

Use of modified water sources by bats in a managed pine landscape

By: M.A.Vindignia, A.D.Morrissa, D.A.Miller, and [M.C. Kalcounis-Rueppell](#)

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Abstract:

In eastern North Carolina, USA, intensively managed pine (*Pinus* spp.) forests, a primary forest type in the Southeastern United States, often are established where water levels are maintained via ditching. In these landscapes, water occurs in numerous linear ditches and several small ponds (heliponds), used by helicopters for the suppression of forest fires. Changes to the physical structure of water sources may be important to bats that use these sources for drinking and foraging. Therefore, we examined bat activity in a managed pine landscape and an adjacent natural wetland in relation to water source type (heliponds, ditches, and natural wetland) and insect abundance. We sampled bat activity using remote acoustic detectors; we sampled insects using passive traps. Insect abundance did not differ among water source types. Bat activity was most concentrated at modified water sources within the managed pine landscape (heliponds and ditches). Feeding activity was highest at heliponds. Heliponds and ditches were important sources of open water and insect prey for bats in the managed pine forest landscape. We suggest management for bats in similar forest landscapes should include maintenance of open and accessible water sources such as heliponds.

Keywords: Bat activity | Chiroptera | Managed pine forest | Insects | Water | Wetlands

Article:

1. Introduction

Intensively managed pine (*Pinus* spp.) forests occur on 18% of coastal plain lands in the southeastern United States and pine is the primary plantation type in coastal North Carolina, USA (Wear and Greis, 2002). Historically, the northern Coastal Plain of North Carolina consisted of wetlands and marsh forests, containing large, calm bodies of water (Chescheir et al., 2003). Establishment of managed pine forests in this area often involves maintenance of water levels via numerous man-made linear ditches (Chescheir et al., 2003). Narrow linear ditches parallel each other through the interiors of forest stands (interior ditches) and along forest edges

(edge ditches). Additionally, small ponds (heliponds) have been established to provide water access for helicopters for suppression of wildfires.

Although bats are important nocturnal predators of insects, few studies have examined bat foraging behavior in managed pine forests (Miller et al., 2003). Many bats drink and forage over open water sources (Hayes, 2004, Korine and Pinshow, 2004, Menzel et al., 2005a) and appear to prefer large, open, calm bodies of water (Mackey and Barclay, 1989, Warren et al., 2000, Siemers et al., 2001), presumably because of higher insect abundance (Jackson and Fisher, 1986, Jackson and Resh, 1989), decreased ultrasound interference (Mackey and Barclay, 1989, Warren et al., 2000, Siemers et al., 2001), and decreased habitat complexity (Mackey and Barclay, 1989). Draining standing water into narrow ditches changes the physical characteristics surrounding water sources and could affect foraging by bats.

Forest managers are increasingly interested in how silvicultural practices affect biodiversity (Guldin et al., 2007, Wigley et al., 2007) and implications of changes to water sources on bats are important to understand. Therefore, we examined how water source type and insect abundance influenced bat foraging behavior within a landscape of intensively managed pine stands in the northern Coastal Plain of North Carolina, USA. Due to differences in insect community structure (Fukui et al., 2006) and structural complexity (Hayes, 2004, Thomas, 1988) among water sources, we hypothesized that bat activity would differ among water source types. Due to differences in habitat requirements for specific bat species (Menzel et al., 2005a, Lacki et al., 2007), we further hypothesized that species-specific activity would differ among water source types. We predicted that water sources would be used according to species' tolerance for structural complexity (Lacki et al., 2007, Morris et al., in press); *i.e.* large species would be active at heliponds and along edge ditches, whereas small maneuverable species may be more active along interior ditches and within natural forested wetland.

2. Study area

We conducted our study in eastern North Carolina, USA from June–July of 2006–2007 on Weyerhaeuser Company's Parker Tract and the Washington County Wetland Site (Fig. 1). The Parker Tract was a 4000 ha mosaic of intensively managed loblolly pine (*Pinus taeda*) stands in various stages of growth and also included 956 ha of mature, unmanaged, natural deciduous stands (Chescheir et al., 2003, Morris et al., in press). Typical silviculture of intensively managed pine stands included clear-cut harvest at 27–35 years old followed by site preparation, planting of pine seedlings on a wide (~6.1 m) row spacing, vegetation control, fertilization, thinning (1–3 times) (Watts and Wilson, 2005), and final harvest. In the Parker Tract, narrow linear ditches occurred within stands every 80–100 m (interior ditches), and along stand borders (edge ditches; Fig. 1). Ditches were 1–2.5 m wide and 0.6–1.2 m deep. We focused our sampling on ditches occurring within and adjacent to mature pine and hardwood stands, due to stand characteristics similar to the wetland site (see below). There were 5 heliponds within the Parker Tract (Fig. 1), each approximately 12 m × 24 m × 2.5 m deep.

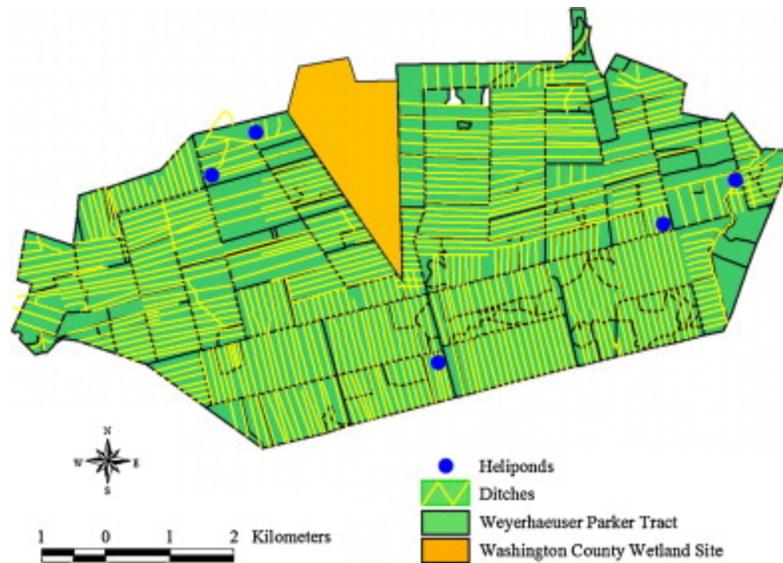


Fig. 1. Study area showing the Washington County Wetland Site, and adjacent Weyerhaeuser Parker Tract, in eastern North Carolina, USA. Water sources (heliponds and ditches) within the managed pine forest are indicated.

The Washington County Wetland Site, a 350 ha remnant natural forested wetland, was adjacent to the Parker Tract (Fig. 1). Trees in the wetland site consisted mainly of bald cypress (*Taxodium distichum*), red maple (*Acer rubrum*), and loblolly pine (Chescheir et al., 2003). Although the wetland site was mature with open canopy structure, scattered storm-damaged trees and branches added structural complexity above the surface of the water [personal observation]. The wetland site was inundated by water for all or most of the year (Chescheir et al., 2003), and represented the natural condition of most of the landscape. During our study, the wetland site had little to no standing water for several weeks during summer 2007, due to drought. Although heliponds and ditches also exhibited variation in water levels, they consistently had standing water throughout our study.

3. Methods

On each night without significant rainfall, we simultaneously sampled bat activity and insect abundance at two of the four water source types (heliponds, interior ditches, edge ditches, or natural forested wetlands). We sampled water source types in a random order with equal sampling effort at each water type. At each site, we simultaneously recorded echolocation calls using two bat detectors (Petterson D240X, Petterson Elektronik AB, Sweden) linked to digital recorders and trapped insects using passive malaise and emergence traps (Kalcounis-Rueppell et al., 2007). Due to a limited number of heliponds ($n = 5$) and accessible natural wetland sites ($n = 3$), we sampled sites at these water sources repeatedly. Therefore, although ditches were prevalent on the landscape (Fig. 1), we also sampled sites at interior ditches ($n = 5$) and edge ditches ($n = 5$) repeatedly.

At each site, we set one detector to heterodyne mode to record real-time echolocation sequences throughout the night. We set the second detector to time-expanded mode to capture full-spectrum sonograms of echolocation calls, which we used to identify bats recorded to species. Bat detector

microphones were angled 45° above horizontal, and pointed directly at or along water sources to minimize vegetation interference on bat detection (Johnson et al., 2002, Patriquin et al., 2003). We set all detectors to record from dusk until dawn. We counted the number of echolocation sequences and feeding buzzes within heterodyne sound files. We qualitatively identified time-expanded echolocation sequences to species using Sonobat software (Sonobat, Arcata, California, USA), and a reference call library (Morris et al., in press, Kalcounis-Rueppell et al., 2007). Our reference library contained echolocation sequences recorded at our study site and sequences previously recorded in the Southeastern U.S. We grouped echolocation sequences from bats of the genus *Myotis* [northern long-eared bat (*M. septentrionalis*) and southeastern myotis (*M. austroriparius*)] because of their similar call structure.

We identified insects to order using a dissecting microscope and taxonomic key (Arnett, 2000). These samples provided counts of insects (by order, and total) for each site where we measured bat activity. Therefore, at each site, we measured bat activity (counts of heterodyne echolocation sequences), bat foraging activity (counts of heterodyne echolocation sequences containing a feeding buzz), bat species activity (counts of time-expanded echolocation sequences recorded per species), and insect abundance.

We used mist net captures to confirm bat species presence and obtain reference echolocation calls from bats. We concentrated mist-netting at heliponds and natural forested wetland sites to increase the likelihood of capturing bats. We set up mist nets (2–6 nets per night; 2.6 m, 6 m, 12 m 4 shelf nets; 38.0 mm mesh, Avinet, Inc. Dryden, New York, USA) at dusk and monitored them at approximately 10 min intervals until about midnight. We removed bats from nets and identified them to species. We recorded reference calls of bats hand-released at the capture site. Bat handling followed the guidelines of the American Society of Mammalogists and the UNCG Institutional Animal Care and Use Committee Protocol #06-11 (Animal Care Use Committee, 1998).

To test the hypothesis that insect abundances did not differ between water source types, we used generalized linear models to compare number of insect captures (total, and by order) across water source types (helipond, edge ditch, interior ditch, and natural wetland). Because our data consisted of repeated measurements, we used generalized estimating equations (GEE) to iteratively fit regression models while accounting for correlations within our data (Ballinger, 2004, Burton et al., 1998, Zorn, 2001). Because we did not sample sites at equal time intervals, we specified a compound symmetrical covariance structure, in which all repeated observations from a site were assumed to be equally correlated (Burton et al., 1998). We used this approach because our primary goal was to make comparisons across water types (between-group effects), and we were less concerned with examining temporal patterns (within-group effects). Furthermore, we expected that measurements of bat activity and insect abundance would vary nightly, and repeated observations would not be strongly correlated.

We also used generalized linear models to test the null hypotheses that overall bat activity (counts of bat echolocation sequences), bat feeding activity (counts of echolocation sequences containing a feeding buzz), and bat species activity (counts of echolocation sequences identified to a given species) were not related to water source type or insect abundance. We modeled counts of echolocation sequences using water source types as categorical (indicator) variables,

and counts of insects (by order and total) as continuous model predictors. This approach allowed simultaneous testing of the effects of water source and prey abundance on bat foraging behavior (Morris et al., in press). As described previously, we used generalized estimating equations to fit models iteratively using a compound symmetrical covariance structure (Ballinger, 2004, Burton et al., 1998, Zorn, 2001). In addition, because counts of echolocation sequences exhibited overdispersion, we fit these models using negative binomial regression (Morris et al., in press). We evaluated candidate models according to their deviance scores and significance ($\alpha = 0.05$) of parameter estimates. We removed non-significant insect abundance terms from final models. We fit and analyzed all models using PROC MIXED and PROC GENMOD in SAS 9.1 (SAS, Cary, North Carolina, USA).

4. Results

We sampled bats and insects on 116 nights during the summers 2006–2007 [heliponds ($n = 28$), interior ditches ($n = 33$), edge ditches ($n = 27$), and natural wetland sites ($n = 28$)]. We captured 17,514 terrestrial and emergent aquatic insects of 23 orders, including Diptera ($n = 13,855$), Homoptera ($n = 800$), Lepidoptera ($n = 646$), Collembola ($n = 401$), Hymenoptera ($n = 345$), Coleoptera ($n = 224$), Thysanoptera ($n = 153$), and Hemiptera ($n = 86$). We recorded 43,708 heterodyne echolocation sequences containing 3961 feeding buzzes. We identified 9982 time-expanded echolocation sequences into 7 species or species groups [red bats (*Lasiurus borealis*; $n = 5558$), big brown bats (*Eptesicus fuscus*; $n = 2391$), tricolored bats (*Perimyotis subflavus*; $n = 750$), evening bats (*Nycticeius humeralis*; $n = 455$), hoary bats (*Lasiurus cinereus*; $n = 302$), Brazilian free-tailed bats (*Tadarida brasiliensis*; $n = 294$), and *Myotis* spp. ($n = 232$)] (mean number of echolocation sequences by species are given in Table 1). We used mist nets to capture 156 bats of 6 species [red bats ($n = 82$), big brown bats ($n = 23$), evening bats ($n = 41$), tricolored bats ($n = 2$), northern long-eared bats ($n = 6$), and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*; $n = 2$)].

Table 1. Means and standard errors (\pm SE) of number of time-expanded echolocation sequences recorded per site per night for each water source type. Data are from acoustic monitoring at water sources within an intensively managed pine forest (Weyerhaeuser Parker Tract), and at the Washington County Wetland Site, eastern North Carolina, USA, during the summers of 2006 and 2007. *Myotis* spp. contains *Myotis septentrionalis* and/or *Myotis austroriparius*.

Species	Helipond	Edge Ditch	Interior Ditch	Natural Wetland
Red bat, <i>Lasiurus borealis</i>	106.64 \pm 19.91	39.96 \pm 12.67	37.09 \pm 15.32	9.61 \pm 2.78
Big brown bat, <i>Eptesicus fuscus</i>	53.04 \pm 10.38	18.04 \pm 5.92	8.15 \pm 2.45	5.36 \pm 2.03
Brazilian free-tailed bat, <i>Tadarida brasiliensis</i>	4.18 \pm 1.34	1.37 \pm 0.57	2.42 \pm 1.48	2.14 \pm 0.70
Hoary bat, <i>Lasiurus cinereus</i>	6.29 \pm 2.60	1.85 \pm 0.79	1.21 \pm 0.53	1.28 \pm 0.42
Tricolored bat, <i>Perimyotis subflavus</i>	23.11 \pm 6.72	1.15 \pm 0.47	1.70 \pm 0.82	0.57 \pm 0.24
Evening bat, <i>Nycticeius humeralis</i>	6.57 \pm 3.02	3.07 \pm 1.81	5.45 \pm 3.49	0.29 \pm 0.18
<i>Myotis</i> spp.	0.79 \pm 0.30	0.85 \pm 0.39	4.06 \pm 1.60	1.89 \pm 0.50

Counts of insects were approximately normally distributed and our generalized linear models fit well using the identity link function. Total insect abundance did not differ across water source types (Table 2). Abundances of Diptera, Homoptera, Hymenoptera, Thysanoptera, Lepidoptera, Hemiptera, Coleoptera, and Collembola did not differ ($p > 0.05$) across water source types (Table 2). The negative binomial distribution fit echolocation sequence counts (Table 3, Table

4). Overall bat activity was higher at heliponds, edge ditches, and interior ditches than at natural wetland sites (Table 3). Counts of echolocation sequences containing feeding buzzes were highest at heliponds (Table 3).

Table 2. Mean (\pm SE) number of insects captured per night for four water sources. Probability values are from tests that insect abundance did not differ across water types. Data are from malaise and emergence trapping at water sources within an intensively managed pine forest (Weyerhaeuser Parker Tract), and the Washington County Wetland Site, eastern North Carolina, USA, during the summers of 2006 and 2007. Only the most commonly captured insect orders are shown.

Order	Helipond	Edge Ditches	Interior Ditches	Natural Wetland	$F_{3,14}$	p
Diptera	155.19 \pm 29.87	87.15 \pm 15.85	95.85 \pm 11.68	156.89 \pm 24.18	1.78	0.20
Lepidoptera	6.70 \pm 1.65	4.03 \pm 0.52	4.91 \pm 0.98	7.33 \pm 1.87	0.40	0.76
Homoptera	10.41 \pm 3.16	8.30 \pm 1.67	4.12 \pm 1.19	6.19 \pm 1.51	1.21	0.34
Hymenoptera	2.41 \pm 0.57	1.73 \pm 0.46	2.52 \pm 0.62	5.63 \pm 1.52	2.53	0.10
Hemiptera	0.96 \pm 0.31	0.58 \pm 0.20	0.33 \pm 0.16	1.26 \pm 0.48	2.12	0.14
Thysanoptera	0.44 \pm 0.18	0.31 \pm 0.12	0.39 \pm 0.17	4.44 \pm 2.33	1.58	0.24
Coleoptera	1.67 \pm 0.44	1.54 \pm 0.44	1.88 \pm 0.37	2.85 \pm 0.64	0.66	0.59
Collembola	0.70 \pm 0.24	0.85 \pm 0.29	10.39 \pm 8.20	0.63 \pm 0.26	1.11	0.38
All Orders	192.57 \pm 34.18	103.70 \pm 16.12	121.03 \pm 14.93	190.29 \pm 28.71	1.72	0.21

Table 3. Parameter estimates for overall bat activity and feeding activity regression models. Models describe total bat activity (count of echolocation sequences), and bat foraging activity (count of feeding echolocation sequences) in relation to water source type (helipond, edge ditch, interior ditch, and natural wetland). Water source types were represented with indicator variables. Significant predictor variables ($p < 0.05$) are denoted by *. The sign and magnitude of parameters describe their relative effect on mean number of echolocation sequences, in comparison to natural wetland sites (positive parameter values indicate higher bat activity). Significance of the over-dispersion parameter ‘Alpha’ implies that the negative binomial model fits well. Data were collected using acoustic monitoring with bat detectors and insect trapping in intensively managed pine forest (Weyerhaeuser Parker Tract), and natural forested wetlands (Washington County Wetland Site) during the summers of 2006 and 2007, in eastern North Carolina, USA.

Variable	Parameter	Estimate	Standard Error	Z	p
Number of echolocation sequences	intercept	4.844	0.069	69.78	<0.001*
	helipond	1.819	0.163	11.13	<0.001*
	edge ditch	0.972	0.201	4.83	0.002*
	interior ditch	0.801	0.356	2.250	0.02*
	<i>alpha</i>	1.566	0.176	8.92	<0.001*
Number of feeding sequences	intercept	3.00	0.233	12.89	<0.001*
	helipond	1.528	0.352	4.34	<0.001*
	edge ditch	0.361	0.351	1.03	0.30
	interior ditch	0.235	0.599	0.390	0.70
	<i>alpha</i>	2.376	0.307	7.73	<0.001*

Table 4. Parameter estimates for negative binomial models of bat species activity. Models describe bat species activity (count of time-expanded echolocation sequences) in relation to water source type and insect abundance. Water source types are represented with indicator variables. Significant predictor variables ($p < 0.05$) are denoted by *. The sign and magnitude of parameters describe their effect on mean number of echolocation sequences, in comparison to natural wetland sites (positive parameter values indicate higher bat activity). Significance of the over-dispersion parameter α implies that the negative binomial model fits well. Data were collected using acoustic monitoring with bat detectors, and insect trapping, at water sources in an intensively managed pine forest (Weyerhaeuser Parker Tract), and natural forested wetland (Washington County Wetland Site) during the summers of 2006 and 2007, in eastern North Carolina, USA. *Myotis* spp. contains *Myotis septentrionalis* and/or *Myotis austroriparius*.

Species	Parameter	Estimate	Standard Error	Z	p
Red bat, <i>Lasiurus borealis</i>	intercept	2.320	0.349	6.65	<0.001*
	helipond	2.344	0.373	6.29	<0.001*
	edge ditch	1.370	0.416	3.30	0.001*
	interior ditch	1.327	0.668	1.99	0.047*
	α	3.03	0.373	8.13	<0.001
Big brown bat, <i>Eptesicus fuscus</i>	intercept	1.704	0.336	5.08	<0.001*
	helipond	2.246	0.363	6.18	<0.001*
	edge ditch	1.159	0.431	2.69	0.01*
	interior ditch	0.437	0.604	0.72	0.47
	α	3.106	0.435	7.14	<0.001
Brazilian free-tailed bat, <i>Tadarida brasiliensis</i>	intercept	0.793	0.389	2.04	0.042*
	helipond	0.628	0.464	1.35	0.18
	edge ditch	-0.493	0.521	-0.95	0.34
	interior ditch	0.104	0.797	0.13	0.90
	α	4.932	0.918	5.37	<0.001
Hoary bat, <i>Lasiurus cinereus</i>	intercept	0.268	0.265	1.01	0.31
	helipond	1.589	0.336	4.73	<0.001*
	edge ditch	0.360	0.412	0.87	0.38
	interior ditch	-0.145	0.603	-0.24	0.81
	α	4.855	0.949	5.11	<0.001
Tricolored bat, <i>Perimyotis subflavus</i>	intercept	-1.506	0.245	-6.14	<0.001*
	helipond	3.395	0.209	16.22	<0.001*
	edge ditch	1.130	0.386	2.93	0.003*
	interior ditch	1.049	0.558	1.88	0.06
	Diptera	0.0064	0.0011	5.75	<0.001*
	α	4.999	1.011	4.95	<0.001
Evening bat, <i>Nycticeius humeralis</i>	intercept	-1.341	0.568	-2.36	0.018*
	helipond	3.214	0.688	4.67	<0.001*
	edge ditch	2.466	0.742	3.32	0.001*
	interior ditch	2.979	0.829	3.59	<0.001*
	α	8.196	1.598	5.13	<0.001
<i>Myotis</i> spp.	intercept	0.675	0.206	32.83	<0.001*
	helipond	-0.927	0.172	-5.39	<0.001*
	edge ditch	-0.852	0.316	-2.70	0.01*
	interior ditch	0.707	0.200	3.54	<0.001*
	α	3.191	0.642	4.97	<0.001

Water source type (Fig. 2) had species-specific effects on bat foraging behavior (Table 4). Five bat species exhibited highest activity at heliponds (Fig. 2, Table 4). Activity of red bats was high at heliponds, edge ditches, and interior ditches (Table 4). Activity of big brown bats was high at heliponds and edge ditches (Table 4). Activity of Brazilian free-tailed bats was not related to water source type or insect abundance (Table 4). Activity of hoary bats was highest at heliponds (Table 4). Activity of tricolored bats was high at heliponds, edge ditches, interior ditches, and was positively related to abundance of Dipterans (Table 4). Activity of evening bats was high at heliponds, edge ditches, and interior ditches (Table 4). In contrast, activity of *Myotis* spp. was high at interior ditches but negatively related to heliponds and edge ditches (Table 4).

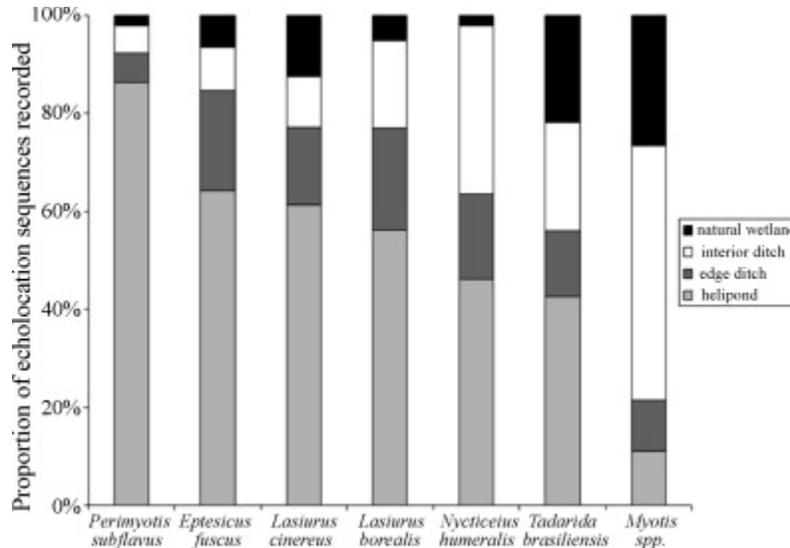


Fig. 2. Percent of time-expanded bat echolocation sequences recorded at four water source types (adjusted for sampling effort). Acoustic data were collected within an intensively managed pine forest (Weyerhaeuser Parker Tract), and natural forested wetland (Washington County Wetland Site) during the summers of 2006 and 2007, in eastern North Carolina, USA.

5. Discussion

Not all species identified in acoustic recordings were captured in mist nets and not all species captured in mist nets were recorded ultrasonically. We recorded hoary and Brazilian free-tailed bats, but did not capture them, likely because they fly high (Kalcounis et al., 1999, Caire et al., 1984) and are therefore difficult to catch. In contrast, we caught two Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) (at a helipond and at a natural wetland site), but did not record this species' echolocation calls, likely because of its low-intensity echolocation calls (Murray et al., 1999). All bat species recorded were present at all four water source types (Fig. 2).

Overall bat activity was higher at modified water sources within the managed pine landscape (heliponds and ditches), than in natural wetlands (Table 3). The high concentrations of bat activity at these sources suggest they may be important resources for bats in this landscape. Consistent with our study, Menzel et al., 2005a, Menzel et al., 2005b found higher bat activity over modified open water sources (restored Carolina bays), than undisturbed wetlands or within forest stands, in the coastal plain of South Carolina (Menzel et al., 2005b). Open, man-made water sources may be important resources for bats in coastal plain forests because they are

accessible and reliable sources of standing water. Heliponds had the highest feeding activity, likely because they were in accessible areas and supported abundant insect prey. Because insect abundance did not differ across water source types, heliponds and ditches may offer similar prey resources to natural wetlands. Additionally, a companion study (Allgood et al., 2009) conducted on our study area found similar Dipteran families between heliponds and natural wetlands.

Species' activity relative to water sources appeared to be determined by each species' foraging habits. Bats of five species (big brown bats, hoary bats, tricolored bats, red bats, and evening bats) exhibited the highest activity levels at heliponds (Fig. 2). Heliponds were likely accessible to many species because they occurred in structurally open areas, and had little overhanging vegetation. Big brown and hoary bats may forage over open water sources, like heliponds, due to their relatively large body size, fast flight, and low frequency echolocation calls (Barclay, 1999, Jacobs, 1999, Sleep and Brigham, 2003, Ober and Hayes, 2008). Tricolored bats, which had high activity at heliponds (Fig. 2), are known to forage over water and are considered riparian specialists (Kalcounis-Rueppell et al., 2007, Fujita and Kunz, 1984, Ford et al., 2005). We found that tricolored bat activity was also correlated with the abundance of Diptera, a component of the species' diet (Carter et al., 2003). This conclusion is further supported by Morris et al. (in press), who, using a different dataset, found that this species' activity patterns were related to abundance of Dipterans in forest stands and along edges on our study area.

Red bats, evening bats, and tricolored bats, which are intermediate in maneuverability (Menzel et al., 2005a), were active at both interior and edge ditches. In contrast, other species displayed strong preferences for interior or edge ditches. Big brown bats were more active along edge ditches, while *Myotis* spp. were more active along interior ditches. Big brown bats may avoid interior ditches because they can maneuver and hunt more effectively in open areas (Menzel et al., 2005a). Big brown bats' use of edge ditches and heliponds is consistent with this species' use of edges and open areas for foraging (Morris et al., in press). *Myotis* spp., which may have been northern long-eared bats (Morris et al., 2009) and/or southeastern myotis, used interior ditches but avoided edge ditches and heliponds. Use of interior ditches and natural wetland sites is consistent with northern long-eared bats' foraging strategy of gleaning prey from substrates and avoidance of open areas (Owen et al., 2003). This pattern is also consistent with the foraging behavior of the southeastern myotis, a small, maneuverable species known to forage over water (Fenton and Bogdanowicz, 2002).

In addition to providing drinking and food resources for bats, linear ditches may function as conduits. Bats are known to move along linear landscape features like streams, roads, corridors (Hein et al., 2008), and forest edges (Morris et al., in press). Furthermore, interior ditches may offer a flyway through structurally complex forest stands that may otherwise be relatively inaccessible. Therefore, the flight corridors created by interior ditches may allow bats to commute and forage within forest stands more efficiently.

Our regression models suggested that natural forested wetland sites had low bat activity. However, this may be due to the large area of wetlands available, rather than non-use by bats. Bat activity was highly concentrated at heliponds and ditches, but likely distributed widely across wetlands. Therefore, the low density of activity at natural wetland sites does not imply

that wetlands are not important sources of water for bats. Natural wetland sites had high insect abundances (Table 2) and likely provide drinking and foraging resources for bats.

6. Conclusion

The high concentrations of bat activity at heliponds and ditches within the managed pine forest suggest that these water sources may be important resources for bats. Heliponds, though few in number, may be key landscape features for bats in managed pine forests as they are reliable sources of open water and prey. Heliponds may be structurally similar water sources to natural wetlands, because they offer an open, flat surface of water. Furthermore, insect communities at heliponds and ditches closely resembled those at natural wetlands, suggesting that modified water sources may provide the same food resources for bats as natural water sources. We recommend that heliponds and ditches be maintained with limited vegetation cover so they remain accessible to a variety of bat species.

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