

Breeding and Recruitment Phenology of Amphibians in Missouri Oak-Hickory Forests

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ABSTRACT.—Knowing the phenologies of species in a region helps guide management and conservation activities in breeding ponds and surrounding terrestrial habitats. We examined the phenology of pond-breeding amphibians in central Missouri oak-hickory forests. Two ponds were monitored for 4 y from 2000–2003 and five other ponds were monitored for 1 y during 2004 using drift fences with pitfall traps. We found 15 species of pond-breeding amphibians, nine of which we captured in sufficient abundance to evaluate breeding phenology. Among the nine species, breeding migrations occur from Feb. to Nov., while subsequent metamorph emigration occurred primarily from May to Oct.. Our ponds were nearly permanent, resulting in salamander-dominated communities in these oak-hickory forests. Pond-use was partitioned by species that differed in their timing of reproduction and post-metamorphic emergence. For example, breeding in the fall gives larval ringed salamanders a potential size advantage over the spring-breeding spotted salamander larvae. However, the fall breeding strategy requires ponds with long hydroperiods that hold water continuously from Aug. through May. Green frogs and central newts also required long hydroperiods for their larval stage (>160 d). American toads, however, are adapted to exploit ponds with shorter, less predictable hydroperiods as they only required ponds to hold water for as little as 60 d. Management for multiple species of pond-breeding amphibians in a landscape benefits from the inclusion of wetlands with a variety of hydroperiods.

INTRODUCTION

Many species of amphibians with complex life cycles use the same ponds for mating, reproduction and larval development. Competition for pond resources necessitates that species partition the aquatic habitat in space or time. Aquatic breeding habitats generally change over time, often seasonally, and amphibian species adjust the timing of reproductive activities to exploit these changing resources (Wilbur, 1980). The resulting differences in breeding phenologies presumably allow more species to coexist through reduced larval competition and predation.

Conditions in the aquatic habitat strongly influence length of the amphibian larval stage, which may last from weeks to years depending on the species (*e.g.*, Werner, 1986; Alford and Harris, 1988). Although timing of and size at metamorphosis are flexible life history traits, minimum size and maximum length of the larval period are generally bounded for species (*e.g.*, Wilbur and Collins, 1973; Smith, 1987; Alford and Harris, 1988). In harsh aquatic environments, larvae metamorphose quickly and at a small size due to rapid pond drying,

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high levels of competition or predation. Under favorable aquatic conditions, larvae may postpone metamorphosis and benefit from increased growth and large size at metamorphosis (Alford, 1999).

Although mechanisms influencing breeding patterns have been tested in experimental communities, few studies have reported the breeding phenology of natural amphibian communities (but *see* Paton *et al.*, 2000; Paton and Crouch, 2002; Todd and Winne, 2006). Pond-breeding amphibians may be broadly classified as winter, spring, summer, or fall breeders. Factors such as rainfall and temperature are important constraints on the seasonal timing of reproduction (*e.g.*, Semlitsch, 1985; Sexton *et al.*, 1990; Redmer, 2002; Todd and Winne, 2006). Some studies have also examined the effects of timing of oviposition on larval performance through “priority effects” and how these community interactions potentially affect breeding and recruitment phenologies (Alford and Wilbur, 1985; Wilbur and Alford, 1985; Morin *et al.*, 1990).

Knowledge of breeding phenologies is necessary for designing appropriate monitoring and inventory assessments and for conserving biodiversity of aquatic communities (Paton and Crouch, 2002). For example, land managers can schedule management activities, such as controlled burning and timber harvesting, to minimize the impacts on amphibians based on their phenologies. Although there is growing concern over the effect of global climate change on breeding phenologies and resulting species interactions (Beebee, 1995; Reading, 1998; Blaustein *et al.*, 2001; Gibbs and Breisch, 2001), few detailed studies have examined phenology of multiple species at multiple locations. Having a baseline to compare phenologies in the future is essential when considering the impacts of global climate change on wildlife populations. Furthermore, the timing and length of the larval period is critical when evaluating hydroperiod, especially for design of restoration and mitigation wetlands.

Our objective was to quantify the breeding and recruitment phenology of pond-breeding amphibians in central Missouri oak-hickory forests. We discuss differences between two sites located approximately 100 km apart. Additionally, we discuss ecological processes potentially contributing to these differences and implications for managing isolated wetlands and the surrounding forests.

METHODS

We studied amphibian breeding and recruitment phenologies from 2000–2004 at two sites in the Outer Ozark Border Subsection of central Missouri (Nigh and Schroeder, 2002). The first site was the University of Missouri’s Thomas S. Baskett Wildlife Research and Education Area (hereafter Baskett), a 911-ha area located in Boone County, Missouri. We studied amphibian populations at two ponds year-round from Apr. 2000 to Sep. 2003. The ponds were constructed as wildlife ponds in the 1930s and are surrounded by forest consisting of oak (primarily *Quercus alba* and *Q. rubra*) and hickory (*Carya* spp.) with an understory of sugar maple (*Acer saccharum*) and dogwoods (*Cornus* spp.). Both ponds are less than 0.1 ha in size. One pond has a nearly permanent hydroperiod while the other dries in most summers.

The second site was the Missouri Department of Conservation’s Daniel Boone Conservation Area (hereafter Boone) in Warren County, Missouri. The conservation area is 1424 ha dominated by oak-hickory forest (*Quercus* spp. and *Carya* spp.) and located approximately 100 km east of Baskett. Of the more than 40 ponds in Boone, we selected five ponds that were fishless, more than 200 m from the nearest public-use road and constructed 27–47 y ago. We monitored these ponds from 20 Feb. through 31 Oct. 2004. All five ponds are semi- to nearly- permanent, contained water for the duration of the study and ranged in

size from 0.016 to 0.034 ha. We used constructed ponds because there are very few natural ponds in Missouri outside of the Missouri and Mississippi River floodplains. Most of the species breeding in these constructed ponds would likely have bred in floodplain ponds which have been drained or filled for agriculture. Additionally, they may have bred in small pools created by large tree blowdowns, which are likely less common now as forests have been harvested, leaving few large trees to create large blowdown ponds. Currently, most pond-breeding amphibians in central Missouri require fishless, constructed ponds due to the absence of suitable natural ponds.

To monitor amphibian populations and phenology, we completely encircled all seven ponds with a drift fence and pitfall traps. The drift fences were constructed of aluminum flashing buried approximately 30 cm into the ground and extending 60 cm above ground. At Baskett, pitfall traps consisted of number 10 coffee cans buried such that the top was flush with the ground. Traps were paired every 4.5 m along each side of the fence. At Boone, pitfall traps were located approximately every 3 m and we used plastic nursery pots for traps (23 cm diameter, 24 cm deep). At both sites, a wooden board was held 4 cm above each trap 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 weather conditions and time of year. We recorded date, species, sex, age class and migration direction for all individuals captured in our traps and we released them on the opposite side of the fence. Some species were also measured and marked (toe-clipped or pit-tagged) as part of population studies, but data on recaptures are not presented here.

The length of time that premetamorphic amphibians require aquatic habitat (from egg oviposition to metamorphosis) is important to consider when planning activities that may alter hydroperiods (*i.e.*, timber harvest, impervious surfaces). We calculated the minimum value by subtracting the Julian date when 5% of the adult females had immigrated from the date when 5% of the metamorphs had emigrated from the ponds. The maximum is calculated from the dates of the 95th percentile of metamorph emigration minus the 5th percentile of female immigration (Paton and Crouch, 2002).

RESULTS

We recorded 13,521 adult and metamorph amphibian captures representing 11 species at the two ponds in Baskett during 4 y (Table 1). All 11 species occurred at both ponds. The western chorus frog (*Pseudacris triseriata*) was the only species not captured in all years. We captured seven species in sufficient abundance (>100 adult or metamorph captures) to examine phenologies.

We recorded 21,041 amphibian captures of 14 species at the five ponds in Boone during 1 y (Table 1). Nine of the species occurred at all ponds. We captured seven species in sufficient abundance (>100 adult or metamorph captures) to examine phenologies. Of the 15 species captured at Baskett and Boone, 10 were present at both sites and most species captured at only one site were found in small numbers. A notable exception was the ringed salamander (*Ambystoma annulatum*), which was among the most abundant species at Boone ponds but was absent from Baskett because the site is outside its geographic range.

The ringed salamander made up 45.0% of all captures at the five ponds in Boone. Ringed salamanders immigrated to breeding ponds from late Aug. through Oct.. Males and females immigrated simultaneously but the majority of males reached the pond prior to females (Table 2; Fig. 1). Following oviposition, the eggs hatched and the aquatic larvae overwintered in the ponds. Most surviving offspring reached metamorphosis and emigrated in May, but metamorph emigration extended into Jul. (Fig. 1).

TABLE 1.—The mean number of captures per pond per year for all pond-breeding amphibian species (SE). Data at the two Baskett ponds were collected from 2000–2003. Data for the five Boone ponds were collected in 2004

Species	Baskett		Boone	
	Adults	Metamorphs	Adults	Metamorphs
Caudata				
<i>Ambystoma annulatum</i>	*	*	1756 (392)	139 (66.5)
<i>Ambystoma maculatum</i>	695 (202)	540 (279)	1318 (208)	269 (96.3)
<i>Ambystoma opacum</i>	*	*	8 (3.2)	0 (0.2)
<i>Hemidactylium scutatum</i>	*	*	4 (1.5)	2 (1.2)
<i>Notophthalmus viridescens</i>	97 (37.7)	193 (165)	244 (63.8)	56 (32.4)
Anura				
<i>Acris crepitans</i>	2 (1.1)	0 (0.5)	2 (1.5)	2 (1.8)
<i>Bufo americanus</i>	14 (8.1)	5 (5.5)	33 (19.6)	0 (0.2)
<i>Hyla versicolor</i>	4 (2.5)	2 (1.1)	7 (1.9)	7 (3.8)
<i>Pseudacris crucifer</i>	43 (28.3)	1 (0.9)	22 (6.1)	4 (2.4)
<i>Pseudacris triseriata</i>	0 (0.2)	2 (2.4)	0	0
<i>Rana catesbeiana</i>	2 (1.4)	5 (3.6)	3 (0.9)	0 (0.2)
<i>Rana clamitans</i>	18 (7.6)	255 (138)	44 (6.0)	234 (88.6)
<i>Rana palustris</i>	18 (12.3)	5 (4.2)	6 (4.6)	0
<i>Rana sphenocephala</i>	4 (1.0)	22 (20.9)	1 (0.4)	0
<i>Rana sylvatica</i>	*	*	7 (3.3)	40 (38.7)

* Baskett was outside the geographic range of these species

Salamanders comprised 85% and 96% of the adult captures and 67% and 62% of metamorph captures at Baskett and Boone, respectively. In addition to ringed salamanders, Boone ponds had large numbers of central newts (*Notophthalmus viridescens louisianensis*) and spotted salamanders (*Ambystoma maculatum*) (Table 1). Some ponds also had small numbers of marbled (*Ambystoma opacum*) and four-toed (*Hemidactylium scutatum*) salamanders (Table 1). Baskett is outside the current geographic range of marbled and four-toed salamanders, but spotted salamanders and central newts still comprised the majority of adult captures at Baskett ponds (Table 1). Although captured in small numbers, frogs constituted the majority of the amphibian species richness at both sites (Table 1).

There was considerable temporal partitioning of the breeding season among species. The majority of adult wood frogs (*Rana sylvatica*), spotted salamanders, central newts, spring peepers (*Pseudacris crucifer*), western chorus frogs, American toads (*Bufo americanus*), pickerel frogs (*Rana palustris*) and southern leopard frogs (*Rana sphenocephala*) immigrated to ponds between 5 Mar. and 30 Apr. at Boone and between 16 Mar. and 27 May at Baskett (Table 2; Fig. 2). The only species with complete overlap in breeding were wood frogs and spotted salamanders at Boone and spring peepers and pickerel frogs at Baskett (Table 2). Central newts had substantial overlap with spotted salamanders and wood frogs, but were also captured in significant numbers during the fall, especially at Boone (Fig. 1). The southern leopard frog was the only species to have a bimodal annual breeding distribution, with immigration and observed oviposition documented from Mar. through Apr. and again from Aug. through Oct. (Fig. 1).

Ninety-percent of metamorphs emerged between 11 May and 25 Oct. at Boone and between 25 May and 16 Oct. at Baskett. At Boone, ringed salamanders were the first to emigrate with the majority leaving the ponds by 25 May. Spotted salamander metamorph

TABLE 2.—Cumulative percent of individuals immigrating and emigrating from the ponds at the Boone and Baskett areas in central Missouri. Minimum days in the pond was calculated by subtracting the Julian date when 5% of females had immigrated from the date when 5% of the metamorphs had emigrated. Maximum days in the pond was calculated by subtracting the 5th percentile of female immigration from the 95th percentile of metamorph emigration

Species	sex	n	Adult immigration			Metamorph emigration			Days in pond	
			5%	50%	95%	5%	50%	95%	minimum	maximum
Daniel Boone Conservation Area										
<i>Ambystoma annulatum</i>	M	2904	20-Aug	30-Aug	3-Oct	11-May	25-May	2-Jul	262	314
	F	1569	22-Aug	17-Sep	9-Oct	6-Jul	20-Aug	13-Oct		
<i>Ambystoma maculatum</i>	M	2249	5-Mar	5-Mar	25-Mar	10-Jun	22-Jun	20-Jul	98	138
	F	1182	4-Mar	11-Mar	25-Mar	31-May	20-Jul	21-Oct	*	*
<i>Bufo americanus</i>	M	59	25-Mar	25-Apr	11-May	9-Jun	10-Jun	20-Jul	97	104
	F	27	25-Mar	30-Apr	15-May	8-Aug	20-Jul	21-Oct		
<i>Pseudacris crucifer</i>	M	27	3-Mar	9-Apr	21-Apr	24-Mar	17-Sep	25-Oct	160	238
	F	34	4-Mar	17-Apr	21-Apr	4-Mar	5-Mar	5-Mar		
<i>Rana clamitans</i>	M	54	21-Apr	8-Jun	27-Oct	1-Mar	5-Mar	5-Mar		
	F	56	1-May	22-Jun	23-Oct	14-Feb	4-Mar	4-Mar		
<i>Rana sylvatica</i>	M	12	29-Feb	4-Mar	7-Mar	24-Feb	4-Mar	4-Mar		
	F	11	4-Mar	5-Mar	24-Mar	1-Mar	5-Mar	5-Mar		
<i>Notophthalmus viridescens</i>	M	397	24-Feb	4-Mar	23-Oct					
	F	403	1-Mar	5-Mar	21-Oct					
Thomas S. Baskett Wildlife Research & Education Area										
<i>Ambystoma maculatum</i>	M	1665	14-Feb	9-Mar	20-Mar	16-Jun	5-Aug	24-Sep	112	212
	F	1186	24-Feb	16-Mar	3-Apr	6-Jul	14-Jul	27-Aug	60	112
<i>Bufo americanus</i>	M	29	11-May	27-May	28-Sep	28-May	4-Jun	19-Jun	84	106
	F	21	7-May	27-May	8-Sep	25-May	13-Jun	5-Oct	*	*
<i>Pseudacris crucifer</i>	M	59	8-Mar	4-Apr	17-Apr	12-Jul	28-Jul	13-Aug	125	157
	F	58	5-Mar	4-Apr	14-Apr	12-Jul	29-Aug	30-Sep	*	*
<i>Rana clamitans</i>	M	29	11-Apr	2-Jul	22-Oct	24-Jul	24-Aug	16-Oct	160	244
	F	30	13-Apr	22-Jun	19-Oct	24-Jul	24-Aug	16-Oct		
<i>Rana palustris</i>	M	84	13-Mar	3-Apr	27-Apr	12-Jul	28-Jul	13-Aug		
	F	34	9-Mar	3-Apr	4-May	12-Jul	29-Aug	30-Sep		
<i>Rana sphenocphala</i>	M	14	6-Mar	5-Apr	1-Oct	12-Jul	29-Aug	30-Sep		
	F	11	9-Mar	24-Apr	22-Oct	12-Jul	29-Aug	30-Sep		
<i>Notophthalmus viridescens</i>	M	244	14-Feb	16-Mar	10-Nov	24-Jul	24-Aug	16-Oct		
	F	303	14-Feb	16-Mar	22-Oct	24-Jul	24-Aug	16-Oct		

* Days in pond not calculated because an unknown portion overwinter as larvae

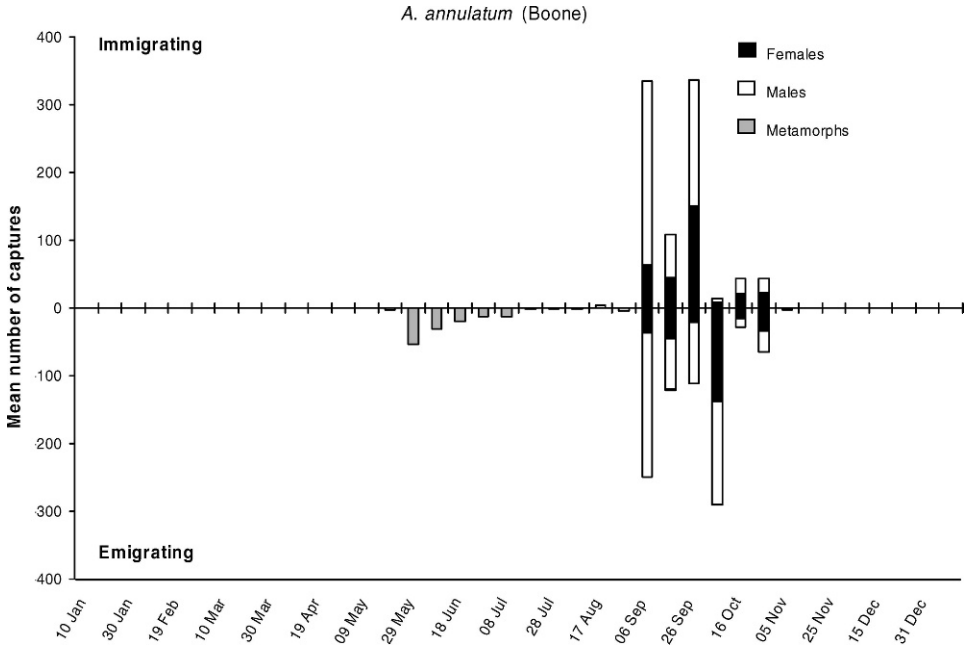


FIG. 1.—Migration phenology of seven species at the Boone sites and seven species at the Baskett sites. Mean number of captures per pond per year is shown in 10 d increments

emigration began immediately following ringed salamander emigration and lasted through Nov. (Fig. 1). Thus, peak spotted salamander metamorph emergence was later at Boone than at Baskett (Table 2; Fig. 1). Similar to spotted salamanders, central newt metamorphs tended to emigrate 2–3 wk later at Boone ponds than from Baskett ponds (Table 2). However, in the case of central newts, the number of days from female immigration until metamorph emigration was similar at the two sites (Table 2). Spring peeper metamorphs emigrated from late-May through July. Metamorphs emigrated earlier and after fewer days at the Baskett ponds than at the Boone ponds (Table 2).

American toads had the shortest time from adult immigration to metamorph emigration. Metamorph emergence occurred between Jul. and Sep., 60–112 d after females entered the ponds (Table 2). We were not able to determine the length of time from female emigration until metamorph emigration for green frogs and southern leopard frogs because an unknown number of tadpoles overwintered in the ponds prior to metamorphosis.

Additionally, our drift fences were not completely effective at capturing adult green frogs (*Rana clamitans*), southern leopard frogs, bullfrogs (*Rana catesbeiana*), gray treefrogs (*Hyla versicolor*), spring peepers, western chorus frogs or northern cricket frogs (*Acris crepitans*). Nor were fences completely effective at capturing metamorphs of the family Hylidae including cricket frogs, spring peepers, chorus frogs and gray treefrogs. Bullfrogs were uncommon in our ponds, whereas cricket frogs and gray treefrogs were observed in large numbers despite avoiding our traps. In separate studies, gray treefrogs in Boone were found to breed from late-Apr. through Jun. and metamorphs emerged in Jul. to early-Sep. (Hocking and Semlitsch, 2007). At Baskett, breeding occurred from mid-May to mid-Jun. in 2003 and 2004, with metamorph emergence from early-Jul. through Sep. (Johnson, 2005).

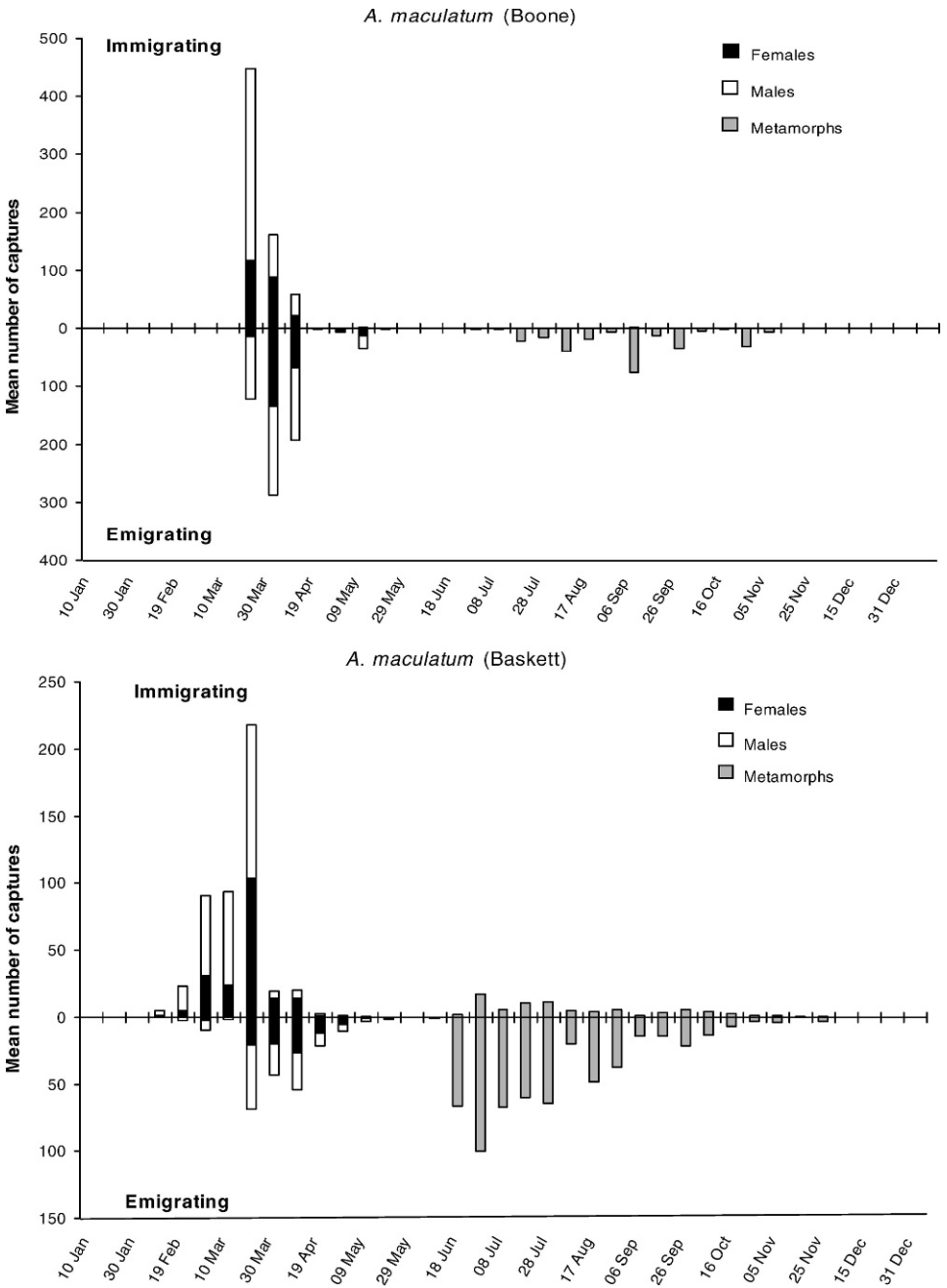


FIG. 1.—Continued

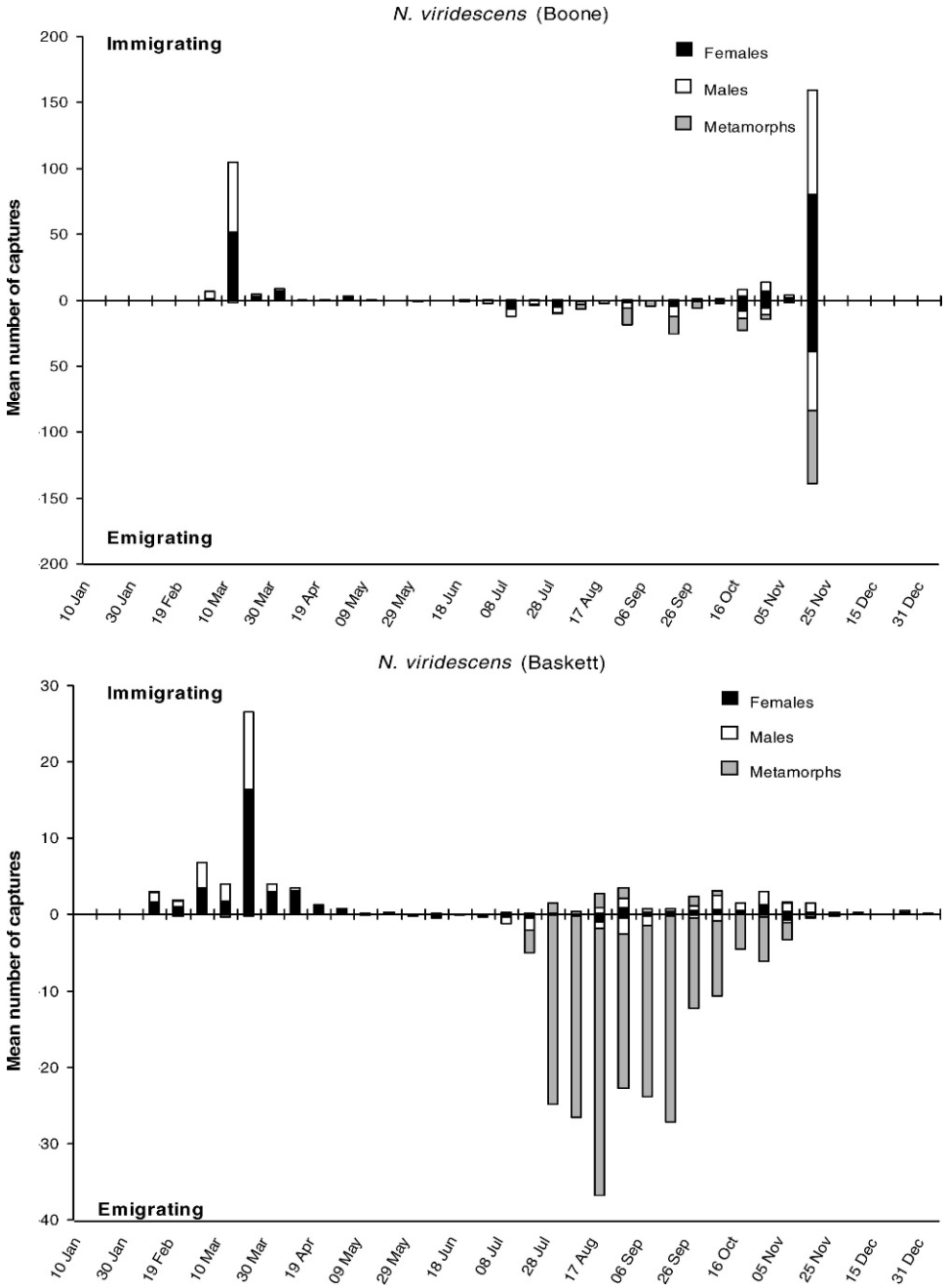


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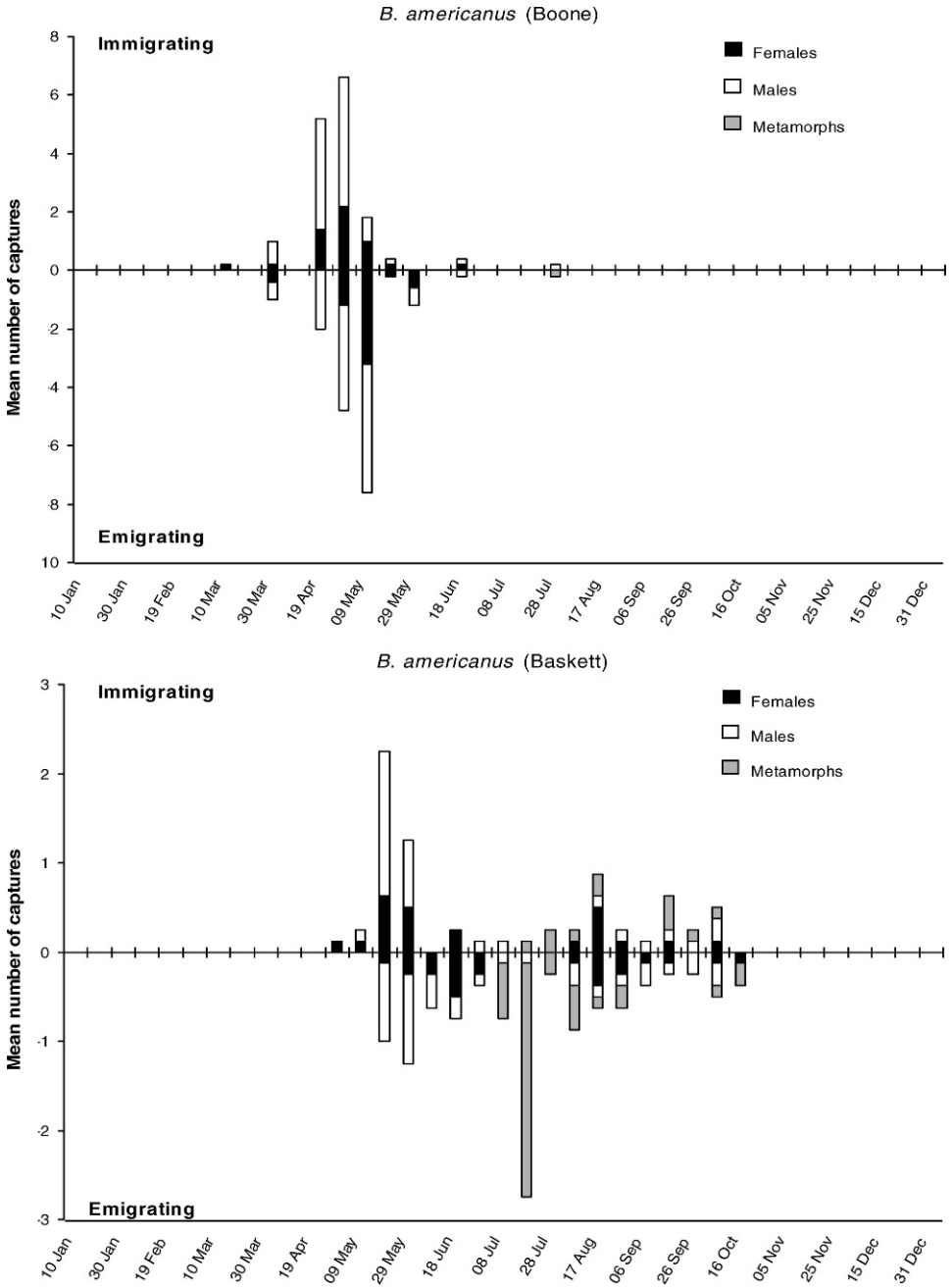


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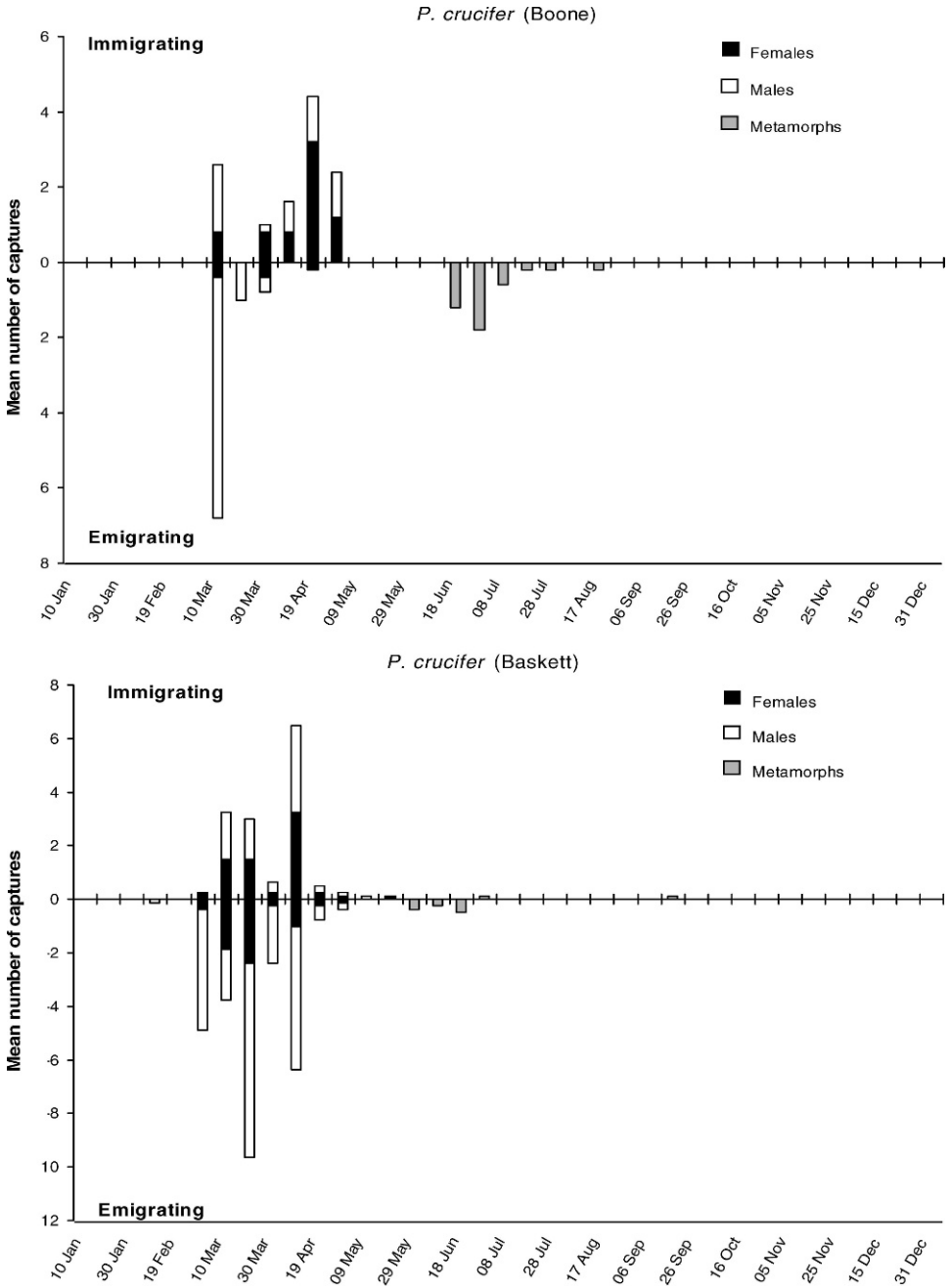


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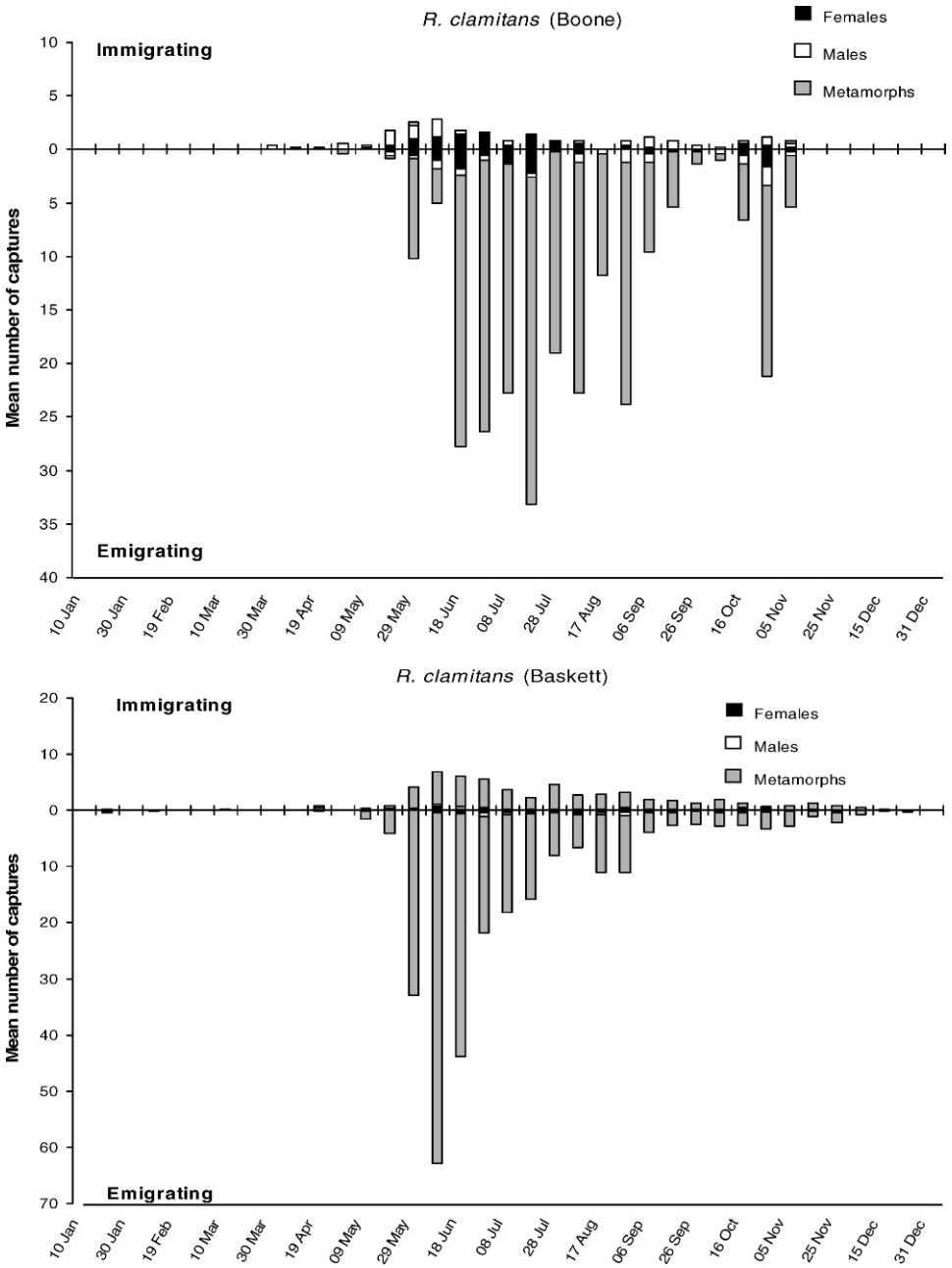


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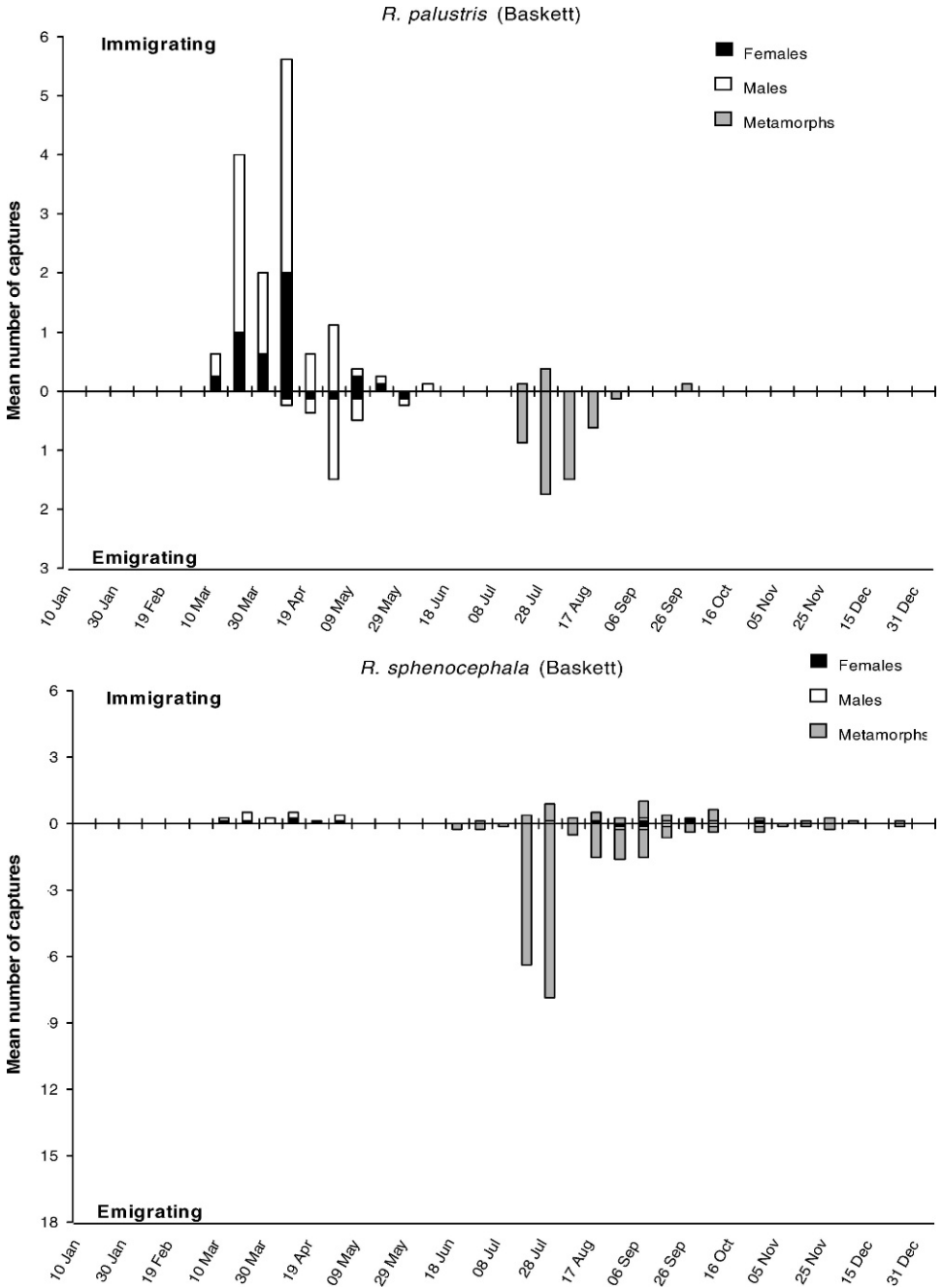


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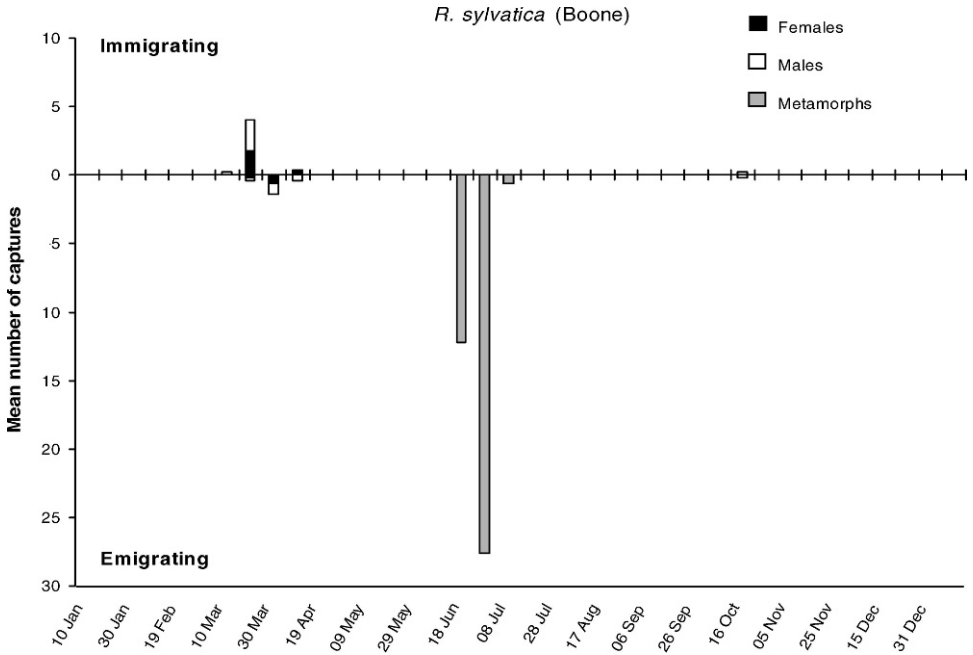


FIG. 1.—Continued

DISCUSSION

Small, isolated wetlands within contiguous forest are important for maintaining biological diversity. We found that ponds in central Missouri oak-hickory forests support a total of 15 species of pond-breeding amphibians, with up to 14 species using a single pond during a year. Species richness was greater than reported in Paton and Crouch (2002) for ponds in Rhode Island, despite having similar breeding phenologies and growing seasons. They found 10 species among the seven ponds studied (Paton and Crouch, 2002) with as many as nine species using a single pond (Paton *et al.*, 2000). Another study in the northeastern U.S. (New Hampshire), found nine species in 42 wetlands with as many as seven in a single wetland (Babbitt *et al.*, 2003). In the southeastern U.S., as many as 27 species of amphibians have been documented at a single wetland (Semlitsch *et al.*, 1996). Other studies in the southeast have also found high species richness (16–22 species in Semlitsch and Bodie, 1998; 24 in Gibbons *et al.*, 2007). The species richness in our study was therefore intermediate between that of the northeast and southeast U.S. and slightly higher than other studies in the midwestern U.S (Upper Midwest: 11 species in Evrard and Hoffman, 2000; Indiana: 10 species in Brodman *et al.*, 2006; Illinois: 10 species in Walston and Mullin, 2007).

The ponds we studied were dominated by salamanders in abundance but supported higher species richness of frogs (Table 1). While drift fences with pitfall traps are more effective for capturing salamanders than anurans (Todd *et al.*, 2007), we observed relatively few anurans in nearby ponds without fences with the exception of *Hyla versicolor*, which were still an order of magnitude less abundant than caudates (Hocking and Semlitsch, 2007). We suggest that the ponds we studied are dominated by salamanders, but relative abundances

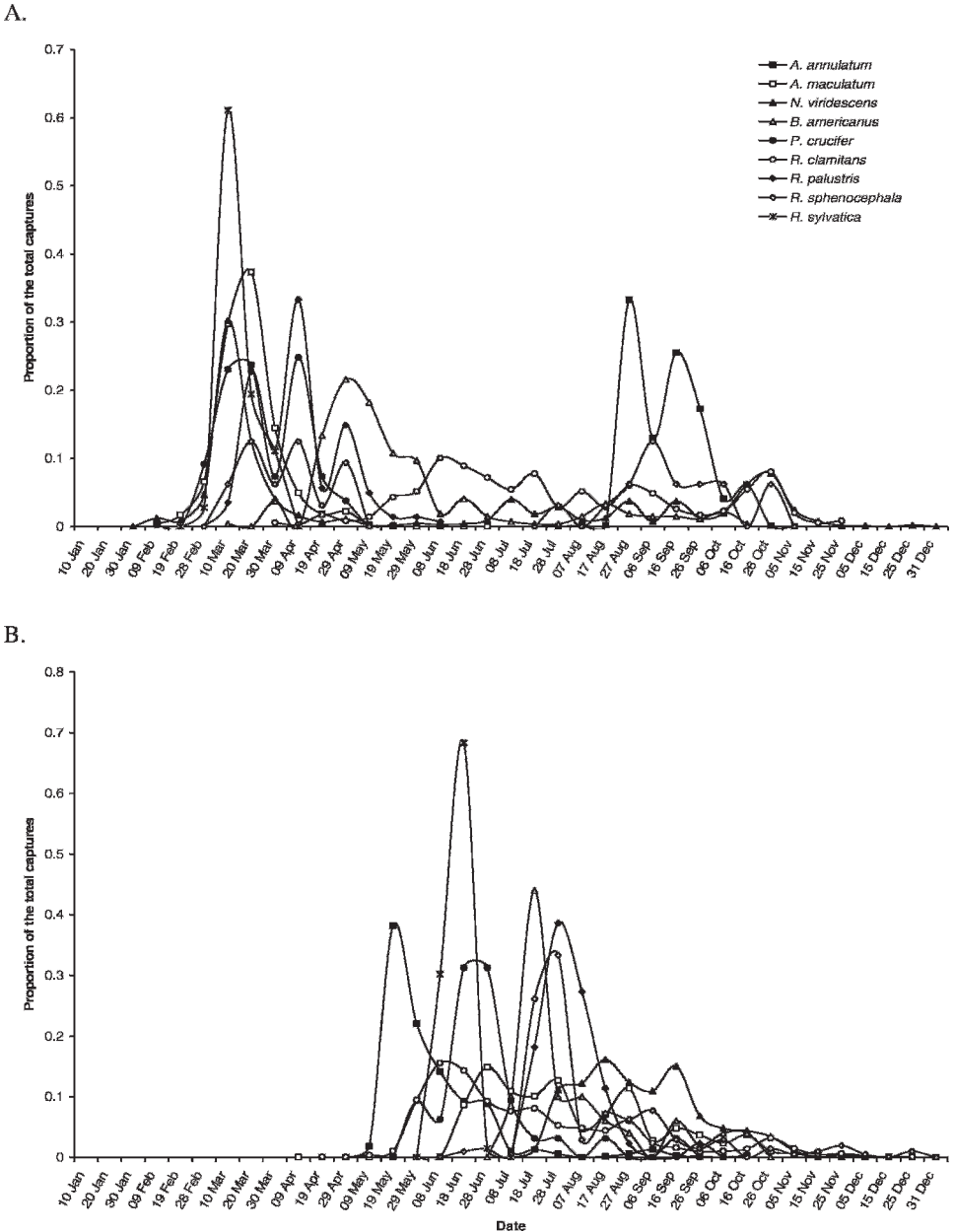


FIG. 2.—Migration phenology of pond-breeding amphibian species in the Outer Ozark Border Subsection of Missouri. Proportion of the annual mean number of captures of each species per pond per year is shown for (A) adults and (B) metamorphs in 10 d increments. Data from the seven ponds sampled at the Boone and Basketts sites were combined to show mean phenologies for the ecoregion

captured are skewed by trap bias. Mark-recapture studies with additional trapping techniques will be necessary to accurately determine the population sizes and relative abundances of all species.

Although most frog and salamander species at our sites are considered spring breeders, there was substantial temporal partitioning in pond-use among species. As found in previous studies, the order of metamorph emigration does not strictly correspond to the order of adult emigration among species (Paton *et al.*, 2000; Paton and Crouch, 2002). For example, although spring peepers bred slightly later than spotted salamanders, spring peeper metamorphs emerged before spotted salamanders due to differences in the length of the larval period (Table 2). Spring peepers and American toads have relatively short larval periods, whereas central newts, ringed salamanders, green frogs and bullfrogs have long larval periods.

Additionally, despite being conducted in a different region of the country and at different latitudes, the timing of adult breeding migrations at our sites is remarkably similar those reported for Rhode Island by Paton *et al.* (2000) and Paton and Crouch (2002). This similarity in amphibian phenology can potentially be explained by annual temperatures and length of the growing season. For example, Missouri and Rhode Island fall within the US Department of Agriculture plant hardiness zones 5b and 6a, respectively (Cathey, 1990). Timing of metamorph emigration at our sites was also remarkably similar to emigration in Massachusetts (Timm *et al.*, 2007).

Another unexpected result was the difference in central newt captures among Baskett and Boone sites (Fig. 1). At the Boone ponds, adult newts were observed moving into and out of the pond in the fall but this phenomenon was never observed at Baskett. Many individuals moving in both directions had morphologies (*i.e.*, laterally compressed tails) suggesting the newts were making frequent, short forays into the terrestrial habitat and intersecting the drift fence. We hypothesize that these migrations may only have occurred at Boone sites due to differences in aquatic food resources and individuals may have been moving into the terrestrial habitat to forage, however, many newts were observed over-wintering in all seven of the ponds. Future research should examine the duration, distance and newt behavior during these fall movements.

Similarly, spotted salamanders exhibited large variability in the duration of their breeding through metamorphosis (112–223 d) and this variation may result from differences in resource availability, thereby altering the length of the larval period. Intraspecific competition among larvae changes as metamorphs emerge and food resources also change through the seasons (Wilbur and Alford, 1985; Morin, 1987; Morin *et al.*, 1990; Ryan and Plague, 2004). Additionally, spatial and temporal differences in pond hydroperiods may help maintain variation in length of the larval period. From the perspective of emigrating and dispersing metamorphs, seasonal climatic factors may influence the timing of metamorphosis. Early metamorphs may benefit from late-spring rains while later emerging metamorphs might benefit by emigrating during cool fall rain events, again maintaining variation in the larval period (Todd and Winne, 2006).

Despite temporal partitioning of resources, interspecific interactions influenced recruitment phenology in our study. We hypothesize that the presence of ringed salamanders caused spotted salamander metamorphs to emerge later in the season and after a longer larval period. We propose two possible explanations. First, spotted salamander larvae may have reduced their activity in the presence of larger ringed salamander larvae, which prey upon spotted salamander larvae (DJH, pers. obs.). The reduction in activity may have reduced foraging opportunities and therefore slowed the growth rates of spotted

salamander larvae. Alternatively, the longer larval period may have been due to competition for common resources. Fall-breeding salamanders gain a size advantage over their spring-breeding congeners, which may give them a competitive advantage (but *see* Stenhouse *et al.*, 1983). The potential influence of ringed salamanders as an abundant predator in pond communities warrants further examination.

The timing of pond drying and length of the hydroperiod are important factors controlling pond communities and phenologies (*e.g.*, Pechmann *et al.*, 1989; Skelly, 2001; Babbitt *et al.*, 2003). In addition to ringed salamanders, bullfrogs, green frogs, and the fall-breeding cohort of leopard frogs produce tadpoles that typically overwintered in our ponds prior to metamorphosis in the spring. These species take advantage of the relative permanence of man-made ponds in central Missouri. With large-scale land alteration from agriculture, timber harvest and development, these man-made ponds are the primary breeding source for many species of amphibians in this region of the country (Knutson *et al.*, 2004). In Missouri, many of the protected amphibian breeding sites in the state were created on Missouri Department of Conservation land and have permanent or semi-permanent hydroperiods (Shulse and Semlitsch, unpubl.). Species with relatively long larval periods that overwinter in ponds have an advantage in ponds with predictably long hydroperiods and no fish.

Species that are greatly affected by high levels of competition or predation often have short larval periods and thus oviposit in ponds with short hydroperiods. Short hydroperiods prevent the accumulation of competitors and aquatic predators (Wilbur, 1987; Skelly, 2001; Babbitt *et al.*, 2003; Baber *et al.*, 2004). In the relatively permanent ponds we studied, however, salamanders comprised the majority of adult and metamorph amphibian captures. Newts and larval ambystomatid salamanders are often important predators in these aquatic communities (Wilbur, 1972; Caldwell *et al.*, 1980; Morin, 1983). Thus, we assume that salamander predators reduced the recruitment of species such as the American toad, spring peeper, pickerel frog, southern leopard frog, western chorus frog and wood frog. Although anurans could potentially alter their breeding phenology to reduce salamander predation on their offspring, the abundance of salamander predators during a large part of the year (*i.e.*, both fall- and spring-breeding species and adult newts) at our sites probably precludes this tactic. Future studies might benefit by experimentally excluding salamanders to examine changes in breeding phenology, length of the larval period and subsequent success of anuran populations.

Constructing ponds with short hydroperiods may be important for the conservation of anuran species in our region, especially a Missouri species of concern like the wood frog. With the increased use of restoration to mitigate for wetland loss and the general increase in concern for biodiversity, considering hydroperiod and amphibian reproductive phenology when designing ponds is essential for amphibian conservation (*e.g.*, Lehtinen and Galatowitsch, 2001; Pechmann *et al.*, 2001; DiMauro and Hunter Jr., 2002; Petranka *et al.*, 2003; Porej and Hetherington, 2005). For our salamander community, particularly the ringed salamander, ponds lacking fish with a semi-permanent to permanent hydroperiod provide ideal breeding habitat (Porej and Hetherington, 2005). Ponds with a long hydroperiod also benefited green frogs. American toads, spring peepers and wood frogs had the shortest larval period and may, therefore, benefit from a short hydroperiod. American toads only need ponds to hold water from Apr. through Aug., while spring peepers and wood frogs need ponds to hold water from Feb. through Jun.. However, considering how the breeding phenology of anurans might differ in the absence of other species, especially salamander predators, is important when creating wetland habitat. In Missouri, ponds that

are dry from Aug. to Nov. might be ideal for many species of frogs that suffer from predation in ponds with long hydroperiods. Overall, community interactions suggest that a matrix of ponds with varying hydroperiods is probably best for maintaining maximum species richness at the landscape scale (Semlitsch, 2000).

Finally, amphibians play an important role in aquatic and forest ecosystems (e.g., Burton and Likens, 1975; Beard *et al.*, 2002; Davic and Welsh, 2004; Regester *et al.*, 2006). Given the importance of amphibians to the ecosystem, land managers conducting management activities that disturb habitat surrounding ponds should account for amphibian reproductive phenologies during the planning stage. Terrestrial management activities such as burning, mowing and timber harvest should be avoided near ponds (within several hundred meters; see Semlitsch and Bodie, 2003; Rittenhouse and Semlitsch, 2007) during peak amphibian migrations, because species such as wood frogs, spotted salamanders and ringed salamanders migrate *en masse* during the peak of breeding. During this peak, a large portion of the population is susceptible to even localized disturbances. We suggest concentrating management activities with high levels of disturbance or traffic in Nov. through early Feb. (Fig. 2). Additional activities could potentially be conducted in Jun.–Aug. during dry periods when amphibian movements are curtailed (Todd and Winne, 2006). While call surveys and other less intensive methods may be used to monitor breeding phenologies, detailed breeding phenologies reported here provide baseline information for the conservation and management of amphibian populations in Missouri, especially in light of expected alterations due to climate change.

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