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ECOLOGICAL COMPARISONS OF SOME CLOSELY RELATED SPECIES OF AMPHIBIANS IN LAND BETWEEN THE LAKES AND THE MID–SOUTH

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ABSTRACT

Several closely related species pairs of amphibians occur in or near Land Between The Lakes (LBL) and over much of the Mid–South. From among these, the following were considered in this study: *Ambystoma maculatum/A. opacum, Bufo americanus/B. woodhousii, Pseudacris crucifer/P. feriarum, Hyla cinerea/H. gratiosa*, and *H. chrysoscelis/H. versicolor*. Preliminary observations indicate that the members of many of these species pairs differ geographically with respect to habitat partitioning, especially regarding seasonal activity and microhabitat selection. A number of ecological and environmental factors may account for these differences, including: interspecific competition, predation, and inhibition; vegetative cover; availability of preferred food; temperature; precipitation; pollution; and pH of soil and water. The following topics are discussed with examples from the above–mentioned species: isolating mechanisms and gene flow; interspecific competition, predation, and inhibition; and habitat partitioning, especially regarding breeding cycles, activity cycles, and microhabitat selection. The purpose of this paper is not so much to report on original research, but to suggest areas for future research on all species of amphibians in LBL.

INTRODUCTION

Land Between The Lakes (LBL) is a 68,800–ha peninsula along the western edge of the Highland Rim section of the Interior Low Plateau province (Smalley 1980). Interfacing with it to the west is the Coastal Plain. The area is rich in both flora and fauna, and the distributional boundaries of many species and subspecies occur there. The area's soils, climate, and forest communities were described by Fralish and Crooks (1988, 1989). Located between the Cumberland and Tennessee rivers in Kentucky and Tennessee, LBL has been the focal point of many recent studies conducted in the lower portion of these drainage basins.

In addition to a variety of terrestrial habitats, LBL contains many types of aquatic habitats that are home to a wide array of amphibian species. Many of these habitats have been examined in studies of LBL and the surrounding region. Included among these were mudflats (Webb et al. 1988), small streams (Bear Creek) (Carpenter and Chester 1988), rivers and reservoirs (Webb and Bates 1989), and stream microhabitats (Phillippi and Richter 1989). Other studies focused on all or portions of the herpetofauna of ponds within LBL (Twombly and Scott 1989; Scott 1988, 1989; Figiel et al. 1989).

Several rather closely related pairs of amphibian species occur in or near LBL and also over much of the Mid–South. From among these, the following species pairs were chosen for consideration in this study: *Ambystoma maculatum/A. opacum* (spotted and marbled salamanders), *Bufo americanus/B. woodhousii* (American and Woodhouse's toads), *Pseudacris crucifer/P. feriarum* (spring peeper and upland chorus frog), *Hyla cinerea/H. gratiosa* (green and barking treefrogs), and *H. chrysoscelis/H. versicolor* (Cope's gray and gray treefrogs).

A major problem when studying some of these species involves proper identification because of physical similarities and possible hybridization. Preliminary observations on many of these species indicate that they differ geographically with respect to habitat partitioning, especially regarding seasonal activity and microhabitat selection. A number of ecological and environmental factors may account for these differences, and should be considered in subsequent studies of these species. Some of these factors are: interspecific competition, predation, and inhibition; vegetative cover; availability of preferred food; temperature; precipitation; pollution; and pH of soil and water. In addition, with respect to recent concerns over declining amphibian populations, studies comparing densities of populations in different habitats and years are needed.

RESULTS AND DISCUSSION

Isolating Mechanisms and Gene Flow

While members of the species pairs *H. chrysoscelis/H. versicolor* and *B. americanus/B. woodhousii* can be distinguished in the field by their respective breeding calls, they are sometimes difficult or impossible to recognize visually (Burkett 1989, 1990). In addition, the range of *H. versicolor* still has not been totally determined, owing partially to its more restrictive habits (Burkett 1989).

A major genetic transition in toads occurs at LBL, with the dwarf form *B. a. charlesmithi* occurring toward the north and west, and *B. a. americanus* occurring toward the south and east. Ecological differences, if any, and exact distribution of these two groups in LBL are not known at present. Hybrid toads involving many species pairs have been found, including the American and Fowler's toads. Sullivan (1986) summarized most previous investigations of hybridization within the Bufonidae of the United States and Canada. Calls of populations of Fowler's and American toads at LBL were not analyzed in detail, but sounded quite distinct, especially in terms of call duration and pulse rate. Sullivan (1989) suggested that sympatric congeners may have influenced divergence in dominant frequency of breeding calls among subspecies of *B. woodhousii*. Zweifel (1968) found that some sympatric populations of *B. w. fowleri* and *B. a. americanus* had similar calls, at least in terms of dominant frequency, a fact that could account in part for some of the hybridization between those two species.

Neither member of the species pair *H. cinerea/H. gratiosa* has been collected at LBL, yet both have been found very near there (Redmond 1985, Van Norman and Scott 1987), and a call record of *H. gratiosa* at Energy Lake was logged during this study. Conant and Collins (1991) show records of both species near LBL and in parts of southwestern Tennessee. Therefore, sympatry of this species pair does occur in the Mid–South. While *H. cinerea* tends to breed in permanent water and *H. gratiosa* in more temporary pools, they often use the same breeding sites. These two species are also known to produce fertile hybrids, which may backcross with either species (Schlefer et al. 1986). My preliminary observations indicate that possible hybridization may be occurring at Meeman–Shelby Forest State Park near Memphis, Tennessee.

Interspecific Competition, Predation, and Inhibition

In amphibians, reproductive potential and mating success are related to body size, growth rate, and length of the larval period, and in turn these factors are influenced by competition and predation during larval development (Berven and Gill 1983, Figiel and Semlitsch 1990, John–Alder and Morin 1990). Facultative timing of metamorphosis may be as important as size and growth rate in species breeding in temporary pools or colonizing new, unpredictable aquatic habitats (Semlitsch and Wilbur 1988). Competition among aquatic larvae may occur for food and oxygen, whereas competition among adults is more likely to occur for food, living space, and breeding sites. Chemical inhibition of tadpole growth in crowded conditions was documented in terms of intraspecific and interspecific effects by Licht (1967), but Walls and Jaeger (1989) determined that *A. maculatum* larvae inhibited *A. talpoideum* larvae primarily through more efficient assimilation of prey and/or foraging behavior.

Predation by larvae and adult amphibians upon other amphibian larvae is well–known. *Ambystoma opacum* was observed preying on eggs and/or larvae of *A. maculatum*, *H. versicolor*, and *B. americanus*, and *A. maculatum* was seen feeding on *H. versicolor* (*chrysoscelis*?) tadpoles (Walters 1975). *Bufo a. charlesmithi* was reported eating dead and dying tadpoles of *Pseudacris streckeri* (Black 1969), and possibly other species as well. A number of other predators feed upon the larvae and/or adults of amphibians, including leeches, dragonfly larvae, aquatic spiders, snakes, turtles, birds, and mammals (Burkett 1984). Figiel et al. (1989) found reduced numbers of all amphibian larvae and reduced growth rates of *A. maculatum* larvae in ponds that also contained fish.

One major difference in the tadpoles of *H. cinerea* and *H. gratiosa* is that *cinerea*, like most other permanent pond inhabitants, is relatively unpalatable to some predatory fish, such as bluegill (*Lepomis machrochirus*) (Blouin 1990). However, tadpoles that inhabit temporary pools (e.g., *H. gratiosa*) tend to be more palatable to predators. These differences in palatability were due to genetic factors, as determined by hybridization experiments. Hall and Mulhern (1984) studied heavy metal uptake in amphibians (mostly ranids and bufonids), and concluded that adult amphibians of certain species can accumulate high levels of copper in the liver, possibly becoming toxic to their predators. They also found that tadpoles ingest and accumulate high levels of several metals, to the point of being poisoned themselves. This mechanism may suggest another way in which amphibians become toxic and unpalatable to predators.

Acidic water is often toxic to amphibians, but the ability to survive in acidic conditions varies within and among species, and is another factor of adaptive significance. Pierce and Harvey (1987) reported that tadpoles of adults from acidic ponds were more acid tolerant than those of adults from less acidic ponds. Breeding experiments indicated that the differences were not genetically based; still they believed that population differences may have had some genetic basis. Thus, species composition of each pond community influences the rate of success of each species, not only because of predation and competition, but also due to factors such as density, interspecific inhibition and adaptation to local conditions.

Habitat Partitioning

Perhaps the major mechanism of reducing interspecific competition among these closely related species of amphibians is habitat partitioning in terms of breeding times and breeding sites. Breeding time appears to be most closely linked to a combination of temperature, precipitation, and changing of day (night?) length, and can be easily compared from different localities and seasons to determine the roles of various ecological parameters.

Ambystoma maculatum found along the Wolf River bottoms in Shelby County, Tennessee, normally breeds the last few days of January in temporary rain–filled woodland pools. By contrast, *A. opacum* breeds in autumn and lays terrestrial eggs that do not hatch until covered with water (Conant and Collins 1991). In 1988, the Wolf River pools filled on 19 November. By mid–winter, well–developed *A. opacum* larvae were present and the eggs of *A. maculatum* had not yet hatched. Water did not collect in the area until mid–January or later in other recent years, and *A. opacum* larvae were not found. From 1986 until 1989, breeding of *A. maculatum* occurred before the end of January, but the pools dried by mid–March before any larvae were able to metamorphose. The 1990 breeding season was evidently more successful, as water remained in the pools well into May, and larvae had disappeared from the pools by the end of April. High mortality rates are apparently common in *A. maculatum* and *A. opacum*. Stenhouse (1987) reported that egg mass mortality varied from 0–100%; premetamorphic mortality was as high as 99.89% in *A. maculatum*, and ranged from 64% to 91.18% over two years in *A. opacum* in North Carolina.

During the 1991 breeding period, the Wolf River pools received their first rain on 29 January, but were not deep enough for breeding to occur until 5 February. Although a major portion of the breeding took place on the latter date, the passage of a relatively dry cold front on 13 February left many of the egg masses exposed and covered with ice. Additional warm rains on 15 February resubmerged the eggs. By contrast, in LBL the breeding period usually begins in late January, peaks in February, and diminishes in March, and breeding occurs in permanent or semipermanent ponds, primarily in or at the edge of woodlands (Scott 1989). Recently metamorphosed young leave the ponds during summer and early fall.

A Massachusetts population of *A. maculatum* studied by Stangel (1988) bred in April, first hatched in mid–May, and began dispersing in mid–July, with most dispersal in late August. Many larvae overwintered and metamorphosed the following year, but were significantly smaller than those dispersing in August. Sexton et al. (1990) determined that the most important factor controlling timing of breeding migration in *A. maculatum* was a soil temperature of at least 4.5°C at a depth of 30 cm, when surface temperature was also warmer. Other studies on similar amphibian communities indicate that temperature plays a dominant role in activity and breeding of several species. Werner and McCune (1979) reported that activity of several species in a northern Michigan pond varied from mid–May until late August. *Pseudacris crucifer*, *R. sylvatica*, and *B. americanus* were mostly active in May, *R. clamitans* and *R. septentrionalis* in June and July, and newly metamorphosed *R. clamitans* were particularly abundant in August.

Bufo americanus and *B. woodhousii* often can be found in the same habitat, but generally breed at different times and in different locations. Table 1 lists sequential dates on which aggregations of frogs were heard calling during this study. At LBL, *B. americanus* tends to breed in small ponds or temporary streams, with the peak of

Table 1. Sequential dates on which assorted aggregations of frog species were heard calling at various locations in the Mid-South.

Species aggregations	Dates
Tennessee	
Shelby County	
Pseudacris feriarum	13-16 Feb.1980—1990 29 Jan—1 Apr1991
P. crucifer, P. feriarum	5 Feb 1991
P. feriarum, Rana utricularia	24 Feb.1991
Bufo woodhousii	11 Mar 1990 6 April-25 Jun 1991 28–29 Aug 1991
P. crucifer	28 Apr 1990
Acris crepitans, B. woodhousii, R. catesbeiana, Hyla cinerea, H. chrysoscelis	12 May 1990
H. cinerea	30 Jun 1988
A. crepitans, H. cinerea, H. chrysoscelis, Gastrophryne carolinensis	23 Jun 1989
Stewart County	
A. crepitans, R. catesbeiana	4-5 Jun 1988
A. crepitans	2-3 Jul 1988
H. chrysoscelis, A. crepitans, G. carolinensis	9 Jul 1988
Tipton County	
H. chrysoscelis, H. versicolor	4–5 Jun 1989
Kentucky	
Trigg County	
B. woodhousii, H. chrysoscelis, H. gratiosa, R. catesbeiana, R. clamitans, R. utricularia, A. crepitans	17 Jun 1989
P. crucifer	14 Mar 1990
B. woodhousii, H. chrysoscelis, H. gratiosa, R. catesbeiana, A. crepitans	18 May 1990
Lyon County	
B. americanus, R. utricularia, P. crucifer	14 Mar 1990

activity in March and April, while *B. woodhousii* breeds in larger, more permanent aquatic sites, mostly from late April through July. By contrast, *B. woodhousii* in Shelby County have been heard most often in temporary rain pools in March and April. At LBL (Lyon County, Kentucky) I recorded *B. americanus* calling only on 14 March 1990, while *B. woodhousii* was recorded several times between 29 April and 17 June 1989 and 1990. In Shelby County, Tennessee, where *B. americanus* was not recorded, *B. woodhousii* was heard in both March and April.

The most unusual example of habitat partitioning that I have witnessed concerning these two species was on 20–21 April 1990, in Winston County, Alabama, at Brushy Creek campground. At dusk, choruses of *Acris crepitans* and *Pseudacris crucifer* were calling from around the lake. Then *Rana catesbeiana*, *R. clamitans*, and *B. woodhousii* joined in. I heard *B. woodhousii* call until 1:00 a.m., then drifted into a light sleep. At 1:30 a.m. I awoke to the calls of *B. americanus*, which continued until dawn. At least on that one night, a total temporal replacement of breeding calls of one toad species by another had occurred. A month later in nearby Lawrence County, in the Sipsey Wilderness, choruses of *R. catesbeiana*, *R. clamitans*, *R. utricularia*, and *B. woodhousii* called regularly all night long, and were occasionally joined by *H. chrysoscelis*.

My observations on the species pair *P. crucifer/P. feriarum* indicate that their breeding seasons often overlap, but the preferred habitat is different in that *P. crucifer* prefers more permanent ponds or lakes, while *P. feriarum* prefers temporary rain pools. Both species begin calling after rains in late winter in the Mid–South, but *P. crucifer* may continue calling until later in spring. The microhabitat for specific calling sites is also quite different for this species pair; *P. crucifer* usually calls from low branches of shrubby vegetation or the water's edge, while *P. feriarum* calls from within the water.

Rapid metamorphosis and growth rates are selectively advantageous to amphibian species, especially inhabitants of temporary ponds. Those species having behavioral adaptations toward congregating in warmer, shallow water, also have an advantage of more rapid growth and development over species that remain in cooler water. However, Black (1969) observed many aggregations of toad tadpoles that appeared to be socially rather than thermally controlled, and that during the low water stage aggregations in deeper depressions of temporary pools often survived. Stangel (1988) summarized data on premetamorphic survival of many species of pond breeding amphibians and found almost all to be below 4%. All species at LBL require further study of their larval development to determine specific patterns for each type of habitat.

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