HABITAT USE AND FORAGING BEHAVIOR OF CACKLING CANADA AND ROSS' GEESE DURING SPRING: IMPLICATIONS FOR THE ANALYSIS OF ECOLOGICAL DETERMINANTS OF GOOSE SOCIAL BEHAVIOR

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Abstract: We studied the foraging ecology of sympatric cackling Canada (*Branta canadensis minima*) and Ross' (*Chen rossii*) geese at a spring staging area in northeastern California. Cackling and Ross' goose resource use patterns diverged as spring progressed and nutrient demands increased. Both species switched from feeding primarily in grain fields during early March to feeding primarily in alfalfa during April. When not feeding in alfalfa, Ross' geese spent more time in wet meadow while cackling geese spent more time in pasture. Cackling geese spent about 65% of their time actively foraging when in alfalfa, pasture, wet meadow, or winter wheat fields. Peck and step rates were faster in habitats with short, dense swards (e.g., winter wheat and pasture). Thus, geese responded to habitat characteristics primarily by modifying feeding rate rather than by changing the proportion of time spent feeding. Cackling geese >4 years old spent more time foraging during mid-day than did younger geese; this may result in higher daily intake rates for older cackling geese. We observed only 6 mated pairs of cackling geese regularly associated and we never observed paired geese with their juveniles. Unlike geese which maintain associations with their mates during winter, paired and unpaired cackling geese did not show sex differences in their time budgets. We suggest the determinants of cackling goose social organization include: (1) predation pressure and other forms of disturbance, (2) population density on primarily a local scale, (3) digestive capabilities relative to metabolic requirements, (4) the distribution, abundance, and predictability of preferred foods, and (5) the response of food plants to being eaten.

Key words: *Anser rossii, Branta canadensis minima,* cackling Canada goose, California, foraging, habitat use, Ross' goose, social behavior.

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Foraging decisions made by arctic-nesting geese during late winter and spring influence potential reproductive success through their affect on nutrient reserve acquisition (Ankney and MacInnes 1978, Raveling 1979, Thomas 1983, Ebbinge 1989, Black et al. 1991, Prop and Deerenberg 1991). Arctic-nesting geese gain weight during spring by feeding intensively and for longer periods than in winter, and by selecting habitats and plants high in protein (e.g., new growth of grasses) and perhaps energy (e.g., seeds) (Owen 1971, Raveling 1979, Prins et al. 1980, McLandress and Raveling 1981*a*, Teunissen et al. 1985, Alisauskas 1988, Alisauskas and Ankney 1992, McWilliams 1993).

Inter- and intraspecific interactions can directly influence whether preferred habitats are used and whether food resources are acquired efficiently. Interspecific competition can affect the distribution and habitat use of geese (Madsen 1985, Madsen and Mortensen 1987). Dominance relations within a species can also affect resource acquisition. In large-bodied geese, individuals that remain associated with their mate and juveniles are socially dominant over smaller families, pairs, and solitary geese (Boyd 1953, Raveling 1970, Lamprecht 1986, Gregoire and Ankney 1990). Dominance often translates into better feeding opportunities during the nonbreeding period (Boyd 1953; Hanson 1953; Raveling 1970; Black and Owen 1989*a, b*).

We studied cackling and Ross' goose foraging behavior and habitat use during March and April, 1989 and 1990, in Big Valley, California. Cackling and Ross' geese are small (ca. 1.2-2.1 kg) and feed primarily by grazing, especially during spring

(Johnson and Raveling 1988). Both cackling and Ross' geese commonly feed in mixed species flocks of 300-4,000 birds in Big Valley. In this paper, we document habitat use of cackling and Ross' geese in Big Valley and examine the degree to which these 2 goose species overlap in their habitat use, and how habitat use changes during March and April for each species. We also investigated the foraging behavior of these geese in the most commonly used habitats. Our study is the first to document the foraging behavior and habitat use of these 2 species during spring and the degree to which cackling and Ross' geese interact during this important time.

Cackling goose social organization during the nonbreeding period is atypical compared with other geese. Based on studies with marked individuals, other geese maintain family groups during most of the nonbreeding period (Owen 1980, Johnson and Raveling 1988, Black and Owen 1989*b*, Owen and Black 1990). In contrast, cackling geese exhibit weak pair and family associations on their wintering grounds, and occur commonly in exceptionally dense flocks during the nonbreeding period (Johnson and Raveling 1988).

Our second major objective was to investigate whether cackling geese exhibit sex, age, and status (paired vs. unpaired) differences in their foraging and aggressive behavior. In large-bodied geese that exhibit a family-based social organization, males are more aggressive and vigilant than females and juveniles resulting in sex- and age-related differences in time budgets (Raveling 1969, 1970, 1981; Black and Owen 1989*a, b*; Austin 1990; Gregoire and Ankney 1990). We expected no age and sex differences in time budgets of cackling geese because they lack the family- and often the pair-based social organization characteristic of other geese. We expected the few paired cackling geese we observed to show the traditional male/female differences in time budgets seen in most other geese.

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METHODS

Study Area

Between February and late April, a portion of the cackling and Ross' goose population inhabits intermountain valleys in northeastern California (Johnson and Raveling 1988). We selected 1 of these valleys, Big Valley (41° 08' N, 121° 04' W), for this study because: (1) a large proportion (up to 75%) of the cackling goose population has used this area in some years, (2) the valley contains a variety of habitats, including wetlands containing mostly native flora (see below), and (3) mixed cackling/Ross' goose flocks occur commonly. During our study, cackling and Ross' goose populations in Big Valley peaked between mid-March and early April at about 6,000 and 10,000 geese, respectively.

Fields in the study area were categorized into 1 of 6 habitat types: pasture, alfalfa, pasture/alfalfa mix, wet meadow, winter wheat, or standing grain (usually wheat or barley planted the previous spring). The pasture component of the alfalfa/pasture mix fields was composed almost entirely of bluegrass (*Poa annua* and *Poa bulbosa*). In contrast, pasture fields included *Poa* spp., but also contained foxtail fescue (*Festuca pratensis*), foxtail (*Alopecurus* spp.), Mediterranean barley (*Hordeum hystrix*), *Bromus* spp., and reed canarygrass (*Phalaris arundinacea*). Wet meadow habitats were dominated by sedges (*Carex* spp.), common tule (*Scirpus acutus*), rushes (*Juncus* spp.), and a mix of grasses, spikerush (*Eleocharis palustris*), clover (*Trifolium* spp.), and cinquefoil (*Potentilla gracilis*).

Habitat Use

In 1989 and 1990, the first cackling and Ross' geese arrived in Big Valley in early February (J. Weldon, Adin, Cal., pers. commun.). We monitored geese beginning 1 March in both years, about 1 week after ≥1,000 Ross' or cackling geese were counted in Big Valley. We continued monitoring goose flocks in Big Valley until the geese departed. In 1989 and 1990, Ross' geese left Big Valley in mid-April, and the last cackling geese left 1-3 May.

Almost daily, 2 or 3 persons located and followed separate flocks of geese from dawn until dusk. We recorded the number of geese using a field and the time the geese spent on that field. When geese were less predictable in their habitat use, we spot-checked locations instead of following individual flocks.

We estimated habitat use by calculating the total and the percentage of total goose-hours spent in each habitat type each day, with 1 goose-hour equal to 1 goose using a field for 1 hr. Daily habitat use was calculated separately for the following intervals: 1-10 March, 12-25 March, 27 March-10 April, and 12-26 April. A day was included in the calculations only when: (1) we recorded goose use for the entire daylight period, (2) we knew where at least 70% of the geese in Big Valley were every hr of the day, (3) >1,000 cackling or Ross' geese were in Big Valley, and (4) geese roosted during mid-day. We were able to accurately estimate goose populations in Big Valley because all geese used a limited number of day roost sites. Because geese roosted during mid-day only on fair weather days (i.e., no precipitation or strong winds), our analysis does not consider habitat use during poor weather.

Foraging Behavior

Plastic neck bands on geese that we observed had been placed on cackling geese between 1982 and 1989 (Raveling et al. 1990) and on Ross' geese during 1989, except 1 Ross' goose that was neck-banded by M. R. McLandress in 1976. We performed focal observations (Altmann 1974) on neck-banded individuals that were feeding. Each time a goose flock was encountered we attempted to record focal observations on all neck-banded individuals. Consequently, focal birds were chosen consecutively until all banded birds had been observed. Usually only 1 focal observation per bird was recorded within a morning (0500-1000 hr), mid-day (1100-1500 hr), or evening (1600-2000 hr) time period. We calculated an average time budget for individuals with more than 1 focal observation on the same day and time period. Focal observations were stopped after 10 min of continuous recording or when we lost sight of the bird. Each time a focal observation was recorded we also noted the extent of cloud cover, temperature and precipitation, time of day, date, location, and neck-band code.

A portable computer or tape recorder was used to record the types of behavior (Table 1), behavioral transitions, and the time each transition occurred. We then calculated the duration and frequency of each behavior, along with peck rates and step rates. Because geese pecked and stepped faster than we could type, we recorded the number of sec that elapsed for 25 pecks or 10 steps. We then converted these values to number of pecks or steps per min prior to statistical analysis. Peck and step rates were counted only when they occurred within an uninterrupted foraging (Table 1) period. Sample sizes for peck and step rates were larger than for time budget analyses because we often recorded peck and step rates on unbanded geese or on neck-banded geese without attempting a complete 10-min focal observation.

Statistical Analysis

We used a repeated measures ANOVA (Neter et al. 1985) to analyze seasonal and annual changes in habitat use of Ross' and cackling geese because we were measuring habitat use of basically the same population of geese over time. The dependent variable for this analysis was the number of goose-hours per day. The independent factors included goose species and habitat type (grain, wet meadow, pasture, alfalfa). The repeated measure for this analysis was the time interval during spring (3 intervals in 1989 and 4 in 1990). We used days within each

Table 1. Behavioral components measured for time budgets of cackling and Ross' geese during March and April, 1989 and 1990, in Big Valley, Calif.

Activity	Definition
Foraging	Head and neck below the horizontal plane of the goose's back; includes pecking at food or stepping.
Walking	Head and neck above plane of back; forward movement.
Standing	Head and neck above plane of back; legs vertically extended, motionless, and bird is awake.
Sitting	Head and neck above plane of back; ventral body surface resting on ground.
Preening	Bill grasping and moving feathers; shaking and fluffing feathers.
Sleeping	White "eyelids" visible or head resting on body.
Agonistic	Inter- and intraspecific aggressive encounters (see Raveling 1970 for details).
Flying	Travel through the air.
Drinking	Consumption of water.
Swimming	Sitting on water.
Pair Bonding	Triumph ceremony and/or copulatory displays (see Fischer 1965 and Raveling 1970 for details).

time interval as replicates. Thus, we assumed that days within each time interval were independent and that days represented "blocks" for which habitat use of geese was repeatedly measured over time intervals. Transforming the data was unnecessary because variances were homogenous across time and goose-hours were approximately normally distributed.

The behavior data set included repeated observations on the same individual geese. We did not use a repeated measures ANOVA for statistical analysis because individual geese did not use all habitats at all times of the day throughout the spring. This differential habitat use resulted in an unbalanced data set (with respect to individual geese) and made a repeated measures analysis inappropriate. Consequently, we used a mixed model ANOVA with both the individual bird effect and the residual error defined as random variables (Snedecor and Cochran 1980). Additionally, the quasi-F statistic was used for mean square comparisons and a Satterthwaite approximation was used for estimating error degrees of freedom (Neter et al. 1985:831-835). We arcsine-transformed the percentage of time spent in each behavior for each focal observation and used these as dependent variables in the mixed model ANOVA. We analyzed each behavior using a separate, but identical, ANOVA. We considered the possible interdependency between behaviors when making our interpretation of the results. The independent factors for this analysis included year, habitat, time-of-day, status (paired or unpaired), sex, and age. We used the general linear models procedure (Type III sums of squares) of the Statistical Analysis System (Crum 1986) for all statistical analysis. The arcsine-transformed data conformed to the assumptions of ANOVA.

We used a completely randomized ANOVA (Snedecor and Cochran 1980) to analyze peck rates and step rates. We ignored sex, age, and status effects in this analysis because more than half of the data were from geese without neck bands. The independent factors for this analysis included goose species, habitat, time-of-day, and season.

RESULTS

Habitat Use

In general, cackling and Ross' geese distributed themselves unequally among habitats (overall habitat main effect: $F = 15.8$; 3, 12 df; $P = 0.0002$; habitat effect within each seasonal period: $F > 7.8$; 3, 12 df; $P < 0.004$), and in a species-specific manner (species x habitat interaction: $F = 17.4$; 3, 12 df; $P = 0.0001$) (Tables 2 and 3). Differences in habitat use between Ross' and cackling geese were significant for both the mid-March and early April periods in both 1989 (species x habitat interaction: $F = 3.4$; 3, 12 df; $P = 0.05$; $F = 5.1$; 3, 12 df; $P = 0.02$, respectively) and 1990 (species x habitat interaction: $F = 10.8$; 3, 12 df; $P = 0.001$; $F = 9.6$; 3, 12 df; $P = 0.002$, respectively), but were significant for the late April period only in 1990 (species x habitat interaction: $F = 22.1$; 3, 12 df; $P = 0.0001$).

We used orthogonal contrasts to identify year and season main effects and their interaction effects because the 7 seasonal intervals (3 in 1989, 4 in 1990) were analyzed as a continuous time effect in the repeated measures ANOVA. Cackling and Ross' goose habitat use patterns changed during March and April (season x habitat interaction: $F = 17.7$; 15, 20 df; $P = 0.0001$; season x species x habitat interaction:

Table 2. Average percent of total goose-hours spent by cackling and Ross' geese in 5 habitats during March and April, 1989, in Big Valley, Calif.

			Habitat types									
			Grain		Wet meadow		Pasture		Alfalfa		Winter wheat	
Dates	Total no. goose-hr[a]	Species	$\bar{x}$[b]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
12,14,18 March	21,825	Cackling	0		6	6	52	25	39	26	3	6
18,19 March	23,584	Ross'	0		21	8	14	9	65	18	0	
1,3,4 April	30,293	Cackling	1	1	5	5	51	23	43	21	0	
3,4 April	21,618	Ross'	2	2	30	11	4	5	62	8	2	3
22,25,26 April	24,162	Cackling	0		2	2	16	13	82	12	0	
17-18,19 April	25,125	Ross'	0		20	28	0		80	28	0	

[a] Sum of the mean number of goose-hours per day for each habitat type.

[b] Mean and SD of each day's percent of total goose-hours spent on each habitat type.

Table 3. Average percent of total goose-hours spent by cackling and Ross' geese in 5 habitats during March and April, 1990, in Big Valley, Calif.

			Habitat types									
			Grain		Wet meadow		Pasture		Alfalfa		Winter wheat	
Dates	Total no. goose-hr[a]	Species	$\bar{x}$[b]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
3, 4, 5 March	16,821	Cackling	77	7	17	5	0		4	3	1	1
3,4 March	44,713	Ross'	67	37	33	37	0		0		0	
12,14,25 March	24,623	Cackling	9	6	31	26	21	20	33	10	6	10
13,14 March	47,600	Ross'	10	14	78	30	0		1	0	11	16
27,28 March & 2 April	20,407	Cackling	2	2	5	1	35	8	57	7	0	
31 March & 4 April	29,089	Ross'	3	2	43	2	11	13	43	1	0	
12-13, 20, 24-26 April	23,146	Cackling	1	1	6	3	36	3	57	16	0	
12, 13 April	15,250	Ross'	6	9	30	15	0		64	6	0	

[a] Sum of the mean number of goose-hours per day for each habitat type.

[b] Mean and SD of each day's percent of total goose-hours spent on each habitat type.

$F = 5.1$; 15, 20 df; $P = 0.0005$). Despite annual differences in total number of goose-hrs in March and April (Tables 2 and 3), these seasonal patterns of habitat use for cackling and Ross' geese did not vary between 1989 and 1990 (year x species x habitat interaction: $F = 1.9$; 9, 26 df; $P = 0.1$). We investigated the importance of changes in total number of geese (reflected in goose-hours) in determining annual and seasonal patterns of habitat use and found its effect to be minor compared to changes in the proportion of geese using each habitat.

During early March in 1990, both cackling and Ross' geese spent most of their foraging time in grain fields and less time in wet meadows (Table 3). Rain and snow during the first 10 days of March in 1989 caused geese to forage throughout the day, rather than roost during mid-day. Consequently, no days were included in the analysis for this time period (Table 2). Observations during early March in 1989 indicated geese fed primarily on waste grain in livestock feed lots and planted fields, but also fed in wet meadows and flooded alfalfa.

By mid-March 1990, cackling and Ross' geese greatly reduced their use of grain and began feeding on new vegetative growth (Table 3). Ross' geese fed primarily in wet meadow, while cackling geese fed frequently in wet meadow, pasture, and alfalfa (Table 3). By mid-March 1989, Ross' geese fed primarily in alfalfa and wet meadow, while cackling geese fed primarily in pasture and alfalfa (Table 2).

By late March/early April, Ross' geese spent most of their feeding time in alfalfa and wet meadow (Tables 2 and 3), with alfalfa usually the most common habitat used for feeding. Pastures were infrequently used by Ross' geese throughout their stay in Big Valley. Cackling geese spent most of their feeding time in alfalfa and pasture (Tables 2 and 3). Unlike Ross' geese, cackling geese used pastures frequently throughout their stay in Big Valley.

Time Budget Comparisons

In 1989, we recorded 624 focal observation periods on 79 neck-banded cackling geese and 1 Ross' goose. In 1990, we recorded 756 focal observation periods on 88 neck-banded cackling and 5 Ross' geese. When the entire data set was analyzed using a mixed model ANOVA, which included an individual bird effect, birds of the same age and sex class differed in foraging behavior in 1990 ($F = 1.68$; 68, 431 df; $P = 0.001$) and nearly did so in 1989 ($F = 1.29$; 67, 257 df; $P = 0.08$). Estimates of individual bird differences revealed that birds that were seldom seen were responsible for the significant bird effect. When birds with fewer than 5 focal observations were excluded from the data, there were no longer differences among birds of the same age and sex class in 1990 ($F = 1.19$; 44, 394 df; $P = 0.20$) or in 1989 ($F = 1.27$; 25, 197 df; $P = 0.18$). For subsequent analyses, we did not include an individual bird effect in the mixed model ANOVA. Observation periods <4 min duration were also excluded from further analysis. Thus, the 1989 and 1990 data used for the analyses included 352 and 495 observation periods on 43 and 51 individual cackling geese and 1 and 5 Ross' geese, respectively. In 1989 and 1990, the mean number of approximately 10-min observation periods recorded for an individual cackling goose was 7.7 ± 4.4 (SD) and 12.6 ± 5.1 (SD), respectively.

Ross' geese spent 60-97% of their time foraging in various habitats. No statistical comparisons of

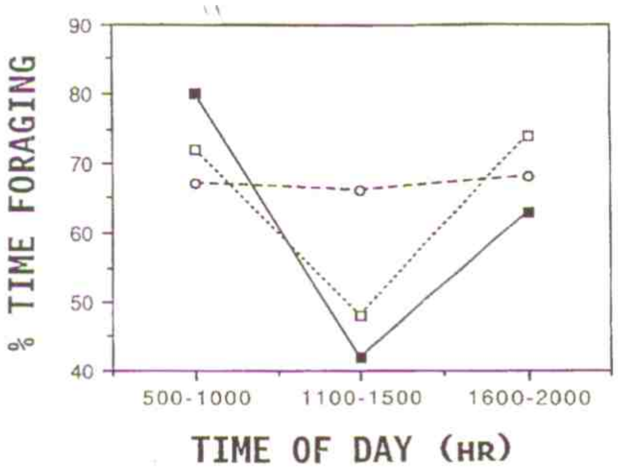

Figure 1. Age differences in the proportion of time spent foraging throughout the day by cackling geese. —■— = 9-10 mo and 21-22 mo (*n* = 29), —□— = 33-34 mo and 45-46 mo (*n* = 63), and —o— = older than 57 month (*n* = 352). The interaction between age group and time-of-day is statistically significant (F = 2.38; 4, 438 df; P = 0.05), while the age and time-of-day main effects were not significant (F = 0.45; 2, 438 df; P = 0.64; F = 1.6; 2, 438 df; P = 0.2; respectively).

Ross' goose time budgets were made because we observed only 6 neck-banded individuals.

Time spent foraging by cackling geese ranged from 56-78% and did not differ significantly among habitats in either 1989 or 1990 (Table 4). Cackling geese spent 20-40% of their time primarily walking, standing, and preening (Table 4). In 1989, cackling geese spent more time standing when in wet meadow and alfalfa than when in alfalfa/pasture mix and winter wheat fields (Table 4). In 1990, cackling geese spent more time walking when in wet meadow and pasture than when in the other 3 habitat types. No significant habitat differences in time spent standing or walking were found in 1990 or 1989, respectively. Cackling geese preened for 1-17% of their time and no habitat differences were detected. Aggressive interactions within cackling goose flocks rarely accounted for more than 1% of their time budget (Table 4). Time spent in aggressive interactions did not change significantly across habitats.

Although the time spent foraging by cackling geese in various habitats was similar, in 1990 there were significant diel differences in foraging time that were age dependent (Fig. 1). In 1989, similar trends were apparent except we recorded no focal observations on birds <2 years of age during mid-day, making the statistical results marginally significant (*F*= 2.41; 2, 197 df; *P*= 0.09). During the morning and evening time periods, all age groups fed for similar proportions of time (Fig. 1). However, when older cackling geese moved off mid-day roost sites, they spent more time feeding than geese <4 yrs old.

Time budgets of paired and unpaired male and female cackling geese were similar (Table 5). Males and females, whether paired or unpaired, did not differ significantly in the proportion of time spent in any of the behavioral categories. Because these values were similar for both 1989 and 1990, only the 1990 values are presented here.

Step Rates and Peck Rates

In 1989, cackling goose step rates were lower when geese were in alfalfa and wet meadows than

Table 4. Time budgets of cackling geese in 5 habitats during March and April, 1989 and 1990, in Big Valley, Calif.

		Habitat types and proportion of time in each behavior												
		Alfalfa/ pasture		Alfalfa		Pasture		Wet meadow		Winter wheat		Habitat comparisons		
Behavior	Year	$\bar{x}$[a]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	df[b]	*F*	*P*
Foraging	1989	70	21	56	25	70	16	60	18	78	19	352	1.55	0.19
	1990	63	19	73	20	68	16	63	26	76	20	477	1.43	0.22
Walking	1989	8	11	7	12	12	12	10	8	11	13	316	1.36	0.25
	1990	6B[c]	6	6B	7	13A	11	11A	11	6B	4	458	3.25	0.01
Standing	1989	12C	14	19AB	19	15BC	17	23A	15	7C	6	346	2.72	0.03
	1990	14	13	10	12	14	11	15	14	9	12	474	1.33	0.26
Preening	1989	6	7	17	15	4	11	3	4	1	1	63	1.27	0.29
	1990	10	12	9	13	2	2	5	6.	9	11	223	1.82	0.13
Agonistic	1989	0.7	1.2	0.5	0.7	0.9	2.7	3.0	2.0	2.3	4.5	87	0.71	0.59
	1990	0.3	0.2	0.6	0.9	0.7	0.7	0.5	0.7	0.6	0.6	141	0.81	0.65

[a] Mean of each ca. 10-min observation period's percent of time spent in each behavior.

[b] Denominator df presented; numerator df is 4 in all cases.

[c] Within a year, means with the same letters are not significantly different (*P* > 0.05) based on least significant difference (LSD) analysis.

Table 5. Time budgets of known sex and status cackling geese during March and April, 1990, in Big Valley, Calif.

				Percent time in each behavior										
				Foraging		Standing		Walking		Preening		Agonistic		Other
Status	**Sex**	*n*[a]	*n*[b]	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$
Paired	Female	6	41	67	20	11	10	7	8	13	16	0.3	0.1	1.7
	Male	6	43	64	20	15	16	7	6	10	13	0.4	0.4	3.6
Unpaired	Female	24	237	69	20	13	12	7	7	8	10	0.7	2.0	2.3
	Male	29	163	70	20	12	12	7	9	9	12	0.6	0.9	1.4
ANOVA results:														
	Status:	*F* =		0.35		3.01		0.36		3.51		0.16		
		P =		0.55		0.08		0.55		0.06		0.69		
	Sex:	*F* =		3.02		0.33		0.47		0.16		1.88		
		P =		0.08		0.56		0.49		0.69		0.17		
	Status by Sex:	*F* =		0.29		0.08		0.10		0.78		0.61		
		P =		0.59		0.77		0.76		0.38		0.44		
		df =		1, 455		1, 452		1, 436		1, 207		1, 128		

[a] Number of neck-collared individuals.

[b] Number of ca. 10-min observations periods.

when in pasture and winter wheat (Table 6, *F*= 6.3; 4, 617 df; *P* = 0.0001), but no changes in step rates among habitats were apparent in 1990 (*F*= 0.04; 4, 329 df; *P*= 0.84). In both 1989 and 1990, step rates were lowest during mid-day ($\bar{x}$ = 35 ± 8 (SD) and 30 ± 9, respectively) and highest in the evening ($\bar{x}$ = 50 ± 13 (SD) and 40 ± 11, respectively) (*F*= 7.39; 2, 617 df; *P*= 0.0007; *F*= 3.94; 2, 329 df; *P* = 0.02; respectively).

In 1989, Ross' geese consistently had higher step rates (*F*= 4.18; 1, 617 df; *P*= 0.04) and, thus, moved faster than cackling geese (Table 6). Step rate differences between species were pronounced only in alfalfa and wet meadow. Less than 5 step rates were recorded for Ross' geese in 1990, so no species comparison was attempted for that year.

Cackling and Ross' geese pecked at similar rates in each habitat both in 1989 (species effect: *F*= 0.06; 1, 1167 df; *P*= 0.81; species x habitat interaction: *F*= 1.11; 4, 1167 df; *P*= 0.33) and in 1990 (species effect: *F*= 0.71; 1, 521 df; *P*= 0.40; species x habitat interaction: *F*= 0.77; 4, 521 df; *P*= 0.38). Average peck rates of both cackling and Ross' geese were lower when geese fed in alfalfa than when they fed in all other habitats in 1990, and all except alfalfa/pasture mix habitats in 1989 (Table 7).

DISCUSSION

Habitat Use

Goose habitat use patterns were similar in 1989 and 1990 except geese switched from feeding on grain to feeding on new vegetative growth earlier in 1990. In both years, Ross' and cackling geese fed primarily in grain fields during early March, and fed

Table 6. Ross' and cackling goose step rates (no. steps/min) on 5 habitat types during March and April, 1989, in Big Valley, Calif.

	Habitat types									
	Alfalfa/Pasture		Alfalfa		Pasture		Wet meadow		Winter wheat	
Goose species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Cackling goose	39.7AB[a]	15.1	31.9B	13.7	45.1A	14.0	31.4B	12.9	42.6A	13.6
n[b]	110		38		205		96		153	
Ross' goose	—		60.0A	15.6	50.8A	14.7	46.2A	13.4	42.3A	11.8
n			7		13		7		10	

[a] Within a goose species, means with the same letters are not significantly different (*P* > 0.05) based on least significant difference (LSD) analysis.

[b] Number of step rates recorded in each habitat for each species.

Table 7. Goose peck rates (no. pecks/min) on 4 habitat types[a] during March and April in Big Valley, Calif. Ross' and cackling goose peck rates are combined because they were not significantly different in either 1989 or 1990.

	Habitat types										
	Alfalfa/Pasture		Alfalfa		Pasture		Wet meadow		Habitat comparison		
Year	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	df	F	P
1989	104.2AB[b]	15.0	96.2B	16.9	135.1A	15.7	124.0A	10.4	1167	5.33	0.001
n[c]	278		134		400		383				
1990	116.3A	18.6	105.6B	19.0	156.3A	19.4	127.1A	11.7	521	14.54	0.001
n	205		190		77		66				

[a] Winter wheat is not included because of small sample size.

[b] Within a year, means with the same letters are not significantly different ($P > 0.05$) based on least significant difference (LSD) analysis.

[c] Number of individual peck rates recorded in each habitat.

primarily in alfalfa fields in April. However, Ross' geese spent more of the remaining feeding time in wet meadow while cackling geese spent more of the remaining feeding time in pasture. As a result, mixed Ross' and cackling goose flocks were common in grain and alfalfa fields and uncommon in pasture and alfalfa/pasture fields. Mixed species flocks were also common in wet meadows, but for less time because cackling geese often departed for pasture or alfalfa fields.

Cackling geese in the fall frequently fed in winter wheat (Raveling and Zezulak 1991). Most geese shift from feeding primarily on high-energy foods such as grain in fall and winter to feeding primarily on high-protein vegetation in spring and summer (Palmer 1976, Owen 1980). This seasonal shift is particularly well documented for Canada geese (Reed et al. 1977; Raveling 1979; McLandress and Raveling 1981*a, b*; Raveling and Zezulak 1991).

We believe that differences in spring habitat use between cackling and Ross' geese result primarily from species differences in plant preferences and the efficiency with which each species eats the vegetation on these habitats. We regularly observed Ross' geese uproot wet meadow plants and then feed on the underground tubers. Bill lamellae of snow geese, and presumably Ross' geese, are harder and at a higher density than Canada geese providing a strong gripping surface used in grubbing for roots and tubers (Bolen and Rylander 1978). Cackling geese were less successful using the grubbing method probably because they have smaller and less powerful bills than Ross' geese (Johnson and Raveling 1988). However, the smaller bill of cackling geese may allow efficient feeding on pasture. Pasture grasses in Big Valley are generally lower in quality than alfalfa (McWilliams 1993) and may require geese to use more selective feeding methods.

Time Budgets and Peck and Step Rates

Time budgets were different among habitats during spring in greater snow geese (*Chen caerulescens atlanticus*) (Gauthier et al. 1984, Bedard and Gauthier 1989), lesser snow geese (*C. c. caerulescens*) (Alisauskas and Ankney 1992), white-fronted geese (*Anser albifrons frontalis*) (Ely 1992), Canada geese (McLandress and Raveling 1981*b*) and many other waterfowl (Paulus 1988). We found little variation among habitats in the proportion of time Ross' and cackling geese devoted to foraging. This was probably because both species were feeding at close to maximum rates in each habitat, and habitats did not vary sufficiently in composition to affect the proportion of time spent foraging.

The percentage of time spent foraging by cackling (56-78%) and Ross' geese (60-97%) was much higher than reported for most other wintering geese (Paulus 1988), but similar to wintering white-fronted (*A. a. albifrons*) (Owen 1972) and barnacle geese (*B. leucopsis*) (Ebbinge et al. 1975, Black and Owen 1989*b*). All 5 habitats for which we compared time budgets contained foods obtained almost entirely by grazing. Grazing on young vegetation during spring enables cackling and Ross' geese to acquire necessary protein, but requires them to feed for a relatively long time to obtain their energy requirements (Raveling 1979, McWilliams 1993).

Ross' and cackling geese stepped and pecked faster in habitats with short, dense swards. Cackling geese took more steps per min in the evening and fewer during mid-day. In addition, Ross' geese had faster step rates on average than cackling geese. This may explain why cackling and Ross' geese in mixed species flocks often become spatially segregated over time. Peck and step rates have proven to be sensitive measures of feeding behavior in studies comparing dominant and subordinate geese (Teunissen et al.

1985), reproductive success and feeding opportunities (Lazarus and Inglis 1978, Prop et al. 1984), and sward characteristics and foraging behavior (Owen 1972, Harwood 1975, Sedinger and Raveling 1988, Black et al. 1992, this study).

We examined foraging behavior of cackling and Ross' geese at 3 distinct levels: (1) time spent in a habitat, (2) proportion of time spent foraging once in a habitat, and (3) the rate of feeding while foraging. Habitat use of Ross' and cackling geese differed for most seasonal intervals and use changed seasonally. Regardless of the habitat type selected, cackling geese always spent about the same proportion of time foraging. In terms of feeding rate, Ross' and cackling geese modified their step and peck rates depending on the habitat type selected and the time of day.

Age Differences in Foraging

Typically, juvenile geese in family groups spend more time foraging than adults (e.g., Frederick and Klaas 1982, Austin 1990) or feed longer without interruptions than juveniles not in family groups (Black and Owen 1989*b*). This offers immediate advantages for maintaining family groups (Black and Owen 1989*b*). However, by spring many family groups of geese in the genus *Branta* have disassociated (Owen 1980, Owen and Black 1990) and juveniles presumably lose this feeding advantage. Black and Owen (1989*b*) found that juvenile barnacle geese with and without their parents fed for similar proportions of time in autumn, winter, and spring. All age classes of cackling geese fed for similar proportions of time during the 2 main feeding periods of the day, but during mid-day birds <4 years of age foraged for a much smaller proportion of time compared with older geese. Instead of foraging, the younger geese spent more time in maintenance behaviors (e.g., preening, bathing). These temporal and age-related differences in time spent feeding may result in higher daily food intake for older geese.

Social Behavior During Spring Staging

Johnson and Raveling (1988) concluded that cackling geese have weaker family and pair associations during the nonbreeding season compared with other goose species and other Canada goose subspecies. Even though we believe mate fidelity in cackling geese is similar to most other geese, we observed only 6 neck-banded pairs regularly associated during spring in either year of this study. We never observed family groups in Big Valley. Thus, our more intensive observations of cackling geese during spring also demonstrated weak family and pair associations in this subspecies of Canada goose.

Individual geese that maintain family associations during the nonbreeding season are socially dominant (Boyd 1953, Raveling 1970, Lamprecht 1986, Black and Owen 1989*a*, Gregoire and Ankney 1990), with males typically spending more time in agonistic interactions and less time feeding than females and their offspring (Lazarus 1978, Prevett and MacInnes 1980, McLandress and Raveling 1981*a*, Fox and Ridgill 1985, Black and Owen 1989*a*, Austin 1990). Paired cackling geese did not maintain associations with offspring, and no sex differences in time spent feeding, vigilant, or aggressive were observed (Johnson 1988, this study). Furthermore, paired and unpaired males and females behaved similarly. We suggest that the advantages of social dominance are sufficiently reduced for cackling geese during the nonbreeding period that the costs associated with maintaining pair associations and dominance relationships (Black and Owen 1988) outweigh benefits (see below).

Determinants of Cackling Goose Social Organization

During fall and spring migration in Alaska (Sedinger and Bollinger 1987, Johnson 1988) and during the breeding season (Sedinger and Raveling 1990), paired cackling geese were conspicuous and active defense of mates was commonly observed. In contrast, cackling geese did not maintain pair associations or dominance relationships on wintering areas in California (Johnson 1988, Johnson and Raveling 1988, this study).

Understanding the implications of small body size for cackling geese is central to understanding their unique social system during the nonbreeding period. Because of their small body size, cackling geese (and Ross' geese) are preyed upon regularly by golden eagles (*Aquila chrysaetos*) and occasionally by bald eagles (*Haliaeetus leucocephalus*) on wintering areas (Raveling and Zezulak 1991, McWilliams et al. 1994). Higher predation pressure could select for gregariousness as a predator-defense strategy. More dense, gregarious flocks that are disturbed regularly by predators would, in turn, increase the costs of maintaining a family-based, social dominance system. Owen and Black (1990:77-78) suggested that degree of disturbance and size of population and wintering groups were the most powerful determinants of family cohesiveness in geese.

Small body size also has direct consequences for foraging strategies. As body size of an herbivore decreases, passage rates increase and digestibility decreases relative to metabolic demands (Demment and Van Soest 1985, Karasov 1990). Geese are small herbivores that have rapid passage rates and digest primarily cell contents and not cell wall (Marriott and Forbes 1970, Mattocks 1971, Sedinger et al. 1989). Consequently, geese must select high quality food plants to meet their nutritional requirements (Owen 1980, Sibley 1981). The small-bodied cackling goose selects high quality food plants and maintains high intake rates for relatively long periods of time (McWilliams 1993). These foraging constraints may directly limit the time cackling geese have available for defense of food resources.

Distribution of food resources directly influences access to and defendability of the food (Brown 1964; Gauthreaux 1978; Lott 1984, 1991). For example, when interior Canada geese (*B. c. interior*) and lesser snow geese ate seeds that were patchily distributed, they engaged in higher levels of aggressive behavior than when they were grazing on vegetation (Raveling 1970, Gregoire and Ankney 1990). Johnson and Raveling (1988) suggested that cackling geese exhibited weak pair and family associations and little aggression during winter in part because they ate primarily grasses which were lower in quality and were more evenly distributed than other food types (e.g., tubers and seeds). However, some geese feed primarily by grazing and retain strong family associations and exhibit frequent aggressive behavior during winter (Black and Owen 1989*b*). The forage eaten by grazing geese usually appears to be evenly distributed; however, much of the forage in a given field is of sufficiently poor quality that geese cannot consume it and maintain a positive nutrient balance (Ydenberg and Prins 1984). Thus, it is necessary to know the distribution, abundance, and quality of preferred foods at feeding sites before evaluating the role of food resources in determining variation in social organization of geese during winter.

We have suggested that high predation pressure on cackling geese may favor dense flocks which in turn increase the costs of maintaining social dominance. Digestive and metabolic constraints require cackling geese to feed on high-quality forage for long periods each day which may further limit their ability to defend food resources. Additionally, evenly distributed, preferred food resources may reduce the benefits of social dominance. Alternatively, if grazing by goose flocks enhances plant quality or quantity (Prins et al. 1980, Cargill and Jeffries 1984), then important benefits emerge for gregariousness. Further research is needed to determine how the distribution and abundance of suitable forage on wintering areas interacts with grazing impacts and predation pressure to influence the social organization of geese.

LITERATURE CITED

Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. Thesis, Univ. W. Ont., London. 261 pp.

——, and C. D. Ankney. 1992. Spring habitat use and diets of midcontinent adult lesser snow geese. J. Wildl. Manage. 56:43-54.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

Ankney, C. D., and C. D. McInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459-471.

Austin, J. 1990. Comparison of activities within families and pairs of wintering Canada geese. Wilson Bull. 102:536-542.

Bedard, J., and G. Gauthier. 1989. Comparative energy budgets of greater snow geese *Chen caerulescens atlantica* staging in two habitats in spring. Ardea 77:3-20.

Black, J., C. Carbone, R. L. Wells, and M. Owen. 1992. Foraging dynamics in goose flocks: the cost of living on the edge. Anim. Behav. 44:41-50.

——, C. Deerenberg, and M. Owen. 1991. Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonized spring staging habitat. Ardea 79:349-358.

——, and M. Owen. 1988. Variations in pair bond and agonistic behaviors in barnacle geese on the wintering grounds. Pages 39-57 *in* M. W. Weller, ed. Waterfowl in winter. Univ. Minn. Press, Minneapolis.

——, and ——. 1989*a*. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. Anim. Behav. 37:199-209.

——, and ——. 1989*b*. Parent-offspring relationships in wintering barnacle geese. Anim. Behav. 37:187-198.

Bolen, E. G., and M. K. Rylander. 1978. Feeding adaptations in the lesser snow goose (*Anser caerulescens*). Southwest. Nat. 23:158-161.

Boyd, H. 1953. On encounters between wild white-fronted geese in winter flocks. Behaviour 5:85-129.

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

Cargill, S. M., and R. L. Jeffries. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. J. Appl. Ecol. 21:669-686.

Crum, L., editor. 1986. SAS system for linear models. 1986 ed. SAS Inst. Inc., Cary, N.C. 211pp.

Demment, M., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. 125:641-672.

Ebbinge, B. 1989. A multifactorial explanation for variation in breeding performance of brent geese *Branta bernicla*. Ibis 131:196-204.

——, K. Canters, and R. Drent. 1975. Foraging routines and estimated daily food intake in barnacle geese wintering in the northern Netherlands. Wildfowl 26:5-19.

Ely, C. R. 1992. Time allocation by greater white-fronted geese: influence of diet, energy reserves and predation. Condor 94:857-870.

Fischer, H. 1965. Das Triumphgeschrei der Graugans (*Anser anser*). Z. f. Tierpsychol. 22:247-304.

Fox, A. D., and S. C. Ridgill. 1985. Spring activity patterns of migrating Greenland white-fronted geese in West Greenland. Wildfowl 36:21-28.

Frederick, R. B., and E. E. Klaas. 1982. Resource use and behavior of migrating snow geese. J. Wildl. Manage. 46:601-614.

Gauthier, G., J. Bedard, and Y. Bedard. 1984. Comparison of daily energy expenditure of greater snow geese between two habitats. Can. J. Zool. 62:1304-1307.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. Pages 17-54 *in* P. P. G. Bateson and P. H. Klopfer, eds. Perspectives in ethology. Plenum Press, New York.

Gregoire, P. E., and C. D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. Auk 107:550-560.

Hanson, H. C. 1953. Inter-family dominance in Canada geese. Auk 70:11-16.

Harwood, J. 1975. The grazing strategies of blue geese, *Anser caerulescens*. Ph.D. Thesis, Univ. W. Ont., London. 186pp.

Johnson, J. C. 1988. Social organization and activity budgets of cackling Canada geese (*Branta canadensis minima*) during winter. M.S. Thesis, Univ. Cal., Davis. 62pp.

——, and D. G. Raveling. 1988. Weak family associations in cackling geese during winter: effects of body size and food resources on goose social organization. Pages 71-89 *in* M. W. Weller, ed. Waterfowl in winter. Univ. Minn. Press, Minneapolis.

Karasov, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. Studies Avian Biol. 13:391-415.

Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour 96:28-48.

Lazarus, J. 1978. Vigilance, flock size and domain of danger in the white-fronted goose. Wildfowl 29:135-146.

——, and I. R. Inglis. 1978. The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledgling period. Behaviour 65:62-88.

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

——. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge Univ. Press, New York, N.Y. 238pp.

Madsen, J. 1985. Habitat selection of farmland feeding geese in West Jutland, Denmark: an example of a niche shift. Ornis Scand. 16:140-144.

——, and C. E. Mortensen. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. Ibis 129:25-44.

Marriott, R. W., and D. K. Forbes. 1970. The digestion of lucerne chaff by Cape Barren geese, *Cereopsis novaehollandiae* Latham. Aust. J. Zool. 18:257-263.

Mattocks, J. G. 1971. Goose feeding and cellulose digestion. Wildfowl 22:107-113.

McLandress, M. R., and D. G. Raveling. 1981*a*. Changes in diet and body composition of Canada geese before spring migration. Auk 98:65-79.

——, and ——. 1981*b*. Hyperphagia and social behavior of Canada geese prior to spring migration. Wilson Bull. 93:310-324.

McWilliams, S. R. 1993. Behavior and ecology of cackling Canada and Ross' geese during spring. Ph.D. Thesis, Univ. Calif., Davis. 195pp.

——, J. P. Dunn, and D. G. Raveling, 1994. Predator-prey interactions between eagles and cackling Canada and Ross' geese during winter in California. Wilson Bull. 106: 272-288.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models. Second ed. R. D. Irwin, Inc., Homewood, Ill. 1,127pp.

Owen, M. 1971. The selection of feeding site by white-fronted geese in winter. J. Appl. Ecol. 8:905-917.

——. 1972. Some factors affecting food intake and selection in white-fronted geese. J. Anim. Ecol. 41:79-92.

——. 1980. Wild geese of the world. B. T. Batsford, Ltd., London. 236pp.

——, and J. Black. 1990. Waterfowl ecology. Chapman and Hall, Inc., New York, N.Y. 194pp.

Palmer, R. S. 1976. Handbook of North American birds. Vol. 2. Yale Univ. Press, New Haven, Conn. 521pp.

Paulus, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: A review. Pages 135-152 *in* M. W. Weller, ed. Waterfowl in winter. Univ. Minn. Press, Minneapolis.

Prevett, J. P., and C. D. MacInnes. 1980. Family and other social groups in snow geese. Wildl. Monogr. 71. 46pp.

Prins, H. H. Th., R. C. Ydenberg, and R. H. Drent. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neerl. 29:585-596.

Prop, J., and C. Deerenberg. 1991. Spring staging in brent geese *Branta bernicla:* feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87:19-28.

——, M. van Eerden, and R. Drent. 1984. Reproductive success of the barnacle goose in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk. Polarinst. Skr. 181:87-117.

Raveling, D. G. 1969. Social classes of Canada geese in winter. J. Wildl. Manage. 33:319-330.

——. 1970. Dominance relationships and agonistic behavior of Canada geese in winter. Behaviour 37:291-319.

——. 1979. The annual energy cycle of the cackling Canada goose. Pages 81-93 *in* R. L. Jarvis and J. C. Bartonek, eds. Management and biology of Pacific flyway geese. Oreg. State Univ. Book Stores, Corvallis.

——. 1981. Survival, experience, and age in relation to breeding success of Canada geese. J. Wildl. Manage. 45:817-829.

——, and D. S. Zezulak. 1991. Autumn diet of cackling Canada geese in relation to age and nutrient demand. Calif. Fish Game 77:1-10.

——, ——, J. G. Silveira, and J. A. Weldon. 1990. Accuracy in recording neck-band codes of cackling Canada geese. Calif. Fish Game 76:205-210.

Reed, A., G. Chapdelaine, and P. Dupuis. 1977. Use of farmland in spring by migrating Canada geese in the St. Lawrence Valley, Quebec. J. Appl. Ecol. 14:667-680.

Sedinger, J. S., and K. S. Bollinger. 1987. Autumn staging of cackling Canada geese on the Alaska peninsula. Wildfowl 38:13-18.

——, and D. G. Raveling. 1988. Foraging behavior of cackling Canada goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119-124.

——, and ——. 1990. Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs. Condor 92:174-181.

——, R. G. White, F. E. Mann, F. A. Burris, and R. A. Kedrowski. 1989. Apparent metabolizability of alfalfa components by yearling Pacific black brant. J. Wildl. Manage. 53:726-734.

Sibley, R. M. 1981. Strategies of digestion and defecation. Pages 109-139 *in* C. R. Townsend and P. Calow, eds. Physiological ecology: an evolutionary approach to resource use. Sinauer Assoc., Inc., Sunderland.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. Seventh ed. Ia. State Univ. Press, Ames. 507pp.

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.

Thomas, V. G. 1983. Spring migration: the prelude to reproduction and a review of its implications. Pages 73-81 *in* H. Boyd, ed. First western hemisphere waterfowl and waterbird symposium. Spec. Publ. Can. Wildl. Serv., Ottawa.

Ydenberg, R. C., and H. H. Th. Prins. 1984. Why do birds roost communally? Pages 123-139 *in* P. R. Evans, J. D. Goss-Custard, and W. G. Hale, eds. Coastal waders and wildfowl in winter. Cambridge Univ. Press, New York, N.Y.