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THE USE OF SOUTHERN APPALACHIAN WETLANDS BY BREEDING BIRDS, WITH A FOCUS ON NEOTROPICAL MIGRATORY SPECIES

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ABSTRACT.—Although loss of wetlands in southern Appalachia has been especially severe, no avian studies have been conducted in the vestiges of these ecosystems. Our research assessed avian use of southern Appalachian wetlands in the breeding seasons of 1999 through 2001. Site analyses included 18 habitat variables, including total wetland area, area of open water, beaver or livestock evidence, edge type (abrupt or gradual), and percent cover of nine vegetation types. We analyzed avian species richness and abundance at the community level and in guilds based on migratory status and breeding habitat preference. Measures of vegetation and habitat—particularly those resulting from beaver activities—and gradual edges were significantly correlated with guild- and community-level variables. Evidence of beaver (i.e., forest gaps where trees had been felled, ponds where drainages had been dammed; hereafter referred to simply as ''beaver evidence'') was significantly correlated with greater community-level species richness and abundance. Both beaver evidence and gradual edge were positively associated with greater species richness and abundance of Neotropical migratory birds (NTMBs) overall, as well as with the late-successional NTMB guild. Presence of gradual edge alone also was significantly correlated with high abundance of birds in the early-successional NTMB guild. Beaver and gradual edge may have contributed to higher-quality breeding habitats with relatively greater overall productivity and structural complexity in some wetlands. *Received 24 November 2004, accepted 22 March 2006.*

Wetlands of the southern Appalachians are perhaps the rarest and most threatened in the southeastern U.S. Weakley and Shafale (1994) estimate that only one-sixth (about 2,000 ha) of the bogs in pre-European settlement southern Appalachia remain today. Historically, post-glacial southern Appalachian wetlands have been maintained by precipitation, groundwater recharge, and natural suppression of woody vegetation (Weakley and Shafale 1994, Lee and Norden 1996); humans, however, have since altered the woody vegetation. Pleistocene megafauna (Weigl and Knowles 1995, Lee and Norden 1996), including elk (*Cervus elaphus*) and American bison (*Bison bison*; Lee and Norden 1996, but see Ward 1990) are believed to have maintained these wetlands in early-successional states via browsing, but all have disappeared concomitant with human settlement. Native American use of fire also may have suppressed the encroachment of woody vegetation (Lee and Norden 1996) into southern Appalachian wetlands (Delcourt and Delcourt 1997). Today, fires are suppressed and quickly extinguished when they do occur (Weakley and Shafale 1994). Widespread loss of beaver (*Castor canadensis*) via the fur trade of the 18th and 19th centuries also reduced the development (Snodgrass 1997) and maintenance of wetlands throughout the landscape (Webster et al. 1975, Naiman et al. 1988, Weakley and Shafale 1994, Lawton and Jones 1995, Lee and Norden 1996). Most recently, the majority of remaining small wetlands in southern Appalachia have been converted to pasture, developed, or manipulated for other human uses (Weakley and Shafale 1994).

Today, the remaining wetlands of southern Appalachia are considered biological hotspots (Murdock 1994); until now, however, no study had focused on the breeding avifauna of these ecosystems. Southern Appalachia's wetlands are important to breeding Neotropical migratory birds (NTMBs). In fact, parts of the region harbor the greatest species richness and abundance of NTMBs in North America (Simons et al. 2000); however, the region's populations of NTMBs are declining more rapidly than anywhere else in North America (Rodriguez 2002). Species preferring open, early-successional habitats or late-successional for-

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ests are undergoing the most rapid declines (Robbins et al. 1989; reviewed in Askins et al. 1990). Of NTMBs that breed in southern Appalachia's early-successional habitats, 76% are declining (Hunter et al. 2001, Thompson and DeGraaf 2001) due to losses of early successional grasslands, scrub-shrub, open-canopy woodlands, and small canopy gaps (Hunter et al. 2001); some of North America's greatest declines in early-successional species have been reported from southern Appalachia (Franzreb and Rosenberg 1997).

Declines among NTMBs that breed in late-successional habitats are due, in part, to forest fragmentation resulting from agricultural, residential, and commercial development (Robbins et al. 1989, Askins et al. 1990, Faaborg et al. 1995). Forest-interior species suffer from increased rates of brood parasitism (Brittingham and Temple 1983, Robbins et al. 1989) and nest predation (Askins et al. 1990), and from increased competition with other bird species (Askins et al. 1990, Zannette et al. 2000) in the smaller habitat patches that result from fragmentation. Although the southern Appalachians contain approximately 80% of the primary forests in the eastern U.S. (Davis 1993), more species are declining in the region (42% of forest-breeding species) than in North America as a whole (27%; Franzreb and Rosenberg 1997).

In southern Appalachia, wetland loss has been concurrent with declines in NTMB populations, although it has not been evaluated as a contributing factor (Hunter et al. 1999). In southern Appalachian wetlands, habitat succession ranges from open, early-successional grasslands to late-successional, forested bogs; thus, these wetlands may provide important breeding habitats for both early- and late-successional breeding species, some of which are undergoing the greatest rates of population decline.

Considering the general scarcity of southern Appalachian wetlands and the disproportionately high rates of decline among NTMB species in that region, research on the use of southern Appalachian wetlands by breeding birds is overdue. Herein, we report the results of such research, focusing specifically on the habitat characteristics that make certain kinds of wetlands attractive to NTMBs in early- and late-successional habitat guilds of breeding birds.

METHODS

Study sites.—We collected data at 57 southern Appalachian wetlands in western North Carolina (*n* = 44), northeastern Tennessee (*n* = 3), and southwestern Virginia (*n* = 10). Wetland elevations ranged from 442 to 1,254 m. The total wetland area in our study was 795 ha. Individual wetland area ranged from 0.40–95 ha (mean = 14 ha); excluding the four largest wetlands, however, mean wetland size was only 0.64 ha. Such small wetland areas are typical in regions of high topographic relief.

All wetland sites were dominated by hydrophytic vegetation and other hydrologic features (i.e., hydric soils, periodic to permanent inundation and/or soil saturation). Forty-four of our sites were used in previous botanical and herpetofaunal studies; we located the others by using natural history records from the North Carolina Natural Heritage Program and the North Carolina Museum of Natural Sciences. All wetlands were classified as one of three palustrine system types (Cowardin et al. 1979): emergent (*n* = 23), scrub-shrub (*n* = 21), or forested (*n* = 13).

Some of our study wetlands were low-pH, precipitation-fed bogs, wherein peat-filled depressions were dominated by a lattice of sphagnum mats and standing water. In these open wetlands, woody vegetation was scarce, although some had a sparse shrub layer (e.g., *Salix* spp., *Alnus* spp., and *Acer rubrum* saplings). Other study wetlands were groundwater-sourced fens characterized by thick covers of mosses, lichens, grasses, and forbs. Most study wetlands were located in floodplains and characterized by a diverse, structurally complex vegetative community. These floodplain wetlands were often the result of historic or current beaver activity and may have been groundwater and/or surface-water fed, though detailed hydrologic characteristics of study sites were not addressed.

All wetlands were owned by Appalachian State University (ASU; *n* = 2), the Blue Ridge Parkway National Park (BRP; *n* = 22), The Nature Conservancy (TNC; *n* = 6), the North Carolina Department of Transportation (NCDOT; *n* = 2), the U.S. Department of Agriculture Forest Service (USFS; $n = 3$), or private landowners ($n = 22$). (Hereafter, all sites other than those owned by private landowners will be referred to as ''publicly owned sites,'' including TNC sites, although we recognize that technically, TNC sites are ''private.'')

In general, publicly owned wetlands are actively managed, whereas privately owned sites are not. Publicly owned wetlands were characterized by fewer land-use disturbances than those that were privately owned, and they were managed for their persistence in the landscape. Privately owned sites generally displayed one or more effects of land use, such as logging, grazing, and mowing, or draining for agriculture, residential development, and/or commercial development.

Small southern Appalachian wetlands are inherently associated with edges, and we classified site edges as either abrupt or gradual. Our qualitative classification of edge type followed that used in other studies of edge-type effects on breeding birds (Suarez et al. 1997, Luck et al. 1999). An abrupt edge displayed a distinct, drastic change in vegetation structure between two vegetation types. Abrupt edges ($n = 29$ sites) usually resulted from persistent land uses, such as mowing or cattle grazing, thus creating a sharp edge between grasses/forbs and forest. In some sites, beaver also had created abrupt edges. For example, sites recently flooded by beaver dams often had no transitional vegetation structure between the new pond and the canopy-level vegetation (Snodgrass 1997).

Twenty-eight sites had a gradual edge, qualitatively defined as a smooth gradient between vegetation types or successional stages (Suarez et al. 1997, Luck et al. 1999). Gradual edges comprised a complex transition between vegetation types, where grasses, forbs, saplings, and shrubs were intermixed. Most of the beaver-impacted wetlands in our study had gradual edges, primarily because there had been sufficient time since beaver invasion for succession to occur; gradual edges did occur in the absence of beaver evidence wherever edges were not maintained by anthropogenic disturbances.

Presence/absence of beaver evidence was assessed via visual observation. Some beaver-impacted wetlands were inundated hardwood forests. Others were inundated gaps in the canopy that had resulted from tree-felling and damming activities; these wetlands often contained much downed, coarse woody debris and many exposed stumps. Some beaver-impacted wetlands had been abandoned, as evidenced by breached dams and exposed sediments, which supported a variety of grasses, forbs, and shrub species (i.e., ''beaver meadows''). Overall, beaver-impacted wetlands were characterized by a diversity of successional seres associated with beaver colonization and abandonment.

Avian censusing.—During the 1999 field season, we conducted a pilot study to compare spot mapping and 50-m fixed-radius point counts. Fixed-radius point counts were superior for this study, as they generated more bird detections in less time than spot-mapping (Ralph et al. 1993), allowing us to increase sample size by visiting more wetlands in 2000 and 2001. Thus, during the breeding seasons of 2000 and 2001, we conducted three 10-min, 50-m fixed-radius point counts in each of the 57 wetlands ($n = 33$ sites in 2000 and $n = 24$ sites in 2001). All point counts were conducted between 15 May and 30 June, from sunrise to 10:00 EST, on days when neither precipitation nor wind conditions interfered with bird detections (Ralph et al. 1995). During each visit, the point count was conducted from the center of the core wetland area (Ralph et al. 1995) and always at the same point location (Johnson 2001). We recorded all birds seen or heard during each count (Ralph et al. 1995), and bird detections were categorized as <25.0, 25.1–50.0, and >50.0 m from the point-count center. The same observer conducted all point counts in all 3 years.

Although point counts—by virtue of standardized and routinely adopted protocols (Ralph et al. 1995)—have become the conventional technique for conducting avian censuses, differences in the detectability of different species may generate inaccurate counts (Thompson 2002). Statistically based detectability adjustments are sometimes used to attempt to compensate for these errors (e.g., double-observer approach, Nichols et al. 2000; distance sampling, Rosenstock et al. 2002; double sampling, Bart and Earnst 2002). We used raw data for our analyses because our sample size ($n = 57$ wetlands over

3 years) and data did not meet all the assumptions necessary for use of distance-sampling methods (Hutto and Young 2003). In addition to our small sample size, we could not be certain that every individual present was counted only once or that precise distances for all detections were estimated accurately. Thus, our raw data were used to assess possible relationships between habitat and bird communities in this short-term study.

We used the number of species and individuals recorded at point counts to calculate community- and guild-level dependent variables for statistical analyses. For each wetland, we calculated community-level species richness as the total number of species observed across all three visits. Therefore, species richness assesses all species observed using a wetland, whether or not they were breeding there; some birds using wetlands for foraging (Pagen et al. 2000) or for extraterritorial copulation forays (Norris and Stutchbury 2001) may not have been present during all census visits. For each wetland, we also calculated community-level avian abundance as the mean number of birds observed during all three visits.

To develop guild-level variables, we assigned all bird species to guilds based upon classifications used by the Breeding Bird Survey (Sauer et al. 2001). We focused on the NTMB guild (as opposed to residents and short-distance migrants). We further classified the NTMBs into two breeding-habitat guilds: ''late-successional'' (i.e., woodland) and ''early-successional'' habitats. All early-successional NTMBs nest in scrub, except the Eastern Meadowlark (*Sturnella magna*)—the only ''grassland'' nester that we observed. Because Eastern Meadowlarks represent a unique subguild of early-successional breeders, and because we observed them in only six sites, we excluded this species from our analyses. Thus, within each of the three guilds (i.e., NTMB and two habitat guilds), we calculated species richness and abundance, which we used as dependent variables in statistical analyses. For each wetland, we calculated within-guild species richness as the total number of species in each guild observed across the three point counts. We calculated within-guild abundance as the mean number of individuals in each guild detected across all three visits.

Vegetation analyses.—At each site, we recorded wetland class (Cowardin et al. 1979), presence or absence of livestock evidence, presence or absence of beaver evidence, edge type, and ownership status; these categorical variables were employed as independent variables in statistical analyses (Table 1). For a given wetland, vegetation sampling and avian censuses were conducted in the same breeding season (following the protocol described in Hamel et al. 1996). At each wetland, all data were collected from an 11.28-m-radius circle surrounding the point-count center (see table 1 in James and Shugart 1970).

Percent cover of several classes of vegetation structure and open water (Table 1) were estimated by using an ocular tube (Hamel et al. 1996). In each of the four cardinal directions, we measured 2, 4, 6, 8, and 10 m from the point-count center. At each of these points we looked downward and upward through a 5.08-cm ocular tube. Presence of vegetation structural layer(s) observed within the field of view of the ocular tube were recorded and used to calculate the percent cover of vertical structural layers in the vegetation plot.

We used a vegetation profile board to assess horizontal vegetation structure in each wetland (Hamel et al. 1996). This method entails using a profile board (50.8 × 50.8 cm) that is divided into a grid of 25 equally sized squares. The board was placed vertically on the ground, 10 m from, and facing, the point center. We recorded number of squares fully visible at 0, 2.5, 5, and 7 m from point center, in each of the cardinal directions. A simple calculation using the number of obstructed squares (across all distances and directions) was used to estimate percent horizontal vegetation density in each wetland (Hamel et al. 1996).

Data analysis.—We used SAS (SAS Institute, Inc. 2000) to conduct stepwise multiple linear regressions (SMLR) with the PROC GLM program for among-site analyses of wetland use by breeding birds at the community and guild levels. Species richness and total abundance values calculated from point-count data were our dependent variables, and vegetation and habitat data collected from each wetland were independent variables. Because data from 2000 and 2001 did not differ (*t*-tests), we pooled data from both years.

TABLE 1. Description of 18 independent variables measured in 57 southern Appalachian wetlands during 2000 and 2001.

Independent variables	Method of measurement
Wetland class	Persistent-emergent, scrub-shrub, or forested (Cowardin et al. 1979)
Livestock evidence	Presence or absence of recent livestock activity (i.e., livestock, trampling, and/or manure)
Edge type	Edge nearest the point-count center was gradual or abrupt
Beaver evidence	Presence or absence of recent beaver activity (i.e., actively maintained dams, freshly felled trees, and/or recently gnawed stumps)
Ownership status	Publicly or privately owned
Blue Ridge Parkway ownership status	Under the jurisdiction (or not) of Blue Ridge Parkway National Park
Size of wetland	Publicly owned sites: information obtained from managers; privately owned sites: estimated (to the nearest 0.1 ha) from 1:24,000 USGS topographic maps
Open water	Percent cover of open water[a]
Stem density of snags	No. snags >10 cm dbh[b]
Stem density of live trees	No. trees >10 cm dbh[b]
Basal area of live and dead trees (cm^2)	Total basal area of trees >10 cm dbh[b] (measured with a Biltmore stick; Hamel et al. 1996)
Canopy cover	Percent canopy cover[a,b]
Midstory cover	Percent cover of total midstory vegetation[a,b]
Shrub cover	Percent cover of shrub vegetation[a,b]
Ground cover	Percent ground cover[a,b]
Forb cover	Percent cover of forb vegetation[a,b]
Grass cover	Percent cover of grass vegetation[a,b]
Vegetation profile	Estimated horizontal density of vegetation[a,b]

[a] Vegetation measures made using the ocular tube method (Hamel et al. 1996).
[b] Measurements taken within 11.28-m circular sample plots.

We checked all dependent and independent variable distributions for outliers using box plots and normal probability plots (Tabachnick and Fidell 1983, Zar 1999). Outlying values for independent variables were confirmed not to have resulted from data entry errors, and were retained for final regression analyses. We also checked all variables for normality using residual scatterplots (Tabachnick and Fidell 1983, Zar 1999) obtained by running preliminary multiple regression models for every dependent variable against all raw data for the independent variables (SAS Institute, Inc. 2000). Residual scatterplots for all dependent variables were normal, and regression models for all dependent variables were considered valid.

Prior to running final regression analyses, we conducted a correlation analysis on all independent variables to eliminate redundancy in habitat measurements. In cases where correlations were ≥0.50, we removed one of the variables before running final regression analyses. For regression models, categorical variables, such as evidence of beaver activity, edge type, and wetland type, were assigned absence/presence values of 0 or 1, respectively. Only parameters significant at $P < 0.05$ were included in final regression models.

RESULTS

During the 2000 and 2001 breeding seasons, we conducted 171 point counts in the 57 study wetlands and detected 2,266 birds representing 90 species (see Appendix for species observed).

Community-level analyses.—Presence of gradual edges, beaver evidence, and private ownership collectively explained 50% of the variation in community species richness of NTMBs (Table 2). Beaver evidence also explained 16% of community abundance, and abundance associated with wetlands on the BRP was lower than it was at wetland sites elsewhere (Table 2).

Guild-level analyses.—Species richness of NTMBs was explained by the presence of gradual edge (42.5% of variation) and evidence of beaver activity (7%; Table 3). Percent ground cover was also positively corre-

TABLE 2. Significant ($P < 0.05$) predictors of community-level avian use at 57 southern Appalachian wetlands during the breeding seasons of 2000 and 2001.

Community-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
Species richness[a]	Gradual edge	23.51	0.96	0.300***[b]	
	Beaver evidence	10.15	1.13	0.111**	0.41**
	Ownership status	9.66	0.96	0.091**	0.50**
Mean avian abundance[c]	Beaver evidence	10.11	4.64	0.155**	
	BRP status	7.05	3.97	0.098*	0.25*

[a] Total number of species detected in all three point counts in each wetland.
[b] *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[c] Mean number of individuals observed during three point-count visits to each study wetland.

lated with species richness, although percent grass cover was negatively associated with species richness (Table 3). As with NTMB richness, NTMB abundance was most strongly associated with gradual edge and evidence of beaver activity; collectively, these variables explained 37% of the model variation. Also, though to a lesser degree, NTMB abundance was positively associated with percent cover of canopy vegetation (Table 3).

Basal area of trees at our sites had the strongest negative effect on species richness and abundance of early-successional NTMBs: it explained 16% of the variation in both richness and abundance models (Table 4). Early-successional NTMB species richness and abundance were positively correlated with grazing and gradual edge, respectively (Table 4). Late successional NTMB species richness and abundance both were positively associated with gradual edge, basal area, and evidence of beaver activity (Table 4). In addition, species richness of late-successional NTMBs was positively associated with canopy cover (accounting for 19% of the variation) and abundance was positively associated with midstory cover (accounting for ~5% of the variation) (Table 4).

DISCUSSION

Although our vegetation sampling areas (11.28-m-radius circular plots) did not correspond exactly with our avian census areas (50-m-radius circular plots), the wetland sizes were small, in which case our quantitative vegetation measurements should have adequately represented the vegetation of most wetlands overall; only the largest wetlands may have been represented inadequately in our 11.28-m vegetation plots. We recognize that this spatial inconsistency may have driven the effects of our qualitative habitat variables (i.e., evidence of beaver activity, edge type) more than the continuous variables (e.g., percent cover of vegetation types) in our regression models. However, relationships between avian community structure and vegetation structure should not be disregarded.

In general, many of our results support existing hypotheses about the effects of land use and environmental variables on NTMB species richness and abundance. At the community and guild levels, species richness and abundance were associated with various habitat characters that can be explained by the habitat preferences of late- and early-succes-

TABLE 3. Significant ($P < 0.05$) predictors of southern Appalachian wetland use by the Neotropical migratory bird (NTMB) guild during the breeding seasons of 2000 and 2001.

Guild-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
NTMB species richness	Gradual edge	40.59	0.62	0.425***[a]	
	Grass cover (%)	4.37	0.01	0.078**	0.50**
	Beaver evidence	7.93	0.83	0.074**	0.576**
	Ground cover (%)	9.68	1.03	0.033*	0.609*
NTMB abundance	Gradual edge	21.53	2.37	0.284***	
	Beaver evidence	7.83	2.80	0.090**	0.374**
	Canopy cover (%)	4.53	0.06	0.063*	0.436*

[a] *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 4. Significant ($P < 0.05$) predictors of southern Appalachian wetland use by early-successional (ES-NTMB) and late-successional (LS-NTMB) Neotropical migratory bird guilds during the breeding seasons of 2000 and 2001.

Guild-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
ES-NTMB species richness	Basal area	10.14	0.00	0.156**[a]	
	Livestock evidence	11.47	0.38	0.148**	0.304**
ES-NTMB abundance	Basal area	10.45	0.01	0.160**	
	Gradual edge	10.84	1.33	0.141**	0.300**
LS-NTMB species richness	Gradual edge	32.60	0.66	0.372***	
	Canopy cover (%)	22.58	0.02	0.185***	0.557***
	Beaver evidence	8.94	0.73	0.064**	0.621**
	Basal area	4.68	0.00	0.031*	0.652*
LS-NTMB abundance	Basal area	40.45	0.01	0.424***	
	Beaver evidence	18.19	1.80	0.145***	0.569***
	Midstory cover (%)	6.40	0.06	0.046*	0.615*
	Gradual edge	4.22	1.62	0.029*	0.644*

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

sional NTMBs. The positive association between private ownership and species richness, however, was unexpected. Although many of the publicly owned wetlands we studied are managed, in part, to promote biodiversity, our results show that private wetlands had greater community-level species richness than sites held in public trust. This may reflect landscape-level influences. We suspect that publicly owned sites often were surrounded by less fragmented landscapes than privately owned sites, which often were embedded in landscapes fragmented by various land uses. The relatively greater number of small habitat patches surrounding privately owned wetlands might have generated a greater diversity of habitats that supported a greater variety of birds (Whitcomb et al. 1981).

The positive effects of gradual edges on the avian community overall, and on NTMBs, were also unexpected. Numerous studies have shown that, in fragmented forest landscapes with high edge-to-interior ratios, area-sensitive NTMBs experience increased predation due to greater predator abundance (Temple and Cary 1988, Wilcove and Robinson 1990, Faaborg et al. 1995) and species richness (Forsyth and Smith 1973, Heske 1995, Chalfoun et al. 2002), as well as greater rates of brood parasitism (Brittingham and Temple 1983, Johnson and Temple 1990). However, the differential effects of gradual versus abrupt edges on NTMBs have received far less attention.

Authors of previous studies have reported greater rates of nest predation along abrupt edges than in gradual edges; they further propose that the more developed vegetation structure in gradual edges provides superior nest concealment (Ratti and Reese 1988) and minimizes the activity and efficiency of predators (Luck et al. 1999). Gradual edges may also provide foraging benefits. Lopez de Casenave et al. (1998) found greater avian species richness and abundance in ''mature,'' or gradual, edges than in surrounding habitats. They concluded that complex, mature edges provided greater fruit production and more foraging niches for birds. Along with these findings, our results suggest that further assessments of parasitism, predation, and foraging efficiency in abrupt versus gradual edges may help determine why edge structure can affect avian community structure.

Overall structure of wetland vegetation affected by beaver activity also may have influenced southern Appalachian bird communities. Grover and Baldassarre (1995) found that wetlands actively maintained by beaver harbored greater species richness of breeding NTMBs and woodland species than other wetlands, primarily due to their structurally diverse edges. In our study, beaver-impacted wetlands were characterized by gradual edges more often than by abrupt edges ($P < 0.05$, $R^2 = 0.302$).

Beaver activity is also thought to enhance avian foraging efficiency by creating structurally diverse habitats with a diversity of foraging niches (Medin and Clary 1990) and by increasing the productivity of insects—the dominant component of NTMB diets (Reese and Hair 1976). Further investigations focusing on differences in wetland vegetation structure and productivity in beaver-impacted versus other wetlands could provide more conclusive results regarding how beaver may enhance habitat quality for nesting NTMBs.

From a management perspective, results from our study and those of previous studies suggest new approaches to managing southern Appalachian wetlands to promote persistence of native birds. ‘‘Gradualizing’’ wetland edges and encouraging beaver could be especially beneficial for NTMBs. Edges are inherent results of current land-use practices, and although the effects of edge quantity on area-sensitive songbirds are well-documented, a better understanding of how edge quality affects these species may help to refine management activities.

Future investigations of how beaver benefit songbirds at local and landscape levels also might be prudent. Paradoxically, populations of avian species with very different habitat requirements are in decline, including those that prefer both early-successional grasslands and late-successional forests. Some researchers have argued that landscapes in the southeastern United States have lost their heterogeneity and are now dominated by homogeneous stands of mid-successional forest (Hunter et al. 2001). Prior to their near extirpation over a century ago, the estimated 60 million beaver in North Carolina alone (McGrath and Summer 1992) would have generated a remarkable mosaic of early- to late-successional ponds, meadows, and forested bogs. The physiographic diversity of these sites, coupled with their productivity, may have benefited bird species with a wide range of resource requirements. Rather than treating beaver as pests, public land managers in the southern Appalachians should encourage beaver in their efforts to restore a heterogeneous landscape capable of supporting a diverse avifauna.

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APPENDIX. Occurrence rates of bird species observed in 57 southern Appalachian study wetlands during 2000 and 2001.

Common name	Scientific name	No. sites where observed (%)
Wood Duck	*Aix sponsa*	2 (3.51)
Mallard	*Anas platyrhynchos*	1 (1.75)
Ruffed Grouse	*Bonasa umbellus*	1 (1.75)
Northern Bobwhite[a,b]	*Colinus virginianus*	1 (1.75)
American Bittern[a]	*Botaurus lentiginosus*	1 (1.75)
Green Heron[a]	*Butorides virescens*	1 (1.75)
Turkey Vulture	*Cathartes aura*	4 (7.02)
Red-tailed Hawk	*Buteo jamaicensis*	1 (1.75)
Killdeer[a]	*Charadrius vociferus*	1 (1.75)
Mourning Dove[a]	*Zenaida macroura*	6 (10.53)
Chimney Swift[a,b]	*Chaetura pelagica*	1 (1.75)
Ruby-throated Hummingbird	*Archilochus colubris*	11 (19.30)
Belted Kingfisher[a]	*Ceryle alcyon*	10 (17.54)
Red-bellied Woodpecker	*Melanerpes carolinus*	6 (10.53)
Yellow-bellied Sapsucker[c]	*Sphyrapicus varius*	3 (5.26)
Downy Woodpecker[b]	*Picoides pubescens*	12 (21.05)
Hairy Woodpecker	*Picoides villosus*	11 (19.29)
Northern Flicker[a,b]	*Colaptes auratus*	2 (3.51)
Pileated Woodpecker	*Dryocopus pileatus*	3 (5.26)
Eastern Wood-Pewee[a,b,c]	*Contopus virens*	12 (21.05)
Acadian Flycatcher[b,c]	*Empidonax virescens*	8 (14.04)
Alder Flycatcher[c]	*Empidonax alnorum*	14 (24.56)
Willow Flycatcher[a]	*Empidonax traillii*	9 (15.79)
Least Flycatcher[a]	*Empidonax minimus*	9 (15.79)
Eastern Phoebe[b]	*Sayornis phoebe*	21 (36.84)
Great Crested Flycatcher	*Myiarchus crinitus*	2 (3.51)
White-eyed Vireo	*Vireo griseus*	4 (7.02)
Blue-headed Vireo[c]	*Vireo solitarius*	16 (28.07)
Red-eyed Vireo	*Vireo olivaceus*	35 (61.40)
Blue Jay[a,b]	*Cyanocitta cristata*	11 (19.30)
American Crow	*Corvus brachyrhynchos*	21 (36.84)
Tree Swallow	*Tachycineta bicolor*	1 (1.75)
Bank Swallow	*Riparia riparia*	1 (1.75)
Barn Swallow	*Hirundo rustica*	1 (1.75)
Carolina Chickadee[a]	*Poecile carolinensis*	32 (56.14)
Tufted Timouse	*Baeolophus bicolor*	28 (49.12)
Red-breasted Nuthatch[c]	*Sitta canadensis*	2 (3.51)
White-breasted Nuthatch	*Sitta carolinensis*	10 (17.54)
Brown Creeper[c]	*Certhia americana*	1 (1.75)
Carolina Wren[b]	*Thryothorus ludovicianus*	17 (29.82)
House Wren	*Troglodytes aedon*	9 (15.79)
Winter Wren[c]	*Troglodytes troglodytes*	1 (1.75)
Golden-crowned Kinglet[c]	*Regulus satrapa*	7 (12.28)
Blue-gray Gnatcatcher[b]	*Polioptila caerulea*	6 (10.53)
Easten Bluebird	*Sialia sialis*	22 (38.60)
Veery[a]	*Catharus fuscescens*	4 (7.02)
Wood Thrush[a,b,c]	*Hylocichla mustelina*	12 (21.05)
American Robin[b]	*Turdus migratorius*	25 (43.86)
Gray Catbird[b,c]	*Dumetella carolinensis*	40 (70.18)
Northern Mockingbird[a]	*Mimus polyglottos*	2 (3.51)
Brown Thrasher[a]	*Toxostoma rufum*	8 (14.04)
European Starling[a]	*Sturnus vulgaris*	9 (15.79)
Cedar Waxwing	*Bombycilla cedrorum*	31 (54.39)
Golden-winged Warbler[a,c]	*Vermivora chrysoptera*	3 (5.26)
Northern Parula[c]	*Parula americana*	21 (36.84)
Yellow Warbler	*Dendroica petechia*	8 (14.04)

APPENDIX. Continued.

Common name	Scientific name	No. sites where observed (%)
Chestnut-sided Warbler[a,c]	*Dendroica pensylvanica*	17 (29.82)
Black-throated Blue Warbler[c]	*Dendroica caerulescens*	14 (24.56)
Yellow-rumped Warbler	*Dendrocia coronata*	1 (1.75)
Black-throated Green Warbler	*Dendroica virens*	2 (3.51)
Blackburnian Warbler[c]	*Dendroica fusca*	2 (3.51)
Pine Warbler	*Dendroica pinus*	3 (5.26)
Prairie Warbler[a,b]	*Dendroica discolor*	3 (5.26)
Black-and-white Warbler[b]	*Mniotilta varia*	10 (17.54)
American Redstart	*Setophaga ruticilla*	5 (8.77)
Worm-eating Warbler[c]	*Helmitheros vermivorum*	2 (3.50)
Swainson's Warbler[b,c]	*Limnothlypis swainsonii*	1 (1.75)
Ovenbird[b]	*Seiurus aurocapilla*	17 (29.82)
Louisiana Waterthrush[c]	*Seiurus motacilla*	7 (12.28)
Common Yellowthroat[a,b]	*Geothlypis trichas*	36 (63.16)
Hooded Warbler[c]	*Wilsonia citrina*	22 (38.60)
Canada Warbler[a,c]	*Wilsonia canadensis*	3 (5.26)
Yellow-breasted Chat[b]	*Icteria virens*	7 (12.28)
Scarlet Tanager[a,b,c]	*Piranga olivacea*	15 (26.32)
Eastern Towhee[a,b]	*Pipilo erythrophthalmus*	38 (66.67)
Chipping Sparrow[b]	*Spizella passerina*	10 (17.54)
Field Sparrow[a,b]	*Spizella pusilla*	13 (22.81)
Song Sparrow[a,b]	*Melospiza melodia*	41 (71.93)
White-throated Sparrow[a]	*Zonotrichia albicollis*	2 (3.51)
Dark-eyed Junco[a,c]	*Junco hyemalis*	16 (28.07)
Northern Cardinal	*Cardinalis cardinalis*	37 (64.91)
Rose-breasted Grosbeak[a]	*Pheucticus ludovicianus*	1 (1.75)
Indigo Bunting[a,b]	*Passerina cyanea*	42 (73.68)
Red-winged Blackbird[a]	*Agelaius phoeniceus*	21 (36.84)
Eastern Meadowlark[a,b]	*Sturnella magna*	5 (8.77)
Common Grackle	*Quiscalus quiscula*	4 (7.02)
Brown-headed Cowbird[a]	*Molothrus ater*	3 (5.26)
House Finch	*Carpodacus mexicanus*	6 (10.53)
American Goldfinch	*Carduelis tristis*	36 (63.16)
House Sparrow[a,b]	*Passer domesticus*	1 (1.75)

[a] Undergoing significant population decline throughout the species' breeding range (Sauer et al. 2001).

[b] Undergoing a moderate or significant population decline in southern Blue Ridge region (Partners in Flight physiographic region 23; Carter et al. 2000, Hunter et al. 1999) or in the Blue Ridge region of the North American Breeding Bird Survey (Sauer et al. 2001).

[c] Considered a priority species in the southern Blue Ridge region (Partners in Flight physiographic region 23; Carter et al. 2000, Hunter et al. 1999) or a species of local concern in the southern Appalachians (North Carolina Natural Heritage Program; LeGrand et al. 2001, Hunter et al. 1993, D. S. Lee and B. Browning unpubl. data).