
Catastrophic Reproductive Failure, Terrestrial Survival, and Persistence of the Marbled Salamander

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Abstract: *Wide variation in reproductive success is common among amphibians that breed in seasonal ponds, but persistence of adults can buffer against these fluctuations, particularly for long-lived species. We hypothesized that the frequent episodes of catastrophic failure of the marbled salamander (*Ambystoma opacum*) enhance the importance of high terrestrial survival. At Rainbow Bay in South Carolina reproductive success was poor (<1 metamorph/breeding female) in nearly half of the 22 years that the species bred. Complete failure occurred in 6 of 22 years. To study catastrophic failure, we adapted an age-structured, individual-based model with density-dependent growth and survival of larvae. The model was based on extensive data from local field studies and experiments. With consistently good survival in the pond stages, the simulated population required survival probabilities in the upland stages (juveniles and adults) near 0.5/year to persist and near 0.8/year to achieve the increases observed. Catastrophic failure, occurring randomly with probability 0.5/year, created additional fluctuations in the population, raised the thresholds of survival required for persistence, and caused extinction under conditions that were otherwise favorable. The marbled salamander at Rainbow Bay is not at great risk of extinction because of catastrophic failure, but the risk increases dramatically if life span is decreased or frequency of failure is increased. Any reduction in terrestrial survival will have deleterious consequences by reducing the breeding populations at equilibrium, even if it does not jeopardize persistence. Our model provides assessments of risk that can be applied to poorly studied species with similar life histories, such as the endangered flatwoods salamander (*A. cingulatum*).*

Keywords: *Ambystoma opacum*, catastrophic reproductive failure, extinction, larval density dependence, pond-breeding salamander, population model, storage effects, terrestrial survival

Fracaso Reproductivo Catastrófico, Supervivencia Terrestre y Persistencia de la Salamandra *Ambystoma opacum*

Resumen: *Es común que los anfibios que se reproducen en charcas temporales tengan una amplia variación en el éxito reproductivo, pero la persistencia de adultos puede amortiguar esas fluctuaciones, particularmente en especies longevas. Probamos la hipótesis de que episodios frecuentes de fracaso catastrófico de *Ambystoma opacum* acentúan la importancia de la supervivencia terrestre alta. El éxito reproductivo fue pobre (<1 metamorfo/bembra reproductiva) en la Bahía Rainbow, Carolina del Sur en casi la mitad de 22 años en que la especie se reprodujo. En 6 de los 22 años hubo fracaso completo. Para estudiar el fracaso catastrófico adaptamos un modelo estructurado por edades basado en individuos con crecimiento y supervivencia de larvas denso dependientes. El modelo se basó en numerosos datos de estudios y experimentos locales. Con buena supervivencia en las etapas acuáticas, la población simulada requirió probabilidades de supervivencia de las etapas terrestres (juveniles y adultos) cerca de 0.5/año para persistir y cerca de 0.8/año para alcanzar los incrementos observados. El fracaso catastrófico, aleatorio y con probabilidad de 0.5/año, creó fluctuaciones adicionales en la población, elevó los umbrales de supervivencia requeridos para persistir y causó la extinción en condiciones otrora favorables. En Bahía Rainbow, la salamandra *Ambystoma opacum* no está en gran riesgo de extinción debido a fracaso catastrófico, pero el riesgo incrementa dramáticamente si se reduce la esperanza de vida, o si aumenta la frecuencia de fracaso. Cualquier reducción en la supervivencia terrestre tendrá consecuencias deletéreas por la disminución de poblaciones reproductivas en equilibrio, aun si no*

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peligra la persistencia. Nuestro modelo aporta evaluaciones de riesgo que pueden ser aplicados a especies poco estudiadas con historias de vida similares, como la salamandra A. cingulatum en peligro.

Palabras Clave: *Ambystoma opacum*, denso dependencia de larvas, efectos de almacenamiento, extinción, fracaso reproductivo catastrófico, modelo poblacional, salamandra de reproducción acuática, supervivencia terrestre

Introduction

The challenges of evaluating apparently widespread amphibian population declines and devising effective conservation measures have sharpened interest in the processes regulating amphibian populations (Semlitsch 2002). In particular the high variance in reproductive success exhibited by pond-breeding amphibians may be important to the design of conservation strategies. The wetland or aquatic stages of the life cycles have received more attention than the terrestrial stages. Explanations of population fluctuations generally emphasize the effects of aquatic factors such as the timing of pond hydroperiod and early pond drying (Pechmann et al. 1989; Semlitsch et al. 1996; Paton & Crouch 2002) or density-dependent competition and predation of larvae (Petranka 1989; Scott 1990; Van Buskirk & Smith 1991; Werner & McPeck 1994) on juvenile recruitment. The link between wetland hydroperiod and production of juveniles is often strong and sometimes dramatic. Years of catastrophic die-off may alternate with years when tens of thousands of juveniles metamorphose (Semlitsch et al. 1996; Alford & Richards 1999). Amphibian reproductive success is also susceptible to wetland disturbance, climate change, and watershed perturbations.

Recent research has examined the interaction of regulatory mechanisms from both sides of the wetland boundary (sensu Berven 1990). From life-stage simulation analyses of stage-structured models for frogs and a toad, Biek et al. (2002) concluded that population growth is generally more sensitive to postmetamorphic vital rates than to premetamorphic vital rates. They also argued for the need to incorporate better estimates of variation in vital rates. From stage-structured models with larval density dependence for a toad and a salamander, Vonesh and De la Cruz (2002) concluded that mortality in postembryonic life stages (including larval density dependence) has much greater influence on population size at equilibrium than does mortality in the egg stage. Their results are consistent with Taylor and Scott's (1997) earlier analyses of an age-structured, individual-based model for a salamander with density-dependent growth and survival of larvae.

Applying this model to marbled salamanders breeding in Ginger's Bay, a seasonal wetland pond in South Carolina, Taylor and Scott (1997) concluded that the population requires either high terrestrial survival or immigration to persist at rates of reproductive success observed during a 9-year study. Either of these conclusions has sub-

stantial implications for management of the pond and surrounding habitat. Extending this analysis to a longer-term study of the species at another pond forced us to consider an additional factor, the risk of catastrophic reproductive failure. We hypothesized that frequent episodes of catastrophic failure will enhance the importance of high terrestrial survival or immigration.

At Rainbow Bay, a seasonal pond on the Savannah River Site (SRS) in South Carolina, results from a long-term population study (1978 to present) have revealed wide annual variation in composition and numbers of metamorphs, including years of complete reproductive failure for every species (Pechmann et al. 1989, 1991; Semlitsch et al. 1996). The marbled salamander colonized Rainbow Bay a few years after the study began. During the 1950s and 1960s, much of the land, including the agricultural land adjacent to Rainbow Bay, was converted to pine plantation. By 1997 nearly 90% of the SRS was forested (Pinder et al. 1997). These changes, combined with reduced disturbances to wetland ponds, probably favored the spread of pond-breeding salamander populations generally on the SRS.

We adapted the Taylor and Scott (1997) model to study effects of catastrophic reproductive failure on population dynamics and persistence of marbled salamanders. We chose this species because extensive local field and experimental data were available to support the model. We also explored the interactions among survival in the upland and pond stages, risk of reproductive failure, and life span on persistence of the population.

Understanding the interactions of factors operating at different stages of the life cycle is essential for focusing management efforts. Analyses of the uniquely well-studied population at Rainbow Bay provide assessments of risk that can be extrapolated to poorly studied species with similar life histories. We also identify situations, depending on life span and risk of reproductive failure, where populations depending on a single breeding pond are unlikely to persist, regardless of the quality of aquatic or terrestrial habitat. Such situations would require management of populations on a broader spatial scale.

Methods

Field Studies at Rainbow Bay

The marbled salamander occurs in much of the eastern United States (Petranka 1998). The terrestrial juveniles

and adults live in soil and leaf litter, where they forage for insects and other invertebrates. In autumn, adults migrate to ponds that are partially or completely dry (Noble & Brady 1933). Unlike most species of ambystomatids, adult marbled salamanders court and breed on land rather than in water (Nussbaum 1985; Krenz & Scott 1994). The female lays eggs in a nest and often remains until the nest is inundated (Petranka et al. 1982; Jackson et al. 1989). The aquatic larvae feed mainly on aquatic microcrustaceans and insects (Petranka & Petranka 1980). In the Southeast the larval period ranges from 2 to 6 months. After metamorphosis, the juvenile salamanders migrate from the pond margin to terrestrial habitats. Maximum adult longevity in the Southeast is approximately 10–11 years (Scott 2005).

On the U.S. Department of Energy's SRS in the Upper Coastal Plain of South Carolina, marbled salamanders breed in Carolina bays, other similar isolated depressional wetlands, and floodplain pools (Gibbons & Semlitsch 1991). Rainbow Bay is an isolated depressional wetland on the SRS that holds water for about 6 months annually (15-year average, Medland & Taylor 2001). The wetland has a maximum inundated area of 1.5 ha (Leeper & Taylor 1998).

Populations of amphibians entering or leaving the wetland have been censused daily since the fall of 1978 at a drift fence that completely encircles the basin (Semlitsch et al. 1996). Water level has been measured weekly at a staff gauge in the deepest part of the basin. For this analysis, we defined hydroperiod as the longest period of continuous inundation during the year. Shorter periods of inundation sometimes occurred before or after the main hydroperiod. We derived a curve relating inundated area to water depth from data in Leeper and Taylor (1998).

Population Model

We developed a computer simulation model (Taylor & Scott 1997) for marbled salamanders from extensive field and experimental data for populations at the SRS, including the unmanipulated population at Rainbow Bay. In the simulations reported here, we modified the model so that the entire larval cohort may be lost because of reproductive failure, which occurs randomly with probability p_{fail} .

As described by Taylor and Scott (1997), the model tracks eggs and larvae as a cohort, and half of the metamorphosing larvae are assumed to be female. The maximum life span is 10 years, counting age from the time of oviposition. Duration of the egg stage is 0.2 years, duration of the larval stage is 0.3 years, and duration of the terrestrial juvenile stage is 0.5 years. One-year-old females are considered adults, although the age at first reproduction varies among individuals. The proportion of the cohort that survives from egg to metamorphosis is determined by the survival probabilities p_{pond} , a constant apportioned between the egg and larval stages, and p_L , a function of

larval density. (In the 1997 model, larval survival depends only on larval density.)

Females are tracked individually in the terrestrial juvenile and adult stages. Size at metamorphosis depends on the population density of larvae; subsequent growth is a function of age and size. Probability of surviving the 0.5-year juvenile stage and each subsequent year of the adult stage is p_{upland} . Probability of breeding depends on age and body size, and fecundity depends on body size. Females may return to breed as early as fall of the year after metamorphosis (age $i = 2$). When the effects of larval density dependence and randomly imposed reproductive failure are negligible, the intrinsic rate of increase for the population is given by r^* :

$$1 = \sum_{i=2}^{10} p_{\text{pond}} p_{\text{upland}}^i b_i \frac{C_i}{2} \exp^{-r^* i}, \quad (1)$$

where b is the probability of breeding and C is number of eggs, half of which are assumed to be female. The value $r^* = 0$ approximates a demographic break-even point for the population.

In these simulations we set p_{pond} to produce a stock recruitment curve fitting the field data for years of good reproductive success at Rainbow Bay. Stock and recruitment were expressed as breeding females and metamorphs, respectively. To examine sensitivity of estimates of p_{pond} to other components of the model, we used stock recruitment curves generated with altered functions for fecundity, probability of breeding, or larval density dependence. To check plausibility of results, we compared life-history statistics from the model with field data for local populations.

Unless noted otherwise, computer simulations were begun with 30 females of age 2, yielding populations similar to those initially observed at Rainbow Bay. The model was implemented with computer programs written in Fortran (code available from B.E.T.). In the simulations, survival of each terrestrial female at the end of each year was determined by drawing a number from a uniform distribution over the interval [0,1] and comparing it with the appropriate probability. The fate of females eligible to breed and the occurrence of reproductive failure were determined similarly. The programs accessed a pseudo-random number generator and other statistical subroutines of the IMSL/Stat Library (Visual Numerics, Houston, Texas). Graphics were produced in S-Plus (MathSoft, Seattle, Washington).

Extinction due to Run of Failures

For an animal with an n -year life span, n successive years of reproductive failure will cause local extinction. If reproduction is successful in year 0, the probability P_k of extinction in year k and the cumulative probability S_k of extinction in or before year k are

$$\begin{aligned}
 P_k &= 0 \quad \text{for } k < n \\
 P_k &= p_{\text{fail}}^n \quad \text{for } k = n \\
 P_k &= (1 - p_{\text{fail}}) p_{\text{fail}}^n \quad \text{for } k = n + 1 \\
 P_k &= (1 - S_{k-n-1})(1 - p_{\text{fail}}) p_{\text{fail}}^n \quad \text{for } k > n + 1 \\
 S_k &= \sum_{i=1}^k P_i.
 \end{aligned} \quad (2)$$

The term $(1 - p_{\text{fail}})$ gives the probability that a new cohort was produced in year $k - n$, a condition that must be met for extinction to occur in year k when $k > n$. This term also ensures that the population does not become extinct in year $k - 1$. The term $(1 - S_{k-n-1})$ gives the probability that the population did not become extinct before year $k - n - 1$, an additional condition that must be met for extinction to occur in year k when $k > n + 1$. The median time to extinction is the year in which the cumulative probability of extinction S_k reaches 0.5.

Results

Breeding female marbled salamanders first appeared at the drift fence at Rainbow Bay in fall of 1980 (the breeding season for 1981), 2 years after the amphibian study began (Fig. 1). The initial breeding populations were 2, 10, and 18 females for the breeding seasons of 1981–1983. Breeding populations ranged up to 1342 females in subsequent years. Hydroperiod ranged from 0 to 390 days (0–13 months; Fig. 2), and the pond typically began to fill in winter (December to February). Maximum inundated area ranged from $< 225 \text{ m}^2$ to 1.5 ha. Hydroperiod and maximum inundated area were strongly correlated ($r^2 = 0.77$, $p < 0.001$).

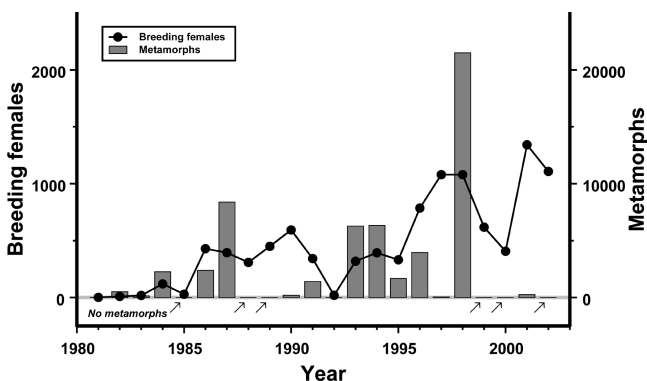


Figure 1. Marbled salamanders censused at the drift fence at Rainbow Bay, 1981–2002. The species was absent or undetected in 1979–1980, the first 2 years of the study. (Data for 1979–1994 in Semlitsch et al. [1996]).

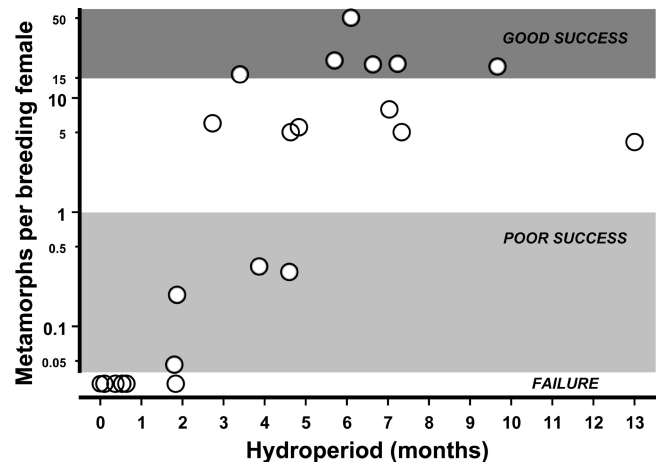


Figure 2. Reproductive success of marbled salamanders in relation to hydroperiod at Rainbow Bay.

Reproductive success was poor (< 1 metamorph per breeding female) in 10 of 22 years, including all years with hydroperiods < 2 months (Fig. 2). Complete failure occurred in 6 of 22 years. Reproductive success was relatively good (> 15 metamorphs per breeding female) in 6 years. The single exceptionally high value was based on a reported population of only 10 breeding females in 1982. Maximum pond area was 0.5–0.7 ha in years of poor success and 1–1.5 ha in years of good success.

By fitting output from the model to the stock recruitment data for Rainbow Bay, we estimated the density-independent component of survival in the pond stage at $p_{\text{pond}} = 0.14$. With the exception of 1 year, field data for years of good reproductive success fell below the range of strong density dependence in the model. Density dependence produces increasing departures from linearity in the stock recruitment curves at populations > 500 breeding females. The model yielded plausible values for age and size at first reproduction (Table 1). From field studies of natural and experimental populations on the SRS (Scott 1994; Pechmann 1995), the average age at first reproduction for females was 2.8–4.0 years, and the average size was 53–60 mm snout-vent length.

In the sensitivity analysis, we altered the functions describing fecundity, probability of breeding, and larval density dependence. Doubling fecundity diminished the fitted estimate of p_{pond} by half (Table 1). Removing the age constraint on breeding had less effect. The decline in age at first reproduction (1–2 years, depending on the intensity of larval density dependence) was partially offset by lower fecundity due to smaller size of the females. Changing the function for density dependence had a negligible effect on the fitted estimate of p_{pond} .

We simulated population growth over a range of values for upland survival (Fig. 3). The density-independent component of pond survival was set to represent (1) good

Table 1. Sensitivity of fitted pond survival estimate to fecundity, age constraint on breeding, and density dependence of larval survival.

Model	Survival probabilities		Larval density dependence ^b	Average snout-vent length of metamorphs (mm)	Females at first reproduction		
	pond p_{pond}	upland p_{upland} ^a (per year)			average age (year)	average snout-vent length (mm)	average brood (eggs)
Unmodified	0.14	0.60	low	50	3.5	64	157
			moderate	35	3.8	54	81
Doubled fecundity	0.07	0.60	low	50	3.5	64	314
			moderate	35	3.8	54	162
Breeding independent of age	0.19	0.45	low	50	1.4	59	119
			moderate	35	2.9	52	68
Halved larval density dependence	0.13	0.61	low	50	3.5	64	157
			moderate	41	3.6	58	109

^aValue chosen to yield $r^* \approx 0.2$.^bLow, density $D_L \rightarrow 0$ larvae/m²; moderate, density $D_L = 20$ larvae/m².

survival at Rainbow Bay without catastrophic reproductive failure ($p_{\text{pond}} = 0.14$, $p_{\text{fail}} = 0$), (2) good survival with failure ($p_{\text{pond}} = 0.14$, $p_{\text{fail}} = 0.5$), or (3) average survival without failure ($p_{\text{pond}} = 0.07$, $p_{\text{fail}} = 0$). Average pond survival represents the time-averaged effect of catastrophic failure on good pond survival. The simulated frequency of catastrophic failure ($p_{\text{fail}} = 0.5$) was higher than the actual frequency of complete failure at Rainbow Bay but close to the combined frequency of poor success and complete failure (10 of 22 years). Breeding females constituted a small portion of the population of terrestrial females (50-year medians were 11–21% for the simulations). Table 2 gives other population statistics.

Only modest effects of catastrophic reproductive failure were apparent at the two higher values of upland survival ($p_{\text{upland}} = 1.0, 0.8$; Figs. 3a, 3b, Table 2). Initial growth was slowed, and fluctuations around the equilibria were less regular than for the corresponding populations with consistently good pond survival. Good pond survival with catastrophic failure produced results similar to average pond survival without catastrophic failure. Additional simulations indicated a small probability of extinction due to long runs of reproductive failure.

At the lowest value of upland survival ($p_{\text{upland}} = 0.6$ /year; Fig. 3c, Table 2), catastrophic failure severely reduced growth of the population. After 30 years, the population with good pond survival was larger by two orders of magnitude. Average pond survival similarly reduced population growth, but additional simulations revealed an important difference in persistence. Good pond survival with catastrophic failure produced extinctions in 30% of 1000 additional 50-year simulations, whereas average pond survival without catastrophic failure produced no extinctions.

The field data for Rainbow Bay fall closest to the simulation with $p_{\text{upland}} = 0.8$ /year with catastrophic reproductive failure. Population increases were initially faster in the field, perhaps because of additional immigration, than in any of the simulations.

We used further simulations to define the interaction among pond survival, upland survival, and catastrophic reproductive failure on population persistence (Fig. 4). The threshold for persistence without failure was defined by $r^* = 0$ (Eq. 1); average probability was 0.85 with range ± 0.03 (based on 1000 50-year simulations for each point tested). The corresponding threshold for persistence with failure was estimated from simulation results; uncertainty of interpolated values of p_{upland} is ± 0.01 unit or less. With very high values of upland survival and high values of pond survival, density-dependent reproductive failure reduces persistence; this region is not delineated.

With or without catastrophic reproductive failure, the populations required moderate to high upland survival to persist. For a population with pond survival near the average for Rainbow Bay, the threshold was $p_{\text{upland}} = 0.58$ /year. For a population with perfect pond survival ($p_{\text{pond}} = 1$, beyond range shown in Fig. 4), the threshold was $p_{\text{upland}} = 0.28$ /year. Catastrophic reproductive failure at $p_{\text{fail}} = 0.5$ /year raised the threshold by as much as 0.056 units of upland survival (at $p_{\text{pond}} = 0.5$) or 0.2 units of pond survival (at $p_{\text{upland}} = 0.4$ /year). Thus, either a small increase in upland survival or a large increase in pond survival could compensate for reproductive failure with probability $p_{\text{fail}} = 0.5$ /year. At low values of pond survival and high values of upland survival, the thresholds were very similar.

The number of colonists affected persistence. In simulations without catastrophic reproductive failure, increasing the number of colonists by an order of magnitude (from 30 to 300) reduced the probability of extinction in 50 years from 0.12 to approximately 0 at $p_{\text{pond}} = 0.07$ and $p_{\text{upland}} = 0.58$ (a point on threshold line in Fig. 4). Decreasing the number of colonists by an order of magnitude raised the probability to 0.85. Each probability was estimated from results of 1000 50-year simulations.

The probability of extinction due simply to a long run of catastrophic reproductive failure (Fig. 5) increased with

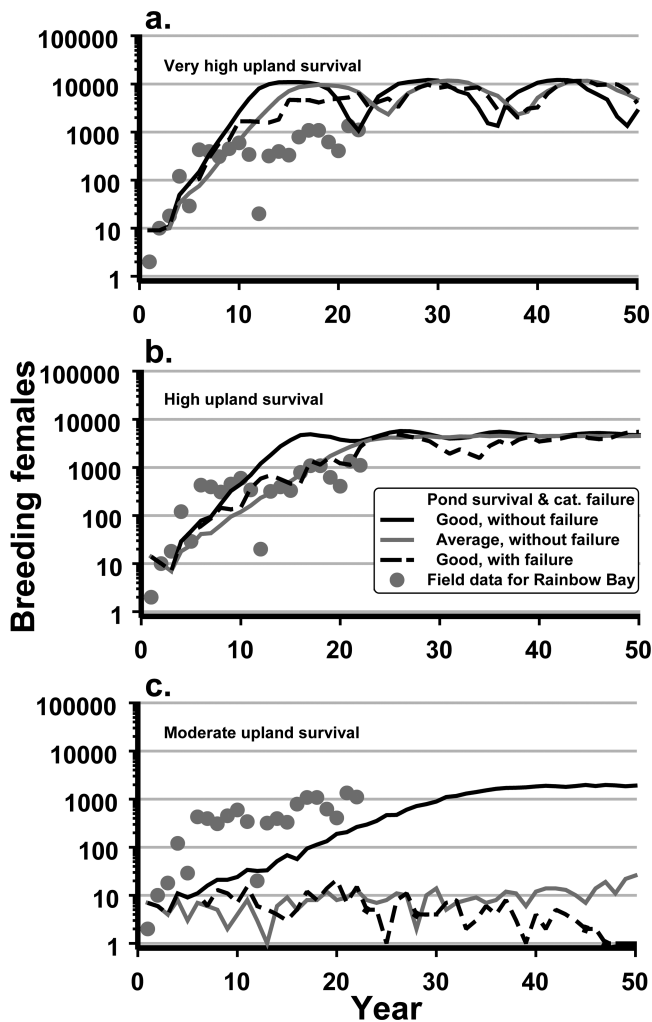


Figure 3. Population dynamics of marbled salamanders in simulations and at Rainbow Bay. Upland survival was set at (a) very high ($p_{\text{upland}} = 1.0/\text{year}$), (b) high ($p_{\text{upland}} = 0.8/\text{year}$), or (c) moderate ($p_{\text{upland}} = 0.6/\text{year}$) probabilities. Pond survival in the simulations corresponded to good survival at Rainbow Bay ($p_{\text{pond}} = 0.14$) or the average result of good survival and catastrophic reproductive failure ($p_{\text{pond}} = 0.07$); failure occurred with probability $p_{\text{fail}} = 0.5/\text{year}$.

probability of failure and decreased with life span. With a 3-year life span and $p_{\text{fail}} = 0.5/\text{year}$, the probability of extinction in 50 years was 0.98 and the median time to extinction was 10 years. With a 10-year life span, the probability of extinction was 0.02 and the median time was more than 1000 years. With a 3-year life span and $p_{\text{fail}} = 0.27/\text{year}$, the frequency of complete failure observed at Rainbow Bay, the probability of extinction in 50 years was 0.52 and the median time to extinction was 48 years. With a 10-year life span, the probability was <0.01 and the median time was nearly 0.5 million years.

Discussion

Catastrophic Reproductive Failure

Randomly imposed catastrophic reproductive failure has several effects on population dynamics of the marbled salamander. We measured these effects by comparing simulations with catastrophic failure to simulations with equivalent average survival. Catastrophic failure created additional fluctuations in the population, raised the thresholds of survival required for persistence, and imposed a possibility for extinction even under environmental conditions that are otherwise entirely favorable. These effects were small for the marbled salamander at Rainbow Bay, but they may have considerable impact for species with shorter life spans or populations breeding in riskier habitats.

Reproductive failure for the marbled salamander at Rainbow Bay was closely tied to natural variation in hydrologic conditions. A hydroperiod of insufficient duration was the main cause of complete failure. Additionally, smaller pond areas in years of short hydroperiod may have intensified density-dependent competition among larvae or resulted in mortality of eggs laid in portions of the basin that remained dry. Early filling of a pond can also diminish reproductive success if invertebrate or vertebrate predators become well established before the eggs hatch (Scott 2005).

With survival well above the thresholds for persistence (Figs. 3a & 3b), the simulated populations with catastrophic failure fluctuated more widely but followed trajectories otherwise similar to the populations with the equivalent average pond survival. Extinction due to long runs of catastrophic failure did occur, even under the best of conditions, but its frequency was low, as predicted by Eq. 2.

With realistic initial conditions, modeled on the early years of marbled salamanders at Rainbow Bay, catastrophic reproductive failure raised the survival thresholds for persistence substantially when terrestrial survival was low (Fig. 3c). In this part of the range, persistence probabilities were more responsive to upland survival than to pond survival, consistent with the generally greater sensitivity of long-lived amphibians to juvenile and adult survival. Number of colonists strongly influenced prospects for reestablishment, highlighting the potential importance of dispersal patterns and proximity to other breeding ponds (Halley et al. 1996).

The model for the marbled salamander functions as a storage model, because persistence of individuals in a long-lived stage buffers against fluctuations of success in other stages (Warner & Chesson 1985). Terrestrial adults represent the storage stage for the marbled salamander. Figuratively, however, these adults have a limited shelf-life. With the 10-year life span modeled for the marbled salamander, this effect is small: the probability of

Table 2. Population statistics of marbled salamanders for simulations in Fig. 3.

Upland survival P_{upland} (per year)	Pond survival P_{pond}	Rate of increase r^* (per year) ^a	Equilibrium	
			breeding females at Rainbow Bay	density-dependent larval survival P_L ^b
1.0	0.14 (good)	0.71	8390	0.15
	0.07 (average)	0.54	8558	0.21
0.8	0.14 (good)	0.49	4864	0.32
	0.07 (average)	0.32	4461	0.47
0.6	0.14 (good)	0.20	1900	0.73
	0.07 (average)	0.03	325	0.97

^aEquation 1.^bRange: 0 (maximum effect) to 1 (no effect).

extinction due simply to catastrophic failures was just 2% in 50 years with a 50% annual risk of catastrophic failure. This probability rises substantially for species with shorter life spans or breeding habitats with greater frequencies of failure.

A run of reproductive failures probably contributed to local extinction of the dwarf salamander (*Eurycea quadridigitata*), a short-lived species at Rainbow Bay. Although hugely abundant in the early 1980s, numbers of breeding females declined abruptly after a 3-year run of complete reproductive failures in 1988–1990 because of insufficient hydroperiod (Semlitsch et al. 1996). From 1994 to 1998, six females were captured, and from 1999

to 2003, none was captured. Dwarf salamanders recolonized Rainbow Bay in 2004, 8 years after the run of reproductive failures (D.E.S.).

Extinction probabilities based on life span and risk of reproductive failure are easy to estimate. They do not require the elaborate computational machinery of an individual-based simulation. Obtaining sound information about life span and risk of reproductive failure may be the greater challenge. Life-history studies normally emphasize reproduction rather than life span, and short-term field studies can yield a misleading picture of risk. For example, in a breeding pond where the annual risk of failure was 50%, 3 years of success or 3 years of failure would each occur with probability of 12.5%. The former outcome might lead to an erroneous assessment from a 3-year study that risk of failure was negligible and the latter might lead to the equally erroneous assessment that the population was not viable.

Although much of the effect of catastrophic reproductive failure on population dynamics was explained

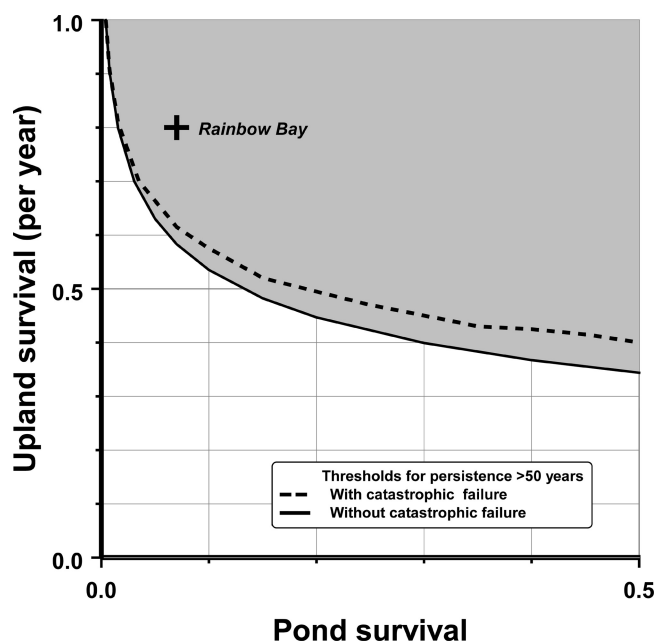


Figure 4. Thresholds for persistence of marbled salamanders. The threshold for persistence without catastrophic reproductive failure is plotted as a function of upland survival P_{upland} and pond survival P_{pond} . The threshold for persistence with failure at $P_{fail} = 0.5/\text{year}$ is plotted as a function of upland survival and the average P_{pond} ($1 - P_{fail}$).

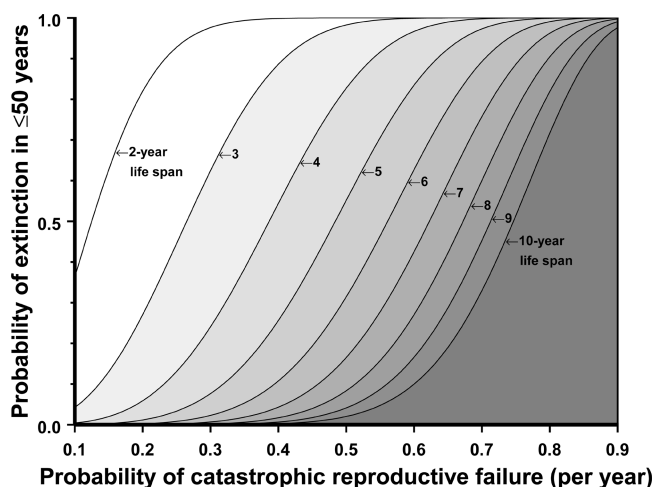


Figure 5. Effect of life span and probability of catastrophic reproductive failure on probability of extinction. Extinction probabilities were computed according to Eq. 2.

by modeling its average effect on pond survival, the additional effects on persistence because of shorter life spans or higher frequencies of failure should not be ignored. With small colonizing populations or low population growth rates, a likely circumstance for threatened or endangered populations, effects of reproductive failure are intensified by demographic stochasticity (Lande 1993).

Terrestrial Survival

For pond-breeding amphibians generally, abundances and other demographic parameters are more sensitive to post-metamorphic processes than to premetamorphic processes (e.g., Marsh & Trenham 2001; Biek et al. 2002; Vonesh & De la Cruz 2002). Stage-specific demographic effects cannot be evaluated in isolation, although life-history attributes such as delayed maturity or low fecundity will always exacerbate vulnerability to reduced survival in the adult stages (e.g., Congdon et al. 1993).

Even the highest of the observed rates of reproductive success were low at Rainbow Bay. Consequently, with or without catastrophic failure, marbled salamanders at Rainbow Bay, as at Ginger's Bay (Taylor & Scott 1997), required either high terrestrial survival or immigration to persist. Survival probabilities for adult ambystomatids generally average 0.6–0.8/year (e.g., Whitford & Vinegar 1966; Raymond & Hardy 1990; Trenham et al. 2000). With pond survival and initial population set in the ranges observed at Rainbow Bay, an upland survival probability near 0.6/year was required for persistence. An upland survival probability near 0.8/year was required to achieve the rate of population growth observed at Rainbow Bay. Upland survival also had a substantial influence on equilibrium population sizes (Table 2), a manifestation of the complicated effects of larval density dependence in models for species with complex life cycles (Wilbur 1996; Taylor & Scott 1997; Vonesh & De la Cruz 2002).

Terrestrial requirements remain poorly known for many pond-breeding amphibians. For marbled salamanders, survival is much better in forested habitat than in old-field (Rothermel 2003) or clearcut habitat (P. Niewiarowski, personal communication). In contrast, mole salamanders (*Ambystoma talpoideum*) survive equally well in clearcut or forested habitats (Chazal & Niewiarowski 1998). Clearcuts and selective canopy removal reduce the relative abundance of terrestrial plethodontid salamanders (Harpole & Hass 1999). Terrestrial plethodontids may experience greater population declines in clearcut habitats than other amphibian groups (deMaynadier & Hunter 1995), but species often persist at reduced abundances in postharvest habitats (Knapp et al. 2003). Species with delayed maturity, such as the marbled salamander, will be particularly vulnerable to reduced terrestrial survival.

Because the endangered flatwoods salamander (*A. cin-gulatum*) has a life span and life history similar to the marbled salamander (Anderson & Williamson 1976; Palis 1995, 1997), it should also require high terrestrial survival. Means et al. (1996) analyzed a 22-year decline in a population of the flatwoods salamander in Florida. The record was not explained by drought, road mortality during breeding migrations, or changes in water chemistry in breeding ponds. They attributed the decline to slash pine silviculture, particularly mechanical alteration of terrestrial habitat. Demographic responses of the marbled salamander support the plausibility of this interpretation, indicating that modest reductions in terrestrial survival can jeopardize persistence. Even if survival remains above the threshold for persistence, reduced terrestrial survival can substantially diminish numbers of adults at equilibrium in populations regulated by density-dependent larval survival.

Conservation Issues

Protecting isolated wetlands is a critical issue for conservation of pond-breeding amphibians such as the marbled salamander. Isolated wetlands are important breeding habitats for amphibians (Petranka 1998). In many regions small, seasonally drying, isolated wetlands are the most valuable for maintaining amphibian biodiversity, but it is precisely these wetlands that are unprotected by current wetland regulations and that are most at risk of alteration (Gibbs 1998; Semlitsch & Bodie 1998). Approximately 97% of the Carolina bays on the Coastal Plain of South Carolina have been altered or severely affected, and fewer than 200 of the original thousands of bays are relatively intact (Bennett & Nelson 1991). Losses are likely to be accelerated by the U.S. Supreme Court's decision in *Solid Waste Agency of Northern Cook County vs. the U. S. Army Corps of Engineers* (Sharitz 2003) unless individual states pass legislation to protect small, isolated wetlands.

If conservation efforts are to be successful, protection must be extended to include terrestrial habitat beyond the boundaries of the jurisdictional wetland (Gibbons 2003). Depending on factors that include life span and risk of catastrophic failure, amphibians breeding in incompletely predictable habitats may require management on spatial scales that encompass additional breeding ponds to offer good prospects for rescue or recolonization when the inevitable occurs. Above all, the example of the marbled salamander underscores the importance of conditions in the upland habitat surrounding breeding ponds.

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