

FORAGING-NICHE DYNAMICS OF GADWALLS AND AMERICAN COOTS IN WINTER

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ABSTRACT.—We examined diet, microhabitat, and feeding method of Gadwalls (*Anas strepera*) and American Coots (*Fulica americana*) and their relationships to food abundance during winter to test several hypotheses relative to niche breadth and overlap. Mass of aquatic vegetation declined over time, and interspecific differences in diet and microhabitat generally occurred only when food abundance was low. Diet and feeding-method niche breadths were negatively related to food abundance, as predicted by niche theory. However, microhabitat niche breadth was not related to food abundance. Overlaps in diet, microhabitat, and feeding-method niches were positively related to food abundance, which is consistent with niche partitioning between potentially competing species. Divergence in foraging niches with declining food abundance was related primarily to behavioral differences between Gadwalls and coots. Both species fed predominantly at the surface in areas dominated by Eurasian watermilfoil (*Myriophyllum spicatum*) in early winter when food was abundant. Most of the Gadwalls left the reservoir when food abundance declined in late winter. Those that remained kleptoparasitized diving coots, or flew to relatively isolated habitats where filamentous algae grew at the surface. Coots, on the other hand, remained in deep-water habitats where they fed by diving for milfoil. Received 19 May 1997, accepted 17 December 1997.

INTERSPECIFIC COMPETITION for food or foraging space has been implicated in patterns of resource use in waterfowl (White and James 1978, Nudds 1983, Allouche and Tamisier 1984, Bustnes and Lonne 1997). Competition exerts its greatest effect on avian assemblages during periods of resource shortage (Baker and Baker 1973, Grant and Grant 1980); however, biologists disagree as to whether resource limitation for waterfowl is highest during the breeding (Nudds and Bowlby 1984, Bethke 1991, Nudds and Wickett 1994) or nonbreeding (DuBowy 1988, 1991) seasons. Although the existence of competition is difficult to determine in highly mobile animals such as waterfowl, niche theory and optimal foraging theory (OFT) provide testable hypotheses regarding resource use (niche breadth) and niche overlap between potentially competing species (Schoener 1986, Stephens and Krebs 1986).

In general, OFT predicts that animals choose food items that yield the greatest net energy per unit time spent foraging; therefore, when high-quality food items are abundant, they should be consumed exclusively. Such foraging decisions directly affect feeding-niche dynamics, niche overlap, and interspecific competition (MacArthur and Pianka 1966, Belovsky 1986a,

b, Abrams 1990). Overlap in food use between species may decrease when food is limited (Grant 1986, DuBowy 1988, Bell and Ford 1990, Miles 1990, Sih 1993), because species specialize on food items that they are adapted to consume (Baker and Baker 1973, Schoener 1982, Grant 1986). When food abundance is low, species also may limit foraging to the microhabitats (patches) in which they forage most efficiently (MacArthur and Pianka 1966, Schoener 1982, Pulliam 1985).

Based on these concepts, we tested several hypotheses regarding niche relationships of wintering Gadwalls (*Anas strepera*) and American Coots (*Fulica americana*; hereafter "coots"). Both species are generalist herbivores in winter and typically occupy similar habitats dominated by submersed aquatic vegetation (Paulus 1982, Hardin et al. 1984, LeSchack 1993). Recognizing that food can be partitioned in several ways, we studied three aspects of the foraging niche: diet, microhabitat, and feeding method. We predicted that as food abundance declined in winter, diet and feeding-method niches of both species would expand, and their niche overlap would decrease. We also predicted that Gadwalls and coots would occupy a more limited set of microhabitats as food abundance declined, resulting in decreased breadth and overlap of the microhabitat niche.

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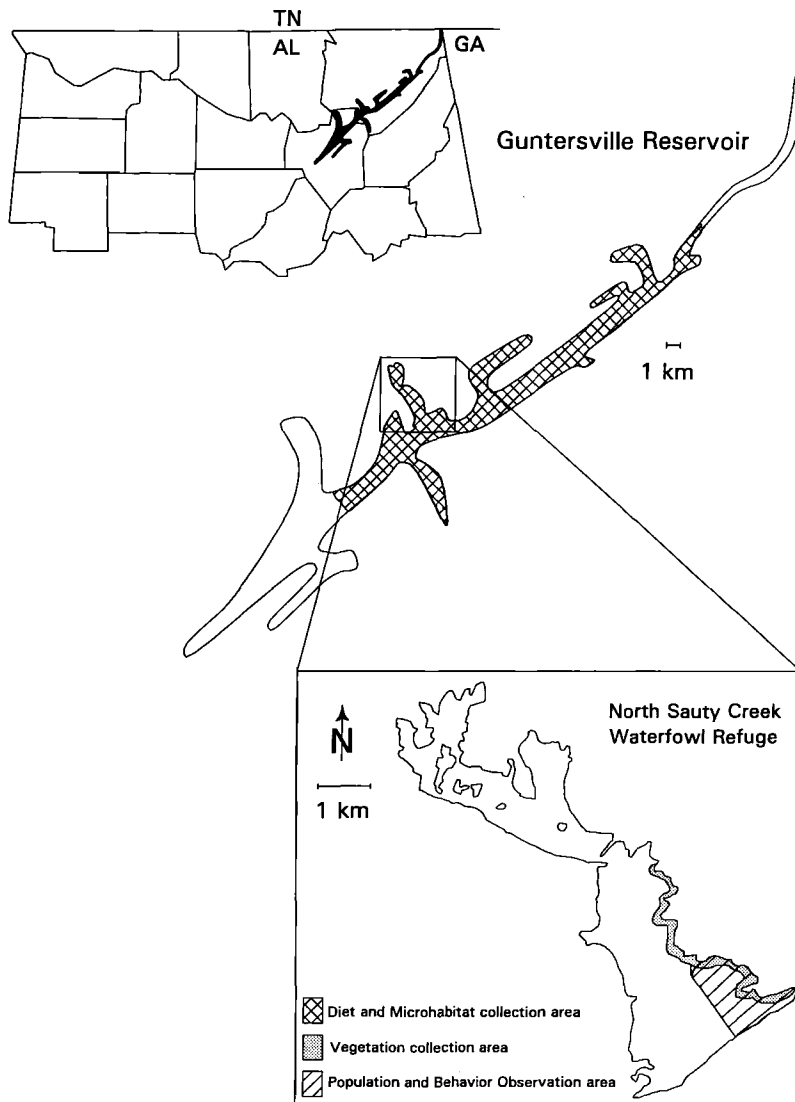


FIG. 1. Map of study area at Guntersville Reservoir, Alabama.

STUDY AREA AND METHODS

Study area.—The study was conducted from October 1992 through February 1993 at Guntersville Reservoir, a 27,479-ha impoundment of the Tennessee River in Jackson and Marshall counties, Alabama, and Marion County, Tennessee (Fig. 1). In September 1992, the reservoir contained 2,426 ha of aquatic macrophytes, with Eurasian watermilfoil (*Myriophyllum spicatum*; hereafter “milfoil”) being the dominant (>90% areal coverage) species (Tennessee Valley Authority unpubl. data).

Bird numbers.—Population counts were conducted weekly (October to March) from 1000 to 1300 CST at the same site within the 2,850-ha North Sauty Creek

Waterfowl Refuge (NSCWR). A 15 to 60 × spotting scope was used to identify and count all birds on a 142-ha section of NSCWR (Fig. 1). Other potential herbivores, such as the American Wigeon (*Anas americana*), occurred in low numbers (<275) and were not included in calculation of total population size.

Vegetation biomass.—We sampled vegetation along the north shore of NSCWR (Fig. 1) every two weeks (November to January) and once in October and February by clipping all vegetation to a depth of 30 cm in six or seven randomly placed 1.0 × 0.5-m plots. Plots were located in water 0.5 to 1.0 m deep, 10 to 100 m from shore. Vegetation samples were placed in sealed plastic bags, refrigerated ≤48 h, and then dried to constant mass and weighed (±0.01 g).

Diet and microhabitat.—Gadwalls and coots were collected from October through February at 30 different locations throughout the reservoir (Fig. 1). Birds were observed feeding ≥ 5 min before being collected with a shotgun. Esophageal and proventricular contents were removed immediately, placed in plastic containers with water, and kept on ice ≤ 8 h and then frozen. Sex was determined by internal examination, and age was determined (Gadwalls only) using plumage characteristics (Carney 1992). Samples of vegetation were clipped from the water surface to 5 cm below the surface within 0.5 m of where the bird had been feeding (microhabitat), placed in plastic bags, and handled similarly to diet samples. Food items within diet samples and plant material within microhabitat subsamples (2 to 3 g, wet) were thawed, sorted, identified, dried to constant mass at 50°C, and weighed (± 0.001 g). Subsampling of microhabitat samples was necessary because of the large amount of time required to sort and identify items. All diet samples weighed less than 2 g (wet). Recognizing an important difference between trace items (i.e. < 0.001 g) and those that do not exist (i.e. 0 g), trace items were given a value of 0.0001 g, an order of magnitude smaller than the lowest measurement. We identified plant material using Godfrey and Wooten (1979, 1981) and Radford et al. (1983), seeds using Martin and Barkley (1961), and invertebrates using Pennak (1978) and Merritt and Cummins (1984).

Diameter of flattened stems ($n = 30$) was measured on wet milfoil plants to classify stem size in three morphologically different parts of the plant; growing tips (small), branched stem segments with whorls of leaves (medium), and unbranched basal stem segments with no leaves (large). The 95% confidence intervals of the three stem categories were calculated and used to set limits for stem size classes. Food items were categorized as milfoil leaves (hereafter "leaves"), small milfoil stems (< 1 mm; "small stems"), medium milfoil stems (1 to 2 mm; "medium stems"), large milfoil stems (> 2 mm; "large stems"), native vegetation, seeds, and invertebrates. Vegetation in microhabitat samples was categorized as milfoil, algae (Chlorophyta), duckweed/mosquito fern (*Lemna* spp. / *Azolla caroliniana*), and other. Food bulk (sensu Belovsky 1984, Prop and Deerenberg 1991) is an important consideration in diet and nutrition studies of animals with limited digestive capacity (Belovsky 1984; see also Sedinger and Raveling 1988, Prop and Deerenberg 1991). However, we measured dry mass of each item because partial drying made it difficult to consistently measure wet mass of numerous small items. We converted dry mass to wet mass using mean percent water values from subsamples ($n = 6$) of milfoil leaf, small milfoil stems, medium milfoil stems, large milfoil stems, and native vegetation (*Lemna* spp., *Spirodella* spp., *Azolla caroliniana*, algae [Chlorophyta]), means of published val-

ues for seeds (*Puccinellia nuttalliana*, *Glyceria glandis*, *Beckmannia syzigachne*, *Scolochloa festucacea*, *Alopecurus aequalis*) and published values for invertebrates (Chironimidae larvae, Cladocera, *Gammarus* sp., Lymnaeidae, Zygoptera naiads; Sugden 1973).

Feeding method.—Feeding method in waterfowl can provide a reliable index to relative feeding depth (Pöysä 1983), because most feeding modes (surface-peck, tip-up, dive, etc.) are associated with characteristic depths below the surface. Diurnal behaviors of Gadwalls and coots were recorded using a 15 to 60 × spotting scope during three time blocks (0.5 h before sunrise to 1000, 1000 to 1400, and 1400 to 0.5 h after sunset) from a blind overlooking the same 142-ha section of NSCWR used in population counts. Each time block was randomly sampled three times per month and divided into 1-h observation periods (e.g. 0700 to 0800). Focal-animal sampling was used to observe and record behaviors (Altmann 1974). An individual was chosen (alternating sexes for Gadwall) by pointing the scope at the center of a flock and observing the bird closest to the center of the field of vision. Although birds were not marked, flocks were usually large enough to avoid repeated sampling of a single individual during consecutive observation periods. Observations of individual birds lasted for 5 min, and behaviors were recorded every 15 s for a total of 20 behaviors per 5-min sampling period. Feeding modes were recorded as surface-peck, head submerged, tip-up, dive, and kleptoparasitize.

Diving coots typically returned to the surface with a strand of vegetation (most often milfoil) in their beak. Once at the surface, they pecked at the newly obtained strand to consume it. We recorded coots as surface-pecking whether or not the food item being consumed was obtained by diving. Hence, some foods consumed while surface-pecking were obtained while diving. We adjusted activity data to reflect this using data collected on diving coots in January 1997 at Gunter'sville Reservoir. We recorded time spent diving (DIVE) and time spent consuming milfoil immediately after it was brought to the surface (CONS) by individual coots. The mean ratio of CONS:DIVE was 1.54 ($n = 66$ diving events) and provided an estimate of the time coots spent consuming food obtained by diving. Original behavioral data were then adjusted by increasing percent of time diving by a factor of 1.54, and reducing percent of time surface-pecking by the same amount. Adjusted data were used in feeding-method niche calculations and analyses.

Niche breadth and overlap.—Niche breadth was calculated after Levins (1968):

$$B = 1 / \sum_{i=1}^n p_i^2, \quad (1)$$

where p_i is the proportion of items in each category

TABLE 1. Monthly numbers of American Coots and Gadwalls, and biomass estimates of aquatic vegetation at North Sauty Creek Waterfowl Refuge, Guntersville Reservoir, Alabama, 1992 to 1993. Values are $\bar{x} \pm SE$.

Month	Bird numbers				Aquatic vegetation	
	<i>n</i>	American Coot	Gadwall	Total	<i>n</i>	Biomass (g/m ²)
October	4	669 ± 233	1,739 ± 757	2,408 ± 855	7	248.8 ± 42.2 A ^a
November	4	1,547 ± 184	1,179 ± 82	2,726 ± 234	13	172.3 ± 38.0 A
December	3	2,037 ± 140	2,135 ± 937	4,171 ± 934	13	106.0 ± 18.2 A
January	4	2,050 ± 219	1,273 ± 144	3,323 ± 184	13	41.3 ± 9.0 B
February	3	1,333 ± 417	614 ± 211	1,948 ± 608	7	8.3 ± 2.5 C
March	3	1,193 ± 431	42 ± 21	1,235 ± 452	—	—

^a Biomass means with different letters differ ($P < 0.05$; Tukey-Kramer).

(i) within a particular niche dimension (e.g. diet, microhabitat, feeding method). Because the range of values of B depends on the number of resources, we standardized it on a scale of 0 to 1 using the following formula (Krebs 1989):

$$B_A = (B - 1) / (n - 1), \quad (2)$$

where n is the number of resource types (e.g. food items). Niche overlap between Gadwalls and coots was quantified using Pianka's (1973) formula:

$$O_{gc} = \frac{\sum_{i=1}^n p_{ig} p_{ic}}{\sum_{i=1}^n p_{ig}^2 \sum_{i=1}^n p_{ic}^2}, \quad (3)$$

where p_{ig} and p_{ic} are the frequency of use of the i th resource by Gadwalls and coots, respectively.

Data analysis.—Vegetation samples were grouped by month before analysis, and the data were log transformed to make the variances independent of the means (Zar 1984). Monthly differences in plant mass were tested with ANOVA and Tukey-Kramer multiple comparisons tests (SAS 1997). Mean monthly numbers of Gadwalls and coots were computed for analysis.

Diet, microhabitat, and feeding-behavior data were grouped by month. Aggregate percentages of diet and microhabitat items (wet mass) were used in analyses. Percent of feeding time using various feeding methods was calculated for each 5-min observation, and mean values were computed for each hour of observation. Diet, microhabitat, and feeding-method data were arcsine transformed to meet assumptions of parametric tests (Sokal and Rohlf 1981). We used multivariate analysis of variance (MANOVA) to examine differences in diet and microhabitat by species, sex, age (Gadwalls only), and month, and differences in feeding method by species and month, using Wilks' Lambda as the test statistic (Harris 1975). Significant independent variables from the MANOVA model were used in ANOVAs, and critical P -values were adjusted for the number of categories tested (diet: categories = 7, critical P -value = 0.007; feeding method: categories = 5, critical

P -value = 0.01; microhabitat: categories = 4, critical P -value = 0.0125). Tukey-Kramer multiple comparisons were used to separate means for factors with significant ANOVAs.

Breadth and overlap of the foraging niche should be related to aquatic plant mass for herbivores such as Gadwalls and coots. Food abundance is a function of the amount of food present and the number of animals potentially using it (Llewellyn and Jenkins 1987). Consequently, we used simple linear or quadratic regression analysis, with mean monthly total population size (Gadwall + coot) as the independent variable, and monthly niche breadth or niche overlap as the dependent variables. Residuals from these analyses represent variation in niche breadth and overlap not explained by population size and were used as the dependent variables in a second set of simple linear regression analyses with aquatic plant mass as the independent variable. We set the level of significance at $P \leq 0.1$ due to the relatively low power of these tests with such small ($n = 5$) sample sizes (Cohen 1977).

RESULTS

Bird numbers and vegetation biomass.—Gadwalls began arriving at Guntersville Reservoir in early October. Average numbers peaked at NSCWR in December and declined through February and March (Table 1). Coots also began arriving in early October, and average numbers were highest in December and January (Table 1). Coot numbers declined in February, but compared with Gadwalls, coots were relatively abundant until mid-March. Dry mass of aquatic vegetation declined ($F = 15.68$, $df = 4$ and 48 , $P < 0.001$) over time (Table 1).

Diets.—We examined diets of coots ($n = 89$) and Gadwalls ($n = 79$). Aggregate percentage wet mass of diet items did not differ by sex (MANOVA, coot: $F = 1.62$, $df = 7$ and 72 , $P = 0.142$; Gadwall: $F = 0.69$, $df = 7$ and 54 , $P =$

0.680), or age (Gadwall: $F = 1.45$, $df = 7$ and 54 , $P = 0.205$), so data were combined across sexes and ages. Overall, coots consumed 95.3% plant material, 1.6% seed, and 3.1% animal matter, and Gadwalls consumed 99.0% plant material, 0.1% seed, and 0.9% animal matter.

Diet composition of coots did not differ (MANOVA, $F = 1.46$, $df = 28$ and 279 , $P = 0.068$) by month, whereas that of Gadwalls did ($F = 3.51$, $df = 28$ and 246 , $P < 0.001$). The proportion of milfoil leaves in the diet decreased ($P < 0.001$) for Gadwalls in January and February, whereas the proportions of native vegetation and invertebrates generally increased in late winter ($P < 0.002$; Table 2). Interspecific differences in diet varied by month (MANOVA, month \times species: $F = 2.33$, $df = 28$ and 549 , $P < 0.001$). Most notably, in February Gadwalls consumed a higher proportion of native vegetation ($F = 16.09$, $df = 1$ and 50 , $P < 0.001$) and a lower proportion of milfoil leaves ($F = 30.51$, $df = 1$ and 50 , $P < 0.001$) than did coots (Table 2).

Microhabitat composition.—There was a sex by month interaction for microhabitat composition of coots (MANOVA, $F = 6.47$, $df = 4$ and 78 , $P < 0.001$). Individual tests by month revealed no sex effect ($P > 0.314$); therefore, data were combined across sexes. Composition of microhabitats used by Gadwalls did not differ by sex or age class (MANOVA, sex: $F = 0.27$, $df = 4$ and 57 , $P = 0.896$; age: $F = 0.58$, $df = 4$ and 57 , $P = 0.681$; sex \times age: $F = 0.62$, $df = 4$ and 57 , $P = 0.648$); therefore, data were combined across ages and sexes.

Composition of microhabitats used by coots and Gadwalls varied by month (MANOVA, coot: $F = 8.24$, $df = 4$ and 84 , $P < 0.001$; Gadwall: $F = 2.87$, $df = 16$ and 218 , $P < 0.001$). Microhabitat of coots consisted mostly of milfoil (97 to 99%; Table 3) but slightly higher ($P < 0.03$) proportions of duckweed/mosquito fern occurred in October and November than in subsequent months. Microhabitat of Gadwalls also contained mostly milfoil, but amounts of milfoil declined ($P < 0.006$) and algae increased ($P < 0.004$) in February (Table 3). Interspecific differences in microhabitat varied by month (MANOVA, month \times species: $F = 3.90$, $df = 16$ and 474 , $P < 0.001$). In February, microhabitat of coots contained a higher proportion of milfoil ($F = 23.95$, $df = 1$ and 50 , $P < 0.001$) and a lower proportion of algae ($F =$

TABLE 2. Diet composition of wintering American Coots and Gadwalls (% aggregate wet mass, $\bar{x} \pm SE$) at Guntersville Reservoir, Alabama, 1992 to 1993.

Month	n	Milfoil leaf	Small stem	Medium stem	Large stem	Native ^a	Seed	Invertebrate
American Coot								
October	11	64.1 \pm 13.2	2.1 \pm 2.1	10.6 \pm 5.5	0	12.1 \pm 9.2	0.1 \pm 0.1	9.1 \pm 9.0
November	16	49.3 \pm 7.5	7.8 \pm 6.2	8.0 \pm 2.9*	7.1 \pm 3.2	25.3 \pm 8.9*	tr	0.2 \pm 0.1
December	18	53.5 \pm 6.5	1.0 \pm 0.4*	12.1 \pm 4.2	13.5 \pm 4.0	11.9 \pm 6.5	5.5 \pm 5.5	0.5 \pm 0.2
January	18	41.1 \pm 7.4	0.2 \pm 0.2*	12.1 \pm 4.9	20.6 \pm 8.3	20.2 \pm 8.6	0.3 \pm 0.2	4.1 \pm 1.7
February	26	67.0 \pm 4.5 ^{b*}	1.2 \pm 0.7	11.3 \pm 2.7	14.5 \pm 3.6	5.2 \pm 2.7*	0.1 \pm 0.1	2.4 \pm 0.6
Gadwall								
October	5	64.7 \pm 17.4 AB ^c	3.9 \pm 2.6	31.4 \pm 18.2	0	0	0	tr
November	13	63.4 \pm 5.6 AB	4.4 \pm 1.6	30.5 \pm 5.5*	1.5 \pm 1.0	0.1 \pm 0.0* B	tr	0.1 \pm 0.0 C
December	18	76.0 \pm 2.9 A	2.6 \pm 0.4*	15.0 \pm 2.2	5.6 \pm 2.3	0.4 \pm 0.3 B	tr	0.4 \pm 0.3 BC
January	17	47.6 \pm 6.0 BC	1.8 \pm 0.4*	13.7 \pm 2.8	9.8 \pm 4.7	25.2 \pm 8.6 AB	tr	1.7 \pm 0.5 A
February	26	28.0 \pm 5.0* C	2.3 \pm 0.7	15.2 \pm 3.4	15.0 \pm 4.1	38.2 \pm 8.2* A	tr	1.0 \pm 0.2 AB

^a Native = predominantly filamentous algae, duckweed, and mosquito fern.

^b Interspecific comparisons: asterisks designate means within months and diet categories that differ ($P < 0.007$; ANOVA) between species.

^c Intraspecific comparisons: means within columns and bird species with different uppercase letters are significantly different ($P < 0.05$; Tukey-Kramer).

TABLE 3. Composition of microhabitats used by wintering American Coots and Gadwalls (% aggregate wet mass, $\bar{x} \pm SE$) at Guntersville Reservoir, Alabama, 1992 to 1993.

Month	<i>n</i>	Milfoil	Algae	DW/MF ^a	Other
American Coot					
October	11	97.1 \pm 2.2 AB ^b	2.5 \pm 2.2 A	0.4 \pm 0.2 A	0.1 \pm 0.0 A
November	16	93.3 \pm 4.0 B	6.1 \pm 3.9 A	0.6 \pm 0.3 A	tr A
December	18	99.8 \pm 0.2 A	0.2 \pm 0.2 A	tr B	tr A
January	18	97.8 \pm 1.5 AB	2.2 \pm 1.5 A	tr B	0 A
February	26	99.6 \pm 0.2 AB ^{c*}	0.4 \pm 0.2* A	0 B	0.1 \pm 0.1 A
Gadwall					
October	5	89.9 \pm 7.7 AB	10.1 \pm 7.6 AB	0 A	tr A
November	13	97.4 \pm 2.5 A	2.5 \pm 2.4 B	tr A	0.1 \pm 0.1 A
December	18	95.3 \pm 3.7 A	4.4 \pm 3.8 B	0.3 \pm 0.1 A	0 A
January	17	98.8 \pm 0.8 A	1.2 \pm 0.8 B	tr A	0 A
February	26	77.1 \pm 5.1* B	22.9 \pm 5.1* A	tr A	0 A

^a Duckweed/mosquito fern.

^b Intraspecific comparisons: means within columns and bird species with different uppercase letters are significantly different ($P < 0.05$; Tukey-Kramer).

^c Interspecific comparisons: asterisks designate means within months and diet categories that differ ($P < 0.05$; ANOVA) between species.

24.31, $df = 1$ and 50, $P < 0.001$) than that of Gadwalls (Table 3).

Feeding method.—Coots were observed for 149 h and Gadwalls for 147 h. Overall, coots and Gadwalls spent >65% of the day feeding. Feeding method varied by month (MANOVA, coot: $F = 53.32$, $df = 4$ and 144, $P < 0.001$; Gadwall: $F = 119.45$, $df = 4$ and 142, $P < 0.001$). Diving by coots increased ($P < 0.006$) after December and peaked in February ($P < 0.001$); surface-pecking was most prevalent from October to December ($P < 0.001$), and declined thereafter ($P < 0.001$; Table 4). Surface-pecking

by Gadwalls peaked in early winter and declined through late winter ($F = 9.90$, $df = 4$ and 142, $P < 0.001$). Kleptoparasitism of coots by Gadwalls was most prevalent in February ($P < 0.001$; Table 4).

Interspecific differences in feeding behavior varied by month (MANOVA, month \times species: $F = 111.43$, $df = 5$ and 285, $P < 0.001$). Coots were not observed tipping-up or kleptoparasitizing, and Gadwalls were not observed diving (Table 4). Gadwalls and coots fed equally by surface-pecking ($P > 0.01$) in all months except February, when Gadwalls surface-pecked

TABLE 4. Feeding activity (%)^a for American Coots and Gadwalls at North Sauty Creek Waterfowl Refuge, Guntersville Reservoir, Alabama, 1992 to 1993.

Month	Surface-peck	Head down	Tip-up	Dive	Kleptoparasitism
American Coot					
October	89.3 AB ^b	4.6 BC	0	6.1 C	0
November	83.9 A	5.7 AB ^{c*}	0	10.4 C	0
December	87.1 A	1.5 C*	0	11.4 C	0
January	63.6 B	10.0 A	0	26.4 B	0
February	40.1 C*	1.4 C	0	58.5 A	0
Gadwall					
October	93.0 A	5.2 BC	1.9 B	0	0 B
November	84.1 AB	11.4* A	4.3 B	0	0.2 B
December	82.7 AB	8.1* AB	9.1 AB	0	0.2 B
January	64.8 C	11.1 AB	22.8 A	0	1.3 B
February	77.0* BC	1.1 C	5.3 B	0	16.6 A

^a For Coots, activity adjusted to account for time spent surface pecking on food obtained while diving (see text for calculations).

^b Intraspecific comparisons: means within columns and bird species with different uppercase letters are significantly different ($P < 0.05$; Tukey-Kramer).

^c Interspecific comparisons: asterisks designate means within months and diet categories that differ ($P < 0.05$; ANOVA) between species. Only feeding methods used by both species (surface peck, head down) were compared statistically.

TABLE 5. Monthly niche breadth and niche overlap indices of wintering American Coots and Gadwalls at Guntersville Reservoir, Alabama, 1992 to 1993.

Niche dimension	October	November	December	January	February
Niche breadth					
Diet					
American Coot	0.20	0.34	0.29	0.40	0.17
Gadwall	0.15	0.17	0.11	0.36	0.45
Microhabitat					
American Coot	0.02	0.04	<0.01	0.01	<0.01
Gadwall	0.06	0.02	0.03	0.01	0.19
Feeding method					
American Coot	0.06	0.10	0.07	0.27	0.25
Gadwall	0.04	0.10	0.11	0.27	0.15
Niche overlap					
Diet	0.93	0.92	0.97	0.97	0.66
Microhabitat	1.00	1.00	1.00	1.00	0.96
Feeding method	1.00	0.99	0.98	0.87	0.55

more ($F = 79.26$, $df = 1$ and 156 , $P < 0.001$) than coots (Table 4). Gadwalls also fed more with their heads submerged than did coots in November ($F = 8.18$, $df = 1$ and 81 , $P = 0.005$) and December ($F = 35.03$, $df = 1$ and 45 , $P < 0.001$).

Niche breadth and overlap.—Diet and feeding-method breadths generally increased over time for Gadwalls and coots (Table 5). Microhabitat breadth was consistently low (<0.04) for coots. Gadwall microhabitat breadth was similarly low, except for a sharp increase in February (Table 5). Diet breadth and feeding-method breadth were negatively related ($P < 0.07$) to food abundance for both coots and Gadwalls (Fig. 2). Breadth of microhabitat was not related to food abundance for either species (coot: $P = 0.466$; Gadwall: $P = 0.298$; Fig. 2). Diet and feeding-method overlap were high from October to January and decreased substantially in February, whereas microhabitat overlap was high in all months (Table 5). Niche overlaps for diet, microhabitat, and feeding method were positively related to food abundance ($P < 0.06$; Fig. 3). Evidence of niche complementarity was not found: overlap was positively correlated in all three pairs of dimensions (feeding method \times microhabitat: $r = 0.962$, $P = 0.009$; feeding method \times diet: $r = 0.916$, $P = 0.029$; microhabitat \times diet: $r = 0.985$, $P = 0.002$).

DISCUSSION

Optimal foraging and diet.—Diets of Gadwalls and coots consisted almost entirely of sub-

mersed vegetation, similar to other studies (Jones 1940, Gates 1957, Kerwin and Webb 1971, Paulus 1982, Allouche and Tamisier 1984, Hardin et al. 1984). Foraging theory predicts that diets should be narrow when high-quality food items are abundant and should expand to include less-nutritious food items only when abundance of more nutritious food declines (MacArthur and Pianka 1966, Stephens and Krebs 1986, Sih 1993). Several species of herbivorous waterfowl select the most nutritious plants or plant parts (Owen 1976, Owen et al. 1977, Sedinger and Raveling 1984, Dawson et al. 1989), which is consistent with optimal foraging theory. Based on digestible energy (Table 6), seeds and invertebrates were under used by Gadwalls and coots in our study. However, Gadwalls and coots are herbivorous in winter and forage in areas with abundant submersed and floating vegetation. It is unrealistic to expect these birds to eat substantial amounts of seeds and invertebrates because, although these foods may supply important nutrients such as essential amino acids (Richardson and Kaminski 1992), their consumption is secondary to maintaining adequate intake of leafy vegetation. Furthermore, seeds and invertebrates probably were too scarce for birds to feed on them exclusively and still meet minimum energetic requirements.

Excluding seeds and invertebrates, diets of Gadwalls and coots still were not consistent with predictions of OFT. Both species main-

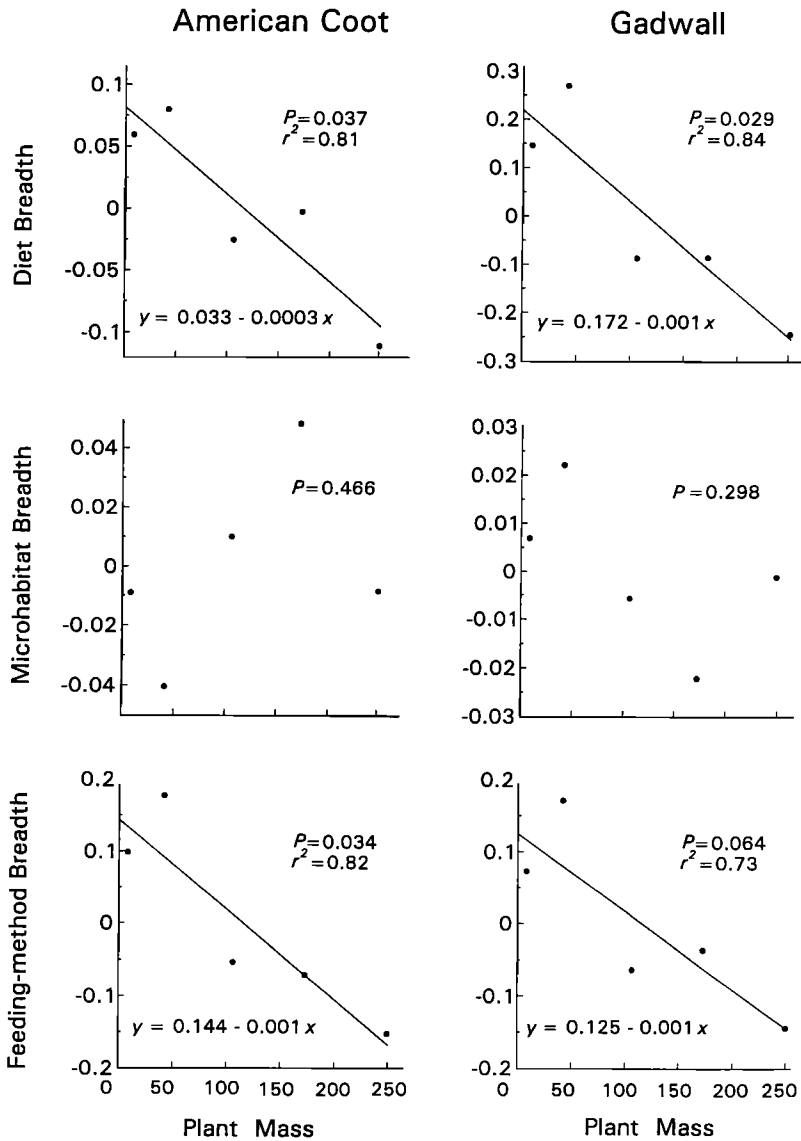


FIG. 2. Regression analyses of plant mass and niche-breadth residuals from niche breadth \times total population regressions for Gadwalls and American Coots at Guntersville Reservoir, October 1992 to February 1993.

tained a mixed diet of milfoil leaves and small, medium, and large stems throughout winter. Perhaps the cost in time and energy required to separate these food items was greater than the relatively small differences in gross energy (Table 6). For many herbivores, foraging is not constrained by energy but by acquisition of adequate levels of protein or other nutrients (Mattson 1980, Belovsky 1984, Sedinger 1997).

McKnight and Hepp (1998) present evidence that dietary preference in Gadwalls at Guntersville Reservoir in December and January was related to protein intake. Food choice, then, probably was a compromise between obtaining adequate levels of energy and protein. Such a tradeoff would explain the mixed diet of milfoil leaves and stems. Presumably, leaves were included in the diet because they contained rel-

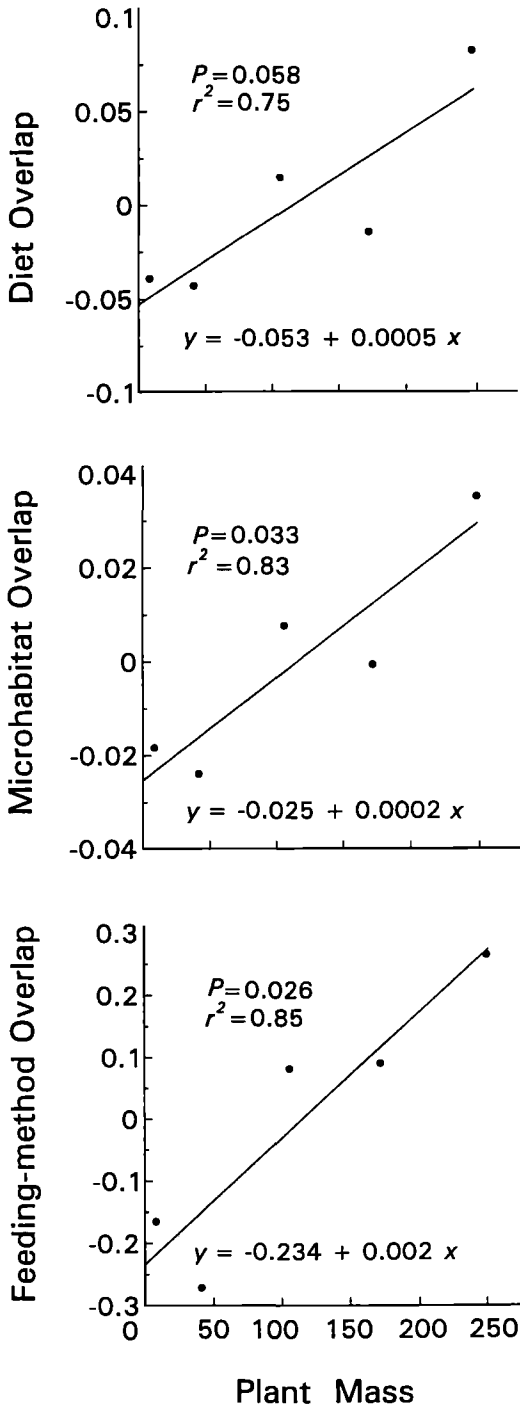


FIG. 3. Regression analyses of plant mass and niche-overlap residuals from niche overlap \times total population regressions for Gadwalls and American Coots at Guntersville Reservoir, October 1992 to February 1993.

TABLE 6. Nutrient content^a of food items consumed by Gadwalls and American Coots at Guntersville Reservoir, Alabama, 1992 to 1993. Values are % dry mass.

Food item	Protein	Fat	NFE ^b	Fiber	Ash	kcal/g ^c
Algae	21.5	1.5	16.1	57.0	4.0	2.01
Leaf	19.6	1.7	27.8	45.9	5.0	2.40
Small stem	15.6	1.0	41.2	41.3	0.9	2.66
Med. stem	11.6	1.5	43.5	41.2	1.2	2.58
Large stem	9.4	1.2	47.7	40.5	1.2	2.60
Seed	10.1	3.5	63.9	16.0	6.5	3.51
Invertebrate	39.4	3.7	13.7	7.9	35.3	3.13

^a Data from McKnight and Hepp (1998).

^b Nitrogen-free extract.

^c Estimated using gross energy values for protein (5.63 kcal/g), fat (9.25 kcal/g), and NFE (4.1 kcal/g).

atively high amounts of protein. Likewise, low-protein stems were included because they were relatively high in digestible energy. Consuming a mixed diet to satisfy competing nutrient demands is consistent with foraging models developed for generalist herbivores (Belovsky 1984, 1986a, b).

Niche breadth.—Low microhabitat diversity values reflect the relatively simple habitat structure of the reservoir during our study. The submersed plant community was dominated by a single species (milfoil), allowing for little variation in microhabitat use (as measured in this study). Coots occurred only in areas dominated by milfoil, and although Gadwalls used habitats with higher relative abundance of algae in October and February, we found no relationship between microhabitat niche breadth and food abundance. Our simple measure of microhabitat likely precluded an adequate test of the hypothesis regarding microhabitat niche breadth. However, the modest increase in microhabitat niche breadth of Gadwalls in February (increased algae) resulted from use of isolated lagoons, near-shore habitats, and ponds adjacent to the reservoir; this increased niche breadth had important effects on their diet.

Standardized diet-breadth indices in our study were similar to those calculated for Gadwalls and Eurasian Coots (*Fulica atra*) wintering in the Camargue, France (Allouche and Tamisier 1984). In both studies, one or a few food items tended to dominate the diet (Camargue: *Potamogeton* spp.; Guntersville Reservoir: milfoil leaf). Gadwalls and coots in our

study exploited a greater variety of food items when food abundance declined (Fig. 3), as predicted by theory. Increased diversity of food items for coots resulted from inclusion of proportionally more large milfoil stems and fewer milfoil leaves. For Gadwalls, increased diet breadth resulted from increased use of filamentous algae. Algae contained the highest level of protein and the lowest level of digestible energy of all food items (Table 6). We cannot determine, however, whether Gadwalls increased their use of algae because milfoil was scarce, or because algae was a better source of protein.

Gadwalls and coots used a greater variety of feeding methods as food abundance declined. Feeding methods fall along a continuum of depth below the water surface, where associated costs differ with respect to energy and vigilance. Surface-pecking exploits only those food items at or near the surface, but allows for greater vigilance for predators (Pöysä 1988). Tipping-up and diving allow individuals to feed farther below the surface but require more energy (Hurter 1979 in Allouche and Tamisier 1984) and allow less time for vigilance (Pöysä 1988). Milfoil was the dominant submersed aquatic plant throughout the study area, and its foliar biomass typically was concentrated within 1 m of the surface (see Nichols and Shaw 1986, Budd et al. 1995). Surface-pecking was used most by Gadwalls and coots when plant biomass was high. As plant mass declined and vegetation near the surface disappeared, use of alternative, more costly feeding methods such as tipping-up and diving were necessary to maintain adequate food intake. Kleptoparasitism of diving coots by Gadwalls also was most frequent at this time (Table 5; LeSchack and Hepp 1995), providing further evidence that food at the surface was relatively scarce while sufficient amounts of food remained at greater depths below the surface.

Niche overlap and partitioning.—Niche overlap between Gadwalls and coots was extremely high during most months of our study. Similar results were reported for migrating Gadwalls and coots in Oklahoma, where diet overlap ranged from 0.80 to 0.99 (Eddleman et al. 1985). High niche overlap is consistent with convergence on a superabundant resource and suggests that food in our study was not limited enough to invoke competition. This probably

was true for the early months of the study, but reduced niche overlap with declining food biomass was consistent with niche partitioning. In the Camargue, France, diet overlap between Gadwalls and Eurasian Coots decreased from August to February, presumably as a result of decreased food at the surface (Allouche and Tamisier 1984). However, these authors did not measure food availability. DuBowy (1988) reported reduced niche overlap in a guild of dabbling ducks during winter, when invertebrate prey items were less abundant. These results are of limited value for the herbivorous ducks in his study (Gadwalls, American Wigeon), however, because these species typically do not eat substantial amounts of invertebrates during winter.

In many communities, species similar along one or more niche dimensions are dissimilar along others (niche complementarity; Cody 1968, Schoener 1986), and niche complementarity has been demonstrated in several waterfowl guilds (Amat 1984, DuBowy 1988, Bustnes and Lonne 1997). However, we found no evidence of niche complementarity. Complementarity can occur only between relatively independent niche dimensions (Armstrong and Nudds 1985), and the niche dimensions measured in our study, especially diet and microhabitat, were not independent. Birds that fed in microhabitats dominated by milfoil were constrained to eat mostly milfoil. Likewise, Gadwalls that fed on algae in late winter apparently went to algae-rich microhabitats to do so.

Gadwalls and coots behaved as predicted by OFT in that they converged on superabundant milfoil growing near the surface and subsequently diverged in resource use when food abundance (i.e. surface milfoil) declined. Divergence in the foraging niche resulted primarily from coots increasing their use of milfoil obtained by diving, and Gadwalls either kleptoparasitizing diving coots or feeding in areas with filamentous algae in February. Gadwalls in Louisiana followed a similar pattern of exploiting algae in late winter when it became abundant (Paulus 1982). Nutritional reasons for the shift in microhabitat use and diet late in the season are discussed above. However, there are at least two alternative explanations. First, abundance of filamentous algae in southeastern lakes typically is low throughout fall and winter and increases in late winter and spring

(see Paulus 1982). Microhabitats with substantial amounts of algae, therefore, may not have been available until February. Second, even if algae were available, disturbance and risk of predation may have precluded the use of these habitats earlier in winter (Nilsson 1972). Because we typically found filamentous algae in ponds adjacent to the reservoir, isolated embayments, and near-shore areas of large embayments, Gadwalls feeding in these habitats would have been more vulnerable to hunting (December to January) than in offshore areas of large embayments and the river channel, where they occurred prior to February. Thus, low availability of algae combined with hunting-related disturbance may explain why Gadwalls did not use these microhabitats prior to February.

LeSchack and Hepp (1995) reported that subordinate (unpaired) Gadwalls kleptoparasitized coots more often and at higher rates than did dominant birds at Guntersville Reservoir, possibly because subordinates were excluded from higher-quality feeding sites. Although we did not determine pair status of Gadwalls collected for diet and microhabitat analysis, age and sex were recorded. Age and sex ratios of Gadwalls collected in milfoil (>90% milfoil) and algae ($\geq 10\%$ algae) microhabitats were not different from 1:1 (milfoil: age, $\chi^2 = 0.82$, $P = 0.366$; sex, $\chi^2 = 2.27$, $P = 0.132$; algae: age, $\chi^2 = 3.27$, $P = 0.071$; sex, $\chi^2 = 0.60$, $P = 0.439$), although a marginally ($P = 0.071$) higher proportion of adults than immatures (11 adults, 4 immatures) occurred in algae microhabitats. Assuming that immature Gadwalls were subordinate to adults (Blohm 1982, McKinney 1992), age ratios provided evidence that algae microhabitats were of equal (or higher) quality than milfoil microhabitats to Gadwalls in February.

We never observed coots in habitats that had substantial amounts of algae (i.e. ponds and isolated lagoons) in late winter. Differential use of microhabitats and foods by Gadwalls and coots in late winter may have resulted from several factors. First, Gadwalls have medium-sized bills with lamellae suited for straining relatively small particles (Kehoe and Thomas 1987), whereas coots have short, pointed, pincer-like bills. Thus, Gadwalls may have been more efficient than coots at manipulating and consuming filamentous algae, although the me-

chanics of this relationship are not clear. Second, because coots can dive for food, milfoil was available to them after surface and near-surface vegetation was unavailable to Gadwalls. Hence, carrying capacity was somewhat higher for coots than for Gadwalls in late winter, as evidenced by their relative numbers in February and March (Fig. 2). Because Gadwalls could not reach much of the remaining milfoil, many left the reservoir beginning in January (Fig. 2). As discussed above, those that remained in milfoil areas kleptoparasitized diving coots, while others increasingly exploited algae-rich microhabitats. Because coots typically roosted in deep-water areas adjacent to milfoil beds (S. K. McKnight pers. obs.), flying to algae-rich microhabitats probably was more energetically costly than swimming to nearby milfoil beds and feeding by diving.

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