ITEROPARITY IN THE VARIABLE ENVIRONMENT OF THE SALAMANDER *AMBYSTOMA TIGRINUM*

Don R. Church,[1,2,4] Larissa L. Bailey,[3] Henry M. Wilbur,[1] William L. Kendall,[3] and James E. Hines[3]

[1]*Department of Biology, University of Virginia, Gilmer Hall, Charlottesville, Virginia 22904 USA*
[2]*Conservation International, Regional Programs Division, 2011 Crystal Drive, Suite 500, Arlington, Virgina 22202 USA*
[3]*USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland 20708-4017 USA*

Abstract. Simultaneous estimation of survival, reproduction, and movement is essential to understanding how species maximize lifetime reproduction in environments that vary across space and time. We conducted a four-year, capture–recapture study of three populations of eastern tiger salamanders (*Ambystoma tigrinum tigrinum*) and used multistate mark–recapture statistical methods to estimate the manner in which movement, survival, and breeding probabilities vary under different environmental conditions across years and among populations and habitats. We inferred how individuals may mitigate risks of mortality and reproductive failure by deferring breeding or by moving among populations. Movement probabilities among populations were extremely low despite high spatiotemporal variation in reproductive success and survival, suggesting possible costs to movements among breeding ponds. Breeding probabilities varied between wet and dry years and according to whether or not breeding was attempted in the previous year. Estimates of survival in the nonbreeding, forest habitat varied among populations but were consistent across time. Survival in breeding ponds was generally high in years with average or high precipitation, except for males in an especially ephemeral pond. A drought year incurred severe survival costs in all ponds to animals that attempted breeding. Female salamanders appear to defer these episodic survival costs of breeding by choosing not to breed in years when the risk of adult mortality is high. Using stochastic simulations of survival and breeding under historical climate conditions, we found that an interaction between breeding probabilities and mortality limits the probability of multiple breeding attempts differently between the sexes and among populations.

Key words: Ambystoma tigrinum; *breeding probability; cost of reproduction; environmental variability; iteroparity; movement; multistate mark–recapture methods; skipping reproduction; survival.*

INTRODUCTION

Organisms that utilize spatiotemporally variable environments must often mitigate risks of reproductive failure. Individuals can postpone maturity until conditions are favorable for reproductive success. Such organisms may use a semelparous life history with their lifetime investment spent in a single bout of reproduction, such as in Pacific salmon, or individuals can use an iteroparous life history to reproduce multiple times over the course of their lives to increase the probability of breeding in an auspicious year (Cole 1954, Hastings and Caswell 1979, Bulmer 1985, Orzack and Tuljapurkar 1989, 2001). Iteroparous individuals may be unable to breed in successive years due to the time required to sequester resources necessary for successful breeding. When the option to breed is open, individuals may postpone reproduction until the environment is auspicious for success. Finally, individuals may invest in reproduction whenever possible because they cannot predict when an investment will succeed. We will refer

to these three adaptations as iteroparity controlled by constraints, facultative breeding, and bet-hedging, although a life history might contain elements of all three. Constraints will generally be determined by the time required to recover from the cost of breeding and time required to sequester resources. Facultative breeding implies a response to external environmental conditions with individuals "choosing" to skip breeding even though they could. Bet-hedging (sensu Slatkin 1974, after Gillespie 1974) implies that individuals are breeding in multiple seasons to reduce variance in reproductive success at the cost to mean investment in the absence of useful cues to predict the success of breeding. Similar arguments can be applied to whether individuals always lay eggs at the same location or invest in dispersal either as a facultative response to environmental cues or as a bet-hedging tactic. This paper considers how the survival, breeding, and movement probabilities of the eastern tiger salamander (*Ambystoma tigrinum tigrinum*) determine its mode of iteroparity.

Several factors can limit iteroparity of organisms, including mortality (e.g., Olsson and van der Jeugd 2002), energy costs of reproduction (e.g., Harris and

Ludwig 2004), and forfeiture of breeding when the probability of reproductive success is low (e.g., Erikstad et al. 1997). The interaction among these constraints under stochastic conditions must be explored in order to calculate the mean number and variance of lifetime breeding attempts by individuals. Estimating how such an interaction limits iteroparity is therefore an important step toward understanding population dynamics and the evolution of life histories.

Variable environments present a twofold dilemma. First, species with the ability to forgo reproduction must choose whether or not to breed based only on conditions during the breeding season without a certain forecast of the conditions that will be faced by their offspring later in the year. This decision is particularly relevant for species that produce large broods (Erikstad et al. 1998), many of which may be unable to reproduce in consecutive years if resources are scarce (e.g., Rivalan et al. 2005). Second, for iteroparous animal species that divide their life cycle between breeding and nonbreeding habitats, reproduction may present mortality risks to adults that do not exist in the nonbreeding habitat. If these mortality risks vary among breeding sites or years, there may be an even greater advantage to adults that are selective about where (Fretwell and Lucas 1970) and when (Williams and Nichols 1984) they breed. However, movements may incur mortality risks of their own and skipping a year of reproduction can be a missed opportunity for reproductive success followed by a risk of dying before the next breeding season arrives (Errington 1946).

Recent advances in multistate mark–recapture methods now permit accurate assessment of mortality risks using simultaneous estimation of survival and movements of organisms in different reproductive states, habitats, and populations (Williams et al. 2002) with the ability to remove sampling variation from the estimates (Gould and Nichols 1998). These multistate models can test hypotheses about how costs of reproduction may vary among and within populations through time (Nichols and Kendall 1995). For species that do not breed every year, it is possible to test whether breeding probability is a random or Markovian process and whether it is dependent on conditions within a year. Here, we present a four-year, capture–recapture (CR) study of the pond-breeding eastern tiger salamander, *Ambystoma tigrinum tigrinum*, designed to evaluate how survival, breeding, and movement probabilities of adult salamanders vary among populations, habitats, and years. We test our predictions that energy costs limit the frequency of reproduction and that attempted breeding in dry conditions incurs episodic survival costs that adults may mitigate by selecting years and sites to breed based on environmental cues. We then interpret how an interaction between mortality and skipping reproduction limits lifetime breeding attempts in the stochastic environments of three populations.

Materials and Methods

Study system

Our study focused on three eastern tiger salamander populations that are associated with three ponds (Pond Two, Oak Pond, and Deep Pond) in the Maple Flats Sinkhole Pond Complex (Buhlmann et al. 1999: Plate 1) at the base of the Blue Ridge Mountains in the Shenandoah Valley of Augusta County, Virginia, USA. *Ambystoma tigrinum* is considered endangered by the state of Virginia and several other Atlantic states. The Maple Flats populations are the only known occurrences in the Ridge and Valley Physiographic Province (Buhlmann and Hoffman 1990, Church et al. 2003). The species is largely subterranean in upland forests and is rarely encountered outside of the breeding season. However, the breeding season is long, with males and gravid females entering the ponds from late August to mid-March and leaving by early April (Fig. 1).

The focal study ponds are arranged in an approximately equilateral triangle (325–400 m apart) and represent three of the nearest neighbor breeding sites of the 10 known breeding sites for tiger salamanders in the complex (Mitchell and Buhlmann 1999). Hydrology of these ponds is complex: ponds fill and dry at different rates within and among years, and water levels may rise in some while receding in others (Fig. 1; Buhlmann et al. 1999). The hydrology of several ponds appears to be regulated more by the local water table than by sheet flow following rainfall. Oak Pond rarely dries but fluctuates greatly in volume. Deep Pond fills quickly and dries only when rainfall is below average. Pond Two dries at least once per year.

Trapping methods

In the summer of 1999, we installed drift fences constructed of aluminum flashing to fully encircle each of the three study ponds. The fences around Deep Pond and Oak Pond were ~290 m in circumference and Pond Two's fence was ~210 m. The fences were buried 10 cm below the ground surface, leaving 50 cm standing above ground. Numbered pitfall traps (19-L plastic buckets) were located every 10 m on both sides of the fence. These traps were opened whenever there was a chance of salamander surface activity, especially during and following rain events and on all days during peak breeding activity. Open traps were checked daily to monitor all animals entering and leaving each pond. Animals were processed and then released on the opposite side of the fence from the point of capture within a few minutes to several hours.

Reconstructing individual capture histories

Adult tiger salamanders have markings that are unique to each animal and that change little after an animal reaches maturity. The capture history of each individual in our study was reconstructed from photographs in three steps. First we compared the images

taken within a year to reconstruct each individual's capture history of entries and exits from a pond within each year. For our analyses, we used only the first and last records for the few animals that entered and left multiple times within a year. Next we compared images between ponds to search for individuals that visited more than one pond within a breeding season. Between-pond movements within a year occurred twice when an animal was intercepted while dispersing from a pond at the end of the breeding season. In these instances, the animal simply crossed through the second pond's basin and exited on the other side within a few days. These records were not viewed as breeding events, and so we did not include them in our analyses. Finally, recaptures across years were found by comparing all images from year 1 (1999–2000 season) of the study against images from year 2 (2000–2001 season). Iterations of between-year comparisons generated a final list of captures of all the individuals captured over four years and each individual's complete recapture history.

Multistate mark–recapture analysis and multimodel inference

Early demographic studies of ambystomatid salamanders (e.g., Husting 1965) and other caudates (i.e., Gill 1978a, b) as well as general knowledge of the natural history of tiger salamanders (reviewed in Petranka 1998) guided our analyses of populations. First, we understood that individual salamanders are likely to skip breeding for one or more years. Second, salamanders may exhibit variation in survival across populations and, possibly, across time. Third, movement of individuals among populations may occur. Finally, we were aware of a "nuisance" parameter associated with drift fence trespass, whereby individual salamanders get under or over drift fences without being detected (Gill 1985, 1987, Nichols et al. 1987). The ability to estimate and accommodate imperfect detection (or capture) probability, allowing for unbiased estimation of survival, movement, and breeding probabilities, is one of the strengths of capture–recapture methods. Our analysis assumes that all individuals depart or die within the breeding pond by the end of the breeding season. We sampled breeding ponds extensively throughout the year using other methods (e.g., dipnetting and funnel trapping) and never encountered an adult tiger salamander within a pond basin during the nonbreeding season.

To calculate maximum likelihood estimates of survival within forest and pond habitats, transitions between breeding and nonbreeding states, movements among populations, and capture probabilities, we used multistate mark–recapture (MSMR) models developed by Bailey et al. (2004) and a modified version of MSSUR-VIV (Hines 1994; modified version *available online*).[5]

Akaike's Information Criterion corrected for small sample size (AIC_c) was used to select among competing models, and Akaike weights (w) were computed to identify the relative "weight" of evidence for each model (Burnham and Anderson 2002). The model structure of Bailey et al. (2004) uses a modified robust design (Pollock 1982) termed a "gateway" robust design (Kendall 2004) to disentangle survival probability between secondary sampling periods (survival while inside the fence) from survival and transition probabilities between primary sampling periods (survival while outside the fence in the forest). The novelty of this approach is that it permits estimation of transitions between observable states (breeders) as well as transitions between observable (breeder) and unobservable (nonbreeder) states. Skipping a year of reproduction implies a transition into the nonbreeding (unobservable) state (Kendall et al. 1997).

W. L. Kendall, L. L. Bailey, and J. Yoshizaki (*unpublished manuscript*) expanded the Bailey et al. (2004) version of the gateway robust design to include multiple unobservable states. For our purposes, animals can occur in one of six states, a breeding and nonbreeding state associated with each of the three populations. Nonbreeding animals remain in the forest, whereas breeding animals divide their year between the pond and the forest; only breeding individuals are subject to capture (i.e., if they are intercepted by the fence between the two habitats). Not all transitions are estimable in the most general case of this model (W. L. Kendall, L. L. Bailey, and J. Yoshizaki, *unpublished manuscript*); movement between two nonbreeding populations cannot be estimated. However, transitions can be estimated from a nonbreeding state to a breeding state in any population and from a breeding state to its counterpart nonbreeding state within the same population (Appendix A). An important feature of our analysis is that it estimates survival probabilities for breeding animals both within ponds and within the forest.

An exploratory set of models determined that survival probabilities of breeders are specific to population, habitat (pond vs. forest), and sex, but only survival within ponds is time-specific; survival within the forest is constant among the four years of our study (Church 2004). Our global model ($S(t$-pd,pop,sx) Ψ (t,pop,sx) p (t,pop,sx)) estimated survival probabilities (S) in ponds (pd) for both sexes (sx) across all three populations (pop) and all four years (t) of the study while forest survival was kept constant among years for each of the three populations; transitions (Ψ) between breeding and nonbreeding states and between all possible pairs of populations for each sex and year; and time-specific capture probabilities (p) for both sexes within each population. Reduced models assumed that survival probabilities were constant across time (years), space (populations), or between the sexes. Probabilities of transitions between states (i.e., between populations and breeding states) were similarly estimated, except that

natural history observations informed additional constraints within all models. For example, movements between some populations were never observed, so these movement probabilities were always constrained to zero to avoid problems in model fitting (e.g., convergence and calculating variance–covariance matrices).

Generally, an unavoidable assumption of MSMR studies with unobservable states is that survival probability is independent of breeding state (assuming nonbreeders are unobservable, U, and breeders are observable, $O:S_i^U = S_i^O = S_i$; see Kendall 2004 and citations within). Biologically, we felt it was more appropriate to assume that survival probabilities of nonbreeders were more closely associated with survival probabilities of breeders in the forest habitat. That is, nonbreeders in the forest during the breeding season were assumed to have the same survival probability as breeders experienced in the forest outside the breeding season [$S_{i1}^U = (S_{i2}^O)^a$], where a is the ratio of time spent in the pond to the time spent in the forest (see Bailey et al. [2004] for more details), the superscripts U and O indicate unobserved (nonbreeder) and observed (breeder) states, respectively, and i indicates the time interval (as an example, "$i1$" and "$i2$" correspond to the breeding and nonbreeding season, respectively, in year i). This approach assumes that habitat, rather than time of year, is the more important factor influencing survival of nonbreeders. We believe that our approach is justified because annual changes in survival within the forest are probably not as large as changes in survival of animals within ponds across years (recall that our exploratory models found survival of breeders during the nonbreeding season to be constant across time). During periods of low precipitation, the dearth of underground refuges within dry ponds may reduce survival (due to predation and desiccation) of animals that have entered the pond basins (breeders) above that experienced by animals residing in the forest (nonbreeders) (Church 2004).

It is important to point out that, although we used biweekly survival probabilities to constrain survival probabilities across different time periods, we converted all survival estimates to realized survival probabilities that represent survival over the periods of interest (i.e., breeding and nonbreeding seasons). That is, for each year we calculated the probability of surviving the entire breeding season and another probability for surviving the entire nonbreeding season; the product of these two probabilities represents the probability of surviving an entire year. Only these realized survival probabilities are presented in our results and discussion.

We tested our prediction that animals were less likely to breed in the third, extremely dry year of our study (2001–2002) by including models with time-specific breeding probability ($\Psi(t)$) in our candidate model set. We also explored whether transition probabilities were random or Markovian with respect to whether animals were breeders (Ψ^{OO}) or nonbreeders (Ψ^{UO}) in preceding years. This permitted us to test our prediction that

energy costs of reproduction limit consecutive breeding attempts. A subset of Markovian models included an additive time effect whereby there was a constant difference in breeding probability, on a logit scale, between animals that bred (Ψ^{OO}) and those that did not breed (Ψ^{UO}) in the preceding year. Some of the additive models did not converge and were therefore disregarded during model selection.

In total, our candidate model set was composed of 42 models (Table 1). Model weights were recalculated for models that, combined, carried >90% of the weight of evidence. Model averaging (Burnham and Anderson 2002) was used to calculate point estimates and standard errors of survival and transition probabilities.

Stochastic simulations of survival and breeding

Breeding and survival probabilities were used in stochastic simulations to calculate mean cumulative adult survival probabilities and breeding attempts over 50 years. An analysis of historical climate data (Appendix B) guided how we assigned frequency values to the survival and breeding probabilities. Simulations were performed with 10 000 replicates for each sex and each population.

RESULTS

Capture data and phenology

Our CR analyses included a total of 1511 captures consisting of 629 female captures (297 individuals) and 882 male captures (417 individuals; Appendix C). The breeding pond residency time, estimated from individuals that were captured entering and departing during a single breeding season, varied greatly among individuals, but, on average, males entered the ponds earlier (Fig. 1) and spent nearly twice as long as females in ponds (Appendix D).

Model selection

A restricted version of our global model with Markovian breeding probabilities fit the data based on Pearson's goodness-of-fit test after pooling cells with small expected values ($S(t$-pd, pop, sx)$\Psi(t$, pop, sx) $p(t$, pop): $\chi^2 = 11.77$, df $= 16$, $P = 0.76$, $\hat{c} = 0.27$; no overdispersion was detected, $\hat{c} < 1$), where t-pd means the parameter is time-specific in the pond habitat, pop refers to population, and sx refers to sex. Because the $S(t$-pd,pop,sx)$\Psi(t$,pop,sx) $p(t$,pop) model is a restricted version of the global model that allows full time-, population-, and sex-specific capture probabilities, an adequate fit of this restricted model implies an adequate fit of the more general model as well.

The two most-parsimonious models ($S(t$-pd,pop,sx)$\Psi(t$,sx) p(pop) and $S(t$-pd,pop,sx)$\Psi(t$,sx) p(pop,sx)) were Markovian with respect to breeding probabilities and together carried 94% of the weight of evidence within the candidate model set (Table 1). Survival of breeders within the pond (breeding season) varied over time (year), population, and sex, whereas

Table 1. Candidate model set ordered by ΔAIC_c.

Model	Transition process	ΔAIC_c	w	Evidence ratio	K
S(t-pd,pop,sx) Ψ (t,sx) p (pop)	Markovian	0.00	0.70	1.00	46
S(t-pd,pop,sx) Ψ (t,sx) p (pop,sx)	Markovian	2.16	0.24	2.94	49
S(t-pd,pop,sx) Ψ (t,sx) p (pop)	random	6.40	0.02	24.53	42
S(t-pd,pop,sx) Ψ (t,sx) p (pop,sx)	random	8.48	0.01	69.41	45
S(t-pd,pop,sx) Ψ (t,sx) p (t,pop)	Markovian	9.51	0.01	116.17	61
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop)	Markovian	9.85	0.01	137.69	62
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop)	additive	10.61	0.00	201.35	56
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop,sx)	Markovian	12.22	0.00	450.36	65
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop,sx)	additive	12.84	0.00	614.67	59
S(t-pd,pop,sx) Ψ (sx) p (pop)	Markovian	13.59	0.00	893.42	42
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop)	random	14.00	0.00	1096.70	50
S(t-pd,pop,sx) Ψ (t,sx) p (t,pop)	random	15.18	0.00	1978.43	57
S(t-pd,pop,sx) Ψ (sx) p (pop)	random	15.31	0.00	2111.30	40
S(t-pd,pop,sx) Ψ (sx) p (pop,sx)	Markovian	15.82	0.00	2724.56	45
S(t-pd,pop,sx) Ψ (t,pop,sx) p (pop,sx)	random	16.25	0.00	3378.08	53
S(t-pd,pop,sx) Ψ (pop,sx) p (pop)	Markovian	17.25	0.00	5569.51	50
S(t-pd,pop,sx) Ψ (sx) p (pop,sx)	random	17.63	0.00	6734.93	43
S(t-pd,pop,sx) Ψ (t,pop,sx) p (t, pop)	additive	18.49	0.00	10 353.33	71
S(t-pd,pop,sx) Ψ (t,pop,sx) p (t,pop)	Markovian	18.83	0.00	12 271.85	77
S(t-pd,pop,sx) Ψ (pop,sx) p (pop,sx)	Markovian	19.72	0.00	19 150.10	53
S(t-pd,pop,sx) Ψ (pop,sx) p (pop)	random	20.11	0.00	23 273.33	44
S(t-pd,pop,sx) Ψ (t,pop,sx) p (t,pop)	random	21.97	0.00	58 986.46	65
S(t-pd,pop,sx) Ψ (sx) p (t,pop)	Markovian	22.12	0.00	63 580.57	57
S(t-pd,pop,sx) Ψ (pop,sx) p (pop,sx)	random	22.57	0.00	79 623.40	47
S(t-pd,pop,sx) Ψ (pop,sx) p (t,pop)	Markovian	25.12	0.00	284 948.40	65
S(t-pd,pop,sx) Ψ (pop,sx) p (t,pop)	random	28.67	0.00	1 681 275.00	59
S(t-pd,pop,sx) Ψ (pop) p (pop)	random	36.33	0.00	77 394 756.00	41
S(t-pd,pop,sx) Ψ (pop) p (pop)	Markovian	37.58	0.00	1.45×10^8	44
S(t-pd,pop,sx) Ψ (pop) p (pop,sx)	random	38.25	0.00	2.02×10^8	44
S(t-pd,pop,sx) Ψ (pop) p (pop,sx)	Markovian	39.58	0.00	3.93×10^8	47
S(t-pd,pop,sx) Ψ (t,pop) p (pop)	random	42.49	0.00	1.69×10^9	44
S(t-pd,pop,sx) Ψ (pop) p (t,pop)	random	43.50	0.00	2.79×10^9	56
S(t-pd,pop,sx) Ψ (pop) p (t,pop)	Markovian	44.04	0.00	3.66×10^9	59
S(t-pd,pop,sx) Ψ (t,pop) p (pop)	Markovian	44.11	0.00	3.79×10^9	50
S(t-pd,pop,sx) Ψ (t,pop) p (pop,sx)	random	44.45	0.00	4.49×10^9	47
S(t-pd,pop,sx) Ψ (t,pop) p (pop,sx)	Markovian	46.15	0.00	1.05×10^{10}	53
S(t-pd,pop,sx) Ψ (t,pop) p (t,pop)	Markovian	46.15	0.00	1.05×10^{10}	65
S(t-pd,pop,sx) Ψ (t,pop) p (t,pop)	random	49.40	0.00	5.33×10^{10}	59
S(t-pd,pop,sx) Ψ (pop) p (t,pop,sx)	random	71.47	0.00	3.31×10^{15}	74
S(t-pd,pop,sx) Ψ (pop) p (t,pop,sx)	Markovian	72.82	0.00	6.5×10^{15}	77
S(t-pd,pop,sx) Ψ (sx) p (t,pop,sx)	random	73.03	0.00	7.22×10^{15}	73
S(t-pd,pop,sx) Ψ (t,pop) p (t,pop,sx)	Markovian	79.26	0.00	1.63×10^{17}	83

Notes: Estimated parameters include survival (S), transition (Ψ), and capture probability (p); these parameters were permitted to vary according to time (t), population (pop), and sex (sx). An exploratory set of models determined that breeders have population-, habitat (pond vs. forest)-, and sex-specific survival probabilities, but only survival within ponds (pd) is time-specific (t-pd); survival within the forest is time-constant. Transition probabilities include transitions between breeding and nonbreeding states within populations as well as movements between populations. Transitions were modeled as random or Markovian processes. A subset of Markovian models was additive to explore the possibility that there were constant time effects on the differences between breeding probabilities of breeders and nonbreeders. Model weights (w) were recalculated for the top two models and used to calculate model-averaged survival, transition, and capture probabilities. Our study focused on three eastern tiger salamander (*Ambystoma tigrinum tigrinum*) populations that are associated with three ponds (Pond Two, Oak Pond, and Deep Pond) in the Maple Flats Sinkhole Pond Complex at the base of the Blue Ridge Mountains in the Shenandoah Valley of Augusta County, Virginia, USA.

survival in the forest (nonbreeding season) varied with sex and population but not time in either top model. Transitions, including breeding and movement probabilities, varied according to sex and year, but not population. The two top models differed only with respect to capture probability structure: the model with population-specific capture probabilities garnered the majority of the weight ($w = 0.70$), but there was some support for sex differences in the second model ($w = 0.24$). Capture probabilities did not appear to vary across time (Table 1).

Model-averaged parameter estimates

Capture probabilities were high; estimates for females were 0.98, 0.98, and 0.96 for populations at Oak Pond, Pond Two, and Deep Pond, respectively. Male capture probabilities in populations at Oak Pond, Pond Two, and Deep Pond were, respectively, 0.98, 0.97, and 0.95. These estimates refer to the probability of capture at each encounter with the fence.

Survival estimates in breeding ponds varied among populations and years and differed between sexes (Fig. 2, Appendix E). Mean survival probability in
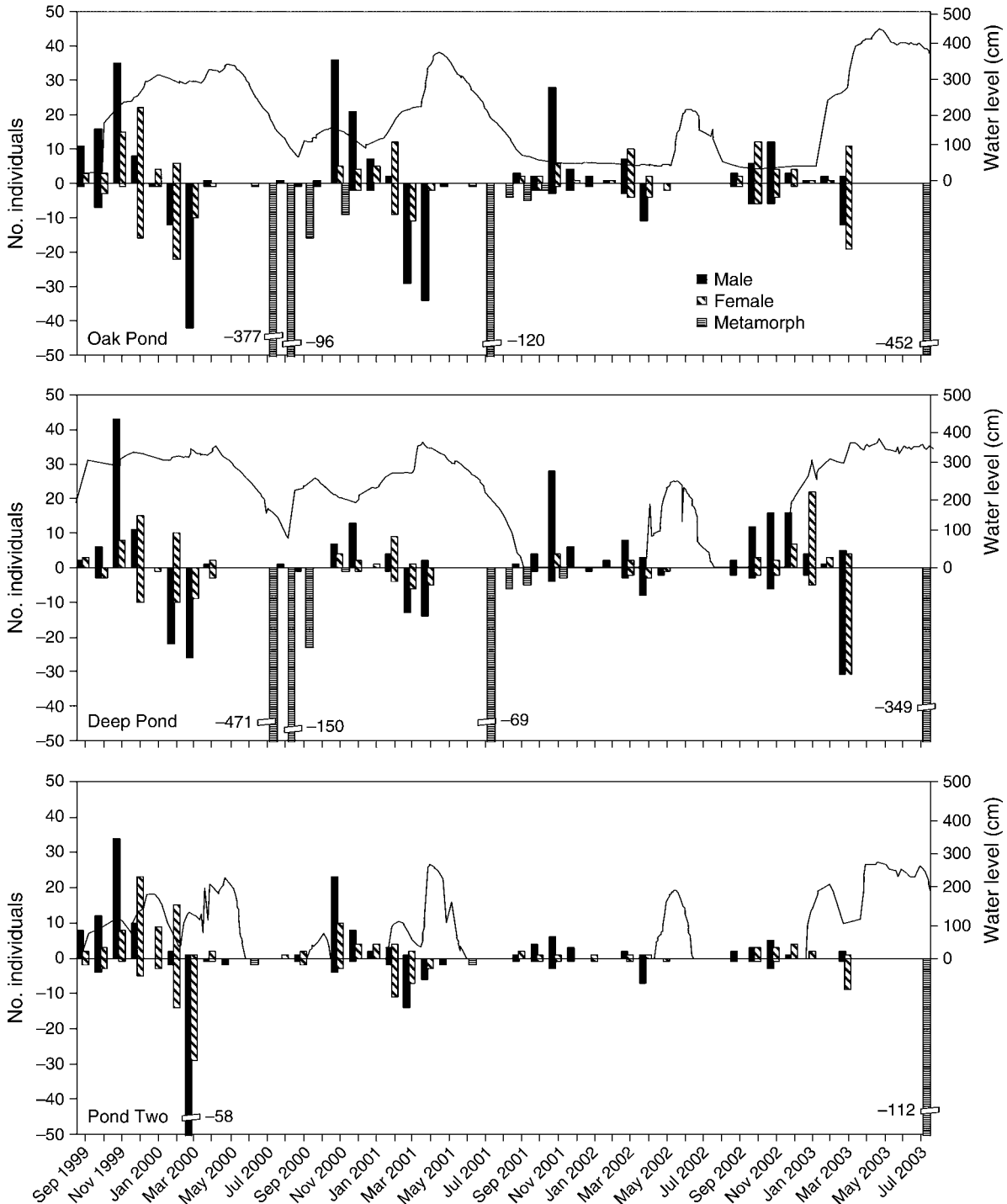
FIG. 1. Phenology of eastern tiger salamander (*Ambystoma tigrinum tigrinum*) breeding activity at Oak Pond, Deep Pond, and Pond Two and each pond's hydrology from 1 September 1999 through 31 August 2003. Pond depth is indicated in centimeters by the trace line. Numbers of animals captured entering the ponds are indicated by the positive numbers on the *y*-axis (above the zero mark), and numbers of animals captured exiting the ponds are represented by the negative numbers (below the zero mark). The bars indicate the numbers of adult males (black bars), adult females (hatched bars), and metamorphs (gray bars) captured entering or exiting the ponds in each month. Note that, in some months, breaks occur in bars that represent the numbers of metamorphs captured exiting ponds; the total number of animals that were captured exiting in each of these months is indicated next to the break. Our study focused on three eastern tiger salamander populations that are associated with three ponds (Pond Two, Oak Pond, and Deep Pond) in the Maple Flats Sinkhole Pond Complex at the base of the Blue Ridge Mountains in the Shenandoah Valley of Augusta County, Virginia, USA.

ponds across all populations and years was 0.85 for females and 0.75 for males. The four-year survival means for males were 0.75, 0.70, and 0.79 and, for females, 0.85, 0.84, and 0.87, for Oak Pond, Pond Two, and Deep Pond, respectively. Variation across years within ponds was due primarily to the especially low survival of both sexes in ponds in the exceptionally dry year of 2001–2002. For example, in Oak Pond the survival of females was estimated as 1.00 in 2000–2001 and only 0.55 the following year, a drop of 45%. It is important to note that the differences in survival estimates between the sexes are not entirely explained by the differences in how males and females divide the year between pond and forest (Appendix D). Our models used probabilities that were scaled entirely to biweekly periods and, therefore, our model selection compared models in which survival was scaled to the same interval of time. The fact that the most parsimonious models were those that assumed different survival for males and females means that there would be differences in male and female survival even if they spent the same amount of time in each habitat.

Both breeders and nonbreeders inhabit the forest during the nonbreeding season but survival could only be estimated directly for breeders. Survival probabilities in the forest varied among populations and between the sexes (Appendix E). Yearly differences in survival reflect only the variation in time spent within the forest by breeders among years (Appendix D). Survival of males was, on average, 12% and 5% lower than that of females in the Oak Pond and Deep Pond populations, respectively, but averaged 10% higher in Pond Two's population. Point estimates of survival probabilities for breeding females in the forest averaged 0.78 for Oak Pond and 0.87 for Deep Pond. Following their exit from ponds, post-breeding females in Pond Two's population had a reduced survival probability of 0.66 in the forest. Mean survival of post-breeding males in the forest was, in contrast, 0.69 for Oak Pond, 0.73 for Pond Two, and 0.83 for Deep Pond.

Our approach for assessing survival costs of reproduction assumes nonbreeders continue to have the same mortality risks in the breeding season (fall–winter) that breeders have when they are in the forest during the nonbreeding season (spring–summer). We believe that this is a reasonable assumption for the following reasons. First, survival in the forest for breeders was constant during the study. Although we were not able to gather direct data on survival in the forest during the breeding season (fall–winter), the constancy of survival in the forest during the spring and summer over four years with extremely variable weather (Church 2004) suggests that survival of salamanders in the forest is buffered from extreme weather events. Indeed, if forest survival were to vary with changes in annual weather patterns, we would expect it to do so during the spring and summer when dry periods are exacerbated by higher temperatures and evapotranspiration by plants. Fur-
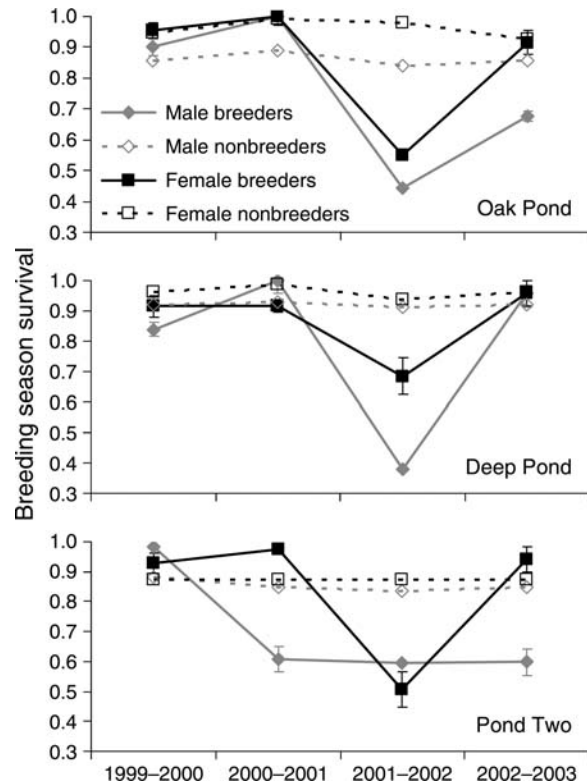

FIG. 2. Model-averaged estimates of survival probabilities (mean ± SE) for adult male and female salamanders during the breeding season (fall–winter) in the four years of the study (1999–2000 through 2002–2003) for populations at Oak Pond, Deep Pond, and Pond Two. Survival estimates for animals in breeding and nonbreeding states are represented to indicate the survival costs to reproduction. Nonbreeder survival probabilities cannot be estimated directly and are therefore borrowed from estimated probabilities of breeder survival during the nonbreeding season (spring–summer). It is assumed that survival of nonbreeders is best approximated by survival of breeding animals during the nonbreeding season because animals in these two states share the same forest habitat, where survival was found to be constant among years.

thermore, more predators are active during the spring and summer (Church 2004). Finally, it is unlikely that tiger salamanders, particularly nonbreeding animals, experience mortality due to freezing temperatures in our populations because radiotelemetry studies at our study site have revealed that their subterranean refuges extend well below the frost line (F. Huber, *personal communication*). Hence, it is reasonable to assume that nonbreeder survival in forests during the fall and winter is at least as high and constant as that of breeders during the spring and summer. Our estimates of survival costs of reproduction are therefore most likely conservative.

Following our assumption about nonbreeder survival during the breeding season, we can see distinct spatiotemporal and sex differences in survival costs of reproduction (Fig. 2). Breeders in the Oak Pond and Deep Pond populations face episodic mortality risks associated with years of low precipitation when ponds
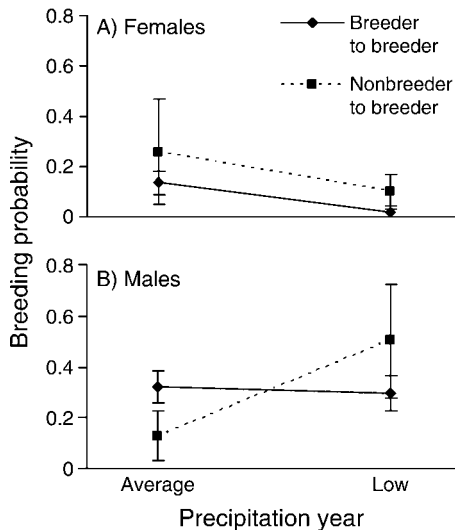
FIG. 3. Model-averaged estimates of breeding probabilities (mean ± SE) for (A) adult female and (B) adult male salamanders transitioning from nonbreeding and breeding states in years with average (1999–2000, 2000–2001, and 2002–2003) and low (2001–2002) precipitation. The weight of evidence supported models in which breeding probabilities were Markovian and in which breeding probabilities for the third (drought) year of our study were estimated independently of other years when precipitation was near or above average.

are dry. Survival probabilities were as much as 54% lower than survival in the forest for males in Deep Pond during the drought year. Females had about half the survival cost owing, in part, to their, on average, later entry into ponds and shorter residence time (Appendix D). Both males and females in Oak Pond incurred a survival cost associated with breeding in the dry year of ~40% $(1 - (S_{br}/S_{nbr})$; br, breeding; nbr, nonbreeding) in the study's third year. Breeding males from Oak Pond suffered an ~20% survival cost in the following year. Although 2002–2003 was an exceptionally wet year, the filling of Oak Pond did not commence until the winter; hence, males that entered the slowly filling Oak Pond in the fall experienced conditions similar to the preceding year. Pond Two, in sharp contrast to Oak and Deep Ponds, appears to provide a benign environment for breeding males only episodically. A 30% survival cost to breeders was constant for males in the last three years of the study. Survival costs were only negligible for males in the first year when intense hurricane rains in the fall were sufficient to fill and maintain this ephemeral pond early in the season (Fig. 1).

Transition probabilities varied between the sexes and among years (Fig. 3). The strong support for models with Markovian transition probabilities is consistent with our prediction that energy costs of reproduction limit the frequency of breeding attempts. The strong support for models with time specificity in transition rates implies that females, at least, are choosy about what years they attempt breeding and are more likely to

skip breeding opportunities, especially in dry years. We found that breeding probabilities for females were reduced by >50% in the third, driest year of the study relative to the three years of near or above mean precipitation. The difference in breeding probability between females changing from a nonbreeding (Ψ^{UO}) and a breeding (Ψ^{OO}) state remained constant (on a logit scale) between the dry and relatively wet years. In contrast, males had relatively constant breeding probabilities when changing from a breeding state (Ψ^{OO}), whereas males that had skipped one or more years of breeding were five times more likely to breed in the dry year than in other years. Overall, these transition estimates suggest that <30% of females and <50% of males attempt breeding in any year and that the proportion of the adult population that breeds is dependent on environmental conditions.

Estimated probabilities of movement by adults between fenced ponds were low. No movements from either Oak Pond or Deep Pond were observed. Five movements from the population of Pond Two were observed, and four of these movements were by males. The estimated movement probability for breeding and nonbreeding state females from Pond Two into Deep Pond was 0.04 and 0.02, respectively. The movement probability of males from Pond Two into Oak and Deep Ponds was 0.06 for breeders and nonbreeders.

Our interpretations of model parameters assume there are no unsampled populations. Inherently, permanent movement to unfenced ponds would be confounded with survival, and any temporary movement would be confounded with breeding probabilities. The high survival probabilities in the forest and the low estimated probabilities of movement among the focal study ponds (which are closer to each other, on average, than they are to other breeding sites for tiger salamanders in the complex) suggest that few such unobserved movements of adults occur. Furthermore, 47 tiger salamanders were captured at unfenced ponds over the course of the study, but none were animals originally captured at the focal ponds.

Stochastic simulations of survival and breeding

Fig. 4 illustrates the manner in which breeding probabilities and cumulative survival probabilities interact to limit multiple breeding attempts of individuals in an environment that simulates stochastic conditions in the region over the past 107 years (Appendix B). The estimated number of years that females survive after their first breeding attempt (mean ± SD) is 4.56 ± 5.10 yr, 2.95 ± 3.39 yr, and 1.41 ± 1.74 yr in the Deep Pond, Oak Pond, and Pond Two populations, respectively. For the same sequence of ponds, males survive 2.88 ± 3.32 yr, 1.50 ± 1.85 yr, and 1.36 ± 1.87 yr post-maturity. These findings agree with an earlier skeleto-chronology study of the same populations (Buhlmann and Mitchell 2000).
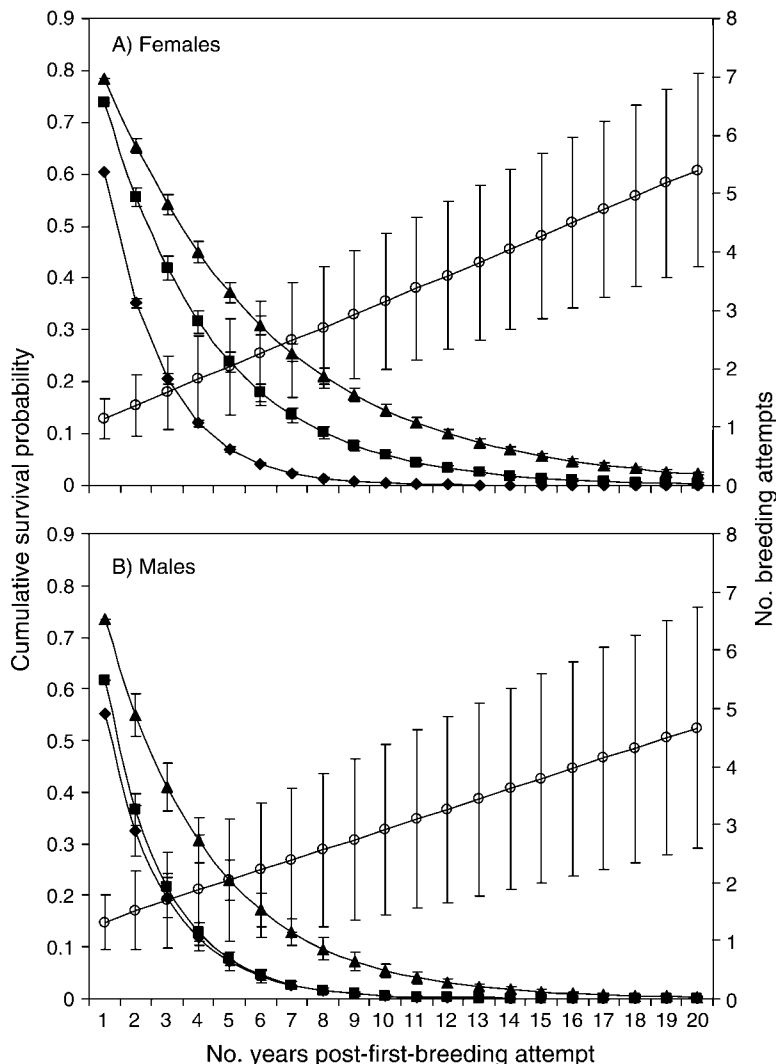
FIG. 4. Cumulative survival probability and number of breeding attempts (mean ± SD) in years after the first breeding attempt, estimated by stochastic simulation for (A) female and (B) male eastern tiger salamanders. Estimates for cumulative survival probabilities are indicated for Deep Pond's population (solid triangles), Oak Pond's population (solid squares), and Pond Two's population (solid diamonds). Estimates of breeding attempts (open circles) are equivalent for the three populations because breeding probabilities were constant among the populations in the most-parsimonious capture–recapture models.

DISCUSSION

Our results indicate that an interaction among energy costs of reproduction, increased forfeiture of breeding opportunities in dry years, and adult mortality limits iteroparity in the populations of tiger salamanders we studied. As evidenced by strong support for our Markovian models, the energy deficit that breeding incurs appears to reduce the probability of consecutive breeding attempts by females. The low probabilities of breeding for females that skipped a year or more of reproduction suggest that energy costs of a single breeding attempt usually force individuals to subsequently defer breeding for more than one year, although our data were insufficient for memory models that would

be needed to explicitly test this hypothesis. This is not surprising given that *Ambystoma tigrinum* females have exceptionally large clutches for their size (Wilbur 1977, Kaplan and Salthe 1979). Males, like females, exhibit overall low breeding probabilities that are Markovian in nature, but they are not necessarily more likely to breed if they had skipped an opportunity in the previous year. Although survival probabilities can be high in our study populations, breeding attempts are so limited, overall, that most individuals of both sexes die before they can breed a second time (Fig. 4). Trenham et al. (2000) also found that California tiger salamanders (*Ambystoma californiense*) rarely survive to breed more than once in the grassland community of central California.

Our study found that breeding probabilities varied among years but not among populations. However, differences in survival among populations interact with these breeding probabilities to produce population-specific probabilities of multiple breeding attempts. Fig. 4A illustrates that a female must survive five years after her initial breeding if she is expected to breed a second time. The population-specific probabilities for a female to survive these five years are 0.07 (Pond Two), 0.24 (Oak Pond), and 0.37 (Deep Pond). An adult female from Pond Two, Oak Pond, and Deep Pond has a 0.01, 0.10, and 0.21 probability, respectively, of surviving the eight years needed, on average, to breed three times. Hence, the three populations are on different points along a continuum of realized iteroparity.

Two factors account for the differences in survivorship curves and, consequently, the differences among populations in the likelihood of multiple breeding attempts. First, survival of breeding females in Deep Pond was nearly 40% greater than in the other ponds during the drought year (Fig. 2). However, we did not expect this difference to account for much of the variation in survivorship curves because, based on historical climate data (Appendix B), such extreme years occurred with a probability of <0.04 in our stochastic simulations. Also, differences in survival within ponds during the drought year do not account for the difference in survivorship curves between females from Pond Two and Oak Pond (Fig. 4A) because animals experienced similar survival costs of breeding in these two ponds (Fig. 2). To test our expectation that the differences in pond survival during dry years do not account for major differences in survivorship curves among populations, we reran our stochastic simulation, incrementally decreasing the probability of dry years by 10% to 0. At a probability of 0 for dry years, the cumulative survival probability of females from Deep Pond decreased by 2% and 6% at ages 5 and 10, respectively, thereby creating a survivorship curve more similar to, but still distinct from, that of females from Oak Pond.

We expected that a second factor, namely differences in survival within the forest during the nonbreeding season, probably accounts for most of the variability in cumulative survival probabilities among populations. Deep Pond females had survival probabilities during the nonbreeding season that were 11% and 22% greater, respectively, than survival of females from the Deep Pond and Pond Two populations. We do not know why survival within the forest differs among the populations, but Pond Two has a greater proportion of its perimeter associated with a 1980 clear-cut that may have residual effects on salamander survival (e.g., Dupuis et al. 1995) and Deep Pond is situated near three drainages that may improve conditions for survival (i.e., increase soil moisture) in the surrounding forest. To test our expectation that differences in survival of animals in the forest play a larger role in creating distinct survivorship curves among populations, we incrementally increased survival probabilities in the forest for Pond Two females and decreased the same probabilities for Deep Pond females while keeping all other parameters constant in our stochastic simulation. When these survival probabilities were similar to those of females from Oak Pond, the three survivorship curves nearly overlap, indicating the importance of variation of survival in the forest in generating the population differences in cumulative survival probabilities. It is interesting to note that, because the model selection in our capture–recapture analysis found survival in the forest to be constant among years and therefore constant under very different weather conditions, we expect the population differences in survivorship curves to be relatively robust to changes in climate during the nonbreeding season. Breeding probabilities may still change under such conditions, however, and thereby shift the position of each population along the continuum of realized iteroparity despite stable survivorship curves. In contrast, we expect that changes in climate that increase the probability of dry breeding seasons could more drastically reduce the iteroparity of females in each population by increasing the steepness of survivorship curves (particularly for the Oak Pond and Pond Two populations) and by increasing the number of years a female needs to live to make additional breeding attempts.

Despite differences in breeding probabilities between males and females (Fig. 3), males must also survive, on average, five years under stochastic conditions if they are to breed a second time (Fig. 4B). Male survivorship curves (Fig. 4B) were steeper than those of females for the Oak Pond and Deep Pond populations due to lower male survival in both the forest and in the ponds. Consequently, males from Deep Pond and Oak Pond are 15% and 16%, respectively, less likely than females to breed more than once. In contrast to animals from Oak Pond and Deep Pond, Pond Two females and males have nearly the same probability of breeding a second time (0.07–0.08). Although male survival probabilities in the pond are, on average, lower than those of females, Pond Two males have a 7% higher probability of survival in the forest during the nonbreeding season that compensates for their lower survival in the pond.

Our stochastic simulations demonstrate that there is high variability in the expected number of breeding attempts for a given post-maturity age in both sexes (Fig. 4). This result reflects the Markovian nature of breeding and, to a lesser extent, the stochastic changes in breeding probabilities due to "wet" and "dry" years. The high variability in number of breeding attempts by age means that there is an advantage of surviving even one additional year after a breeding attempt, despite the fact that the average individual must survive several additional years before it attempts breeding again.

It is important to note that because our study did not experimentally manipulate the animals that were ex-

posed to conditions within the ponds during the breeding season, our estimates of survival costs of breeding may reflect nonrandom (e.g., condition-dependent) sets of animals that choose to breed in a given year. For example, if only high-condition animals breed, their costs of reproduction are presumably lower than the costs that would be suffered by animals in inferior condition.

Given the anticipated survival costs of breeding in the drought year, we expected that breeding probabilities would be lower in the third year of our study. Long-term studies have reported decreased numbers of individuals in amphibian breeding migrations during dry years (e.g., Semlitsch et al. 1993). The weight of evidence in our model selection (Table 1) supports the hypothesis that females, at least, avoid mortality risks by choosing not to breed in a dry year (Fig. 3A). However, we did not eliminate other possible explanations. For example, rather than serving as a cue that conditions in a pond are poor, low rainfall may simply reduce the probability that animals residing at greater distances will reach the pond within a breeding season.

The breeding probabilities of males were remarkably low overall (Fig. 3B). Males did lose, on average, 20% of their body mass (data not shown) during the extended breeding season (Appendix D), suggesting that they may have to recoup energy losses by skipping breeding opportunities. However, this generalization is directly contradicted by our finding that, in average precipitation years, males that bred in the previous year (Ψ^{OO}) had a higher breeding probability than those that had skipped (Ψ^{UO}). This finding may be due to a group, possibly a cohort, of individuals in our study population that were especially well conditioned due to especially good home ranges or long-term effects of large size at metamorphosis (e.g., Scott 1994). In further contrast with females, males had only a slightly lower probability of remaining a breeder (Ψ^{OO}) in the dry year, and, especially surprising, males that had skipped breeding were nearly five times more likely to become breeders in the dry year than in the years with average and above-average precipitation. This may also be due to some kind of group effect in which, for example, a relatively large subset of our male population had recouped sufficient energy stores to attempt breeding in the 2001–2002 season. It remains remarkable, however, that more males did not avoid breeding in a year that posed such extreme mortality risks. A possible explanation is that because males have lower survival in the forest and overall steeper survivorship curves, they may be less likely to forgo a breeding opportunity even when mortality risks are high. This might be especially plausible if there is a risk of falling out of breeding condition (in terms of energy resources) by the next breeding season.

Based on the spatiotemporal variation in reproductive success and survival in our study populations, as well as the relatively high movement probabilities (0.0–0.24)

known for *Ambystoma californiense* (Trenham et al. 2001), we expected that movement probabilities would be high among ponds in our study. Instead, no movements were observed from Oak Pond or Deep Pond and estimated probabilities of movement for Pond Two animals were only 0.03–0.06 (Appendix F). In keeping with movement theory (e.g., Fretwell and Lucas 1970), all of the emigration occurred from the population with greatest risks of mortality and reproductive failure. However, the overall low probabilities of movement in such a variable environment suggest that there may be costs to movement. These costs are not necessarily in terms of survival; instead, adult *Ambystoma tigrinum* may simply be poor prospectors for breeding sites, making fidelity to a single pond a more advantageous strategy. Furthermore, some theory indicates that, under certain conditions, spatial risk spreading may be a far less efficient strategy for contending with spatiotemporal variation than is temporal risk-spreading (Seger and Brockmann 1987). Juveniles in our study populations have higher movement probabilities than adults, as high as 0.20 (D. R. Church and H. M. Wilbur, *unpublished data*), which is in keeping with findings for other pond-breeding amphibian species in which adults exhibit fidelity to a breeding site whereas juveniles are likely to disperse from their natal pond by the time they breed for the first time (e.g., Sinsch 1997).

Bull and Shine (1979) proposed that a "low frequency of reproduction" may evolve when energy or survival savings associated with skipped breeding opportunities can be diverted to increase lifetime reproductive output above what could be achieved through annual reproduction. They contend that these savings are usually associated with reduction in an activity that is accessory to reproduction (e.g., migration to the breeding site). In the case of tiger salamanders, such divertible savings must be very large or there must be an additional advantage to investing heavily at each breeding because most individuals die before they can breed a second time. Furthermore, smaller (i.e., fewer eggs or less time courting females in the pond) but more frequent investments would increase their chances of intercepting auspicious years. Presumably, the temporal variability in reproductive success and survival are not sufficient for such a bet-hedging strategy to outweigh unknown advantages of consolidating reproductive effort into relatively few breeding attempts.

We conclude that reproduction by tiger salamanders probably incurs a high energy cost that constrains the frequency of breeding attempts. After these costs have been recovered females, at least, may only attempt reproduction in years that present favorable environments for adult and larval survival. Our estimates of low adult movement probabilities and low expected number of breeding attempts by both sexes suggest that adult dispersal and iteroparity are not dominant bet-hedging strategies in the life history of this species. Because the environment poses high variability in larval survival

among years and because detection of "optimal" years for reproduction is imperfect, we expect that other adaptations permit individuals to hedge their evolutionary bets. Juveniles from a single cohort do mature at different ages within our study populations (D. R. Church and H. M. Wilbur, *unpublished data*). Variable age at maturity may introduce a population storage effect (sensu Chesson 1982) and thereby substitute iteroparity as a dominant adaptation for contending with environmental variability.

LITERATURE CITED

Bailey, L. L., W. L. Kendall, D. R. Church, and H. M. Wilbur. 2004. Estimating survival and breeding probabilities for pond-breeding amphibians: a modified robust design. Ecology 85:2456–2466.

Buhlmann, K. A., and R. L. Hoffman. 1990. *Ambystoma tigrinum tigrinum*. Herpetological Review 21:36.

Buhlmann, K. A., and J. C. Mitchell. 2000. Age of adult eastern tiger salamanders (*Ambystoma tigrinum tigrinum*) in a Virginia sinkhole pond complex: implications for conservation. Journal of the Elisha Mitchell Scientific Society 116:239–244.

Buhlmann, K. A., J. C. Mitchell, and L. R. Smith. 1999. Descriptive ecology of the Shenandoah Valley sinkhole pond system in Virginia. Banisteria 13:23–51.

Bull, J. J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. American Naturalist 114:296–303.

Bulmer, M. G. 1985. Selection for iteroparity in a variable environment. American Naturalist 126:63–71.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer-Verlag, New York, New York, USA.

Chesson, P. L. 1982. The stabilizing effect of a random environment. Journal of Mathematical Biology 15:1–36.

Church, D. R. 2004. Population ecology of *Ambystoma tigrinum* and occupancy dynamics in an Appalachian pond-breeding amphibian assemblage. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Church, S. A., J. M. Kraus, J. C. Mitchell, D. R. Church, and D. R. Taylor. 2003. Evidence for multiple Pleistocene refugia in the postglacial expansion of the eastern tiger salamander, *Ambystoma tigrinum tigrinum*. Evolution 57:372–383.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103–137.

Dupuis, L. A., J. N. Smith, and F. Bunnel. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology 9:645–653.

Erikstad, K. E., M. Asheim, P. Fauchald, L. Dalhaug, and T. Tveraa. 1997. Adjustment of parental effort in the Puffin: the roles of adult body condition and chick size. Behavioral Ecology and Sociobiology 40:95–100.

Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79:1781–1788.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology 21:144–177.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Gill, D. E. 1978a. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145–166.

Gill, D. E. 1978b. Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Evolution 32:839–849.

Gill, D. E. 1985. Interpreting breeding patterns from census data: a solution to the Husting dilemma. Ecology 66:344–354.

Gill, D. E. 1987. Reply to Nichols et al. Ecology 68:217–220.

Gillespie, J. H. 1974. Natural selection for variance in offspring numbers: a new evolutionary principle. American Naturalist 111:1010–1014.

Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79:2531–2538.

Harris, R. N., and P. M. Ludwig. 2004. Resource level and reproductive frequency in female four-toed salamanders, *Hemidactylium scutatum*. Ecology 85:1585–1590.

Hastings, A., and H. Caswell. 1979. Role of environmental variability in the evolution of life history strategies. Proceedings of the National Academy of Sciences (USA) 76:4700–4703.

Hines, J. E. 1994. MSSURVIV user's manual. Biological Resources Division, USGS, Laurel, Maryland, USA.

Husting, E. L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965:352–362.

Kaplan, R. H., and S. N. Salthe. 1979. The allometry of reproduction: an empirical view in salamanders. American Naturalist 113:671–689.

Kendall, W. L. 2004. Coping with unobservable and misclassified states in capture–recapture studies. Animal Biodiversity and Conservation 27:97–107.

Kendall, W. L., J. D. Nichols, J. S. Sauer, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Mitchell, J. C., and K. A. Buhlmann. 1999. Amphibians and reptiles of the Shenandoah Valley Sinkhole Pond System in Virginia. Banisteria 13:129–142.

Nichols, J. D., G. R. Hepp, J. E. Hines, and K. H. Pollock. 1987. The Husting dilemma—a methodological note. Ecology 68:213–217.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835–846.

Olsson, O., and H. P. van der Jeugd. 2002. Survival in king penguins *Aptenodytes patagonicus*: temporal and sex-specific effects of environmental variability. Oecologia 132:509–516.

Orzack, S. H., and S. Tuljapurkar. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. American Naturalist 133:901–923.

Orzack, S. H., and S. Tuljapurkar. 2001. Reproductive effort in variable environments, or environmental variation is for the birds. Ecology 82:2659–2665.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

Rivalan, P., A. C. Prevot-Julliard, R. Choquet, R. Pradel, B. Jacquemin, and M. Girondot. 2005. Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. Oecologia 145:564–574.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396.

Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Oxford Surveys in Evolutionary Biology 4:182–211.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1993. Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influence. Journal of Animal Ecology 62:334–340.

Sinsch, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112:42–47.

Slatkin, M. 1974. Hedging one's evolutionary bets. Nature 250: 704–705.

Trenham, P. C., D. W. Koenig, and B. H. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82: 3519–3530.

Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). Copeia 2000:365–377.

Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. American Naturalist 111:43–68.

Williams, B. K., and J. D. Nichols. 1984. Optimal timing in biological processes. American Naturalist 123:1–19.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

APPENDIX A

A figure showing estimable transitions in the study following methodologies of Bailey et al. (2004) and W. L. Kendall, L. L. Bailey, and J. Yoshizaki (*unpublished manuscript*) (*Ecological Archives* E088-055-A1).

APPENDIX B

A figure showing historic precipitation data and methods for assigning frequencies to survival and breeding probabilities in our stochastic simulations (*Ecological Archives* E088-055-A2).

APPENDIX C

A table showing numbers of individual adult and recently metamorphosed *Ambystoma tigrinum tigrinum* entering and exiting the study ponds over four years (Ecological Archives E088-055-A3).

APPENDIX D

A table showing the number of days spent within pond basins by adult female and male *Ambystoma tigrinum tigrinum* captured over four years (*Ecological Archives* E088-055-A4).

APPENDIX E

A table showing model-averaged survival probability estimates for adult *Ambystoma tigrinum tigrinum* (*Ecological Archives* E088-055-A5).

APPENDIX F

A table showing model-averaged transition probability estimates between breeding and nonbreeding states within and between populations of *Ambystoma tigrinum tigrinum* (*Ecological Archives* E088-055-A6).