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STRUCTURE AND DYNAMICS OF RINGED SALAMANDER (*AMBYSTOMA ANNULATUM*) POPULATIONS IN MISSOURI

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Abstract: We report a detailed account of the structure and dynamics of five populations of Ringed Salamanders (*Ambystoma annulatum* Cope, 1886) in Missouri, USA, studied over a 4-yr period. The average date of capture for breeding males varied from 30 August to 2 October, and average date of capture for breeding females varied from 9 September to 7 October. The sex ratio was consistently male biased and averaged 2.05 males to each female. The smallest breeding female was 77 mm snout–vent length ([SVL]; mean = 96.3 mm) and the smallest breeding male was 66 mm SVL (mean = 94.2 mm). Eggs and larvae were present in September and October each year, and the larval period varied from 7 to 9 mo. Juveniles metamorphosed in all years in every pond, albeit in low numbers (6–631). The mean SVL of metamorphosing juveniles among all years and ponds was 39.2 mm. Intra-annual body size of emerging juveniles declined over time; juveniles that metamorphosed early were larger in body size than those metamorphosing later in the summer. Production of juveniles per female averaged 0.76 (range, 0.056–2.929), and survival of juveniles from egg to metamorphosis averaged 0.2% (range, 0.01%–0.75%). Both females and males can reach reproductive maturity at 1 yr of age, but most return at 2–3 yr of age. Management of the Ringed Salamander must focus on all life-history stages; protecting the aquatic stage to maximize the number and fitness of metamorphosing juveniles, managing the terrestrial habitat to maximize survival to first reproduction, and monitoring connectivity to promote metapopulation dynamics.

Key words: Body size; Breeding migration; Juvenile production; Maturity; Ozark Highlands; Population size; Sex ratio

Knowledge of basic population processes is essential for understanding species declines and for developing conservation or restoration solutions. Comparing species using such information is also important for understanding why some species decline and others persist or appear stable under similar conditions. Furthermore, basic information on population processes in multiple geographic locations within the range of species can provide important comparative data on species adaptations, susceptibility to diseases, competition with invasive species, and understanding the long-term effects of climate-change—all factors important for making management decisions.

Pond-breeding salamanders are well suited for studies of population processes because adults use small ponds for annual reproduction, and both juveniles and adults migrating in or out can be effectively censused each year (Semlitsch et al., 1996). Although some species of mole salamanders (family Ambystomatidae), such as the Spotted Salamander (*Ambystoma maculatum*) and Marbled Salamander (*A. opacum*), have been well studied across their ranges (e.g., Shoop, 1974; Scott, 1990, 1994), the lesser known species, including the Ringed Salamander (*A. annulatum*), are the subjects of few studies (but see Spotila and Beumer, 1970; Hutcherson et al., 1989; Peterson et al., 1992; Briggler, 2005). No studies on *A. annulatum* have described variability in breeding populations or juvenile production that is critical for understanding population persistence. *Ambystoma annulatum* is a fall-breeding species that is endemic to the Ozark Highlands and Ouachita Mountains of southern Missouri, Arkansas, and eastern Oklahoma, USA (Trapp, 1956; Petranka, 1998). Ringed Salamanders are of management concern in Missouri because of their restricted range and the lack of basic information on population dynamics. In this study, we add to the information of Mole Salamanders by providing a detailed account of the structure and dynamics of five populations of Ringed Salamanders (*Ambystoma annulatum* Cope, 1886) in Missouri studied over a 4-yr period. Our objective is to provide

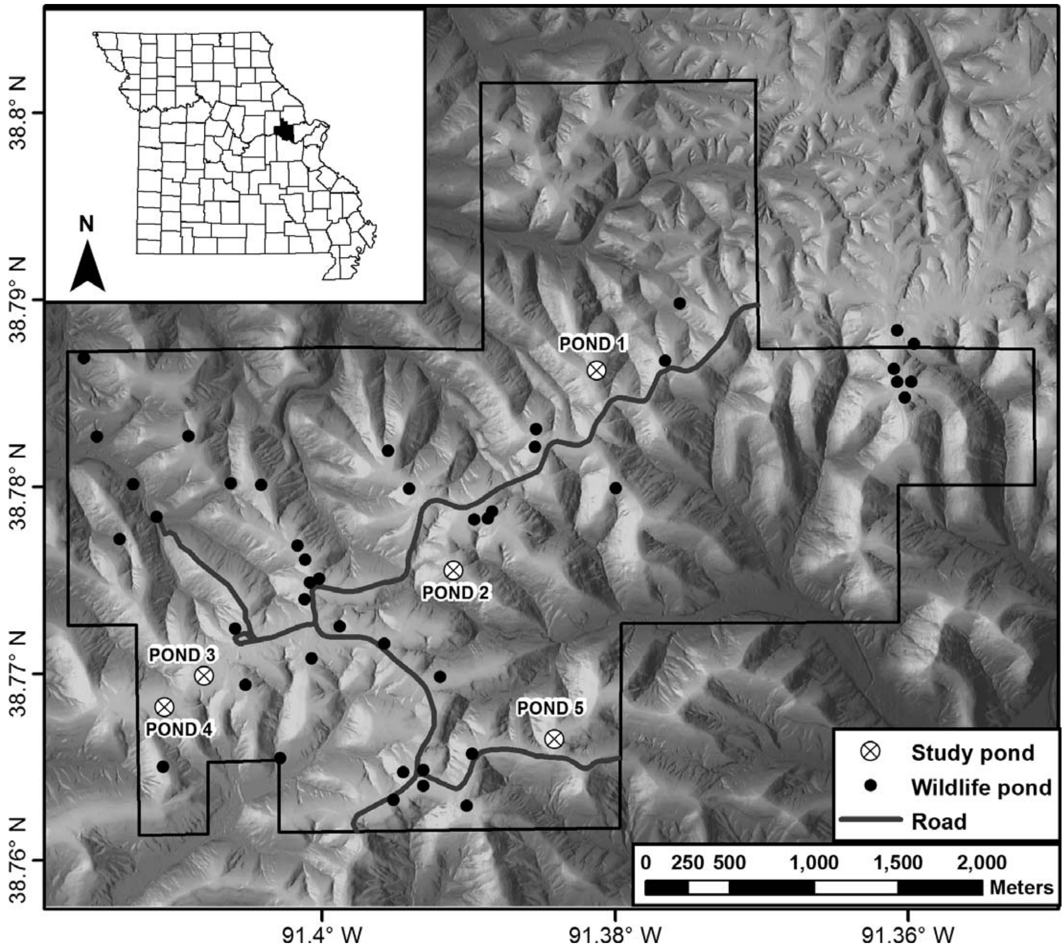

FIG. 1.—Map of Missouri with inset of Warren County and the Daniel Boone Conservation Area delineated boundary lines in black. All wildlife ponds are indicated with circles and our study ponds are indicated with X's in the circles and noted Ponds 1–5.

information on annual breeding phenology, breeding population size, sex ratio, adult body size, larval growth, juvenile emigration and production, and size and age at maturity. We then compare our results with those of other studies of *A. annulatum* and to other select species in the family Ambystomatidae.

Materials and Methods

Study Area

Our study was conducted within the Daniel Boone Conservation Area (DBCA); 1,424.5 ha) in the upper Ozark Highlands in Warren County, Missouri (Fig. 1). We selected five breeding ponds that were (1) representative of the >40 ponds present, (2) >200 m from public-use roads, and (3) spaced across the DBCA (interpond distance ranged from 0.38 to 1.35 km; Semlitsch et al., 2008, 2009). Ponds were located in a mature (80–100-yr-old), second-growth forest of oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with varying amounts of sugar maple (*Acer saccharum*) in the understory. Portions of the forest surrounding ponds was subject to varying levels of timber harvest that were allowed to undergo natural succession (Semlitsch et al., 2009). All ponds were originally constructed for other wildlife (e.g., turkey and deer), similar in size (high water area, 160–330

TABLE 1.—Dates of immigration into five breeding ponds for *Ambystoma annulatum* in Missouri, 2004–2007.

		Female immigration date		Male immigration date	
Year	Pond	First capture	Mean capture	First capture	Mean capture
2004	1	21 August	9 September	9 August	30 August
	2	21 August	9 September	9 August	1 September
	3	27 August	17 September	21 August	6 September
	4	23 August	15 September	21 August	5 September
	5	21 August	19 September	27 July	3 September
2005	1	16 August	17 September	14 September	14 September
	2	24 August	16 September	14 September	11 September
	3	15 September	19 September	14 September	19 September
	4	16 August	18 September	16 August	17 September
	5	16 August	18 September	14 September	15 September
2006	1	5 September	19 September	20 August	17 September
	2	12 September	21 September	20 August	19 September
	3	12 September	26 September	12 September	22 September
	4	12 September	22 September	28 August	20 September
	5	5 September	22 September	30 August	21 September
2007	1	8 September	29 September	8 September	25 September
	2	8 September	5 October	7 September	1 October
	3	8 September	7 October	8 September	2 October
	4	8 September	3 October	8 September	28 September
	5	8 September	5 October	8 September	27 September
Mean dates		21 August	21 September	9 August	16 September

m^2), <1.2 m in depth, and 27–47 yr old, and they have been naturally colonized by up to 16 species of amphibians (Hocking et al., 2008). All five ponds were nearly permanent, fishless, and contained water for the duration of our study, except for a short period in late summer during a drought in 2005.

Drift Fences and Monitoring

We completely encircled each breeding pond with a drift fence and pitfall traps from October to December 2003. The drift fences enabled us to census the breeding population and metamorphosing juveniles each year. Drift fences were constructed of aluminum flashing buried ~30 cm into the ground and they extended 60 cm above ground (Gibbons and Semlitsch, 1982). Pitfall traps consisted of plastic plant pots (23 cm in diameter, 24 cm in depth) buried such that the top was flush with the ground and against the fence. Traps were paired along each side of the fence every 3.0 m. A wooden board was fixed 4 cm above each trap by using metal stakes to reduce predation, and a moist sponge was placed in the bottom of each trap to reduce desiccation. Traps were checked every 1–3 d, depending on season of activity and rainfall, starting in February and ending in November for 2004–2007. We recorded trap location, date, sex, age class, and migration direction for all individuals captured in our traps, and we released them on the opposite side of the fence. A subsample of up to 50 adults at each pond and year were also measured for body size (snout–vent length [SVL], ±1 mm), and these adults were marked by toe-clipping or with passive integrated transponder-tags. All juveniles were measured (SVL) and cohort marked by toe-clipping. Rainfall gauges were placed at Ponds 1 and 4 during 2004–2006 to estimate precipitation amounts from 15 August to 15 November. For 2007, precipitation data was taken from the National Oceanic and Atmospheric Administration weather station at Warrenton, Missouri, approximately 40 km from the study location.

RESULTS

Breeding Migrations

We captured 15,111 breeding adult *A. annulatum* at drift fences migrating into ponds between August and October 2004–2007 (Table 1). The earliest male capture occurred on 27 July 2004, and the earliest female was captured on 16 August 2005, but first captures varied by year. The average date of capture for

Table 2.—Breeding population sizes for males and females, and sex ratios, of *Ambystoma annulatum* at five ponds in Missouri, 2004–2007.

Year	Pond	No. of females	No. of males	Sex ratio (male:female)
2004	1	545	903	1.66
	2	317	520	1.64
	3	119	326	2.74
	4	230	550	2.39
	5	347	574	1.65
2005	1	704	1267	1.80
	2	247	540	2.19
	3	177	278	1.57
	4	250	485	1.94
	5	325	545	1.68
2006	1	392	957	2.44
	2	156	374	2.40
	3	98	303	3.09
	4	144	321	2.23
	5	202	417	2.06
2007	1	324	646	1.99
	2	103	216	2.10
	3	120	221	1.84
	4	175	357	2.04
	5	130	206	1.58
Mean		255	500	2.05

males varied from 30 August to 2 October, and average date of capture for females varied from 9 September to 7 October among ponds and years (Table 1). The first males arrived slightly earlier most years than any of the females. The last male and female were both captured entering a breeding pond on 7 November 2007, at different ponds (Table 1).

Breeding Populations

The total breeding population size captured at drift fences showed wide variation across ponds and years with as few as 319 adults in Pond 2 in 2007 to as high as 1971 adults in Pond 1 in 2005 (Table 2). The number of males entering each year varied from 206 to 1267, with a mean of 500 males among all ponds over the 4 yr. The number of females entering each year varied from 98 to 704, with a mean of 255 females among all ponds over the 4 yr. Ponds varied in the number of breeding adults, with Pond 1 consistently having more breeding adults each year than the other four ponds (Kruskal–Wallis chi-square test: 11.76, $df = 4$, $P = 0.02$; Table 2). Variation among years in the number of breeding adults was correlated with amount of rainfall during the migration season; more adults bred during years of higher rainfall (15 August–15 November; Spearman's rho: 0.46, $P = 0.03$). The sex ratio of males to females was consistently male biased in all years and averaged 2.05 males to each female (binomial exact test: $P < 0.0001$; Table 2).

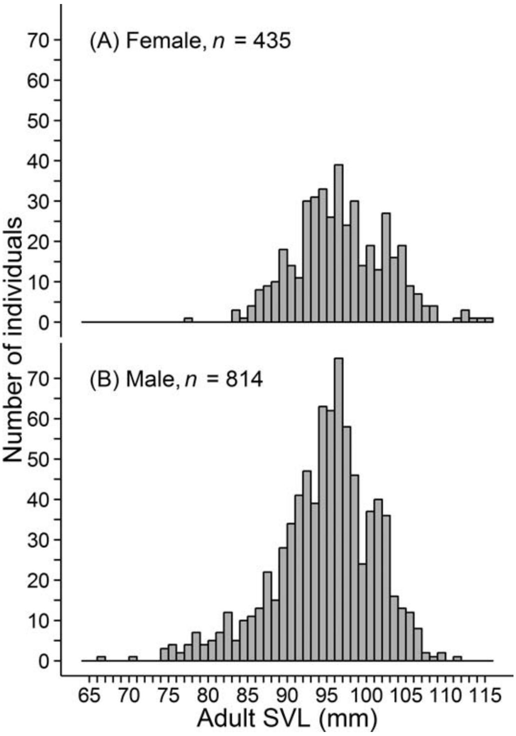

Fig. 2.—Size-frequency distribution of snout–vent length (SVL; mm) of *Ambystoma annulatum* breeding adults, (A) females and (B) males, captured at five ponds in Missouri, 2004–2007.

There was sexual size dimorphism in SVL of breeding adults; females were larger than males (male SVL = 94.2 ± 0.23 mm [mean ± SE]; female SVL = 96.3 ± 0.28 mm; Mann–Whitney U chi-square = 19.25, $df = 1$, $P = 0.0005$; Fig. 2). The smallest breeding female was 77 mm SVL, and the smallest breeding male was 66 mm SVL (Fig. 2). There were differences in SVLs of both females and males as a function of pond (Kruskal–Wallis test: female chi-square = 27.60, $df = 4$, $P < 0.0001$; male chi-square = 23.13, $df = 4$, $P = 0.0001$) and year (Kruskal–Wallis test: female chi-square = 20.87, $df = 3$, $P = 0.0001$; male chi-square = 33.30, $df = 3$, $P < 0.0001$).

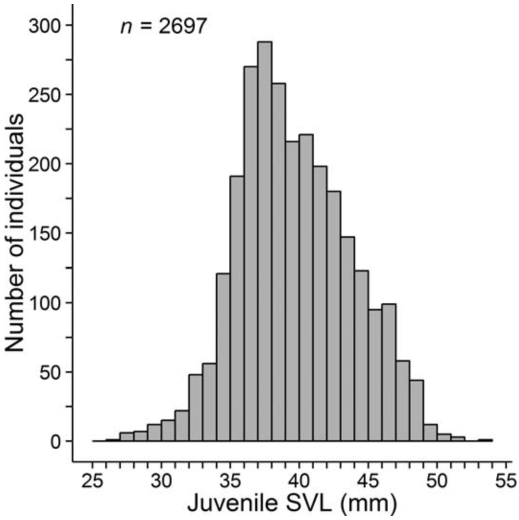

FIG. 3.—Size-frequency distribution of snout–vent length (SVL; mm) of metamorphosing *Ambystoma annulatum* juveniles captured at five ponds in Missouri, 2004–2007.

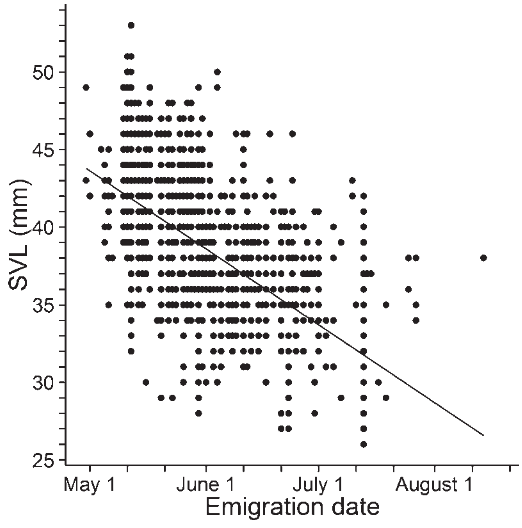

FIG. 4.—Relationship between the snout–vent length (SVL; mm) of metamorphosing *Ambystoma annulatum* juveniles and their date of emigration from five ponds in Missouri, 2004–2007. The Spearman's correlation coefficient for the line is –0.60.

Juvenile Production

Eggs and larvae were present in September and October each year at all five ponds. Based on egg masses hatched in the laboratory, larvae averaged 11.5 ± 0.29 mm in total length during the first few days after hatching. Larvae overwintered in the ponds, under the ice. No metamorphosing juveniles were found emigrating from ponds until April the following spring. We captured a total of 3065 juveniles metamorphosing from ponds across all years 2004–2007. The earliest capture of a metamorphosing juvenile at the drift fence occurred on 29 April 2006, and the average date of juvenile emigration varied from 14 May to 11 June among ponds and years. Based on the average date of arrival of breeding females and the average date of juvenile emigration, larval period ranged from 7 to 9 mo, including overwintering.

The smallest juvenile to metamorphose from ponds was 26 mm SVL on 13 July 2005 (Fig. 3). The mean body size of metamorphosing juveniles among all years and ponds was 39.2 ± 0.08 mm SVL (range, 26–53 mm). Juveniles that metamorphosed early were larger in body size than those metamorphosing later in the summer (Spearman's rho = –0.60, $P < 0.0001$; Fig. 4).

Juveniles metamorphosed from all ponds and years, albeit in low numbers (Table 3). The fewest number of juveniles to metamorphose from a pond was six individuals in 2006 at Pond 4. The greatest number to metamorphose from a pond was 630 individuals in 2005 at Pond 2. The average number metamorphosing from ponds was 153 individuals per year. The production of juveniles per female averaged 0.76 (range, 0.056–2.929; Table 3). Percentage of survival of juveniles from egg to metamorphosis averaged 0.2% (range, 0.01%–0.78%; number of juveniles/number of breeding females × 390 eggs per female; Hutcherson et al., 1989). The production of juveniles (total metamorphs, metamorphs/female, and metamorphs/egg) did not vary among ponds or years (all $P > 0.05$).

Reproductive Maturity

Based on the recapture of marked metamorphosing juveniles at our drift fences, the average body size at first reproduction was 80.3 ± 8.4 mm SVL. A total of 163 marked juveniles ($n = 116$ males; $n = 43$ females; $n = 4$ unknowns; Table 4) was captured for the first time entering our study ponds during the fall breeding season. Only a small percentage

Table 3.—Juvenile production of *Ambystoma annulatum* from five breeding ponds in Missouri, 2004–2007.

Year	Pond	Juvenile production	Juveniles/female	Juvenile survival/egg[a]
2004	1	378	0.694	0.0020
	2	24	0.069	0.0002
	3	10	0.040	0.0002
	4	158	1.612	0.0020
	5	125	1.214	0.0010
2005	1	256	0.808	0.0010
	2	630	0.895	0.0073
	3	27	0.083	0.0004
	4	52	0.361	0.0006
	5	340	2.833	0.0030
2006	1	230	1.933	0.0017
	2	70	0.283	0.0013
	3	21	0.054	0.0006
	4	6	0.030	0.0001
	5	150	0.857	0.0021
2007	1	138	0.600	0.0012
	2	11	0.062	0.0003
	3	329	2.109	0.0078
	4	7	0.022	0.0001
	5	103	0.792	0.0023
Mean		153	0.760	0.0020

[a] Survival was estimated dividing the total number of juveniles produced by the total number of eggs estimated using 390 eggs per clutch (in Missouri; Hutcherson et al., 1989) multiplied by the total number of females captured at breeding ponds.

returned in their first year (11.7%), 5–6 mo after metamorphosis; most returned in the second (34.4%) and third (53.9%) years (Table 4).

Discussion

The population dynamics of the Ringed Salamander in Missouri appears similar to that other fall breeding species in the family Ambystomatidae (Petranka, 1998). Breeding migrations occurred primarily in September and October at our study ponds. The onset and peak of breeding migrations were influenced by the amount and frequency of rainfall during late summer and autumn. Unlike the Marbled Salamander, the Ringed Salamander requires water to lay eggs, although anecdotal observations show females occasionally lay eggs in dry pond beds (DS, personal observation). Nearly all adults emigrated out of ponds after breeding during October, and no adults were observed overwintering in ponds. Our results support past observations for *A. annulatum* of breeding during September and October in Missouri (Hutcherson et al., 1989; Peterson et al., 1992) and Arkansas, USA (Trapp, 1956; Spotila and Beumer, 1970). Although previously reported, we have no information supporting breeding during winter at this site (Trauth et al., 1989).

The breeding populations of *A. annulatum* at our study sites were relatively large, ranging from 98 to 704 breeding females each year, and they appeared stable across years despite timber harvests in areas around our study ponds (Semlitsch et al., 2008, 2009). Although most previous studies of Ringed Salamanders did not census whole breeding ponds, Peterson et al. (1992) found 150–230 adult females at a pond in southern Missouri. The breeding population sizes we found are comparable to those of other species of mole salamanders (e.g., Shoop, 1974; Semlitsch, 1983, 1987; Semlitsch et al., 1996; Taylor et al., 2005). We also found the sex ratio of breeding adults to be male biased, as has been shown for most other species in Ambystomatidae (Petranka, 1998). We observed less variability in the number of breeding adults each year at our ponds, however, relative to other long-term studies of *Ambystoma* populations. We attribute this finding to our ponds being nearly permanent and never completely drying compared with highly variable hydroperiods found in more seasonal ponds (e.g., Massachusetts, USA, Shoop, 1974; South Carolina, USA, Semlitsch et al., 1996; Taylor et al., 2005). We also found low-level juvenile

Table 4.—Recapture of marked (2004–2006) *Ambystoma annulatum* returning to breed for the first time (2005–2007) at five ponds in Missouri. Sex of returning animals is shown in parentheses.

	Year of recapture			
Year of cohort mark	2004	2005	2006	2007
2004	0	19 (17 male, 2 female)	20 (13 male, 7 female)	21 (10 male, 11 female)
2005	—	0	33 (31 male, 2 female)	53 (30 male, 21 female)
2006	—	—	3 (3 unknown sex)	16 (15 male, 1 unknown sex)
2007	—	—	—	0

production at our ponds every year; therefore, we documented neither the high levels of recruitment nor the reproductive failures previously found for several species (Semlitsch et al., 1996; Taylor et al., 2005). In fact, every pond produced juveniles every year of our study.

Along with other species of salamanders present at our sites (Spotted Salamanders, Marbled Salamanders, and Red-Spotted Newts [*Notophthalmus viridescens*]), Ringed Salamanders were numerically dominant in these small, permanent wildlife ponds (D.L. Drake, personal communication). These salamander-dominated ponds contained relatively few anuran species. The timing of their fall breeding might allow Ringed Salamanders to establish dominance and exert negative predatory effects on other salamanders and anuran prey species breeding in spring, thereby decreasing abundance and occupancy of other species (Stenhouse, 1987; Stenhouse et al., 1983; Segev and Blaustein, 2007).

We found a relatively long larval period for Ringed Salamanders, lasting 7–9 mo, including 2–4 mo of cold water temperatures in ponds during the winter. Hutcherson et al. (1989) also reported that the larval period varied from 6 to 8.5 mo in southern Missouri. The larval period of *A. annulatum* is comparable to that of another fall-breeding species, Marbled Salamander, in northern regions (New York, USA, Bishop, 1941; Illinois, USA, Smith, 1961), but it is much longer than fall-breeding *Ambystoma cingulatum* found in southern regions (11–13 wk in Florida, USA, Palis, 1995; Sekerak et al., 1996). Metamorphosing juveniles of Ringed Salamanders began emerging in April, and we found that emerging juveniles decreased in body size as the season progressed; the opposite pattern found in other species such as Spotted Salamander (Shoop, 1974; TLA, personal observation). Thus, for any Ringed Salamander larvae unable to metamorphose early and escape the potential for early pond drying, they suffer the added disadvantage of metamorphosing at a small body size and perhaps experiencing lower fitness (e.g., Semlitsch et al., 1988; Scott, 1994). The mean SVL at metamorphosis at our site was 39.2 mm, and this comprised 59% and 51% of the average body size of breeding adult males and females, respectively. The largest juveniles at our sites were >50 mm SVL (Fig. 3), and they were 76% and 65% of the average body size of breeding adult males and females, respectively. It has been shown repeatedly that a large body size at metamorphosis increases the probability of juveniles surviving, a younger age at first reproduction, and populations persisting over the long term (Semlitsch et al., 1988; Taylor et al., 2005; Harper et al., 2008).

Although we do not have the data to test the importance of size at and time to metamorphosis on reproductive traits, a small percentage of Ringed Salamander (11.7%, representing both males and females) reached maturity at 1 yr of age. We found that most individuals bred for the first time at 2–3 yr of age, and almost three times as many males (71.2%) breed by age 3 yr as females (26.4%). We do not know what percentage of individuals reached maturity, dispersed, and bred in other ponds at DBCA, so our estimates on first reproduction are conservative. Another fall-breeding species, Marbled Salamander, similarly has only a small percentage of individuals that reach maturity at 1 yr of age (4.9%); most reach maturity at 2 yr (55.1%) and 3 yr (40.0%) of age (Scott, 1994).

Based on our results and ongoing studies in Missouri, we suggest that conservation and management efforts for Ringed Salamander be focused on maintaining fishless, permanent ponds for breeding and larval development. A continuous hydroperiod from September through the end of June appears to maximize juvenile production for this species, and therefore the potential for recruitment into the adult population. Drying of ponds during late summer, even after short droughts (e.g., 2005) had no apparent effect on their juvenile production because they metamorphose earlier than spring breeding species such as Spotted Salamander (Hocking et al., 2008; TLA, personal observation), that can be devastated by summer drying (Semlitsch et al., 1996; Taylor et al., 2005). A lack of rain and pond filling during September and October appear to reduce Ringed Salamander breeding effort and egg deposition (TLA, personal observation), but we never recorded a complete absence of breeding activity at our sites during any year.

Additional recommendations for management of Ringed Salamanders include protection of the terrestrial core habitat surrounding each breeding pond out to a radius of 200–500 m from the pond edge (Semlitsch, 1998; Rittenhouse and Semlitsch, 2007; Peterman et al., in press; Scott et al., 2013). For other species with overlapping generations of breeding adults (e.g., Spotted Salamanders), minimizing juvenile mortality by maintaining high-quality, forested habitat can decrease local extinction probability (Harper et al., 2008). Furthermore, protecting or restoring breeding ponds in small clusters within 300 m of each other increases the abundance of three species of mole salamander larvae, including Ringed Salamanders (Peterman et al., in press). Maintaining clusters of ponds, with adequate terrestrial habitat between them for dispersal and recolonization promotes metapopulation dynamics and long-term persistence. Thus, management for the Ringed Salamander must focus on protection of the aquatic stage to maximize the number and fitness of metamorphosing juveniles, conservation of forested terrestrial habitat to maximize survival to first reproduction, and maintenance of connectivity to promote metapopulation dynamics. Future studies should focus on the spatial dynamics of populations across a broader landscape for understanding long-term persistence of this endemic species at a regional level.

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