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FOOD DEFENDABILITY AND ANTIPREDATOR TACTICS: IMPLICATIONS FOR DOMINANCE AND PAIRING IN CANVASBACKS[1]

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Abstract. Activity and foraging aggression of Canvasbacks (*Aythya valisineria*) were compared among five different habitats used during fall, winter, or spring migration. Time spent in aggression and rates of aggressive encounters during the day were higher in habitats where food items were larger relative to food densities. Foraging aggression was rare in estuarine bays where most Canvasbacks wintered. Relative dominance of males and females varied among sites during fall and winter; but when pairing began during spring migration, paired females were more aggressive and dominant than all other classes of sex and pair status. In estuarine bays, predation pressure by Great Black-backed Gulls (*Larus marinus*) apparently caused Canvasbacks and other diving ducks (Aythyini) to stay in dense flocks, in which feeding-site defense was unfeasible, and antipredator tactics (selfish herding, confusion effect) conflicted with maintaining proximity to particular individuals. It appears that (1) foods of Canvasbacks over much of their wintering range are not scarce and economically defendable consistently enough to justify costs of maintaining pair-bonds for dominance purposes; and (2) feeding-site defense and proximity of mates required to maintain and benefit from pair-bonds conflict with antipredator tactics of Canvasbacks in open water. These factors may partly explain the absence of early pairing in Canvasbacks and other species of *Aythya*.

Key words: Canvasback; Aythya valisineria; *food defendability; foraging; predation; flocking; pairing chronology.*

INTRODUCTION

Unlike most other migratory birds which form pair-bonds only in the breeding season, the family Anatidae (waterfowl) contains some species with lifetime pair-bonds and others that pair in fall or winter well before nesting activities. Within the two main genera of prairie-nesting ducks in North America, the dabbling ducks *Anas* spp. and the diving ducks or pochards *Aythya* spp., there is much interspecific variation in chronology of pair-bond formation (Weller 1965, Paulus 1983, Hepp and Hair 1984, McKinney 1986, Rohwer and Anderson 1988). Nevertheless, the genera differ broadly in that many species of dabbling ducks pair in fall and early winter, whereas pochards do not pair until late winter or spring.

Proposed explanations for early pairing in dabbling ducks have centered on the benefits to one or both sexes of enhanced dominance in foraging aggression. In a variety of dabbling ducks, pair members dominate unpaired individuals (Paulus 1983, 1988), and one study suggests that paired males protect their mates from foraging interference (Hepp and Hair 1984). In both *Anas* and *Aythya,* pair-bonds are formed earlier by species with higher proportions of low-quality foliage in the diet (Paulus 1983). Consequent need for greater foraging time or efficiency by females is presumed to justify costs of pair-bond maintenance in return for increased dominance. Females of some species, being otherwise subordinate, may have more to gain by early pairing than do males (Afton and Sayler 1982, Rohwer and Anderson 1988). However, males also appear to accrue dominance benefits from pairing: paired males consistently dominate unpaired males in foraging aggression (Paulus 1983, 1988; Hepp and Hair 1984; Lovvorn 1987), even though before pairing they were subordinate to the same unpaired males (latter data available only for Shelducks [*Tadorna tadorna*], Patterson 1982; see also Raveling 1970, Ashcroft 1976, and Scott 1980 for examples of lowered dominance in individuals while separated from pair and family members).

Pochards, however, although they commonly exhibit foraging aggression, feeding-site defense, and dominance throughout fall and winter, do

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not pair until late winter and mostly spring (Weller 1965; Alexander and Hair 1979; Alexander 1980b, 1987; Lovvorn 1987). Thus if dominance in foraging aggression is the primary benefit of early pairing to one or both sexes, I believe the correct question is not whether dominance and hence early pair-bonds are advantageous, but rather whether pair-bond dominance is a more appropriate aggressive strategy than individual dominance during late fall and winter.

Marked spatial or temporal variation in costs and benefits of feeding-site defense will call for foraging interactions ranging from no aggression and defense to strong aggression and defense (Theimer 1987). Occasional dominance advantages of being paired might be outweighed by costs of maintaining pair-bonds when they provide no foraging benefits. Pairing in ducks may be delayed if conditions are unsuitable (Brodsky and Weatherhead 1985, Hepp 1986). However, because of time and effort required for mate selection and pair-bond establishment, and the probability of mobile individuals becoming separated while ranging independently, dissolved pair-bonds might not be easily replaced or reformed. A system of individual dominance is favored when (1) costs of pair-bond maintenance are high in terms of energetics or risk, or (2) benefits of aggression are either low or highly variable.

In the nonbreeding period, Canvasbacks (*Aythya valisineria*) exhibit strong foraging aggression in some habitats but essentially no aggression in others, and experience substantial changes in quality and abundance of food (Alexander and Hair 1979; Alexander 1980a, 1980b, 1987; Bellrose 1980; Cely 1980; Lovvorn 1987; see below). In this paper, I examine the occurrence of foraging aggression among Canvasbacks in various habitats throughout winter and spring migration, and concurrent factors affecting costs and benefits of maintaining pair-bonds.

METHODS

I analyzed data on Canvasback behavior from five habitats during different periods of the annual cycle. Canvasbacks arriving in coastal North Carolina in early November concentrate on Lake Mattamuskeet, and in December move 5–45 km away to Pamlico Sound until departing north beginning in late February (Lovvorn 1989). I studied Canvasbacks on Lake Mattamuskeet from 11 November–13 December 1982 and 7 November–31 December 1983; and on Pamlico Sound (Rose Bay and the Neuse River near the town of Oriental) from 31 December 1983–12 January 1984. During spring migration, I recorded Canvasback behavior at inner Long Point Bay on the north shore of Lake Erie from 11 March–12 April 1984, and on Pool 8 of the Mississippi River near La Crosse, Wisconsin, from 23 March–5 April 1983. Data on behavior of Canvasbacks in impounded ponds in coastal South Carolina (November–March 1975–1978) were available from another study (Alexander 1980b), in which sampling methods were essentially the same as those I used.

On each day of sampling I stratified daylight hours into three equal periods, and randomly chose 2–3 hr from each period for observations. During a 1-hr sampling interval, I randomly selected four males and four females in alternate sequence and observed each continuously for 5 min through a 15–60 × spotting scope. Subjects were chosen by swinging the spotting scope across the range of visible birds, and then selecting the individual closest to the center of the field of view of the scope wherever it came to rest. Canvasbacks almost always dived and surfaced without significant lateral movement, so unmarked individuals could be followed continuously during feeding bouts (see also Alexander and Hair 1979, Anderson 1984). I recorded the activity of the focal individual at 20-sec intervals, and continuously monitored all aggressive interactions for that bird.

I used the behavioral terminology of Alexander (1980a, 1980b), except that I consider the display termed Head-pump by Alexander to be a Neck-stretch display of appeasement (Lovvorn 1987). I defined low-intensity aggression as including Approach threats, Bill-in-water, Bill-jabs, and Bill-on-chest displays; and high-intensity aggression as including Pushing contests, chases, and fights. I did not analyze data on Displacement-by-presence (Alexander 1980b) because I probably did not detect all such interactions. In this paper I examine aggressive behavior occurring in disputes over feeding sites, which does not include aggression among Canvasbacks that were actively courting as evidenced by courtship displays (Lovvorn 1987). Wins in aggressive encounters were defined by which bird supplanted the other, and percent wins were calculated as percentages of interactions with clear winners.

In some contexts, feeding-site defense (terri-

TABLE 1. Areal mass density and size of Canvasback foods at different sites where behavior was studied. Values reflect conditions at the beginning of Canvasback use periods.

Site	Use period	Principal food[a]	g ash-free dry mass/m^2	g ash-free dry mass/item
S. Carolina ponds[b]	Nov–Mar	*Nymphaea mexicana* tubers	20	1.09
Lake Mattamuskeet[c]	Nov–Dec	*Vallisneria americana* tubers	5	0.02
Pamlico Sound	Dec–Mar	*Macoma* spp. clams		0.06[d]
Long Point	Mar–Apr	*Vallisneria americana* tubers		0.03[d]
La Crosse[e]	Mar–Apr	*Sagittaria rigida* tubers	73	0.26
		Vallisneria americana tubers	20	0.11

[a] Comprising >80% volume or dry mass of esophagus contents, except for South Carolina ponds for which Cely (1980) did not provide quantitative data for specific habitats.

[b] Alexander (1980b, p. 169–170).

[c] Lovvorn (1987).

[d] Based on contents of Canvasback esophagi (Lovvorn 1987; unpubl.).

[e] Korschgen et al. (1988), Lovvorn (unpubl.). Percent volume of esophagus contents were for *S. rigida* 48% and *V. americana* 40% (J. A. Barzen and C. E. Korschgen, unpubl.).

toriality) and foraging aggression are considered separate entities (Myers 1984). In Canvasbacks, foraging aggression typically occurs when a feeding bird defends an area around itself 1–2 m in diameter, usually for less than 10 min. Thus I did not distinguish between feeding-site defense and foraging aggression.

In fall 1983, I established transects for tuber sampling in four areas of Lake Mattamuskeet heavily used by Canvasbacks the previous fall (Lovvorn 1989). Three substrate cores per station (total of 210 cores) were taken at 50-m intervals along the transects from 20 September–5 October before Canvasbacks arrived. Cores were 11 cm in diameter, and varied in depth from 0–37 cm depending on how far the sampler could be pushed into substrates of varying hardness (Lovvorn 1989).

Data were tested for normality and homogeneity of variance and rank-transformed when appropriate. I used chi-square, percentage (Sokal and Rohlf 1969, p. 607), and z-tests (Student 1907) to detect differences among percentages and frequencies.

RESULTS

FOOD SIZE AND AREAL MASS DENSITY

Principal Canvasback foods in different areas varied substantially in mean areal mass density and size (Table 1). *Nymphaea mexicana* tubers in South Carolina were quite large and of only moderate mass densities. *Sagittaria rigida* tubers at La Crosse were also large, with relatively high mass densities. Tubers of *Vallisneria americana* at Lake Mattamuskeet and Long Point were much smaller, with very low mass densities at Mattamuskeet.

Although tuber abundance was not surveyed at Long Point, food appeared to be limited there for much of the study period: Canvasbacks were often restricted to the same small holes in the ice (Lovvorn 1987), and new leads developing from these holes commonly were packed with intensely foraging Canvasbacks. Because the mass of *Macoma* clams varies greatly among individuals, available data on total numerical densities could not be used to estimate mass densities available (see Lovvorn 1989). However, average food content of *Macoma* clams is small (Table 1).

ACTIVITY AND AGGRESSION IN DIFFERENT HABITATS

Variation in time-activity budgets (Table 2) resulted partly from seasonal differences, but there appear to be strong habitat effects. Canvasbacks eating clams on Pamlico Sound spent essentially no time in aggression, and less time feeding and more time above water (swimming, resting) and alert than when eating *V. americana* tubers on Lake Mattamuskeet. Time spent in aggression was also low on Mattamuskeet. Systematic observations on Pamlico Sound were discontinued when Canvasbacks began feeding nocturnally and sleeping during daylight except when disturbed. At Long Point where Canvasbacks also fed on *V. americana* tubers, feeding time was again high and foraging aggression increased. The most striking change was the much greater time spent in aggression at La Crosse and South Carolina ponds. In South Carolina, data spanned fall through early spring and little courtship and no pairing were observed (Table 2; Alexander 1980b); whereas at La Crosse, data were only from spring migration when courtship and pair-

TABLE 2. Mean percent of daylight hours spent in various activities by Canvasbacks in different areas and months. Means in the same row followed by the same letters are significantly different.[a]

	S. Carolina ponds Nov–Mar[b]	Lake Mattamuskeet Nov–Dec	Pamlico Sound Dec–Jan	Long Point Mar–Apr	La Crosse Mar–Apr
n[c]	1,639	1,573	452	857	608
Feeding	33.4 AB	45.0 AC	29.0 CDE	40.0 BD	36.3 E
Swimming	19.6 ABCD	9.5 AEF	10.7 BEG	7.4 CGH	13.1 DFH
Resting[d]	33.6 ABC	33.0 D	49.7 ADEF	27.5 BE	27.0 CF
Comfort movements	10.6 A	7.6 ABC	8.2 D	10.7 BE	13.1 CDE
Alert		0.4 A	0.7 A	0.3	0.4
Aggression	2.2 ABC	0.3 ADE	0.0 BFG	0.6 CDFH	1.8 EGH
Courtship	0.3 ABC	0.0 ADE	0.1 FG	8.6 BDFH	5.7 CEGH

[a] Means for South Carolina ponds were compared with other means by percentage tests; differences among other sites were tested by Bonferroni multiple comparisons on rank-transformed data. For all tests combined, experimentwise $\alpha < 0.05$.

[b] Alexander (1980b, p. 87–90).

[c] Number of 5-min, focal-individual samples.

[d] Includes sleeping, whose values were for Lake Mattamuskeet 30.2, Pamlico Sound 46.0, Long Point 22.0, and La Crosse 17.4.

ing were common (Table 2; Lovvorn 1987) (note that aggression among actively courting birds was not included in foraging aggression). However, at both sites Canvasbacks were eating large food items (Table 1) which apparently were defendable.

Rates of aggressive encounters among foraging Canvasbacks (Fig. 1) also corresponded to habitat. Aggression was high among Canvasbacks feeding on larger tubers (c.f. Table 1) and during spring migration. Low-intensity aggression was uncommon and high-intensity aggression almost nonexistent on Pamlico Sound.

At Lake Mattamuskeet, foraging Tundra Swans (*Cygnus columbianus*) altered the local availability of *V. americana* tubers. Feeding swans unearthed many tubers which floated to the surface and were picked up by other species, and their digging apparently facilitated benthic foraging by Canvasbacks. Canvasbacks sometimes vigorously defended areas around swans, and at other times merely fed near them without obvious defense. High-intensity aggression was greater among Canvasbacks feeding <1 m from swans, whereas trends for low-intensity aggression were inconsistent between years (Table 3).

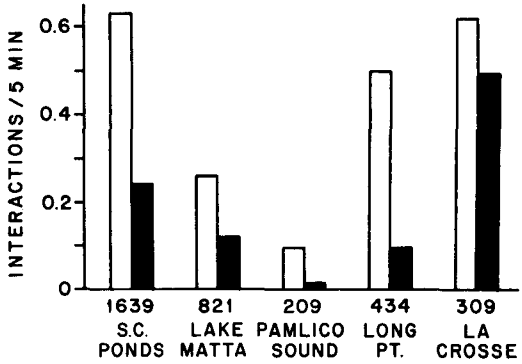

FIGURE 1. Rates of aggression of low (open bars) and high (solid bars) intensity among foraging Canvasbacks. Numbers of 5-min, focal-individual samples are below the abscissa. Rates of the same intensity class in different areas are all significantly different (z-tests, experimentwise $\alpha = 0.05$) except for high-intensity aggression at Lake Mattamuskeet vs. Long Point ($P = 0.089$). Data for South Carolina ponds are from Alexander (1980b, p. 63–64). Data from Lake Mattamuskeet are for Canvasbacks >1 m from swans.

On Lake Mattamuskeet, aggression between males and females was less frequent than expected, whereas aggression within sexes occurred more often than expected (Table 4). There was no appreciable difference in aggressiveness or dominance between males and females at Mattamuskeet. On Pamlico Sound, most aggression

TABLE 3. Rates of aggression (interactions/5 min) of low and high intensity among Canvasbacks foraging on *Vallisneria americana* tubers near and away from Tundra Swans at Lake Mattamuskeet, North Carolina.

		Distance from swans		
Year		>1 m	<1 m	*P*[a]
1982	*n*[b]	185	46	
	Low	0.135	0.435	0.001
	High	0.011	0.239	<0.001
1983	*n*	636	106	
	Low	0.297	0.104	<0.001
	High	0.156	0.226	0.076
Total	*n*	821	152	
	Low	0.261	0.204	0.090
	High	0.123	0.230	0.004

[a] z-test.

[b] Number of 5-min, focal-individual samples.

TABLE 4. Number of encounters observed, relative aggression (encounters observed/encounters expected[a]), and percent wins among foraging Canvasbacks in North Carolina.[b] Percentages in the same column followed by the same letter are not significantly different (percentage test, experimentwise $\alpha < 0.05$).

	Lake Mattamuskeet[c]			Pamlico Sound		
Initiator-receiver	Obs.	Obs./exp.	% wins	Obs.	Obs./exp.	% wins
Male-male	84	1.38	98.6 A	6	0.80	100.0 A
Male-female	64	0.82	89.7 B	15	2.66	80.0 B
Female-male	61	0.79	90.4 B	0	0/5.64	
Female-female	106	1.07	91.1 B	2	0.47	100.0 A
P[d]		<0.005			<0.005	

[a] Expected = (proportion of first sex in population) × (proportion of second sex in population) × (total interactions). Proportion male was 0.44 on Lake Mattamuskeet, 0.57 on Pamlico Sound.

[b] Number of 5-min, focal-individual samples were for Lake Mattamuskeet: males 416, females 405; for Pamlico Sound: males 106, females 103.

[c] >1 m from swans.

[d] Chi-square goodness-of-fit test.

was by males toward females, with males strongly dominant (Table 4); however, aggression there was extremely rare (Table 2, Fig. 1). For Long Point and La Crosse, I could not construct dominance matrices relating paired and unpaired Canvasbacks, because when concentrating on focal individuals in flocks I often could not identify the pair status of their opponents with certainty. Attacks by unpaired females on both sexes were more frequent than expected, the females winning most of these encounters with males (Table 5). Paired females were especially aggressive toward other females, whereas paired males were never observed to attack females. Paired females rather than their mates were responsible for most foraging aggression by pairs, and were more successful than paired males in dominating both males and females (Table 5).

DISCUSSION

SELECTIVITY OF ATTACKS

Of the 93% (872/942) of all aggressive interactions having clear winners, 96% were won by the individuals initiating them, indicating that Canvasbacks seldom attacked birds that they could not dominate. Similar results have been reported for other species (Patterson 1982; Paulus 1983, 1988; Hepp and Hair 1984). This finding has notable implications for evaluating dominance among categories of sex, age, and pair status when all birds observed are not individually marked. Among marked Canvasbacks on South Carolina ponds, adult females won only 1% of their encounters with adult males but 36% of those with juvenile (<1 year old) males; whereas juvenile females won none and 10% of encounters with

TABLE 5. Number of encounters observed, relative aggression (encounters observed/encounters expected[a]), and percent wins among foraging Canvasbacks during spring migration at Long Point Bay, Ontario, 1984, and the upper Mississippi River near La Crosse, Wisconsin, 1983.[b] Percentages in the same column followed by the same letter are not significantly different (percentage test, $\alpha < 0.05$ for each pairwise comparison).

		Long Point			La Crosse		
Focal individual	Opponent	Obs.	Obs./exp.	% wins	Obs.	Obs./exp.	% wins
Unpaired male	male	94	0.76	61.3 A	151	0.86	69.4 ABC
	female	41	0.85	65.9 AB	49	0.83	65.2 AB
Paired male	male	3	0.32	66.7 ABC	23	1.27	81.0 AC
	female	1	0.28	0	0	0/6.05	
Unpaired female	male	76	1.78	53.9 AD	61	1.31	62.1 B
	female	29	1.75	44.8 CD	23	1.48	18.2
Paired female	male	6	0.65	100.0 E	29	1.60	100.0
	female	8	2.21	87.5 BE	10	1.65	87.5 C
P[c]			<0.005			<0.005	

[a] Expected = (proportion of focal individual's sex and pair status in population) × (proportion of opponent's sex in population) × (total interactions). Proportions were at Long Point: unpaired males 0.67, paired males 0.05, unpaired females 0.23, paired females 0.05; at La Crosse: unpaired males 0.68, paired males 0.07, unpaired females 0.18, paired females 0.07 (Lovvorn 1987).

[b] Number of 5-min, focal-individual samples were at Long Point: unpaired males 393, paired males 29, unpaired females 337, paired females 67; at La Crosse: unpaired males 281, paired males 24, unpaired females 137, paired females 51.

[c] Chi-square goodness-of-fit test.

adult and juvenile males, respectively (Alexander 1987). Unmarked females in the same areas won 34% of 634 encounters with unmarked males (Alexander 1980b, p. 90–91), suggesting that most male-female aggression involved adult females and juvenile males. Thus variations in age structure of observed populations might have appreciable effects on the incidence and outcome of aggressive interactions among unmarked Canvasbacks.

During spring migration, paired and unpaired female focal individuals won 100% and 58%, respectively, of their encounters with males (Table 5). Thus if sex and pair status were the only criteria for selecting victims, unpaired males (whom most male-female aggression apparently involved, Table 5) should have won no more than 42% (100% − 58%) of their encounters with females, this maximum occurring if all females they attacked were unpaired. However, a random sample of unpaired, focal-individual males won over 65% of such encounters (Table 5). This difference indicates that subsets of particular classes of sex, age, and pair status were consistently attacked, while larger subsets of the same classes were recognized as potentially dominant and seldom attacked. Frequent attacks on small subsets of individuals could misrepresent overall dominance relations among social classes. Such bias might have affected a number of studies involving interactions among unmarked birds (Raveling 1970; Alexander 1987; Paulus 1983, 1988; Hepp and Hair 1984). The importance of this factor is difficult to assess without capturing and marking all individuals observed, which is virtually impossible for many species during winter and migration.

FOOD CHARACTERISTICS, FOOD REQUIREMENTS, AND AGGRESSION

Feeding-site defense benefits an individual if food is both scarce and economically defendable (Brown 1964, see also Myers 1984). Effective scarcity of foods depends not only on food availability, but also on the dynamics of food requirements. In captive Canvasbacks held outdoors in Maryland, food intake corresponded to changes in body mass (Perry et al. 1986). Food intake (ca. 144 g/day) and weight gain (ca. 1.9 g/day) were high in November, declining after body mass peaked in December. In January–February, food intake and weight change dropped to lows of about 107 and −1.9 g/day, followed by rapid increase in food intake (ca. 127 g/day) and body mass (ca. 1.4 g/day) in March–April (Perry et al. 1986). Seasonal patterns of body mass in these captive birds closely resembled those of free-ranging Canvasbacks in the same region (Perry et al. 1986; Lovvorn 1987, 1989). Thus food intake in wild Canvasbacks is probably high from November through mid-December, followed by a decline from January through February, and an increase in March and April.

Food patchiness (see Wiens 1976) and hence defendability is difficult to quantify in these habitats; but consideration of probable patterns of food requirements and the sizes and areal densities of foods (Table 1) yields insight into the occurrence of foraging aggression (Tables 2–5, Fig. 1). Tubers of *N. mexicana* and *S. rigida* are large, and the relatively high mass density of the latter may be offset by the apparently high food requirements of Canvasbacks during spring migration. Tubers of both species are often too large to be swallowed easily, and are commonly if not always brought to the surface for further manipulation (Alexander 1980b; Cely 1980; Lovvorn, pers. observ.). The frequency with which these tubers are brought to the surface indicates that a number of dives concentrated in the same spot are necessary to procure them. These characteristics suggest that feeding-site defense should be favored in these habitats.

Food requirements appear to be high in November (Lake Mattamuskeet) and in March and April (spring migration at Long Point and La Crosse) (Perry et al. 1986; Lovvorn 1987; J. A. Barzen, unpubl.). Feeding-site defense is expected at these sites whenever tubers are dispersed so as to be defendable. Foraging aggression may not be favored on Pamlico Sound in January because clams are small (Lovvorn 1989; Table 1) and food intake is probably low at that time (Perry et al. 1986).

Aggression of Canvasbacks was altered when swans changed effective food availability in the same habitat (Bailey and Batt 1974; Table 3), and feeding-site defense was frequent on South Carolina ponds during the same period that aggression on Pamlico Sound was extremely low (Fig. 1; Tables 2, 4; Alexander 1980b). Thus foraging aggression among Canvasbacks in fall and winter seems more a function of food abundance and defendability than of aggressive physiological state (see Tamisier 1970). It appears that even when feeding-site defense is not observed, the potential for such behavior among Canvasbacks always exists and will be expressed if suitable conditions arise. Other species have shown similar behavioral flexibility (Zahavi 1971, Gill and Wolf 1975, Carpenter and MacMillen 1976, Lott 1984).

CONSISTENCY OF DOMINANCE BENEFITS

Reports of feeding-site defense in South Carolina ponds (Alexander and Hair 1979; Alexander 1980a, 1980b) led to the suggestion that male dominance in foraging aggression largely explains the latitudinal gradient in sex ratio among Canvasbacks on the Atlantic Coast (78% male in New York to 31% in South Carolina) (Nichols and Haramis 1980). However, Canvasbacks wintering in *N. mexicana* habitats in South Carolina make up less than 2% of the Atlantic Flyway population (Cely 1980, U.S. Fish and Wildlife Service Midwinter Inventories). An average of 72% of this population winters in Chesapeake Bay and North Carolina sounds, similar environments where Canvasbacks eat mostly *Macoma* clams (Lovvorn 1987, 1989; Perry and Uhler 1988). Aggression among foraging Canvasbacks was rare in this habitat (Tables 2, 4; Fig. 1).

Canvasbacks wintering on the West Coast (primarily San Francisco Bay) eat mostly clams, but diets in the lower Mississippi River Valley and Gulf Coast include clams, insect larvae, and various tubers (Bellrose 1980). Tubers of *V. americana* and *Potamogeton pectinatus* were historically more important in the diet of East Coast Canvasbacks before widespread decline of submerged aquatic vegetation in Chesapeake Bay (Perry and Uhler 1988). However, currently and probably historically (Lovvorn 1989), much of the Canvasback population has spent significant portions of winter eating clams whose economic defendability appears very low. Long periods when foraging aggression is not called for would reduce the net effects of dominance behavior (Theimer 1987) and discourage a strategy of pair-bond dominance. A system of individual dominance would obviate costs of pair-bond maintenance during periods when pair-bonds have no foraging benefits.

PREDATION PRESSURE AND ANTIPREDATOR TACTICS

Great Black-backed Gulls (*Larus marinus*) were common on Lake Mattamuskeet and Pamlico Sound, and had dramatic effects on water-bird flocking behavior (Sobkoviak 1986; Lovvorn, pers. observ.). Great Black-backed Gulls killed between 4.6 and 7.3% of an average 725 (SD = 545) American Coots (*Fulica americana*) present on Lake Mattamuskeet from late October to mid-December 1983 ($n = 55$ days). Interactions in which gulls singled out and pursued, struck, or killed coots ranged from 0.111 to 0.571/hr ($\bar{x} = 0.270$/hr, $n = 441$ hr) (Sobkoviak 1986, p. 40–43). Relatively poor diving and flying abilities of coots made them the primary target of gull attacks on Lake Mattamuskeet, but other water birds were often approached and sometimes killed when in their own flocks or mixed with coots. Predation rates on other water birds were not quantified, but gulls were observed to kill two Ruddy Ducks (*Oxyura jamaicensis*) and one Canvasback (known to be crippled by hunters) on Lake Mattamuskeet. Canvasbacks always ceased diving when gulls approached (S. Sobkoviak and J. R. Lovvorn, unpubl.).

After Canvasbacks moved from Lake Mattamuskeet to Pamlico Sound in early December, they occurred in flocks of several hundred to several thousand diving ducks including Greater and Lesser scaup (*Aythya marila* and *A. affinis*) and Ruddy Ducks. Most dabbling ducks also disappeared from Lake Mattamuskeet at this time, and Great Black-backed Gulls concentrated their efforts on diving ducks in the sound. The gulls attempted to displace these flocks almost hourly to isolate crippled or otherwise vulnerable individuals (see also Mansueti 1961, Tamisier 1970, Sobkoviak 1986). While doing other fieldwork, I incidentally observed gulls kill two Ruddy Ducks and two Canvasbacks on Pamlico Sound.

Flock density on Pamlico Sound eventually increased until individuals could no longer be followed and systematic data collection was discontinued. Constant movement of flocks often resulted in diving ducks surfacing to find the raft had moved away while they were underwater, a potentially dangerous situation provoking obvious nervousness in the isolated bird. Within several weeks of their shift to Pamlico Sound, and perhaps after prewinter fat levels were attained (Lovvorn 1987), Canvasbacks mostly stopped foraging during daylight and moved to feeding areas only after the gulls had left for nighttime roosts. It is possible that during the day, either Canvasbacks were unwilling to sacrifice vigilance while underwater (see Poysa 1987), or else food densities were too low to support profitable foraging by birds constrained by predators to remain in dense flocks. In Chesapeake Bay where Great Black-backed Gulls are also common (Mansueti 1961; Lovvorn, pers. observ.), Canvasbacks sleep in large flocks by day and disperse into small, loose groups while feeding at night (Perry and Uhler 1988). In North Carolina this behavior appeared independent of hunting disturbance, which was very low in 1982–1983 (closed season on Canvasbacks with little hunting of other diving ducks) but heavy in 1983–1984 (first open season on Canvasbacks in 10 years, with much diving duck hunting).

Bald Eagles (*Haliaeetus leucocephalus*) were present at Lake Mattamuskeet (Sobkoviak 1986) and La Crosse, and provoked similar antipredator responses. However, they approached Canvasbacks rarely compared to the frequent and persistent harassment by Great Black-backed Gulls on Lake Mattamuskeet and especially Pamlico Sound. Eagles and Great Black-backed Gulls were not observed at Long Point, and were seen very rarely at South Carolina ponds (W. C. Alexander, pers. comm.).

ANTIPREDATOR TACTICS AND PAIR-BOND ECONOMICS

Upon approach by a Bald Eagle or Great Black-backed Gull, dabbling ducks on Lake Mattamuskeet relied primarily on quickly taking flight and outdistancing the predator (see also Tamisier 1970). However, in my study areas, the first defense of pochards was to form dense rafts rather than to flush. This difference might result from pochards' lack of vigilance while feeding underwater, and their higher wing loading and slower take-off time (Raikow 1973). These factors may contribute to their staying in characteristically dense flocks when predators are active, and to reports that diving ducks are more easily captured when flushed by eagles than are dabbling ducks (Sharp 1951, Todd et al. 1982). In forming dense rafts to elude predators, selfish herding mandates escape at the expense of nearest neighbors (Hamilton 1971), and the confusion effect demands that prey abandon spatial affinities with other individuals that would make them appear different (Milinski 1977, Hobson 1978, Pitcher 1986). Maintaining proximity to a mate in areas where flocks are large and attacks frequent would seem difficult and dangerous.

Direct evidence that pair-bond maintenance costs increase in dense flocks when predators are active is hard to obtain. Among Snow Geese (*Chen caerulescens*) highly concentrated on migration staging areas, confusion when flocks were flushed by predators or other disturbance often caused breakup of individually marked pairs and families (Prevett and MacInnes 1980). Separation results in strong reduction of dominance in foraging interactions, and searching behavior for lost family members (Raveling 1970, Prevett and MacInnes 1980, Scott 1980). In response to Bald Eagles and Gyrfalcons (*Falco rusticolus*), Steller's Eiders (*Polysticta stelleri*) remain in very large, dense rafts, in which interference by other birds forces pairs to leave flocks for brief bouts of copulation important to pair-bond reinforcement (McKinney 1965). Whether this indicates conflict between antipredator and pair-bond behavior, or rather that such behaviors are in fact compatible, requires further study.

In addition to possibly increased costs of maintaining pair-bonds when predators are active, benefits of pair-bond dominance may be reduced in dense flocks (Johnson and Raveling 1988). Even if birds feed while in dense rafts as *Aythya* often do, feeding-site defense is unfeasible because of swamping effects (Raveling 1970, Moore 1977, Myers et al. 1979, Myers 1984). Thus pair-bond dominance in foraging may be of little value even if costs of pair-bond maintenance were acceptable. In North Carolina during winter, constraints of antipredator flocking behavior on both social bonds and feeding-site defense should be stronger in *Aythya* than in *Anas* because of the denser and much larger flocks of pochards, and their greater reliance on selfish herding and confusion effect on the water surface than on quickly taking flight and outdistancing predators in the air.

IMPLICATIONS FOR PAIRING CHRONOLOGY

It has been suggested that timing of pair formation in *Anas* and *Aythya* depends on a balance of benefits to females (primarily nutrient storage and survival) and to males (mate acquisition) vs. costs to males of mate defense and vigilance (Afton and Sayler 1982, Rohwer and Anderson 1988). Rohwer and Anderson (1988) proposed that *Aythya* generally pair later than *Anas* because diving as a foraging mode makes it more difficult for males to defend feeding sites and attend their mates. Although I agree with the general approach, I believe these constructs underemphasize the dominance benefits to males of being paired, the costs to females of maintaining pair-bonds, and the capability of pochards to defend feeding sites.

Female Canvasbacks initiated and won a large fraction (49%) of their encounters with males on Lake Mattamuskeet (Table 4). On South Carolina ponds, unmarked females won 34% of 595 low-intensity interactions with males, and 46% of 39 high-intensity interactions with males, the latter difference between sexes being nonsignificant (Alexander 1980b, p. 72, 74, 90–91). These data for unpaired Canvasbacks emphasize that simply being male often does not ensure dominance over females, and hence many males in the population would have much to gain from pair-bond dominance. Among paired Canvasbacks at Long Point and La Crosse, males and females did not differ in percent time spent foraging (males: $\bar{x} \pm \mathrm{SE} = 45.5 \pm 5.9$, n of 5-min, focal-individual samples = 54; females: 36.5 ± 3.8, $n = 119$) or dives/min (males: 1.5 ± 0.2, females 1.2 ± 0.1) (Wilcoxon's rank sum tests, $P > 0.22$). Paired males and females both dominated unpaired individuals in foraging interactions (Table 5; Lovvorn 1987). On the breeding grounds male Canvasbacks do defend their mates, and female foraging rates exceed those of males (Anderson 1985). However, before accelerated nutrient storage for egg production in late migration (J. A. Barzen, unpubl.), foraging benefits of pairing do not accrue mainly to female Canvasbacks at the expense of males, as paired females are more aggressive and successful than paired males in defending foraging sites (Table 5; Lovvorn 1987). Furthermore, Anderson (1984) found that pair-bond reinforcement behaviors of maintaining proximity, coordinating activities, and initiating displays were greater in paired female Canvasbacks than in paired males from migration through the prelaying period, and that only during laying did males take the lead in pair-bond maintenance. These data suggest that pairing chronology in ducks should not be viewed solely in terms of costs and benefits to males, with pairing always being of benefit to females because of mate defense by males.

Rohwer and Anderson (1988) proposed that diving as a foraging mode makes it more difficult among *Aythya* than *Anas* for males to defend feeding sites and attend their mates. Closer examination of this hypothesis suggests a more ultimate reason that foraging mode of diving ducks might constrain site defense and mate attendance. Measures of relative effort for defense of feeding sites by pochards vs. dabbling ducks are currently unavailable, but site defense by pochards is common and effective in a variety of habitats (Alexander and Hair 1979; Alexander 1980a, 1980b, 1987; this study). Canvasbacks, for example, appear fully capable of site defense at any time of year when food is appropriately distributed. Furthermore, both *Anas* and *Aythya* show a range in winter diet among species from predominantly foliage to mostly invertebrates (Bellrose 1980), suggesting that if foods of *Aythya* are less defendable, it is not solely or predominantly because of the way these foods are distributed. However, in open water where most Canvasbacks and other *Aythya* winter, diving may indirectly reduce feeding-site defense and the potential for mate attendance through its influence on antipredator flocking behavior. Because of swamping effects, Canvasbacks and scaup could not have defended foraging sites in the dense flocks apparently formed to counter avian predators in North Carolina. Regardless of sexual differences, costs of maintaining proximity to mates would perhaps be too high for Canvasbacks and other *Aythya* in the presence of avian predators, especially if foods are not consistently scarce and economically defendable.

In summary, it appears that (1) foods of Canvasbacks over much of their wintering range are not scarce and economically defendable consistently enough to justify costs of maintaining pair-bonds for dominance purposes; and (2) feeding-site defense and proximity of mates required to maintain and benefit from pair-bonds conflict with antipredator tactics of Canvasbacks in open water. Such tactics (dense flocking, selfish herding, confusion effect) probably have been favored by diving as a foraging mode, because loss of vigilance while underwater and morphological constraints on take-off abilities have led to slower response time and less reliance on escape flights when predators are active. These factors may partly explain the absence of early pairing in Canvasbacks and other species of *Aythya*.

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LITERATURE CITED

AFTON, A. D., AND R. D. SAYLER. 1982. Social courtship and pairbonding of Common Goldeneyes wintering in Minnesota. Can. Field-Nat. 96:295–300.

ALEXANDER, W. C. 1980a. Aggressive displays in nonbreeding Canvasbacks. Auk 97:198–201.

ALEXANDER, W. C. 1980b. The behavioral ecology and sociobiology of nonbreeding diving ducks (Aythyini). Ph.D.diss. Clemson Univ., Clemson, SC.

ALEXANDER, W. C. 1987. Aggressive behavior in wintering diving ducks. Wilson Bull. 99:38–49.

ALEXANDER, W. C., AND J. D. HAIR. 1979. Winter foraging behavior and aggression of diving ducks in South Carolina. Proc. Annu. Conf. S. E. Assoc. Fish and Wildl. Agencies 31:226–232.

ANDERSON, M. G. 1984. Parental investment and pair-bond behavior among Canvasback ducks (*Aythya valisineria,* Anatidae). Behav. Ecol. Sociobiol. 15:81–90.

ANDERSON, M. G. 1985. Social behavior of breeding Canvasbacks (*Aythya valisineria*): male and female strategies of reproduction. Ph.D.diss. Univ. Minnesota, Minneapolis.

ASHCROFT, R. E. 1976. A function of the pairbond in the Common Eider. Wildfowl 27:101–105.

BAILEY, R. O., AND B.D.J. BATT. 1974. Hierarchy of waterfowl feeding with Whistling Swans. Auk 91: 488–493.

BELLROSE, F. C. 1980. Ducks, geese and swans of North America. 3rd ed. Stackpole, Harrisburg, PA.

BRODSKY, L. M., AND P. J. WEATHERHEAD. 1985. Time and energy constraints on courtship in wintering American Black Ducks. Condor 87:33–36.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

CARPENTER, F. L., AND R. E. MACMILLEN. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639–642.

CELY, J. E. 1980. Distribution and feeding ecology of Canvasback ducks along the South Carolina coast. M.S. thesis. Clemson Univ., Clemson, SC.

GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333–345.

HAMILTON, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:292–311.

HEPP, G. R. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. Auk 103:477–484.

HEPP, G. R., AND J. D. HAIR. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of the sexes. Condor 86:251–257.

HOBSON, E. S. 1978. Aggregating as a defense against predators in aquatic and terrestrial environments, p. 219–234. *In* E. S. Reese and F. J. Lighter [eds.], Contrasts in behavior. Wiley, New York.

JOHNSON, J. C., AND D. G. RAVELING. 1988. Weak family associations in Cackling Geese during winter: effects of body size and food resources on goose social organization, p. 71–89. *In* M. W. Weller [ed.], Waterfowl in winter. Univ. Minnesota Press, Minneapolis.

KORSCHGEN, C. E., L. S. GEORGE, AND W. L. GREEN. 1988. Feeding ecology of Canvasbacks staging on Pool 7 of the upper Mississippi River, p. 237–249. *In* M. W. Weller [ed.], Waterfowl in winter. Univ. Minnesota Press, Minneapolis.

LOTT, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266–325.

LOVVORN, J. R. 1987. Behavior, energetics, and habitat relations of Canvasback ducks during winter and early spring migration. Ph.D.diss. Univ. Wisconsin, Madison.

LOVVORN, J. R. 1989. Distributional responses of Canvasback ducks to weather and habitat change. J. Appl. Ecol. 26:113–130.

MANSUETI, R. J. 1961. Waterfowl predation by and records of the Great Black-backed Gull in Chesapeake Bay during winter and spring. Chesapeake Sci. 2:102–104.

MCKINNEY, F. 1965. The spring behavior of wild Steller Eiders. Condor 67:273–290.

MCKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks, p. 153–171. *In* D. I. Rubenstein and R. W. Wrangham [eds.], Ecological aspects of social evolution. Princeton Univ. Press, Princeton, NJ.

MILINSKI, M. 1977. Experiments on selection by predators against spatial oddity of their prey. Z. Tierpsychol. 43:311–325.

MOORE, F. R. 1977. Flocking behaviour and territorial competitors. Anim. Behav. 25:1063–1066.

MYERS, J. P. 1984. Spacing behavior of nonbreeding shorebirds. Behav. Mar. Anim. 6:271–321.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96:551–561.

NICHOLS, J. D., AND G. M. HARAMIS. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. Condor 82:406–416.

PATTERSON, I. J. 1982. The Shelduck. Cambridge Univ. Press, Cambridge.

PAULUS, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. Auk 100:947–952.

PAULUS, S. L. 1988. Social behavior and pairing chronology of Mottled Ducks during autumn and winter in Louisiana, p. 59–70. *In* M. W. Weller [ed.], Waterfowl in winter. Univ. Minnesota Press, Minneapolis.

PERRY, M. C., W. J. KUENZEL, B. K. WILLIAMS, AND J. A. SERAFIN. 1986. Influence of nutrients on feed intake and condition of captive Canvasbacks in winter. J. Wildl. Manage. 50:427–434.

PERRY, M. C., AND F. M. UHLER. 1988. Food habits and distribution of wintering Canvasbacks, *Aythya valisineria,* on Chesapeake Bay. Estuaries 11: 57–67.

PITCHER, T. J. 1986. Functions of shoaling behaviour in teleosts, p. 292–337. *In* T. J. Pitcher [ed.], The behavior of teleost fishes. Johns Hopkins Univ. Press, Baltimore.

POYSA, H. 1987. Feeding-vigilance trade-off in the Teal (*Anas crecca*): effects of feeding method and predation risk. Behaviour 103:108–122.

PREVETT, J. P., AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. Wildl. Monogr. 71.

RAIKOW, R. J. 1973. Locomotor mechanisms in North American ducks. Wilson Bull. 85:295–307.

RAVELING, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37:291–319.

ROHWER, F. C., AND M. G. ANDERSON. 1988. Female-based philopatry, monogamy, and the timing of pair formation in migratory waterfowl, p. 187–221. *In* R. F. Johnston [ed.], Current ornithology. Vol. 5. Plenum Press, New York.

SCOTT, D. K. 1980. Functional aspects of the pair bond in winter in Bewick's Swans (*Cygnus columbianus bewickii*). Behav. Ecol. Sociobiol. 7:323–327.

SHARP, W. M. 1951. Observations on predator-prey relations between wild ducks, Trumpeter Swans and Golden Eagles. J. Wildl. Manage. 15:224–226.

SOBKOVIAK, S. 1986. Greater Black-backed Gull and Bald Eagle predation on American Coots. M.S. thesis. McGill Univ., Montreal.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman, San Francisco.

STUDENT. 1907. On the error of counting with a haemacytometer. Biometrika 5:351–360.

TAMISIER, A. 1970. Signification du gregarisme diurne et de l'alimentation nocturne des Sarcelles d'Hiver *Anas crecca crecca* L. Terre et Vie 4:511–562.

THEIMER, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate Dark-eyed Juncos, *Junco hyemalis.* Anim. Behav. 35:1883–1890.

TODD, C. S., L. S. YOUNG, R. B. OWEN, AND F. J. GRAMLICH. 1982. Food habits of Bald Eagles in Maine. J. Wildl. Manage. 46:636–645.

WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82:227–235.

WIENS, J. A. 1976. Population responses to patchy environments. Annu. Rev. Ecol. Syst. 7:488–493.

ZAHAVI, A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. Ibis 113:203–211.