DOMINANCE IN WINTERING WATERFOWL (ANATINI): EFFECTS ON DISTRIBUTION OF SEXES

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ABSTRACT.—Aggressive behavior of six species of dabbling ducks was studied from November through February in 1978–1979 and 1979–1980, to investigate effects of dominance on distribution of sexes. Eighty-nine percent of aggressive interactions ($n = 1,266$) were intraspecific. Rate and intensity of aggression remained approximately stable throughout winter. Sex, pair status and aggressiveness influenced dominance rank. Individuals initiating conflicts usually won the encounters. In intraspecific interactions, males dominated females when both were either paired or unpaired, but paired individuals dominated unpaired individuals regardless of sex. Early pair-formation may be advantageous in wintering dabbling ducks because the resulting higher dominance may give better access to food.

Sex ratios differed among the six species. Males predominated in all species; however, species that formed pair bonds early in the winter had less disparate sex ratios than species pairing later. Differences in sex ratios among species may have been in response to the influence that pair status had on dominance rank. Paired females were more dominant than unpaired females and were protected by their mates from engaging in aggressive encounters. Females of late-pairing species remained subordinate for a greater proportion of the fall and winter. We suggest that females of late-pairing species are more likely to be excluded from preferred feeding sites, which may necessitate moving to other areas. These results support the hypothesis that behavioral dominance influences differential distribution of males and females during the nonbreeding period.

In certain ducks (see Bellrose et al. 1961, Nichols and Haramis 1980, Sayler and Afton 1981, Alexander 1983) and other species of birds (see Ketterson and Nolan 1976), the sexes have different distributions during the nonbreeding season (e.g., males predominate at more northerly latitudes). Behavioral dominance is one mechanism that may influence differential winter distribution by sex and age (Gauthreaux 1978). Dominance can result from aggressive interactions and may affect access to preferred resources (i.e., food, mates or nest sites). Dominance rank may be influenced by sex (Balph 1975, Dunbar and Crook 1975, Ketterson 1979), age (Wilson 1975), size (Fretwell 1969, Baker and Fox 1978), plumage coloration (Rohwer 1975), aggressiveness (Patterson 1977), and familiarity with an area (Brown 1963, Smith 1976). Gauthreaux (1978) suggested that when food is scarce, subordinates (e.g., females and juveniles), through competitive interaction, are forced to either occupy inferior habitats or go elsewhere.

Dominant individuals have certain advantages over subordinates. In the nonbreeding season, dominants have greater access to food (Craig et al. 1982), lose less weight (Baker and Fox 1978), and survive better than subordinates (Murton et al. 1971, Dunbar and Crook 1975, Kikkawa 1980). Behavioral dominance during fall and winter can influence distribution and survival patterns of avian species, and perhaps affect future reproductive success.

In this study, we examined characteristics of aggressive behavior in wintering waterfowl (*Anas* spp.). Our objective was to determine the effect of behavioral dominance on differential distribution of the sexes during the nonbreeding period.

STUDY AREA AND METHODS

The study was conducted in the nonbreeding season from November through February in 1978–1979 and 1979–1980 on Bodie Island, part of the Cape Hatteras National Seashore, Dare County, North Carolina. Behavioral data were collected by observing from a blind in a slightly brackish marsh just north of Pea Island National Wildlife Refuge. The marsh was uniformly shallow (10.2–20.3 cm) and the lack of emergent vegetation, except on the perimeter, facilitated observation.

We observed free-ranging populations of six species of wintering waterfowl that were neither given artificial food supplement nor hunted: American Black Duck (*Anas rubripes*),

TABLE 1. Summary of aggressive interactions of dabbling ducks in the fall and winter, 1978–1979 and 1979–1980.[1,2]

Species attacking	Species attacked						
	Black Duck	Gadwall	Wigeon	Shoveler	Pintail	Green-winged Teal	Total
American Black Duck	107	6	3	0	52	1	169
Gadwall	0	154	2	5	3	5	169
American Wigeon	0	3	86	5	0	5	99
Northern Shoveler	0	1	1	206	0	10	218
Northern Pintail	0	3	5	3	223	26	260
Green-winged Teal	0	0	0	0	0	351	351
Total	107	167	97	219	278	398	1,266

[1] Data from focal individual and ad lib. samples were combined.
[2] Total time (h) of focal individual sampling: Black Duck (54.9), Gadwall (67.8), Wigeon (35.9), Shoveler (63.8), Pintail (62.9) and Green-winged Teal (69.2).

Gadwall (*A. strepera*), American Wigeon (*A. americana*), Northern Shoveler (*A. clypeata*), Northern Pintail (*A. acuta*) and Green-winged Teal (*A. crecca carolinensis*). Data on aggressive encounters were compiled using focal individual and ad libitum sampling (Altmann 1974). Using focal individual sampling, every month we attempted to watch each species during each hour of daylight. During sample periods, 10 focal individuals (5 males and 5 females) were selected randomly and observed separately, each for 5 min. All behavior was recorded continuously on a cassette tape recorder. Ad libitum sampling was used to record aggressive interactions that did not occur within normal sample periods. For each conflict we recorded: species and sex of participants, winner and loser (winner displaced the other participant), initiator of the interaction (individual who attacked or displayed first), pair status of individuals, intensity of the encounter, and activity of participants before the encounter.

Several criteria were used to determine pair status and were based on experience derived from many hours of observation. The best criterion was sustained proximity to a member of the opposite sex. Paired individuals remained near their mate and performed all activities close to each other, often touching as they foraged. In contrast, unpaired birds did not tolerate this degree of closeness with any individual. Other forms of behavior indicative of paired birds and often used with the proximity criterion were: inciting by the female, following of a particular male by a female, and defense of the female by a male.

We recognized four levels of intensity based on presumed energetic costs of aggression to the participants: (1) supplanting—lowest intensity encounters that were settled when an individual simply moved into an area and the loser moved away without further confrontation; (2) threat—displays such as open-bill, head pump, bill up, bill down on the breast,

etc. (Johnsgard 1965); (3) chase—short chases across the water without physical contact; (4) fight—interactions involving physical contact.

Sex ratios for each species were determined from weekly counts conducted in the morning (08:00–11:00). Excellent visibility and small population sizes generally allowed a complete count of individuals. Mean monthly estimates of sex ratios were calculated by combining data across years after testing for homogeneity.

We estimated the percentage of paired female dabbling ducks by using females who had been selected during focal individual sampling. Pair status of these randomly chosen females was determined, and percentage paired was calculated for each sample period. Samples were combined each month to calculate the mean percentage of paired females for each species.

Before analyses, we tested our data on aggressive encounters for differences between sampling techniques; except where differences were significant, data were combined. After testing for seasonal homogeneity, data were combined and goodness of fit between observed and expected frequencies was tested with a G-test (Sokal and Rohlf 1969:560). Aggressive interactions were divided into categories of low intensity (supplanting and threats) or high intensity (chases and fights); a chi-square test for linear trend was used to test whether the encounters became more intense as winter progressed (Snedecor and Cochran 1967:246). Linear regression was used to analyze the relationship between rate of aggressive interaction (encounters/h) and progression of the winter season. Rate of aggression was calculated for each focal sample. Regression lines did not differ significantly ($P > 0.05$) by year, so data for both years were combined for analysis (Neter and Wasserman 1974).

RESULTS

Most (89%) of the 1,266 conflicts were intraspecific (Table 1). Rate of interaction (encoun-

ters/h) decreased significantly (b = −2.21; P < 0.05) during winter for American Black Ducks, but did not vary significantly (P > 0.05) by month for other species. In addition, the proportion of aggressive encounters classified as high intensity did not increase significantly (P > 0.05) as the winter progressed.

DETERMINANTS OF DOMINANCE

When pair status of the sexes was the same (both paired or both unpaired), males won significantly more intersexual encounters than expected by chance (Table 2). Heterogeneity among species was not significant (P > 0.50), so data were pooled (P < 0.005).

The **inter**sexual dominance relationship changed when paired females interacted with unpaired males. After females formed pair bonds with males, they dominated unpaired males more often than would be expected if males and females were equal in dominance status (86 of 93 encounters; G = 73.14, df = 1, P < 0.001). In **intra**sexual encounters, furthermore, paired birds of both sexes were dominant to unpaired individuals. Paired males dominated unpaired males in 153 of 160 encounters (G = 161.26, df = 1, P < 0.001), and paired females dominated unpaired females in 18 of 21 encounters (G = 10.19, df = 1, P < 0.005). Dabbling ducks that paired early, therefore, were dominant to unpaired members of the population.

We combined all species to test the effect of initiating an encounter on the outcome of the interaction (G_H = 7.78, df = 5, P > 0.10). Ducks that initiated aggressive interactions won significantly more often than expected by chance (1,035 of 1,070; G = 1,166.31, df = 1, P < 0.001). This suggests that individuals assessed the dominance status of other members in the flock and initiated encounters only when they were likely to be successful. For instance, in interactions between paired individuals (dominant) and unpaired individuals (subordinate), aggressive interactions were initiated by paired birds significantly more often than by unpaired birds (G = 279.20, df = 1, P < 0.001). In addition, males (dominant) initiated significantly more interactions with females (subordinate) than vice versa when their pair status was the same (G = 25.21, df = 1, P < 0.001).

FREQUENCY OF AGGRESSIVE BEHAVIOR BY SEX

Species of dabbling ducks established pair bonds at different times in fall and winter (Table 3). Female Black Ducks and Gadwalls paired earliest, followed in order by Wigeons, Shovelers and Pintails; female Green-winged

TABLE 2. Outcome of intersexual aggressive interactions when male and female were of same pair status (both paired or both unpaired).[1,2]

Species	Female wins, male loses	Male wins, female loses
American Black Duck	3	12
Gadwall	8	13
American Wigeon	4	13
Northern Shoveler	12	23
Northern Pintail	13	28
Green-winged Teal	18	38
Total	58	127

[1] $G_{Heterogeneity}$ = 2.07, df = 5, P > 0.50.
[2] G_{Pooled} = 25.59, df = 1, P < 0.005.

Teals paired latest of all. Because pair bonds affected dominance relationships in these birds, the relative period when pair bonds were formed may have influenced the degree to which sexes were involved in aggressive behavior. For each species, the number of encounters by sex (male-male, female-female, male-female and female-male) were analyzed to determine if sexes participated in a greater or lesser proportion of interactions than expected on the basis of their frequency in the population (Table 4). Differences among species may have been related to variations in the timing of pair-bond formation. This was most clear when species were separated into an early-pairing category (EP: Black Duck and Gadwall), mid-pairing category (MP: Wigeon and Shoveler), and a late-pairing category (LP: Pintail and Green-winged Teal).

For EP species, participation by sexes in aggressive interactions differed significantly from expected (Black Duck, P < 0.001; Gadwall, P < 0.001). Major differences occurred in intrasexual interactions. Male-male interactions were more frequent than expected and female-female interactions were less frequent. Differences in intersexual interactions also occurred. Male Gadwalls initiated fewer interactions with females (male-female) than expected, and female Black Ducks initiated fewer interactions with males (female-male). Deviations from expected values also were highly significant for LP species (Pintail, P < 0.001; Green-winged Teal, P < 0.001), but differences were not the same as for EP species. For example, in **intra**sexual encounters female-female interactions were more frequent than expected, and male-male interactions were approximately the same as expected values. In **inter**sexual encounters, females of LP species initiated fewer interactions with males than expected, and male-female interactions were observed in approximately the same frequencies as expected. Deviations from expected values for MP

TABLE 3. Variation of mean percentage ($\pm$SD) of paired females among populations of dabbling ducks wintering in coastal North Carolina, 1979–1980.

	Month			
Species	November	December	January	February
American Black Duck	6[1] (30)[2]	10 (50)	9 (45)	2 (10)
	96.7 ± 8.2a	98.0 ± 6.3a	100.0a	100.0a
Gadwall	10 (50)	10 (50)	9 (45)	8 (40)
	91.5 ± 11.1ab	96.0 ± 8.4a	97.8 ± 6.7a	100.0a
American Wigeon	10 (33)	4 (17)	2 (91)	
	82.0 ± 22.9b	71.0 ± 21.7b	84.0 ± 5.7ab	—
Northern Shoveler	10 (48)	10 (42)	8 (38)	6 (30)
	9.0 ± 11.7c	41.7 ± 21.6c	67.5 ± 18.3b	96.7 ± 8.2a
Northern Pintail	10 (47)	10 (45)	9 (45)	6 (30)
	0.0c	11.0 ± 19.1d	84.4 ± 13.3ab	100.0a
Green-winged Teal	10 (49)	10 (46)	9 (41)	9 (44)
	2.0 ± 6.3c	0.0d	34.1 ± 33.6c	80.0 ± 20.0b
P[3]	***	***	***	**

[1] Number of samples.
[2] Total number of females recorded.
[3] ANOVA (**$P < 0.01$; ***$P < 0.001$) followed by a Duncan's multiple range test; means in each column without the same letter are significantly different ($P < 0.05$).

species were significant only for Shoveler ($P < 0.005$). Male-male interactions were more frequent than expected and females initiated fewer interactions with males.

These results suggest that females of the EP species were protected from participating in aggressive encounters because their mates engaged in a greater proportion of disputes. This concept is supported when the overall participation in such encounters by males and females is analyzed (Table 5). Females of the EP species participated in significantly fewer aggressive interactions than expected based on their frequency in the population (Black Duck, $P < 0.001$; Gadwall, $P < 0.001$), whereas females of the LP species participated in more aggressive encounters. The difference for LP species was significant only for Green-winged Teal ($P < 0.001$). MP species did not differ significantly, but the trend in male and female participation for Wigeon and Shoveler was similar to that in EP species.

Lower aggressiveness by paired females became more evident when interactions of female Pintail were analyzed. We used that species because interactions could be separated into periods when a majority of females were either unpaired (November and December) or paired (January and February; Table 3). Early in the season, when few pair bonds had formed, females participated in more encounters than expected (122 of 266 participants were female, expected = 94; $G = 12.42$, df = 1, $P < 0.001$); as pair bonds were established, however, this relationship changed, and females participated in fewer interactions than

expected (46 of 180 participants were female, expected = 70; $G = 14.28$, df = 1, $P < 0.001$).

SEX RATIOS

Monthly sex ratios differed significantly ($P < 0.05$) among species of dabbling ducks (Table 6). Males predominated in all species; however, American Black Ducks and Gadwalls generally had less disparate sex ratios than either MP or LP species. Green-winged Teal had the highest proportion of males in their population during December, January and February with peak numbers (80%) occurring in January. The percentage of males in populations of dabbling ducks wintering on the study area was negatively correlated with the percentage of females that had formed pair bonds (Kendall's Rank Correlation Coefficient, Tau = -0.47, $P < 0.001$).

DISCUSSION

DETERMINANTS OF DOMINANCE

Sex. Male dabbling ducks dominated females when their pair status was identical. This supports the findings of other investigators who also have shown that males were dominant to females in the nonbreeding season (Balph 1975, Dunbar and Crook 1975, Alexander and Hair 1979, Ketterson 1979). Such a situation must exist for behavioral dominance to explain differential dispersion of dabbling duck sexes during the nonbreeding period.

Pair bonds. Pair status also was important in determining dominance rank of wintering dabbling ducks. Dominance status of females as a group increased when pair bonds formed.

TABLE 4. Frequency of aggressive interactions observed by sex and expected values, which were calculated from population sex ratios.[1]

| | Early-pairing | | | | Mid-pairing | | | | Late-pairing | | | |
| | Black Duck | | Gadwall | | Wigeon | | Shoveler | | Pintail | | Green-winged Teal | |
Interaction	Ob.	Ex.	Ob.	Ex.	Ob.	Ex.	Ob.	Ex.	Ob.	Ex.	Ob.	Ex.
Male-male	60	37	80	51	44	38	109	93	100	89	188	198
Female-female	7	20	12	27	10	10	24	23	45	30	62	23
Male-female	23	25	20	38	19	19	48	45	49	52	60	65
Female-male	17	25	42	38	13	19	25	45	29	52	41	65
G scores	26.38***		35.26***		3.04		13.50**		20.14***		56.10***	

[1] Expected frequency = (proportion of first sex in population) × (proportion of second sex in population) × (total observations).
** $P < 0.005$; *** $P < 0.001$.

Paired females were still subordinate to paired males but were dominant to unpaired males. Paired birds of both sexes were dominant in intrasexual encounters with unpaired individuals. Patterson (1977) reported similarly that the hierarchy of captive, male Common Shelducks (*Tadorna tadorna*) was changeable, and advancements within the hierarchy were associated with formation of pair bonds. Low-ranking male Shelducks improved their dominance status after forming pair bonds. Females interacted too infrequently to permit analysis in Patterson's (1977) study.

It would seem advantageous for wintering dabbling ducks to form pairs early because of higher dominance rank, which may be associated with greater access to resources (Craig et al. 1982). However, dominance rank is just one aspect related to the economics of pairing. Other factors may be more important in determining the best time of pair-bond formation for the later-pairing Northern Pintail and Green-winged Teal. The best behavior usually is the product of a complex set of selective pressures that often change temporally or with species, age, and sex (see Paulus 1980, Afton and Sayler 1982). Perhaps costs (e.g., energy expenditure) of early courtship activity for LP species were greater than potential benefits received from formation of pair bonds. The intra- and interspecific differences in costs and benefits of pairing must be ascertained in order to evaluate the importance of these variations on pairing chronology.

Aggressiveness. Those dabbling ducks who initiated conflicts won an overwhelming proportion of these interactions. Success of initiators could have resulted from convenience ordering, whereby individuals could participate in group activities with a minimum of aggression (see Craig et al. 1982). Convenience ordering would be expected to occur if the benefits of increased status were small compared to the costs of acquiring and maintaining higher dominance rank. For example, if individuals were similar in status and resources such as food were low in quality or perhaps evenly distributed, then costs of defending the resource would be greater than potential benefits, and individuals would be expected to devote less time and energy to aggressive behavior. Individuals who began conflicts under these circumstances would be expected to win because of less resistance by the other participant. Convenience ordering can be disregarded if either a clear advantage can be related to dominance rank, or interactions are not initiated arbitrarily.

Our data suggest that aggression was not arbitrary, but that individuals recognized dominance status of flock members and became aggressive only when they were likely to succeed. For example, when pair status was the same, females initiated fewer interactions with

TABLE 5. Overall participation in aggressive interactions by males and females, with expected values which were calculated using the population sex ratios.[1]

| | Early-pairing | | | | Mid-pairing | | | | Late-pairing | | | |
| | Black Duck | | Gadwall | | Wigeon | | Shoveler | | Pintail | | Green-winged Teal | |
Sex	Obs.	Ex.	Obs.	Ex.	Obs.	Ex.	Obs.	Ex.	Obs.	Ex.	Obs.	Ex.
Female	54	90	86	130	52	58	121	136	168	164	225	176
Male	160	124	222	178	120	114	291	276	278	282	477	526
G scores	26.38***		27.02***		0.80		2.50		0.18		17.22***	

[1] Expected frequencies = (proportion of sex in population) × (total observations).
*** $P < 0.001$.

TABLE 6. Variation of mean percentage (±SD) of males among populations of dabbling ducks wintering in coastal North Carolina, 1978–1979 and 1979–1980.

Species	Month				
	November	December	January	February	March
Early-Pairing					
American Black Duck	5[1] (374)[2] 61.6 ± 2.2ab	3 (184) 57.7 ± 1.5c	1 (35) 51.4	3 (209) 53.3 ± 3.2e	—
Gadwall	8 (1,039) 57.6 ± 1.4b	6 (851) 58.2 ± 1.7c	7 (1,183) 56.9 ± 2.8bc	7 (989) 56.3 ± 3.5de	8 (1,130) 55.6 ± 1.5b
Mid-Pairing					
American Wigeon	8 (1,110) 66.6 ± 5.6a	4 (556) 64.2 ± 4.9bc	5 (974) 64.0 ± 2.9b	1 (88) 66.0	—
Northern Shoveler	7 (523) 69.1 ± 6.2a	4 (432) 67.5 ± 6.6b	6 (349) 64.2 ± 6.5b	7 (523) 70.1 ± 3.1ab	4 (295) 65.0 ± 3.5a
Late-Pairing					
Northern Pintail	8 (1,003) 68.4 ± 10.1a	6 (1,108) 62.3 ± 7.6bc	7 (1,537) 62.4 ± 1.8b	4 (728) 61.7 ± 6.3cd	2 (66) 55.5 ± 2.1b
Green-winged Teal	8 (1,913) 65.7 ± 8.0a	6 (1,938) 76.0 ± 7.9a	7 (1,603) 79.6 ± 5.6a	7 (2,545) 74.4 ± 4.8a	8 (1,762) 61.7 ± 5.7a
P[3]	*	***	***	***	**

[1] Number of samples.
[2] Total number of individuals recorded.
[3] ANOVA (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) followed by a Duncan's multiple range test; means in each column without the same letter are significantly different ($P < 0.05$).

males than expected; but males initiated encounters with females approximately proportional to their abundance in the population. This suggests that females were avoiding conflicts with more dominant males. Patterson (1977) reported similar results for Common Shelducks and showed that individuals attacked only their subordinates. Sex was an obvious indicator of status; however, cues used by dabbling ducks to assess dominance status when individuals interacted intrasexually were less clear. Some species of birds use differences in plumage to communicate dominance (Rohwer 1975), and perhaps subtle plumage variation exists in wintering waterfowl. Further research is needed on the extent to which this or other variables are used to signal dominance.

ROLE OF DOMINANCE IN THE DISTRIBUTION OF THE SEXES

Differences in sex ratio were greatest between early-pairing species (Black Duck and Gadwall) and Green-winged Teal. These differences may have been in response to variation in chronology of pair-bond formation and the subsequent effect of pair status on dominance rank. For EP species, courtship activity began early in the fall and most females became paired early. Paired females were protected by their mates from engaging in aggressive encounters, which may have allowed females to devote more energy to other activities such as foraging (Ashcroft 1976, Paulus 1980, Scott 1980). Green-winged Teal females remained subordinate members of the population for a longer

period than females of other species. Females of late-pairing species (Pintail and Green-winged Teal) interacted more frequently overall than those of EP species, especially with other females, and our data suggest that subordinate females avoided interactions with males.

The percentage of males in dabbling duck populations was negatively correlated with the percentage of females that were paired. Green-winged Teal, for example, were the last to form pair bonds and had the greatest percentage of males in the population. Female Green-winged Teal predominate at more southerly wintering areas (Palmer 1976:362). Diving ducks (Aythyini) resemble teal in these respects: their reproductive behavior does not begin until late winter (Alexander 1980), most pair bonds are not formed until March and April (Weller 1965) and northern wintering populations often have many more males than females (Bellrose et al. 1961, Alexander 1980). Species of waterfowl that initiate courtship behavior and form pair bonds in fall or early winter appear to have less disparate sex ratios and less segregation of sexes than species that form pair bonds later.

We suggest that late-pairing females, being subordinate for a longer period, are more likely to be excluded from preferred feeding sites, which may necessitate their moving to other areas when food becomes limited. Our results are consistent with the hypothesis that behavioral dominance influences the differential distribution of males and females during the nonbreeding period. However, this hypothesis does

not predict the direction of dispersal. Other hypotheses (see Myers 1981) need to be invoked to explain southward distribution of females. We agree, therefore, with Ketterson and Nolan's (1979) proposal that differential distribution of sexes results from interactions of several factors.

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