproductive stage from juvenile stages and is able to account for the different sources of mortality affecting eggs, tadpoles, and metamorphs during the first year of life.

Individuals are counted as juveniles *J* (1 yr old) or adults *A* (≥ 2 yr old) at the end of the dry season each year, just before reproduction takes place. A schematic representation of the model is shown in Fig. 1. The $A \rightarrow J$ transition describes the reproduction and survival of *B. marinus* throughout larval and juvenile development during the first year. The $J \rightarrow A$ transition, on the other hand, describes the survival throughout the juvenile stage (pre-reproductive), during the second year. Toads may also survive as adults after the second year and reproduce in the following breeding seasons. The $A \rightarrow A$ transition describes the survival of older adults. The dynamics of the system are thus defined as follows:

$$N_{t+1} = M_t N_t \quad (1)$$

where t is measured in years;

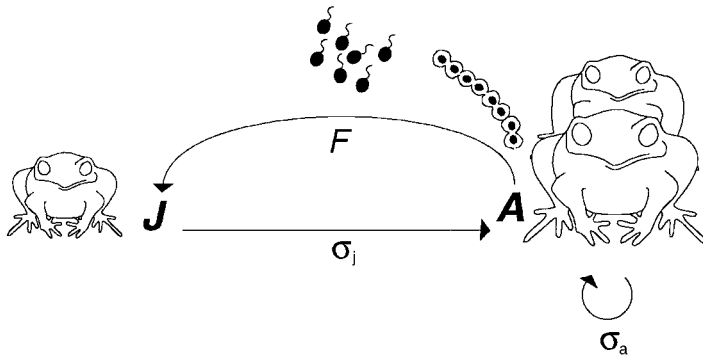


FIG. 1. *Bufo marinus* life cycle. F describes the recruitment to the juvenile stage, J ; σ_j the survival from juvenile to adult, A , and σ_a the survival of adults beyond the first year. Transition times correspond to 1 year.

$$M_n = \begin{pmatrix} 0 & F \\ \sigma_j & \sigma_a \end{pmatrix} \text{ and } N_t = \begin{pmatrix} A \\ J \end{pmatrix}_t \quad (2)$$

where σ_j and σ_a are the annual survival in juvenile and adult classes, respectively, and F is the product of toad fertility and survival from the egg to the juvenile stage (Fig. 1).

The model was parameterized with data from different sources. Estimates for clutch size and survival of eggs, metamorphs, and adults are summarized in Table 1. Clutch size, ϕ , was approximated by the number of oocytes inside females shortly before the breeding season in Venezuela (Lampo and Medialdea 1996) and Australia (Hearnden 1991). Estimated clutch sizes indicated that a single female may mature 3200–84 000 oocytes at once, depending on her body size or mass (Hearnden 1991, Lampo and Medialdea 1996). No evidence has been found suggesting that *B. marinus* has a greater reproductive ability in Australia than in South America. On the contrary, average fecundities estimated over three sites in Australia (Hearnden 1991) and four sites in Venezuela (Lampo and Medialdea 1996) have shown that South American toads tend to be more fecund than Australian ones (77.121 oocytes/g of body mass for Venezuela, from Lampo and Medialdea 1996; 51.023 oocytes/g of body mass for Australia, from Hearnden 1991; $t = 3.90$, $df = 79$, $P < 0.0001$).

Data on egg survival, σ_e , were only available from two Australian sites (Hearnden 1991). This study indicated that egg survival (71.8%) is most affected by cannibalism by *B. marinus* tadpoles when different cohorts overlap. Moreover, experimental evidence has suggested that eggs of this species are not palatable to most fish and many aquatic insects from South America (C. Ramos, *personal communication*) or Australia (Hearnden 1991). If predation by native species is not an important mortality source for *B. marinus* eggs, we do not expect differences in egg survival between continents. Therefore, values for egg survival estimated in Australia were used to predict adult densities in both continents.

Metamorph survival, σ_m (from metamorphosis to juvenile stage), on the other hand, was estimated in both continents. In Brazil, Bayliss (1994) followed cohorts under natural conditions from metamorphs to the juvenile stage and estimated recruitment to the juvenile stage by mark–recapture methods. In Australia, Cohen and Alford (1993) used enclosure experiments at three sites. They suggested that desiccation is the main mortality source when metamorphs leave the water and move into the forest to find refuges, and argued that density may affect survival if the availability of retreat sites is limited. Unfortunately, there are no data allowing us to estimate the density-dependent function for metamorph survival. We therefore assumed that a con-

TABLE 1. Population parameters for *Bufo marinus*.

Population parameter	Mean	Range	Site	Source
Clutch size (ϕ)	15 000	7500–20 000	Australia	Hearnden (1991)
	19 472	3200–84 000	Venezuela	Alford et al. (1995) Lampo and Medialdea (1996)
Egg survival (σ_e)	71.8%	68.8–73.8%	in situ, Australia	Hearnden (1991)
Metamorph survival (σ_m)	5%	1.2–17.6%	in situ, Brazil	Bayliss (1994)
			in situ, Australia	Cohen and Alford (1993)
Juvenile survival (σ_j)	2%	1–5%	in situ, Brazil	Bayliss (1994)
		3–7% †	Australia †	
Adult survival (σ_a)		15–46%	in situ, Brazil and Venezuela	Bayliss (1994) and M. Lampo, <i>personal observation</i> Alford et al. (1995)
		30–70%	in situ, Australia	

Note: Density-dependent larval survival is discussed in the text.

† Juvenile survival for Australia was assumed to be 10% of adult survival, σ_a , there.

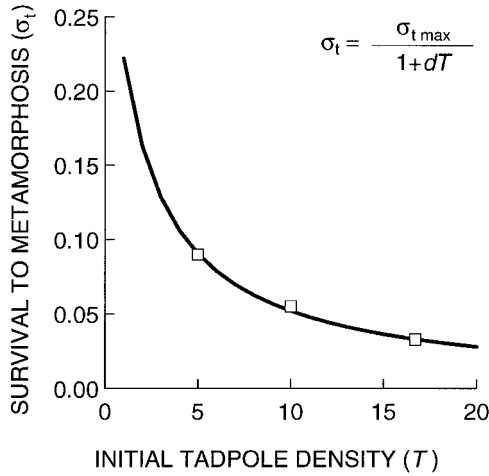


FIG. 2. Relationship between tadpole survival and initial tadpole density (from Hearnden 1991). The curve represents the best least square fit to the data; tadpole maximum survival, $\sigma_{t \max}$, is 0.3499 tadpoles/L (95% CI = 0.31, 0.39); d , a coefficient of intraspecific competition, is 0.5771 tadpoles/L (95% CI = 0.37, 0.77).

stant fraction of metamorphs, σ_m , survive to the juvenile stage each year ($\sigma_m = 5\%$ for South America; $\sigma_m = 1.2\text{--}17.6\%$ for Australia).

Juvenile and adult survival were estimated by mark-recapture methods in Brazil (Bayliss 1994) and Venezuela (M. Lampo, unpublished data). Bayliss (1994) found that juvenile survival ($\sigma_j = 2\text{--}5\%$) was $\sim 10\%$ of the adult survival ($\sigma_a = 15\text{--}46\%$). In Australia, adult yearly survival was assessed by Alford et al. (1995) from skeletochronological estimates of the population age structure ($\sigma_a = 30\text{--}70\%$). Unfortunately, an estimate for juvenile survival in Australia was not available. However, it is likely that nocturnal juveniles experience sources of mortality similar to those of adults, because of their similar activity patterns. Based on this premise, we assumed that juvenile mortality in Australia is also 10% of the adult survival there (i.e., $\sigma_j = 3\text{--}7\%$).

There is evidence suggesting that tadpole survival is density dependent. Hearnden (1991) showed that the number of tadpoles that survived to metamorphosis in field enclosures decreased with tadpole density. Although the data set considers only three initial densities, these are the only data relating tadpole density to tadpole survival in the field. We explored the functional relationship between tadpole survival, $\sigma_t(T)$ and the initial tadpole density, T , by fitting to these data the following function (Fig. 2):

$$\sigma_t(T) = \frac{\sigma_{t \max}}{1 + dT} \quad (3)$$

where $\sigma_{t \max}$ is the tadpole maximum survival and d is a measure of the intensity of intraspecific competition during this stage. Other functional relationships were tested, but none affected the outcome as long as we

used a decreasing monotonic function for larval survival. By assuming a sex ratio of 1:1, the recruitment success F is thus defined as

$$F(T) = \frac{1}{2} \phi \sigma_e \sigma_t(T) \sigma_m$$

where

$$T = \frac{1}{2} \phi \sigma_e A.$$

Therefore, F can be expressed as a function of adult density A :

$$F(A) = \frac{1}{2} \phi \sigma_e \frac{\sigma_{t \max}}{\left(1 + d \frac{1}{2} \phi \sigma_e A\right)} \sigma_m.$$

Because no equivalent estimates were available from South America and we had no evidence that either tadpole maximum survival is lower or intraspecific competition is more intense there, we used those parameters estimated in Australia for South America.

To test the consistency of the model predictions with empirical data, adult equilibrium densities and tadpole survival at equilibrium were calculated for all parameter values estimated in South America and Australia. Equilibrium densities were calculated by setting $N_{t+1} = N_t \equiv \hat{N}$ in Eq. 1. The analytic expressions for the adult, \hat{A} , and juvenile, \hat{J} , nontrivial equilibrium densities are given by

$$\hat{A} = \frac{1}{d} \left[\frac{\sigma_{t \max} \sigma_m \sigma_j}{(1 - \sigma_a)} - \frac{2}{\phi \sigma_e} \right] \quad (4)$$

and

$$\hat{J} = \frac{1}{d} \left[\frac{\sigma_{t \max} \sigma_m \sigma_j}{(1 - \sigma_a)} - \frac{2}{\phi \sigma_e} \right] \frac{(1 - \sigma_a)}{\sigma_j}. \quad (5)$$

Tadpole survivals at equilibrium, $\hat{\sigma}_t$, were calculated by substituting Eqs. 4 and 5 into Eq. 3:

$$\hat{\sigma}_t = \frac{2}{\phi \sigma_e \sigma_m} \left[\frac{(1 - \sigma_a)}{\sigma_j} \right]. \quad (6)$$

Eqs. 4 and 5 indicate that a nontrivial equilibrium exists if and only if

$$R_0 = \frac{\sigma_e \sigma_{t \max} \sigma_m \sigma_j \phi}{2(1 - \sigma_a)} > 1 \quad (7)$$

where R_0 is the basic reproductive number. That is, a nontrivial equilibrium exists as long as the number of females produced by an adult female during its lifetime in the absence of density-dependent constraints is greater than one. The stability of the equilibrium was explored according to the classical local stability analysis for nonlinear systems (Beddington 1974, Caswell 1989), as described in the Appendix. The analytical expression describing the stability conditions (Appendix, Eq. A.3) is identical to that defining the existence

TABLE 2. Comparison of model predictions for equilibrium densities and empirical data from both continents. Densities are expressed as the number of adult toads in 100 m of shoreline.

Continent	Model predictions range	Empirical data		
		Range	Median	Source
South America	0–127	3–116	32	Lampo and Bayliss (1996)
Australia	0–1 245	27–3 715	1 096	Alford et al. (1995)

of the nontrivial equilibrium (Eq. 7). Therefore, when the equilibrium is feasible (>1), it is also stable.

A scaling factor based on the water available to tadpoles in each meter of shoreline was derived to compare the number of individuals per liter of water predicted by the model with the observed number of adults along the shoreline. Because *B. marinus* females lay eggs preferentially in shallow waters (Evans et al. 1996), tadpoles are usually distributed within the first two meters of water in depths usually ≤ 0.5 m (M. Lampo, *personal observation*). If the volume available to tadpoles consists of a wedge 2 m from the shoreline into the water by 0.5 m deep, 500 L of water are equivalent to 1 m of shoreline. Thus, the predicted number of adults in a 100-m transect was obtained by multiplying the equilibrium densities by a factor of 50 000. Because the shape of waterbodies used by tadpoles is not different in the two continents, the same scaling factor was used for South America and Australia.

A sensitivity analysis was carried out by varying each parameter while setting all others constant (Caswell 1989). To perform the analysis, we chose the maximum of all parameter values reported in Table 1 for South America as a reference set, because it represents the most favorable condition in the native habitat. This set of values was then used as a baseline to identify which parameters (fecundity and survival in various development stages) need to increase further to obtain densities as high as those observed in Australia. In this way, we were able to identify which parameter is most likely to explain the high densities reported in Australia.

RESULTS

Model predictions

The adult equilibrium densities predicted by the model are consistent with those reported in each continent (Table 2). For South America, estimates range from 0 to 127 adults/100 m of shoreline (Table 2) and fit very well observed field densities. In Australia, the maximum predicted density is three times smaller than the maximum density reported in the field, but the observed median (1096 adults/100 m of shoreline) is within the range of density predicted by the model (0–1245 adults). Moreover, differences in predicted densities between continents are of the same order of magnitude as those observed in the field. It is worth noting that, although estimates of absolute densities might be affected by a biased assessment of the scaling factor

(the average water volume available to tadpoles in 1 m of shoreline), the difference between the predicted densities in South America and Australia is not, the shape of waterbodies being similar in the two continents.

Tadpole survival rates at equilibrium predicted by Eq. 6 were consistent with field estimates. For South America, Eq. 3 predicts that $\sim 5\%$ of tadpoles should survive to metamorphosis each year; field estimates at one site in Brazil (Bayliss 1994) indicated that $\sim 10\%$ of tadpoles survive to metamorphosis each breeding season. In Australia, our estimates of tadpole survival at equilibrium (1.4%) are consistent with field experiments by Alford et al. (1995), who reported values ranging between 0.025% and 4% at field densities, depending on the presence of odonates or older *Bufo marinus* cohorts. Tadpole survival at equilibrium does not depend upon the intraspecific competition coefficient, d , or the maximum tadpole survival $\sigma_{t \max}$, but upon the clutch size ϕ and survivals at other stages (i.e., σ_e , σ_m , σ_j , and σ_a). Thus, only variations in these parameters may potentially affect the tadpole survival estimates at equilibrium.

Finally, the mean basic reproductive number (Eq. 7) estimated for South America and Australia is much greater than 1 (3.2 and 17.5, respectively), confirming the enormous reproductive and invasion potential of *B. marinus*.

Sensitivity analysis

Adult equilibrium density, as given by Eq. 4, depends upon four parameter aggregates: (1) it increases linearly with the product of $\sigma_{t \max}$, σ_m , and σ_j ; (2) it increases hyperbolically with adult survival σ_a ; (3) it increases hyperbolically but levels off with the product of clutch size ϕ and egg survival σ_e ; and (4) it decreases hyperbolically with the competition coefficient d . The actual sensitivity of adult equilibrium density over a realistic range of model parameters is quite variable and depends upon which parameter is considered.

Adult equilibrium densities showed little sensitivity to variations in either female fecundity or egg survival (Fig. 3a, b). Given that a density-dependent mechanism regulates larval survival, even a substantial increase in ϕ or σ_e could only account for an increment in the equilibrium densities to a maximum value of 127 adults/100 m of shoreline (Fig. 3a).

On the other hand, tadpole maximum survival, metamorph, and juvenile survivals showed linear relation-

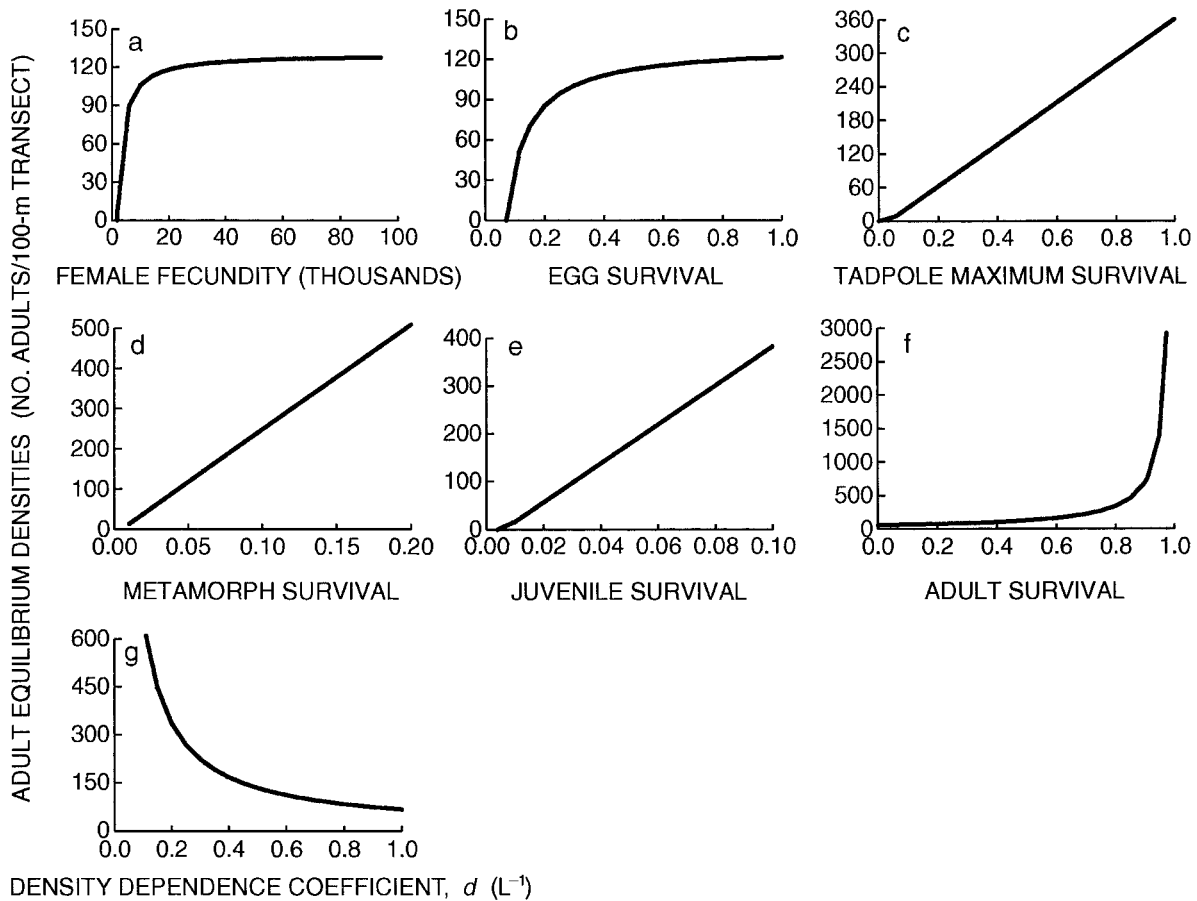


FIG. 3. Sensitivity of adult equilibrium densities to variations in population parameters, as predicted by the model. Each parameter was varied within the range of values reported in both continents, while fixing all others to the maxima reported in South America.

ships with the adult equilibrium densities (Figs. 3c–e). However, the slopes of these lines indicate that adult density at equilibrium is one order of magnitude less sensitive to $\sigma_{t\max}$ (373) than to σ_m or σ_j (2608 and 2835, respectively). Therefore, even if we assumed that no tadpoles died at low densities ($\sigma_{t\max} = 1$), the model would predict only 370 adult toads/100 m of shoreline. On the other hand, metamorph and juvenile survivals should increase unrealistically, i.e., from three to six times greater than the maximum value recorded in Australia, in order to predict densities similar to the median density reported in Australia. Thus, the individual contributions of these parameters to adult equilibrium densities are not sufficient to explain the differences observed between continents.

Predicted densities show little sensitivity to variations in adult survival (Fig. 3f) for the typical range of values reported in South America (i.e., $\sigma_a < 50\%$), but are very sensitive to adult survival for the typical range of values reported for Australia ($>50\%$). Although a net increase (over that in native habitat) in adult survival cannot fully explain the upper range of densities reported in Australia, the high sensitivity of

toad densities to σ_a (compared to other postmetamorphic survivals) suggests that adult survival is more likely to provide the largest contribution to the densities reported in Australia.

Finally, adult equilibrium densities increased asymptotically as the intraspecific competition coefficient d decreased (Fig. 3g). This suggests that it is possible to explain differences in densities between continents based on differences in the strength of the intraspecific interactions between tadpoles. However, variations in the estimated competition coefficient within one order of magnitude of the value reported in Australia have little effect on the equilibrium adult densities (Fig. 3g). Thus, it is unlikely the differences in densities are the result of differences in the competition coefficients.

DISCUSSION

Two factors appear to have a distinct impact on the equilibrium densities of the model described herein. The first is a density-dependent mechanism at the larval stage that regulates the number of individuals surviving to metamorphosis. Given such a mechanism and the high recruitment of tadpoles observed in this species,

variations in female fecundity and egg survival exert little effect on the equilibrium densities of adult toads, because most tadpoles die. Hence, only postmetamorphic survivals contribute to adult equilibrium densities. The second factor is related to the survival and life expectancy of adults. Because adults may survive beyond the first year, generations will tend to overlap and individuals will accumulate in this stage. As a result, adult equilibrium densities are increasingly sensitive to increments in adult survival.

Density dependence of larval survival has been demonstrated in many anuran species, including *Bufo marinus* (Brockelman 1969, Licht 1974, Wilbur 1977, Cecil and Just 1979, Dash and Hota 1980, Berven 1990, Hearnden 1991). In most cases, a reduction in survival may be produced by interference and exploitation competition (see review in Alford, *in press*) or by slowed developmental rates that increase the mortality risks by desiccation (Newman 1987) or predation. Experimental observations indicate that high densities may also reduce the size of anuran tadpoles at metamorphosis (Brockelman 1969, Smith 1983, Morin 1986, Blaustein and Margalit 1996), decreasing their chance of survival to first reproduction (Smith 1987). For *B. marinus*, field experiments have demonstrated that high densities reduce the survival of tadpoles to metamorphosis and reduce tadpole size at metamorphosis (Hearnden 1991). Moreover, larger tadpoles may also prey on smaller conspecifics at high densities (Hearnden 1991), which suggests that the selective pressures imposed by the need to grow rapidly under severe resource limitations must be very high. Therefore, intraspecific competition or predation at the larval stage act as a bottleneck regulating the number of toads reaching the reproductive stage.

Because of the lack of quantitative data, the potential effect of larval density on postmetamorphic survival via reduction in tadpole size at metamorphosis was not explicitly modeled. However, it makes no difference in the adult equilibrium densities whether density-dependent effects at the pre-juvenile stage translate into tadpole or postmetamorphic survival, as long as they regulate the number of individuals surviving to the reproductive stage.

Survival estimates suggest that the mean life expectancy of an adult toad is slightly >1 yr in South America, but almost 3 yr in Australia. Thus, adult toads will tend to accumulate more rapidly in Australia, where generations overlap to a greater extent. However, the major mortality sources for adult toads are not well understood. Schwarzkopf and Alford (1996) noticed that the scarcity of day retreat sites may be an important mortality source for adult toads in Australia. On the other hand, Zug and Zug (1979) suggested that moisture stress and predation are the major mortality sources for all reproductive classes in Panama. Similarly, Bayliss (1994) found that adult survival rates in Brazil were inversely correlated with predation rates.

Moreover, he also found that survival was correlated with insect availability, although insects were more scarce in the wet late season when predation was higher. In any case, although some form of density dependence in the adult stage cannot be ruled out, the fact that densities estimated in Australia are even higher than those predicted by the model suggests that densities may still be below the level at which density-dependent mortality in the adult stage may occur. Therefore, density-dependent survival in the larval stages would regulate population sizes to densities below those at which intraspecific competition in the adult stages becomes important.

Although it is unclear which are the major species preying upon *B. marinus*, anecdotal information suggests that small vertebrates and some reptiles may prey on adult toads, and birds may pick up recently metamorphosed toadlets in South America. Similarly, pathogens and parasites could also affect the survival of adult toads by lowering their physiological condition and, thus, increasing their risk of mortality due to dehydration or predation. Parasites commonly found in/on adult toads in South America are less common, when not totally absent, in Australia (D. Barton and C. L. Loureiro, *personal communication*), presumably because many parasites were left behind during the process of introduction. Lampo and Bayliss (1996b) showed that ticks, absent from Australian toads, may have impact on the survival and size-specific mass of this species in native habitats. The sensitivity of adult equilibrium densities to variations in the fecundity and stage-specific survival of *B. marinus* have profound implications for control of this species in Australia. *Bufo marinus* is a successful invader species in its native habitat (Zug and Zug 1979, Lampo and Bayliss 1996a) as well as in those areas where it has been introduced (Zug et al. 1975, Cohen and Alford 1993). This success may be partly explained by its R_0 and extraordinary plasticity in the scheduling of reproductive events, which allows this species to reproduce successfully in extremely unpredictable environments (Hearnden 1991, Lampo and Medialdea 1996). Given such reproductive success, it also seems unlikely that this species can be eradicated from Australia. However, although high fecundity seems crucial to the success of this species as an invader, this parameter has little effect on the population density at high densities. Not surprisingly, size-specific fecundities are higher in South America, yet toad densities are lower there. Thus, any control strategy targeted toward fecundities or pre-larval stages will have very little effect on the population densities of this species, because a reduction in the recruitment to tadpoles will be compensated by a density-dependent increase in their survival. Thus, the most effective strategy to reduce toad densities in Australia seems to be the reduction of adult survival. For example, according to the model, a reduction in adult survival down to 20% will decrease adult den-

sities to values within the range reported in South America. However, it would be necessary to suppress either egg or larval maximum survival to 0.7% or 3–4%, respectively, to achieve an equivalent reduction in adult densities. Recently, an iridovirus has been isolated from adult toads in South America, as a first step toward the evaluation of potential control agents for this species in Australia (López et al. 1997).

The model presented here is by no means a predictive, but rather an analytical, tool. Because its structure has been dictated by a principle of simplicity, and some gaps in the available data need to be filled, there are some limitations in its predictive power. For example, the model cannot fully account for the range of density values reported in Australia. This could be explained by an underestimation of juvenile survival, the only parameter for which no data are available from Australia. Thus, further studies need to focus on juvenile survival in Australia. On the other hand, inclusion of a density-dependent mechanism, as the result of limited retreat sites for metamorphs (Cohen and Alford 1993, 1996, Alford et al. 1995), is likely to reduce the sensitivity of adult densities to metamorph survival (as observed with the tadpole survival). This would reinforce the importance of juvenile and adult survival as the actual determinants of toad densities in both continents. Despite these limitations, there is general consistency between predicted and observed patterns. Thus, we believe that our study brings important insights on factors driving the enormous reproductive success of Australian toads and on strategies to control their rate of increase.

ACKNOWLEDGMENTS

This work was supported by the Commonwealth for Scientific and Industrial Research Organisation (CSIRO) and the Italian Ministry of Research. We thank Brian Green and the Australian Embassy at Caracas who made possible the interaction between the South American and Australian research teams. We are also pleased to thank Ross A. Alford, Andy Dobson, Marino Gatto, Diego Rodríguez, Jon Paul Rodríguez, and anonymous referees who carefully read the manuscript and helped to improve the work, and to acknowledge Simon Levin and Andy Dobson, who made possible our collaboration during a postdoctoral visit to the Department of Ecology and Evolutionary Biology of Princeton University.

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APPENDIX

The stability of the equilibrium is determined by linearizing in the region around the equilibrium and examining the eigenvalues of the linearized matrix. The Jacobian matrix \mathbf{M}_8 for model (Eq. 2) and the equilibrium vector $\hat{\mathbf{N}}$ (based on Eqs. 4 and 5) is given by

$$\mathbf{M}_8 = \begin{bmatrix} 0 & \frac{2(1 - \sigma_a)^2}{\phi \sigma_e \sigma_t \max \sigma_m \sigma_j^2} \\ \sigma_j & \sigma_a \end{bmatrix}. \quad (\text{A.1})$$

The nontrivial equilibrium is stable if the modules of the eigenvalues of \mathbf{M}_8 are smaller than unity. Thus, for the characteristic equation

$$\lambda^2 - \lambda \sigma_a - \frac{2(1 - \sigma_a)^2}{\phi \sigma_e \sigma_t \max \sigma_m \sigma_j^2} = 0 \quad (\text{A.2})$$

the necessary and sufficient conditions for the eigenvalues to be < 1 are given by

$$R_0 = \frac{\sigma_e \sigma_t \max \sigma_m \sigma_j \phi}{2(1 - \sigma_a)} > 1 \quad (\text{A.3})$$

and

$$R_0 \frac{(1 + \sigma_a)}{(1 - \sigma_a)} = \frac{(1 + \sigma_a) \sigma_e \sigma_t \max \sigma_m \sigma_j \phi}{2(1 - \sigma_a)^2} > 1. \quad (\text{A.4})$$

Inequality A.4 is satisfied if A.3 holds true, and A.3 is necessary and sufficient for feasibility.