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BAT RESPONSE TO CAROLINA BAYS AND WETLAND RESTORATION IN THE SOUTHEASTERN U.S. COASTAL PLAIN

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Abstract: Bat activity in the southeastern United States is concentrated over riparian areas and wetland habitats. The restoration and creation of wetlands for mitigation purposes is becoming common in the Southeast. Understanding the effects of these restoration efforts on wetland flora and fauna is thus becoming increasingly important. Because bats (Order: Chiroptera) consist of many species that are of conservation concern and are commonly associated with wetland and riparian habitats in the Southeast (making them a good general indicator for the condition of wetland habitats), we monitored bat activity over restored and reference Carolina bays surrounded by pine savanna (*Pinus* spp.) or mixed pine-hardwood habitat types at the Savannah River Site in South Carolina. In order to determine how wetland restoration efforts affected the bat community, we monitored bat activity above drained Carolina bays pre- and post-restoration. Our results indicate that bat activity was greater over reference (i.e., undrained) than drained bays prior to the restorative efforts. One year following combined hydrologic and vegetation treatment, however, bat activity was generally greater over restored than reference bays. Bat activity was also greater over both reference and restored bays than in random, forested interior locations. We found significantly more bat activity after restoration than prior to restoration for all but one species in the treatment bays, suggesting that Carolina bay restoration can have almost immediate positive impacts on bat activity.

Key Words: bat activity, Carolina bay, mixed pine-hardwood, pine savanna, Savannah River Site, timber harvest, wetland restoration

INTRODUCTION

During the 20th century, more than half of the wetlands in the United States were drained for agricultural use, forestry, or development (Mitsch and Gosselink 1993). Within the Atlantic Coastal Plain of the southeastern United States, the reduction of one wetland type, Carolina bays, has been particularly severe (Sharitz 2003). Carolina bays are isolated, elliptically-shaped, shallow wetlands of uncertain geologic origin that range in size from 1 to 3,600 ha and that commonly contain either woody or emergent vegetation (Wharton 1978, Savage 1982, Sharitz 2003). Found along the lower and interior portions of the Atlantic Coastal Plain from Maryland to Florida, Carolina bays are most numerous in South Carolina, Georgia, and North Carolina. Bennett and Nelson (1991) found that approximately 80% of the 2,651,500 mineral soil Carolina bays surveyed had been substantially impacted by anthropogenic disturbance. At the Savannah River Site (SRS) in South Carolina, Kirkman et al. (1996) showed that at least 66% of the approximately 300 Carolina bays on site had been disturbed by either draining or ditching.

Carolina bays are important regional biodiversity hotspots for many organisms, including several rare species of plants (Knox and Sharitz 1990), microcrustaceans and macroinvertebrates (Krajick 1997), and many amphibian and reptile species (Plummer and Congdon 1994, Semlitsch et al. 1996). Because of the ephemeral nature of Carolina bays and their relative isolation from other water sources, these wetlands are extremely important for wildlife on a local landscape scale. Based in part on the important roles that Carolina bays play in the life cycle of many wildlife species, these bays are currently the focus of an intensive restoration and adaptive management study at the SRS. There, natural resource managers are restoring the numerous area bays that were ditched and drained for agriculture prior to governmental acquisition of the site in the early 1950s. Not surprisingly, this offers opportunities to address ecological questions that are critical for future Carolina bay restoration and management relating to wetland restoration responses from area flora and faunal communities.

Bat feeding and commuting activity is generally concentrated in riverine and lacustrine habitats in temperate and subtropical regions of the world (Grindal et al. 1999, Ciechanowski 2002, Menzel et al. 2005). For example, Wilhide et al. (1998) captured nine bat species, including two species that are federally endangered (Indiana bat, *Myotis sodalis* Miller and Allen and gray bat, *M. grisescens* Howell) and one species of special concern (small-footed myotis, *M. leibii* Audubon and Bachman), in nets placed over water-filled road ruts and small wildlife ponds in Arkansas. This aspect of bat foraging ecology suggests that, prior to being drained, wetland habitats such as Carolina bays probably provided very important foraging habitat for bats in the Atlantic Coastal Plain of the southeastern United States.

Recent studies have also shown that riparian areas in forested environments often serve as important foraging habitat for bats. Menzel (1998) found greater levels of flight and foraging activity around Carolina bays than any other habitat type monitored. Additionally, Law and Chidel (2002) recently compared bat activity in unlogged and regrowth forests in Australia and found that bat activity was greatest in forested tracts and riparian zones. Nonetheless, there is a paucity of quantitative information concerning the importance of aquatic systems to bats in the southeastern United States. Although descriptive studies suggest that wetland habitats are important to bats in the Southeast, none have incorporated robust manipulative experimental designs with pre- and post-treatment sampling. We used a ''before and after control impact'' design (BACI) to assess bat response to restoration efforts in Carolina bays. Our objectives were to (1) determine the level of bat foraging activity above Carolina bays relative to upland habitats without bays; (2) determine if the level of bat activity over restored Carolina bays differs from activity levels over natural, undisturbed Carolina bays; and (3) determine if the type of habitat surrounding restored Carolina bays affects bat activity and species composition of bats foraging over the Carolina bays.

STUDY AREA

We conducted our study on the Department of Energy's 80,000-ha Savannah River Site located in Aiken, Barnwell, and Allendale counties in the Upper Coastal Plain physiographic province of west-central South Carolina. The SRS, located approximately 20 km southeast of Augusta, Georgia, was established in 1950 as a nuclear materials production facility. In 1972, the SRS was designated as the United State's first National Environmental Research Park. Approximately 90% (69,200 ha) of the SRS is forested (Workman and McLeod 1990). Although forest types on the SRS include bottomland hardwoods (approximately 12,000 ha), upland hardwoods (approximately 3,000 ha), and pine/hardwood communities (approximately 4,000 ha), the forested areas on the SRS consist predominately of loblolly (*Pinus taeda* L.), longleaf (*P. palustris* P. Mill.), and slash pine (*P. elliotii* Engelman.) forests (approximately 50,000 ha; Workman and McLeod 1990). Aquatic habitats such as ponds, marshes, and Carolina bays are common throughout the site (Workman and McLeod 1990). Much of the upland pine areas on the SRS are managed under plantation silviculture systems. The SRS has a warm-temperate to subtropical climate, with an average summer and winter air temperature of 27 and 9 °C, respectively, and an average annual rainfall of 120 cm (Workman and McLeod 1990, Menzel 2003).

METHODS

The Carolina bay restoration project at the SRS (Barton et al. 2004) has incorporated wetlands that were ditched and drained >50 years ago and had developed mixed forests of upland trees, primarily loblolly pine and sweetgum (*Liquidambar styraciflua* L.), within the bays. Restoration activities, which occurred during the fall and winter of 2000, involved removing the upland forest and closing the drainage ditch with an earthen plug. Additionally, the upland margins surrounding the bays (within a 100-m radius from the wetland boundary) were managed for one of two habitat types − mixed pine-hardwood and fire-maintained pine savanna. The mixed pine-hardwood margins consisted of a closed canopy forest dominated by loblolly pine and sweetgum, from which fire was excluded. In the pine savanna margins, hardwoods were removed and pines were selectively thinned to an open pine savanna structure managed by frequent prescribed fire resulting in a forest condition that is thought to more closely mimic pre-settlement upland forest conditions (Van Lear and Harlow 2002).

We acoustically monitored bats in three restored Carolina bays (hereafter, treatment bays) within each of the two upland margin treatments (i.e., three restored bays surrounded by a mixed pine-hardwood margin and three surrounded by an open pine savanna). We also monitored bats at six undisturbed bays (hereafter, reference bays) that had not been ditched and drained in the past and that remained functional emergent wetlands. These bays were dominated by herbaceous species, including maidencane (*Panicum hemitomon* Schult.) and southern cut grass (*Leersia hexandra* Swartz). To approximate the vegetative margins of the treatment bays, we selected three reference bays surrounded by open-canopy pine forest and three surrounded by closed-canopy, mixed pine-hardwood forest. All Carolina bays were approximately the same size (0.5–1.5 ha) to standardize the surface area of the bays and ranged a distance of 1.6 to 16.1 km from one another. Finally, we monitored bats at three locations in mature upland pine forest interior, distant (approximately 3.2 km) from any wetland (hereafter, interior forest). Thus, our design included 15 sites (three each of pine savanna treatment, mixed pine-hardwood treatment, pine savanna reference, mixed pine-hardwood reference, and interior forest).

The bat community at SRS has been extensively mist-netted and surveyed in conjunction with numerous research projects conducted at the site (Menzel 1998, Menzel et al. 2002, Menzel 2003, Menzel et al. 2003, Carter et al. 2004). We used a bat call library collected from previous studies to identify acoustically monitored calls collected over the Carolina bays and from the forest interior. During summers (June–August) of 2000 and 2001, we used frequency division (Anabat) detectors linked to laptop computers through Zero Crossing Analysis Interface Modules (ZCAIM, Titley Electronics, Ballina, Australia) to survey levels of bat activity. During summer 2000, we deployed bat detectors over the bays to establish a baseline of bat activity prior to any restorative efforts. One bat detector was placed at ground height (i.e., 1–2 m above the ground) over each of the treatment and reference bays.

During summer 2001, we simultaneously surveyed bat activity levels with two detectors at two sampling heights, 1–2 m above the ground and above the forest canopy. The canopy sampling height was approximately 30 m (this height varied slightly at each site because we attempted to position detectors 2 m above the height of the surrounding canopy). Depending on the habitat type, above-canopy detectors were deployed at 30 m using climbing ladders, rope and pulley systems, or 14-cubic-m helium-filled blimps (Scientific Sales, Lawrenceville, NJ). The sampling cones of all the detectors were adjusted during both years of sampling prior to deployment to ensure that the volume of sampling space was equal among all habitat types. We conducted surveys nightly except during rain or winds >9 km/h. Sampling was conducted simultaneously at each sampling height for 30 minutes at random time intervals between dusk and midnight. See Menzel et al. (2005) for additional details on sampling methods.

We used the program ANALOOK to identify the species of bat that emitted all call sequences containing >3 calls. Calls were identified by comparing the spectrograms of our known-identification calls to the spectrograms of unknown calls (Fenton and Bell 1981, O'Farrell et al. 1999). We categorized calls with characteristics dissimilar to the calls in our call library, as well as all call sequences containing <3 calls, as unidentifiable.

Prior to statistical analyses, counts of bat calls were transformed using a square-root transformation to correct for heteroskedasticity (Zar 1984). We used a paired *t*-test to determine differences in bat activity before and after restoration in the treatment and reference bays (SAS Institute 1990). Next, at each sampling height (ground and canopy), we used one-way analysis of variance (ANOVA) to compare levels of bat activity among treatment bays, reference bays, and forest interior sites prior to restoration and post-restoration (SAS Institute 1990). We used *a priori* orthogonal linear contrasts to determine how levels of bat activity differed among site types before and after restoration efforts. We had five treatment levels, enabling us to conduct four linear orthogonal contrasts for each sampling height: interior forest vs. treatment bays, interior forest vs. reference bays, all treatment vs. all reference bays, and pine-hardwood treatment vs. pine savanna treatment bays. Significance was determined at $P \leq 0.05$.

RESULTS

During our pre-treatment surveys, we recorded 216 calls at all sites. No feeding buzzes were detected. Known species recorded included eastern red/Seminole bats (*Lasiurus borealis* Gray/*L. seminolus* Rhoads; n = 130; we grouped the two species because we were unable to distinguish between their calls reliably), evening bats (*Nycticeius humeralis* Rafinesque; n = 39), eastern pipistrelles (*Pipistrellus subflavus* Cuvier; n = 10), southeastern myotis (*Myotis austroriparius* Rhoads; n = 10), hoary bats (*L. cinerius* Beauvois; n = 3), and big brown bats (*Eptesicus fuscus*

Table 1. Comparison of bat activity (calls/30 min.) at ground height between all reference bays and all treatment bays prior to (2000) and post (2001) restoration on the Savannah River Site in South Carolina. Statistical test is a paired *t*-test on square-root tranformed data.

Species	Mean	SE	Mean	SE	*t*	*P*
	Reference bays 2000		Reference bays 2001			
Red and Seminole bats	10.56	6.51	4.88	1.37	3.39	0.001
Eastern pipistrelles	0.87	0.60	1.17	0.49	−0.04	0.662
Evening bats	3.24	1.76	1.01	0.62	2.26	0.029
Big brown bats	0.08	0.08	0.20	0.45	−1.98	0.047
Hoary bats	0.25	0.17	0	0	2.44	0.019
Southeastern myotis	0.10	0.10	0.71	0.41	−1.97	0.049
Total bat activity	16.80	1.09	9.42	2.69	3.20	0.003
	Treatment bays 2000		Treatment bays 2001			
Red and Seminole bats	0.50	0.29	8.21	3.87	15.91	0.001
Eastern pipistrelles	0	0	2.83	1.71	9.58	0.001
Evening bats	0.10	0.10	1.29	0.78	5.47	0.001
Big brown bats	0	0	0.33	0.29	3.68	0.001
Hoary bats	0	0	0.04	0.04	2.36	0.027
Southeastern myotis	0.90	0.78	1.17	0.50	2.01	0.057
Total bat activity	1.80	8.95	14.46	6.54	13.64	0.001

Beauvois; n = 1). We found significant differences in bat activity before and after bay restoration. There was significantly more bat activity for red bats, evening bats, hoary bays and total activity in reference bays before restoration than after restoration (Table 1). We found the strongest response in the treatment bays, with all species except for the southeastern myotis having significantly greater activity over treatment bays after restoration (Table 1). When comparing reference to treatment bays prior to restoration, total bat activity was significantly greater over reference bays than treatment bays (Table 2). Although not statistically significant, there was a general trend of greater bat activity for each species over the reference bays than the treatment bays. Bat activity levels did not differ between pine-hardwood and pine treatment bays (Table 2).

After restoration, we recorded 1,474 calls and 109 feeding buzzes above and below the canopy. Species detected included eastern red/Seminole bats (n = 591

Table 2. Comparison of bat activity (calls/30 min.) at ground height between all reference bays and all treatment bays, and pine-hardwood treatment bays and pine savanna treatment bays, on the Savannah River Site in South Carolina during May-August, 2000 (means and SE are from untransformed data, *F* and *P* are results of orthogonal contrasts).

Species	Mean	SE	Mean	SE	*F*	*P*
	All reference bays		All treatment bays			
Red and Seminole bats	10.56	6.51	0.50	0.29	1.50	0.275
Eastern pipistrelles	0.87	0.60	0	0	3.41	0.124
Evening bats	3.24	1.76	0.10	0.10	5.24	0.071
Big brown bats	0.08	0.08	0	0	0.45	0.533
Hoary bats	0.25	0.17	0	0	2.99	0.144
Southeastern myotis	0.10	0.10	0.90	0.78	3.05	0.141
Total bat activity	16.80	1.09	1.80	8.95	15.64	0.011
	Pine-hardwood treatment bays		Pine savanna treatment bays			
Red and Seminole bats	0.80	0.37	0.20	0.20	1.45	0.282
Eastern pipistrelles	0	0	0	0	N/A	N/A
Evening bats	0	0	0.20	0.20	0.40	0.555
Big brown bats	0	0	0	0	N/A	N/A
Hoary bats	0	0	0	0	N/A	N/A
Southeastern myotis	1.80	1.56	0	0	0.44	0.538
Total bat activity	0.20	0.20	0.40	0.40	0.01	0.908

Table 3. Comparison of bat activity (calls/30 min.) at ground height between forest interior sites and treatment bays, forest interior sites and reference bays, pine-hardwood reference bays and pine-hardwood treatment bays, and pine savanna reference bays and pine savanna treatment bays on the Savannah River Site in South Carolina during May-August, 2001 (*F* and *P* are results of orthogonal contrasts).

Species	Mean	SE	Mean	SE	*F*	*P*
	Forest interior		Treatment bays			
Red and Seminole bats	0.06	0.06	8.21	3.19	6.33	0.015
Eastern pipistrelles	0	0	2.83	1.63	3.86	0.048
Evening bats	0.06	0.06	1.29	0.58	2.72	0.104
Big brown bats	0	0	0.33	0.22	0.64	0.426
Hoary bats	0	0	0.04	0.04	1.07	0.305
Southeastern myotis	0	0	1.17	0.36	6.29	0.015
Total bat activity	0.31	0.22	14.46	5.56	6.09	0.017
	Forest interior		Reference bays			
Red and Seminole bats	0.06	0.06	4.88	1.03	2.21	0.143
Eastern pipistrelles	0	0	1.17	0.40	0.55	0.460
Evening bats	0.06	0.06	1.38	0.50	3.11	0.083
Big brown bats	0	0	0.83	0.38	4.02	0.049
Hoary bats	0	0	0	0	N/A	N/A
Southeastern myotis	0	0	0.71	0.31	2.32	0.133
Total bat activity	0.31	0.22	9.42	2.04	3.80	0.046
	All reference bays		All treatment bays			
Red and Seminole bats	4.88	1.37	8.21	3.87	0.27	0.613
Eastern pipistrelles	1.17	0.49	2.83	1.71	0.06	0.809
Evening bats	1.01	0.62	1.29	0.78	0.08	0.776
Big brown bats	0.20	0.45	0.33	0.29	2.62	0.127
Hoary bats	0	0	0.04	0.04	1.25	0.281
Southeastern myotis	0.71	0.40	1.17	0.50	1.28	0.276
Total bat activity	9.42	2.69	14.46	6.54	0.00	0.969
	Pine-hardwood treatment bays		Pine savanna treatment bays			
Red and Seminole bats	11.25	6.20	5.17	1.54	0.04	0.837
Eastern pipistrelles	5.25	3.17	0.42	0.26	2.51	0.134
Evening bats	1.42	1.07	1.17	0.49	1.10	0.312
Big brown bats	0.50	0.42	0.17	0.17	0.31	0.588
Hoary bats	0.08	0.08	0	0	2.50	0.135
Southeastern myotis	1.33	0.63	1.00	0.37	0.53	0.477
Total bat activity	20.75	10.83	8.17	2.25	0.00	0.978

calls/60 feeding buzzes), evening bats (n = 357/11), eastern pipistrelles (n = 153/0), big brown bats (n = 130/0), southeastern myotis (n = 100/7), and hoary bats (n = 11/3). Total bat activity and the activity of eastern red/Seminole bats, eastern pipistrelles, and southeastern myotis all were greater over the treatment bays than in the forest interior at the ground level (Table 3). Total bat activity and the activity of big brown bats were greater over reference bays than in the forest interior at the ground level (Table 3). When comparing bat activity after restoration between reference and treatment bays, we found no significant difference in activity between the two bays. However, there was a general trend of greater levels of activity over the treatment bays than reference bays. Bat activity levels did not differ between pine-hardwood treatment and pine savanna treatment bays (Table 3). However, there was generally more activity over the pine-hardwood treatment bays than the pine savanna treatment bays.

Bat activity was generally lower above the forest canopy than below. In 2001, we recorded only 213 calls (14% of the total number of calls recorded) at heights above the surrounding forest canopy. Despite the low level of activity, we detected some statistical differences in bat activity among treatments above the canopy. We did not detect any bat activity above the canopy in the forest interior (Table 4). When comparing bat activity above all reference bays to all treatment bays after restoration, only evening bats were found significantly more over reference bays (Table 4). Additionally, there was no difference in bat activity above pine-hardwood and pine savanna treatment

Table 4. Comparison of bat activity (calls/30 min.) at canopy height between forest interior sites and treatment bays, forest interior sites and reference bays, all reference bays and all treatment bays, pine-hardwood and pine savanna treatment bays on the Savannah River Site in South Carolina during May-August, 2001 (*F* and *P* are results of orthogonal contrasts).

Species	Mean	SE	Mean	SE	*F*	*P*
	Forest interior		Treatment bays			
Red and Seminole bats	0	0	0.84	0.35	10.07	0.006
Eastern pipistrelles	0	0	0.23	0.18	1.00	0.334
Evening bats	0	0	0.38	0.31	1.36	0.262
Big brown bats	0	0	0.57	0.45	2.87	0.111
Hoary bats	0	0	0.05	0.05	0.18	0.676
Southeastern myotis	0	0	0.27	0.27	0.91	0.354
Total bat activity	0	0	2.95	1.50	16.07	0.001
	Forest interior		Reference bays			
Red and Seminole bats	0	0	1.71	0.63	17.56	0.001
Eastern pipistrelles	0	0	0.17	0.51	2.17	0.162
Evening bats	0	0	0.88	0.35	9.94	0.007
Big brown bats	0	0	1.21	0.75	8.09	0.012
Hoary bats	0	0	0.17	0.09	1.75	0.206
Southeastern myotis	0	0	0.08	0.46	0.82	0.380
Total bat activity	0	0	5.71	1.81	33.18	0.001
	All reference bays		All treatment bays			
Red and Seminole bats	1.71	0.63	0.84	0.35	1.35	0.264
Eastern pipistrelles	0.17	0.51	0.23	0.18	0.30	0.592
Evening bats	0.88	0.35	0.38	0.31	5.43	0.034
Big brown bats	1.21	0.75	0.57	0.45	1.79	0.201
Hoary bats	0.17	0.09	0.05	0.05	1.10	0.310
Southeastern myotis	0.08	0.46	0.27	0.27	0.01	0.943
Total bat activity	5.71	1.81	2.95	1.50	4.07	0.062
	Pine-hardwood treatment bays		Pine savanna treatment bays			
Red and Seminole bats	1.09	0.48	0.58	0.23	0.68	0.423
Eastern pipistrelles	0.45	0.37	0	0	2.75	0.118
Evening bats	0.27	0.27	0.50	0.34	0.75	0.401
Big brown bats	0.73	0.63	0.42	0.26	0.22	0.643
Hoary bats	0.09	0.09	0	0	0.50	0.489
Southeastern myotis	0.36	0.36	0.17	0.17	0.00	0.980
Total bat activity	3.82	1.96	2.08	1.03	0.12	0.730

bays, although we recorded more total calls of all species, except evening bats, above bays with a pine-hardwood margin.

DISCUSSION

Our study indicates the importance of wetlands to bats in the southeastern Coastal Plain landscape. It also suggests how quickly bats are able to respond positively to Carolina bay restoration. Interior forest locations at our study site were typified by extremely low levels of bat activity both above and below the canopy, suggesting that, in the absence of water, the upland forest interior is poor foraging habitat for bats. Both Bradshaw (1996) and Owen et al. (2004) demonstrated that cluttered environments such as dense forest interiors are poor foraging habitat for most bat species. Dense forests provide a complex habitat through which it is difficult and energetically expensive for a bat to navigate (Broders et al. 2003). Therefore, it is not surprising that most bat research has shown that bats are more likely to be present around open wetland habitats than upland forests (Zimmerman and Glanz 2000, Seidman and Zabel 2001, Russo and Jones 2003, Menzel et al. 2005). The absence of bat activity at our forest interior sites corroborates the results of these previous studies.

Additionally, because many insects consumed by bats are water-dependent during at least a portion of their life cycle, the drier conditions of an interior forest are commonly unfavorable for insects (Imes 1992). The absence of these insect species in dry forest interiors further reduces bat foraging opportunities in these habitats. Lastly, because bats drink from wetlands such as bays, ponds, and streams, it is reasonable to assume that they would frequently concentrate their flight activity over aquatic habitats.

Prior to bay restoration, bat activity was lower over drained bays than reference bays. The drained bays contained little or no water and were covered by a closed-canopy forest. The drained bays thus supported a habitat more similar to interior-forest non-wetland locations than to the reference bays. Additionally, the low level of bat activity we detected prior to bay restoration probably was influenced by the severe, prolonged drought that occurred throughout much of the Southeast between 1998 and 2001 (NOAA 2001). During this period, most of the Carolina bays at the study site, including the reference bays, were either dry or had very low water levels. Despite the drought, however, we detected several significant trends in bat activity around the Carolina bays following bay restoration.

Restoration of Carolina bays generally had a positive effect on activity levels of all bat species one year after treatment. In fact, post-restoration sampling indicated more bat activity in the treatment bays than in the reference bays. These high levels of bat activity over the treatment bays were most likely due to the combination of vegetation removal and the hydrologic response in these bays. A clutter-free wetland area was created in a landscape of drier habitat types, apparently enhancing foraging opportunities for bats. Our results mimicked the bat response to canopy removal in bottomland hardwood stands at the SRS detected by Menzel et al. (2002). Menzel et al. (2002) detected greater levels of bat activity in bottomland stands where harvesting had occurred than in locations within the bottomland interior. The installation of the earthen plugs and the removal of the overstory vegetation (which reduced evapotranspirative water loss) resulted in an increase in the depth and duration of flooding in treatment bays (Barton et al. 2004). This reflooding was likely an equally significant factor leading to the increase in bat activity following restoration (i.e., as significant as the reduction in structural complexity in the foraging area caused by the removal of the canopy). Following treatment, there was less vegetation in the treatment than the reference bays, which resulted in the treatment bays holding more water than the reference bays (C. D. Barton, unpubl. data). This hydrologic difference between the treatment and reference bays may explain the difference in bat activity we observed.

We did not determine that the type of habitat surrounding bays significantly altered the level of bat activity over the bays. At ground level, however, the absolute number of calls detected over pine hardwood bays was more than over pine savanna bays for all species. The same trend was observed above the canopy for all but one species. This finding is somewhat puzzling. Pine savanna is the habitat that historically (i.e., pre-European settlement) dominated the SRS upland landscape (White and Gaines 2000, Imm and McLeod 2005). Thus, most Carolina bays were most likely surrounded by pine savanna during pre-settlement, and it is probably the habitat in which species that forage over Carolina bays evolved. The relatively low levels of bat activity in the pine savanna treatment bays may have been due to the lack of vegetative structure. We sampled during the first growing season after the pine savanna margins had been thinned but before the understory had time to recover from the harvesting operation. Other than the residual trees, little vegetation existed in the margins. Habitats void of vegetation generally are poor foraging habitat for bats (Kalcounis et al. 1999, Menzel et al. 2002). Good bat foraging habitat commonly contains some structure and is moderately cluttered. Insects commonly require a low shrub layer for refuge. Without such a layer, insect densities are typically reduced (Tibbels and Kurta 2003). The structure of a mature pine savanna, with its well-developed ground and understory layer and open mid-story, may meet these requirements. Whether bat activity will increase as the understory and mid-story of the pine savanna margins develops, or whether the pine-hardwood margins represent foraging habitat superior to pine savannas remains unclear. An additional hypothesis for the lower amount of bat activity surrounding pine savanna bays may be that bat activity could have been more spread out in these bays due to the lack of vegetative structure in the landscape. In the pine-hardwood bays, the forest edge was more complex, and thus, bats may have been forced to forage less in the forest edge and more over the bays surrounded by pine-hardwoods. This would result in a high detection rate of bats in the pine-hardwood bays compared to the pine savanna bays.

Our study of the short-term impact of bay restoration on bat activity on the SRS indicates that Carolina bay restoration results in increased flight and foraging activity for bat species that commonly forage over undisturbed bays. Although our post-treatment sampling was only one year after restoration, effects of restoration were already detectable. It remains unclear how bat activity will respond once vegetation reclaims the restored Carolina bays. If an overstory remains absent, it is probable that bats will continue to use the restored Carolina bays, particularly when water is present. Therefore, we believe that Carolina bay restoration can be an important bat conservation tool in the southeastern United States.

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