Wilson Bull., 93(3), 1981, pp. 310–324

HYPERPHAGIA AND SOCIAL BEHAVIOR OF CANADA GEESE PRIOR TO SPRING MIGRATION

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Several papers have emphasized the evolutionary and functional significance of spring accumulated body reserves for reproduction by geese (Barry 1962; Hanson 1962; Ryder 1970; Ankney 1977; Raveling and Lumsden 1977; Ankney and MacInnes 1978; Raveling 1978a, 1979a, b; McLandress and Raveling 1981). Numerous studies have contributed information on behavior of Canada Geese (*Branta canadensis*) (see Johnsgard 1975 and Bellrose 1976 for reviews). However, no study of wild geese has described or quantified the hyperphagia presumably associated with their increase in body weight in spring. The objective of our study was to document behavior of Giant Canada Geese (*B. c. maxima*) prior to their arrival on their nesting grounds. Emphasis was placed on behavior related to accumulation and use of energy reserves to enhance our knowledge of the evolution and proximate control of avian reproductive and social organization systems.

METHODS

We studied Giant Canada Geese wintering at Silver Lake, in the city of Rochester, Minnesota (43°55′N, 92°30′W). These birds nest between Lake Winnipeg and Lake Manitoba-Winnipegosis, in Canada, 885 km northwest of Rochester (see Hanson 1965, Gulden and Johnson 1968, Raveling 1978b). Refuges at both wintering and nesting areas of these birds and the urban environment of Rochester provided a unique situation for close observation of wild geese which were habituated to human activity. Data were collected within a 30 km radius of Rochester from 3 February–6 April 1974. The last major migration occurred on the latter date. Measurements of temperature, wind and snow cover were obtained from the U.S. Dept. of Commerce, Weather Bureau, Rochester, Minnesota.

On a daily basis, time that geese spent in feeding areas and on lake roosting areas was determined for the flock as a whole. Major flights of geese to and from these areas were visible from almost anywhere in the study area and indicated transition between feeding and roosting periods. Daily feeding regimes, defined as the duration of time spent away from lake roosting areas by at least half of the population, were categorized as follows: (A) more than half the flock did not leave lake roosting areas or left for less than 1.5 h; (B) geese were in feeding areas from 1.5–4.5 h without returning to water roost areas; (C) geese remained away from lake roosting areas from 4.5–7.5 h (usually, there were distinct morning and evening feeding periods, but one long period was normal on overcast days); (D) geese were in feeding areas from 7.5–10.5 h during the day, typically in one continuous period; and (E) geese spent more than 10.5 h in feeding areas because at least half the flock did not return to lake roosting areas for at least part of the night.

Over 200 individually identifiable neck-banded adult geese were available for observation (see Raveling 1978b). Numbers of geese in feeding areas were estimated when possible and all marked birds observed were recorded. The proportion of time spent in these fields actually

devoted to feeding by marked individuals (and their mates, when present) was recorded for sample periods of approximately 10 min (timed by stopwatch).

Family status of geese was determined from behavioral associations (see Raveling 1969), especially the triumph ceremony. This display involves extensive head and neck movements with associated vocalizations and is usually exhibited only by mated pairs of adults and among members of a family (see Fischer 1965, Raveling 1970). The occurrence of triumph ceremonies and aggressive interactions involving physical contact between individuals were recorded for timed periods averaging 30 min.

The number of sexual displays was recorded when a majority of the goose population was at Silver Lake. Approximately 1000 birds were observed when sexual displays were being recorded so as to have reasonably comparable samples from which to compare rates of sexual behaviors. Sexual behavior noted included copulation and the pre-copulatory neck-dipping display (Klopman 1962). Sperm transfer could not be determined but copulation was considered unsuccessful only when the post-copulatory display (Klopman 1962) was not exhibited by either sex following coition. Size and behavior of unmarked geese was used to identify sex of the individual initiating neck-dipping and terminating incomplete sexual displays when possible.

Proportions of timed sample periods spent feeding by individuals and frequencies of triumph ceremonies and aggressive interactions, measured as the number of displays or contacts per unit time per bird, were ranked and analysed with Mann-Whitney *U*-tests (Sokal and Rohlf 1973:218). Changes in intensity of triumph ceremonies and aggressive interactions, which were categorized according to vigor and duration of displays (see description in Results), were compared with Chi-square tests (Sokal and Rohlf 1973:300). Significance of the regression of changes in frequency of sexual behavior over time was also tested (Sokal and Rohlf 1973:248).

RESULTS

Changes in food habits and body composition determined from geese collected during this study are reported elsewhere (McLandress and Raveling 1981). In summary, the results were: (1) body weight of adult female and male geese increased 36% and 26%, respectively, above average winter (February) weights; (2) adult geese without mates weighed less before the weight gain period and gained less weight than paired geese; (3) geese shifted from a winter diet of corn (*Zea mays*) to a diversity of food items in spring dominated by bluegrass (*Poa pratensis*); and (4) bluegrass was rich in protein (>26%), which is a requirement that may limit clutch-size in Canada Geese (Raveling 1979a).

Feeding behavior.—Ambient temperatures ranged from −28 to 16°C. Under the coldest conditions geese remained at Silver Lake with bills tucked under their scapular feathers. As temperature increased, geese spent more time in feeding areas (Table 1: $r = 0.87$, $P < 0.001$). This resulted in geese feeding 7.5 h or longer (category D or E), for 25 of 34 days (74%) for which feeding regime data were obtained from 1 March to the 6 April mass migration. Only 5 extended feeding regimes (22%) were recorded for 23 days of data between 3 and 28 February. Geese fed during the night (category E) only when temperatures remained above or near 0°C between

TABLE 1

DAILY FEEDING PATTERN OF GIANT CANADA GEESE UNDER DIFFERENT TEMPERATURES PRIOR TO SPRING MIGRATION (3 FEBRUARY–6 APRIL 1974)[a]

Feeding regime[b]	Max. / Min.	Daily temperature ranges (°C)					
		<−10° / <−10°	−10°–−5° / <−10°	>−5° / <−10°	>−5° / −10°–−5°	>−5° / −5°–0°	>0° / >0°
A (0–1.5 h)		2[c]	1				
B (1.5–4.5 h)			7	2			
C (4.5–7.5 h)			2	7	5	1	
D (7.5–10.5 h)				1	7	15	3
E (>10.5 h)						1	3
Total days		2	10	10	12	17	6

[a] No data for 6 days within this period.
[b] See text.
[c] Actual daylight maximum temperatures for these days were −16°C and −13°C.

2 and 6 March. These warm nights, although partially overcast, coincided with a full moon. Patterns of decreased feeding (category B or C) returned 17–24 March when minimum temperatures were less than −5°C and maximums were seldom above 0°C.

Changes in feeding location corresponded with decreasing snow depth in February (Table 2). Geese fed rarely in grass fields and frequently in creeks and ponds when recorded snow depth was greater than 20 cm. Geese were more dispersed when at creeks and ponds than when in cornfields. Thawing occurred first around the bases of trees and where clumps of vegetation extended through the snow. These snow-free patches exposed grass when recorded snow depth fell below 20 cm. Geese fed at these patches as soon as they appeared. Snow was 18 cm deep on 1 March and all but gone by 6 March. Snow fell on 6 days after 11 March but accumulation did not exceed 8 cm for the remainder of the study.

Corn remained an important food item throughout the study. Waste corn, frozen in top soil, became available to geese as the soil thawed (9–16 March). More geese in feeding areas were observed in cornfields in this week than during any other time period when snow depth was less than 20 cm. Proportions of feeding geese that used pastures increased after 25 March and peaked just before the 6 April migration. Generally, geese fed in cornfields and pastures bordering creeks and rivers flowing into Silver Lake.

The average size of the Giant Canada Goose population during our study was 12,000–15,000 birds. Thirty-one flocks of geese feeding in cornfields of approximately 65 ha (160 acres) averaged 1996 ± 311 birds during February. Flock size in cornfields in early March (869 ± 111 birds, N = 123

TABLE 2
FEEDING LOCATIONS OF GIANT CANADA GEESE PRIOR TO SPRING MIGRATION, 1974

Date	Total geese observed[a]	% of geese in:		
		Corn	Grass	Creeks and ponds
Snow depth >20 cm:				
3–28 February	30,290	86	1	13
Snow depth <20 cm:				
3–28 February	36,197	63	36	1
1–8 March	44,870	62	31	6
9–16 March	40,580	86	11	3
17–24 March	46,620	71	24	5
25 March–1 April	72,063	47	51	2
2–6 April	16,842	38	62	0

[a] Summation of all geese in feeding flocks estimated to size; most flocks were repeatedly observed over the time period—see text for average flock size.

flocks) was significantly smaller ($t = 4.16$, $P < 0.001$) and it diminished still further ($t = 4.52$, $P < 0.001$) to 339 ± 35 geese (N = 122 flocks) in the 2 weeks prior to the 6 April migration. Decreasing flock size was related to an increase of distance between individuals. No significant change was detected in flock size of grass feeding geese among comparable time periods. Geese feeding in 65 ha (160 acres) pastures averaged 360 ± 42 geese (N = 183 flocks).

Proportions of marked geese of known social status feeding in grass changed markedly ($\chi^2 = 8.89$, df = 2, $P < 0.002$) during spring (Table 3). The percentage of marked birds that were paired declined slightly as spring progressed, although the actual number of paired geese showed little change. In contrast, the number of marked geese never observed with a mate doubled between each observation period from early to late

TABLE 3
PROPORTIONS OF INDIVIDUALLY MARKED ADULT GIANT CANADA GEESE OF DIFFERENT SOCIAL STATUS OBSERVED IN GRASS FIELDS DURING SPRING 1974

Date	N	Status		
		Paired	Unpaired	Undetermined
18 February–9 March	56	44 (79%)	5 (9%)	7 (13%)
9–24 March	69	53 (77%)	10 (15%)	6 (9%)
24 March–6 April	79	49 (62%)	22 (28%)	8 (10%)

TABLE 4

PROPORTION OF TIME ACTUALLY DEVOTED TO FEEDING BY GIANT CANADA GEESE OF DIFFERENT SEX AND SOCIAL STATUS DURING SPRING (3 FEBRUARY–6 APRIL 1974)

Sex and social status of geese	Feeding site			
	N[a]	Cornfield	N[a]	Grass field
Males				
In pairs	31	38%[b] 26–53[c]	20	51% 45–77
Others	55	38% 32–52	30	64% 37–81
Females				
In pairs	32	52% 39–62	22	65% 54–79
Others	51	24% 17–33	37	52% 36–79

[a] Number of approximate 10 min sample periods in which a marked individual's proportion of time spent feeding was recorded.
[b] Median.
[c] Confidence limits (cf. Snedecor and Cochran 1967:124).

spring. Accurate determinations of social status of geese in cornfields were difficult in February and early March due to large flock sizes.

While in grass fields, paired geese spent higher proportions of their time actually feeding than when they were in cornfields (Table 4: $t_s = 1.66$ males and 1.83 females, $P < 0.05$). Similarly, "other" females (referring to individuals without identifiable mates in the vicinity) spent a higher proportion of time feeding while in pasture than in cornfields ($t_s = 3.60$, $P < 0.001$). "Other" males showed a tendency toward the same feeding pattern ($t_s = 1.59$, $P < 0.1$). Paired females tended to feed for a greater proportion of time than paired males when in either cornfields ($t_s = 1.50$, $P < 0.1$) or grass fields ($t_s = 1.49$, $P < 0.1$). Also, when both members of a pair were observed simultaneously, females spent more time feeding than males on 73% of observations (N = 63). Proportions of time spent feeding by "other" and paired males were similar but "other" females spent less time feeding when in cornfields than either paired females ($t_s = 3.60$, $P < 0.001$) or "other" males ($t_s = 2.85$, $P < 0.005$).

Social behavior.—No significant differences were detected among frequencies of triumph ceremonies determined from observations at Silver Lake, either among periods of time during the day (i.e., morning—07:00–10:00, mid-day—10:00–15:00 and evening—15:00–19:00) or between February and March. A significantly higher frequency ($t_s = 3.45$, $P < 0.001$)

TABLE 5

FREQUENCY AND INTENSITY DIFFERENCES OF TRIUMPH CEREMONY DISPLAYS AND AGGRESSIVE INTERACTIONS OF GIANT CANADA GEESE AT AND AWAY FROM SILVER LAKE DURING SPRING 1974

	Silver Lake		Other areas	
	3–28 Feb.	1 Mar.–6 Apr.	3–28 Feb.	1 Mar.–6 Apr.
	Triumph ceremonies (T.C.)			
Frequency[a]				
Median (N)[b]	2.6 (26)	5.4 (6)	12.0 (5)	20.0 (2)
95% C.L.	1.9–4.8	1.3–7.5	3.3–38.0	13.3–26.7
Intensity				
T.C.'s categorized	199.0	60	37	24
Reduced (%)	19.1	42	3[b]	17[b]
Normal (%)	63.3	42	32	46
Exaggerated (%)	17.6	17	65	38
	Aggressive interactions (A.I.)			
Frequency[a,d]				
Median (N)	0.5 (6)	5.3 (3)	8.2 (4)	24.4 (2)
95% C.L.	0.0–2.7	1.3–6.7	8.0–12.0	10.7–38.1
Intensity				
A.I.'s categorized	114.0	35	31	28
Pecking (%)	36.8	69	29	36
Chasing (%)	49.1	23	61	54
Fighting (%)	14.0	9	10[b]	11[b]

[a] Displays/1000 birds/min.
[b] N = number of observation periods (ca. 30 min each).
[c] Combined with closest category for χ^2 test due to infrequent occurrence.
[d] Mid-day (10:00–15:00) observations only.

of displays was recorded for observations in areas other than Silver Lake compared to Silver Lake in March (Table 5).

Triumph ceremony intensity was classified "normal" when the components (see Raveling 1970), rolling (neck extended upward and forward) and cackling (neck extended downward and forward), were displayed with about equal frequency. Intensity was considered "reduced" when: wing-flicking (shown to some extent during "normal" displays) was not exhibited by either adult; cackling exceeded rolling; head and neck waving during the rolling component were more restricted; and vocalizations were less raucous and prolonged than in "normal" triumph displays. "Exaggerated" displays involved vigorous rolling by males and extended raucous vocalizations. The criterion for classification in this category was that contact was made between adults. Typically, adult males used their bills to grasp

the female's neck near the back of her head or base of the black neck stocking. Occasionally, females grasped the breast feathers of males.

There was a significant change in proportions of triumph ceremony displays of different intensity exhibited at Silver Lake (Table 5: $\chi^2 = 13.38$, df = 2, $P < 0.005$) and at areas other than Silver Lake ($\chi^2 = 4.39$, df = 1, $P < 0.05$) between February and March. "Reduced" intensity displays increased at all areas. Little change occurred in the proportion of "exaggerated" intensity displays at Silver Lake but these were greatly reduced at other areas. The percentage of "normal" displays was less in March than in February at Silver Lake.

Proportions of triumph ceremonies of different intensity at areas other than Silver Lake differed significantly from displays at Silver Lake in February ($\chi^2 = 38.06$, df = 2, $P < 0.001$) and in March ($\chi^2 = 6.46$, df = 2, $P < 0.05$). At areas other than Silver Lake, highly vigorous displays were much more common (or "reduced" intensity triumph ceremonies were much less common) than at Silver Lake.

Triumph ceremonies were most commonly associated with aggressive conflicts among geese (76% of 191 displays for which circumstances were recorded). Pairs often displayed prior to conflict and immediately following retreat of an opponent. The intensity of display increased with the duration of aggressive interaction and the degree of physical conflict. Most triumph ceremonies associated with aggressive conflicts (N = 145) were classified as either "normal" (47%) or "exaggerated" (33%) in intensity. Aggressive interactions were involved in 48 (94%) of the 51 most intense triumph ceremonies.

If mated pairs were spatially separated for any reason, triumph ceremony occurred when they were reunited. In March, triumph ceremony was occasionally (9 times) observed when 1 member of a pair involved had just awakened (separation in a temporal sense). Triumph ceremonies following either type of separation comprised 24% of the 191 displays. Proportionately fewer high intensity displays and more low intensity displays were noted for triumph ceremonies following separation of mates ("exaggerated" = 7%, "normal" = 50%, "reduced" = 43%, N = 46) than for triumph ceremonies related to aggression ($\chi^2 = 16.82$, df = 2, $P < 0.001$). The proportion of "reduced" intensity displays was highest for triumph ceremonies related to reunion of mates after awakening (7 of 9, 78%).

Only frequencies of aggressive interactions obtained from observations at mid-day (10:00–15:00) are presented (Table 5) because significant differences were found among different time periods of the day and too few observations were taken during other time periods for further comparisons. A difference in frequency of interactions was detected for these mid-

day observations between February and March at Silver Lake ($U_s = 17$, $P < 0.025$). In addition, geese at locations away from Silver Lake were involved in higher frequencies of aggressive encounters than geese at Silver Lake ($U_s = 54$, $P < 0.001$).

A total of 208 aggressive interactions between geese were classified according to degree of physical exertion (Table 5). "Pecking" involved 1 goose striking another with its bill, followed by a short retreat or immediate submission by the loser. "Chasing" was characterized by the victorious goose chasing the loser with no fighting involved. "Fighting" referred to encounters in which 2 geese grasped each other at the base of the neck with their bills and hit each other with their wings. Proportions of aggressive encounters of different physical involvement observed at Silver Lake in March changed significantly from proportions recorded for geese in February aggressive encounters ($\chi^2 = 11.01$, df = 2, $P < 0.005$). The proportion of aggressive encounters which involved "pecking" doubled from February–March and because the frequency of conflicts was greater, the absolute amount of "chasing" and "fighting" may have increased as well. These differences between months were not evident at areas other than Silver Lake. There was a significant difference in the proportion of interactions of different exertion between geese at and away from Silver Lake in March ($\chi^2 = 6.76$, df = 1, $P < 0.01$), but not in February.

Sexual behavior.—Copulation attempts by geese were observed 69 times during spring although 6 (9%) were considered incomplete due to lack of the post-copulatory display. In addition, the pre-copulatory display, neck-dipping, was not followed by coition on 67 occasions. The frequency of all sexual behaviors (which included successful copulation, neck-dipping not followed by coition and unsuccessful copulation) increased exponentially from 3 February–6 April (Fig. 1: $Y = 0.05e^{0.60X}$, $t_s = 5.72$, $P < 0.001$). Although the highest rate of sexual displays was recorded in the first week of April, only 8% (1 of 13) of sexual interactions resulted in successful coition compared to 53.6% (60 of 112) for March sexual displays ($\chi^2 = 9.81$, df = 1, $P < 0.005$). The frequency of successful copulations was highest in the last week of March.

Males initiated neck-dipping on 19 of 27 (70%) occasions when sexes of both members of the pair were identified—a significantly higher proportion than an expected equal contribution by each sex ($\chi^2 = 4.48$, df = 1, $P < 0.05$). The copulatory behavior sequence was terminated by the female before coition on 14 of 20 (70%) observations when sex of the birds could be determined, which tended to be a higher rate than would be expected from equal contribution by either sex ($\chi^2 = 3.20$, df = 1, $P < 0.10$). Similar findings were reported by Klopman (1962).

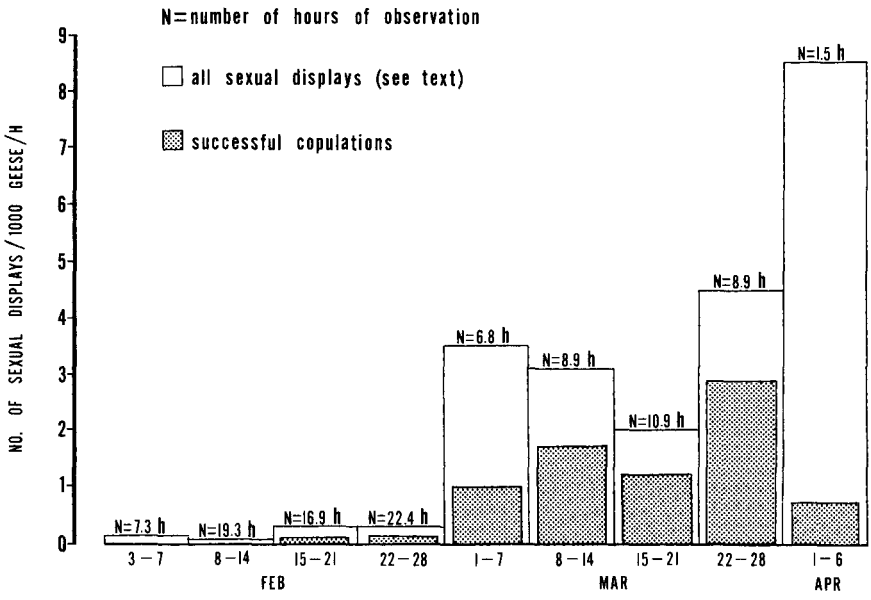

FIG. 1. Frequency of displays of the copulatory sequence of Giant Canada Geese during spring 1974.

DISCUSSION

Environmental factors affecting food consumption.—Daily ambient temperature range appeared to influence the amount of time spent in feeding areas by Giant Canada Geese during spring. Raveling et al. (1972) reported that cold had little influence on the length of the feeding period of Todd's Canada Geese (*B. c. interior*) in southern Illinois and concluded that cloudy conditions caused them to spend more time in feeding areas in winter. In this study, temperature seemed to be the most important influence on daily duration of feeding by geese. Cloud cover was, however, related to patterns of feeding. Geese usually had distinct morning and evening feeding periods on clear days, whereas, on cloudy days of similar temperature ranges they typically had single feeding periods of prolonged duration, but total time per day spent in feeding areas was unchanged.

Higher temperatures melted snow and thawed soil enabling geese to use previously inaccessible food resources. These conditions corresponded with geese spending all day and some nights in feeding areas. In contrast to the results of this study, *B. c. interior* held in captivity and supplied food ad libitum, increased energy intake with decreasing ambient temperature regardless of photoperiod (Williams 1965). However, Raveling et al. (1972) reported that temperatures at or below −9°C (15°F) caused wild

B. c. interior to cease activity. Similarly, in this study, on 2 days when temperature remained below −13°C (9°F), geese stayed at Silver Lake. LeFebvre and Raveling (1967) predicted that immature female Giant Canada Geese could not sustain the energetic demand caused by prolonged heat loss at temperatures less than −15°C (5°F). Raveling et al. (1972) suggested that inactivity which reduces energy loss is the most adaptive response of geese to extreme cold. Thus, the behavioral response of Canada Geese to changing energetic demands is flexible and can be altered by increased food availability. After appropriate photo-stimulation (see reviews by Lofts and Murton 1968, 1973; Farner and Lewis 1971; Lofts 1975), the expression of hyperphagia by geese may be regulated by temperature and food availability in spring. Such control would maximize positive energy balance during the fattening period.

The insulating effect and translucent quality of snow may provide sufficient warmth and light for survival and early germination of grasses in years of ample snow cover (see Tieszen 1972). During the spring of 1974, geese were able to obtain protein-rich green grass (McLandress and Raveling 1981) from beneath melting snow 11 days prior to the major thaw in early March. Winters with little precipitation or frequent thawing of snow cover could result in decreased survival of subnivean grass and delay in the emergence of new grasses. Conversely, mild spring weather might allow geese earlier access to grasses.

Social factors and food intake.—Appropriate behavior between members of pairs is necessary for follicle maturation in many birds (see review by Lofts and Murton 1973). Results of our study indicate that pair relations may also be important to spring fat accumulation. All geese spent a greater percentage of time devoted to feeding when in grass fields than in cornfields. Paired geese preceded non-paired birds to grass fields in spring and paired females spent more time actually feeding when in cornfields than unpaired females. Finally, unpaired geese initially weighed less and gained less weight in the period of fat accumulation (McLandress and Raveling 1981).

Decreases in density of flocks of geese feeding in cornfields could have been due to diminishing amounts of waste corn as spring progressed. However, density of flocks in pastures remained unchanged and essentially equaled the final density of geese recorded for cornfields in spring. A higher percentage of geese feeding in pastures coincided with the decrease in density of flocks of geese feeding in cornfields. Flocks of geese feeding in pastures contained higher proportions of unpaired geese in the 2 weeks prior to spring migration than earlier in spring. Possibly, this reflects later initiation of hyperphagia in potentially non-reproductive geese.

The preponderance of rolling and cackling components of triumph ceremonies displayed in different releasing situations in this study were not as clearly separable as Fischer (1965) reported for Greylag Geese (*Anser anser*). Rather, these components appeared to form a continuum from exclusively cackling in the mildest triumph ceremonies, to predominantly rolling in displays of the highest intensity. Rolling is almost exclusively a male behavior and has been accepted as a predominantly aggressive display (Lorenz 1959, Fischer 1965, Raveling 1970, Radesater 1974). Radesater (1974) suggested that the frequency of rolling may depend on testosterone levels as frequency increased during seasons when agonistic encounters were common in captive geese. The decrease in proportion of "exaggerated" (rolling predominated) triumph ceremonies by Giant Canada Geese as well as the lower proportion of "chasing" and "fighting" noted in aggressive interactions as spring progressed, would appear to contradict a correlation with higher testosterone levels indicated by increasing testis size (McLandress and Raveling, unpubl.). However, geese became progressively more dispersed in feeding areas through spring, thus reducing intensity and/or frequency of agonistic stimuli. Less conspicuous chasing and threatening behavior than during winter has also been reported for Canada Geese upon their arrival at the breeding grounds in spring (Raveling and Lumsden 1977).

As spring progressed, the frequency of triumph ceremonies did not change significantly despite a decrease in the proportion of aggressive related displays. The lower proportions of "normal" and "exaggerated" displays were balanced by an increasing number of "reduced" intensity triumph ceremonies. "Reduced" intensity triumph ceremonies (predominated by cackling) observed in this study, as in other studies (Lorenz 1959, Fischer 1965, Raveling 1970, Radesater 1974), often occurred in the absence of agonistic stimuli. Hanson (1953) and Raveling (1970) concluded that families and mates remaining together have an adaptive advantage in the social hierarchy of Canada Geese in winter. The dominance order provides benefits in terms of food and space acquisition, and reduction of aggressive encounters. The higher number of "reduced" intensity triumph ceremonies may be a reflection of increased stimulation of geese to be with mates in spring. This would be adaptively advantageous to: (1) enhance the status of paired geese in the dominance hierarchy during the period of hyperphagia, nest-site selection and territorial defense; (2) insure that pairs arrive together on the breeding grounds; and (3) stimulate pair formation in unmated geese.

Termination of spring hyperphagia.—Raveling (1978a) concluded that factors that stimulate the gonadotropin release responsible for follicle maturation in female Canada Geese occur at the same time as, or just before,

final migration to nesting grounds. The yolk of eggs of Canada Geese takes 12–13 days to develop (Raveling 1978a). Geese in this study migrated 2–6 April, arrived on nesting grounds on 8 and 9 April and began egg-laying 19 and 20 April. However, nest initiation was probably delayed by a lack of meltwater at nest-sites (see also Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975). Minor follicular development had occurred in female geese collected during March, but rapid yolk deposition was evident only in geese collected 4–6 April. Based on average size of the largest follicles of 4 females collected 4–6 April (23 mm; McLandress and Raveling, unpubl.), it is likely that rapid ovarian follicular development began during the last week of March.

Digestive organs which were enlarged in geese collected 14–16 March had decreased in size in birds collected 4–6 April (McLandress and Raveling, unpubl.) indicating that hyperphagia had already ended. The exponential increase in sexual displays (Fig. 1) during spring corresponded with enlargement of testes and ovarian follicle size of collected geese (McLandress and Raveling, unpubl.). Despite the highest frequency of displays of the sexual sequence occurring in the first week of April, copulatory success indicated that the most important week for coition was 21–28 March. Coincidentally, 9 of 15 (60%) post-copulatory displays, for which information was recorded during the week of 21–28 March, included the female. This frequency was significantly greater ($\chi^2 = 6.84$, df = 1, $P < 0.01$) than 4 female postcopulatory displays of 22 (18%) copulations observed throughout spring by Klopman (1962). Thus, rapid ovarian follicle growth began before migration, coincided with the decrease in size of digestive organs enlarged during hyperphagia, and was correlated with and perhaps, as suggested by Raveling (1978a), stimulated by copulatory behavior.

Giant Canada Geese of this study population have consistently arrived on their nesting grounds in Manitoba between 5 and 9 April, 1968–1975 (Raveling, unpubl.). Day length, the most consistent indicator of season (Follett 1973), is likely the primer for migration and associated physiological changes. Secondary factors may modify timing of migration, final development of ovarian follicles and termination of hyperphagia, once photoperiod is permissive.

Hyperphagia and the resulting weight gain of geese began 1 March when warming temperatures and melting snow allowed geese to have prolonged access to new grass. Pre-reproductive body weight gain was attained by the end of March. Young grass eaten by geese contained high levels (>26%) of protein (McLandress and Raveling 1981). Young grass remains highly digestible for approximately 1 month during spring, at which time digestibility abruptly decreases (McDonald et al. 1973). Thus, duration of

the fattening period of Canada Geese and their use of fertile lowlands along creeks coincided with availability of maximum quality of grass. Cold weather which was related to reduced feeding efforts occurred 17–24 March. Perhaps the required increase of weight could occur more rapidly in years of even more clement weather.

SUMMARY

Behavioral changes of Giant Canada Geese associated with accumulation of body weight prior to spring migration were studied in southeastern Minnesota. Daily duration of time spent in feeding areas by geese increased with increasing temperature. The percentage of geese feeding in grass fields increased, but cornfields remained important feeding sites throughout spring. Adult geese spent more time actually feeding when in pastures than when in cornfields. Paired females devoted more time to feeding than males in either cornfields or pastures and more time than females without mates in cornfields. Increased dispersal of geese in spring coincided with proportionately fewer vigorous triumph ceremonies and a lower percentage of aggressive encounters which involved actual fighting. However, the frequency of all triumph ceremonies and aggressive encounters may have increased. Sexual behavior increased exponentially through spring, but the highest frequency of successful copulations coincided with the onset of rapid yolk formation and with the termination of hyperphagia 1 week prior to migration. Hyperphagia and the associated accumulation of body reserves by Giant Canada Geese occurred in a period of less than 1 month prior to departure for the breeding grounds which coincided with availability of the highest level of protein in new growth grass.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grant GB-38788. We are grateful for permission from the P. Curry and A. Vincent families to study at East Meadows Ranch, Manitoba, and from the Rochester Parks Board and the Minnesota Department of Natural Resources (MDNR) to study at Silver Lake, Rochester. N. Gulden, R. Holmes and R. Jessen (MDNR) supplied equipment and handled many administrative matters. J. Gilbertson (MDNR) and G. Yaeger of the Rochester Post Bulletin were invaluable in dealing with public relations. Many thanks are due to A. Stegen (MDNR), L. Salata and M. Wege of the University of California, Davis (UCD) for their assistance in the field. Additional help was provided by R. Christman of Macalester College, L. King, Manager of East Meadows Ranch, and K. Brace of the Canadian Wildlife Service. R. Schwab and W. Hamilton (UCD) provided valuable critiques of early drafts. We are especially grateful to Ilse McLandress who helped with fieldwork and typed earlier drafts of the manuscript.

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DEPT. WILDLIFE AND FISHERIES BIOLOGY, UNIV. CALIFORNIA, DAVIS, CALIFORNIA 95616. ACCEPTED 20 SEPT. 1980.

RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering a research grant of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her banding or ornithological background, the project plan and a budget to the joint selection committee chairman: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. The deadline for receipt of applications is 15 March 1982.