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DEMOGRAPHICS OF A GEOGRAPHICALLY ISOLATED POPULATION OF A THREATENED SALAMANDER (CAUDATA: AMBYSTOMATIDAE) IN CENTRAL ILLINOIS

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Abstract.—Amphibian populations that use small isolated wetlands are often small in size, susceptible to stochastic extinction processes, and have little to no contact with other populations. One can ascertain the persistence of such populations only by obtaining data that allow the prediction of future changes in population's size, and propensity to achieve a sustainable number of individuals. The number of metamorphosing larvae leaving a pond predicts the viability of a salamander population, and thus, the number recruited into the terrestrial adult population. The Jefferson Salamander, *Ambystoma jeffersonianum*, is a listed threatened species in Illinois, occurring at fewer than 15 ponds statewide. In 2004 and 2005, individuals at an isolated breeding pond in Lincoln Trail State Recreation Area (LTSRA) were captured using a drift fence-pitfall trap array. Once captured, we determined sex, measured snout-vent length, and using a unique combination of toe clips, marked the salamanders. We also determined the number of egg masses, average percentage of successfully hatched eggs, and number of juveniles leaving the pond. We incorporated this information into a matrix for a stage-based population model. Model simulations predicted that on average, the population at the LTSRA pond would persist for four more years, with survivorship from larvae to juvenile being the most important parameter. Increasing survivorship during the larval period increased abundance as well as average persistence time. Active management at the breeding pond to increase the time available for successful metamorphosis might facilitate persistence of the salamander at this site.

Key Words.—*Ambystoma*; ephemeral wetland; Jefferson Salamander; management; persistence; population; recruitment

INTRODUCTION

The study of amphibian populations has warranted greater attention due to three distinct trends: (1) the recent (since the 1980's) increase in reports of declining populations and species extinctions; (2) these declines occurring simultaneously and over great distances within a species geographic distribution; and (3) the decline of amphibian populations in protected, natural areas (Blaustein et al. 1994; Heyer et al. 1994; Blaustein and Kiesecker 2002; Wake and Vredenburg 2008). Among the causes of decline (reviewed in Collins and Storfer 2003), habitat fragmentation and/or degradation (Caughley and Gunn 1996) has arguably one of the largest potential impacts on amphibian species, especially when it results in an isolated population (Laan and Verboom 1990).

Studies involving isolated populations of salamanders are few in number. Isolated salamander populations might exhibit a depressed population size, and/or a decline in individual health or fitness similar to that seen in other groups (Fahrig and Merriam 1985; Portnoy 1990; Ash et al. 2003). Small, isolated populations lacking any contact with other populations can become increasingly susceptible to environmental and demographic stochasticity and natural catastrophes

(Lacy 1992). Stochasticity can also cause small populations of many species to suffer erratic swings in size from year to year (Caughley and Gunn 1996), especially if mating opportunities are rare. Small populations are also threatened by the loss of genetic variation. Inbreeding and the associated increase in homozygosity can also exacerbate demographic problems experienced by the species (Lacy 1992; Caughley and Gunn 1996). In addition to these factors, geographic isolates often occupy marginal habitat. The poor quality of this habitat might compromise individual reproductive success and, therefore, longevity of the population inhabiting the area (Lesica and Allendorf 1995).

To identify actual causes of population decline, a quantitative link needs to be made between observed reductions in certain life history stages and the effect that those reductions manifest on the population overall (Akçakaya et al. 1999; Biek et al. 2002; Wheeler et al. 2003). Quantitative population models can be effective conservation tools because they evaluate management options for each life history stage and can predict the chances of decline or recovery of the population. Effective methods to acquire the information needed for a quantitative model of an amphibian population include a combination of aquatic sampling for eggs and aquatic



FIGURE 1. One of the adult Jefferson Salamanders (*Ambystoma jeffersonianum*) that was trapped in 2004 as part of a two-year population study at Lincoln Trail State Recreation Area, Clark County, Illinois, USA. (Photographed by Stephen Mullin)

larvae, and terrestrial sampling with a drift fence-pitfall trap array for metamorphs and adults (Semlitsch 2002). In order to assess the population status of the Jefferson Salamander (*Ambystoma jeffersonianum*; Fig. 1), we conducted a study at an isolated pond within Lincoln Trail State Recreation Area (LTSRA; Fig. 2A-B).

The Jefferson Salamander is associated with hardwood forests and requires woodland ponds for breeding (Minton 2001). These ponds are usually ephemeral, having a high density of emergent plants and dead plant debris that provide refuges for breeding adults and developing larvae from various predators (Thompson et al. 1980; Petranka and Sih 1986; Rowe et al. 1994). Isolated populations of *A. jeffersonianum* are found in two counties in east-central Illinois (Petranka 1998, IDNR 2003) and breed at fewer than 15 ponds, most of which are small and unprotected (occurring on privately owned property; IDNR 2003). The restricted distribution of this species in Illinois stimulated its designation as state-threatened (Phillips et al. 2001). We estimated the size and structure of the *A. jeffersonianum* population at LTSRA and, using a stage-based population model, identify the needed conservation efforts. In addition to quantifying the number of individuals representing each life history stage, we also recorded sex ratio, body size, and percent hatching success.

MATERIALS AND METHODS

Study site.—The breeding pond at LTSRA (8 km south of Marshall, Clark County, Illinois) is a triangular body of water (0.03 ha), semi-permanent, and lies along

the southwestern edge of the park property (Fig. 2C). The surrounding forest consists of mixed deciduous hardwoods (*Carya* sp., *Acer* sp., and *Quercus* sp.) with an understory of vines (e.g., *Parthenocissus*, *Toxicodendron*) and occasional herbaceous ground cover (e.g., *Urtica*, *Podophyllum*). Grasses and forbs dominate the immediate periphery of the pond. The terrain on the pond's northeastern side slopes toward the pond, allowing the water to drain into it. The western side of the pond is separated from a county road (LTSRA boundary) by a narrow (< 15 m) strip of forest that slopes towards a drainage ditch alongside the road. The south side of the pond is in similar proximity to a LTSRA boundary, beyond which is a pine tree plantation.

Sampling procedure.—To capture and process salamanders that entered and exited the breeding site, we enclosed the pond with a drift fence and pitfall traps. This technique provided an annual census of breeding adults and juvenile recruitment (the number of juveniles produced per adult entering the pond to breed at the beginning of that particular activity season; Semlitsch et al. 1996). The fence consisted of 45-cm tall silt cloth supported by wooden stakes. We buried the bottom 5–10 cm of the fence to prevent any salamanders from passing underneath it. We placed pitfall traps (plastic buckets, 30 cm deep and 13 cm in diameter) on both sides of the fence every 5–7.5 m. The buckets were immediately adjacent to the fence, flush with the ground, and had holes in the bottom to allow for drainage. We sealed the buckets with lids during the non-activity season to prevent the capture of any non-target animals.

We monitored the drift fence on an alternate-day schedule from mid-February until mid-December of 2004, and early February until early June of 2005. We obtained the sex and snout-vent length (SVL) of each amphibian and then marked it with a unique combination of toe clips (Heyer et al. 1994). Salamanders were released to the opposite side of the drift fence from where they originated. We also determined the sex of individuals of other amphibian species caught (when possible), measured their SVL, and marked them by year (also using toe-clips). In March 2004, we surveyed individuals in the pond using several sweeps of a D-frame net.

Because ambystomatid salamanders are sexually dimorphic (Petranka 1998), we calculated the sex ratio of adult *A. jeffersonianum* based on the individuals collected in the traps. We counted egg masses once breeding adults ceased to enter the pond, but before we detected any larvae. To count egg masses, we established linear transects every 3 m across the entire pond area. While walking these transects, we counted all visible *A. jeffersonianum* egg masses, and scaled up

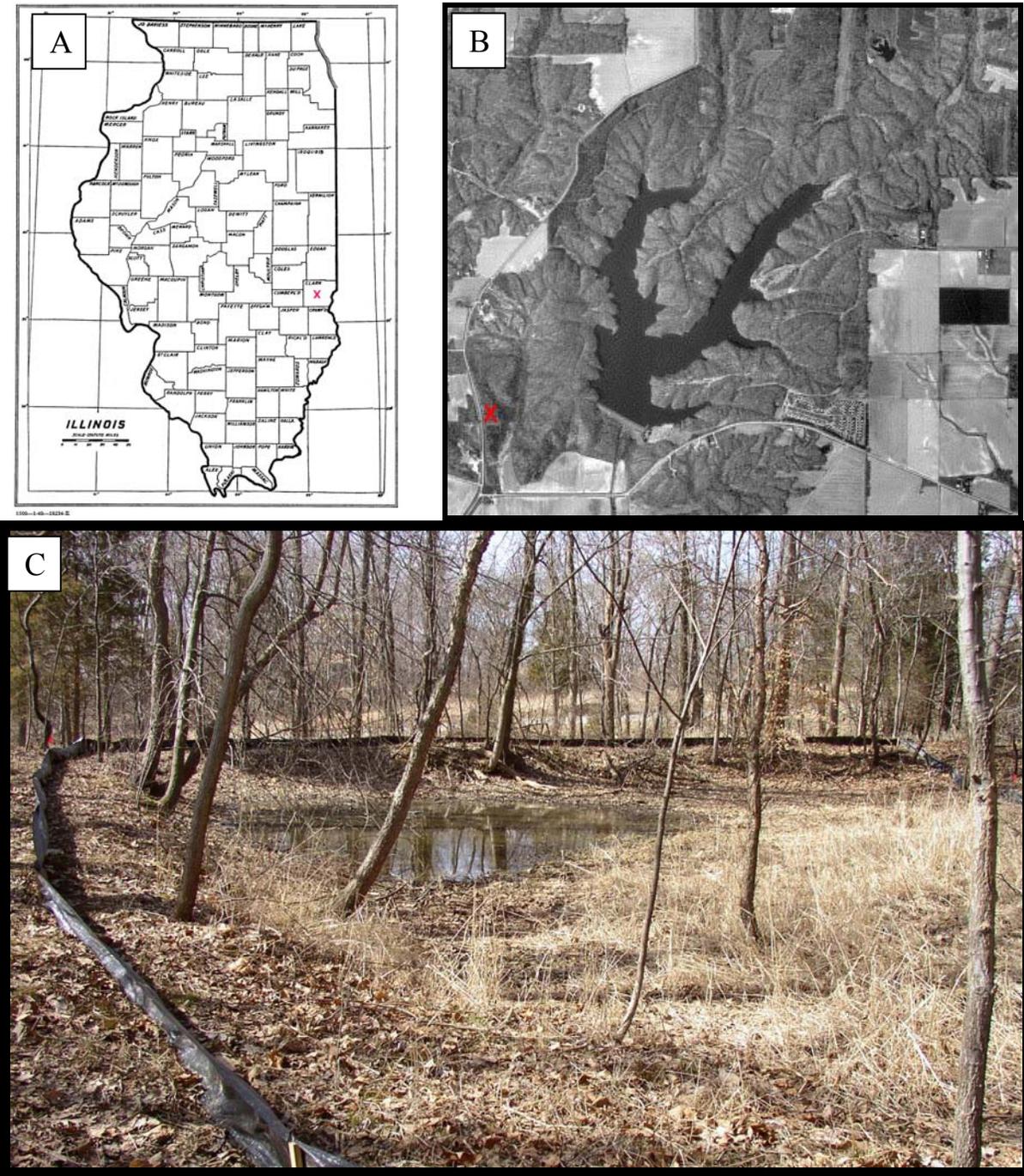


FIGURE 2. The site for a population study of the Jefferson Salamander (*Ambystoma jeffersonianum*) in 2004 and 2005. (A) Clark County, Illinois, is indicated by an “X” (taken from ??); (B) a Digital Orthophoto Quadrangle (DOQ) of Lincoln Trail State Recreation Area: the study pond is in the southwest corner of the property, as indicated by an “X” (aerial photograph from ??); (C) the study pond before it had completely filled with precipitation in February 2004: the left side of the image shows a portion of the drift fence used to sample amphibians. (Photographed by Stephen Mullin)

this total to the pond area. We gently lifted submerged limbs that were out of sight from the water's surface and examined them for egg masses. We used care to ensure that all egg masses remained attached to their original substrate. We counted eggs in a sub-sample of four haphazardly chosen masses to document the mean number of eggs per mass.

We determined the percentage of *A. jeffersonianum* eggs that hatched successfully by placing an egg mass into each of four chambers (12 x 12 x 24 cm) within a 38-L aquarium maintained at the LTSRA pond. If a mass was attached to substrate or positioned under debris, we transferred those objects with the egg mass into the aquarium. We counted the number of eggs present in each clutch and positioned the lower 15 cm of each aquarium in the pond. The remaining height of each aquarium protruded above the pond surface and we covered it with wire screen. The placement provided protection from predation, but allowed the egg masses to experience the same water temperature and light levels as the eggs that remained in the pond. We replaced the water in the chambers with pond water on a weekly basis. We concede that the geochemical processes occurring within the aquarium were likely different from those occurring in the pond. For logistical reasons, however, and to best simulate physical characteristics of the pond (e.g., temperature and photoperiod), we view this as a reasonable simulation of what the eggs would experience *in situ* (Graney et al. 1994).

The mean percent survivorship to hatching for all four masses was used to estimate the viability for all egg masses within the pond. Because we counted egg masses during the breeding season and calculated the mean number of eggs per mass, we could extrapolate this percentage to the whole pond. We then used this percentage to estimate the number of larvae present in the pond during each study year.

Newly hatched *A. jeffersonianum* typically reach the juvenile stage in 2–4 months (Petranka 1998); after this time period at the LTSRA pond, we recorded the new metamorphs as they encountered the pitfall traps when exiting the pond. We calculated the fecundity for this *A.*

jeffersonianum population based on a ratio between number of juveniles leaving and the number of adults entering the pond.

Stage-based Population Model.—We placed data collected at LTSRA in a stage-based population model (Fig. 3A; Halley et al. 1996). This type of model is appropriate because it allows individuals to be grouped according to the developmental stages that are important to survival and reproduction of the population (Caswell 2001). Our model included ceiling contest competition as a density dependent effect (RAMAS EcoLab Software 1999) for the following reasons (1) The number of suitable oviposition sites for adult females might have been limited by pond size (Kinkead and Otis 2007); (2) oxygen availability for eggs and larvae might have been a limiting factor; and (3) intraspecific competition among ambystomatid larvae is generally well documented (Semlitsch 1987; Semlitsch and Gibbons 1990), including that described as contest competition (Petranka 1989; Van Buskirk and Smith 1991). These aspects mean that pond size at LTSRA likely limited resource availability during aquatic life-history stages.

We made predictions about the population's response to changes in survivorship in each life-history stage (Fig. 3B; Akçakaya et al. 1999). In constructing this model, we assumed that the initial population was stable and closed (i.e., isolated from all other breeding populations within the county; Robert A. Szafoni, pers. comm.). We further assumed that the probability of survival, reproduction, and the fecundity did not vary among individuals of the same stage (Akçakaya et al. 1999).

Because we could not determine the survival from juvenile to adult and interannual survival of adults during the study period, we used values from Williams (1973; 50% and 25%, respectively). We ran the model through 1,000 iterations and simulated environmental stochasticity by using a standard deviation matrix that considered 10% of the survival rates (including those obtained from Williams 1973) and the standard deviation of the fecundity rate (Akçakaya et al. 1999). We used a sensitivity analysis to measure the change in population

TABLE 1. Life-history parameters for a population of Jefferson Salamanders (*Ambystoma jeffersonianum*) surveyed in 2004 and 2005 at Lincoln Trail State Recreation Area, Clark County, Illinois, USA. Values are based on individuals observed (adults, emerging juveniles, body size), or estimates based on quantified subsampling (egg masses) or survivorship (larvae). Means are reported ± 1 standard error.

Life history trait	2004	2005	Mean
Adults	100	84	
Number of females	68	47	57.5
Number of males	32	37	34.5
Sex ratio (female:male)	2:1	1.3:1	1.7:1
Female snout-vent length (mm)			82.0 \pm 0.7
Male snout-vent length (mm)			84.5 \pm 0.9
Number of emerging juveniles	2	0	1
Number of larvae	6,750	5,447	6,098
Number of eggs (egg mass)	8,766 (487)	7,074 (393)	7,920 (440)
Number of Eggs/Female (egg mass)	129 (7)	151 (8)	140 (7.5)

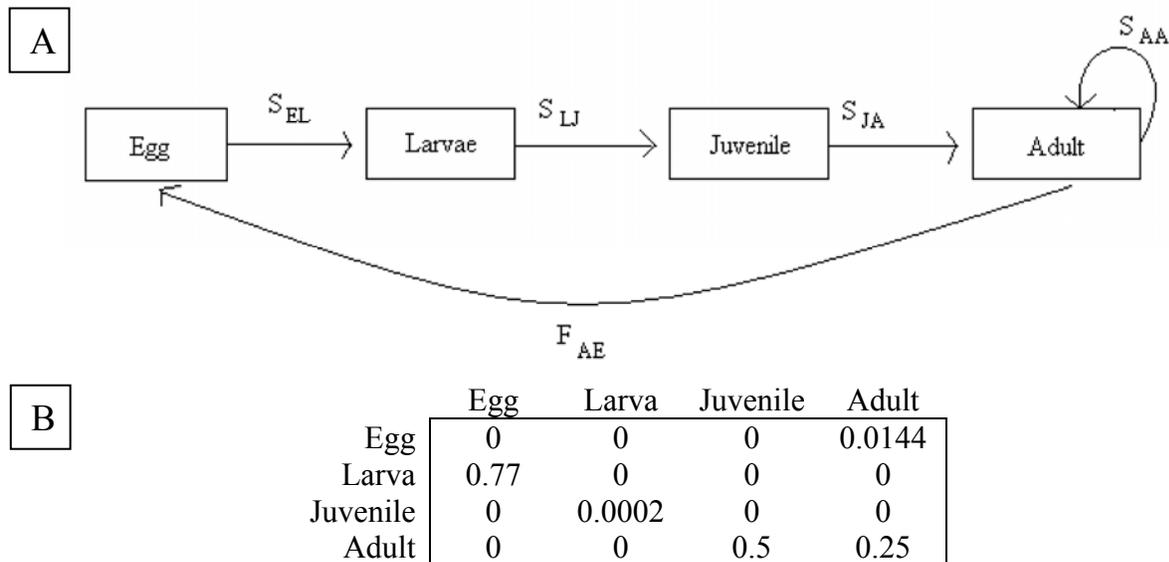


FIGURE 3. A stage-based population model of the Jefferson Salamander (*Ambystoma jeffersonianum*) at Lincoln Trail State Recreation Area, Clark County, Illinois, USA. In (A), the subscripts E, L, J, and A refer to egg, larva, juvenile, and adult, respectively. Survival (S) from one stage to the next is represented by arrows passing from one box to another. Fecundity (F) is represented by the arrow passing from adult to egg. Because adults may remain in the adult stage for multiple years, the survival arrow loops back on itself. (B) The model matrix, in which values for juvenile to adult and interannual adult survival, was obtained from Williams (1973).

trajectory when varying different parameters of the population (Akçakaya et al. 1999). We performed all population modeling with the stage-based module within RAMAS EcoLab (RAMAS EcoLab Software 1999, Setauket, New York, USA).

RESULTS

Demographics.—In 2004, 104 adult *A. jeffersonianum* were associated with the LTSRA pond. We captured more adult females at the pond than males (Table 1). Our sub-sample sweeps with a D-frame net in March did not detect any unmarked *A. jeffersonianum*. The eggs maintained in the aquaria had a 77% survival rate to hatching. Therefore, we estimate that there were approximately 6,750 larvae in the pond. In the middle of May, the breeding pond completely dried and most larvae did not have adequate time to metamorphose and leave. Based on the two juveniles caught in pitfall traps, fecundity was calculated at 0.029.

In 2005, we observed egg masses in the pond prior to our opening the trap array in early February, presumably a result of breeding migrations during a few days of uncharacteristically warm and rainy weather in early January. We recorded all census data after this early migration; thus, we believe our population size estimate is conservative. As with the previous year, more adult females used the pond than adult males (Table 1); there were 15 recaptures (10 females and 5 males) from the previous year. Fewer egg masses were produced in 2005

and, using the 77% probability for hatching success from 2004, fewer larvae as well (Table 1). The pond dried completely in April and all larvae perished prior to metamorphosis. Recruitment and fecundity were negligible.

Based on the data from both years, we calculated mean values for each age class (Table 1) and used these

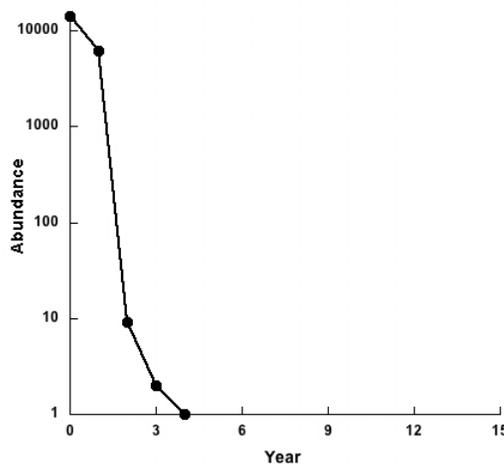


FIGURE 4. Population trajectory summary (logarithmic scale) for the Jefferson Salamander (*Ambystoma jeffersonianum*) at Lincoln Trail State Recreation Area, Clark County, Illinois, USA for 15 years. The stage-based model generating these values used 1,000 iterations to account for stochasticity.

TABLE 2. Number of individual salamanders (regardless of ontogenetic stage) calculated in each year when larval survival rate (LSR) is increased from 0.02%. Data were generated in a stage-based population model for the Jefferson Salamander (*Ambystoma jeffersonianum*) at Lincoln Trail State Recreation Area, Clark County, Illinois, USA.

LSR (%)	Number of individuals						
	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10
0.10	1	-	-	-	-	-	-
0.50	6	1	-	-	-	-	-
0.70	8	2	-	-	-	-	-
1	11	3	1	-	-	-	-
5	53	15	4	1	-	-	-
30	313	91	27	9	3	1	-
30	524	155	51	18	6	2	-

values in the population model (Fig. 3B). Based on the recapture rate of adults during the second year of the study, we conservatively estimated the adult population size to be 969 individuals. We recorded eight other amphibian species at the LTSRA pond: Smallmouth Salamander (*Ambystoma texanum*), Spotted Salamander (*A. maculatum*), Redback Salamander (*Plethodon cinereus*; leadback phase), American Toad (*Anaxyrus* [*Bufo*] *americanus*), Blanchard's Cricket Frog (*Acris crepitans*), Spring Peeper (*Pseudacris crucifer*), Western Chorus Frog (*P. triseriata*), and Southern Leopard Frog (*Lithobates* [*Rana*] *sphenocephalus*).

Population modeling.—We averaged values of the two-year study period for inclusion in the matrix: adult fecundity was 0.015, survival rate of egg to larvae was 77%, and survival from larvae to juvenile was 0.02%. The values for juvenile to adult (50%) and inter-annual survival of adults (25%) were values adopted from Williams (1973). The stage-based population model predicted the population trajectory for 15 years. Following this time period, all iterations predicted extinction of the population under realistic survivorship values. Given the parameters recorded at LTSRA, the model predicted that, on average, the *Ambystoma jeffersonianum* population could persist for another four years (Fig. 4) with only one individual remaining in that last year. The finite rate of increase (λ) was 0.257. Increasing the larval survivorship from 0.02% successfully increased the number of individuals per year (Table 2). Varying parameters other than larval survivorship in the model had little to no effect on the population trajectory.

DISCUSSION

Pond dynamics.—Variability in hydroperiod, and its effects on amphibian recruitment and population size are well documented (Shoop 1974; Pechmann et al. 1989; Skelly 1996). A 16-year study by Semlitsch et al. (1996) documented four years of short hydroperiod (≤ 100 days) with complete or nearly complete reproductive failure for most species at their study sites. Juvenile production for all species was erratic with large numbers

of metamorphs being produced in only a small number of the 16 years (as few as one for some species; Semlitsch et al. 1996). Jefferson Salamanders at the LTSRA pond appeared to experience a similar fate within the scope of our study, even though annual precipitation fell below-average levels only in 2005 (National Oceanic & Atmospheric Administration [NOAA], 2005. National Weather Service Weather Forecast Office, Available from <http://www.crh.noaa.gov/ilx/> [Accessed 29 April 2008]). The time of drawdown either provided this species with barely enough time to complete its larval stage, or resulted in the mortality of all larvae. Small populations of amphibians, such as the one at LTSRA, are especially sensitive to an erratic hydroperiod because of its impact on juvenile recruitment (Semlitsch 2002).

Demographics.—The sex ratio for *A. jeffersonianum* in the LTSRA pond (1.65:1 female:male) indicates a higher proportion of females using this site than has been reported for other populations (ranging between 1:1.04 to 1:3, Williams 1973; Petranka 1998). Our inter-annual recapture rate of adult *A. jeffersonianum* at the LTSRA pond (17.8%) is similar to the 25% survivorship value reported by Williams (1973). Because some individuals migrated to the pond before the traps were open in 2005, our recapture rate is likely a conservative estimate of inter-annual adult survival. Williams (1973) also reported a 90% hatching success for the eggs, compared to 77% at LTSRA, and a 0.08% survivorship during the larval period, compared to 0.02% at LTSRA. The lower values reported here likely reflect the fact that the hydroperiod of the LTSRA pond is often too short support the larval development of *A. jeffersonianum*.

Population model.—The Jefferson Salamander population inhabiting this LTSRA pond might be extirpated by 2010. Short pond hydroperiods resulted in low recruitment for both years. The only matrix element in the model (Fig. 3B) that had any substantial affect on abundance was larval survivorship. Increasing the survivorship of the adult age class to 50% increased the population size, but the results were comparable to increasing larval survivorship to 0.7%. Modeling also

suggested that increasing fecundity and egg, juvenile, or adult survivorship had little impact on individual abundance within the population. Our results parallel those of other studies that report very low (Williams 1973) or no (Thompson et al. 1980) *A. jeffersonianum* survivorship at the larval stage. Clearly, assuring larval survival is critical for the persistence of this species at LTSRA, as well as populations of other ambystomatid salamanders (Anderson et al. 1971; Petranka 1989).

Conservation implications.—Only rarely do amphibians experience a year in which a large proportion of any cohort emerges from their larval pond following metamorphosis (Semlitsch 1983; Pechmann et al. 1989; Berven 1990). In many instances, these aperiodic events are enough to sustain the population. The *A. jeffersonianum* population using the LTSRA pond is both isolated and small, increasing its extinction probability in the event that “good” recruiting years do not occur with sufficient frequency. NOAA (2005, *op. cit.*) classified 2005 as a drought year for central Illinois, so the probability of larval survivorship used in our model likely underestimates the normal stochastic processes experienced by this population. Kinkead and Otis (2007) noted that as many as 90% of adult ambystomatids might forego breeding during drought years, so our estimate of adult population size might also be conservative.

Jefferson Salamanders typically require a hydroperiod of 2–3 months in order for the larvae to attain a size suitable for successful metamorphosis (Phillips et al. 1999). Even though survivorship of *A. jeffersonianum* larvae was very low, we observed several metamorphs of other amphibians (e.g., *Pseudacris crucifer* and *P. triseriata*) exiting from the pond. Because *A. jeffersonianum* larvae feed on *P. triseriata* and *P. crucifer* tadpoles (Smith 1983), food limitation is an unlikely explanation for the low survivorship of the salamander species examined in our study (i.e., although these frogs were not trapped frequently at this site, they were regularly heard chorusing, and their larvae were observed in this study pond). The LTSRA pond would occasionally refill following heavy rain events in the late spring, so it could still support populations of pond-breeding amphibians that reproduce later within the context of an activity season (e.g., *Anaxyrus (Bufo) americanus* and *Lithobates (Rana) sphenocephalus*). Because of interspecific variation in the timing of adult reproductive activity, and egg and larval development, different species may benefit more than others from these weather events in certain years. Regardless of when breeding occurs, this pond appears to be a valuable resource for pond-breeding amphibians in the LTSRA (and adjacent) landscape (Klueh 2005).

The Jefferson Salamander is threatened in Illinois and management efforts are needed in order to assure the

species' persistence along the western limit of its range. Our study reinforces the importance of the larval stage to survivorship of amphibian populations (Semlitsch et al. 1996; Semlitsch 2002). Because hydroperiod is vital to larval survival, increasing the amount of time the LTSRA pond holds water is essential for continued *A. jeffersonianum* presence at that site. Possible restoration strategies to improve recruitment include: (1) deepening the breeding pond to slightly lengthen the hydroperiod (see Pechmann et al. 1989); (2) create one or more additional breeding ponds in adjacent areas of the LTSRA property where suitable habitat for *A. jeffersonianum* exists (see Semlitsch 2000); or (3) a combination of these strategies. Future conservation strategies should include research agendas to validate the effectiveness of these actions on the population status of *A. jeffersonianum* at LTSRA (Klueh 2005).

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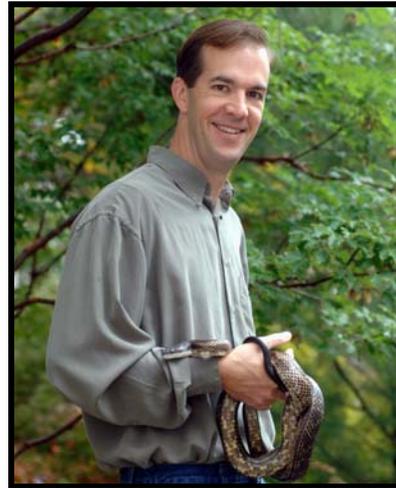
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Mullin and Klueh.—Jefferson's Salamander in Illinois.

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