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ACORN SELECTION BY FEMALE WOOD DUCKS

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Abstract: Acorns of southern bottomland red oaks (*Quercus* spp.) are important winter foods of wood ducks (*Aix sponsa*). Therefore, we tested if captive, wild-strain female wood ducks would exhibit preferences among different species of common bottomland red oak acorns, including willow oak (*Q. phellos*), water oak (*Q. nigra*), cherrybark oak (*Q. falcata* var. *pagodaefolia*), and Nuttall oak (*Q. nuttallii*) during winter 1991–92. Willow oak acorns were selected over all other equally available acorns, whether presented in mixed- or single-species feeding trials. Willow oak acorns had smallest top width, thinnest shell, and greatest meat : shell mass ratio, which perhaps facilitated ingestion and nutrient assimilation by wood ducks. Future research should clarify mechanisms for acorn selection by wood ducks and mallards (*Anas platyrhynchos*) in captive and natural environments. Managers might use willow oak and other appropriate tree species (i.e., considering geographical, hydrological, and soil conditions) in restoration of lowland hardwood forests.

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Key words: acorns, *Aix sponsa, Anas platyrhynchos,* foraging, forested wetlands, mallard, Mississippi, oak, *Quercus* spp., waterfowl, winter, wood duck.

The wood duck is the only *Aix* species endemic to North America (Batt 1992). Although nearly extirpated or at low population levels in the early 1900s in some parts of its range (Bellrose 1990), wood ducks have been 1 of the most abundant and frequently harvested ducks in the Mississippi and Atlantic flyways (Gamble 1990, Serie and Chasko 1990, Bellrose and Holm 1994: 109). Consistent with the name wood duck, the species predominantly uses forested wetlands during its life cycle. Oak bottomlands are especially important habitats for wood ducks; they forage on acorns and other natural foods in these areas (Thompson and Baldassarre 1988, Heit-

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meyer and Fredrickson 1990*a*, Bellrose and Holm 1994:76).

Bellrose (1976:194) stated, "Acorns are the favored foods of more wood ducks in more places than any other plant food from New Hampshire to South Carolina to Mississippi to Wisconsin." Acorns have been reported to account for as much as 74% (by vol) of the esophageal contents of wintering wood ducks (Delnicki and Reinecke 1986). Wood ducks consume acorns from a variety of bottomland red oak species (Bellrose and Holm 1994:397–398, 407–413), including cherrybark oak (Hall 1962), Nuttall oak (Delnicki and Reinecke 1986), pin oak (*Q. palustris*) (McGilvrey 1966, Drobney and Fredrickson 1979), water oak (Hall 1962, McGilvrey 1966, Allen 1980, Delnicki and Reinecke 1986), and willow oak (Hall 1962, Drobney and Fredrickson 1979, Allen 1980, Delnicki and Reinecke 1986). Acorns are important sources of energy for migrating, wintering, and prebreeding wood ducks because the nuts contain relatively high levels of saturated fatty acids (Heitmeyer and Fredrickson 1990*b*) and nitrogen-free extract (NFE) (Ofcarcik and Burns 1971, Short 1976, Landers et al. 1977).

Despite the nutritional value of acorns, we were unaware of any published results from controlled experiments that have investigated acorn selection by wood ducks. Although Allen (1980) reported that free-ranging wood ducks wintering in Texas "preferred" water oak over willow oak acorns, he did not provide empirical evidence relating acorn consumption by wood ducks to acorn availability in sampled habitats. Therefore, our primary objective was to test if female wild-strain wood ducks, in a captive and controlled experimental environment, would select among cherrybark, water, willow, and Nuttall oak acorns, which are commonly consumed during winter by wood ducks in Mississippi (Hall 1962, Delnicki and Reinecke 1986) and elsewhere in southern United States (Bellrose and Holm 1994:407–413). Secondly, we measured dimensional, nutrient, and tannin characteristics of these acorns to investigate potential mechanisms affecting acorn use by wood ducks. Our study has important implications for understanding wood duck foraging ecology and managing bottomland hardwood forests.

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STUDY AREA

We conducted experiments and confined wood ducks in 2 outdoor aviaries located about 2 km southeast of MSU in eastcentral Mississippi (33°27'N, 88°46'W). Characteristics of the aviaries have been described (Richardson and Kaminski 1992).

METHODS

Acorn Collection and Preservation

We collected fresh cherrybark, water, and willow oak acorns on the MSU campus and in Starkville, Mississippi during autumns 1990–91. We obtained Nuttall oak acorns from several sites in western Mississippi, within the Mississippi Alluvial Valley, where Nuttall oak occurs commonly (Duncan and Duncan 1988:287). Immediately following collection, we placed cupless acorns in a bucket containing water, discarded those that floated (i.e., acorns with cracked or insect-damaged shells [Allen 1989: 11]), and froze remaining nuts in a household chest freezer to prevent decomposition before use in experiments.

Captive Wood Ducks and Confinement

During spring 1989, we collected fresh eggs laid by wild, free-ranging wood ducks in nest boxes at Noxubee and Yazoo National Wildlife Refuges in eastcentral and western Mississippi, respectively. Eggs were artificially incubated, hatched, and ducklings reared in captivity at MSU. Annually in autumn, we clipped all dextral remiges of the ducks to render birds flightless. Wood ducks were maintained before and during experiments in accordance with a protocol approved by the Institutional Animal Care and Use Committee, MSU.

On 2 December 1991, we randomly selected 30 females of this flock and randomly assigned each individual to a separate cage (71 cm wide x 122 cm long x 64 cm high). Cages were placed within an outdoor, roofed aviary with chain-link fence sides (Richardson and Kaminski 1992: 534). Three vertical sides of each cage were built of plywood; 1 side was a vertically sliding door for access inside each cage. Top and front sides of each cage were covered with 2.54-cm-diameter mesh wire to admit natural light. We arranged cages in the aviary to prevent visual interaction among wood ducks. Bottoms of cages were uncovered and rested directly on a concrete floor. Within each cage, we placed 3 circular rubber tubs (43-cm diam. x 11.5 cm deep) and filled each daily with fresh water. We also placed about 50 mL of grit in each tub to aid wood ducks' digestion of experimental acorn diets. Cages and the concrete floor were sprayed clean with water daily and disinfected with bleach weekly.

Acorn Selection Experiments

Pre-experimental Period.—Before cage assignment, wood ducks received ad libitum access to a commercial, high-protein, pelleted ration (Richardson and Kaminski 1992:533) and fresh water. On 2 December 1991 (3 weeks before first acorn feeding trial), each female received ad libitum access to acorns equally and randomly allocated among the 3 tubs of water. Each female was given 30 cherrybark, 30 water, or 30 willow oak acorns, with each acorn species provided in a separate tub (i.e., "homogenous" patches of acorns); or 10 acorns of each of the 3 species for a total of 30 acorns per tub (i.e., "heterogenous" patches). The composite total among 3 tubs was 90 acorns/duck/day within each patch type. We provided acorns to wood ducks before experiments in the same manner that acorns would be offered during experiments to familiarize ducks with experimental acorn diets and to acclimate birds' digestive systems to hard mast. Because wood ducks used in this study were hatched and reared in captivity and fed only commercial ration, they had no prior exposure to acorns. We fed commercial ration to ducks every third day to avoid possible nutritional deficiencies caused by an exclusive acorn diet and to condition birds to this frequency of impending ration availability during experiments.

Calculations, involving existence energy requirements (eqs 1 and 3 [Richardson and Kaminski 1992:533]) applied to wood ducks in the acorn-selection experiments (approx mass = 500 g/bird [Barras 1993:47]) and true metabolizable energy (TME [Miller and Reinecke 1984]) acquired by mallards from water and willow oak acorns (approx 2 kcal/g dry weight of acorns [K. J. Reinecke, Nat. Biol. Serv., Vicksburg, Miss., unpubl. data]), indicated that 90 acorns/duck/day would potentially provide 58% more energy than needed by 500-g ducks for daily existence in our outdoor aviaries during winter. Thus, we assumed provision of 90 acorns/day for 2 consecutive days, followed by ad libitum commercial ration for a day, provided an adequate maintenance diet. Data on body mass of wood ducks from this study suggested this assumption was valid (see Results).

Experimental Periods.—We performed 21 feeding trials in Experiment I between 23 December 1991 and 23 February 1992. Cherrybark, water, and willow oak acorns were used in this experiment. In Experiment II, Nuttall oak acorns were offered with cherrybark and willow oak acorns during 3 feeding trials between 24 February 1992 and 3 March 1992. We excluded water oak acorns from Experiment II, because wood ducks ingested significantly fewer of these than willow and cherrybark oak acorns (see Results), and we were interested in examining wood ducks' use of Nuttall oak acorns.

Each feeding trial was 24 hours in duration and consisted of wood ducks receiving ad libitum access to acorns in either a homogenous or a heterogenous patch assigned randomly. The alternate patch type was administered on the next day. Each day of acorn feeding was considered an observation within a feeding trial period (i.e., 2 consecutive days of acorn availability [both patch types presented] followed by a day of ration availability). Patch types were selected to simulate natural aggregations of acorns in flooded hardwood bottomlands (e.g., homogenous patches of acorns of an oak species under trees of that species, and heterogenous patches of multiple acorn species due to acorn mixing from hydrology).

We counted all acorns of each species that remained in water tubs after each 24-hour feeding trial. Number of acorns of a species recorded as ingested per duck was the difference between total presented (i.e., $n = 30$ acorns/oak species/duck/day) and number of acorns remaining/oak species after 24 hours. We meticulously inspected water tubs, cage interiors, and floor space around each cage to ensure accurate determination of ingested acorns. Small rodent control was practiced within and around the aviary to alleviate possible acorn consumption by rodents that entered the aviary. Acorn counting and husbandry of wood ducks were performed daily from about 1200–1400 hours; ducks were not disturbed otherwise.

Body-mass Monitoring.—We measured body mass (± 2 g) of wood ducks weekly during both experiments to monitor their masses and safeguard against any major weight loss from malnutrition or the birds' possible aversion to consume acorns. We also measured mass weekly of 15 female wood ducks (7 adults and 8 immatures) confined communally in a separate, outdoor aviary without a roof (approx 150 m away); these birds were provided the same commercial ration and water ad libitum as the acorn-selection experimental birds (Demarest 1993:7, 23). We obtained mass data from these females fed commercial ration to compare their mean weekly mass with that of females in the acorn-selection experiments, as another means to monitor and thwart any malnourishment of ducks fed acorn diets.

Acorn Measurements

We measured dimensional characteristics of acorns to test if these were related to consumption by wood ducks. For Experiments I and II, we randomly selected 100 acorns of each of the 4 oak species from frozen lots and measured acorn shell thickness (± 0.01 mm) midway between the base and tip of acorns, using digital calipers. For Experiment I, we measured maximum length and width (both ± 1 mm) of cherrybark, water, and willow oak acorns for 420 randomly selected acorns of each oak species (i.e., 10 acorns/oak species x 2 patch types x 21 feeding trial periods). We also measured length and width of 420 randomly selected acorns of each oak species not eaten during Experiment I. For Experiment II, we measured length and width (± 1 mm) of cherrybark, Nuttall, and willow oak acorns for 60 acorns of each oak species (i.e., 10 acorns/oak species x 2 patches x 3 feeding trial periods). We also measured length and width of 60 randomly selected acorns of each oak species not consumed by wood ducks during Experiment II.

Proximate and Tannin Assays

We compared nutrient and tannin characteristics of acorns from the same lots used in experiments to discern if wood duck use of acorns was related to these characteristics. We submitted 10, 100-g (wet mass) samples of each of the 4 acorn species to the Mississippi State Chemical Laboratory for proximate and tannin assays. Nutritional assays of acorns included determining percentages of ash, crude fat, crude fiber, crude protein, moisture, and NFE, following techniques of the Association of Official Analytical Chemists' (AOAC) Official Methods of Analysis (1990:69–80). Hydrolyzable and condensed tannins were also assayed. Hydrolyzable tannin levels were estimated using tannic acid as a standard for precipitating tannin (AOAC 1984:607). The acidified vanillin assay was used to estimate condensed tannins (Burns 1971); these were expressed as percent catechin equivalents precipitated by acorn tannins.

Statistical Analyses

We tested hypotheses at alpha = 0.05. We used the Statistical Analysis System (SAS) for all tests (SAS Inst. Inc. 1985).

For wood ducks in the acorn-selection experiment, we tested the null hypothesis of no difference in mean body mass among weeks of the study, using analysis of variance (ANOVA) in a randomized complete block design (RCBD) with individual ducks as blocks (SAS Inst. Inc. 1985:130). Because of unequal numbers of ducks within weeks due to mortality, we used a least square means procedure in SAS to compare mean body mass of wood ducks each week during the acorn-selection experiment to the birds' pre-experiment mean mass at cage assignment (SAS Inst. Inc. 1985:444). In addition, we used an independent-samples t-test (SAS Inst. Inc. 1985:798) to test the null hypothesis of no difference in mean weekly body mass between wood ducks in the acorn-selection experiments and those fed commercial ration in a separate aviary.

We tested the null hypothesis of no difference in numbers of acorns consumed by wood ducks in relation to acorn species, patch types, and feeding trial periods, using a split-plot ANOVA in a RCBD with repeated measures of acorn consumption (i.e., during consecutive trial periods) by ducks (i.e., blocks). In this ANOVA, patch types and acorn species were whole- and split-plots, respectively. We detected a 3-way interaction ($P < 0.001$) for number of acorns consumed by wood ducks among acorn species, patch types, and periods. Therefore, we tested the null hypothesis of no difference in numbers of acorns consumed by wood ducks within each feeding trial period among acorn species and between patch types, using an ANOVA in a RCBD with ducks as blocks (SAS Inst. Inc. 1985: 130). To meet assumptions of ANOVA, we transformed acorn consumption data by taking the square root of each datum + 0.375, because sometimes no acorns of certain species were consumed (Zar 1974:188). Following ANOVAs within feeding trial periods, we made all pair-wise comparisons among oak species in mean number of acorns consumed by wood ducks, using Student-Newman-Keuls test (Zar 1974: 151–155).

We used ANOVA to test the null hypotheses of no differences among acorn species in length, width, and shell thickness of acorns before feeding nuts to wood ducks, and in proximate- and tannin-analysis data (SAS Inst. Inc. 1985:127). Preceding ANOVA to meet assumptions, we transformed acorn dimensional data using a natural log or natural log of each datum + 1 (Steel and Torrie 1980:235). We transformed acorn nutrient and tannin percent data using an arcsine-square root transformation (Steel and Torrie 1980:236). We used Ryan-Einot-Gabriel-Welsch test to make all pair-wise comparisons among acorn species for pre-experiment acorn data (SAS Inst. Inc. 1985:117; Day and Quinn 1989). We tested null hypotheses of no difference in acorn length and width between pre-experiment samples of acorns and those not eaten by wood ducks, using a paired t-test (SAS Inst. Inc. 1985:799).

RESULTS

Mortality

Three of 30 wood ducks died during Experiment I. Necropsy by clinicians at the MSU College of Veterinary Medicine indicated that 2 birds died from aspergillosis. Cause of death of the third duck was uncertain, but the bird was not emaciated at death.

Body Mass

Mean mass of females in Experiments I and II differed ($F = 9.70$; 13, 359 df; $P < 0.001$) among all weeks of the study. Mean mass of females 1 week after birds were caged and provided acorns was lower ($P < 0.001$) than their mean mass at pen assignment on 2 December 1991. Subsequent mean weekly masses of females fed acorns either did not differ ($0.09 \leq P \leq 0.87$) or were greater ($P < 0.01$) than the ducks' pre-experiment mean mass, except on 2 March 1992 when mean mass was lower ($P = 0.001$) than pre-experiment mean mass.

Pre-experiment mean mass of females in the acorn-selection experiment and females fed commercial ration in the nearby aviary did not differ ($t = 1.54$, 43 df, $P = 0.13$). Thereafter, mean weekly mass of females fed acorns was greater ($2.27 \leq t \leq 3.49$, 43 df, $0.001 \leq P \leq 0.028$) than mean mass of the other captive group of females during the same weeks in 9 of 14 weeks. During remaining weeks, mean masses did not differ ($0.44 \leq t \leq 1.33$, 43 df, $0.19 \leq P \leq 0.66$) between the 2 groups of wood ducks.

Acorn Selection

Experiment I.—Of 107,640 acorns offered to female wood ducks between 23 December 1991 and 22 February 1992, 42,676 (40%) apparently were consumed by the ducks, including 23,093 willow (54%), 13,853 cherrybark (33%), and 5,730 water (13%) oak acorns. In 20 of 21 feeding trials, patch type had a marginal effect or none ($0.06 \leq P \leq 0.98$) on number of acorns of an oak species consumed by wood ducks; thus, acorn consumption data were pooled across patch types and mean consumption compared among acorn species. In all 21 feeding trials, differences among acorn species were detected in numbers of acorns consumed by wood ducks ($18.98 \leq F \leq 101.62$; 2, 133–148 df; $P < 0.001$). Wood ducks consumed significantly more willow than cherrybark oak acorns in 18 of 21 feeding trials and significantly more willow than water oak acorns in all trials (Table 1). Significantly more cherrybark than water oak acorns were consumed during 19 of 21 feeding trials (Table 1).

Experiment II.—Female wood ducks apparently consumed 5,104 (35%) of 14,580 acorns offered between 24 February 1992 and 2 March 1992. Of those eaten, 3,203 (63%) were willow, 1,856 (36%) were cherrybark, and 45 (1%) were Nuttall oak acorns. Patch type did not influence ($0.29 \leq P \leq 0.83$) acorn consumption by wood ducks in 2 of 3 feeding trials. Thus, acorn consumption data were pooled across patch types. In all 3 feeding trials, differences were detected

Table 1. Numbers of willow, cherrybark, and water oak acorns eaten by 27–30 female wood ducks during 21 feeding trial periods between 23 December 1991 and 23 February 1992, Mississippi State University.

Period	Willow oak		Cherrybark oak		Water oak	
	$\bar{x}$[a]	95% CL[b]	$\bar{x}$	95% CL	$\bar{x}$	95% CL
23–25 Dec	18.83A[c]	16.65–21.14	5.19B	3.62–7.01	7.22B	5.31–9.41
26–28 Dec	17.34A	15.41–19.38	7.40B	5.49–9.57	4.72C	3.27–6.42
29–31 Dec	19.24A	16.21–22.52	9.09B	6.80–11.70	7.28B	5.11–9.81
01–03 Jan	19.04A	16.50–21.75	8.20B	6.07–10.64	5.34C	3.66–7.32
04–06 Jan	17.28A	14.59–20.20	10.27B	8.07–12.72	4.55C	3.04–6.34
07–09 Jan	16.67A	14.16–19.38	13.02B	10.59–15.69	3.16C	1.97–4.59
10–12 Jan	18.63A	16.14–21.31	10.61B	8.48–12.99	2.79C	1.74–4.06
13–15 Jan	14.41A	11.70–17.39	13.60A	11.61–15.74	2.65B	1.77–3.69
16–18 Jan	14.30A	11.95–16.86	11.19B	9.47–13.06	1.52C	1.00–2.11
19–21 Jan	15.43A	12.76–18.33	13.82A	11.87–15.91	1.72B	1.10–2.43
22–24 Jan	12.68A	10.67–14.86	13.18A	11.34–15.14	1.71B	0.98–2.59
25–27 Jan	19.97A	17.33–22.78	15.90B	14.13–17.77	2.88C	1.83–4.12
28–30 Jan	18.07A	15.63–20.69	12.12B	10.49–13.86	2.33C	1.42–3.42
31 Jan–2 Feb	17.26A	14.87–19.81	12.21B	10.30–14.27	2.67C	1.66–3.89
3–5 Feb	19.29A	16.37–22.44	9.19B	7.04–11.62	2.71C	1.64–4.02
6–8 Feb	22.63A	20.55–24.81	8.49B	6.75–10.42	3.76C	2.59–5.13
9–11 Feb	22.44A	20.24–24.75	9.59B	7.33–12.13	3.51C	2.28–4.97
12–14 Feb	18.99A	16.62–21.52	6.75B	4.97–8.78	2.89C	1.93–4.02
15–17 Feb	23.15A	20.58–25.86	8.46B	5.88–11.50	3.64C	2.25–5.33
18–20 Feb	21.94A	19.93–24.05	6.84B	5.01–8.94	2.35C	1.45–3.42
21–23 Feb	20.02A	18.13–22.00	5.55B	3.86–7.52	2.23C	1.48–3.11
Grand mean	18.29	17.73–18.86	9.83	9.35–10.32	3.30	3.03–3.59

[a] $n = 60$ ($n = 30$ wood ducks × 2 patch types = 60/period. See methods for description of patch types.), 23 Dec 1991–18 Jan 1992; $n = 58$, 19–21 Jan; $n = 55$, 22–24 Jan; $n = 54$, 25 Jan–23 Feb.
[b] CLs based on back-transformed data (Sokal and Rohlf 1969:381–382).
[c] Means within rows with unlike letters differ ($P \leq 0.05$).

among acorn species in numbers of acorns consumed by wood ducks ($177.97 \leq F \leq 251.63$; 2, 133 df; $P < 0.001$). Wood ducks consumed significantly more willow than cherrybark oak acorns and significantly more cherrybark than Nuttall oak acorns in all feeding trials (Table 2).

Acorn Measurements

Shell Thickness.—Mean shell thickness differed ($F = 121.20$; 3, 396 df; $P < 0.001$) among the 4 acorn species. Willow oak acorns had the thinnest shells, followed by cherrybark, Nuttall, and water oak acorns (Table 3).

Acorn Size, Experiment I.—Mean widths of willow, cherrybark, and water oak acorns differed ($F = 594.74$; 2, 1,257 df; $P < 0.001$). Willow oak acorns were narrowest, water oak acorns intermediate, and cherrybark oak acorns widest (Table 3). Uneaten cherrybark, willow, and water oak acorns were wider ($2.80 \leq t \leq 3.47$, 419 df, $0.001 \leq P \leq 0.005$) than pre-experiment samples of each species.

Mean lengths of willow, cherrybark, and water oak acorns differed ($F = 99.49$; 2, 1,257 df; $P < 0.001$). Cherrybark oak acorns were longer than willow oak acorns, which were longer than water oak acorns (Table 3). Uneaten cherrybark

Table 2. Numbers of willow, cherrybark, and Nuttall oak acorns eaten by 27 female wood ducks during 3 feeding trial periods between 24 February 1992 and 3 March 1992, Mississippi State University.

Period	Willow oak		Cherrybark oak		Nuttall oak	
	$\bar{x}$[a]	95% CL[b]	$\bar{x}$	95% CL	$\bar{x}$	95% CL
24–26 Feb	20.31A[c]	18.14–22.59	10.44B	8.44–12.64	0.26C	0.12–0.41
27–29 Feb	16.81A	14.26–19.55	9.79B	7.94–11.82	0.12C	0.03–0.22
1–3 Mar	19.65A	17.30–22.14	11.51B	9.55–13.64	0.20C	0.09–0.33
Grand mean	18.89	17.52–19.61	10.57	9.46–11.74	0.19	0.13–0.26

[a] $n = 54$ ($n = 27$ wood ducks × 2 patch types = 54/period).
[b] CLs based on back-transformed data (Sokal and Rohlf 1969:381–382).
[c] Means within rows with unlike letters differ ($P \leq 0.05$).

Table 3. Dimensional variables of willow, cherrybark, water, and Nuttall oak acorns used in wood duck foraging experiments, Mississippi State University, winter 1991–92.

Variable	Willow oak		Cherrybark oak		Water oak		Nuttall oak	
	$\bar{x}$[a]	95% CL[b]	$\bar{x}$	95% CL	$\bar{x}$	95% CL	$\bar{x}$	95% CL
Shell thickness (mm)	0.38A[c]	0.37–0.39	0.40B	0.39–0.42	0.55C	0.53–0.57	0.44D	0.43–0.46
Experiment I								
Width (cm)	1.16A	1.15–1.17	1.39B	1.38–1.40	1.26C	1.26–1.27	[d]	
Length (cm)	1.16A	1.15–1.16	1.18B	1.17–1.19	1.10C	1.10–1.11		
Experiment II								
Width (cm)	1.15A	1.13–1.17	1.34B	1.31–1.36			1.50C	1.47–1.53
Length (cm)	1.16A	1.14–1.18	1.14A	1.12–1.16			1.90B	1.85–1.95

[a] n = 100 acorns for shell thickness; n = 420 acorns for acorn width and length in Experiment I; n = 60 for these variables in Experiment II. See Methods for computation of n in Experiments I and II.
[b] CLs based on back-transformed data (Sokal and Rohlf 1969:381–382).
[c] Means within rows with unlike letters differ ($P \leq 0.05$).
[d] Blanks denote that Nuttall and water oak acorns were not included in Experiments I and II, respectively.

oak acorns were longer (t = 2.61, 419 df, P = 0.009) than pre-experiment samples of the species, but there were no differences ($0.36 \leq t \leq 0.52$, $0.64 \leq P \leq 0.72$) in length between pre-experiment samples and uneaten water and willow oak acorns.

Acorn Size, Experiment II.—Mean widths of willow, cherrybark, and Nuttall oak acorns differed (F = 206.35; 2, 177 df; $P < 0.001$). Nuttall oak acorns were wider than cherrybark oak acorns, which were wider than willow oak acorns (Table 3). Uneaten cherrybark, willow, and Nuttall oak acorns were wider ($2.16 \leq t \leq 4.41$, 59 df, $0.001 \leq P \leq 0.035$) than pre-experiment samples of each species.

Mean lengths of willow, cherrybark, and Nuttall oak acorns differed (F = 783.03; 2, 177 df; $P < 0.001$). Nuttall oak acorns were longer than willow and cherrybark oak acorns, which did not differ (Table 3). Mean lengths of uneaten and pre-experiment samples of cherrybark, Nuttall, and willow oak acorns did not differ ($0.11 \leq t \leq 1.81$, 59 df, $0.08 \leq P \leq 0.92$).

Acorn Proximate and Tannin Analyses

Proximate Analyses.—Percentages of crude fat, crude protein, NFE, fiber, moisture, and ash differed ($12.81 \leq F \leq 577.66$; 3, 36 df; $P < 0.001$) among acorn species. Cherrybark oak acorns were highest in crude fat and crude protein, followed by willow, water, and Nuttall oak acorns (Table 4). Percent ash exhibited a similar pattern among acorn species. Nuttall oak acorns contained most NFE, followed by water and willow oak acorns, which did not differ; cherrybark oak acorns had least NFE. Nuttall oak acorns were lower in crude fiber than the other 3 species, which did not differ. Nuttall oak acorns were highest in moisture; other species did not differ.

Tannin Analyses.—Percentages of condensed tannin from the vanillin assay and hy-

Table 4. Percentages of nutrients and tannin for 100-g samples of willow, cherrybark, water, and Nuttall oak acorns assayed at Mississippi State University, winter 1991–92.

Acorn constituent	Willow oak		Cherrybark oak		Water oak		Nuttall oak	
	$\bar{x}$[a]	95% CL[b]	$\bar{x}$	95% CL	$\bar{x}$	95% CL	$\bar{x}$	95% CL
Nutrients								
Fat	14.13A[c]	13.86–14.40	15.85B	15.56–16.14	13.15C	12.81-13.49	7.60D	7.17–8.03
Protein	3.52A	3.34–3.64	4.33B	4.22–4.44	3.27C	3.16–3.38	3.01D	2.92–3.10
NFE	33.92A	32.25–35.58	31.79B	30.13–33.45	35.17A	33.33–37.01	37.80C	36.73–38.88
Fiber	18.78A	17.39–20.22	18.30A	16.52–20.16	19.53A	17.85–21.27	13.15B	12.42–13.89
Moisture	28.36A	27.89–28.83	28.34A	27.55–29.13	27.77A	27.06–28.48	37.32B	36.67–37.97
Ash	1.28A	1.21–1.29	1.36B	1.28–1.44	1.06C	1.02–1.10	1.11C	1.05–1.17
Tannin indices								
Catechin	0.85A	0.75–0.95	1.01A	0.73–1.35	0.76A	0.69–0.83	2.33B	1.66–3.10
Tannic acid	3.88A	3.06–4.80	1.32B	1.28–1.35	1.36B	1.29–1.43	1.52B	1.28–1.77

[a] n = 10 for all means.
[b] CLs based on back-transformed data (Sokal and Rohlf 1969:381–382).
[c] Means within rows with unlike letters differ ($P \leq 0.05$).

drolyzable tannins from the tannic acid assay differed ($21.96 \le F \le 53.16$; 3, 36 df; $P < 0.001$) among acorn species (Table 4). Nuttall oak acorns contained greater levels of condensed tannins than cherrybark, willow, and water oak acorns; the 3 latter species did not differ. Willow oak acorns were highest in hydrolyzable tannins, followed by similar tannin levels in Nuttall, water, and cherrybark oak acorns.

DISCUSSION

Mortality and Body Mass

Although 3 wood ducks died during Experiment I, their deaths seemed unrelated to acorn test diets. During most weeks of the study, mean masses of females in the acorn-selection experiment were similar to, or greater than, both their pre-experiment mass and masses of females provided commercial ration ad libitum in a nearby aviary. We conclude that females in the acorn-selection experiment were well nourished, and their acorn foraging behavior was indicative of healthy, captive wood ducks.

Acorn Selection

Female wood ducks consumed significantly more willow oak acorns than other equally available species, suggesting a preference for this acorn species. Indeed, wood ducks could have foraged preferentially on larger and heavier acorn species under the free-choice environment of our experiments, but instead wood ducks elected to eat greater numbers and mass (≥ 2 times on average) of willow oak acorns compared with other available acorn species. We conclude that greater consumption of willow oak acorns by wood ducks was not a strategy (or consequence) to compensate for willow oak acorns' lesser mass relative to the other species. Wood ducks selected willow oak acorns over other species regardless of patch type, suggesting that the increased compositional complexity of heterogenous acorn patches did not hinder wood ducks' selection for willow oak acorns. Although wood ducks seemed to prefer willow oak acorns over the others under the experimental conditions of this study, mechanisms for this apparent selection cannot be deduced unequivocally from our results. Nevertheless, we discuss possible mechanisms for this selection below.

Willow oak acorns had the smallest width and thinnest shells. Analysis conducted after this study revealed that willow oak acorns had greater ($F = 41.5$; 3, 76; $P = 0.0001$) mean meat : shell mass ratio than cherrybark, water, and Nuttall oak acorns (R. M. Kaminski, unpubl. data). These collective attributes of willow oak acorns may have facilitated ingestion, digestion, and nutrient uptake by wood ducks. Similar inference has been proposed regarding selection of small acorns by blue jays (*Cyanocitta cristata*) (Darley-Hill and Johnson 1981, Scarlett and Smith 1991) and small mussels (*Dreissena polymorpha, Mytilus edulis*) by tufted ducks (*Aythya fuligula*) (Draulans 1982, 1984; De Leeuw and Van Eerden 1992) and common eiders (*Somateria mollissima*) (Bustnes and Erikstad 1990). Acorn width and shell pliancy may be proximate cues (Hildén 1965) used by wood ducks to select among available acorns, based on wood ducks' selection of small and thin-shelled willow oak acorns, and because uneaten acorns of all 4 oak species were wider than pre-experimental samples. However, we do not overlook the possibility that wood ducks discriminated among acorns visually, because birds were observed seemingly looking at acorn patches in the shallow-water tubs. Tactile cues and encounters with acorns may be more important than visual cues for wood ducks foraging in natural bottomlands where acorns may be concealed by turbid water and/or leaf litter.

Wood ducks ingested water oak acorns least of all acorns in Experiment I. Water oak acorns had the thickest shells of all acorns, despite being smallest in length. Thick shells of water oak acorns may have decreased shell pliancy and thus digestive efficiency. Also, water oak acorns have a comparatively long and acute apex, which could lacerate esophagi and/or impair swallowing (Bellrose and Holm 1994:391).

Pyke (1984) stated that optimal foraging models usually assume a positive relation between energy acquisition and fitness. Acorns used in this and other studies generally were high in crude fat and NFE (i.e., indicators of energy content) (Ofcarcik and Burns 1971, Short 1976, Landers et al. 1977). Although wood ducks selected willow oak acorns over others, willow oak acorns were not highest in crude fat and NFE. Perhaps wood ducks did not maximize net energy intake (i.e., be "energy maximizers" [sensu Pyke 1984]) during feeding trials, based on ingested crude fat and NFE of willow oak acorns. De Leeuw and Van Eerden (1992) hypothesized that captive tufted ducks may have acquired more net energy by selecting greater numbers of small mussels instead of fewer larger ones with thicker shells. Similarly, we hypothesize that wood ducks may increase net nutrient intake by selecting small, thin-shelled willow oak acorns with high meat:shell mass ratios. Collectively, these attributes of willow oak acorns may lower handling times and processing rates compared with larger acorns having higher levels of crude energy. Hamilton et al. (1994) reported that several diving ducks (Tribes: Aythyini, Mergini) were size selective for zebra mussels (*D. polymorpha*); these ducks preyed preferentially on relatively large mussels (11–21 mm in length) but avoided mussels smaller and larger than this range, perhaps because the largest mussels would be difficult to ingest and crush (Hamilton et al. 1994). Willow oak acorns in this study averaged 11–12 mm in both length and width, suggesting that wood ducks and diving ducks examined by Hamilton et al. (1994) may exhibit different prey-size selectivity.

K. J. Reinecke (Natl Biol. Serv., Vicksburg, Miss., unpubl. data) found that mallards derived 2.33, 1.73, and 1.44 kcal/g of TME from willow, water, and Nuttall oak acorns, respectively. Interestingly, Strong (1986:54) reported that proportional use of these 3 acorn species by captive, wild-strain mallards corresponded to the ranked order of above TME values for these acorn species. Wood ducks in our study also may have derived greatest TME from willow oak acorns, based on willow oak acorns' small size, shell thinness, and high meat : shell mass as described above. However, TME values for the above acorn species and cherrybark acorns have not been determined for wood ducks to test this hypothesis about acorn consumption and TME.

Crude protein generally is low in acorns (Ofcarcik and Burns 1971, Short 1976, Landers et al. 1977). Wood ducks in our study selected willow oak acorns, which contained second highest levels of crude protein. Wood ducks may have been able to meet daily protein needs by consuming commercial ration every third day of the experiment and from body reserves, similar to wild wood ducks which supplement plant-dominated diets by foraging on invertebrates (Delnicki and Reinecke 1986, Drobney 1990). Furthermore, significant gains in body mass and absence of emaciation in surviving and deceased wood ducks support our contention that wood ducks obtained adequate dietary protein from regular access to commercial ration.

Acorn selection by female wood ducks seemed independent of tannin concentrations in acorns. Before and during the experiment, wood ducks may have acquired a search image for preferred acorn species (Scarlett and Smith 1991) and/or became physiologically adapted to tannin levels in the acorns (Smallwood and Peters 1986). Although willow oak acorns contained greatest levels of hydrolyzable tannins, we did not observe any major decrease in wood duck body mass despite abundant consumption of willow oak acorns. Tannin toxicity from acorn ingestion is known to cause weight loss in blue jays (Johnson et al. 1993), fox squirrels (*Sciurus niger*) (Havera and Smith 1979), and white-footed mice (*Peromyscus leucopus*) (Smallwood and Peters 1986). Supplementation of wood ducks' diet with a nutritious commercial ration probably circumvented any detrimental effect of tannins.

Nuttall oaks were highest in condensed tannins, which Koenig (1991) indicated had a greater negative effect on acorn TME for acorn woodpeckers (*Melanerpes formicivorus*) than hydrolyzable tannins. Little use of Nuttall oak acorns by captive wood ducks in our study may have been related to high condensed tannin content, their large size and perhaps increased handling and digestive constraints, and/or the ducks' lesser familiarity with them. Nonetheless, free-ranging wood ducks consume Nuttall oak acorns (Delnicki and Reinecke 1986).

MANAGEMENT IMPLICATIONS

Female wood ducks preferred willow oak acorns, used cherrybark oak acorns approximately proportional to their availability, and ingested water and Nuttall oak acorns significantly less. When bottomland site conditions are appropriate within the geographic range of these oak species (Allen 1989:22, Duncan and Duncan 1988), managers may desire to plant more willow and cherrybark oak acorns or seedlings than other oak species tested in this study. Willow and cherrybark oak acorns are consumed frequently by wood ducks (Hall 1962) and mallards (Heitmeyer 1985:272), and both tree species produce quality timber on sites with suitable soil and hydrology (Allen 1989:22).

Although wood ducks in this study consumed more willow and cherrybark oak acorns than water and Nuttall oak acorns, free-ranging wood ducks consume a variety of mast species, including acorns ingested infrequently by wood ducks in this study (Delnicki and Reinecke 1986).

Also, mast production can vary annually within and among oak species, with periodic mast failures occurring in some species and locales. Therefore, we do not recommend establishment of monotypic stands of willow oak. Instead, geographical, hydrological, and soil conditions should dictate selection of oak species to promote seed germination, seedling survival, and acorn and timber production (Allen 1989:22). This strategy should also enhance oak species diversity and ensure acorn production for waterfowl and other wildlife during years of poor mast production. We also recommend that managers examine historical aerial photos of proposed hardwood restoration sites and nearby remnant forests to gain information on past species composition and distribution of bottomland hardwoods before clearing occurred. This insight would facilitate selection and location of indigenous tree species for restoration.

Future research should determine TME and protein values derived by wood ducks from acorns used in this study along with pin oak; all these are consumed by wood ducks (Drobney and Fredrickson 1979) and mallards (Heitmeyer 1985:272). Also, potential metabolizable nutrient differences between acorns containing and without weevil larvae (*Curculio* spp.) warrant testing (Johnson et al. 1993). These data may clarify underlying mechanisms for acorn selection by ducks, aid in development of optimal foraging models for ducks, and increase accuracy of estimates of waterfowl foraging carrying capacity of hardwood bottomlands (Reinecke et al. 1989).

We also suggest that researchers test if male wood ducks exhibit the same patterns of acorn use as females in this study. In addition, field trials should be conducted to test if acorn foraging patterns by captive wood ducks are repeatable in natural habitats. Other field or captive experiments could include tests of optimal prey size and patch selection (e.g., Strong 1986; Draulans 1982, 1984; De Leeuw and Van Eerden 1992, Hamilton et al. 1994), effects of patch dynamics and depletion (e.g., De Leeuw and Van Eerden 1992), and effects of interspecific interactions (e.g., between wood ducks and mallards) and duck density on foraging patch use. Finally, we suggest that researchers field test predictions of Reinecke et al. (1989:228–229) regarding interrelations of waterfowl foraging in hardwood bottomlands, forest stand characteristics (i.e., percent basal area composed of red oaks), and acorn availability to formulate forest management beneficial to waterfowl and timber production.

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