

INTERSPECIFIC RELATIONSHIPS BETWEEN AMERICAN COOTS AND WATERFOWL DURING FALL MIGRATION

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Interactions between American Coots (*Fulica americana*) and waterfowl during the breeding season are well-documented (Ryder 1959, Nudds 1981). Ducks and coots use similar nesting, feeding, brooding, and loafing sites during the breeding season (Munro 1939, Sooter 1945, Ryder 1959). Coots create potential nest sites, repulse predators, provide predation buffers for ducks (Sooter 1945; Ryder 1958, 1959), and also may destroy eggs and young of other marsh-nesting birds (Munro 1937, Burger 1973, McNicholl 1975). Coots, ducks, and swans often feed cooperatively (Ryder 1959, Anderson 1974, Ryan 1981); and American Wigeon (*Anas americana*) and Gadwall (*A. strepera*) may rob feeding coots (Knapton and Knudsen 1978, Ryan 1981). Interspecific aggression between coots and waterfowl usually occurs when ducks approach coot nests or broods (Ryan and Dinsmore 1979). Despite these interactions, the numbers of duck broods produced in areas in Utah with nesting coots and in areas where coots had been removed were similar (Ryder 1958, 1961). Densities of coots and ducks, and brood counts of coots and ducks for a 26-year period in Saskatchewan also indicated no significant relationship between numbers of coots and waterfowl (Nudds 1981).

Coots and waterfowl from large areas of breeding habitat concentrate on smaller areas during the nonbreeding season (Weller 1975:102). These species may also change diets and habitats during migration and while wintering (Weller 1975). This study documents associations between waterfowl and coots during fall migration and examines feeding and behavioral interactions between coots and waterfowl in mixed flocks. Specifically, we (1) describe temporal and spatial overlap among migrations of coots and waterfowl, (2) present behavioral interactions among species, and (3) document food habits of birds feeding sympatrically during fall migration in Oklahoma.

STUDY AREAS

Field work was conducted on lakes in north-central and eastern Oklahoma. Activities of mixed flocks of coots and ducks were observed on Lake Carl Blackwell, Sooner Lake, Perry Lake, and Lake McMurtry (Payne and Noble counties) (described by Baumgartner 1942, Eddleman et al. 1985), and at Sequoyah National Wildlife Refuge (NWR) (Haskell, Muskogee, and Sequoyah counties). The former are within tallgrass prairie and cross-timber vegetation

types, while the refuge is predominately within the bottomland hardwood vegetation type on Robert S. Kerr Reservoir (Duck and Fletcher 1943). Cultivation of wheat and soybeans for migratory waterfowl is the major land-use on the refuge. Most observations of mixed flocks were made on the upper end of the reservoir and at the mouth of the Canadian River. Cattail (*Typha latifolia*) marshes, beds of Eurasian watermilfoil (*Myriophyllum brasiliense*), open water, beds of water primrose (*Ludwigia repens*), flooded dead timber, and intermittent mud flats were the principal habitats used by coots and ducks.

METHODS

Aerial and ground counts of coots and waterfowl during fall migration determined migration chronology on all lakes but Robert S. Kerr Reservoir. Aerial counts were conducted every five days from September through December 1979 and 1980. The surveys were supplemented with ground counts on Lake Carl Blackwell and Sooner Lake every one to five days from September through December 1979–1981. Temporal overlap was determined by comparison of the chronology of coot migration with the chronology of migration for each species of duck. Coots differed in migration chronology among lakes in the same year and among years on the same lake; thus, chronology data for each lake and year were analyzed separately (Eddleman et al. 1985). To determine correlations among numbers of coots and numbers of ducks, we calculated Spearman rank correlation coefficients (Conover 1980:251), which minimized problems of nonnormal distribution of count data. Dates of counts were used as sample points, and correlation analyses were conducted for all lakes and for Lake Carl Blackwell and Sooner Lake yearly. Significant positive correlations were interpreted as significant overlap in chronology between coots and the species under consideration, and significant negative correlations were interpreted as a lack of significant overlap in chronology.

Given temporal overlap, species may not overlap spatially. Spatial overlap was determined by observation of flocks of coots and waterfowl. During ground counts (all years) and some aerial counts (1980), species composition of all waterbird flocks was recorded. Flocks were used as sample points to calculate coefficients of interspecific overlap (Ochiai 1957). We used Ochiai's coefficient

$$r_o = \frac{A}{(A + B)(A + C)},$$

where A is the number of flocks containing both species, B is the number of flocks containing species one but not species two, and C is the number of flocks containing species two but not species one. Ochiai's coefficient was chosen because it satisfies the six necessary criteria for overlap indices (Janson 1981). The coefficient was calculated for each coot-duck species-pair for all duck species observed. Ochiai's coefficient ranges from zero (no overlap in use of space) to one (total overlap in use of space). To determine if spatial overlap changed through fall migration, we combined data for all years and calculated Ochiai's coefficient for September through December.

During ground counts, we observed mixed flocks of coots and waterfowl for at least 5 min to determine the principal behavioral interactions between coots and each duck species in flocks.

Because a similar diet between coots and a waterfowl species may partially explain behavioral interactions, we collected coots and three common species of ducks at sympatric feeding sites to determine overlap in diet. Gadwalls, wigeons, and coots were collected from all reservoirs. Redheads (*Aythya americana*) rarely fed at Robert S. Kerr Reservoir and therefore were collected only on Lake Carl Blackwell and Sooner Lake.

Birds were collected after they were observed feeding for ≥ 10 min. Esophageal contents were removed immediately and flushed into bottles containing 80% ethanol to prevent post-mortem digestion (Swanson and Bartonek 1970). Appropriate references (Pennak 1953, Fassett 1957, Martin and Barkley 1961, Steyermark 1963, Borrer et al. 1976) were used to identify esophageal contents in the laboratory. Foods were oven dried to constant weight for 10–12 hours at 100°C and weighed to the nearest mg on a Mettler analytical balance. Food-habit data were expressed as percentage dry weight and percent frequency of occurrence.

The degree of diet overlap among species was computed as:

$$C_0 = \frac{2 \sum_i^t (X_i Y_i)}{X_i^2 + Y_i^2}$$

where t is the total number of food species and X_i and Y_i the proportions of the diet comprised of food species i for two avian species (Morisita 1959). Values vary from 0, for distinctly different samples, to 1, when diets are identical. As foods differed among lakes, diets of birds were compared only when collected from the same lake. Statistical analyses were performed using the Statistical Analysis System (SAS Institute, Inc. 1982).

RESULTS

Twenty-one species of ducks and geese were present on the lakes, but the single White-winged Scoter (*Melanitta fusca*) seen was excluded from the analysis. Numbers of geese, Wood Ducks (*Aix sponsa*), Ring-necked Ducks (*Aythya collaris*), Common Goldeneyes (*Bucephala clangula*), and Buffleheads (*B. albeola*) were not significantly correlated with numbers of coots. All of these species except Ring-necked Ducks occurred in small numbers relative to other waterfowl. Numbers of Mallards (*Anas platyrhynchos*), Hooded Mergansers (*Lophodytes cucullatus*), and Common Mergansers (*Mergus merganser*) were significantly negatively correlated with numbers of coots for at least one lake or one year (Table 1). Numbers of Northern Shovelers (*Anas clypeata*), Gadwalls, American Wigeons, and Redheads were positively correlated with numbers of coots. Finally, significant correlations, both positive and negative, with coot numbers were found with Green-winged Teal (*Anas crecca*), Northern Pintails (*A. acuta*), Blue-winged Teal (*A. discors*), Canvasbacks (*Aythya valisineria*), and Lesser Scaup (*A. affinis*) (Table 1).

A total of 1099 flocks of coots and waterfowl were observed during fall 1979–1981, with 14 species of ducks recorded in mixed flocks (Table 2). Gadwalls and American Wigeons were most frequently recorded in mixed flocks, followed by Mallards, Redheads, and Ring-necked Ducks. Spatial overlap between coots and waterfowl species was highest for American Wigeon and Gadwall. Spatial overlap between coots and Ring-necked Ducks and American Wigeons increased through November, but declined in December (Table 3). Mallards and Gadwalls increased their relative

TABLE 1
SPEARMAN CORRELATION COEFFICIENTS BETWEEN NUMBERS OF AMERICAN COOTS AND NUMBERS OF WATERFOWL DURING FALL MIGRATION IN NORTH-CENTRAL OKLAHOMA, 1979-1981 (ONLY SPECIES WITH SIGNIFICANT CORRELATIONS ARE PRESENTED)

Species	Lake and year						
	1979		1980			1981	
	Carl Blackwell	All	Carl Blackwell	Sooner	All	Carl Blackwell	All
Mallard	-0.69 ^c	0.36 ^a	-0.52 ^b	-0.60 ^c	-0.21	0.08	0.06
Blue-winged Teal	-0.27	0.18	-0.06	0.37 ^a	0.11	0.03	0.30
Northern Shoveler	0.01	0.15	-0.27	0.18	0.25	0.42 ^a	0.51 ^b
Gadwall	-0.04	0.43 ^a	0.04	0.21	0.43 ^b	0.62 ^c	0.63 ^c
American Wigeon	0.06	0.28	0.16	0.28	0.46 ^b	0.52 ^b	0.58 ^c
Canvasback	-0.19	0.37 ^a	-0.34	-0.13	0.05	0.27	0.36 ^a
Redhead	0.03	0.41 ^a	0.00	0.24	0.30	0.38 ^a	0.26
Lesser Scaup	-0.00	0.40 ^a	-0.24	-0.20	-0.16	0.35	0.29
Hooded Merganser	-0.13	0.19	-0.18	-0.58 ^c	-0.34 ^a	-0.17	-0.21
Common Merganser	-0.44 ^a	0.25	-0.41 ^a	-0.24	-0.13		
Ruddy Duck	0.44 ^a	0.39 ^a	-0.53 ^a	0.17	0.30	0.27	0.37 ^a

^a 0.01 < P < 0.05.

^b 0.001 < P < 0.01.

^c P < 0.001.

occurrence in mixed flocks through December. Nearly 75% of the waterfowl in 184 mixed flocks did not interact with coots (Table 4). Cooperative feeding (ducks feeding on matter churned up by coots and vice versa) occurred between coots and Mallards, Gadwalls, American Wigeons, Redheads, and Ring-necked Ducks. Wigeons and Gadwalls were the only species observed robbing food from coots. Aggressive interactions between coots and ducks occurred in <5% of all flocks.

Submerged aquatic vegetation was the most common food for all species on all lakes. Vegetation eaten by coots, Gadwalls, and wigeons on Robert S. Kerr Reservoir included Eurasian watermilfoil, filamentous algae (*Cladophora* sp.), and floating-leaved pondweed (*Potamogeton nodosus*). Coots also grazed on sedges (*Cyperus* sp.), rushes (*Juncus* sp.), and cattail. A large number of snails was found in one coot. Aquatic insect larvae and adults were frequently eaten by coots, but amounts by dry weight were low.

On Sooner Lake, naiads were the principal food of coots, Gadwalls, and wigeons. Redheads also ate naiads, but sago pondweed (*Potamogeton pectinatus*) was found in most birds. One coot and one Gadwall contained only muskgrass (*Chara vulgaris*). Coots and Redheads ate small amounts of pondweed seeds. Naiads were also the most common food of coots,

TABLE 2
 COEFFICIENTS FOR INTERSPECIFIC OVERLAP BETWEEN AMERICAN COOTS AND COMMON
 WATERFOWL SPECIES IN NORTH-CENTRAL OKLAHOMA, FALL 1979-81^a

Species	Index of interspecific overlap ^{b,c}	Number of flocks with coots	Total number of flocks
Mallard	0.10 ± 0.01 D	43	367
Blue-winged Teal	0.02 ± 0.02 B	3	42
Northern Shoveler	0.02 ± 0.03 B	2	15
Gadwall	0.20 ± 0.04 F	70	262
American Wigeon	0.20 ± 0.04 F	68	239
Canvasback	0	0	25
Redhead	0.12 ± 0.04 E	30	141
Lesser Scaup	0.02 ± 0.02 B	3	54
Hooded Merganser	0.03 ± 0.20 C	3	24
Common Merganser	0	0	19
Ruddy Duck	0.01 ± 0.02 A	1	28

^a Number of flocks = 1099; number of flocks with coots = 483.

^b Ochiai's coefficient of interspecific overlap ± 95% confidence interval.

^c Means having the same letter are not significantly different (*t*-test, *P* = 0.01).

Redheads, Gadwalls, and wigeons on Lake Carl Blackwell, where muskgrass was the only food found in one coot and one wigeon.

Coots and ducks fed on many of the same foods during fall. Coots, Gadwalls, and wigeons ate similar foods within all lakes (Table 5). Redheads and coots ate similar foods on Lake Carl Blackwell, but Redheads were the only species eating narrow-leafed pondweed on Sooner Lake, accounting for the low diet overlap with coots.

DISCUSSION

Chronology of migration of most coots and ducks in our study differs both seasonally and daily. Negative correlations among the migration chronology of coots and other species were related to early migration of Blue-winged Teal or to late migration of Mallards and Common Mergansers relative to coot migration. For those species with migration positively correlated with migration of coots, such as Gadwall, American Wigeon, and Northern Shoveler, differences between migration timing of coots and individual species of ducks were explained by differences between responses of migrating coots and ducks to the passage of cold fronts. Waterfowl characteristically arrive ahead of or just behind fronts and frequently migrate during the day (Richardson 1978). Coots, however, follow cold fronts and are night migrants (Ryder 1963). Therefore, peak numbers of coots often followed peak numbers of waterfowl by one day. Because most coots and ducks usually left our study lakes within one to

TABLE 3
CHANGES IN SPATIAL OVERLAP BETWEEN AMERICAN COOTS AND COMMON WATERFOWL SPECIES THROUGH FALL MIGRATION, SEPTEMBER-DECEMBER 1979-81

	September		October		November		December	
	Index* of overlap	n_1/n_2^b	Index of overlap	n_1/n_2	Index of overlap	n_1/n_2	Index of overlap	n_1/n_2
Mallard	0.05 (A)	1/5	0.07 (A)	14/112	0.17 (B)	16/139	0.23 (C)	12/111
Gadwall	0.08 (A)	2/9	0.21 (B)	50/178	0.22 (B, C)	14/63	0.23 (C)	4/12
American Wigeon	0.14 (A)	5/20	0.18 (B)	42/170	0.33 (C)	16/37	0.29 (D)	5/12
Redhead	0	0/1	0.12 (A)	23/109	0.16 (B)	7/31		
Ring-necked Duck	0	0/1	0.06 (A)	8/59	0.13 (B)	5/23	0.08 (C)	1/6

* Ochiai's index for interspecific overlap using flocks as sample points, indices having the same letter are not significantly different (t -test, $P = 0.01$).

^b Number of flocks containing coots (n_1)/number of flocks containing waterfowl species (n_2).

TABLE 4
BEHAVIORAL INTERACTIONS BETWEEN WATERFOWL AND AMERICAN COOTS IN 184 MIXED FLOCKS, FALL 1979-81

Species	Behavioral interaction					Total no. of flocks observed containing species
	None	Aggression toward coots	Aggression toward ducks	Cooperative feeding	Food robbery	
Mallard	19 (90.5) ^a	0	0	2 (9.5)	0	21
Northern Pintail	6 (85.7)	0	1 (14.3)	0	0	7
Blue-winged Teal	3 (75.0)	0	1 (25.0)	0	0	4
Gadwall	33 (70.2)	1 (2.1)	1 (2.1)	7 (14.9)	5 (10.6)	47
American Wigeon	36 (70.6)	1 (2.0)	1 (2.0)	8 (15.7)	5 (9.8)	51
Redhead	19 (67.9)	0	0	9 (32.1)	0	28
Ring-necked Duck	8 (66.7)	0	0	4 (33.3)	0	12
All species	137 (74.5)	2 (1.1)	5 (2.7)	30 (16.3)	10 (5.4)	184

^a Number of interactions in each category (% of total for the species).

two days (Eddleman et al. 1985), potential temporal overlap of coots and waterfowl was minimized.

Spatial overlap for all coot-waterfowl pairs increased as the season progressed. This increase may indicate a proportional decrease of all aquatic food plants. As waterfowl deplete food in shallow water, the activities of coots make food available in deeper water as a result of churning, thus permitting food robbery by ducks. Coots fed on matter churned up by ducks only once. Food robbery was initiated by American Wigeon and Gadwall, two species that usually do not dive in deep water and which consume foods similar to those eaten by coots (Knapton and Knudsen 1978, Paulus 1982). Cooperative feeding and food robbery allowed dabbling ducks to obtain food that was ordinarily unavailable to them (Knapton and Knudsen 1978, Ryan 1981). Cooperative feeding may also benefit coots (Ryder 1959, Anderson 1974). We found no evidence that coots robbed food from ducks, although this behavior has been observed in coots and Ring-necked Ducks on wintering areas (L. D. Vangilder, pers. comm.).

We noted few instances of aggression between coots and ducks during fall migration. Interspecific behavioral interactions between breeding coots and ducks peak after hatching of coot broods (Ryder 1959, Ryan and Dinsmore 1979). At that time coots tenaciously defend broods against any species of duck entering their territory.

Overlap in diet among coots and the four principal waterfowl species was high on certain lakes in our study, especially between coots and

TABLE 5

DIET OVERLAP VALUES (MORISITA 1959) BETWEEN AMERICAN COOTS AND GADWALLS, AMERICAN WIGEONS, AND REDHEADS ON ROBERT S. KERR RESERVOIR, SOONER LAKE, AND LAKE CARL BLACKWELL DURING FALL 1980

	Gadwalls	American Wigeons	Redheads
Robert S. Kerr Reservoir	0.80	0.75	
Sooner Lake	0.99	0.99	0.24
Lake Carl Blackwell	0.86	0.90	0.86

Gadwall and American Wigeon. This overlap may explain the high incidences of behavioral interactions between coots and these two species compared with other ducks. Redheads differed from coots in eating mostly sago pondweed on Sooner Lake. Overall diets were similar in that vascular aquatic vegetation predominated in the diets of both species.

Interactions between coots and waterfowl on nesting areas usually benefit waterfowl or have little effect on densities of waterfowl (Ryder 1959, Knapton and Knudsen 1978, Nudds 1981). Similar conclusions are apparent during migration, although food robbery by ducks and churning up of food material by coots provide foods otherwise unavailable to some dabbling ducks.

SUMMARY

Temporal, spatial, and behavioral relationships between migrating American Coots (*Fulica americana*) and ducks were investigated in fall 1979–1981 in Oklahoma. Diets of coots, Gadwalls (*Anas strepera*), American Wigeons (*A. americana*), and Redheads (*Aythya americana*) were studied in fall 1980. Arrivals and departures of coots differed from those of waterfowl for all species, mainly because waterfowl migrated ahead of cold fronts and often diurnally, while coots migrated behind cold fronts and nocturnally. Significant positive correlations occurred between numbers of coots and numbers of Northern Shovelers (*Anas clypeata*), Gadwalls, American Wigeons, and Redheads on at least some lakes in most years. Waterfowl occurred in mixed flocks with low frequency. Gadwalls and American Wigeons were most frequently recorded with coots. Most ducks did not interact with coots in mixed flocks. Cooperative feeding and food robbery were the most frequently recorded behavioral interactions, especially between coots and Gadwalls or American Wigeons. Foods of coots and ducks were similar in most lakes and consisted mostly of aquatic vegetation. Interspecific interactions between coots and ducks are minimal because of temporal and spatial segregation during migration, and behavioral interactions that are mostly neutral or beneficial to ducks.

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