Amphibian and Reptile Communities Associated with Beaver (*Castor canadensis*) Ponds and Unimpounded Streams in the Piedmont of South Carolina

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ABSTRACT

We used drift fence arrays with pitfall traps to compare amphibian and reptile assemblages at the peripheries of beaver (*Castor canadensis*) ponds of two age-classes ("new": ≤ 5 yr old, and "old": ≥ 10 yr old) and unimpounded streams in the Piedmont of South Carolina. The richness and total abundance of amphibians were not significantly different among new beaver ponds, old beaver ponds, and unimpounded streams, although several species of anurans were captured predominantly or exclusively at beaver ponds. Amphibian community overlap and diversity also were similar among the three habitats. In contrast, the richness and total abundance of reptiles were significantly higher at old beaver ponds when compared to new beaver ponds and unimpounded streams. The degree of reptile community overlap also was relatively low, with significant differences in diversity among all three habitats. Differences in amphibian and reptile community attributes between beaver ponds and unimpounded streams likely were related to the lentic or lotic habitat requirements of individual species and the effects of beaver impoundments on surrounding upland habitats.

INTRODUCTION

Beavers (*Castor canadensis*) are among the few animals with the ability to substantially modify habitats and even entire landscapes to suit their needs (Grasse 1951, Hill 1982, Johnston and Naiman 1990). Beaver impoundment of free-flowing streams significantly modifies several ecosystem processes (Snodgrass and Meffe 1998), including the availability, cycling, and transport of nutrients, decomposition dynamics, water characteristics, and the diversity of both aquatic and terrestrial habitats (Hodkinson 1975, Edwards and Guynn 1984, Naiman et al. 1986, Johnston and Naiman 1990, Smith et al. 1991, Yavitt et al. 1992, Snodgrass 1997, Klotz 1998, Snodgrass and Meffe 1998). The dam-building activities of beavers also influence the composition of aquatic and terrestrial animal communities (Snodgrass 1997). Several studies have documented that beaver ponds and/or the peripheral upland habitats altered by impoundment support more diverse communities of invertebrates, fishes, waterfowl, non-game birds, and mammals when compared to unimpounded streams (Beard 1953, Neff 1957, Hanson and Campbell 1963, Pullen 1971, Reese and Hair 1976, Lochmiller 1979, Webster et al. 1985, Clifford et al. 1993, McCall et al. 1996, Snodgrass and Meffe 1998). However, little is known about the impacts of beaver impoundments on communities of amphibians and reptiles (herpetofauna). Additionally, most studies of beaver pond ecology have been conducted in northern latitudes (> 35° N), although the historical range of *C. canadensis* encompasses most of North America (Hill 1982, Snodgrass and Meffe 1998). Our objective was to survey and compare the herpetofaunal assemblages inhabiting the margins of beaver ponds and unimpounded streams in the Piedmont of South Carolina.

METHODS

Study Area and Sampling Sites

We conducted the study on the 7,024-ha Clemson University Experimental Forest (CUEF) in Anderson, Pickens, and Oconee Counties in the Piedmont of South Carolina. The CUEF is characterized by moderately rolling hills with elevations to 305 m above sea level. Streams on and adjacent to the CUEF drain into Lake Hartwell, a 22,640-ha reservoir, and numerous beaver colonies exist on these streams (Davis and Guynn 1993). With the exception of occasional trapping to reduce flooding of timber, beavers are not actively managed on the CUEF and no commercial or recreational trapping is allowed. Dominant overstory vegetation on the CUEF consists of managed, multi-aged stands of pine, hardwood, and pine-hardwood mixtures (Moorman et al. 1999).

From within the CUEF, we selected two beaver ponds in each of two age categories, ≤ 5 years old ("new ponds") and ≥ 10 years old ("old ponds"). The two old ponds were approximately 1.2 ha in size and 1.5 m deep; each was created by a single long dam (25-35 m) and supported abundant submersed and emergent vegetation. Both new ponds were approximately 0.5 ha in size and 0.5-1 m deep; they were created by a series of three to four narrow (4-8 m) dams and supported little submersed or emergent vegetation. The average zone of influence (i.e., the degree of flooding and upland vegetation removal) of beavers at old ponds extended 35 m from the edge of permanent water and was significantly greater than the zone of influence (27 m) at new ponds (Edwards and Guynn 1984). We also selected two unimpounded streams, each similar to beaver ponds with respect to topography and surrounding upland vegetation, as control sites. A closed canopy of mixed-mesophytic hardwood species bordered each stream.

Herpetofaunal Sampling

We installed 10 linear drift fences with pitfall traps (Gibbons and Semlitsch 1981) at the periphery of each pond and stream, just above the anticipated high-water mark. The fences, spaced at regular intervals around each pond and at 10-m intervals along each stream, were 5 m long, constructed of 60 cm high aluminum flashing supported with wood stakes and buried at least 10 cm in the ground. Pitfall traps (19-L buckets) were sunk to ground level and were flush with the ends of each side of the fence (four buckets/fence). Moist sponges were placed in the buckets to prevent desiccation of herpetofauna. We operated drift fences simultaneously at each of the six sites for five consecutive days each month from November 1981 through October 1982, excluding January and February. All herpetofauna captured were identified to species and released on the opposite side of the fence from which they were captured. Taxonomy for all species was updated to follow Conant and Collins (1998).

Analyses

We determined differences in the total richness and abundance of amphibians and reptiles among streams, new ponds, and old ponds using a completely randomized, one-way analysis of variance (ANOVA; SAS Institute 1995). When the ANOVA yielded a significant F-statistic, we used Tukey's honestly significant difference (HSD) to identify significant differences among means. We used the Sorenson Coefficient of Community Similarity (CC_S; Brower et al. 1998) to estimate the degree of community overlap (i.e., the number of shared species) among the three habitats. We also calculated the Shannon diversity index (H') for amphibian and reptile communities within each of the three aquatic habitats and used Student's t-tests to determine significant differences in community diversity between beaver ponds and unimpounded streams (Brower et al. 1998). Statistical significance was accepted at $\alpha \leq 0.05$ for all tests.

RESULTS

Amphibians

A total of 20 species of amphibians was captured from all three aquatic habitats combined (Table 1). The species richness of amphibians was not significantly different ($F = 4.78$, $df = 5$, $p = 0.117$) among unimpounded streams, new beaver ponds, and old beaver ponds. Similarly, the Sorenson Coefficient of Community Similarity indicated a high degree of community overlap among all three aquatic habitats (Table 2), but with the greatest degree of overlap between new ponds and old ponds and the lowest overlap between new ponds and unimpounded streams. According to the Shannon diversity index, amphibian species diversity was highest at unimpounded streams, intermediate at old beaver ponds, and lowest at new beaver ponds (Fig. 1). However, significant differences in diversity were detected only between unimpounded streams and new beaver ponds (unpaired $t = 2.07$, $df = 2962$, $p < 0.05$).

A total of 466 amphibians was captured from the three aquatic habitats combined (Table 1). *Rana clamitans* (bronze frog) was the numerically dominant species and comprised 28% of all amphibian captures, followed by *Bufo americanus* (American toad; 14%), *Rana utricularia* (southern leopard frog; 12%), and *Rana catesbeiana* (bullfrog; 9%). Although more amphibians, particularly anurans, were captured at old beaver ponds than at either new ponds or unimpounded streams (Table 1), these differences were not significant ($F = 0.925$, $df = 5$, $p = 0.486$).

Reptiles

A total of 18 species of reptiles was captured from the three aquatic habitats combined (Table 1). We captured significantly ($F = 91.5$, $df = 5$, $p = 0.002$) more species of reptiles at old beaver ponds than at new beaver ponds or unimpounded streams. The Sorenson Coefficient of Community Similarity indicated a relatively low degree of reptile community overlap among all three habitats (Table 2), but with the lowest degree of overlap between new ponds and unimpounded streams. Reptile species diversity was highest at old beaver ponds, intermediate at new beaver ponds, and lowest at unimpounded streams (Fig. 1). Significant differences ($p < 0.05$) in reptile diversity were detected among all three habitats (streams vs. new ponds:

Table 1. The pooled species and numbers of amphibians and reptiles captured from the periphery of unimpounded streams (n = 2), and new (≤ 5 years old; n = 2) and old (≥ 10 years old; n = 2) ponds created by beavers (*Castor canadensis*) on the Clemson University Experimental Forest (CUEF), in the Piedmont of South Carolina. Numbers in parentheses indicate totals for each site.

Species	Streams	New Ponds	Old Ponds	Total
AMPHIBIANS				
Salamanders				
Desmognathus fuscus	14	4	3	21
Desmognathus ochrophaeus	3	1	1	5
Desmognathus quadramaculatus	1	0	0	1
Eurycea bislineata	8	6	1	15
Eurycea longicauda	2	6	7	15
Gyrinophilus porphyriticus	0	2	0	2
Notophthalmus viridescens	0	0	12	12
Plethodon glutinosus	6	2	3	11
Pseudotriton montanus	0	0	9	9
Pseudotriton ruber	1	0	1	2
Anurans				
Acris crepitans	0	11	10	21
Bufo americanus	0	9	55	64
Bufo woodhousii	7	7	3	17
Gastrophryne carolinensis	1	2	13	16
Pseudacris crucifer	4	0	12	16
Pseudacris triseriata	1	0	0	1
Rana catesbeiana	4	33	4	41
Rana clamitans	13	49	70	132
Rana palustris	0	0	9	9
Rana utricularia	0	40	16	56
Total Amphibians	65 (38/27)	172 (141/31)	229 (165/64)	466
REPTILES				
Turtles				
Chelydra serpentina	0	0	1	1
Chrysemys picta	0	1	2	3
Kinosternon subrubrum	0	0	2	2
Sternotherus odoratus	0	0	3	3
Terrapene carolina	3	1	3	7
Lizards				
Anolis carolinensis	2	0	4	6
Cnemidophorus sexlineatus	0	0	1	1
Eumeces inexpectatus	0	1	2	3
Eumeces laticeps	1	0	1	2
Sceloporus undulatus	0	0	9	9
Scincella lateralis	1	1	2	4
Snakes				
Carphophis amoenus	0	1	3	4
Diadophis punctatus	0	0	1	1
Nerodia sipedon	0	1	0	1
Opheodrys aestivus	0	1	0	1
Storeria dekayi	0	1	0	1
Storeria occipitomaculata	1	0	1	2
Thamnophis sirtalis	0	0	1	1
Total Reptiles	8 (3/5)	8 (4/4)	36 (17/19)	52
Grand Total	**73**	**180**	**265**	**517**

unpaired t = 3.45, df = 2135; streams vs. old ponds: unpaired t = 4.56, df = 3524; new ponds vs. old ponds: unpaired t = 3.02, df = 1435).

A total of 52 reptiles was captured from unimpounded streams and beaver ponds combined (Table 1). *Sceloporus undulatus* (eastern fence lizard) was the numerically dominant species and comprised 17% of all reptile captures, followed by *Terrapene carolina* (eastern box turtle; 13%), *Anolis carolinensis* (green anole; 12%), *Scincella lateralis* (ground skink; 8%), and *Carphophis amoenus* (eastern worm snake; 8%). Significant differences (F = 98.0, df = 5, p = 0.001) were detected in the total abundance of reptiles among the three habitats, with significantly more reptiles captured at old beaver ponds than at new beaver ponds or unimpounded streams.

Table 2. Sorenson Coefficient of Community Similarity (CC_S) for amphibian and reptile communities from the periphery of unimpounded streams (n = 2), and new (≤ 5 years old; n = 2) and old (≥ 10 years old; n = 2) ponds created by beavers (*Castor canadensis*) on the Clemson University Experimental Forest (CUEF), in the Piedmont of South Carolina. Values closer to 1.0 indicate greater community similarity between habitats.

	Streams	New Ponds
Amphibians		
New Ponds	0.692	
Old Ponds	0.733	0.800
Reptiles		
New Ponds	0.307	
Old Ponds	0.500	0.435

DISCUSSION

Impoundment of streams by beavers apparently had little influence on the species richness or composition of amphibians within the CUEF. Likewise, we also failed to detect significant differences in the total abundance of amphibians among unimpounded streams, new beaver ponds, and old beaver ponds. The latter is at least partially related, however, to the large among-site (within-habitat) variability of amphibian captures at both new and old beaver ponds. Such variation probably is related to local differences in vegetation, hydrology, topography, or other habitat features at individual ponds (Edwards and Guynn 1984, Davis and Guynn 1993, Snodgrass and Meffe 1998). When individual sites are pooled, several species of relatively abundant anurans including *Acris crepitans* (northern cricket frog), *Bufo americanus*, *Rana catesbeiana*, *R..clamitans*, and *R. utricularia*, as well as the salamander *Notophthalmus viridescens* (red-spotted newt) were captured predominantly or exclusively along the margins of beaver ponds. In contrast, *Desmognathus fuscus* (northern dusky salamander) was captured most frequently from the periphery of unimpounded streams. The dominance of a few species of amphibians at beaver ponds is reflected in the lower estimates of community diversity at these sites when compared to unimpounded streams (Brower et al. 1998).

Differences in the abundance of some amphibians between beaver ponds and unimpounded streams are related to species-specific life history traits and habitat preferences. Although *A. crepitans*, *B. americanus*, and *R. clamitans* may opportunistically use a variety of aquatic habitats for reproduction, these species typically are most abundant along the grassy, open margins of ponds, marshes, and ditches (Martof et al. 1980, Conant and Collins 1998). In contrast, *D. fuscus* is associated with small free-flowing streams, brooks, and springs but usually is absent from large, slow-moving streams and lentic ponds where predatory fish may occur (Martof et al. 1980, Conant and Collins 1998). Thus, the availability as well as the variability of freshwater lentic habitats that result from beaver impoundments likely are important determinants of amphibian biodiversity both within the CUEF and across the southeastern Piedmont.

The relatively high richness but low abundance of reptiles partially is attributable to biases associated with drift fence sampling. In particular, many species of lizards and large snakes escape from pitfall traps and crawl over drift fences (Gibbons and Semlitsch 1981, Greenberg et al. 1996). Also, because our drift fences were installed at the terrestrial margins of ponds and streams, we likely underestimated the abundance of aquatic turtles (Gibbons and Semlitsch 1981).

Despite these sampling biases, the significantly greater richness, abundance, and diversity of reptiles that we detected at old beaver ponds likely are an accurate reflection of reptile community composition both within the CUEF and across the South Carolina Piedmont (Martof et al. 1980). Although *Sternotherus odoratus* (common musk turtle), *Chrysemys picta* (painted turtle), *Kinosternon subrubrum* (eastern mud turtle), and several other species of turtles may occur along the margins of streams (Martof et al. 1980, Mitchell 1994, Kellison et al. 1998), preferred habitats for these species are shallow, slow-moving or standing water with abundant

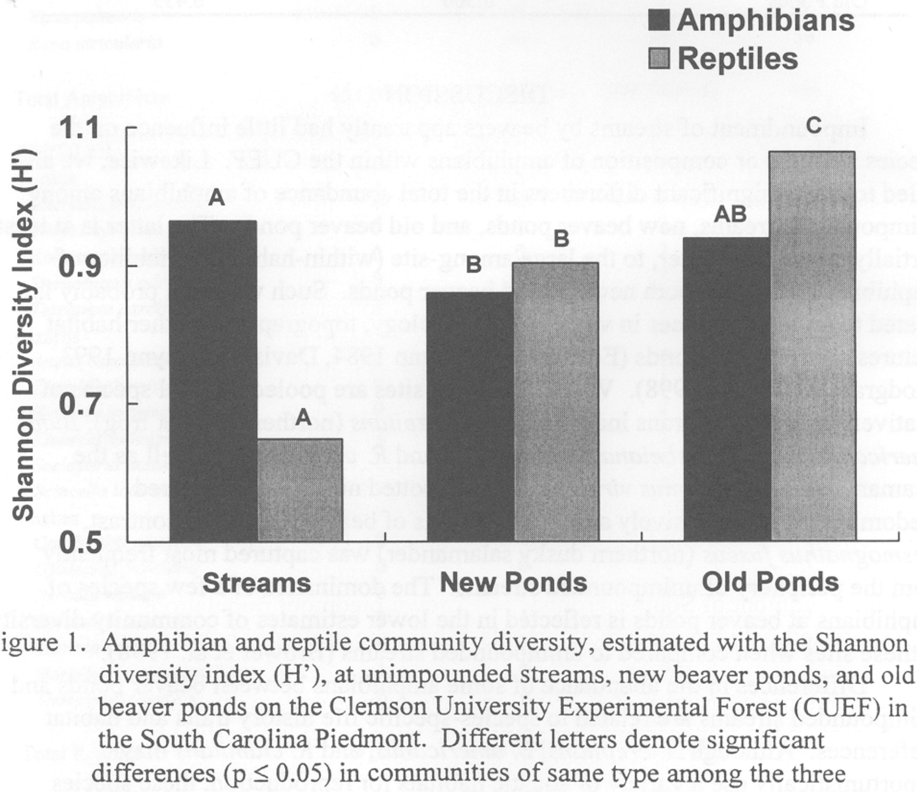

Figure 1. Amphibian and reptile community diversity, estimated with the Shannon diversity index (H'), at unimpounded streams, new beaver ponds, and old beaver ponds on the Clemson University Experimental Forest (CUEF) in the South Carolina Piedmont. Different letters denote significant differences ($p \leq 0.05$) in communities of same type among the three habitats.

submersed and emergent vegetation and soft organic substrates (Ernst et al. 1994, Mitchell 1994). Additionally, these species hibernate in similar aquatic habitats under logs, stumps, and in the lodges of beavers and muskrats (Mitchell 1994), and *C. picta* requires floating logs or other emergent substrates for thermoregulatory basking (Ernst et al. 1994, Mitchell 1994). Accordingly, in our study all captures of *C. picta*, *K. subrubrum*, and *S. odoratus* occurred along the margins of old beaver ponds where submersed and emergent vegetation, standing water, soft organic substrates, and floating logs were abundant (Edwards and Guynn 1984). Among turtles, only *Terrapene carolina* was captured at unimpounded streams and new beaver ponds. However, *T. carolina* is a largely terrestrial and wide-ranging species that enters water only temporally for hibernation, drinking, or dispersal (Ernst et al. 1994, Mitchell 1994).

The greater abundance and diversity of reptiles at old beaver ponds also may be related to the association of many species of lizards (e.g., *Sceloporus undulatus*) with early-successional habitats (Mitchell 1994, Conant and Collins 1998). The degree of habitat alteration (i.e., zone of influence) surrounding beaver impoundments is related to the distance that beavers must travel to obtain foraging and dam construction materials. Over time, as trees near the water are consumed, feeding must occur farther away from the edge of permanent water. Thus, the zone of influence in the upland stands surrounding beaver ponds is positively correlated with pond age (Edwards and Guynn 1984). The greater amount of early-successional terrestrial habitat surrounding old ponds may explain the increased richness and abundance of lizards at these sites when compared to more recently created impoundments and free-flowing streams with closed canopies.

Beavers were nearly extirpated from South Carolina and other southeastern states by the early 1900's but have reoccupied much of their former range during the last 40 years due in part to an aggressive reintroduction program coupled with restrictions on trapping (Hill 1982, Webster et al. 1985). Increasing beaver populations have increased habitat diversity across southeastern landscapes, leading to increased diversity of many plant and animal species (Snodgrass 1997). Expanding populations of beavers likely have directly benefited herpetofauna in the Piedmont of South Carolina. Early surveys of herpetofauna in the region indicated that *K. subrubrum* and *S. odoratus* were scarce or absent (Pickens 1927, Bruce 1965, Martof et al. 1980), although both species now appear to be abundant (Platt et al. 1999). Whether the lack of early records indicates a real increase in the abundance of these species or the sampling biases of earlier surveys remains unclear (Platt et al. 1999), but it is likely that the increased availability of beaver-created lentic habitats over the last 40 years has benefited these and other species of Piedmont herpetofauna. Additionally, Snyder and Platt (1997) and Platt et al. (1999) documented a recent range expansion of *Hyla cinerea* (green treefrog) from the Coastal Plain into the southern Piedmont of South Carolina. All known piedmont populations of *H. cinerea* are associated with beaver impoundments, where the preferred habitat features of this species (e.g., floating and emergent vegetation along the swampy edges of ponds, lakes, and marshes; Martof et al. 1980) are abundant. Because most alluvial floodplains in the southeastern Piedmont have been heavily modified by hydroelectric dam construction and decades of sedimentation from agricultural runoff (Martof et al. 1980, Kellison et al. 1998), beaver-created wetlands can be expected to play an increasingly important role in maintaining historical patterns of herpetofaunal distribution and abundance within the region.

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