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SPATIAL AND TEMPORAL ECOLOGY OF EASTERN SPADEFOOT TOADS ON A FLORIDA LANDSCAPE

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ABSTRACT: Effective amphibian conservation must consider population and landscape processes, but information at multiple scales is rare. We explore spatial and temporal patterns of breeding and recruitment by eastern spadefoot toads (*Scaphiopus holbrookii*), using nine years of data from continuous monitoring with drift fences and pitfall traps at eight ephemeral ponds in longleaf pine-wiregrass sandhills. Breeding events (≥25 adults at a pond within a month) occurred 23 times on nine occasions at seven of the eight study ponds, but substantial recruitment (≥100 metamorphs) followed only five events. Recruitment ranged from 0–4648 among ponds. Only four ponds functioned as population "sources", and only during some years. The other ponds, and even "source" ponds during some years, functioned either as "sinks," where breeding occurred with no resulting recruitment, or were not used at all for breeding. Most recruitment occurred during four years. Recruitment was correlated with adult breeding effort, but only during some years. Recaptures were rare, and inter-pond exchange of adults was minimal and short-distance (<130 m; one was 416 m). Most (83.5%) individuals captured were metamorphs, and 15.9% were ≥51 mm (est. ≥4 yr). We conservatively estimated a 7-yr lifespan. Adult "population" trends clearly reflected breeding effort rather than numbers per se; capture rates fluctuated dramatically among years, but showed no overall trends during the 9-yr study. Our paper is provides empirical information that can be used to generate realistic metapopulation models for *S. holbrookii* as a tool in conservation planning.

Key words: Amphibian populations; Anuran breeding; Ephemeral ponds; Hydroperiod; Metapopulation; *Scaphiopus holbrookii*; Spadefoot toads; Temporary wetlands; Wetlands

AT FIRST glance, pond-breeding amphibians represent ideal metapopulation models using a "ponds as patches" paradigm, where populations continually become extinct and are recolonized by amphibians from neighboring ponds (Marsh and Trenham, 2001). However, this paradigm may not be realistic, either because metapopulation dynamics of a given species are not as they appear, or because assumptions are not met. Assumptions include: (1) extinctions and recolonizations commonly occur, (2) local extinctions are the result of stochastic processes in otherwise suitable breeding habitat, and (3) inter-pond distances influence recolonization processes due to limited dispersal ability by amphibians (Marsh and Trenham, 2001). In addition, perceived extinctions may be biased by sampling problems, such as species that are missed in surveys, skipped breeding seasons when climate or pond conditions are unsuitable, or explosive breeding followed by long periods without breeding (Marsh and Trenham, 2001).

Accurate perceptions of amphibian metapopulation dynamics and population trends require long-term, landscape-scale studies to distinguish between local extinction and recolonization, natural population fluctuations, and true declines at a regional level (Blaustein et al., 1994; Gibbons et al., 1997; Pechmann et al., 1991). Long-term sampling at a single site provides vital information about amphibian pond use and life history, but sacrifices a landscape-scale perspective of community and metapopulation dynamics (Dodd, 1992; Semlitsch et al., 1996). Conversely, repeated "snapshot" sampling across multiple sites provides a broader spatial perspective, but sacrifices information about community and population dynamics (Cody, 1996; Semlitsch et al., 1995) and may miss information regarding distribution or site use (Skelly et al., 1999, 2003). Only intensive, concurrent, and continuous sampling of multiple sites over an

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extended period of time can capture the temporal and spatial variability of breeding, recruitment, longevity, and inter-pond movement that creates metapopulations.

Eastern spadefoot toads (*Scaphiopus holbrookii*) breed exclusively in fish-free, isolated, ephemeral ponds, and inhabit the surrounding uplands for most of their adult lives (Moler and Franz, 1987). Breeding is highly dependant on weather patterns and resulting pond hydrology; adults select ponds that have dried and recently refilled, likely to avoid high densities of invertebrate predators (Moler and Franz, 1987). Explosive breeding in this species occurs after heavy rains (Gosner and Black, 1955; Wright, 2002; Greenberg and Tanner, 2004). However, not all seemingly suitable ponds are selected for breeding, and not all heavy rains elicit explosive breeding by *S. holbrookii* (Greenberg and Tanner, 2004). Therefore, population persistence likely depends upon an interplay between weather, chance, and the suitability of both breeding ponds and the surrounding uplands (Delis et al., 1996). Much of what is known about *S. holbrookii* is derived from observation (Neill, 1957), short-term studies at one or a few sites (Bragg, 1961; Pearson, 1955), studies in upland habitat (Pearson, 1955), or experiments in artificial pools (Alford, 1989; Petranka and Kennedy, 1999; Wilbur et al., 1983; Wilbur, 1987). Little is known about the spatial and temporal dynamics of breeding ecology, or whether a metapopulation model fits the population ecology of *S. holbrookii* at the landscape level.

In this paper we use data from nine years (February 1994–January 2003) of continuous monitoring at eight, isolated, ephemeral ponds in Florida longleaf pine-wiregrass uplands to explore spatial and temporal patterns of breeding and recruitment by *S. holbrookii*. We examine life-history and behavioral attributes that could influence metapopulation dynamics. Specifically, we ask: (1) is breeding or juvenile recruitment spatially or temporally autocorrelated? (4) does breeding effort by adults affect recruitment levels, or is successful recruitment commonly subject to stochastic processes? (2) are extinctions and recolonizations common? (3) how might spatial and temporal patterns of breeding affect perceptions of population "blinking" and landscape-level population trends? Our paper is intended to provide empirical information that can be used to generate realistic metapopulation models for *S. holbrookii* as a tool in conservation planning.

Methods

Study Area

This study was conducted at eight small (0.1–0.37 ha) isolated, ephemeral sinkhole ponds in longleaf pine-wiregrass sandhills on the Ocala National Forest in Marion and Putnam Counties, Florida. Ponds 1–4 were in fire-suppressed, hardwood- and sand pine-invaded sandhills. Despite attempts at habitat restoration (hardwood reduction) by burning at 1–4 year intervals during the past two decades, hardwood density and wiregrass cover remained patchy around Ponds 1–4. Ponds 5–8 were in savanna-like sandhills with a continuous wiregrass ground cover, widely spaced longleaf pine trees, and few hardwoods. Since 1976 the upland matrix surrounding these ponds has been regularly, successfully burned at 2–3 yr intervals (see Greenberg, 2001 for specific habitat characteristics; also see Greenberg and Tanner, 2004). Ponds 1–3 are within 10–30 m of the regularly burned sandhills on one side, separated by a sand road. Ponds 7 and 8 are approximately 9.5 km south of the others.

Drift Fence Sampling

We installed drift fences 7.6 m long and spaced 7.6 m apart around 50% of each pond, and placed pitfall traps (19-liter buckets) on the inside and outside of both ends of each fence (four per fence) to detect directional movement by amphibians to and from ponds. We placed a sponge in each pitfall trap. Sponges were moistened as needed during trap checks to reduce the likelihood of desiccation. We positioned a double- or single-ended funnel trap at the midpoint of each fence on both sides (two per fence).

Traps were routinely checked three times weekly from February 1994 through January 2003. Our resident volunteer alerted us when explosive breeding events occurred, and traps were checked the next day. When capture rates were low, we measured all first-captured

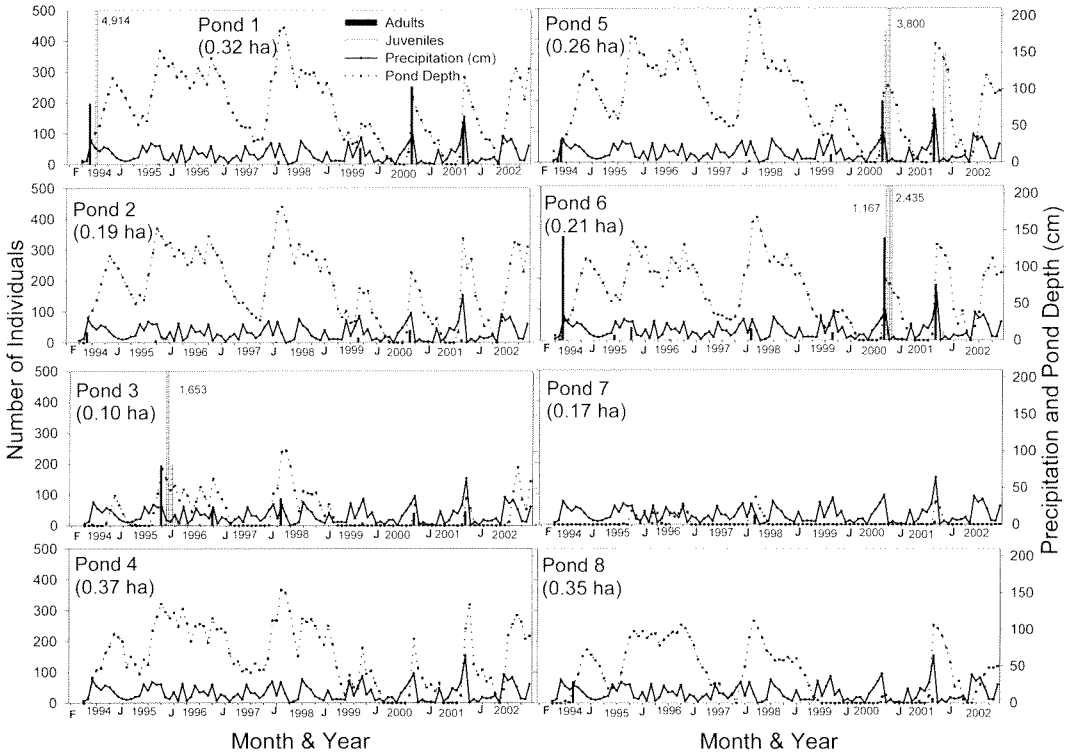

FIG. 1.—Monthly precipitation, pond depth, and total first-captures of adult and metamorphic (≤17 mm SVL) *S. holbrookii* during February (F on x-axis) 1994–January (J on x-axis) 2003 at eight isolated, ephemeral ponds within longleaf pine-wiregrass sandhills, Ocala National Forest, Marion and Putnam Counties, Florida.

individuals and weighed them to the nearest 0.1 g using a hand-held Pesola spring scale, sexed them (except metamorphs), and marked each according to pond number and year of capture by toe clipping. Recaptured animals were (rarely) re-clipped for original pond and year if needed. During breeding events only a subsample (ca. 30 per pond) of adults were measured and weighed, but all were sexed and toe-clipped. Similarly, newly metamorphosed toads were counted, but only a subsample was measured when they emigrated en masse; most were too small (ca. ≤11 mm) to toe-clip. Recaptured toads were not measured. Animals were released on the opposite side of the fence at the point of capture.

We measured water depths weekly beginning in March 1994, and recorded temperature and rainfall daily at 0700 h beginning in April 1994. We used a Global Positioning System (GPS) to estimate distances among ponds.

Statistical Analyses

We used Wright's (2002) cohort classifications to classify individuals, using SVL categories, as <1-yr old "metamorphs" (8.5–17 mm), or "adults", 1–(18–25 mm), 2–(26–37 mm), 3–(38–50 mm) 4–(51–61 mm), 5–(62–72 mm), or 6–(73–83 mm) yr old. For statistical analyses we considered all individuals ≥18 mm as adults (but adults <51 mm were rarely captured, suggesting that they were nonbreeding subadults). Recruits were conservatively defined as the number of metamorphs exiting ponds. We defined a breeding "event" as $n \geq 25$ adults at any single pond during a one-month period, and a breeding "period" as the date of breeding at one or multiple ponds. In all statistical analyses we used only first-captured animals to eliminate potential confusion caused by inclusion of multiple captures of the same individuals.

Because *S. holbrookii* larvae develop rapidly, most breeding events and subsequent recruit-

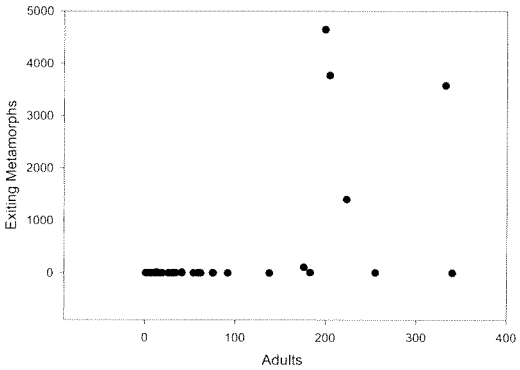

FIG. 2.—Relationship between the total (entering and exiting) number of first-captured *S. holbrookii* adults and number of recruits (exiting metamorphs) from eight isolated, ephemeral ponds during nine years, Ocala National Forest, Marion and Putnam Counties, Florida.

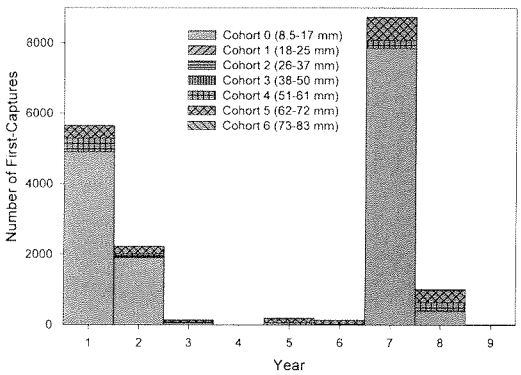

FIG. 3.—Annual size-distribution (%) and population trends of *S. holbrookii* captured annually February 1994–January 2003 at eight isolated, ephemeral ponds, Ocala National Forest, Marion and Putnam Counties, Florida. Size classes correspond with approximate age (years) (Wright, 2002).

ment occurred during the same calendar year. As a result of a 13 October 1995 breeding, metamorphs exited Pond 3 from 6 November 1995 through May 1996 (but most by February 1996). All metamorphs from this breeding event were included with the 1995 data for correlation analysis.

We used Pearson product-moment correlations to examine the relationship between breeding effort by adults ($\geq$18 mm SVL) and the number of recruits ($\leq$17 mm SVL); all pond-years (one year at one pond) with at least one adult capture were included in the analysis. Visual inspection of the data suggested that we use an exponential model in this analysis.

We examined population trends over the 9-yr study period using Pearson's product-moment correlations. Population data for adults were square-root transformed for this analysis. We used paired *t*-tests to compare the arcsine square-root transformed proportion of total (immigrating + emigrating) males to females per pond during breeding events. We considered $P < 0.05$ as statistically significant in our analyses.

RESULTS

Breeding and Recruitment

A total of 23 breeding events by *S. holbrookii* occurred during nine periods (dates) at seven of the eight study ponds (Fig. 1). Most (six of nine) breeding periods occurred during September or October, but breeding also occurred during February, March, and June. Breeding was explosive, with up to 340 adults captured at any given pond within a 1–2 day breeding period, but rarely otherwise (Fig. 1). Breeding occurred at only 1–5 ponds per period, and only during seven of the nine years reported. Breeding events with >175 adults captured occurred in only 1–2 ponds per period, and only during four of the study years. Four of the eight study ponds (Ponds 1, 3, 5, and 6) were used most frequently for breeding, and they produced most (99.8%) of the recruits (Fig. 1).

Most metamorphs (89.5%) were captured emigrating from ponds. Recruitment ranged from 0–4648 among ponds in any given year, and 0–7370 (ponds combined) among years. Most recruitment occurred during 1994, 1995, 2000, and 2001; and then only one or two of the four "productive" ponds (Ponds 1, 3, 5, and 6) produced most of the recruits. The remaining ponds were never used (Pond 4), used once (Ponds 7 and 8), or twice (Pond 2) for breeding, but none resulted in recruitment (Fig. 1). Substantial recruitment ($\geq$100 metamorphs exiting ponds) occurred only five times during the 9-yr period, or after only 22% of breeding events.

TABLE 1.—Total number of same-year and prior-years adult *S. holbrookii* recaptured annually at eight isolated ephemeral ponds, Ocala National Forest, Marion and Putnam counties, Florida.

	Year of first capture											
Recap year	1	2	3	4	5	6	7	8	9	Total 1st cap	Total recap	Percent recap
1	109	0	0	0	0	0	0	0	0	738	109	14.8
2	38	16	0	0	0	0	0	0	0	322	54	16.8
3	4	10	3	0	0	0	0	0	0	79	17	21.5
4	0	0	0	0	0	0	0	0	0	5	0	0
5	1	10	4	1	12	0	0	0	0	189	28	14.8
6	1	0	0	1	1	18	0	0	0	143	21	14.7
7	0	0	2	0	1	19	65	0	0	884	87	9.8
8	0	0	0	0	0	0	3	61	0	618	64	10.4
9	0	0	0	0	0	0	0	0	0	8	0	0
Total	153	36	9	2	14	37	68	61	0	2986	380	12.7

No substantial recruitment (≥100 metamorphs) occurred following any breeding event (at a given pond) where <175 adults were captured, but did following five of the eight breeding events where >175 adults were captured (Figs. 1, 2). A few (1–16) metamorphs exited ponds following 11 other breeding events. We found a significant, exponential relationship between adult breeding effort and recruitment of metamorphs (r^2 = 0.3364; RMSE = 755.36; $F_{1,55}$ = 27.88; P < 0.0001), indicating a threshold for the number of breeding adults, below which recruitment was negligible (Fig. 2). When examining the years separately, however, we found a significant relationship between adult breeding effort and recruitment during 1995 (r^2 = 0.9325; *RMSE* = 135.31; $F_{1,6}$ = 82.84; P < 0.0001), 1996 (r^2 = 0.9646; *RMSE* = 3.79; $F_{1,3}$ = 81.81; P < 0.005), and 2000 (r^2 = 0.5285; *RMSE* = 1261.14; $F_{1,6}$ = 6.73; P = 0.04), but not during other years.

Population Structure and Trends

A total of 2986 individual adult *S. holbrookii* and 15,145 metamorphs was captured; most (97.6%) were captured in pitfall traps. Study-related mortality was 5.3%, and was heaviest for adults due to suffocation by other *S. holbrookii* piled in pitfall traps. We captured significantly more males (57.6%) than females (42.4%) during breeding events (t = –3.52; df = 22; P < 0.005).

Most (83.5%) captured *S. holbrookii* were metamorphs. Most adults were either in the 4 yr old (34.7%) or 5 yr old (62.1%) age classes (Fig. 3). Very few individuals in the smallest age classes (1–3 yr: 2.3%) were found; most of these were captured during nonbreeding periods. Individuals in the oldest cohort (6 yr:

TABLE 2.—Total number of same-pond and other-pond adult *S. holbrookii* recaptured during February 1994–January 2003 at eight isolated ephemeral ponds, Ocala National Forest, Marion and Putnam counties, Florida.

	Pond of origin										
Recap pond	1	2	3	4	5	6	7	8	Total 1st cap	Total recap	Recap (%)
1	64	4	2	0	0	0	0	0	664	70	10.5
2	3	8	1	0	0	0	0	0	123	12	9.8
3	2	6	89	0	0	0	0	0	497	99	19.9
4	0	0	0	1	0	0	0	0	15	1	6.7
5	0	0	0	0	49	0	0	0	505	49	9.7
6	0	0	0	0	0	132	0	0	990	132	13.3
7	0	0	0	0	0	0	2	0	71	2	2.8
8	0	0	0	0	0	0	1	16	121	17	14.0
Total	69	18	92	1	49	132	3	16	2986	380	12.7

0.9%) also were rare; the largest individuals captured were 80 mm SVL (Fig. 3).

We found no consistent relationship between study year and number of adults (≥18 mm) ($F_{1,7} = 0.11$; $P = 0.7493$), indicating that, overall, the population did not increase or decrease during the 9-year study period (Fig. 3).

Multi-year Recaptures and Inter-pond Movement

A total of 12.7% of first-captured adults were recaptured (380 of 2986). Most recaptures occurred during the same year as their original capture (Table 1). However, several individuals were captured ≥2 yr after, indicating that they were at least three years old (because most metamorphs were too small to toe-clip); two individuals were recaptured after five years, and one was recaptured after six years, indicating that *S. holbrookii* can live at least seven years (Table 1).

Most (95%) adult recaptures occurred at the pond where they were first captured (Table 2). Minimal exchange of adults occurred among Ponds 1, 2, and 3 (maximum distance 130 m), and one individual was recaptured at Pond 8, approximately 416 m from Pond 7 where it was originally marked (Table 2). Because most metamorphs were not marked we could not determine whether they used nonnatal ponds for breeding as adults.

Discussion

Our data provide empirical information that can be used in developing realistic metapopulation models for *S. holbrookii*. We found that all ponds were not "created equal" either as breeding sites or as sources of juvenile recruitment. *S. holbrookii* bred in variable numbers among some, but not all seemingly suitable ponds. Among the eight ponds we studied, only half (Ponds 1, 3, 5, and 6) were used frequently, though irregularly, for breeding. Only this subset of ponds functioned as population "sources" (Pulliam, 1988), producing most (99.8%) metamorphs during the 9-year study period. Yet, even the four "source" ponds were sources of recruitment during only one (Ponds 1, 3, and 6) or two (Pond 5) of the nine years studied; they functioned as "sinks" (where breeding resulted in no recruitment) or were not used at all for breeding during the other years. The other ponds functioned either as "sinks," where breeding occurred rarely and in low numbers, but resulted in no recruitment (Ponds 2, 7, and 8), or were never used for breeding (Pond 4). Among-pond differences in breeding and recruitment did not appear related to hydrology, which was similar among most ponds (Greenberg and Tanner, 2004).

Conceptually, a "metapopulation" incorporates at least some dispersal among distinct populations (in this case, ponds) (Hanski and Simberloff, 1997). We found minimal "rescue" (Pulliam, 1988), or dispersal by adults among ponds, and short distances (except once) when it occurred. Yet, the interval between breeding events at a given pond exceeded the apparent lifespan of most individuals (we estimated a maximum lifespan of 7 yr); too long to sustain a viable population if ponds did not receive immigrants from surrounding ponds. For example, large numbers of adults bred at Ponds 5 and 6 in 2000, although the last substantial recruitment occurred sometime before the study began in 1994 (at least 7.5 yr earlier). This incongruity between apparent pond fidelity versus within-pond recruitment intervals that should lead to local extinction, could be because (1) adult *S. holbrookii* are philopatric but live longer than we estimated, (2) adults move among ponds more than we detected, or (3) metamorphs disperse and breed in nonnatal ponds as adults.

Because we did not mark emigrating metamorphs we could not assess their dispersal. Most metamorphs entering ponds were captured during mass exodus events from those ponds, suggesting that they were part of the same recruitment event. However, our data did suggest that some short-distance inter-pond movement occurred (Greenberg and Tanner, 2004). Genetic analyses would shed more light on the metapopulation connectivity among ponds.

Although breeding events were highly synchronized among subsets of ponds during each breeding period, recruitment was not. Breeding effort was an important determinant of recruitment during some, but not all years. Substantial recruitment never occurred when <175 adults were captured during a breeding event at any given pond, suggesting that there may be a critical threshold of breeding effort,

eggs, or tadpoles for substantial survival to metamorphosis to occur. Dodd (1992) reported only one large *S. holbrookii* breeding event in five years at a pond in north-central Florida, but no recruitment. Semlitsch et al. (1996) also reported one successful recruitment of *S. holbrookii* despite repeated breeding events over 16 years in a Carolina Bay in South Carolina.

Recruitment was essentially an "all or none" occurrence. Substantial recruitment occurred following only five of 23 breeding events, and was not spatially or temporally synchronized across the study ponds. Recruitment occurred at only one of eight ponds during three years (1994, 1995, and 2001), and at two ponds during 2000. Other studies have shown that survival of anuran larvae to metamorphosis is affected by numerous factors including water temperature (Gosner and Black, 1955), premature pond-drying, intra- and interspecific competition, predation on eggs or larvae by vertebrate and invertebrate predators, and a complex interplay of predator phenology and prey assemblages (Alford, 1989; Petranka and Kennedy, 1999; Wilbur, 1983, 1987). We suggest that predation on eggs and larvae had a major effect on recruitment success because (1) breeding events were strongly associated with ponds that had recently dried and refilled—one way to avoid high predator densities that may increase with longer hydroperiods, (2) each substantial recruitment occurred only in ponds that had recently dried and refilled prior to breeding events (Greenberg and Tanner, in press), and (3) there was an apparent "minimum threshold" of breeding adults—likely resulting in densities of eggs and larvae that were potentially high enough to "swamp" predators—thereby allowing substantial recruitment to occur. Causes aside, *S. holbrookii* recruitment is clearly heavily subject to stochastic processes. This lack of spatial autocorrelation may have important implications for developing probabilistic models of patch occupancy by amphibians (Knapp et al., 2003; Trenham et al., 2003).

Despite dramatic differences in adult captures and recruitment among ponds and years, the adult population was relatively stable over the life of our study. Sampling over a shorter subset of years, however, might have led us to conclude that the population was declining, or even locally extinct. Our data show that, based on trapping at breeding ponds, perceptions of *S. holbrookii* abundance are heavily biased by weather, pond hydrology (Greenberg and Tanner, 2004), and breeding phenology. In our study, apparent reduced populations of adult *S. holbrookii* during some years clearly reflected suspended breeding activity rather than low densities. The probability that only a portion of the potential adult breeding pool actually breeds during any given breeding event further biases population estimates (Gosner and Black, 1955). In our study, individuals 18–50 mm SVL were rarely captured at ponds; most captured individuals were 51–72 mm SVL, or about 4–5 yr old (Wright, 2002). This indicates that large numbers of juvenile and subadult *S. holbrookii* remain in uplands surrounding ponds for 3–4 years before appearing at ponds for their first breeding at age 4 or 5. Population "reservoirs" that are not detected at breeding ponds thwart accurate estimation of populations and population trends, and may give a misleading impression of among-pond extinctions and recolonizations that have important implications for metapopulation modeling.

Similarly, sampling any subset of our eight study ponds might have left us with a very different impression of *S. holbrookii* breeding and recruitment dynamics. This result illustrates the importance of long-term, landscape-level studies to distinguish natural amphibian population fluctuations, or perceptions of population fluctuations, from true declines (Pechmann and Wilbur, 1994). Even the relatively larger spatial and temporal scope of our study is likely inadequate to capture the true time-landscape complexity of their population dynamics.

Effective amphibian conservation must be built upon metapopulation models that incorporate accurate, empirical knowledge of spatial and temporal population dynamics and species-specific life-history traits that affect persistence at a landscape level. Our study illustrates the potential contribution of each individual wetland, regardless of its proximity to others, as evidenced by wide differences in breeding events and recruitment among ponds, among years within ponds, and by the apparent rarity of long-distance movement or inter-pond "rescues" by adult *S. holbrookii*.

Although we could not track inter-pond movement by metamorphs, it appears likely that they "rescue" local populations by breeding—4 or 5 years later—in nonnatal ponds as adults. Our inability to substantiate that *S. holbrookii* function as metapopulations further emphasizes the importance of conserving multiple wetlands. Closely clustered wetlands would likely increase the likelihood of recruitment success within a landscape neighborhood during at least some years and ponds, and enhance the probability of inter-pond movement. Clusters of ponds that are spaced at varying distances from one another may increase the likelihood of population persistence at a larger scale.

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