

AGGRESSIVE BEHAVIOR OF WINTERING DIVING DUCKS (AYTHYINI)

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ABSTRACT.—Intraspecific aggression, behavioral dominance, and the influence of behavioral dominance on habitat use by the sexes was studied in free-ranging flocks of Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), Ring-necked Ducks (*A. collaris*), and Lesser Scaup (*A. affinis*) that overwintered in coastal South Carolina. During three field seasons 4316 focal individuals were observed for 5 min each. In Canvasbacks, aggression was more frequent and was more intense than in the other three species. Males of each species dominated females in aggressive encounters that occurred primarily while foraging. In Canvasbacks there was a partial segregation of male and female foraging areas where food resources were distributed irregularly, with greater proportions of males inhabiting the higher quality food areas. Received 12 Apr. 1985, accepted 15 July 1986.

Aggressive behavior in animals is a mechanism by which individuals compete for essential, and often limited, resources (e.g., mates, food). Because of aggressive behavior there is frequently an unequal disposition of resources, with dominant individuals having priority of access (Brown 1975, Gauthreaux 1978). Moreover, some researchers indicate that dominant individuals have greater survival probabilities than subordinates (e.g., Smith 1976).

In birds, aggressive behavior is a common phenomenon associated with the reproductive period when males establish territories and compete for mates. Lack (1954) and Fretwell (1972), however, have suggested that, in terms of survival, the nonbreeding period is the more critical portion of the annual cycle. Lack (1966) further suggested that many bird populations are regulated by food supply during the nonbreeding period. In most bird species, a postbreeding tendency to form flocks generates a situation in which aggression is common (e.g., Marler 1971, Jenkins et al. 1975, Patterson 1977). Oftentimes this aggression involves asymmetric contests where males dominate females in competition for food (Brown 1963, Sayler and Afton 1981, Grubb 1982), although the opposite sometimes occurs (e.g., Thompson 1960, Samson 1977). In waterfowl, behavioral dominance has been studied in dabbling ducks (e.g., Paulus 1983, Hepp and Hair 1984), but is poorly understood in diving ducks.

Here, I (1) compare aspects of wintering intraspecific aggression and behavioral dominance in four species of coexisting diving ducks, Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), Ring-necked

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Ducks (*A. collaris*), and Lesser Scaup (*A. affinis*); and (2) evaluate the effect of behavioral dominance on local habitat use by males and females of each species.

STUDY AREA

I studied free-ranging diving ducks on four coastal manmade impoundments near Georgetown, Georgetown County, South Carolina. The four impoundments ranged from 7.75 to 12.85 ha in size and from 0.50 to 1.50 m in depth. The ponds supported approximately 3500 diving ducks daily from early November to March during 1975, 1976, and 1977. Canvasbacks and Ring-necked Ducks fed on banana water-lily (*Nymphaea mexicana*) tubers in the three freshwater impoundments. All four species fed on muskgrass (*Chara* spp.) and widgeon grass (*Ruppia maritima*) in the one brackish pond.

METHODS

Behavioral sampling.—Diving ducks were observed with 8.5× binoculars, or a 15–60× spotting scope, either from permanent blinds or a vehicle. The behavior of each species was recorded daily during four 40-min intervals spaced 3 h apart. Behavioral data were collected in 4-day cycles throughout each field season, with the 40-min intervals beginning 30 min later each day. Shifting the observation intervals assured that data collected were not biased toward a particular portion of the day. I attempted to study each of the four species every day, but Redheads and Lesser Scaup were frequently absent from the impoundments; species were sampled in a random sequence.

The 40-min observation intervals were partitioned into eight sample periods of 5-min each in which individual birds of a single species were followed continuously. When feasible, equal numbers of males and females were observed within each 40-min interval. Beginning each 5-min sample period, a focal individual was selected from the flock by directing binoculars, or a spotting scope, toward the flock and selecting the individual nearest the center of the field. This bird was the focal individual for the 5-min period, and each behavioral event performed by the bird was recorded in sequence (see Altmann 1974). In agonistic encounters (Scott and Fredericson 1951), the initiator, winner, and loser of the encounter were tabulated.

I defined an aggressive display as any behavioral act performed by one individual that caused the displacement of a second individual. An "intention movement" involved a jab with the bill or a slight movement by one bird toward another bird that was less than 1 m away. A "chase" occurred when one bird paddled rapidly across the water, with its head thrust forward and its bill slightly opened in pursuit of a retreating bird. "Fighting" involved exchanges of biting and striking with the wings. A bird was considered supplanted in an aggressive encounter when it retreated from another individual as a result of a threatening posture or overt activity (e.g., chase). Further descriptions of aggressive displays and fighting are in Alexander (1980a).

Sex and age determination.—Juvenile Aythyini resemble adults by late fall or early winter, and cannot be separated visually in the field. To assess age-related dominance in these species, birds were bait-trapped, aged according to a combination of cloacal characteristics (Hochbaum 1942) and plumage development (Carney 1964), and color-marked with patagial streamers.

Analytical procedures.—The intensity of aggression between wintering diving ducks was assessed by ranking the agonistic encounters on an ordinal scale from levels 1 to 4. Encounters were recorded as level 1 when the presence of one individual supplanted another, as level

2 when one individual supplanted another by an intention movement (e.g., bill thrust), as level 3 when one individual chased another, and as level 4 when two individuals were engaged in a fight (e.g., exchanges of biting and striking with the wings).

Intraspecific sex differences in dominance between unmarked individuals were evaluated by chi-square tests, and dominance matrices (Brown 1975) were used to establish a sex- and age-hierarchy between marked individuals within species.

Once I established intraspecific dominance relationships, I examined the effect of intersexual dominance on flock structure (i.e., male-female encounters more or less frequent than expected by chance). The distribution of intraspecific aggressive encounters between the sexes was analyzed by the goodness of fit to a theoretical distribution with a chi-square test. The existing sex ratio of each species (Hailman 1975) and focal bird sex ratio were considered in calculating the theoretical distribution of encounters. Sex ratio counts were made in early morning while birds were flocked in open water. The sex ratio of each species did undergo some temporal variation on individual ponds, but a decrease in birds on one pond was typically followed by an increase on a nearby pond. Therefore, an average sex ratio was calculated over all ponds. Often, when a population sex ratio has been determined, the proportions of males and females are used to compute an expected distribution of aggressive encounters (e.g., Hepp and Hair 1984). In focal individual sampling, these expected values are biased if the proportions of focal males and females are not also included in the computation of expected values. I calculated expected values for each interaction as follows:

- (1) Male-Male = $P_{fm} \times P_{mp} \times TI$
- (2) Male-Female = $P_{fm} \times P_{fp} \times TI + P_{ff} \times P_{mp} \times TI$
- (3) Female-Female = $P_{ff} \times P_{fp} \times TI$

In the previous equations, P_{fm} = proportion males in focal sample, P_{mp} = proportion males on ponds, TI = total aggressive interactions, P_{fp} = proportion females on ponds and P_{ff} = proportion females in focal sample.

If males and females within species used impoundments independently, the distribution of the sexes within a given pond should occur at random. As I selected focal birds, I also recorded the sex of the nearest conspecific to the focal individuals on each pond. The goodness of fit of male-male, male-female, and female-female associations to a theoretical distribution was tested by the chi-square statistic (see Ketterson 1979). Calculation of expected values included sex ratios and focal bird ratios as above.

Vegetation sampling. — Three impoundments on the study area supported stands of banana water-lily. Aerial photographs indicated that two ponds had uniform distributions of the plant, but at one pond (Middleton) water-lilies had a patchy distribution. On this pond some patches of water-lily leaves covered approximately 100% of the surface area, while in other patches only about 50% of the surface was covered. Bottom sampling for banana water-lily tubers was conducted at 3 m intervals along parallel transects through two contiguous patches near my observation blind. Hereafter, these patches are referred to as areas *a* (100% leaves/m²) and *b* (50% leaves/m²). Bottom samples were collected with a sharpened core sampler that extended 20.3 cm into the substrate. Sampling was conducted in October 1978 to estimate the banana water-lily tuber crops in the two areas before birds arrived. In March 1979 sampling was conducted again to document any seasonal decline of tuber crops within the two areas.

RESULTS

Canvasback aggression. — Intraspecific agonistic behavior occurred significantly more often in Canvasbacks than in the other three species (Table

TABLE 1
MEAN NUMBER $\pm$ SD OF INTRASPECIFIC AGGRESSIVE INTERACTIONS PER 5-MIN SAMPLE PERIOD IN WINTERING DIVING DUCKS

	Canvasback	Redhead	Ring-necked Duck	Lesser Scaup
Mean $\pm$ SD	1.02 $\pm$ 1.7 ^a	0.47 $\pm$ 1.04 ^b	0.55 $\pm$ 1.18 ^b	0.58 $\pm$ 1.36 ^b
Number of sample periods	1639	452	1441	784

^a One-way ANOVA ($F = 42.90$, $P < 0.001$). Means not followed by the same letter are significantly different using a Duncan's multiple range test ($P < 0.05$).

1). Moreover, male Canvasbacks initiated 837 intraspecific aggressive encounters during 817 sample periods, while females initiated 495 encounters in 822 sample periods, a difference that was highly significant ($t = 3.24$, $P < 0.001$). In six encounters I could not determine the initiator of the interaction. Of 1338 encounters, 30% involved chasing and fighting. Thirty-one percent of male-male and male-female encounters were at levels 3 and 4, while 26% of female-female encounters were at these levels.

Aggressive encounters between male and female Canvasbacks occurred at a rate of 0.08 interactions/min. A total of 634 aggressive encounters between unmarked males and females was observed, with males winning 416 encounters and females winning 218 ($\chi^2 = 61.8$, $df = 1$, $P < 0.001$). Male Canvasbacks initiated significantly more intersexual encounters than did females ($\chi^2 = 10.6$, $df = 1$, $P < 0.005$).

The dominance relationships among sex- and age-classes of Canvasbacks were determined from interactions among 25–40 of 86 marked birds. Adult male Canvasbacks were dominant, followed by juvenile males, adult females, and juvenile females (Table 2). This dominance structure closely parallels differences in body size of the respective sex- and age-classes in the species (see Alexander 1980b for morphological measurements on all four species).

Unmarked Canvasbacks were involved in 1338 intraspecific aggressive encounters. Male-male encounters occurred more often than expected, while female-female encounters occurred less often than expected (Table 3). Similarly, male-male associations were higher than expected and female-female were lower (Table 4). The similarity between these data could suggest an explanation for high male-male and low female-female aggressive encounters based upon frequency of association; however, a χ^2 test for heterogeneity indicated that aggressive interactions in Canvasbacks were not due to proximity alone ($\chi^2 = 14.5$, $df = 2$, $P < 0.001$).

During this study greater proportions of male Canvasbacks were ob-

TABLE 2
INTRASPECIFIC DOMINANCE RELATIONSHIPS FOR SEX- AND AGE-CLASSES OF WINTERING
DIVING DUCKS

Species ^a	Winner	Loser				% wins
		Adult male	Juvenile male	Adult female	Juvenile female	
Canvasback	Adult male	—	35	71	29	98
	Juvenile male	2	—	27	9	43
	Adult female	1	15	—	30	32
	Juvenile female	0	1	0	—	2
Ring-necked Duck	Adult male	—	40	7	1	100
	Juvenile male	0	—	2	13	27
	Adult female	0	0	—	3	25
	Juvenile female	0	0	0	—	0
Lesser Scaup	Adult male	—	18	28	18	99
	Juvenile male	0	—	5	11	46
	Adult female	1	1	—	11	28
	Juvenile female	0	0	0	—	0

^a Redheads were deleted from this table because of insufficient data.

served diving in the dense patches of banana water-lily at Middleton Pond. By comparing the Canvasback sex ratio on the pond over a two year period to the sex ratio in densely vegetated area *a*, a pattern of partial sexual segregation while foraging was detected. In addition, the proportion of males using area *a* rose from 38% in November to 86% in January (Table 5). The prevalence of male Canvasbacks in area *a* was likely a result of better food resources there. The bottom samples of banana water-lily tubers from area *a* (100% leaves/m²) and area *b* (50% leaves/m²) of Middleton Pond were markedly different. In October 1978 area *a* had whole tubers that were significantly heavier than in area *b* ($t = 2.24$, $P < 0.05$). Moreover, the total weight of whole tubers and fragments cut by the core sampler from area *a* (82.9 g/m²) was 2.4 times that of area *b* (35.0 g/m²). When tuber sampling was repeated in March 1979, area *a* had sustained a 50% decline in tubers that was not statistically significant, but area *b* had suffered a highly significant 88% tuber decline ($t = 3.39$, $P < 0.001$). I did not perform similar analyses for the other three species of diving ducks because they did not exhibit sexual differences in foraging patterns on any of the ponds.

Redhead aggression. — Intraspecific agonistic behavior in Redheads was significantly less frequent than in Canvasbacks, but did not differ statistically from Ring-necked Ducks and Lesser Scaup (Table 1). Male Redheads initiated 128 intraspecific aggressive encounters in 239 sample pe-

TABLE 3
 χ^2 GOODNESS-OF-FIT TESTS OF THE DISTRIBUTION OF AGGRESSIVE ENCOUNTERS WITHIN SEX CLASSES OF EACH DIVING DUCK SPECIES

Species	Male-male	Male-female	Female-female	χ^2	Probability
Canvasback	485/253 ^a	635/668	218/416	308.5	<0.001
Redhead	47/47	104/103	53/55	0.1	>0.050
Ring-necked Duck	232/277	363/364	138/101	20.9	<0.001
Lesser Scaup	163/183	235/228	51/39	6.1	<0.050

^a Observed frequency of encounters within each category/Expected frequency of encounters within each category (corrected for sex ratio and focal bird differences in each species).

riods, and females initiated 64 encounters in 213 sample periods ($t = 0.81$, $P > 0.05$). In Redheads, 15% of 204 aggressive encounters involved chasing and fighting. Six percent of male-male encounters were at levels 3 and 4, while 15% of male-female and 23% of female-female encounters were at these levels.

Aggressive encounters between male and female Redheads occurred at a rate of 0.04 interactions/min. A total of 102 intersexual aggressive encounters between unmarked males and females was observed, with males winning 86 encounters and females winning 16 ($\chi^2 = 49.9$, $df = 1$, $P < 0.001$). Male Redheads initiated significantly more intersexual encounters than did females ($\chi^2 = 20.0$, $df = 1$, $P < 0.001$).

Unmarked Redheads were involved in 204 intraspecific aggressive encounters. The distribution of male-male, male-female, and female-female encounters was not significantly different ($P > 0.05$) from a random distribution based upon the existing sex ratio and focal bird sex ratio (Table 3). The frequencies of aggressive encounters differed from the frequencies of associations between the sex of the focal individual and that of the nearest conspecific (Table 4). Male-female associations were higher than expected, female-female associations were lower than expected, and male-male associations were about as expected. The distribution of aggressive encounters in Redheads was significantly different from the distribution of associations ($\chi^2 = 8.9$, $df = 2$, $P < 0.025$).

Ring-necked Duck aggression.—Male Ring-necked Ducks initiated 473 intraspecific aggressive encounters in 730 sample periods, and females initiated 257 encounters in 711 sample periods ($t = 3.97$, $P < 0.001$). Only 14% of 733 interactions involved chasing and fighting. Sixteen percent of male-male encounters, 10% of male-female encounters, and 20% of female-female encounters were at levels 3 and 4.

Aggression between the sexes in Ring-necked Ducks occurred at a rate of 0.06 interactions/min. A total of 366 intersexual aggressive encounters

TABLE 4

χ^2 GOODNESS-OF-FIT TESTS OF THE DISTRIBUTION OF ASSOCIATIONS BETWEEN RANDOMLY SELECTED FOCAL INDIVIDUALS AND THEIR NEAREST CONSPECIFIC NEIGHBOR

Species	Male-male	Male-female	Female-female	χ^2	Probability
Canvasback	334/196 ^a	464/519	241/325	124.7	<0.001
Redhead	53/67	206/161	64/96	26.2	<0.001
Ring-necked Duck	288/341	539/461	102/128	26.7	<0.001
Lesser Scaup	164/266	371/331	119/57	111.3	<0.001

^a Observed frequency of associations within each category/Expected frequency of associations within each category (corrected for sex ratio and focal bird differences in each species).

was observed between unmarked individuals, with males winning 339 encounters and females 27 ($\chi^2 = 266.0$, $df = 1$, $P < 0.001$). Male Ring-necked Ducks initiated significantly more intersexual encounters than did females ($\chi^2 = 45.8$, $df = 1$, $P < 0.001$).

Dominance relationships between sex- and age-classes of Ring-necked Ducks were determined from interactions among 40 to 60 of 105 marked individuals. Adult males were dominant, followed by juvenile males, adult females, and juvenile females (Table 2). This dominance order follows the size differences among sex- and age-classes of the species (Alexander 1980b). Only four adult females, however, were trapped and marked during this study, rendering any conclusions about size differences and dominance between adult and juvenile females tentative.

Unmarked Ring-necked Ducks had 733 intraspecific aggressive encounters. Male-male encounters were less frequent than expected, male-female encounters about as expected, and female-female more frequent than expected (Table 3). These data do not coincide with the distribution of associations between the sex of focal individuals and that of the nearest conspecific (Table 4). The frequency of male-male and female-female associations was less than expected, but male-female associations were higher. The distribution of aggressive encounters and distribution of associations in Ring-necked Ducks differed significantly ($\chi^2 = 24.4$, $df = 2$, $P < 0.001$).

Lesser Scaup aggression. — Male Lesser Scaup initiated 310 intraspecific aggressive encounters in 388 sample periods, while females initiated 138 encounters in 396 sample periods ($t = 0.97$, $P > 0.05$). Of 499 interactions in Lesser Scaup, 12% involved chasing and fighting. Thirteen percent of male-male encounters were at levels 3 and 4, while 12% of male-female encounters and 8% of female-female encounters were at these levels.

Aggressive encounters between Lesser Scaup males and females occurred at a rate of 0.06 interactions/min. A total of 235 aggressive en-

TABLE 5
SEASONAL COMPARISON OF OVERALL CANVASBACK SEX RATIOS ON MIDDLETON POND WITH
SEX RATIOS IN AN AREA OF CONCENTRATED FOOD^a

Period	Overall			Area <i>a</i>		
	Males	Females	% males	Males	Females	% males
1 Nov.–15 Nov.	150	213	41	11	18	38
16 Nov.–30 Nov.	370	457	45	75	70	52
1 Dec.–15 Dec.	357	412	46	101	74	58
16 Dec.–31 Dec.	388	230	60	135	50	73
1 Jan.–15 Jan.	577	616	48	158	43	79
16 Jan.–31 Jan.	416	529	44	49	8	86

^a Data were tabulated during 1976/77 and 1977/78. Because the two years were similar, data were combined (overall heterogeneity $\chi^2 = 1.87$, $P > 0.05$; area *a* heterogeneity $\chi^2 = 2.30$, $P > 0.05$).

counters was tabulated between unmarked males and females, with males winning 205 encounters and females 30 ($\chi^2 = 130.3$, $df = 1$, $P < 0.001$). In addition, males initiated more intersexual encounters than females ($\chi^2 = 22.7$, $df = 1$, $P < 0.001$).

Dominance among sex- and age-classes of Lesser Scaup was determined from interactions among 20 to 40 of 115 marked individuals. Adult males were the dominant class followed by juvenile males, adult females, and juvenile females (Table 2). In general the dominance structure followed the size differences among sex- and age-classes (Alexander 1980b).

Unmarked Lesser Scaup had 449 intraspecific aggressive encounters. Male-male encounters were lower than expected, male-female encounters were higher than expected, and female-female encounters were higher than expected (Table 3). These data coincide with the associations found between the sex of the focal individual and that of the nearest conspecific (Table 4). The frequency of male-male associations was lower than expected, but male-female and female-female associations were higher than expected. The distribution of aggressive encounters and distribution of associations in Lesser Scaup were significantly different ($\chi^2 = 23.3$, $df = 2$, $P < 0.001$).

DISCUSSION

Fretwell (1972) reported that behavioral dominance in winter resulted in the dispersal of birds into an "optimal habitat" in which dominant birds have relatively high survivorship throughout the winter, and a sub-optimal "fringe habitat" inhabited by subordinate birds that have relatively low survivorship through the winter. Gauthreaux (1978) reported that important determinants of dominance are sex, age, and size. The

dominance of Canvasback males over females created a partial segregation of foraging areas at Middleton Pond where food resources were irregularly distributed. Males fed more often in areas where banana water-lily tubers were larger, and females fed in less optimal portions of the habitat. Consistently higher proportions of female Canvasbacks were counted swimming into the emergent cattail on this impoundment during foraging, and this area was frequented by predators (e.g., river otters, *Lutra canadensis*; alligators, *Alligator mississippiensis*) during most of the winter. The loss of visual contact with other individuals while foraging in the emergent cattails would make female Canvasbacks more vulnerable to predation. Errington (1946) suggested that individuals forced into marginal habitats by intraspecific competition are often captured by predators. Though little documentation exists on the impact of river otters and alligators on waterfowl, I have observed alligators taking waterfowl (Lesser Scaup, Bufflehead [*Bucephala albeola*], Red-breasted Merganser [*Mergus serrator*]) on three occasions in open water. Indirect evidence that river otters take waterfowl on the study area was derived from observations of duck feathers in feces near otter slides.

The segregation of male and female Canvasbacks, while foraging at Middleton Pond, was not obvious on the other three impoundments where the food resources were regularly distributed; however, the distributions of aggressive interactions and frequency of associations among male-male, male-female and female-female components of the population on all ponds suggested a more frequent association among males. These data seem to indicate that some segregation of the sexes in Canvasbacks takes place on each of the ponds, although it is more subtle in areas where food is regularly distributed, and they support the earlier observations of Olson (1965) concerning an apparent segregation of adult male and female Canvasbacks in the fall.

Redheads, Ring-necked Ducks, and Lesser Scaup did not demonstrate local segregation of the sexes during this study. Moreover, the distribution of aggressive interactions, and the frequency of associations among male-male, male-female, and female-female components of these populations suggested that males and females are found together more often than in Canvasbacks. The close association of the sexes in Redheads, Ring-necked Ducks, and Lesser Scaup may be a result of interspecific competition for food between these three species and the larger Canvasbacks. Male and female Canvasbacks clearly dominated and excluded these species from feeding areas when possible (preliminary data in Alexander and Hair 1979, Alexander 1980b). The three subordinate species seemed to compete more effectively with the larger birds when in pairs or small groups, and this may have produced closer associations among males and females in these species. Their subordination to Canvasbacks may have stimulated more

intense intraspecific competition for food and fighting in Canvasbacks. As well as their competing directly with Canvasbacks for food, the subordinate species might be expected to exploit other less-than-optimal areas in the same habitat, or to migrate to other wintering sites with few or no Canvasbacks. As Redheads and Ring-necked Ducks show some segregation of the sexes by latitude in parts of North America (Alexander 1983), additional research on these species as well as on Lesser Scaup is needed in wintering areas with few Canvasbacks to determine if any sexual segregation occurs there.

Local habitat segregation between wintering male and female Canvasbacks may reduce the rate of aggressive encounters associated with intersexual competition for food. In a variety of nonbreeding woodpecker species, aggression associated with intersexual competition was reduced when males and females segregated feeding niches (Kilham 1965, Ligon 1968, Hogstad 1976, Peters and Grubb 1983) or displayed differences in foraging behavior (Wallace 1974; Hogstad 1977, 1978). If the complete, or partial, segregation of male and female birds at the local or geographic level is a widespread phenomenon during the wintering period, it could be a significant factor in population regulation. Many researchers have demonstrated that the mortality of females exceeds that of males during the nonbreeding period: Phalacrocoracidae (Potts 1969), Anatidae (Geis 1959, Smith 1963, Cooke and Sulzback 1978), Phasianidae (Nelson and Janson 1949), Muscicapidae (Curio 1959), Sturnidae (Davis 1959, Coulson 1960), Icteridae (Darley 1971), and Ploceidae (Ward 1965). If female birds choose suboptimal areas in winter to avoid competition with dominant males, or are forced into these areas, lower quality food or predation could exacerbate the effects of bad weather, increase female mortality, and ultimately skew the population sex ratio in favor of males. If this is so, intersexual competition for food during this period may be an important factor in the regulation of natural populations of these species.

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