HABITAT USE AND PREFERENCES OF BREEDING FEMALE WOOD DUCKS

KEVIN M. HARTKE,1 School of Forestry and Wildlife Sciences, Auburn University, 108 M. White Smith Hall, Auburn, AL 36849, USA
GARY R. HEPP,2 School of Forestry and Wildlife Sciences, Auburn University, 108 M. White Smith Hall, Auburn, AL 36849, USA

Abstract: Female wood ducks (Aix sponsa) feed primarily on plant foods in the prelaying period and switch to a diet of mostly invertebrates during egg production. If nutrient acquisition is habitat-specific, then selection and use of habitats may differ between these reproductive stages. A better understanding of these processes is needed to assist future habitat conservation and management efforts. In January–May 1999 and 2000, we monitored movements and habitat use of radiomarked females (n = 47) during the prelaying and egg-production periods of first nests. Home-range size averaged 367 ha and did not vary with reproductive period, year, or female age. Habitat use did not differ between periods of prelaying and egg production; consequently, data were combined. Habitat use varied between years, female age, and periods of nest initiation (i.e., early vs. late). Use of beaver ponds (BP), temporary wetlands (TW), managed impoundments (MI), and lake habitats (LK) declined in 2000 compared to 1999, possibly due to reduced precipitation. Nest initiation date was independent of female age. Adult females used BP more than yearlings, and early-nesting females used BP and MI more than late-nesting females. Females selected habitats nonrandomly when habitat composition of the study area was compared to that of home ranges (second-order selection). Lake-influenced wetlands (LI) and MI were ranked highest in preference. Home-range size was inversely related to percentage of the home range comprised of MI and LI, supporting the idea that MI and LI were high-quality habitats. However, we found no relationship between nest initiation date (an important index to reproductive performance) and the combined area of MI and LI in home ranges. Habitat selection did not differ from random when habitat composition of home ranges was compared to that of radio locations (third-order selection). Although MI and LI were preferred, high-quality habitats, our results suggest that breeding female wood ducks can satisfy requirements for egg production using a variety of wetland habitats. We suggest that providing a diversity of habitat types will increase the probability of meeting needs of breeding females throughout the breeding season, especially in areas where wetland conditions frequently change.

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Wood ducks rely on food resources obtained on breeding grounds to provide all nutrients needed for reproduction (Drobney 1990), a nutrient-acquisition pattern that differs from many other duck species (Alisauskas and Ankney 1992). Female mallards (Anas platyrhynchos), for example, accumulate lipid reserves used for reproduction prior to arriving at breeding areas and then use exogenous sources of protein during egg production (Krapu 1981, Young 1993). During the prelaying period, female wood ducks accumulate lipid reserves by feeding on plant foods high in carbohydrates and fats (Drobney 1982). These lipid reserves are used by female wood ducks for egg production and provide them with energy to gather exogenous protein for egg development (Drobney 1980). Diets of prelaying female wood ducks include equal parts of plant and animal foods, but change to mainly protein-rich invertebrates during egg laying (Drobney and Fredrickson 1979). Availability of high-quality breeding habitats that provide food resources necessary for reproduction is important to female wood ducks. However, with exception of the brood-rearing period (Smith and Flale 1985, Cottrell et al. 1990), little is known about habitat use and preferences of breeding female wood ducks.

We radiomarked female wood ducks and examined movements and habitat use during the prelaying and egg-laying periods. Our objectives were to (1) test whether habitat use differed between prelaying and egg-production periods, when nutrient requirements of females change; (2) examine sources of variation in habitat use that included year, female age, and nesting date; and (3) examine habitat preferences of females by comparing use and availability of habitats at 2 spatial scales. If habitat use differed from availability (i.e., nonrandom), we predicted that females making greater use of preferred habitats would initiate nests earlier than those that did not. Nesting date
is an important reproductive parameter for many species of birds including wood ducks. Early-nesting females at southern latitudes produce larger clutches, hatch more young from successful nests, are at less risk from predators, and are more likely to initiate a second nest than females nesting late (Hepp and Kennamer 1993).

STUDY AREA

We conducted our study at Eufaula National Wildlife Refuge (ENWR) and the surrounding area (32°N, 85°W). Located in southeast Alabama and southwest Georgia, USA, ENWR (4,520 ha) is centered on Lake Eufaula, an impoundment of the Chattahoochee River. Dominant aquatic habitats included open water on the lake, farm ponds, beaver ponds, managed impoundments, and littoral areas of the lake. Flooded hardwood habitat existed in small, widely distributed patches. Forested habitats generally were dominated by young trees that provided few natural cavities; therefore, most wood ducks used nest boxes on ENWR, which provided relative ease in locating and monitoring nests.

METHODS

Capture and Radiomarking of Females

In January and February, we installed automatic nest-box traps modified from Zicus (1989) in nest boxes (1999: n = 25; 2000: n = 28) to capture female wood ducks. During this period, local, nonmigratory females were visiting nest boxes and searching for suitable nest sites (Bellrose and Holm 1994). Migrant wood ducks also were present in the area during this time; consequently, we used nest-box traps to target and capture nonmigratory females. We aged females as yearling or adult (Harvey et al. 1989) and banded them with U.S. Fish and Wildlife Service leg bands.

We subcutaneously implanted radiotransmitters (model RI-2BM, Holohil Systems, Ltd., Carp, Ontario, Canada) with mortality switches immediately posterior to the nape (Korschgen et al. 1996, Schulz et al. 1998). The radiotransmitters weighed 6.6 g and had a life expectancy of 180 days. We anesthetized females during surgery by administering propofol (PropoFlo®, Abbott Laboratories, North Chicago, Illinois, USA) through the medial metatarsal vein by means of a 25-gauge winged infusion set combined with a 3 mL syringe. We monitored heart rate and respiration throughout the entire procedure using a stethoscope. We soaked surgical instruments, sutures, and the transmitter in chlorohexidine diacetate solution (Nolvasan®, Aveco Company, Fort Dodge, Iowa, USA) prior to each procedure. After surgery, we held females 1 to 2 hr in a dark, well-ventilated box to allow full recovery from anesthesia before being released near the nest box where they were captured. Hepp et al. (2002) provide more complete descriptions of anesthetic and surgical procedures.

Advantages of implanting transmitters relative to other attachment techniques include higher local survival and return rates (Dzus and Clark 1996), more normal behavior (Pietz et al. 1993), and improved reproduction (Paquette et al. 1997, Garrettson and Rohwer 1998). We found no differences in behavior, reproduction, and annual return rates between females implanted with radiotransmitters and those that were not radiomarked (Hepp et al. 2002).

Radiotelemetry

After a 72-hr adjustment period, we attempted to locate radiomarked females at least once daily from 1 hr before sunrise to 1 hr after sunset. Because of transportation and workload constraints, radiomarked females were assigned to groups (i.e., based on previous location and proximity to others) and located during 3 scheduled periods (1 hr before sunrise–1000 hr; 1000–1500 hr; 1500 hr–1 hr after sunset). Groups were reassigned (nonrandom) to a different period each day. Females were located using triangulation (≥3 bearings) from telemetry receiving stations of known coordinates. Because we were interested in habitat use and movements of females when they were not at nest sites, we attempted to exclude locations when they were inspecting nest sites or laying eggs. Radiotransmitters emitted a loud and stationary signal when females were inside or on top of nest boxes, and we did not attempt to triangulate until females moved and signal strength weakened, indicating that they were away from the nest box. Similarly, when some females were at natural cavity sites in wooded habitats (upland and wetland), a loud and stationary signal indicated use of a tree cavity; therefore, we recorded the female’s location only after she departed. When females could not be located from the ground, we used a fixed-wing aircraft equipped with antennas to search our study area (Gilmer et al. 1981).

We used Locate II (Nams 2000) and the maximum-likelihood method (Lenth 1981) to estimate radio locations and 95% error ellipses.
Mean error ellipse size (1999: 1.85 ± 0.05 ha; 2000: 2.63 ± 0.05 ha) was similar to or less than mean size of most habitat types (Table 1); therefore, we felt confident that radio locations were assigned to the correct habitat type. Any misclassification that did occur likely would have made detecting nonrandom patterns of use more difficult, thus our results may be viewed as conservative (Samuel and Kenow 1992).

**Home-range Estimation**

We estimated home-range size of female wood ducks for the prelaying and egg-production periods separately and combined. We used the Animal Movement Program 2.0 (Hooge et al. 1999), an extension for ARCGIIS (Environmental Systems Research Institute 2000a), to calculate minimum convex polygon (MCP). Before estimating MCPs, we removed 5% of outlying locations by the harmonic mean method (Dixon and Chapman 1980, White and Garrott 1990). When number of locations is low (n < 50), such as in our study (Table 2), fixed kernel methods overestimate home-range size (Seaman et al. 1999).

**Determination of Reproductive Periods**

We considered the prelaying period of radio-marked females to have begun the day following the 72-hr adjustment period and to have ended the day before rapid follicular growth (RFG) began. The period of RFG begins when yolk starts to accumulate in the first ovarian follicle and ends when the last follicle of the clutch is ovulated (Alisauskas and Ankney 1992). For female wood ducks, RFG starts 7 days before the first egg is laid (Drobney 1980); therefore, we estimated the beginning of RFG by subtracting 7 days from the nest initiation date. The egg production period extended from the first day of RFG to the day preceding the start of incubation.

We checked nest boxes (n = 71) at ENWR approximately once per week from January to June 1999 and 2000 to monitor nesting activity. We estimated date of nest initiation by subtracting the number of eggs in the nest from the date when the active nest was first found. If the number of eggs was greater than the number of days between nest-box checks (i.e., dump nest), we assumed that the nest began on the day after that nest box was last checked. Eggs were candled during early incubation (<7 days), and we estimated the first day of incubation by subtracting the number of days of egg development (Hanson 1954) from the date that eggs were candled (Folk 2001).

We did not examine eggs of females using natural cavities. For these females (n = 4), we assumed that incubation began on the day we first located a female in a natural cavity in the afternoon. To estimate the start of egg production for these females, we calculated the average length (x = 19 days) of the egg-production period of females nesting in boxes and subtracted this...
average from the date when incubation was estimated to have started.

Habitat Map

We used ARCINFO® (Environmental Systems Research Institute 2000b) and ARCVIEW® GIS to create a habitat map of our study area. We delineated the boundary for the study area each year by connecting the outermost vertices of all 95% MCP home ranges of females that were present during prelaying and egg-production periods. Habitats within this boundary were identified in the field and located on a mosaic of digital orthophoto quarter quadrangles (DOQQ). Next, we digitized individual habitat units within the study area from the DOQQ base map and assigned a habitat code to each unit. We classified habitats into the following categories (Table 1): (1) BP, (2) farm pond (FP), (3) TW, (4) creek (CR), (5) MI, (6) LK, (7) LI, and (8) upland. We recorded few radio locations in upland habitats, and these occurred only when we found females (n = 4) incubating a clutch in natural cavities on upland sites. We therefore excluded upland habitats from analyses.

Statistical Analyses

Home Range.—Home-range estimates and the interval length (number of days) in which the home range was estimated were log_{10} transformed, because data were not normally distributed. Home-range sizes for prelaying and egg-production periods were positively related to interval length. Therefore, we computed residuals from a regression of home-range size and interval length and checked them for nonlinearity. We used normally distributed residuals in a paired t-test to compare home-range sizes between reproductive periods. We used analysis of covariance with interval length as the covariate to test whether home-range size varied with year, female age, and their interaction. Slopes were homogeneous between years and age.

Habitat Use.—We used compositional analysis to test whether habitat use varied with reproductive period, year, age, and nesting date (Aebischer et al. 1993b). Proportions of the 7 habitats used by each female were calculated from radio-location data. We calculated 6 log-ratios by dividing proportions of BP, FP, TW, CR, MI, and LK by the proportion of LI, and taking the log. Habitat proportions with zero values were replaced with 0.00001. Choices of habitat to use as denominator and number to replace zero values do not affect results (Aitchison 1986, Aebischer et al. 1993a).

We used a split-plot MANOVA with log-ratios as the response variables to test for differences in habitat use in relation to reproductive period, year, female age, nesting date, and females. We made nesting date a categorical variable to facilitate multiple pairwise comparisons between levels of explanatory variables and for simplicity when interpreting effects of interactions between nesting date and other explanatory variables. We categorized radiomarked females as early (<median date) or late (≥median date) nesters based on median standardized nest initiation date of radiomarked females. We used variation due to the interaction term of females (year × female age × nesting date) as the error term to test whether habitat use differed with year, female age, nesting date, and 2-way interactions. Residual error was used to test for female [year × female age × nesting date]; to account for repeated measures) and reproductive period effects and remaining interactions.

We calculated log-ratios of habitats used for our overall study period (prelaying and egg-production periods combined) and used a regular MANOVA to test for variation due to year, female age, nesting date, and all possible interactions. We compared use of habitats relative to use of LI between levels of explanatory variables in the final fitted model by testing whether least-squares means of log-ratios were different from each other. In all appropriate analyses, backward stepwise procedures were used to eliminate nonsignificant terms, beginning with the highest-order interactions.

Habitat Preference.—We compared use of habitats to their availability at 2 spatial scales (Johnston 1980). First, we compared proportions of each habitat type within home ranges of females to habitat proportions available on our study area (second-order selection). Next, we compared proportions of radio locations occurring in each habitat type to habitat proportions available within individual home ranges (third-order selection). We used compositional analysis to test for significant nonrandom selection of habitats at each level of selection (Aebischer et al. 1993b).

Log-ratios of used and available habitat proportions were calculated as done for analyses of habitat use. We used MANOVA to test for nonrandom selection of habitats at each scale. If nonrandom selection of habitats occurred (P ≤ 0.05), we constructed a matrix of paired t-tests by using differences of log-ratios between habitats of interest to rank habitat preference and determine where ranks differed (Aebischer et al. 1993b).
Table 2. Mean (± SE) number of locations, number of days females were monitored, and home-range size (ha) of radiomarked female wood ducks during prelaying, egg-production, and both periods combined at Eufaula National Wildlife Refuge in Alabama and Georgia, USA, 1999–2000.

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of locations</th>
<th>No. of days</th>
<th>Home-range size (ha)²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>x ± SE</td>
<td>x ± SE</td>
</tr>
<tr>
<td>Preluining</td>
<td>45</td>
<td>39.3 ± 3.1</td>
<td>41.2 ± 3.4</td>
</tr>
<tr>
<td>Egg production</td>
<td>47</td>
<td>17.2 ± 0.6</td>
<td>19.0 ± 0.4</td>
</tr>
<tr>
<td>Combined</td>
<td>47</td>
<td>54.8 ± 3.0</td>
<td>58.5 ± 3.3</td>
</tr>
</tbody>
</table>

² 95% minimum convex polygon.
ᵇ 95% confidence limits.

Home-range size generally is related to the amount and distribution of quality habitats within the home range (Orians 1973, Nuells and Ankney 1982). We assumed that preferred habitats (from compositional analysis) represented habitats of high quality. We used partial correlation analysis that controlled for variation in the number of days that females were radiotracked to test the relationship between the combined percentage of highest ranked habitats (from compositional analysis) in each home range and home-range size.

Female wood ducks that nest early have many advantages over females that nest late (Hepp and Kennamer 1993). We used partial correlation analysis to test the relationship between date of nest initiation and the combined area of the highest ranked habitats in each home range. We used overall home-range size as the partial term in the analysis. We standardized date of nest initiation of radiomarked females by expressing nesting date relative to the date (day 1) when the first radiomarked female started nesting each year. Nesting date often is influenced by age; we therefore conducted correlation analysis separately for adults and yearlings. All correlation analyses were conducted using Spearman rank correlation because of small sample sizes.

We were limited in our ability to measure reproductive performance relative to habitat use. Nest parasitism occurred frequently (1999: 58%, 2000: 62%) among wood ducks breeding at ENWR; therefore, we could not use clutch size as a metric of reproductive performance. We also did not consider nest success because many females abandoned nests after being captured during incubation. Data summaries and analyses were completed using SAS (SAS Institute 1988).

RESULTS

We implanted radiotransmitters in 29 females (11 adults, 18 yearlings) in 1999 and in 33 females (27 adults, 6 yearlings) in 2000. Two females (3.2%) died ≤5 days after release, predators killed 4 females (6.5%), and 4 females (6.5%) either temporarily emigrated or experienced premature transmitter failure. Of the 52 remaining females, 22 of 24 (91.7%) nested in 1999 and 28 of 28 (100%) nested in 2000; however, we used data from 47 nesting females in analyses because 3 females had few (≤20) radio locations. Four females (1999: n = 1; 2000: n = 3) initiated their first nest in a natural cavity. We used only data associated with first nest attempts. Average date of nest initiation in 1999 was 23 March (range = 15 Feb–24 May), and in 2000 was 24 March (range = 14 Feb–15 May).

Home Range

In 1999, home ranges of 2 females could not be estimated for the prelaying period because RFG was initiated ≤7 days after the first day of radiotracking. After controlling for interval length (number of days), home-range size of females did not differ between reproductive periods (t = 0.202, n = 45, P = 0.84). We therefore pooled radio locations across reproductive periods and estimated home-range size for the overall study period. Home-range size of breeding females prior to incubation did not differ by year (F₁,₄₆ = 1.98, P = 0.17) or by female age (F₁,₄₆ = 0.66, P = 0.42) and averaged 367 ha (Table 2).

Habitat Use

Female use of habitats did not differ between reproductive periods (Wilks’ λ = 0.799, F₀,₃₉ = 1.64, P = 0.16). We therefore combined locations across reproductive periods and recalculated proportional use of habitats. Use of habitats in relation to LI differed between years (Wilks’ λ = 0.724, F₆,₃₈ = 2.41, P = 0.045), age class (Wilks’ λ = 0.683, F₆,₃₈ = 2.94, P = 0.019), and nesting date (Wilks’ λ = 0.647, F₆,₃₈ = 3.45, P = 0.008). Interactions between year, female age, and nesting date were not significant (P-values ≥ 0.34).

Relative to use of LI (the denominator of log-ratios), female use of BP, TW, MI, and LK was greater in 1999 than in 2000, but use of FP and
CR did not differ between years (Table 3). With the exception of BP, use of habitat types was similar between age classes (Table 3). Beaver ponds were used more by adults than by yearling females. Frequency of adults and yearlings comprising the early- and late-nesting periods did not differ (χ² = 0.045, df = 1, P = 0.83); therefore, age and nesting period were independent for our sample of females. Early-nesting females used BP and MI habitat types more than late nesters (Table 3). For all remaining habitat types, we found no differences in habitat use between early- and late-nesting females.

Habitat Preferences

Use of habitats was nonrandom (Wilks’ λ = 0.441, F₆,₈₇ = 18.36, P < 0.001) when habitat composition of individual home ranges was compared with habitat proportions available on our study area (second-order selection). Managed impoundments were ranked highest but did not differ significantly (P = 0.16) from LI; however, MI was ranked significantly higher than other habitat types (Table 4). Rankings of LI, BP, and LK did not differ from each other, but all were preferred to other habitats (Table 4). Analysis of third-order selection showed that proportional use of habitats (radio locations) by females did not differ from the availability of habitats within home ranges (Wilks’ λ = 0.899, F₆,₈₇ = 1.62, P = 0.15).

Home-range size was inversely related to the combined percentage of MI and LI habitats within the home range (partial ρ = −0.58, n = 47, P < 0.001; Fig. 1), which is expected if these preferred

Table 3. Annual, age, and nesting date differences in mean (± SE) percenta use of aquatic habitats by breeding female wood ducks during prelaying and egg production periods at Eufaula National Wildlife Refuge in Alabama and Georgia, USA, 1999–2000.

<table>
<thead>
<tr>
<th></th>
<th>MI</th>
<th>LI</th>
<th>BP</th>
<th>LK</th>
<th>CR</th>
<th>FP</th>
<th>TW</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
</tr>
<tr>
<td>1999 (n = 21)</td>
<td>15.45</td>
<td>4.46</td>
<td>2.58</td>
<td>2.15</td>
<td>8.64</td>
<td>4.77</td>
<td>0.80</td>
</tr>
<tr>
<td>2000 (n = 26)</td>
<td>22.35</td>
<td>5.65</td>
<td>3.02</td>
<td>1.30</td>
<td>2.08</td>
<td>1.74</td>
<td>1.39</td>
</tr>
<tr>
<td>Adult (n = 32)</td>
<td>0.009</td>
<td>0.152</td>
<td>2.47</td>
<td>1.57</td>
<td>1.13</td>
<td>0.49</td>
<td>34.54</td>
</tr>
<tr>
<td>Yearling (n = 15)</td>
<td>4.06</td>
<td>1.69</td>
<td>3.58</td>
<td>3.00</td>
<td>10.44</td>
<td>6.52</td>
<td>1.12</td>
</tr>
<tr>
<td>Early (n = 23)</td>
<td>26.52</td>
<td>6.08</td>
<td>1.37</td>
<td>0.79</td>
<td>2.01</td>
<td>1.26</td>
<td>0.21</td>
</tr>
<tr>
<td>Late (n = 24)</td>
<td>12.32</td>
<td>3.95</td>
<td>4.23</td>
<td>2.18</td>
<td>7.89</td>
<td>4.43</td>
<td>2.01</td>
</tr>
</tbody>
</table>

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**Table 4.** Matrix of mean (± SE) log-ratio differences of all habitat pairings for proportions of habitats within home ranges compared to proportions of available habitats in our study area (second-order selection) for female wood ducks at Eufaula National Wildlife Refuge in Alabama and Georgia, USA, 1999–2000. Significant differences (P ≤ 0.05) are marked with an asterisk.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>MI</th>
<th>LI</th>
<th>BP</th>
<th>LK</th>
<th>CR</th>
<th>FP</th>
<th>TW</th>
</tr>
</thead>
<tbody>
<tr>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
<td>SE</td>
</tr>
<tr>
<td>MI</td>
<td>0.79</td>
<td>0.56</td>
<td>1.35*</td>
<td>0.55</td>
<td>1.86*</td>
<td>0.66</td>
<td>4.03*</td>
</tr>
<tr>
<td>LI</td>
<td>−0.79</td>
<td>0.56</td>
<td>0.55</td>
<td>0.65</td>
<td>1.06</td>
<td>0.59</td>
<td>3.24*</td>
</tr>
<tr>
<td>BP</td>
<td>−1.35*</td>
<td>0.55</td>
<td>−0.55</td>
<td>0.65</td>
<td>0.51</td>
<td>0.59</td>
<td>2.69*</td>
</tr>
<tr>
<td>LK</td>
<td>−1.86*</td>
<td>0.66</td>
<td>−1.06</td>
<td>0.59</td>
<td>0.51</td>
<td>0.59</td>
<td>2.18*</td>
</tr>
<tr>
<td>CR</td>
<td>−4.03*</td>
<td>0.49</td>
<td>−3.24*</td>
<td>0.53</td>
<td>−2.69*</td>
<td>0.50</td>
<td>−2.16*</td>
</tr>
<tr>
<td>FP</td>
<td>−5.16*</td>
<td>0.59</td>
<td>−4.37*</td>
<td>0.67</td>
<td>−3.81*</td>
<td>0.56</td>
<td>−3.30*</td>
</tr>
<tr>
<td>TW</td>
<td>−5.19*</td>
<td>0.61</td>
<td>−4.40*</td>
<td>0.62</td>
<td>−3.84*</td>
<td>0.59</td>
<td>−3.33*</td>
</tr>
<tr>
<td>Rankc</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
</tr>
</tbody>
</table>

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a Percentages computed by averaging percent use of each habitat by females in each level of the explanatory variables.

b BP = beaver pond; FP = farm pond; TW = temporary wetland; CR = creek; MI = managed impoundment; LI = lake; LK = lake influenced wetland.

c P-values for the null hypothesis that use of habitats relative to use of LI were similar between levels of explanatory variables.
Habitats represent habitats of high quality. However, tests of yearlings (partial $r_2 = 0.20$, $n = 15$, $P = 0.49$) and adults (partial $r_2 = 0.29$, $n = 32$, $P = 0.11$) separately and combined (partial $r_2 = 0.26$, $n = 47$, $P = 0.08$) showed no relationships between the combined area of MI and LI in the home range and nest initiation date, after controlling for home-range size.

DISCUSSION

Home-range Size

Prior to incubation, breeding female wood ducks in our study used home ranges almost 3 times larger than that of pre-incubation female wood ducks using natural cavities in north-central Minnesota ($\bar{x} = 127$ ha; Gilmer 1971). This difference may be attributed to variations in the quality and distribution of wetland habitats between study areas. Natural cavities used by radiomarked wood ducks breeding in north-central Minnesota were located <0.5 km from the nearest wetland or shoreline, and most (68%) of these nest sites were ≤0.16 km from the nearest wetland habitat (Gilmer 1971). Wood duck nest boxes at ENWR were located within or on the edge of wetlands, but breeding females still moved extensively.

Bellrose and Holm (1994) suggested that wood duck home ranges would be large where essential habitat components are dispersed or where constantly fluctuating water levels alter habitat quality. Water levels on our study area, especially in LI and MI habitats, fluctuated during the breeding season and may have influenced the size of areas used by breeding wood ducks. Manipulation of the water level at Lake Eufaula by the U.S. Army Corps of Engineers altered habitat conditions of LI, and water levels of MI at ENWR were lowered to manage these areas for wintering waterfowl.

Predictability of wetland productivity also may influence home-range size. Ringelman et al. (1982) suggested that small home ranges of breeding black ducks (*Anas rubripes*) in south-central Maine resulted from low variability in wetland productivity. Black ducks expanding their home range would have little chance of finding habitats higher in quality than those already being used (Ringelman et al. 1982). Efficiently exploiting habitats is difficult where productivity over time is uncertain (i.e., low predictability; Brown and Orians 1970). Therefore, large home-range size could result when wetland productivity is uncertain (Orians 1973, Nudds and Ankney 1982).

Habitat Use and Preferences

Nutrient requirements of female wood ducks differ between periods of prelaying and egg production, and females respond by changing their food habits during these periods. Prelaying female wood ducks in southeastern Missouri accumulated lipid reserves on breeding areas by feeding on seeds high in fat and carbohydrates and then switched to a diet of protein-rich invertebrates during egg production (Drobney and Fredrickson 1979; Drobney 1980, 1982). We predicted that habitat use of female wood ducks would differ between reproductive periods if availability of nutrients varied among major habitat types. However, habitats used by female wood ducks breeding at ENWR were similar between reproductive periods, suggesting that females did not need to change habitats to meet the changing nutritional demands of reproduction. In eastern North Dakota and west-central Minnesota, use of different classes of wetland basins by female mallards also did not vary between periods of prenesting and egg production (Krapu et al. 1997). Krapu et al. (1997) suggested that these wetland basins provided females with productive foraging opportunities during both reproductive periods.

The possibility exists that we made errors in assigning females to reproductive periods. For example, nests at ENWR were frequently parasitized (1999: 58%; 2000: 62%), but we were unable to distinguish radiomarked females that dumped eggs. Some radiomarked females likely laid parasitic eggs. These females would have been incorrectly placed in the prelaying category until initi-
ating their own nests, thereby helping to conceal potential differences in habitat use between the prelaying and egg-production periods.

Habitat use of female wood ducks varied between years, female age, and nesting date. Annual variation in use of habitats by waterfowl is common and often is related to variation in environmental factors such as precipitation. In South Dakota, preferences of wood duck broods for semipermanent wetlands and tributaries outside of floodplains increased when floodplain wetlands were dry (Granfors and Flake 1999). Blue-winged teal (Anas discors) breeding in the prairie potholes moved to semipermanent wetlands late in summer as seasonal wetlands became dry (Swanson and Meyer 1977). At ENWR, cumulative rainfall in 2000 was lower than in 1999, especially after March (Apr–May 1999: 17.7 cm; Apr–May 2000: 2.7 cm). Kennamer (2001) showed that precipitation patterns in the southeastern United States influence wetland availability. The 2-fold increase in use of LI habitats in 2000 may have resulted from decreased quality of other aquatic habitats caused by reduced precipitation. For example, water levels of ENWR impoundments were lowered each year during the growing season to help propagate annual seed-bearing plants for wintering waterfowl. After drawdown, wood ducks were able to use areas within impoundments where water remained. However, many of these depressions dried during the breeding season of 2000.

Adult females in our study area used BP more than yearlings. Age-specific differences in habitat use are common in birds and frequently are caused by variation in dominance status (Gauthreaux 1978, Wunderle 1991). Dominant adults often displace juveniles and cause them to use habitats of lower quality (Goss-Custard et al. 1982, Sol et al. 2000). Wood ducks breeding at southern latitudes migrate short distances or may reside near breeding areas year-round (Bellrose and Holm 1994). Young wood ducks tend to migrate longer distances than adults (Hepp and Hines 1991), and may return to breeding areas later (Semel and Sherman 2001). Adults, by virtue of migrating short distances or not migrating at all, may occupy habitats of higher quality like BP. However, further research is needed to help understand differences in habitat use of yearling and adult females.

Early nesters used MI and BP more heavily than late nesters. Temporal differences in habitat use were probably related to variation in the phenology of wetland vegetation. In early spring, woody and shrub/scrub vegetation provide important cover for wood ducks when herbaceous aquatic vegetation is absent (Bellrose and Holm 1994). Species such as red maple (Acer rubrum), button-bush (Cephalanthus occidentalis), black willow (Salix nigra), and alder (Alnus serrulata) were abundant in heavily used, early-season habitats. As the breeding season progressed, availability of herbaceous aquatic plants increased in habitats like LI and provided females with additional cover and foraging substrate.

The highest-ranked habitat types (second-order selection) in our study area were MI and LI. The importance of MI to prelaying and egg-laying females may have been exaggerated because most (89%) nest boxes at ENWR were located in MI and all boxes used by radiomarked females were located in MI. However, among radiomarked females (n = 43) that nested in MI, approximately half of radio locations recorded in MI occurred in MI that did not include the nest box where females nested. In addition, female wood ducks typically search for nest sites and lay eggs in the early morning (Bellrose and Holm 1994, Semel and Sherman 2001), but we recorded approximately 56% of radio locations in MI from 1000 hr until 1 hr after sunset, also suggesting that MI habitats were important to females for a variety of activities besides nesting.

The combined percentage of MI and LI in home ranges of females was negatively related to home-range size, which is consistent with the idea that these habitats represented areas of high quality. We predicted that female wood ducks would prefer food-rich habitats and that females having greater access to these habitats would initiate nests early. Many species of birds initiate nests early when food is abundant (Martin 1987), and nesting date is an important predictor of reproductive success for wood ducks breeding at southern latitudes (Hepp and Kennamer 1993). However, we found no evidence that home ranges of early-nesting females at ENWR were comprised of larger areas of preferred habitats than that of late-nesting females.

**MANAGEMENT IMPLICATIONS**

Managed impoundments at ENWR contained nest boxes and were preferred habitats of breeding female wood ducks. Females used MI throughout the day, not just in the morning when most nesting activity (e.g., prospecting for nests and egg laying) occurs. This indicates that these wetlands were important in helping
females meet the nutrient demands of reproduction. Drawdown (managed or natural) of aquatic habitats can influence patterns of habitat use by wood ducks. On our study area, annual variation in use of MI habitat by female wood ducks coincided with a shift to drier conditions during the breeding season in 2000. Where managed wetlands are associated with nest sites of wood ducks, maintaining water levels may be necessary throughout the breeding season, especially during dry conditions. This could be accomplished by not completely draining impoundments. Water levels in most impoundments at ENWR were managed in this way. Alternatively, if managers have access to several impoundments that are close together, they could manage some areas as moist-soil units while permanently flooding other impoundments to promote cover and foraging substrate for wood ducks.

Wood ducks that initiate nests early in the season have many advantages over females that nest later (Hepp and Kennamer 1993). Early-nesting females prepare for reproduction before wetland plants have experienced spring growth. Early-nesting females on our study area used MI and BP habitats that were characterized by abundant woody and shrub/scrub vegetation. We suggest that conservation and improvement of early-season cover such as shrub/scrub vegetation should be an important consideration in managing wetlands for breeding wood ducks.

Finally, with the exception of MI, wetland habitats were widely distributed throughout our study area. Females moved extensively and used wetlands inside and outside ENWR during prelaying and egg-production periods. Wetlands used by females had diverse cover types that included emergent vegetation, temporarily flooded forests, shrub/scrub, and wooded creeks. Nesting date, a good index to reproductive performance, was not related to use of preferred habitats, suggesting that breeding wood ducks can satisfy requirements of reproduction using a diversity of wetland habitats.

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