In: Proceedings of the 2nd Longleaf Alliance Conference; 1998 November 17-19; Charleston, SC. Longleaf Alliance Report No. 4. Auburn University, AL; Longleaf Alliance: 92-95.

Metapopulation dynamics of amphibians using isolated, ephemeral ponds in longleaf pine uplands of Florida

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ABSTRACT: Several species of southeastern amphibians completely or facultatively depend upon small, ephemeral isolated ponds for reproduction, and inhabit surrounding uplands for much of their adult lives. However, spatio-temporal dynamics of pond use is little known. Since 1994, eight ephemeral ponds embedded within frequently (n=4) or infrequently (n=4) burned longleaf pine uplands in the Ocala National Forest, Florida, have been continuously sampled for herpetofaunal use. Drift fences were spaced to encircle 50% of each pond. Pitfall and funnel traps were positioned to detect directional movement to and from ponds. Breeding attempts and success was highly variable among species, ponds and years. Although patterns cannot be determined in four years, some trends in reproductive output were observed. Some species are produced in enormous quantities every few years, and from a fraction of available ponds (spadefoot toads, *Scaphiopus holbrookii*). Others are produced in moderate numbers more consistently among years and ponds (leopard frogs, *R. utricularia* and Florida gopher frogs, *R. capito*). Yet others produce in smaller numbers every few years, and only from a few of seemingly available ponds. Apparently complex interactions between abiotic factors (weather, hydroperiod), underwater interactions (competition, predation) that vary among ponds, and life history traits result in complex local metapopulation dynamics that differ among species. Clearly, multiple isolated, ephemeral ponds within a landscape may be required to maintain amphibian populations in longleaf pine-wiregrass sandhills.

INTRODUCTION

Several species of southeastern amphibians completely or facultatively depend upon small, ephemeral isolated ponds for reproduction, and inhabit surrounding uplands for much of their adult lives. Isolated pond-dependent species that may be declining within their range include the Florida gopher frog (*Rana capito capito*) and striped newt (*Nothphthalmus perstriatus*), both denizens of the longleaf pine-wiregrass ecosystem.

Seasonally flooded ponds frequently offer protection from predatory fish and reduced numbers of predatory invertebrates. Very small (0.5-1.3ha) ephemeral ponds can produce enormous numbers of juvenile amphibians (Goin 1938; Pechman et al. 1989; Dodd 1992). Since many amphibian species disperse into upland habitats following metamorphosis, one small pond could potentially supply over 1,000 ha of uplands with amphibians (Moler and Franz 1987).

Decades of fire suppression have altered the ecosystem processes by permitting hardwood invasion and consequent decline of the fire-carrying wiregrass understory. A few studies suggest that fire suppression in the longleaf pine ecosystem results in lower herpetofaunal species diversity (Christman and Campbell 1982; Mushinsky 1985). Hardwood invasion of the longleaf pine-wiregrass ecosystem could reduce habitat quality by changing soil moisture or texture, root mass, cover, prey availability, and shade conditions. Tree diversity in surrounding uplands also could affect pond hydrology (Dominique 1998; Vickers et al. 1985), possibly indirectly affecting pond use by amphibians.

Environmental conditions and life history patterns result in high spatio-temporal variability in breeding attempts and success, hence amphibian populations at a local scale (Dodd 1992). Such variability, along with dependence upon ephemeral ponds for breeding, the use of uplands during much of their adult lives, and probable inter-pond colonization makes some amphibian species excellent candidates for studying metapopulation dynamics at a landscape scale. While a few long-term studies at single sites provide vital information on amphibian pond use and life history (eg., Shoop 1965; Dodd 1992), few have continually sampled multitude ponds over several years (Pechman et al. 1989; Dominique 1998).

The objectives of this ongoing study are to: (1) quantify the effects of fire suppression on herpetofaunal use of small, isolated ephemeral ponds situated within an upland sandhills habitat matrix; (2) determine the metapopulation dynamics, or the spatio-temporal dynamics of breeding attempts and success by

amphibians; and (3) obtain information on life histories and habitat requirements of many amphibian species.

METHODS

Since 1994, eight isolated ephemeral ponds < 0.4 ha have been continuously sampled for herpetofaunal use. Four are embedded within frequently burned, savanna-like longleaf pine-wiregrass habitat (SL), and four within infrequently burned, hardwood-invaded longleaf pine uplands (HI) in the Ocala National Forest, Florida. Three of the four ponds within the HI-invaded treatment are surrounded by hardwood invaded sandhills only on three sides. A sand road separates these ponds from SL sandhills on the fourth side. Two ponds in the SL habitat are approximately 9.5 km south of the other six ponds.

Habitat measurements of uplands surrounding study ponds indicated that on average, basal area of hardwoods and sand pine was significantly higher in the HI treatment. Ground cover (primarily wiregrass) was significantly higher in the SL treatment, and leaf litter cover higher in the HI treatment. SL habitat received significantly more light than HI. However, variability in these measurements among plots in the HI habitat was high, indicating that habitat quality was patchy.

Drift fences (7.6-m) are spaced at 7.6-m intervals to encircle 50% of each pond. Pitfall (1.9-liter buckets) and funnel traps are positioned to detect directional movement to and from the ponds. A vertically positioned PVC pipe is placed between each fence.

Traps are checked 3 times weekly. Animals are marked according to pond number and year of capture by toe clipping, and released on the opposite side of the fence from which they were captured. Water depth, air temperature, and rainfall are monitored.

RESULTS

Between 1994 and 1997 pond depths ranged from 0-1.3 meters. Pond depths and hydroperiods were similar among many of the ponds in both treatments. Ponds 1, 2, and 4 in the HI treatment and ponds 5, 6, and 8 in the SL treatment held water continuously from June 1994 through 1997. Each treatment has one very shallow pond (pond 3 in HI and pond 7 in SL) with more frequent and longer periods of dry-down than the others do. Pond levels so far tend to peak in late fall and winter, and reach their lowest levels from March through summer. Rainfall was highest from June through October or so, and lowest in winter and spring.

Between February 1994 and December 1997 over 21,301 (17,808 amphibian and 3,493 reptile) individuals of 50 species of reptiles (32 species) and amphibians (18 species) were captured from eight ponds. There was no significant difference in relative abundance or species richness of amphibians between treatments. Detection of potential differences between treatments may be obscured by the proximity of the treatments, and/or variability of habitat quality within the treatments. Extreme spatio-temporal variability in pond use and production of juveniles may preclude detection as well, in the absence of long term data.

Breeding attempts and success were highly variable among species, ponds, and years. Although patterns cannot be determined in four years, some trends in reproductive output were observed. Some species are produced in enormous quantities every few years and from a fraction of available ponds. For example, in 1994 nearly 5,000 juvenile spadefoot toads emerged from pond 1, but not from any other pond. In 1995 nearly 2,000 spadefoot toads emerged from pond 3, but no others.

Other species were produced in moderate numbers more consistently among years and ponds. Juvenile leopard frogs (*Rana utricularia*) metamorphosed from most ponds in most years, although the quantity varied greatly among seemingly similar ponds within a year, and within ponds among years. Gopher frogs also successfully metamorphosed and emerged in moderate numbers from many ponds in most, but not all years.

Other species produced in small numbers every few years, and only from a few of seemingly available ponds. Juvenile narrowmouth toads (*Gastrophryne carolinensis*) emerged from several ponds in 1994, but not since then. Similarly, oak toads (*Bufo quercicus*) were produced from several ponds only in 1994. Southern toads (*B. terrestris*) were produced from two ponds in 1996, but in no other year thus far.

In some cases, the apparent cause of reproductive failure is self-evident. For example, in 1994, southern toads bred at pond 4 in February and early March. Before the larvae had a chance to metamorphose (larvae require 1-2 months), pond 4 dried up. However, explanations of why breeding attempts are or aren't successful are not always as clear cut. Southern toads bred in moderate numbers at pond 3 in 1996, and moderate numbers of young emerged. They also apparently bred at pond 6, but no young emerged. In both cases the timing of adult breeding attempts was similar, and in neither case did the pond dry up in the interval between breeding and juvenile emergence. Clearly, hydroperiod can be important, but it does not always explain the outcome of reproductive attempts.

Explosive breeding attempts were made by spadefoot toads in 1994 at ponds 1 and 6. Despite similar adult effort on the same date, and similar hydrology (eg., time since most recent dry-down and similar water levels) at both ponds, nearly 5,000 juveniles emerged from pond 1 but none from pond 6 in 1994. Also note that all ponds dried up in spring, 1994, but breeding attempts were made only in these two ponds. In 1995 about 200 adults bred following a dry period in pond 3 and nearly 1,900 juveniles emerged less than a month later.

Gopher frog reproduction is also variable among ponds and years. The number of adults captured is consistently low, suggesting that they trespass fences or escape traps easily. Hence, number of adult captures may not be a valid gauge of adult reproductive effort for this species. In 1994 no juveniles emerged from any pond. In 1995 and 1996 juveniles were captured at most ponds, but the number varied considerably among ponds. Some ponds (ponds 6 and 8) seem to produce more young than others. Virtually no juveniles were produced in 1997, although ponds did not dry up that year.

Most ponds in the study area (both treatments) reached very low water levels in the spring of 1994, and dried up completely in May. A plausible explanation for the absence of young at any pond in 1994 might be that concentrating larvae and their invertebrate predators, and/or the warmer water of shallow ponds affected larval development or survival. However, this explanation does not suffice for all species. For example, the apparent reproductive effort by both leopard frogs and Florida gopher frogs (low captures of both species makes it difficult to gauge reproductive effort, but adults of both species were captured) had quite different outcomes. These two species are in the same genus, and are similar in size. Both tend to breed in winter and early spring. The tadpoles of both require 3-5 months to metamorphose. Despite these similarities, about 220 leopard frog but no gopher frog juveniles emerged from pond 5 in 1994.

Inter-pond and inter-annual differences in breeding attempts and outcomes for the closely related and morphologically similar (except for size) southern and oak toads were also apparent. In 1994 southern toads either did not breed or bred in low numbers at pond 1 from February-June (n=18), but no young emerged. In the same pond, oak toads bred (n=99) in June following the virtual drying, then refilling of the pond and juveniles (n=62) emerged at the end of July.

Reproductive success varied among species breeding in the same pond in the same year, as well. For example narrowmouth toads bred in June, July, and August at Pond 1 in 1994. Juveniles emerged from July through September in small numbers. Reproduction was successful here and at pond 4 but no others, despite the fact that all dried down that year. Conversely (again) spadefoot toads bred on June 23 following a drenching rain, and juveniles emerged three weeks later. Florida gopher frogs did not produce any young at Pond 1 (or any pond) in 1994 despite a (very low) capture rate of adults similar to other years when young were produced. Leopard frog juveniles emerged in low numbers from pond 1 at the end of April and beginning of May. Hence, a single pond may attract breeding attempts by some, but not all species, and produce anything from zero to large numbers of juveniles in a given year.

Only a few instances of inter-pond movement by amphibians have been documented thus far (except for some "spillover" movement among ponds 1-3). One gopher frog traveled from Pond 7 to 8 (ca. 0.4 km),

and one leopard frog from pond 5 to 6 (ca 0.5 km). Most recaptures are individuals returning to the same ponds in the same or different years.

CONCLUSIONS

Data are inconclusive regarding the differences in pond use by amphibians between hardwood invaded versus savanna-like longleaf pine-wiregrass habitat. Greater physical separation between treatments and/or less habitat variability within treatments may be required to detect differences if they exist. In addition, the detection of differences in habitat use by species that exhibit such dramatic spatio-temporal variation in breeding attempts and success clearly necessitates a very long-term data set.

Based on the four years of data, several observations may be made, although caution must be used in ascribing patterns in reproductive attempts and success among species using such a short time frame. Spatial, temporal and specific use of ponds is high. Some species are produced in enormous quantities every few years and only from a fraction of the ponds on the landscape (eg. spadefoot toads). Others seem to be produced more consistently among years and ponds (eg. Leopard frogs and gopher frogs). Still other species are apparently produced in smaller numbers every few years and only from a few ponds on the landscape (eg. Narrowmouth toads, oak toads and southern toads).

The outcome of reproductive attempts is partially affected by timing. Sufficient time for larvae to develop and metamorphose is required, and must coincide with timing of rainfall patterns, hydroperiod, and depth of ponds. However, other, less obvious factors clearly affect reproductive attempts and success, as well. These "mystery factors" include: (1) pond selection by adults for breeding. Only a fraction of apparently similar ponds are selected by a given species during a given year. Morphologically similar species may or may not attempt to breed in a given pond or year. (2) The outcome of attempts may differ dramatically both within and among species, ponds, and years. Apparently complex interactions between abiotic factors (weather, hydroperiod), underwater interactions (competition, predation) that vary among ponds, and life history traits result in complex local metapopulation dynamics that differ among species. Clearly, multiple ponds within a landscape with different filling regimes may be required to maintain amphibian populations.

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