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WOOD DUCK AND MALLARD WINTER MICROHABITATS IN MISSISSIPPI HARDWOOD BOTTOMLANDS

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Abstract: Wood ducks (Aix sponsa) and mallards (Anas platyrhynchos) use southern hardwood bottomlands and greentree reservoirs extensively during winter, but possible differential microhabitat use by these species in forested wetlands has not been investigated. Consequently, we quantified aspects of forest structure, relative availability of potential foods (e.g., acorns and invertebrates), and water depth at microhabitats of wood ducks and mallards in 3 greentree reservoirs in Mississippi during winters 1988–90 to test the null hypothesis that species' microhabitats did not differ. Species' microhabitats differed ($P \le 0.03$) in 1 or both winters. Compared with wood ducks, mallards used microhabitats with greater "openness" (i.e., less canopy closure, tree density, and understory cover), lower tree species diversity, and shallower water. Our results provide additional support for the continued need to conserve southern forested wetlands through preservation and restoration of bottomland hardwoods, and integration of waterfowl habitat management with ecologically sound bottomland hardwood silviculture and timber harvesting.

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Habitat use by birds is guided by instinctive and learned responses to environmental and social stimuli (Hildén 1965). Regarding migratory species, habitat use can be viewed as a hierarchical process of selection from macroscales to microscales (Kotliar and Wiens 1990). For example, migratory waterfowl may make a "first-order" selection of a physiographic region, next a "second-order" selection of wetland habitats within regions, and finally a "third-order" selection of microhabitats within wetlands (Wiens 1973, Johnson 1980). Ricklefs (1990:816) defined microhabitat as segments of habitat that animals use during their activities.

Wood ducks and mallards are important migratory waterfowl in the Mississippi and Atlantic flyways from harvest, management, and research perspectives (Bellrose 1976, Fredrickson et al. 1990, Gamble 1990, Serie and Chasko 1990). The Mississippi Alluvial Valley (MAV) and other riverine flood plains in the southeastern United States are important physiographic landscapes for these species (Nichols et al. 1983, Ladd 1990:122). In this region, forested wetlands, particularly bottomlands containing red oak species (Quercus spp. subgenus Erythrobalanus), are valuable habitats for both species (Bellrose 1976, Heitmeyer 1985, Fredrickson and Heitmeyer 1988, Thompson and Baldassarre 1988, Heitmeyer and Fredrickson 1990a). Additionally, impounded hardwood bottomlands (i.e., greentree reservoirs [GTR's]) have been widely established in the southern United States to provide winter and migrational habitat for these and other waterfowl species (Reinecke et al. 1989, Wigley and Filer 1989).

Differential use of wetland habitats by mallards and wood ducks wintering in the MAV has been reported (Heitmeyer 1985, Combs 1987, Dell et al. 1987, Heitmeyer and Fred-

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rickson 1990a, Reinecke et al. 1992). Despite these studies and the functional importance of forested wetlands for migrating and wintering wood ducks and mallards, microhabitat use within forested wetlands by these species has not been investigated. Because wintering wood ducks and mallards exploit similar resources in hardwood bottomlands (e.g., mast and invertebrates [Allen 1980, Delnicki and Reinecke 1986, Fredrickson and Heitmeyer 1988, Kirby 1990, Heitmeyer and Fredrickson 1990b]), microhabitat differences within habitats, regional geographic separation, asynchronous annual events, different foraging modes and body morphology, and/or competitive interactions may occur between species to reduce potential resource overlap (Fredrickson and Heitmeyer 1988). To address the first alternative (i.e., potential microhabitat differences), we measured variables characteristic of microhabitats where wood ducks and mallards were observed in several Mississippi GTR's. Specifically, we desired to test the null hypothesis that wood duck and mallard microhabitats were similar within study areas and years, to discern any patterns in species' microhabitat use between study areas and years, and to make management and research recommendations consistent with our results.

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STUDY AREA

We conducted our study in GTR's 1 and 2 at Noxubee National Wildlife Refuge in eastcentral Mississippi, and West GTR in Delta National Forest in westcentral Mississippi (Sherman et al. 1992). Delta National Forest and Noxubee Refuge are located in the MAV and Interior Flatwoods physiographic regions of Mississippi, respectively (Pettry 1977). Because of alternate-year flooding of GTR's at Noxubee Refuge, GTR's 2 and 1 were used as study areas during winters 1988–89 and 1989–90, respectively. West GTR was inundated and used as a study area during both winters.

GTR's 1 and 2 were contiguous bottomland hardwood impoundments separated by a levee containing a water control structure with flowthrough capability. Water from adjacent Bluff Lake flowed via gravity to flood both GTR's. When flooded, the GTR's were inundated from late November-early December through late February-early March. GTR 1 encompassed approximately 240 ha; GTR 2 impounded about 200 ha. However, extent and depth of flooding varied with precipitation and periodic overflows from the nearby (<0.5 km) Noxubee River. Average flooded area was 144 and 107 ha in GTR's 1 and 2, respectively. Dominant overstory tree species were overcup oak (Q. lyrata), willow oak (Q. phellos), water oak (Q. nigra), cherrybark oak (Q. falcata var. pagodaefolia), and sweetgum (Liquidambar styraciflua) (Young 1990). West GTR encompassed 228 ha of flooded hardwood bottomland. Dominant trees included overcup oak and Nuttall oak (Q. nuttallii), water hickory (Carya aquatica), and sugar hackberry (Celtis laevigata) (Alexander 1990). Additional details concerning these sites and physiographic regions have been described elsewhere (Pettry 1977, Reinecke et al. 1989, Alexander 1990, Sherman 1990, Young 1990).

METHODS

Transect Lines

Wood ducks and mallards were observed from transect lines located throughout the GTR's (Sherman 1990, Sherman et al. 1992). Approximately 7 km (8 lines), 5 km (5 lines), and 7 km (6 lines) of parallel transect lines, spaced 200 m apart, were established in a north–south orientation in GTR 1, GTR 2, and West GTR, respectively. Lines were marked by blazes of yellow or white latex or spray paint on trees along or immediately adjacent to transects. Trees were marked at close, irregular intervals to ensure easy following of transects during ground surveys. No vegetation was cleared or otherwise modified along transect lines.

Waterfowl Surveys and Microhabitats

Line-transect surveys of wood ducks and mallards were conducted in the GTR's at Noxubee Refuge and Delta National Forest during winters 1988-89 and 1989-90 (Sherman 1990, Sherman et al. 1992). The same 2 observers conducted all surveys usually at 7- to 10-day intervals (range = 6-21 days) at both study areas between early December and early March. Surveys began at daylight and continued until either all transects were traversed or 1-2 hours before dusk. Attired in camouflaged clothing, the observers walked together slowly and quietly during surveys and observed ducks visible from transect lines. The observers visually noted sites where ≥2 wood ducks or mallards were seen feeding, resting, and/or courting. Pairs or flocks of ducks observed swimming or that seemed alert to the observers' presence were not considered for microhabitat sampling. The center of sites where ducks were initially sighted and accurately marked was deemed the microhabitat. Insufficient sample size prevented analysis of microhabitat data by flock size, sex ratio, and date. Microhabitats were marked with flagging tape, and observers returned to them in ≤1 day to measure site variables.

Microhabitat Variables

We measured 11 variables within 0.01-ha circular plots centered on microhabitats. Tree species diversity (Shannon and Weaver 1949) and basal area of all trees with a diameter at breast height (dbh) of ≥7.6 cm (Duncan and Duncan 1988) were determined for all microhabitat plots. Tree density was the number of all trees within plots having the above dbh criterion. Height of overstory trees within or closely (≤10 m) surrounding each plot was determined using a range finder. Percent understory cover (i.e., woody stems < 7.6 cm dbh and/or herbaceous vegetation) above water was estimated with a modified density board (Nudds 1977). Portions of the board (30 × 243 cm) covered by vegetation were determined by 1 observer positioned at plot center, while the other observer held the density board at each cardinal directional location around the circumference of the plots. The resulting 4 density values were averaged for each plot. Water depth also was measured at these 4 locations and averaged likewise. Percent canopy openness was estimated at plot center, using a spherical densiometer (Lemmon

1957). Readings were taken in each cardinal direction and averaged for each plot. All exposed or floating substrates within plots were counted as an index of possible waterfowl loafing sites. Distance to nearest cover was measured with a range finder or by pacing. Cover was defined as any downed trees or other woody/ herbaceous vegetation that was deemed sufficient to conceal ducks previously observed at the microhabitat. To index availability of sound acorns and other hard mast (i.e., submerged nuts resting on the substrate) and invertebrates as potential duck foods, a sweep net (20 × 46 × 30 cm), with its handle bent 45° upward from horizontal (Voigts 1976), was used to collect 1 sample of available mast and invertebrates in each plot. The net was moved along the substrate at plot center for 1 m and then lifted vertically through the water column. All potential foods were counted in the field, recorded. and then discarded.

Statistical Analyses

We used discriminant function analysis (DFA), with stepwise inclusion of variables (P ≤ 0.1), to test for differences between wood duck and mallard microhabitats within study areas and years (Klecka 1975; 1989). DFA enables a multivariate test of difference between ≥2 groups, using the same set of independent variables measured for each group. DFA also allows prediction of group membership for samples, with accuracy related to discriminating ability of measured variables. DFA was not used unless sample size within species and years was ≥20. Except for mallard microhabitats in West GTR in winter 1988–89 (n = 12), n ranged from 23 to 48 within study areas, years, and species. We used an independent 2-sample t-test (Zar 1984) to compare wood duck and mallard microhabitat variables for West GTR in winter 1988-89.

Microhabitat variables were transformed to meet assumptions of DFA (Klecka 1989). Variables that were counts (e.g., n loafing sites, n mast, n invertebrates) and all percent data (e.g., canopy openness, understory cover) were transformed using square-root and arcsine square-root transformations, respectively (Zar 1984). Remaining variables were transformed using either square-root or natural logarithmic transformations (Zar 1984). Possible collinearity among variables was assessed using simple correlation analysis and variance inflation factors

Table 1. Variables measured at sites where wood ducks and mallards were observed in 2 greentree reservoirs, Noxubee National Wildlife Refuge, Mississippi, winters 1988-89 and 1989-90.

Variable		Wood	duck		Mallard				
	1988-89		1989–90		1988-89		1989-90		
	ź	SEa	Ī	SEª	ž	SEb	î	SEb	
Canopy openness (%)	7.3	1.2	10.4	3.2	11.5	2.3	10.7	1.4	
Understory cover (%)	13.7	2.5	9.9	2.1	8.6	1.4	9.8	1.0	
Tree diversity (natural bels)	0.81	0.09	0.81	0.11	0.62	0.09	0.59	0.08	
Water depth (cm)	43.6	3.5	39.3	3.8	39.0	3.1	31.3	2.4	
Tree height (m)	25.8	1.8	29.1	0.8	27.7	0.7	28.8	0.6	
Basal area (m²/ha)	28.4	3.5	27.4	4.4	30.2	4.2	27.7	3.7	
Loafing sites (n)	2.1	0.3	1.3	0.2	2.1	0.3	1.8	0.4	
Cover proximity (m)	24.7	3.7	63.0	8.3	26.1	4.8	45.8	5.1	
Hard mast (n/m²)	4.7	1.5	3.0	2.2	2.7	0.7	5.6	2.0	
Invertebrates (n/m^2)	53.1	11.1	47.3	14.5	87.0	. 32.1	39.0	6.6	

^a n=31 and 23 for wood ducks in 1988–89 and 1989–90, respectively. b n=30 and 36 for mallards in 1988–89 and 1989–90, respectively.

(VIF's) (Wiesberg 1985). Klecka (1975) considered extreme collinearity to exist when $R^2 \ge$ 0.64. We decided a priori that correlated (i.e., $R^2 \ge 0.36$) pairs of variables and VIF's ≥ 10 would provide evidence of collinearity (Kleinbaum et al. 1988). Generally, basal area, tree density, and percent canopy openness were correlated either positively or negatively with each other, so only canopy openness was included in DFA. We used canopy openness in DFA instead of basal area and tree density, because we assumed that ducks descending into GTR's would be influenced first by canopy openness and subsequently by forest structure and other microhabitat characteristics below the canopy. Nonetheless, we also included basal area and tree density in our analyses by comparing these variables between wood duck and mallard microhabitats within years and study areas with an independent 2-sample t-test. All variables used in DFA's were deemed sufficiently independent (i.e., $VIF \le 4.04$, $0.00 \le R^2 \le 0.35$), based on the aforementioned established criteria. Significance level for DFA's and t-tests was set a priori at alpha = 0.05.

RESULTS

Noxubee National Wildlife Refuge

Microhabitat data were obtained for 54 wood duck (31 in 1988-89, 23 in 1989-90) and 66 mallard sites (30 in 1988-89, 36 in 1989-90). DFA and standardized discriminant function coefficients (SDFC) revealed that percentages of canopy openness (SDFC = 0.93) and understory cover (SDFC = -0.92) separated (P = 0.008) wood duck and mallard microhabitats with approximately equal importance in winter 1988-89. Wood duck sites exhibited less canopy openness (approx 4%) and more understory cover (approx 5%) than mallard sites (Table 1). The DFA model explained 39% of the variation between wood duck and mallard microhabitats and correctly classified 65% and 60% of the species' sites, respectively.

In winter 1989-90, DFA and SDFC's revealed that water depth (SDFC = 0.79) and tree species diversity (SDFC = 0.75) distinguished (P = 0.03) wood duck from mallard microhabitats with nearly equivalent strength. Wood ducks were observed at sites with greater average water depth (8 cm) and tree species diversity (0.22 natural bels) than mallard microhabitats (Table 1). Although canopy openness was not a significant discriminant variable in winter 1989-90, tree density/plot (i.e., a negative correlate of canopy openness) was greater (t = 2.96, P = 0.004, 57 df) at wood duck $(\bar{x} =$ 5.0 trees/plot, SE = 0.56, n = 23) than mallard sites ($\bar{x} = 3.0$ trees/plot, SE = 0.39, n = 36). The DFA model accounted for 34% of the variation between wood duck and mallard microhabitats and correctly classified 61% and 75% of the species' sites, respectively.

Delta National Forest

We located and marked 88 wood duck microhabitats (48 in 1988-89, 40 in 1989-90) and 39 mallard sites (12 in 1988-89, 27 in 1989-90). Univariate analyses were performed on the 1988-89 data set because of a small sample of

Table 2. Variables measured at sites where wood ducks and mallards were observed in a-greentree reservoir, Delta National Forest, Mississippi, winters 1988–89 and 1989–90.

Variable	Wood duck				Mallard			
	1988-89		1989-90		1988-89		1989-90	
	ž	SEa	ž	SEa	ŕ	SEb	ź	SEb
Canopy openness (%)	4.2	0.5	8.5	1.2	8.1	2.4	10.7	2.2
Understory cover (%)	22.8	2.6	26.2	2.6	18.0	3.9	18.5	2.2
Tree diversity	1.04	0.07	0.95	0.06	0.74	0.18	0.86	0.09
(natural bels) Water depth (cm)	34.2	.1.8	35.9	1.8	36.2	3.1	35.7	2.0
Tree height (m)	24.2	0.5	25.1	0.6	25.0	1.1	26.3	0.7
Basal area (m²/ha)	32.0	3.8	48.5	6.9	33.9	8.5	44.6	7.0
Loafing sites (n)	1.6	0.4	1.2	0.3	1.1	0.4	1.0	0.3
Cover proximity (m)	13.2	1.5	22.2	3.0	14.6	3.1	27.0	3.8
Hard mast (n/m^2)	3.0	0.7	3.0	0.9	3.6	1.6	1.6	0.4
Invertebrates (n/m^2)	105.7	14.5	54.4	11.1	72.9	12.0	90.0	21.8

a n=48 and 40 for wood ducks in 1988–89 and 1989–90, respectively. b n=12 and 27 for mallards in 1988–89 and 1989–90, respectively.

mallard microhabitats. Percent canopy openness was less (t = -2.53, P = 0.014, 58 df) at wood duck than mallard microhabitats in winter 1988–89 (Table 2). Conversely, tree density was

greater (t=2.57, P=0.013) at wood duck ($\bar{x}=5.6$ trees/plot, SE = 0.43, n=48) than mallard sites ($\bar{x}=3.2$ trees/plot, SE = 0.54, n=12).

In winter 1989–90, DFA and SDFC's revealed that percentages of canopy openness (SDFC = 1.02) and understory cover (SDFC = -0.71) differentiated (P = 0.03) species' microhabitats. Absolute values of SDFC's suggested that canopy openness was more important than understory cover in separating wood duck from mallard microhabitats. Wood ducks 'were associated with sites having less canopy openness (approx 2%) and more understory cover (approx 2%) than mallard microhabitats (Table 2). The DFA model accounted for 32% of the variation between species' microhabitats and classified 63% of the sites correctly for each species.

DISCUSSION

Wood duck and mallard microhabitats differed at both study areas and in both years, but precision and accuracy of DFA models were marginal. The majority of measured variables did not differ significantly between wood duck and mallard microhabitats, which resulted in the DFA models explaining relatively little of the total variation (<40%) and moderate correct classification (60–75%) of species' microhabitats. Thus, we concluded that our models were not useful for predicting wood duck and mallard microhabitats in our study areas and perhaps other GTR's and similar forested wetlands.

Some of the similarity between wood duck and mallard microhabitat variables may have been due to observer disturbance during linetransect surveys, despite our attempts to observe ducks from a distance, move quietly and very slowly, and measure variables only at microhabitats where ducks were seemingly undisturbed. Several other factors may have contributed to variation in microhabitat variables and overlap between species' microhabitats. These factors may have included variation in flock size and physiological, behavioral, sexual, age, and social-status differences of individuals within and among observed groups (Fredrickson and Heitmeyer 1988); plasticity in microhabitat use within and between species (Mulhern et al. 1985); use of similar resources at different times (Fredrickson and Heitmeyer 1988); and climatic variation among surveys influencing waterfowl use of different local habitats (Sherman et al. 1992). Additionally, decreased potential for discerning differences at a microhabitat scale of sampling (Wiens 1985, 1989) and small sample size in at least 1 case (i.e., mallard microhabitats at Delta National Forest in winter 1988-89 [n = 12]likely reduced statistical power and detection of potential differences.

Despite potential reasons for variability and habitat overlap, wood duck and mallard microhabitats differed most consistently between areas and years with respect to forest structural characteristics and water depth. Wood ducks diverged from mallards along microhabitat gradients of increasing canopy closure, understory cover, tree density, tree species diversity, and water depth. Like Nudds (1982), we lacked data

on resource use by ducks to determine whether detected microhabitat differences were related to competition for resources (e.g., food). Nevertheless, we concur with Nudds (1982) that it seemed unnecessary to suggest that interference competition (i.e., direct agonistic interactions [Pianka 1974:134]) between wood ducks and mallards influenced microhabitat differences. Fredrickson and Heitmeyer (1988) also suggested that wood ducks and mallards reduced potential competition for food and habitat resources by exhibiting specific differences in winter distribution, chronology of annual events, ecology, morphology, and behavior. Our study did not permit behavioral sampling to investigate other possible interactions between mallards and wood ducks. Thus, we were unable to resolve whether observed microhabitat differences of coexisting wood ducks and mallards resulted from other forms of competition (e.g., exploitation [Pianka 1974:134]) and/or from species-specific habitat selection. Dubowy (1988, 1991) concluded that competition was an important force resulting in winter habitat partitioning within a guild of dabbling ducks (Anas spp.) in California (cf. Bethke 1991). Regardless of cause(s) for microhabitat differences between wood ducks and mallards, an alternative and perhaps superior endeavor is to study individuals within communities or guilds and address their survival and reproduction (Wiens 1989, 1992), and subsequently implement habitat management that augments these fitness components (Martin 1992).

Water depth and tree species diversity also differed between wood duck and mallard microhabitats but only at Noxubee Refuge in winter 1989-90. Despite decreased mean water depths in Noxubee GTR's between winters 1988-89 and 1989-90, wood ducks continued their association with deeper microhabitats than mallards. Increased water depth may not inhibit wood duck feeding as much as mallards, because wood ducks typically forage on or slightly below (1-3 cm) the surface; whereas mallards mainly feed in forested wetlands by subsurface dabbling for acorns and invertebrates (Fredrickson and Heitmeyer 1988:319). Barnes and Nudds (1990) found temporal constancy in microhabitat use by grebes (Podiceps auritus, Podilymbus podiceps) and American coots (Fulica americana) despite annual variation in water depth and wetland resources. They reported that microhabitat separation among these species was greatest due to water depth in years of reduced wetland depth and availability. Thus, water depth may be a habitat feature used by waterfowl for niche partitioning in wintering habitats (White and James 1978, Dubowy 1988, our study) and on the breeding grounds (Dubowy 1988).

MANAGEMENT AND RESEARCH IMPLICATIONS

Our data suggest that wood ducks used microhabitats with greater forest structural density and diversity than those used by mallards. Therefore, preservation and restoration of bottomland hardwood communities seem prudent measures to benefit this species; such action also would provide habitat for numerous other wildlife species that inhabit lowland forested wetlands (Fredrickson 1978). Moreover, these strategies are consistent with goals of the North American Waterfowl Management Plan and other cooperative public and private wetland conservation initiatives, such as the Conservation Reserve and Wetlands Reserve Programs (e.g., Sparrowe et al. 1989).

Mallards were associated with more "open" sites in GTR's than were wood ducks. In fact, wood duck microhabitats exhibited more understory cover (0.2–5%) than randomly located sites within 150 m and 360° of wood duck microhabitats, whereas mallard microhabitats contained less understory cover (2–4%) than corresponding random sites (Alexander 1990:43, 45). Greater openness at mallard compared with wood duck microhabitats may facilitate entry and exodus of hardwood bottomlands by mallards, which do not nearly exclusively use forested wetlands as do most wood ducks.

If timber harvest or understory thinning is prescribed by forest and wildlife managers, these could enhance hardwood bottomlands for migrating and wintering mallards. Creating small clearcut areas (e.g., 0.5-4 ha) is a recommended practice for harvesting bottomland hardwoods and for regenerating shade-intolerant red oak species that produce acorns consumed by wood ducks and mallards (Reinecke et al. 1989, Moorhead et al. 1991). However, any timber harvesting or prescribed silviculture should be implemented thoughtfully with ecological principles to ensure sustainability of southern forest ecosystems (Sharitz et al. 1992). In clearcut areas, moist-soil plants also frequently regenerate, augmenting availability of seed and

invertebrate foods for waterfowl (Harrison and Chabreck 1988, Fredrickson and Heitmeyer 1988, Wehrle 1992). To facilitate food accessibility by waterfowl in forested wetlands, water depths should be kept <45 cm (Allen 1980, Heitmeyer 1985, Fredrickson and Heitmeyer 1988, our study).

Future research should address waterfowl and other avian use (e.g., neotropical migrant landbirds) of GTR's and unmanaged forested wetlands relative to size, shape, and dispersion of tracts and clearcut openings within them (e.g., Askins et al. 1990, Christman 1984, Hagan and Johnston 1992, Mitchell and Lancia 1990). During such studies, regeneration and survival of red oak species within clearcut areas also should be evaluated relative to these factors and seasonal hydrology. Additionally, researchers should test for selection ("preference") of bottomland microhabitats by waterfowl and other birds by comparing characteristics of used and randomly selected microhabitats (Alldredge and Ratti 1986, 1992). Finally, we suggest our study be replicated at a northern latitude to determine whether migrating wood ducks and mallards exhibit patterns of microhabitat use similar to wintering conspecifics.

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