COURTSHIP AND AGGRESSION IN CANVASBACKS: INFLUENCE OF SEX AND PAIR-BONDING[1]

JAMES R. LOVVORN[2]

Department of Zoology, University of Wisconsin, Madison, WI 53706

Abstract. Time-activity budgets, courtship, and aggression of paired and unpaired Canvasbacks (*Aythya valisineria*) were studied on the upper Mississippi River and on Long Point Bay, Lake Erie, during spring migration. Of Canvasbacks present, 25–28% were female of which 17–27% were paired. Paired Canvasbacks spent more time in foraging aggression and initiated and won more encounters than did unpaired individuals. Paired females engaged in more courtship-related threats, chases, and neck-stretches than did unpaired females. Paired females exceeded paired males in foraging aggression and in courtship behaviors such as neck-stretches and chases, with the trend in all chases reversing just before or upon arrival at nesting sites. Thus in the early stages of pairing, females rather than males appeared to assume the primary role in foraging aggression and repelling courtship advances of other males.

Key words: Canvasback; Aythya valisineria; courtship; aggression; pair-bonding.

INTRODUCTION

In monogamous birds, pair-bonded individuals are often behaviorally dominant to unpaired individuals (Raveling 1970, Ashcroft 1976, Scott 1980, Patterson 1982, Paulus 1983, Hepp and Hair 1984, Teunissen et al. 1985, Lamprecht 1986, Hepp 1989). In northern ducks on the breeding grounds (Dwyer 1974, Ashcroft 1976, Afton 1979, Stewart and Titman 1980, Wishart 1983, Anderson 1985a) and in dabbling ducks (Anatini), geese, and swans on wintering areas (Scott 1980, Hepp and Hair 1984, Teunissen et al. 1985), females especially appear to benefit from pair-bonds owing to mate defense by males. Whether defense by the male constitutes indirect reproductive investment in the female's body condition, or simply protection of his paternity or pair-bond integrity (see Anderson 1985a), an important result is presumed to be enhancement of the female's foraging efficiency (Dwyer 1974, Ashcroft 1976, Afton 1979, Stewart and Titman 1980, Wittenberger and Tilson 1980, Afton and Sayler 1982, Hepp and Hair 1984, McKinney 1986; see also LeFebvre and Henderson 1980).

Costs and benefits of pair-bonding, however, may differ both between males and females (Afton and Sayler 1982, Hepp and Hair 1983) and

among individuals. Time of pairing, "choosiness" in mate selection, and pair-bond maintenance effort are all expected to reflect not only the relative reproductive effort of the sexes, but also the availability of potential mates to a given sex or individual (review in Thornhill 1986). Factors affecting the choices available include the operational sex ratio of the population (Emlen and Oring 1977) and the relative "quality" of different individuals as mates (Searcy 1982). Such qualities are expected to have greater influence on differential mating success in the sex that is numerically dominant (Emlen and Oring 1977) or that has lower but still appreciable reproductive effort (Burley 1977).

In Canvasbacks, *Aythya valisineria,* males outnumber females about three to one (Bellrose 1980), and females alone incubate and care for broods. However, during the nesting period, males apparently provide indirect reproductive investment by defending their mates from harassment by other males or pairs, by watching for predators, and by chasing away parasitic Redheads, *A. americana* (Anderson 1984, 1985a, 1985b).

Established theory (Emlen and Oring 1977, Wittenberger and Tilson 1980, Thornhill 1986) predicts that male Canvasbacks, because of their much greater abundance and lesser reproductive investment, should compete among themselves for females and defend their mates from other males. In turn, females should use their control over the pairing process to encourage their mates

[369]

to defend them from unwanted intruders. However, these same circumstances are also expected to increase the importance of male-quality variations in mate choice by females (Burley 1977, Petrie 1983a), possibly altering anticipated patterns in pair-bond behavior by the sexes. Male-quality variations should also have greater effects on options for mate desertion by either sex early in the pairing process, when there are more unpaired females available (more pairing opportunities for high-quality males) and little behavioral synchronization between mates has occurred.

I studied time-activity budgets, display frequencies, and aggressive relations of paired and unpaired Canvasbacks during spring migration (see also Lovvorn 1989). In this paper, I examine (1) the influence of pair-bond formation on aggression and dominance, and (2) the relative roles of paired males and females in aggression toward other Canvasbacks.

MATING SYSTEM

Canvasbacks form new pair-bonds each spring, primarily during migration. Females respond to courtship displays of males by threatening or chasing them, and by various signals that encourage male courtship. The female exhibits initial choice by performing inciting displays and mutual neck-stretches with the chosen male while threatening or chasing other males (display descriptions in Palmer 1976, p. 150). Stability of these initial pair-bonds has not been studied in wild, marked individuals; but females in seemingly well-established pairs are courted frequently by unpaired as well as paired males. Pair-bonds are apparently reinforced by displays such as mutual neck-stretches, by copulation, and by aggression toward rival males and pairs. Paired males foster extra-pair liaisons with other paired females, but forced copulations are rare and pairs typically remain together for renesting attempts (Hochbaum 1944; Anderson 1984, 1985a, 1985b).

METHODS

I studied Canvasbacks at two stopover areas during spring migration in different years (see also Lovvorn 1989). In 1983 on Navigation Pool 8 of the Mississippi River near La Crosse, Wisconsin, I recorded Canvasback behavior during the peak of migration, 23 March–5 April. In 1984 at Long Point Bay, Lake Erie, I documented be-

havior throughout the time Canvasbacks were present, 11 March–12 April.

Sex ratios were tallied through a spotting scope in areas near and including sites where Canvasback behavior was studied. Aerial counts by the U.S. Fish and Wildlife Service (La Crosse) and the Canadian Wildlife Service (Long Point) provided data on local numbers of Canvasbacks.

Each day 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 and dive and pause times for that bird.

I used the behavioral terminology of Palmer (1976, p. 150) and Alexander (1980a, 1980b), except that I consider the display termed head-pump by Alexander to be a neck-stretch. I believe neck-stretches are appeasement displays that mitigate aggression among courting birds or mates (McKinney 1961) as well as among noncourting individuals. I included bill-jabs in the category of threats because of apparent similarity of function and low frequency of bill-jabs. I did not analyze data on displacement-by-presence (Alexander 1980a) because I probably did not detect all such interactions. Wins in aggressive encounters were defined by which bird supplanted the other, and the percentages of wins were calculated as percentages of interactions with clear winners. Threats, chases, and fights occurring in disputes over feeding sites were categorized as foraging aggression; whereas courtship aggression included threats and chases among Canvasbacks that were actively courting as evidenced by courtship displays.

Canvasbacks were classified as "paired" based on a combination of spatial proximity, coordination of activities, mutual neck-stretches, inciting by the female, and selective threats and chases. If at the end of a 5-min sampling period
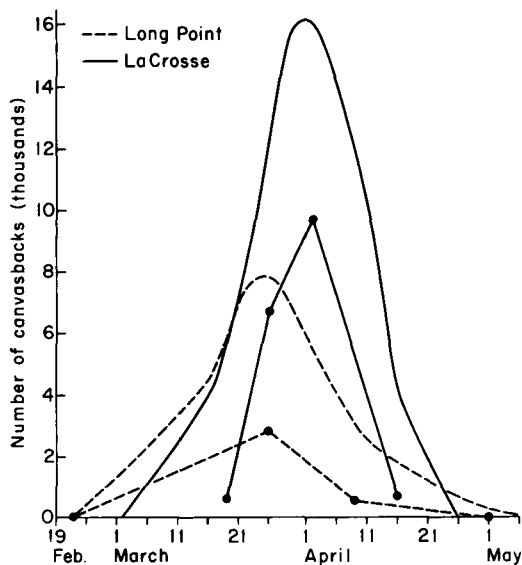
FIGURE 1.   Numbers of Canvasbacks in 1984 at Long Point Bay, Ontario, and the Mississippi River near La Crosse, Wisconsin (connected points); and averaged for Long Point (1972, 1975, 1979, 1984) and La Crosse (1979–1984) (smooth curves).
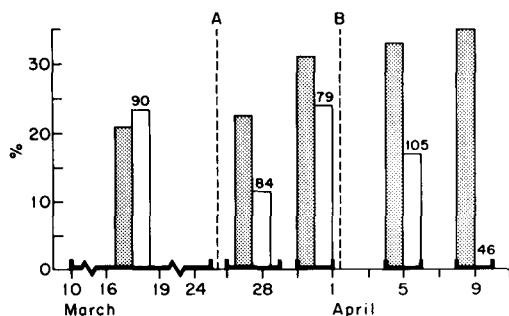

FIGURE 2.   Percentage of Canvasbacks that were female (stippled bars) and percentage of females that were paired (open bars) in 1984, at Long Point Bay, Ontario. Numbers of birds sexed during the five successive periods were 1,556, 789, 454, 955, and 360. Numbers of 5-min, focal-individual samples of females used to determine pair-status percentages are notated above bars. Days over which observations were combined are bracketed at the bottom. First thaw exposing many new holes in the ice occurred at point A; general breakup of ice was at point B.

I was unsure of an individual's pair status, I continued to watch the bird until an accurate determination was possible. Random selection of focal individuals was necessary to quantify the percentage of Canvasbacks that were paired, but resulted in unequal samples of paired and unpaired birds.

Data were tested for normality and homogeneity of variance, and rank-transformed when necessary. Percentage tests (Sokal and Rohlf 1969, p. 607) and z-tests (Student 1907) were used to test differences in percentages and frequencies. For time-activity data, characteristically high variances gave multifactor analyses unacceptably low power for detecting differences. Consequently, I used combinations of univariate tests.

RESULTS

CHRONOLOGIES OF MIGRATION, SEX RATIOS, AND PAIR STATUS

Staging chronologies of Canvasbacks at Long Point and La Crosse in 1984 resembled long-term averages (Fig. 1); data were insufficient to construct plots for 1983. First arrival and peak numbers generally occur earlier at Long Point than at La Crosse; and for Canvasbacks migrating from the East Coast toward prairie nesting areas, stopover at La Crosse occurs later in migration.

Sex ratios and predominance of paired birds changed markedly throughout the staging period at a single location (Fig. 2). Apparent departure of many paired females from Long Point during 26–29 March (Fig. 2) coincided with the opening of many new holes in the ice. Overall at Long Point in 1984, the population was 28% female (average of five periods in Fig. 2) and 17% of 404 females observed as focal individuals were paired. At La Crosse in 1983, females comprised 25% of the population ($n = 14,430$ over a 14-day period) and 27% of 188 focal-individual females were paired.

NONCOURTSHIP ACTIVITY AND AGGRESSION

In general, Canvasbacks spent more time swimming and in foraging aggression (Table 1) and exhibited higher rates and intensities of aggression (Table 2) at La Crosse in 1983 than at Long Point in 1984. At La Crosse, the Canvasback diet included 48% (by volume) *Sagittaria rigida* tubers, 20% winter buds of *Vallisneria americana,* and 25% *Hexagenia* spp. nymphs (J. A. Barzen and C. E. Korschgen, unpubl.); whereas at Long Point, Canvasbacks fed only on winter buds of *V. americana* (Lovvorn 1987). *Sagittaria rigida* tubers were much larger, less continuously distributed, and occurred deeper in the substrate

TABLE 1. Mean percentage of time spent in different activities by Canvasbacks during spring migration in 1984 at Long Point Bay, Ontario, and in 1983 at the Mississippi River near La Crosse, Wisconsin. Means in the same row followed by the same letter are significantly different (Bonferroni multiple comparisons of rank-transformed data, $P < 0.05$).

Activity	Long Point				La Crosse			
	Male		Female		Male		Female	
	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired
n^a	393	29	337	67	281	24	137	51
Feeding	33.4A	43.3	46.0AB	35.7	34.0B	42.9	38.0	37.6
Swimming	8.0A	4.5BCD	7.7EF	7.3GHJ	14.3ABFHI	6.9I	13.6CEG	12.5DJ
Resting	5.9A	3.2	5.8	5.2BC	11.5AC	12.5	8.2B	9.7
Sleeping	22.0	21.3	20.4	29.9A	19.4	17.1	14.7A	13.8
Comfort movements	14.9	14.9	12.8AB	7.3C	13.0	10.4	17.4BC	13.7A
Alert	0.4	0.4	0.1	0.2	0.4	0.6	0.4	0.7
Aggression^b	0.4ABC	0.0DE	0.9FGH	0.9	1.5BI	2.4ADHI	1.7G	3.1CEF
Courtship	13.2ABC	8.8	4.8BDE	12.0DE	5.7A	6.9	5.9C	8.8

^{a} Number of 5-min, focal-individual samples.
^{b} Primarily foraging.

than winter buds of *V. americana* (Lovvorn 1989). At La Crosse, there was widespread defense of feeding sites and increased swimming by Canvasbacks, especially unpaired males, apparently in search of foraging opportunities (Table 1; note that swimming during courtship is included in courtship time). At both sites, time spent feeding was greater in paired than unpaired males, but did not differ significantly between paired and unpaired females.

There were no significant main effects or interactions among sex or pair status in dives/minute, dive durations, pause durations, or ratios of dive and pause durations at the same area. However, all these parameters were greater (with no interactions) at La Crosse in 1983 than at Long Point in 1984 (Bonferroni multiple comparisons of rank-transformed data, $P < 0.001$ except for dives/minute, $\bar{x} = 3.4$ vs. 1.5, $P = 0.23$). I detected no meaningful patterns in times spent resting, sleeping, alert, or in comfort movements among sex, pair status, or location (Table 1).

Of the 97% (583/604) of all aggressive encounters having clear winners, 98% were won by individuals initiating them; so the percentage of wins in Table 2 is essentially equivalent to relative aggressiveness. Paired females initiated and won 100% of their encounters with males (there was no aggression between mates), and 89–100% of those with females (Table 2). Unpaired females won only 40–66% of encounters with males, and 0–50% of those with females. Paired males won 67–100% of their interactions with males, but none of their encounters with females. Paired males were also threatened and chased more commonly than paired females, but less often than unpaired males. In terms of aggression initiated [(encounters/5 min) × (% wins)], paired females threatened other females more frequently than did paired males (z-test, $P = 0.02$). There were no other significant differences between paired males and females in initiation of non-courtship aggression.

COURTSHIP

The fraction of the diurnal period spent in courtship by unpaired Canvasbacks was higher in males than in females at Long Point, but was similar for both sexes at La Crosse (Table 1). Average duration of the courtship period (in days) may differ between sexes, so that comparison of total time devoted to courtship by males vs. females is not possible with these data. Neverthe-

less, it was clear that courtship is time-consuming and energetically costly for females as well as males.

Frequencies of courtship displays (head throw, kink-neck call, sneak) generally were greater in paired males and lower in unpaired males at La Crosse than at Long Point (Table 3). Neck-stretches by paired males and females, and threats by paired females, were more frequent at Long Point, concurrently with greater courtship activity among unpaired males (Tables 1 and 3). Unlike paired females, paired males almost never threatened or chased other males in a courtship context. Inciting displays by paired females occurred at rates of 0.51 and 0.18 per 5 min at Long Point and La Crosse, respectively. Only one copulation was observed at Long Point, and none at La Crosse.

CHRONOLOGY OF SEXUAL ROLES IN CHASES

To examine chronological changes in the relative roles of paired males and females in chasing conspecifics, I compared my data with those of Anderson (1985a, p. 81–82). Anderson studied Canvasbacks on small breeding ponds with few birds present, and expressed chase frequencies as chases per number of Canvasbacks available to chase. This approach was inappropriate for my study sites, where large areas and numbers of Canvasbacks made it difficult to quantify how many birds were "available" to chase. Consequently, I used ratios of the numbers of chases performed by paired males and females ("chaser ratios") for comparisons. I combined my data for chases in both courtship and foraging contexts to conform to Anderson's presentation.

Paired females did more chasing than paired males during migration, especially at Long Point (Table 4). However, chaser frequencies of paired males far exceeded those of paired females from arrival at the nesting area through incubation (end of April through early June). The higher chaser ratio at La Crosse than at Long Point was primarily owing to increased male chases in foraging contexts (compare Tables 2 and 3).

DISCUSSION

I studied Canvasback behavior at different sites in different years, so that effects of location and year could not be distinguished. However, concerning time-activity budgets and aggression according to sex and pair status, trends discussed

TABLE 2. Frequencies of foraging aggression (encounters/5 min) and percentage of wins by focal individuals (in parentheses) among migrating Canvasbacks in 1984 at Long Point Bay, Ontario, and in 1983 at the Mississippi River near La Crosse, Wisconsin.

Aggression type and sex of opponent	Long Point				La Crosse			
	Male		Female		Male		Female	
	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired
n^a	393	29	337	67	281	24	137	51
Threat								
Male	0.19 (60)	0.10 (67)	0.20 (55)	0.07^b (100)^{bc}	0.29^c (65)	0.58^{bc} (77)	0.25 (66)^c	0.25^{ce} (100)^{bc}
Female	0.08^d (62)	0^b	0.08^d (50)^c	0.12^c (88)^{bd}	0.11^d (62)	0^{bd}	0.07^d (11)^{cde}	0.12^c (100)^{be}
Chase								
Male	0.04 (65)	0^b	0.01^c (40)^c	0.01 (100)^b	0.21^c (71)	0.33^c (86)	0.12^c (62)^c	0.27^c (100)^{bc}
Female	0.02 (86)^d	0.03 (0)^b	0.01 (0)^{cd}	0	0.05^d (85)^d	0^{bd}	0.07^d (22)^{cde}	0.02^d (100)^b
Fight								
Male	0	0	0	0	0.04^d (100)	0.04 (100)	0.03 (50)^c	0.02 (100)^b
Female	0.01 (50)	0	0	0	0.01 (50)^d	0	0.03 (25)^{cd}	0

^{a} Number of 5-min, focal-individual samples.
^{b} Different from unpaired, percentage test, $P < 0.05$.
^{c} Different from opposite sex of same pair status at same location, z-test, experiment-wise $\alpha < 0.05$.
^{d} Different from male opponent for same sex and pair status of focal individual, test as in (c).
^{e} Different from same sex and pair status at Long Point, test as in (c).

TABLE 3. Frequencies of courtship and pair behaviors (behaviors/5 min) of migrating Canvasbacks in 1984 at Long Point Bay, Ontario, and in 1983 at the Mississippi River near La Crosse, Wisconsin.

	Long Point				La Crosse			
	Male		Female		Male		Female	
Behavior	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired	Unpaired	Paired
n^a	393	29	337	67	281	24	137	51
Head throw	0.27	0.10[b]			0.24	0.62[d]		
Neck-stretch	0.26	0.72[b]	0.60[c]	1.87[bc]	0.22	0.42	0.63[c]	0.76[d]
Kink-neck call	0.71	0.34[b]			0.42[d]	0.54		
Sneak	0.28	0.21			0.19[d]	0.38		
Threat to male	0.01	0	0.52[c]	1.82[bc]	0.02	0.04	0.64[c]	1.02[bcd]
Chase of male	0.01	0	0.12[c]	0.06	0.02	0	0.04[d]	0.16[c]

[a] Number of 5-min, focal-individual samples.
[b] Different from unpaired, z-test, experiment-wise $\alpha < 0.05$.
[c] Different from male of same pair status at same location, test as in (b).
[d] Different from same sex and pair status at Long Point, test as in (b).

below were consistent for both data sets regardless of any site or year differences.

AGGRESSION

I could not construct dominance matrices relating paired and unpaired Canvasbacks of either sex, because when concentrating on focal individuals in flocks I often could not identify the pair status of their opponents with certainty. It is also not possible to identify ages of Canvasbacks at a distance, and age can influence the outcome of aggression between males and females. On wintering areas in South Carolina, adult female Canvasbacks won 36% of encounters with juvenile males, but only 1% of encounters with adult males (Alexander 1987). Of Canvasbacks I collected at Long Point in spring 1984, eight of 34 males and two of 16 females were juveniles, and most juveniles were collected in the last 5 days of the staging period when no pairs were observed in the area. At La Crosse in spring 1984, none of 22 males and three of 23 females collected near the peak of migration were juveniles (J. A. Barzen, unpubl.). Consequently, most of the aggression I documented probably occurred among adults.

Paired Canvasbacks tended to spend more time in aggression and initiated and won more aggressive encounters than unpaired Canvasbacks (Tables 1 and 2). Similar trends have been described in other ducks (Ashcroft 1976, Patterson 1982, Paulus 1983, Hepp and Hair 1984). However, documenting this relationship does not indicate whether pairing enables dominance or rather that dominant individuals tend to pair (Patterson 1982). Among captive Common Shelducks, *Tadorna tadorna,* Patterson (1982)

reported that females did not pair with males that were initially most dominant, and that the dominance rankings of paired males were readjusted to the original rankings of their mates. Paired Common Shelducks were, however, dominant to unpaired individuals. In field studies of Common Eiders, *Somateria mollissima* (Ashcroft 1976), and Tundra Swans, *Cygnus columbianus* (Scott 1980), in winter, females were less successful in aggressive encounters, were threatened more frequently, and spent less time feeding when separated from their mates than when close to them. These findings suggest that in these species pairing leads to dominance rather than the reverse. In captive American Black Ducks, *Anas rubripes,* dominant individuals were more likely than subordinates to form pair-bonds, and the prepairing dominance ranks of mates were positively related (Hepp 1989). The primary benefit of dominance in American Black Ducks

TABLE 4. Ratios of numbers of chases performed by paired Canvasbacks (male/female) during spring migration (this study) and on breeding areas near Minnedosa, Manitoba (Anderson 1985a). For laying and incubation, first and renesting attempts are combined.

Period	Chaser ratio
Migration	
Long Point	0.4
La Crosse	0.9
Breeding	
Postarrival	11.0
Prelaying	21.5
Laying	17.8
Incubation	24.7

appeared to be priority in pair-bonding rather than improvement of winter body condition.

Moreover, in the reproductive season it cannot be assumed that enhanced foraging efficiency (food intake per unit effort) automatically results from, or, in fact, motivates aggression by paired birds. Both male and female may benefit from chasing behavior for reasons other than foraging, such as protecting the male's paternity, the female's choice of mate, or any compatibility or synchronization developed by the pair up to that point. It is also insufficient to show that paired birds feed more, because greater feeding effort could result from the behavioral or hormonal stimulus of being paired (Akesson and Raveling 1981). Functionally relating the aggressiveness of paired birds to their feeding efficiency in spring will require foraging data on individuals when (1) their endocrine levels are manipulated to mimic those of birds of different pair status (Bluhm et al. 1984, Moore 1984), (2) their pair status or proximity to mates changes, and (3) food abundance and dispersion are such that any effects of pair aggressiveness on foraging efficiency are expressed.

COURTSHIP

Courtship-related threats, chases, and neck-stretches were much more frequent in paired than in unpaired female Canvasbacks (Table 3). This trend might result from unpaired males directing courtship differentially toward desirable females that are already paired. When concentrating on focal individuals in flocks, I was unable to determine consistently the pair status of females courted by focal-individual males (other than their own mates); so I cannot evaluate this possibility. Among wild Mallards (*A. platyrhynchos*), unpaired males in fact displayed more frequently to unpaired females (Bossema and Roemers 1985). The difference in behavior of female Canvasbacks after pairing might also result from pair-bond-related behavior discussed below.

RELATIVE BEHAVIOR OF PAIRED MALES AND FEMALES

In early spring, paired female Canvasbacks exceeded paired males both in foraging aggression and in sexual neck-stretches and chases, with the trend in all chases reversing just before or upon arrival at nesting sites (Tables 1–4). Thus in early stages of pairing, male Canvasbacks did not assume a primary role in defending their mates from foraging aggression or the courtship advances of other males, and did not thereby increase the females' foraging time (Table 1, Lovvorn 1989). This situation is in marked contrast to patterns reported for Common Eiders, Gadwalls (*A. strepera*), and American Wigeons (*A. americana*) on wintering areas (Ashcroft 1976, Paulus 1983, Wishart 1983); for Gadwalls, Blue-winged Teals (*A. discors*), and American Wigeons on breeding areas (Dwyer 1974, Stewart and Titman 1980, Wishart 1983); and for Canvasbacks after arrival at nesting sites (Table 4; Anderson 1985a, 1985b). However, Weller (1967) noted that in Redheads females "were responsible for most pair-defense" in late winter and during migration. Furthermore, Anderson (1984) found that pair-bond-reinforcement behaviors of maintaining proximity, coordinating activities, and initiating mutual 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. Possible alternative explanations for trends in relative aggressiveness of male and female Canvasbacks include: (1) newly paired females continue to test rival males as potential mates; and (2) female aggression toward rival males strengthens the pair-bond, signals the female's commitment to her mate, and thereby protects her extensive investment in the mate-selection process.

Evaluation of these alternatives is complicated because threats and chases appear to be used by female Canvasbacks both to test potential mates during courtship (and perhaps to elicit such courtship), as well as to repel strange males later in the breeding sequence (Anderson 1985a). Relative to alternative 1 above, it seems that mate switches must occur or else males would not continue to court paired females. Courtship of paired females by males other than their mates continues into the nesting period, during which mate switches occur in about 17% of pairs (Anderson 1985b). No data exist on the stability of new pair-bonds in wild, marked Canvasbacks during migration. However, Anderson (1984) documented greater pair-bond reinforcement by females than by males during early stages of pairing (see above), which provides independent evidence for alternative 1 vs. 2 based on different behavioral criteria than were used in my study. Anderson's results support the interpretation that female

threats and chases (Tables 2–4) involve more than continued assessment of rival males (alternative 1), and are in fact intended to reinforce her existing pair-bond (alternative 2).

Alternative 2 is of interest regarding the influence of relative pair-bond benefits on "control" of the pairing process by either males or females (see Afton and Sayler 1982, Anderson 1984, McKinney 1986, Thornhill 1986). In Canvasbacks, annual survivorship among adults is 75% in males and 56% in females (Nichols and Haramis 1980), and among juveniles is 36% in males and 30% in females (Office of Migratory Bird Management, U.S. Fish and Wildlife Service, unpubl.). The skewed sex ratio (>70% male, Bellrose 1980) dictates that three-fourths of Canvasback males cannot pair in a given year. Hence, heritable traits that influence whether a female's male offspring will ever obtain mates, or the age at which they first obtain mates, would seem extremely important to her fitness (Cook and Siegel 1974, Boag 1982). Superabundance of males relative to females is expected to increase the influence of male-quality variations in mate choice by females (Burley 1977; Thornhill 1980; Petrie 1983a, 1983b). The fitness value of male traits such as body condition, aggressiveness, and skill in courtship (e.g., Lambrechts and Dhondt 1986, Lamprecht 1986) would be extremely difficult to establish in wild Canvasback populations. However, the importance of male quality in Canvasbacks is suggested by the extensive time and effort a female expends in mate selection (Tables 1 and 3), in which the relative quality of the mate she chooses represents the net gain from her investment. The fact that a paired male continues to court other females could result in greater pair-bond reinforcement by his new mate, and perhaps confirmation of her commitment to the pair-bond through vigorous rejection of rival males (Erickson and Zenone 1976, Anderson 1984).

Established theory holds that mate selection will be controlled by the sex with greater reproductive investment, lower numbers, or both (Emlen and Oring 1977, Wittenberger and Tilson 1980, Thornhill 1986). In keeping with these principles, female Canvasbacks clearly retain the primary role in mate selection (Bluhm 1985). However, superimposed on broad between-sex differences, there appear to be variations in male quality that oblige females to invest heavily in mate-selection processes, and that may result in

female defense of chosen males until new pair-bonds are firmly established (Table 4; see Burley 1977, Bossema and Kruijt 1982). Such mechanisms may explain the female aggression now well documented in Canvasbacks (Anderson 1984, Bluhm 1985, this study) that seems inconsistent with theories not considering the importance of male-quality variations to females. If male quality does affect pair-bond reinforcement by newly paired females, such behavior would not depend on between-sex differences in cumulative reproductive effort (see Anderson 1984), but rather on the probability of early mate desertion based on alternatives available to different individuals (Boucher 1977). Further study of other taxa throughout the breeding sequence might provide more evidence of mate defense when suitable mates superficially do not appear to be scarce (e.g., Thornhill 1980; Petrie 1983a, 1983b).

ACKNOWLEDGMENTS

LITERATURE CITED

AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. Wilson Bull. 91:42–49.

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

AKESSON, T. R., AND D. G. RAVELING. 1981. Endocrine and body weight changes of nesting and nonnesting Canada Geese. Biol. Reprod. 25:792–804.

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

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

ALEXANDER, W. C. 1987. Aggressive behavior of wintering diving ducks (Aythyini). 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. 1985a. Social behavior of breeding Canvasbacks (*Aythya valisineria*): male and female strategies of reproduction. Ph.D.diss., Univ. Minnesota, Minneapolis.

ANDERSON, M. G. 1985b. Variations on monogamy in Canvasbacks (*Aythya valisineria*). Ornithol. Monogr. No. 37. American Ornithologists' Union, Washington, DC.

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

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

BLUHM, C. K. 1985. Mate preferences and mating patterns of Canvasbacks (*Aythya valisineria*). Ornithol. Monogr. No. 37. American Ornithologists' Union, Washington, DC.

BLUHM, C. K., R. E. PHILLIPS, W. H. BURKE, AND G. N. GUPTA. 1984. Effects of male courtship and gonadal steroids on pair formation, egg-laying, and serum LH in Canvasback ducks (*Aythya valisineria*). J. Zool. (Lond.) 204:185–200.

BOAG, D. A. 1982. How dominance status of adult Japanese Quail influences the viability and dominance status of their offspring. Can. J. Zool. 60:1885–1891.

BOSSEMA, I., AND J. P. KRUIJT. 1982. Male activity and female mate acceptance in the Mallard (*Anas platyrhynchos*). Behaviour 79:313–324.

BOSSEMA, I., AND E. ROEMERS. 1985. Mating strategy, including mate choice, in Mallards. Ardea 73:147–157.

BOUCHER, D. H. 1977. On wasting parental investment. Am. Nat. 111:786–788.

BURLEY, N. 1977. Parental investment, mate choice, and mate quality. Proc. Natl. Acad. Sci. USA 74:3476–3479.

COOK, W. T., AND P. B. SIEGEL. 1974. Social variables and divergent selection for mating behaviour of male chickens (*Gallus domesticus*). Anim. Behav. 22:390–396.

DWYER, T. J. 1974. Social behavior of breeding Gadwalls in North Dakota. Auk 91:375–386.

EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

ERICKSON, C. J., AND P. G. ZENONE. 1976. Courtship differences in male Ring Doves: avoidance of cuckoldry? Science 192:1353–1354.

HEPP, G. R. 1989. Benefits, costs, and determinants of dominance in American Black Ducks. Behaviour 109:222–234.

HEPP, G. R., AND J. D. HAIR. 1983. Reproductive behavior and pairing chronology in wintering dabbling ducks. Wilson Bull. 95:675–682.

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

HOCHBAUM, H. A. 1944. The Canvasback on a prairie marsh. American Wildlife Institute, Washington, DC.

LAMBRECHTS, M., AND A. A. DHONDT. 1986. Male quality, reproduction, and survival in the Great Tit (*Parus major*). Behav. Ecol. Sociobiol. 19:57–63.

LAMPRECHT, J. 1986. Social dominance and reproductive success in a goose flock (*Anser indicus*). Behaviour 97:50–65.

LEFEBVRE, L., AND D. HENDERSON. 1986. Resource defense and priority of access to food by the mate in pigeons. Can. J. Zool. 64:1889–1892.

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. Food defendability and antipredator tactics: implications for dominance and pairing in Canvasbacks. Condor 91:826–836.

McKINNEY, F. 1961. An analysis of the displays of the European Eider *Somateria mollissima mollissima* (Linnaeus) and the Pacific Eider *Somateria mollissima v. nigra* Bonaparte. Behaviour Suppl. 7.

McKINNEY, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks, p. 153–161. *In* D. I. Rubenstein and R. W. Wrangham [eds.], Ecological aspects of social evolution. Princeton Univ. Press, Princeton, NJ.

MOORE, M. C. 1984. Changes in territorial defense produced by changes in circulating levels of testosterone: a possible hormonal basis for mate-guarding behavior in White-crowned Sparrows. Behaviour 88:215–226.

NICHOLS, J. D., AND G. M. HARAMIS. 1980. Inferences regarding survival and recovery rates of winter-banded Canvasbacks. J. Wildl. Manage. 44:164–173.

PALMER, R. S. 1976. Handbook of North American birds. Vol. 3. Yale Univ. Press, New Haven, CT.

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.

PETRIE, M. 1983a. Mate choice in role-reversed species, p. 167–179. *In* P. Bateson [ed.], Mate choice. Cambridge Univ. Press, Cambridge.

PETRIE, M. 1983b. Female Moorhens compete for small fat males. Science 220:413–415.

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

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.

SEARCY, W. A. 1982. The evolutionary effects of mate selection. Annu. Rev. Ecol. Syst. 13:57–85.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

STEWART, G. R., AND R. D. TITMAN. 1980. Territorial behaviour by prairie pothole Blue-winged Teal. Can. J. Zool. 58:639–649.

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

TEUNISSEN, W., B. SPAANS, AND R. DRENT. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. Ardea 73:109–119.

THORNHILL, R. 1980. Competitive, charming males and choosy females: was Darwin correct? Fla. Entomol. 63:5–30.

THORNHILL, R. 1986. Relative parental contribution of the sexes to their offspring and the operation of sexual selection, p. 113–136. *In* M. H. Nitecki and J. A. Kitchell [eds.], Evolution of animal behavior. Oxford Univ. Press, London.

WELLER, M. W. 1967. Courtship of the Redhead (*Aythya americana*). Auk 84:544–559.

WISHART, R. A. 1983. The behavioral ecology of the American Wigeon (*Anas penelope*) over its annual cycle. Ph.D.diss., Univ. Manitoba, Winnipeg.

WITTENBERGER, J. F., AND R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. Annu. Rev. Ecol. Syst. 11:197–232.