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Structure and Dynamics of Spotted Salamander (*Ambystoma maculatum*) Populations in Missouri

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ABSTRACT: Comparisons of spatial and temporal variation in demographic rates are crucial to understanding population dynamics. Yet, even well-studied species are often lacking in comparisons of such variability in demographic data, making these contrasts imperative to conduct in population ecology research. We conducted a long-term monitoring study of Spotted Salamanders (*Ambystoma maculatum*) at five ponds in Missouri, USA. We sampled populations using drift fences, and monitored breeding immigration dates, adult population sizes, sex ratio, juvenile recruitment, metamorph sizes, and metamorph emigration dates. Generally, we found that our study populations exhibited characteristics similar to other populations across their distribution. We also found spatial and temporal variation among populations in nearly all demographic parameters, however, indicating that multipopulation and multiyear studies will likely improve our inferential abilities in understanding population dynamics. We observed an overall positive relationship between metamorph size and date of metamorphosis, but this pattern was not consistent across ponds or years, indicating that different environmental pressures might influence selection on these traits. Finally, we identified rainfall amounts and frequency as the primary factors that influenced adult and metamorph movement patterns to and from ponds. Overall, the spatial and temporal variation in demographic data we provided can be useful for population modeling or conservation planning, in addition to furthering our understanding of population ecology of Spotted Salamanders.

Key words: Body size; Breeding migration; Demography; Maturity; Metapopulation; Sex ratio; Spatiotemporal variation

SPATIAL and temporal variation in population dynamics is foundational to understanding species persistence (Pulliam 1988; Harrison 1991; Hanski 1999). How demographic parameters such as population size, larval and adult survival, or size and age at maturity vary is critical for understanding their dynamics. Such parameters are also important for developing population models, especially projection or viability analyses to determine declines, time to extinction, or the impact of land use on persistence or of management strategies on conservation and recovery (Morris et al. 2002). The study of population dynamics is complex, however, and compared with studying temporal variation (e.g., Shoop 1974; Semlitsch et al. 1996), studies of spatial variation are historically uncommon (Harrison 1991; Tilman and Kareiva 1997; Oro 2013). Thus, comprehension of how population dynamics vary in both time and space can increase understanding of how populations are regulated, whether local populations vary independently, and how annual differences in environmental conditions contribute to the variation. Furthermore, understanding spatiotemporal variation in population parameters is a necessary element to describe metapopulation structure of connected populations (e.g., source–sink versus island–mainland).

Pond-breeding amphibians are well-suited for studying population and metapopulation dynamics because their complex life cycle is centered on spatially discrete aquatic habitats patches (Wilbur 1980) that are often connected by infrequent dispersal events (Trenham et al. 2001; Gamble et al. 2007; Griffiths et al. 2010). However, the ponds-as-patches metapopulation paradigm must also include the terrestrial habitat surrounding breeding ponds, where adults and juveniles live, usually within short distances of ponds (100–300 m; Semlitsch 1998; Rittenhouse and Semlitsch 2007; but see Scott et al. 2013). During the reproductive season, adults migrate to ponds where they breed and oviposit eggs that eventually hatch into aquatic larvae. Larvae grow and develop over a period of 3–9 mo, depending on species, and metamorphose into terrestrial juveniles. Survival to metamorphosis is typically low (1–5%; Shoop 1974; Semlitsch et al. 1988), yet juveniles are recruited into the adult population and are likely the regulatory stage for pond-breeding species (Biek et al. 2002; Vonesh and De la Cruz 2002; Harper et al. 2008). For some species, ~91% of juveniles that survive to maturity remain near their natal pond to replenish the adult population, whereas ~9% disperse to new breeding populations (Gamble et al. 2007). The life history of pond-breeding species allows biologists to sample individuals at multiple ponds over multiple years with apparent effectiveness (Shoop 1974; Semlitsch et al. 1996), although only a few studies have attempted to monitor multiple patches over several years to characterize metapopulation structure (Gill 1978; Trenham et al. 2001; Gamble et al. 2007; Griffiths et al. 2010).

This article presents material that was to be the basis for Ray Semlitsch's lecture as the 2015 Distinguished Herpetologist at the annual meeting of the Herpetologists' League (HL). Ray succumbed to leukemia on 10 June 2015, however, before he could deliver that lecture. The Editor and the HL Past President, Jim Spotila, are grateful to Tom Anderson for his assistance in the posthumous publication of this contribution from Ray's lab group.

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The primary objective of our study was to describe both spatial and temporal variation in life-history and population parameters of Spotted Salamanders (*Ambystoma maculatum*; Shaw 1802). We chose a common species so that the numbers of adults and juveniles would be adequate to quantitatively analyze spatial and temporal variation, especially for estimating larval survival, and age and size at maturity. We selected five replicate ponds for our study and collected data over a 4-yr period so that we might encompass enough variation to make some general inferences about the population dynamics of *A. maculatum*. Although we collected data from specimens occurring in ponds that are within known dispersal distances for the species, and likely form a metapopulation, we report on information from individual populations (i.e., ponds) because we do not have direct movement data among populations to characterize metapopulation structure or capacity. Secondly, we provide information on other life-history parameters such as annual breeding phenology, sex ratio, adult body size, juvenile size, and juvenile emigration, to add to the growing literature on salamander ecology. We also examined the abiotic factors influencing adult breeding immigration patterns, as well as metamorph emigration patterns during metamorphosis from each wetland. Finally, we determined whether or not any biotic factors influenced the relationship of size and date of metamorphosis for metamorphs, because these traits are considered to be under strong selective pressures (Wilbur and Collins 1973; Searcy et al. 2014).

MATERIALS AND METHODS

Study Area

Our study was conducted within the Daniel Boone Conservation Area (DBCA, 1424.5 ha) in the upper Ozark Highlands in Warren County, Missouri, USA. The five breeding ponds were representative of other ponds at DBCA and were part of a series of studies (Hocking and Semlitsch 2007; Semlitsch et al. 2008, 2009, 2014; Rittenhouse et al. 2009). The ponds were located in mature (80–100 yr old), second-growth forest of oak (*Quercus* sp.) and hickory (*Carya* sp.) overstory, with varying amounts of sugar maple (*Acer saccharum*) in the understorey. The forest surrounding ponds was subject to varying levels of timber harvest (March 2004–January 2005) that was allowed to undergo natural succession (Semlitsch et al. 2009). All ponds were originally constructed for game species (e.g., turkey [*Meleagris gallopavo*] and deer [*Odocoileus virginianus*]), similar in size (high-water area from 160 m² to 330 m²), <1.2 m deep, 0.38–1.35 km apart, 27–47 yr old, and have been naturally colonized by up to 16 species of amphibians (Hocking et al. 2008). All five ponds were nearly permanent, and contained water for the duration of our study except during a short period in late summer during a drought in 2005.

Drift Fences and Monitoring

We completely encircled the study ponds with a drift fence and pitfall traps during October–December 2003. The drift fences were used to census the adult breeding population and metamorphosing juveniles each year. Drift fences were constructed of aluminum flashing that was buried ~30 cm in the ground and extended 60 cm above ground (Gibbons and Semlitsch 1981). Pitfall traps consisted of plastic plant pots (23 cm diameter, 45 cm

deep) buried with the top flush to the ground and against the fence. Traps were paired along each side of the fence every 3.0 m. A removable wooden board was positioned 4 cm above each trap with metal stakes to reduce predation, and a moist sponge was placed in the bottom of each trap to reduce the risk of desiccation. Traps were checked every 1–3 d depending on activity season of species and rainfall events from February to November each year from 2004 to 2007. We recorded trap location, date, sex, age class, and migration direction (in or out) for all individuals captured in our traps and released them within 15 min on the opposite side of the fence. A subsample of individuals at each pond and year was measured for body size (snout–vent length [SVL], mm; $n = 2264$ males, $n = 1488$ females, $n = 1756$ juveniles). Metamorphosing juveniles were marked by toe-clipping two adjacent toes on the rear foot and adults were marked with passive integrated transponder- (PIT-) tags. Double toe-clips usually regenerate within 1–2 yr, but are still recognizable years later because of scarring (Semlitsch et al. 1988; Scott 1994). Daily rainfall totals and air temperature were averaged from weather stations in Warrenton, Missouri, Washington, Missouri, and Hermann, Missouri, each ~20–30 km from the study location (High Plains Regional Climate Center, see <http://www.hprcc.com>). Where appropriate, values are presented as mean \pm 1 SE.

Statistical Analyses

To understand and compare spatial and temporal variation, we conducted several two-way analyses of variance (ANOVA) with pond and year as fixed categorical factors. Our adult response variables included the abundance of total adults, male abundance, female abundance, mean SVL for each sex, and mean emigration date. We also estimated survival in two ways. First, we approximated the number of eggs laid in each pond by multiplying the number of captured females by the estimated clutch size in this species (224 eggs; Shoop 1974). We then divided the number of metamorphs captured by the estimated egg total for each pond-year combination (hereafter, metamorphs/egg). For our second measure of survival, we divided the number of metamorphs by the number of breeding females (metamorphs/female). We initially compared several different error structures for the abundance data, including normal, log-normal, Poisson, Gamma, and negative binomial using Akaike's Information Criterion (Burnham and Anderson 2002). Based on this, log-transformed abundance was the most highly supported and best approximated normality; the overall inferences generally did not change regardless of error distribution. We used a logit transformation for the metamorphs/egg survival model (Warton and Hui 2011) and a log-transformation for the metamorphs/female survival model. Residuals from all other models fit normal distribution assumptions.

We tested whether adult SVL and immigration date differed between sexes using a linear mixed model using all individual data points, with pond and year as random effects (R package lme4; Bates et al. 2014). We tested for significance of each term in the mixed models using the “Anova” function in R (Fox and Weisberg 2011), which computes a Wald chi-square statistic, which is a comparable test to the standard *F*-test in ANOVA. To understand the

TABLE 1.—Population sizes and sex ratios of breeding adults of Spotted Salamanders (*Ambystoma maculatum*) captured at five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

Pond	Year	Total adults	Females	Males	Sex ratio (male:female)
1	2004	1042	309	733	2.37
	2005	1083	340	743	2.19
	2006	984	496	488	0.98
	2007	838	373	465	1.25
2	2004	514	180	334	1.86
	2005	223	67	156	2.33
	2006	237	81	156	1.93
3	2004	546	177	369	2.08
	2005	448	157	291	1.85
	2006	449	164	285	1.74
4	2004	412	98	314	3.20
	2005	742	266	476	1.79
	2006	692	216	476	2.20
5	2004	485	135	350	2.59
	2005	305	48	257	5.35
	2006	514	217	297	1.37
Mean	2004	366	144	222	1.54
	2005	202	93	109	1.17
	2006	228	79	149	1.89
Mean	550.25	184.65	365.60	2.59	

TABLE 2.—Mean and range (earliest and last) of breeding movements of adult Spotted Salamanders (*Ambystoma maculatum*) captured at five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

Pond	Year	Females			Males		
		Mean	First	Last	Mean	First	Last
1	2004	9 Mar	5 Mar	22 Apr	7 Mar	2 Mar	22 Apr
	2005	24 Mar	7 Feb	24 Apr	6 Mar	7 Feb	12 May
	2006	15 Mar	9 Mar	19 Apr	11 Mar	29 Jan	6 Apr
	2007	21 Mar	10 Mar	15 Apr	15 Mar	25 Feb	11 Apr
2	2004	14 Mar	5 Mar	24 Apr	11 Mar	2 Mar	22 Apr
	2005	9 Apr	7 Mar	14 May	13 Mar	7 Feb	22 Apr
	2006	17 Mar	10 Mar	31 Mar	13 Mar	8 Mar	2 Apr
3	2004	23 Mar	10 Mar	25 Apr	17 Mar	1 Mar	25 Apr
	2005	12 Mar	5 Mar	20 May	6 Mar	2 Mar	1 May
	2006	31 Mar	13 Feb	24 Apr	7 Mar	7 Feb	18 Apr
4	2004	15 Mar	6 Mar	6 Apr	10 Mar	29 Jan	31 Mar
	2005	18 Mar	10 Mar	11 Apr	15 Mar	25 Feb	27 Apr
	2006	9 Mar	5 Mar	22 Apr	6 Mar	1 Mar	22 Apr
5	2004	23 Mar	13 Feb	14 Apr	5 Mar	7 Feb	22 May
	2005	16 Mar	6 Mar	6 Apr	10 Mar	29 Jan	19 Apr
	2006	22 Mar	10 Mar	11 Apr	16 Mar	25 Feb	11 Apr
Mean	2004	15 Mar	5 Mar	24 Apr	13 Mar	5 Mar	29 Mar
	2005	11 Apr	14 Feb	22 Apr	9 Apr	7 Feb	22 May
	2006	22 Mar	6 Mar	6 Apr	14 Mar	29 Jan	19 Apr
Mean	20 Mar	2 Mar	19 Apr	12 Mar	17 Feb	20 Apr	

abiotic factors that influenced daily adult captures, we assessed the relative strengths of the amount of precipitation the previous 24 hr, the maximum daily temperature, the minimum daily temperature, and the number of days since rain (DSR). These factors have been identified as important in other studies of amphibian movement patterns (Semlitsch 1985; Todd and Winne 2006). We performed these tests using linear mixed-effect models with each covariate centered and scaled, and we included pond and year as random effects. We also computed 95% bootstrapped confidence intervals for each covariate to assess whether the effects were significantly different from zero.

For metamorphs, we tested whether abundance, mean emigration date, and mean SVL varied by pond or year using two-way ANOVAs. Abundance was again log-transformed, whereas models of size and date both had normally distributed residuals. Using linear regression separately for each pond-year combination, we also tested whether the relationship of metamorph SVL and emigration date differed among both ponds and years. We sought to explain variation in size-date relationships; specifically, we were interested in potential covariates that would explain the slope of this relationship, and tested for such effects using Spearman's correlation tests. We examined any potential correlations among mean values of all adult and metamorph metrics using Spearman's correlations. Finally, we tested the abiotic factors that influenced metamorph emigration patterns (maximum and minimum temperature, rainfall, and DSR) in an identical manner to adult immigration patterns.

RESULTS

We captured 11,005 total breeding adults along the drift fences across all years and ponds (Table 1). The total breeding population size captured showed wide spatiotemporal variation, with as few as 202 adults in Pond 5 in 2006, to as many as 1083 adults in Pond 1 in 2005. The number of

males entering each year varied from 109 to 743 with a mean of 366 males among all ponds over the 4 yr. The number of females entering each year varied from 48 to 496 with a mean of 185 females among all ponds over the 4 yr. Ponds varied in the number of breeding adults, and Pond 1 consistently had more breeding adults each year than the other four ponds ($F_{4,12} = 6.51$, $P = 0.01$; Table 1). The number of males varied among ponds ($F_{4,12} = 5.32$, $P = 0.01$) but not years, with Pond 1 having the most males. The number of females also varied among ponds ($F_{4,12} = 8.89$, $P = 0.001$) and years ($F_{3,12} = 4.76$, $P = 0.02$). The sex ratio of males to females was consistently male-biased in all years, and averaged 2.59 males to each female (Table 1).

We captured breeding adults migrating into ponds between January and May 2004–2007 (Table 2). The earliest male capture occurred on 29 January 2006 and the earliest female was captured on 7 February 2005, but first captures varied by year. The average date of capture for males varied from 5 March to 9 April, and average date of capture for females varied from 9 March to 11 April among all ponds and years (Table 2). For male salamanders, the mean arrival date tended to vary among ponds ($F_{3,12} = 3.02$, $P = 0.06$) but not among years. Arrival date for females varied both among ponds ($F_{3,12} = 28.74$, $P < 0.001$) and years ($F_{3,12} = 4.83$, $P = 0.01$). On average, males arrived 8 d earlier than females (Wald chi-square = 413.07, $df = 2$, $P < 0.001$), although in some years this difference was minimal (Table 2). Larger females tended to arrive later in the breeding in the season (interaction term Wald chi-square = 3.24, $df = 1$, $P = 0.07$). The last male and female individuals were captured entering a breeding pond on 22 May 2005 at Pond 4, and 20 May 2004 at Ponds 3, respectively (Table 2). The only covariates that explained adult movements included linear and quadratic terms for DSR, and the linear term for the amount of precipitation that occurred during the previous 24 hr (Table 3). The effect of DSR was

TABLE 3.—Parameter estimates for Spotted Salamanders (*Ambystoma maculatum*) adult immigration and metamorph emigration daily captures over 4 yr at Daniel Boone Conservation Area, Missouri, USA. Precip = the amount of precipitation the previous 24 hr, DSR = days since rain, Max temp = maximum daily temperature, and Min temp = minimum daily temperature. Superscripts indicate quadratic terms. Estimates are the restricted maximum likelihood estimates, SE values are the standard errors, and lower and upper are the 95% bootstrapped confidence intervals. Significant values are indicated in boldface.

Adults					
Covariate	Estimate	SE	t-value	Lower	Upper
Intercept	1.872	0.100	18.653	1.667	2.056
Precip	0.588	0.256	2.296	0.119	1.058
Precip ²	-0.360	0.243	-1.482	-0.816	0.123
DSR	-0.808	0.230	-3.506	-1.306	-0.328
DSR ²	0.601	0.216	2.784	0.145	1.065
Max temp	0.395	0.437	0.904	-0.432	1.287
Max temp ²	-0.449	0.446	-1.007	-1.399	0.374
Min temp	0.313	0.221	1.416	-0.163	0.685
Min temp ²	-0.349	0.213	-1.640	-0.718	0.092

Metamorphs					
Covariate	Estimate	SE	t-value	Lower	Upper
Intercept	1.070	0.156	6.870	0.788	1.398
Precip	0.483	0.150	3.229	0.194	0.770
Precip ²	-0.372	0.140	-2.670	-0.649	-0.101
DSR	-0.393	0.150	-2.623	-0.710	-0.085
DSR ²	0.163	0.139	1.173	-0.128	0.446
Max temp	0.003	0.405	0.008	-0.745	0.851
Max temp ²	-0.147	0.397	-0.370	-0.976	0.643
Min temp	0.370	0.237	1.560	-0.103	0.838
Min temp ²	-0.192	0.234	-0.821	-0.670	0.269

TABLE 4.—Survival of Spotted Salamanders (*Ambystoma maculatum*) from five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA. See text for descriptions of how survival estimates were calculated.

Pond	Year	Abundance	Juveniles/egg	Juveniles/female
1	2004	271	0.004	0.877
	2005	37	0.0005	0.109
	2006	252	0.002	0.507
2	2007	266	0.003	0.711
	2004	606	0.015	3.367
	2005	36	0.002	0.537
3	2006	19	0.001	0.235
	2007	49	0.004	0.925
	2004	117	0.003	0.661
4	2005	25	0.001	0.158
	2006	411	0.011	2.491
	2007	265	0.012	2.677
5	2004	51	0.001	0.192
	2005	41	0.001	0.190
	2006	137	0.005	1.015
Mean	2007	47	0.004	0.979
	2004	300	0.006	1.382
	2005	51	0.002	0.354
Mean	2006	279	0.013	3.000
	2007	113	0.006	1.430
	Mean	168.7	0.005	1.090

negative, whereas the effect of precipitation was positive (Table 3).

Adult female *A. maculatum* were larger than males (male SVL = 85.48 ± 0.11 mm; female SVL = 93.94 ± 0.13 mm; Wald chi-square = 29.27, df = 1, P < 0.001; Fig. 1). The smallest breeding female was 75 mm SVL and the smallest breeding male was 56 mm SVL. There were differences in mean SVL of both female and male individuals as a function of pond (female, F_{4,12} = 4.05, P = 0.03; male, F_{4,12} = 5.97, P = 0.01), but not among years (P > 0.05 for both male and female individuals).

We captured 3373 total juveniles metamorphosing from ponds during the study. Juveniles metamorphosed from all ponds and years, albeit in low numbers (Table 4). The fewest juveniles to metamorphose from a pond was 19 individuals from Pond 2 in 2006. The greatest number to metamorphose was from the same pond, where 606 individuals were captured in 2004. The mean number of juveniles emerging from ponds was 169 individuals/yr (Table 4). The production of juveniles per female averaged 1.09 (range = 0.11–3.37; Table 4). The percent survival of juveniles from egg to metamorphosis averaged 0.5% (range = 0.05–1.5%; Table 4). The production of juveniles varied among years (P = 0.03) but not ponds (P > 0.05). The abundance of *A. maculatum* metamorphs was greater only when females bred earlier (Spearman's ρ = -0.60, P = 0.01), and did not vary as a function of either metamorphs/egg or metamorphs/female.

The mean body size of metamorphosing juveniles among all years and ponds was 31.4 ± 0.1 mm SVL (range = 21–45 mm SVL; Fig. 2), and did not vary among either spatiotemporal grouping. The earliest capture of a metamorphosing juvenile at the drift fence occurred on 9 June 2005, and the average date of juvenile emigration varied from 6 July to 8 September among ponds and years. The body size of juvenile individuals increased as the activity season progressed (Spearman's ρ = 0.49, P < 0.001; Fig. 3). The amount of precipitation that occurred during the previous 24 hr (linear and quadratic terms) and the linear term for DSR were the

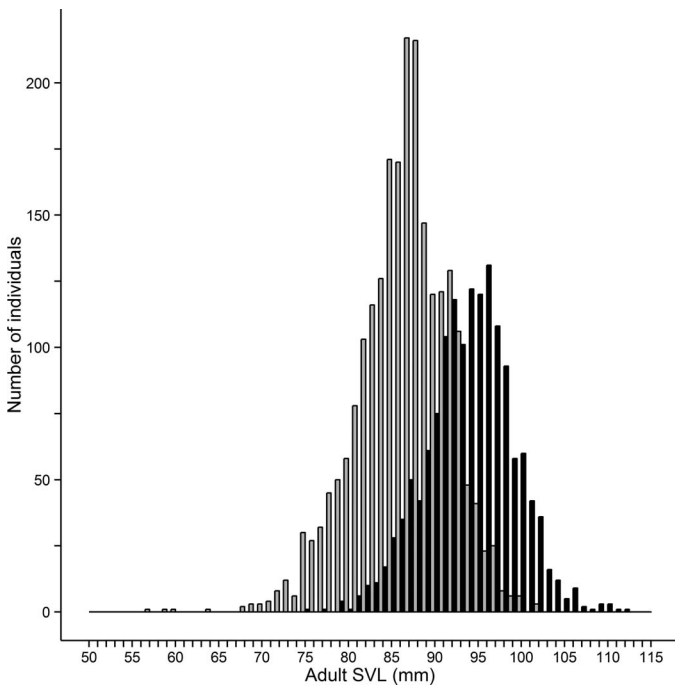


FIG. 1.—Distribution of snout-vent length (SVL, in mm) for male (gray bars, n = 2007) and female (black bars, n = 1403) Spotted Salamanders (*Ambystoma maculatum*) from five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

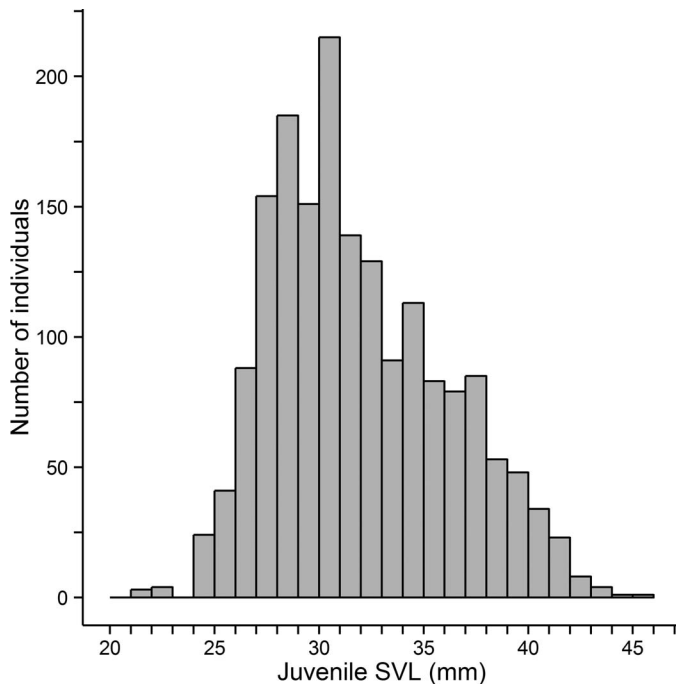


FIG. 2.—Distribution of snout-vent length (SVL; in mm) of metamorphic Spotted Salamanders (*Ambystoma maculatum*; $n = 2579$) from five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

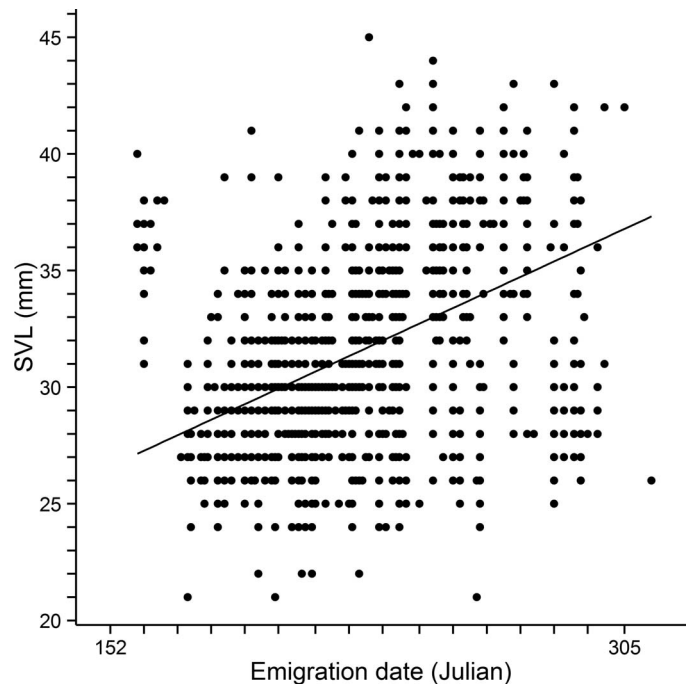


FIG. 3.—Relationship of snout-vent length (SVL; in mm) and date of capture for emigrating Spotted Salamanders (*Ambystoma maculatum*) from five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

only reliable predictors of juvenile emigration patterns (Table 3). Variability in size–date relationships also was apparent, where slope values between these parameters ranged from -0.1 to 0.13 (Fig. 4). The only factor we measured that predicted these slope values was survival; the slope was increasingly positive when more individuals survived (Spearman's $\rho = 0.69$, $P = 0.002$).

We recaptured 24 total adults that had been marked as metamorphosing juveniles at drift fences. All of these recaptures came in 2006: 15 individuals were captured reproducing at age 2, and 9 individuals were captured reproducing at age 1, with a male-biased sex ratio in each cohort (11:4 and 5:4, respectively). The smallest female at first reproduction was 81 mm SVL and the smallest male was 83 mm SVL. Across both sexes, average body size at first reproduction was 88.7 ± 2.3 mm SVL. Interestingly, one of the first-year returning females was captured immigrating on 11 October 2006, and was visibly gravid.

DISCUSSION

Baseline demographic data provides reference information on the requirements and attributes of a species needed to understand its population ecology, its role within a food web, and for successful conservation efforts. Furthermore, understanding temporal and spatial variation in demographic parameters can help differentiate variability in populations stemming from natural processes or anthropogenic effects (Pechmann et al. 1991). Our results indicate that these five populations of Spotted Salamanders in Missouri exhibit population dynamics and a life history typical of other parts of its range (reviewed in Petranka 1998). We identified spatial and temporal variation in several population parameters, which are features that are often lacking from

demographic studies. Thus, our findings (1) fill this essential gap in knowledge for Spotted Salamanders, and (2) show that the relative importance of spatial and temporal variation can vary for different life-history parameters (e.g., abundance versus body size).

At our study sites, most males arrived at our study ponds during the first 2 wk of March. Females followed males by a few days or weeks, matching migration phenology reported in other studies in Missouri (e.g., Sexton et al. 1990). This timing is earlier than reported for populations of *A. maculatum* in more northerly regions of the United States (e.g., Baldauf 1952; Peckham and Dineen 1955; Husting 1965; Stangel 1988). Most of the migratory pattern each year was related to the timing and amount of rainfall events in late winter and early spring. The number of individuals captured each day was best predicted by the number of days since rain and the amount of rainfall, which supports the general conclusions from other studies of amphibian breeding movements (Semlitsch 1985; Todd and Winne 2006). Sexton et al. (1990) also found that mean daily temperature played a role in Spotted Salamander migration patterns, but our analyses did not support temperature as an influential factor (either minimum or maximum daily value).

The breeding population sizes were seemingly large for our relatively small ponds (160–340 m²), averaging 366 males and 185 females across ponds and years. Only a handful of other studies have attempted to census whole breeding populations (i.e., ponds) of Spotted Salamanders. Comparable numbers have been reported, however, in the U.S. states of Michigan (111–315 males, 69–155 females, pond size = 1066 m²; Husting 1965) and Indiana (136–244 males, 51–84 females, pond size = 1214 m²; Peckham and Dineen 1955). In contrast, other studies have reported lower numbers in the

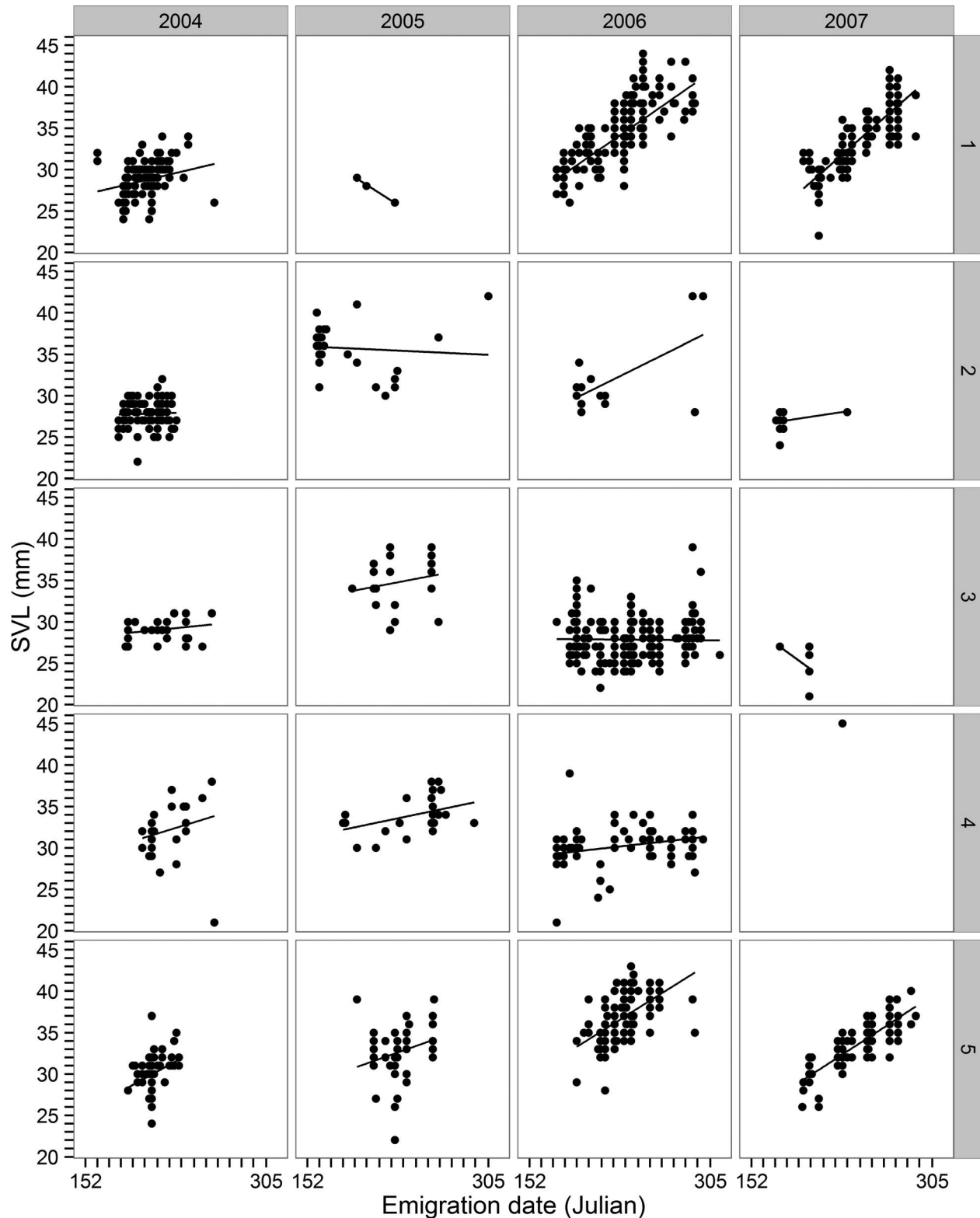


FIG. 4.—Relationship of snout-vent length (SVL; in mm) and date of metamorphosis for Spotted Salamanders (*Ambystoma maculatum*) separated by pond (gray panels on right axis) and year (gray panels on top axis), from five ponds over 4 yr at Daniel Boone Conservation Area, Missouri, USA.

states of Massachusetts (16–67 females, pond size = 177 m²; Shoop 1974) and Alabama (111 males, 70 females, pond size = 250 m²; Blackwell et al. 2003). Few studies have monitored multiple populations even for a few years (e.g., Shoop 1974; Petranka et al. 2004), leading to a dearth of information on

spatial variation compared with temporal variation. This is a common problem for many amphibian taxa because of the labor- and time-intensive nature of data collection on terrestrial life stages (e.g., Trenham et al. 2001; Whiteman and Wissinger 2005; Church et al. 2007; Gamble et al. 2007,

2009; Semlitsch et al. 2014). Such data, in conjunction with movement data, are necessary to inform our understanding of spatial dynamics, and to determine whether clusters of ponds function as metapopulations or a single demographic unit (Petranka et al. 2004). Genetic data from our study sites (collected ~10 yr after this study was conducted) showed low genetic differentiation among ponds, indicating some dispersal occurs among our study sites (Peterman et al. 2015). Other studies conducted on Spotted Salamanders across their range indicate that gene flow can be either highly structured at shorter interpond distances (Richardson and Urban 2013) or show limited genetic structure at greater interpond distances (i.e., Whiteley et al. 2014; Peterman et al. 2015). Taken together, these studies suggest that inferences on metapopulation structure based on pond distance alone might be inaccurate, and that direct movement data and/or genetic data are needed to describe both source populations and overall metapopulation structure. Identifying these high-quality (i.e., source) populations is critical to afford them conservation protection such that the entire metapopulation does not collapse (Marsh and Trenham 2000).

The sex ratios of adult *A. maculatum* at our ponds were consistently male-biased with a mean of 2.59 males/female. The sex ratios reported in other studies were also strongly male-biased (2.67–2.9:1, Peckham and Dineen 1955; 1.61–2.19:1, Husting 1965; 1.42–2.55:1, Sexton et al. 1986; 1.59:1, Blackwell et al. 2003), and appear to be a general pattern for ambystomatid salamanders (Petranka 1998). In practice, however, the actual sex ratio might differ from what is captured at drift fences because of either sampling bias (Husting 1965), or male ambystomatids having higher survival probabilities (Gamble et al. 2009).

The body sizes of breeding male and female *A. maculatum* in our study ponds were intermediate compared with values reported from other sites within their range. The largest body sizes of Spotted Salamanders were recorded in the states of Alabama (males = 98.1 mm; females = 110.7 mm; Blackwell et al. 2003), whereas adult body sizes were smaller in Michigan (males = 74.3 mm, females = 84.2 mm; Husting 1965) and New York (males = 80.5 mm; females = 89.3 mm; Wilson 1976). Although these comparisons are incomplete across the entire distribution of *A. maculatum*, these data appear consistent with Adams and Church (2008), who contended that salamanders do not follow Bergmann's Rule.

Annual production of juvenile *A. maculatum* varied widely among ponds and years; yet all ponds produced some juveniles each year, indicating no pond was a consistent sink for the overall metapopulation. Although survival rates from egg to metamorphosis were low (ranging from 0.05% to 1.5%), no year was a complete reproductive failure as frequently occurs in more ephemeral breeding ponds (Semlitsch et al. 1996; Taylor et al. 2006; Anderson et al. 2015). Our ponds were nearly permanent and dried only in an extreme drought year, so spring breeding species such as Spotted Salamanders typically had enough time to develop and metamorphose. In spite of a relatively short period of larval development (Wacasey 1961; Stangel 1988), larval *A. maculatum* metamorphosing later in the summer emerged at larger body sizes (Shoop 1974; Phillips 1992), which potentially increases fitness (Semlitsch et al. 1988). Larger sizes at metamorphosis also facilitate greater terrestrial survival (Scott 1994), meaning that ponds with bigger

metamorphs might differentially contribute individuals to future cohorts within the metapopulation.

The correlation of metamorph size with later emergence date was not consistent across ponds or years. The positive relationship between larval size and time to metamorphosis was affected only by overall survival to metamorphosis, indicating a potential density-dependent response occurring late in larval ontogeny. Ringed Salamanders (*Ambystoma annulatum*) exhibit the opposite pattern, metamorphosing at smaller body sizes at later emigration dates (Semlitsch et al. 2014). Ringed Salamanders likely gain more larval growth advantages by hatching in the autumn, overwintering as larvae, and reaching a maximum size early by late April or early May. It appears that only small, slow-growing Ringed Salamander larvae remain in ponds later into the summer perhaps just to reach minimum body size to metamorphose, whereas *A. maculatum* metamorphose as early as possible to escape the potential of pond drying (Wilbur and Collins 1973; Semlitsch and Wilbur 1988). Spotted Salamander larvae have also been found to overwinter in ponds in Rhode Island, USA (Whitford and Vinegar 1966), Nova Scotia, Canada (Bleakney 1952), Kentucky, USA (TLA, personal observation), and in Missouri (Phillips 1992; TLA, personal observation).

Although we have a relatively small sample of marked metamorphs that were recaptured at first reproduction, it is apparent that some individuals can reach reproductive maturity 1 yr after hatching (whereas the majority appear to wait ≥ 2 yr). More males than females returned to breed at ages 1 and 2 yr. The smallest males (83 mm SVL) and females (81 mm SVL) captured at first reproduction were larger than the smallest unmarked breeding individuals (males 56 mm SVL, females 75 mm SVL), indicating that even smaller and possibly younger individuals are part of the breeding population. The ability of metamorphosing juvenile ambystomatids to breed at 1 yr of age in natural populations has now been documented for *Ambystoma talpoideum* (Semlitsch et al. 1988), *Ambystoma opacum* (Scott 1994), and *A. annulatum* (Semlitsch et al. 2014).

The populations of *A. maculatum* at our study site appear stable and are producing an adequate number of new juveniles each year to maintain relatively large adult populations. Pond hydroperiod seemed to have little effect on successful reproduction, and factors such as invertebrate predation might play a larger role in larval success at our ponds. In other areas of Missouri, the ephemeral nature of some breeding ponds can contribute to reproductive failure rates as high as 34% in *A. maculatum* (Anderson et al. 2015). Our study ponds were fishless, so the impact of this predator type was eliminated. All five study ponds were surrounded by high-quality forest habitat that likely facilitates juvenile and adult survival. Despite the terrestrial habitat homogeneity, we still observed spatiotemporal variation in aquatic parameters, indicating further long-term studies on basic demographic information are needed to characterize those factors that contribute to such variation. Furthermore, most of the information available for many ambystomatids is for adults, and primarily concerns breeding migrations and population sizes. Data for metamorphs from natural populations are underrepresented compared with the adult stages, which is an important omission given juveniles' critical role in population regulation (Biek et al. 2002; Vonesh and De la Cruz 2002). Studies investigating spatiotemporal variation in both the

metamorph and other stages, however, will ultimately lead to a greater understanding of both population and metapopulation dynamics, and the assembly of such data sets will be useful in both demographic modeling and conservation actions (Trenham and Shaffer 2005; Harper et al. 2008, 2015).

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