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BEHAVIORS ASSOCIATED WITH SEASONAL REPRODUCTION AND LONG-TERM MONOGAMY IN CANADA GEESE

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ABSTRACT.—We measured seasonal changes in the incidence of various social behaviors performed by members of a captive flock of Canada Geese (*Branta canadensis moffitti*) in order to determine (a) which of these behaviors were associated with reproduction in a species with long-term monogamy, (b) sexual differences in their expression, and (c) their temporal relationship with nesting events. Breeding and nonbreeding geese were compared.

Aggression, Triumph Ceremony, and Calling by breeding male geese reinforced pair bonds and were performed most frequently in the context of territorial display. The Triumph Ceremonies of breeding females also strengthened pair bonds and were probably essential for establishing a territory and reproductive success. Breeding males behaved aggressively most frequently before the initiation of nesting through the incubation period. During incubation, females became increasingly unresponsive to their mate's Triumph Ceremony and by the time their goslings were two weeks old the frequency of their aggressive behaviors was closer to that of their mates than at any other time of the year. These changes coincided with an increase in social gregariousness during brood rearing and molt.

Retreat was more common in nonbreeding than breeding geese. Nonbreeding males were not aggressive and performed few Triumph Ceremonies. Their behavior did not elicit supportive responses from nonbreeding females and probably inhibited pair formation.

The timing of reproduction of many avian species in seasonal habitats is confined by the periodic availability of resources (Lack 1968). Canada Geese (*Branta canadensis*) nest predominantly in northern latitudes (Delacour 1954, Palmer 1976) and reproductive events occur within a relatively short period of time. Nesting generally begins as soon as secure nest sites become available, and growth of goslings coincides with the growth of sedges and grasses during the summer (MacInnes 1962, Vermeer 1970, MacInnes et al. 1974, Raveling and Lumsden 1977, Raveling 1978). The timing of nesting is also influenced by intra-pair activities (Lofts and Murton 1973:81, Silver 1978) and social conditions (Lott et al. 1967). Formation of life-long pair bonds and intensification of mutual behaviors by pairs of Canada Geese before arrival on their breeding grounds permit nesting to begin without the delay of pair formation.

The social behavior of Canada Geese is well documented (e.g., Hanson 1953, Collias and Jahn 1959, Klopman 1962, 1968, Brakhage 1965, Raveling 1970), but few investigators have quantified such behavior using individuals with known histories in a well defined social environment. In this paper, we report the frequency with which previously described behaviors were performed by breeding and nonbreeding Canada Geese (*B. c. moffitti*). Our objective was to identify behaviors that were important to intra-pair synchrony and nesting success in order to increase our understanding of the behavioral role of the sexes in a species that has long-term pair bonds and nests within a restricted period of time.

METHODS

STUDY ANIMALS AND FACILITY

Geese used in this study either originated from eggs collected at Lake Almanor, Plumas Co., California, during 1971, or were offspring of these birds. Neck collars (Sherwood 1966) and leg bands were used for individual identification. The geese were kept outdoors in a large ($91 \times 44 \times 8$ m high), completely enclosed pen which contained a permanent pond (45×15 m) and three islands. Primary flight feathers on one wing were clipped to render the geese flightless. The pen was located on the Davis campus, University of California (38°32'N). It was surrounded by fallow fields to which access by humans was controlled. Grass and a variety of grains were available to the geese at all times and commercial pigeon pellets (20% protein) were provided during the repro-

ductive and molt periods (February through July). Blood samples were taken from the geese weekly for study of their circulating steroid hormones (Akesson and Raveling 1981).

We classified the geese as "immatures" if they were less than one year old, "yearlings" if between one and two years old, and "adults" if two or more years old. We referred to paired geese as "breeding" birds if the gander defended a territory and the female incubated a clutch.

BEHAVIOR SAMPLING

We observed and recorded the behaviors of the geese and the times of their occurrence from a blind using a spotting scope and a portable tape recorder. Most observation sessions lasted from 1 to 3 h and were conducted between sunrise and 10:00 or 14:00 and dark. We sampled behaviors for 253 h between 9 Oct. 1976 and 3 June 1977 and 236 h between 8 Dec. 1977 and 6 June 1978. In 1976–1977, we observed six pairs of breeding adults and 10 unpaired yearlings. In 1977–1978, the study flock consisted of five of the same pairs of breeding adults, the same 10 unpaired geese (now adults), and one additional unpaired adult male. None of the unpaired yearlings or adults had previous breeding experience, whereas all of the breeding adults had successfully bred in the past. In addition to the study animals, there were geese in the pen whose behavior was not recorded. In 1976–1977, these additional geese included three unpaired adult males and one unpaired adult female. In 1977–1978, they included one pair of breeding adults and one unpaired adult female.

We recorded only behaviors that were expressed completely, i.e., we did not include certain developmental or transitional behaviors in our analysis. For the purposes of analysis, we combined the various aggressive behaviors into one category (Aggressive Approach, Table 1). Similarly, we lumped retreat behaviors and sexual behaviors into single categories (Table 1). Components of the Triumph Ceremony (Table 1) of breeding geese were analyzed separately but, in nonbreeding geese, they occurred so infrequently that we combined them in the analysis.

The time when specific reproductive events occurred among individual pairs of geese differed by as much as three to four weeks within a breeding season. To facilitate comparison among breeding pairs, we therefore standardized the time when these events occurred with respect to the date when the first egg of each pair was laid. Using this as a reference point, the study season was divided into six periods:

A. The beginning of the study period in each year until three weeks before the first egg.

B. Three weeks before the first egg until the first egg was laid.

C. First egg to initiation of incubation.

D. The incubation period.

E. First two weeks posthatching.

F. Two weeks posthatching until the end of the study period in each year.

We used the average dates of the above events to separate data from nonbreeding geese into comparable periods.

We used Spearman's rank correlation (Siegel 1956) to test for statistically significant relationships between the frequencies of behaviors.

RESULTS

Families, pairs, and unpaired geese remained together as a gregarious flock during autumn and winter. Flock size varied from 22 to 37 individuals and most of this variation was due to the presence or absence of young of the previous or current year. Reproductively active birds began to defend territories, from which they also excluded their offspring, in late February or early March. We removed young of the previous year to a separate pen at that time, leaving the number of breeding adults, yearlings, or nonbreeding adults described above. Eggs were usually laid in mid-to-late March. Incubation averaged 27 days ($n = 9$) and within two or three weeks after hatching, families joined to form a flock.

BREEDING ADULTS

In 1977, six pairs attempted to breed and five pairs raised a total of 23 young; in 1978, four of five breeding pairs raised a total of 18 young.

Aggressive Approach and Retreat. The frequency of Aggressive Approach by breeding males increased before and during egg-laying (periods B and C) and remained high throughout incubation (period D, Table 2). By the time females began to lay eggs, territories were usually well established and breeding males seldom retreated from the aggressive behaviors of other geese. Seasonal changes in the Retreat behavior of breeding males and females were similar, but the frequency of Agressive Approach among females peaked sharply only during egg-laying. During periods D–F, the frequency of Aggressive Approach declined in males, rose in females, and when the goslings were more than two weeks old, the frequency of aggression by breeding females was closer to that of their mates than during any other period.

Triumph Ceremony. Cackling by breeding males and Facing-away by breeding females were similar in frequency (Table 3), i.e., paired

TABLE 1. Categories and descriptions of behaviors of the Canada Goose.

Category of behavior	Specific behaviors within category	Description of specific behaviors
Aggressive Approach[a]	Attack	Active movement toward receiver.
	Initiated-attack	Attack begun, but not carried through.
	Threat	Little or no active movement toward receiver.
	Threat-at	Aggressor distant to receiver; reaction of receiver usually mild.
Retreat	Flee	Active movement away from attacker.
	Low-intensity flee	"Casual" movement away from attacker.
	Avoid	Fleeing behavior or submissive posture[b] without any discernible act of aggression by the avoided individual.
Triumph Ceremony, male behaviors	Cackling	Neck outstretched, head low to the ground, usually oriented toward mate or family, often associated with a "snoring" vocalization; accompanied by Triumph Ceremony behavior(s) of mate or family (see below).
	Cackling-at	Same as Cackling, but mate or family do not respond with Triumph Ceremony behavior(s); e.g., female ignores or walks away from the male.
	Rolling[b]	Vigorous rotating and waving movements of the head, often associated with a honking vocalization.
Triumph Ceremony, female behaviors	Facing-away	Submissive posture in response to male's Cackling.
	Yipping[d]	Vocalization characterized by irregular staccato sounds of variable pitch; almost exclusively a vocalization of paired females in the presence of the mate.
Calling		Any sustained honking vocalization produced by either sex; distinguishable from Yipping in female geese by its comparatively monotonous, regular repetition of sounds.
Head-tossing		Vertical flicking of the head, a behavior communicating the intention to move to a new location.[e]
Sexual Behavior[d,f]		Precopulatory Head-dipping (repeated, stereotyped immersion of the head and neck into water), copulation, and postcopulatory display (breast, neck, and head tilted backwards, bill upturned).
Head-pumping[g]		Repeated lowering and raising of the head in a vertical plane.

[a] See Blurton Jones (1960), Klopman (1968), and Raveling (1970).
[b] See Raveling (1970).
[c] See Fischer (1965) and Radesäter (1974a).
[d] See Collias and Jahn (1959).
[e] See Raveling (1969a).
[f] See Klopman (1962).
[g] See Blurton Jones (1960) and Raveling (1970).

females usually responded to their mate's Cackling (Table 3). Females were less responsive to their mate's Cackling during periods D–F (Table 4). Triumph Ceremony behaviors were performed more commonly by both sexes of breeding adults during periods A–C of 1977–1978 than in 1976–1977 (Table 3).

Rolling was most common among breeding males during periods B–D (Table 3). Seasonal variations in frequency of Rolling and Cackling were significantly correlated ($r_s = 0.943$, $P < 0.01$) in 1977–1978, but not in 1976–1977 ($r_s = 0.771$). The proportion of Rolling to Cackling increased during the incubation period (period D) and remained high during brood rearing in 1977, but not in 1978 (Table 4). Seasonal changes in the frequency of Rolling and Aggressive Approach were also significantly correlated in both years (1976–1977: $r_s = 0.886$, $P < 0.05$; 1977–1978: $r_s = 1.000$, $P < 0.01$). In other words, the Rolling component of the Triumph Ceremony was associated with both pair-bond maintenance and aggression, but more predictably with aggression.

Seasonal variations in the frequency of Facing-away and Yipping of breeding females (Table 3) were significantly correlated, both in 1976–1977 ($r_s = 0.943$, $P < 0.01$) and 1977–1978 ($r_s = 1.000$, $P < 0.01$). This was not unexpected as we considered both these behaviors as integral components of the female's Triumph Ceremony. The frequency with which females performed the Triumph Ceremony was not significantly correlated with the frequency of either their own or their mates' Aggressive Approach in 1976–1977. However, in 1977–1978, Facing-away and Yipping were significantly correlated with their mate's aggressive behaviors ($r_s = 0.943$, $P < 0.01$), supporting the view that the female's Triumph Ceremony behaviors serve to redirect her mate's aggression (Raveling 1970).

Calling. Breeding males did most of the

TABLE 2. Seasonal variations in the frequency (acts/h) of Aggressive Approach and Retreat behaviors of Canada Geese. Values in the table are means ± SE.

Year and period	Aggressive Approach				Retreat			
	Breeding adults		Yearlings and nonbreeding adults		Breeding adults		Yearlings and nonbreeding adults	
	Males	Females	Males	Females	Males	Females	Males	Females
1976–1977[a]								
A	1.18 ± 0.32	0.18 ± 0.08	0.05 ± 0.01[b]	0.02 ± 0.01[b]	1.01 ± 0.44	0.71 ± 0.17	1.00 ± 0.15[b]	0.82 ± 0.09[b]
B	2.85 ± 0.55	0.24 ± 0.04	0.05 ± 0.01	0.04 ± 0.01	1.39 ± 0.39	1.30 ± 0.35	2.06 ± 0.18	2.10 ± 0.14
C	3.77 ± 0.71	1.26 ± 0.33	0.11 ± 0.07	0.00 ± 0.00	0.64 ± 0.21	0.84 ± 0.26	2.51 ± 0.24	2.73 ± 0.37
D	3.54 ± 0.31	0.49 ± 0.20	0.07 ± 0.05	0.03 ± 0.02	0.17 ± 0.07	0.09 ± 0.03	3.00 ± 0.21	2.90 ± 0.27
E	2.43 ± 0.36	0.80 ± 0.10	0.05 ± 0.03	0.06 ± 0.01	0.21 ± 0.14	0.29 ± 0.16	1.67 ± 0.10	2.07 ± 0.22
F	1.41 ± 0.20	0.91 ± 0.13	0.03 ± 0.02	0.02 ± 0.01	0.20 ± 0.08	0.22 ± 0.11	0.96 ± 0.18	1.09 ± 0.13
1977–1978[c]								
A	1.72 ± 0.40	0.11 ± 0.03	0.08 ± 0.04[d]	0.01 ± 0.01[d]	0.71 ± 0.25	0.63 ± 0.19	0.79 ± 0.09[d]	0.86 ± 0.13[d]
B	2.29 ± 0.41	0.18 ± 0.04	0.07 ± 0.04	<0.01	0.52 ± 0.22	0.52 ± 0.25	1.27 ± 0.11	1.27 ± 0.06
C	3.34 ± 0.44	1.01 ± 0.30	0.23 ± 0.12	0.03 ± 0.02	0.38 ± 0.21	0.40 ± 0.21	2.90 ± 0.25	3.19 ± 0.39
D	2.16 ± 0.28	0.22 ± 0.11	0.22 ± 0.14	0.13 ± 0.07	0.06 ± 0.02	0.03 ± 0.02	1.81 ± 0.16	2.15 ± 0.43
E	1.41 ± 0.33	0.66 ± 0.07	0.17 ± 0.09	0.06 ± 0.03	0.29 ± 0.23	0.28 ± 0.24	1.66 ± 0.23	1.56 ± 0.22
F	1.14 ± 0.29	0.87 ± 0.08	0.17 ± 0.13	0.02 ± 0.02	0.30 ± 0.11	0.42 ± 0.21	1.35 ± 0.07	1.20 ± 0.12

[a] Sample sizes are six of each sex for breeding adults and five of each sex for yearlings.
[b] Yearlings.
[c] Sample sizes are five of each sex for breeding adults and six male and five female nonbreeding adults.
[d] Nonbreeding adults; same geese that were yearlings in 1976–1977.

Calling (Table 5). Their Calling frequency was significantly correlated with Aggressive Approach in 1976–1977 ($r_s = 0.886$, $P < 0.05$), but not in 1977–1978 ($r_s = 0.771$). However, Calling was not significantly related to the Aggressive Approach of breeding females. Yipping was the predominant vocalization of breeding females during periods A and B (Table 4), but Calling increased during periods C and D and became the major vocalization during periods E and F. It declined rapidly after goslings were two weeks of age (period F).

Head-tossing. Head-tossing occurred most frequently in breeding males (Table 6), although it was rare among territorial geese during egg laying and incubation (periods C and D). Consequently, seasonal changes in its frequency did not correlate with changes in frequency of Aggressive Approach, Triumph Ceremony, or Calling.

Sexual Behavior. Breeding males occasionally exhibited Sexual Behavior during period A (0.04 acts/h during 1976–1977 and 0.01 acts/h during 1977–1978). However, breeding females rarely did so at this time (0.01 acts/h in 1976–1977 and none in 1977–1978). Such

TABLE 3. Seasonal variation in the frequency (acts/h) of Cackling (Ck), Cackling-at (Ck-at), Rolling (R), Facing-away (FA), and Yipping (Y) among breeding adult Canada Geese; and of Triumph Ceremony (TC) behaviors of yearling and nonbreeding adults. Values in the table are means ± SE. Sample sizes are as in Table 2.

Year and period	Breeding adult males			Breeding adult females		Yearlings and nonbreeding adults	
	Ck	Ck-at	R	FA	Y	Males TC	Females TC
1976–1977							
A	0.84 ± 0.16	0.02 ± 0.01	0.29 ± 0.09	0.71 ± 0.16	0.25 ± 0.07	<0.01[a]	0.00[a]
B	2.55 ± 0.49	0.27 ± 0.09	1.25 ± 0.35	2.46 ± 0.49	1.20 ± 0.33	0.09 ± 0.03	0.02 ± 0.02
C	2.91 ± 0.57	0.41 ± 0.22	1.36 ± 0.65	2.90 ± 0.59	0.98 ± 0.20	0.05 ± 0.03	0.01 ± 0.01
D	1.68 ± 0.32	0.77 ± 0.25	1.50 ± 0.58	1.52 ± 0.28	0.78 ± 0.28	0.06 ± 0.03	0.28 ± 0.18
E	0.56 ± 0.20	0.23 ± 0.04	0.53 ± 0.21	0.50 ± 0.18	0.14 ± 0.07	0.15 ± 0.06	0.57 ± 0.21
F	0.04 ± 0.02	0.05 ± 0.02	0.06 ± 0.03	0.04 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.04 ± 0.04
1977–1978							
A	1.68 ± 0.57	0.18 ± 0.08	0.93 ± 0.41	1.52 ± 0.49	0.67 ± 0.29	0.10 ± 0.05[b]	0.02 ± 0.01[b]
B	2.95 ± 0.77	0.53 ± 0.32	1.46 ± 0.71	2.71 ± 0.76	1.40 ± 0.55	0.29 ± 0.14	0.05 ± 0.04
C	3.85 ± 0.43	0.88 ± 0.47	1.54 ± 0.63	3.56 ± 0.41	1.91 ± 0.52	0.42 ± 0.18	0.09 ± 0.09
D	1.17 ± 0.14	0.72 ± 0.14	1.11 ± 0.43	0.94 ± 0.08	0.43 ± 0.09	0.38 ± 0.16	0.06 ± 0.06
E	0.30 ± 0.17	0.51 ± 0.16	0.15 ± 0.10	0.13 ± 0.08	0.02 ± 0.01	0.38 ± 0.16	0.08 ± 0.08
F	0.01 ± 0.01	0.01 ± 0.01	0.00	0.01 ± 0.01	0.00	0.00	0.00

[a] Yearlings.
[b] Nonbreeding adults; same geese that were yearlings in 1976–1977.

TABLE 4. Seasonal changes in the Cackling-at and Rolling behaviors of breeding male Canada Geese and Yipping behavior of breeding females, expressed in proportional terms. Values in the table are percentages.

Behavior	Year	Period					
		A	B	C	D	E	F
Cackling-at/(Cackling + Cackling-at)[a]	1976–1977	2.3	9.6	12.4	31.4	30.0	55.6
	1977–1978	9.7	15.2	18.6	38.1	63.0	50.0
Rolling/(Cackling + Cackling-at + Rolling)[a]	1976–1977	25.2	30.7	29.1	38.0	40.2	40.0
	1977–1978	33.3	29.6	24.6	37.0	15.6	
Yipping/(Yipping + Calling)[b]	1976–1977	86.2	87.6	57.3	56.1	46.7	20.0
	1977–1978	85.9	68.6	63.2	25.6	2.7	0.0

[a] Based on data in Table 3.
[b] Based on data in Tables 3 and 5.

behavior was most common among pairs during periods B and C (in 1977, frequencies during periods B and C were 0.16 and 0.14 acts/h for males, respectively, and 0.09 and 0.10 acts/h for females, respectively; in 1978, frequencies during these same time periods were 0.10 and 0.05 for males and 0.03 and 0.03 for females). We did not see any Sexual Behavior after incubation began.

Head-pumping. Head-pumping was expressed almost exclusively by parents with broods (periods E and F, a range of 0.36 to 0.82 acts/h) and was not correlated with other behaviors.

Rates of behaviors in relation to nesting events. The influence of Aggressive Approach and Triumph Ceremony behaviors on reproductive performance was best illustrated by observations of one low-ranking, reproductively experienced pair. The male was subordinate to all but one of the other breeding males prior to the incubation period and used the Aggressive Approach much less than average (Table 7). The female infrequently responded to her mate's Triumph Ceremony. In periods B and C, this male expressed Cackling-at three to seven times more often than the average of other breeding males (Table 7). In periods A and B, we did not see this pair show any interest in the nest site that they eventually used; not until the afternoon when the female laid her first egg did her mate begin to defend the surrounding territory. At this time (period C), the female's expression of Facing-away and Yipping and the male's expression of Aggressive Approach became dramatically more frequent, from well below average in periods A and B to well above average (Table 7). The male's low rank and his abrupt transition to successful defense of a territory paralleled the female's infrequent performance of Triumph Ceremony behaviors during the pre-nesting periods and sharply increased performance of such behaviors during the egg-laying period.

YEARLINGS AND NONBREEDING ADULTS

Because nonbreedings adults and yearlings remained unpaired throughout the study, we could not observe the nesting behavior of geese that lacked previous breeding experience. Be-

TABLE 5. Seasonal variation in the Calling behavior (calls/h) of Canada Geese. Values in the table are means ± SE. Sample sizes are as in Table 2.

Year and period	Breeding adults		Yearlings and nonbreeding adults	
	Males	Females	Males	Females
1976–1977				
A	0.51 ± 0.14	0.04 ± 0.02	0.01 ± 0.01[a]	0.02 ± 0.02[a]
B	1.32 ± 0.21	0.17 ± 0.04	0.04 ± 0.03	0.11 ± 0.08
C	2.07 ± 0.46	0.73 ± 0.15	0.06 ± 0.05	0.22 ± 0.09
D	2.41 ± 0.29	0.61 ± 0.14	0.11 ± 0.04	0.22 ± 0.09
E	0.71 ± 0.22	0.16 ± 0.09	0.43 ± 0.14	0.38 ± 0.08
F	0.11 ± 0.05	0.04 ± 0.02	0.46 ± 0.21	0.36 ± 0.11
1977–1978				
A	0.84 ± 0.25	0.11 ± 0.06	0.06 ± 0.03[b]	0.19 ± 0.20[b]
B	1.63 ± 0.61	0.64 ± 0.37	0.27 ± 0.13	0.30 ± 0.24
C	2.33 ± 0.83	1.11 ± 0.50	0.37 ± 0.18	0.46 ± 0.33
D	2.33 ± 0.35	1.25 ± 0.17	0.69 ± 0.22	0.72 ± 0.34
E	0.89 ± 0.21	0.72 ± 0.37	0.42 ± 0.14	0.49 ± 0.21
F	0.05 ± 0.03	0.05 ± 0.03	0.40 ± 0.23	0.16 ± 0.13

[a] Yearlings.
[b] Nonbreeding adults; same geese that were yearlings in 1976–1977.

TABLE 6. Seasonal variation in the Head-tossing behavior (acts/h) of Canada Geese. Values in the Table are means ± SE. Sample sizes are as in Table 2.

Year and period	Breeding adults		Yearlings and nonbreeding adults	
	Males	Females	Males	Females
1976–1977				
A	0.65 ± 0.17	0.05 ± 0.04	<0.01[a]	<0.01[a]
B	0.99 ± 0.17	0.02 ± 0.01	0.06 ± 0.03	0.02 ± 0.01
C	0.62 ± 0.18	0.00	0.08 ± 0.06	0.01 ± 0.01
D	0.02 ± 0.01	0.00	0.20 ± 0.09	0.04 ± 0.02
E	0.88 ± 0.24	0.37 ± 0.08	0.53 ± 0.32	0.11 ± 0.07
F	0.71 ± 0.22	0.37 ± 0.10	0.77 ± 0.35	0.62 ± 0.27
1977–1978				
A	0.41 ± 0.09	0.05 ± 0.04	0.12 ± 0.05[b]	0.17 ± 0.09[b]
B	0.16 ± 0.06	0.21 ± 0.17	0.08 ± 0.04	0.08 ± 0.05
C	0.02 ± 0.01	0.00	0.07 ± 0.04	0.05 ± 0.02
D	0.00	0.00	0.38 ± 0.18	0.20 ± 0.07
E	0.46 ± 0.04	0.19 ± 0.04	0.18 ± 0.08	0.02 ± 0.02
F	0.64 ± 0.19	0.38 ± 0.07	0.44 ± 0.25	0.36 ± 0.19

[a] Yearlings.
[b] Nonbreeding adults; same geese that were yearlings in 1976–1977.

haviors that we recorded occurred less frequently than in breeding adults, except Retreat (Table 2); and in periods E and F, Calling (Table 5) and Head-tossing (Table 6).

Yearling males and females exhibited Aggressive Approach, Retreat (Table 2), and Calling (Table 5) at similar frequencies. However, yearling females performed the Triumph Ceremony more often than did yearling males during periods D and E (Table 3), whereas yearling males did more Head-tossing (Table 6) in periods D and E than females. Head-tossing and Calling were significantly correlated in both yearling males ($r_s = 1.000$, $P < 0.01$) and yearling females ($r_s = 0.886$, $P < 0.05$). We did not see Sexual Behavior by yearling males but yearling females occasionally behaved sexually during periods B through E (0.01 to 0.04 acts/h).

Nonbreeding adult males exhibited Aggressive Approach slightly more often than did nonbreeding adult females, but their rates of Retreat were similar (Table 2). Triumph Ceremony behaviors were more frequently expressed by nonbreeding adult males than females (Table 3), but there was little sexual difference in Calling (Table 5) and Head-tossing (Table 6). Unlike the situation for yearlings, seasonal changes in Head-tossing and Calling were not significantly correlated among nonbreeding adult males ($r_s = 0.600$) or females ($r_s = -0.429$). Nonbreeding adult males rarely behaved sexually (<0.01 to 0.01 acts/h) during periods C–E, while we saw no such behavior among nonbreeding adult females. In summary, the behaviors of nonbreeding geese differed little between sexes and were expressed less often than by breeding birds.

DISCUSSION

COMPARISON OF CAPTIVE FLOCK WITH WILD POPULATION

Naylor (1953) studied *B. c. moffitti* at Honey Lake, Lassen Co., California, which is approximately 72 km east of the site where our breeding stock was collected. The elevations differ by less than 150 m. Periods of egg-laying, incubation, and hatch in our study were within the dates reported by Naylor, indicating that the conditions of captivity did not affect nesting phenology.

Wood (1964) found that crowding may inhibit reproduction in captive Canada Geese,

TABLE 7. Frequencies (acts/h) of Aggressive Approach and Triumph Ceremony behaviors of one pair of Canada Geese compared to the average frequencies with which all other breeding pairs ($n = 5$) expressed these behaviors in 1976–1977.

Period	Aggressive Approach		Cackling-at		Facing-away		Yipping	
	Male of the pair	Other breeding males	Male of the pair	Other breeding males	Female of the pair	Other breeding females	Female of the pair	Other breeding females
A	0.57	1.30	0.01	0.02	0.36	0.78	0.11	0.27
B	1.06	3.20	0.60	0.20	0.63	2.83	0.32	1.38
C	5.37	3.44	1.49	0.19	3.80	2.72	1.36	0.91

especially if the flock members differ greatly in social status. Craighead and Stockstad (1964) concluded that a much higher proportion of wild Canada Geese breed at the age of two and three years than is the case for captive geese. This may explain why none of our two- and three-year-old geese reproduced, since density was high and established breeding pairs were present year-round. However, the conditions of captivity did not necessarily depart greatly from conditions that the birds would experience in the wild. Both Naylor (1953) and Miller and Collins (1953) concluded that the principal reason for nest failure of Canada Geese in northeastern California was desertion due to over-crowding in preferred nesting areas.

Nonetheless, the conditions of captivity did cause artifacts. Since our geese were unable to fly, their decreased mobility may have resulted in fewer high intensity attacks and more low intensity aggression (threats). This did not appear to affect the spacing of nests, however, because two years before the present study (spring 1975), seven pairs of breeding adults capable of flight occupied territories that were similar in size to the six territories occupied in the 1976–1977 season.

The continual presence of subordinate geese near the dominant birds also probably affected our results. Outcomes of aggressive interactions at times when the geese were not territorial were more predictable than probably would have been the case if the geese were not familiar with each other. During the territorial phase of the annual cycle, the outcomes of aggressive interactions between breeding geese were less consistent, but the low status of nonbreeding birds was even more pronounced.

AGGRESSION, TRIUMPH CEREMONY, AND CALLING BY BREEDING MALES

The expression of Aggressive Approach and Triumph Ceremony behaviors was clearly temporally associated with reproduction because these behaviors were most common when the geese were territorial (periods B–D; Tables 2 and 3). The importance of this temporal association was further illustrated by the abrupt transition to territorial defense by the low-ranking gander of one pair (Table 7).

Fischer (1965) and Raveling (1970) found that the Rolling component of the Triumph Ceremony is often displayed in conflict situations and may serve as the highest intensity threat. Radesäter (1974a) also suggested that aggression and Rolling share a common motivational basis. Our results support these observations: seasonal changes in the frequency of Rolling (Table 3) correlated with the Cackling of breeding males (Table 3), but especially with Aggressive Approach (Table 2). Cackling was most often directed to the mate or family and may maintain or strengthen family ties. Wild Canada Geese generally call less during the incubation period (Raveling and Lumsden 1977); persistent calling among our breeding geese was probably due to the comparatively high density of nesting pairs in the enclosure. It appeared to function primarily as an assertive display and therefore to be seasonally associated with reproduction because seasonal changes in the incidence of Calling (Table 5) and Aggressive Approach (Table 2) were similar in both years of the study and significantly correlated in 1976–1977. We expected this because the raucous vocalizations that are an integral part of the Rolling component of the male's Triumph Ceremony were included in the Calling category.

AGGRESSION, TRIUMPH CEREMONY, AND CALLING BY BREEDING FEMALES

Breeding females performed the Aggressive Approach most commonly during the egg-laying period (Table 2), supporting Kossack's (1950) observation that females participate in territorial defense during the early stages of its establishment.

Raveling (1970) concluded that a female's response to the Triumph Ceremony of her mate serves to inhibit and redirect his aggression. Facing-away, which is an appeasement behavior, develops in the Cackling ceremonies of goslings during the first few days of life (Radesäter 1974b), but it was infrequently expressed by unpaired females in the present study. Yipping was the characteristic response of females to high-intensity Triumph Ceremonies expressed by their mates. This, together with the finding that the incidence of Facing-away and Yipping (Table 3) were significantly correlated among paired females, suggests that their supportive responses to the male's aggressive and Triumph Ceremony displays were essential for maintaining or strengthening pair bonds and reproductive success. The sudden increase in Facing-away and Yipping by the female of one pair at the time of egg-laying (Table 7) further indicates the probable importance of mutual pair behaviors in relation to nesting events.

Calling activity of breeding females (Table 5) was not correlated with Aggressive Approach (Table 2) and it became more common than Yipping as the breeding season progressed (Table 4). Therefore, we suggest that Calling was not an important component of the female's breeding behavior.

HEAD-TOSSING

Raveling (1969a) concluded that Head-tossing was primarily a preflight behavior, although at low intensities Rolling is sometimes indistinguishable from it. We rarely observed Head-tossing unless a bird was about to move to a new location. Motions that were similar to Head-tossing also occurred during conflict encounters, but were not usually sustained.

HEAD-PUMPING

Blurton Jones (1960) and Raveling (1970) concluded that Head-pumping was the outcome of balanced conflicting tendencies to attack and flee. We rarely observed this behavior in individuals other than parents with goslings. It was probably not seen at other times of the year because the dominance rank order of the geese in our flock was well established. The reluctance of pairs with newly hatched goslings to flee when threatened by a dominant individual resulted in the expression of ambivalent behaviors such as Head-pumping.

NONBREEDING YEARLINGS AND ADULTS

Aggressive Approach (Table 2) and Triumph Ceremony (Table 3) were less commonly expressed by nonbreeding geese than breeding geese, suggesting that the ability to perform these behaviors was closely associated with the recruitment of a bird into the breeding population. With few exceptions, behaviors differed little in frequency between sexes of nonbreeding geese.

Yearling females performed the Triumph Ceremony (periods D and E; Table 3) more than did yearling males, and exhibited some Sexual Behavior, whereas yearling males did not. During the following year, when these individuals were adults, the opposite was true: nonbreeding adult males expressed Aggressive Approach and Triumph Ceremony more frequently; and Sexual Behavior was recorded among males but not females. This apparent reversal was probably related to differences in flock composition between the breeding seasons. In 1976–1977, yearling females responded to the Triumph Ceremony and Sexual Behavior of three unpaired adult males, one of whom had bred previously and another which had been previously paired. However, no experienced, unpaired adult males were present during most of the 1977–1978 season. The Triumph Ceremonies and Sexual Behavior expressed by nonbreeding adult males in 1977–1978 were directed at females of their own age class, but the latter rarely responded to them.

Rates of Calling by yearlings, in contrast to breeding geese, increased during periods E and F and correlated significantly with Head-tossing. Both activities were also common among nonbreeding adults late in the study season. These behaviors appeared to be associated with avoidance reactions to newly mobile families.

In summary, the behavioral patterns of yearlings and adults with no reproductive experience were clearly different from those of breeding adults. Aggression and Triumph Ceremony behaviors were uncommon, Retreats were frequent, and these differences appeared to be intimately related to the lack of reproductive success.

BEHAVIORS IN RELATION TO REPRODUCTIVE HABITS

Orians (1969) proposed that monogamous mating systems will maximize reproductive fitness when the contributions of both parents are essential during incubation and/or brood rearing. Incubation in Canada Geese is performed exclusively by the female, which allows the gander to devote his time to defense of the territory. The division of labor (and the need to synchronize roles) early in the breeding season is further reflected by seasonal changes in the frequency of behaviors expressed by pair members. Before incubation, females were much less aggressive than males (Table 2) and were highly responsive to their mate's Triumph Ceremony (Table 3). After the young hatched, ganders performed fewer Aggressive Approaches, but their mates exhibited this behavior more frequently (at nearly the frequency of the males; Table 2). Supportive responses to the male's Cackling also decreased sharply (Table 3). Thus, by the time the family became mobile, sexual differences in roles were much less pronounced. Parents began to molt within three to four weeks after families became mobile and these behavioral changes were consistent with what we believe is an increased advantage of social gregariousness during this time of the year.

Families of Canada Geese remain intact all winter (Raveling 1969b). Family members are socially dominant to pairs and single geese and enjoy the advantages of relative freedom from harassment and access to limited food or space (Hanson 1953, Raveling 1970). Individuals are highly traditional in returning to their winter quarters (Raveling 1979), and inexperienced family members may improve their chances of surviving to breeding age by following their parents to safe or preferred roosting and feeding areas. Nonbreeding adults in our study frequently retreated from aggressive family members and failed to express behaviors closely associated with nesting success

(Aggressive Approach and Triumph Ceremony) in the presence of established breeding pairs. This observation suggests the possibility that within wild populations, the proportion of physiologically capable, but reproductively inactive, individuals may vary annually with the population structure in relation to the availability of food and space.

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