

# TIME ALLOCATION BY GREATER WHITE-FRONTED GEESE: INFLUENCE OF DIET, ENERGY RESERVES AND PREDATION<sup>1</sup>

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**Abstract.** I determined the amount of time Greater White-fronted Geese (*Anser albifrons frontalis*) allocated to various activities from September to May, 1980-1982 at their primary wintering areas in the Pacific Flyway of North America. The length of time spent on roosts during the day was positively correlated to day length. Geese at roost sites spent the majority of their time sleeping (24-46%), alert (17-40%), walking or swimming (6-24%), and in comfort behaviors (3-25%). The amount of time geese fed each day varied little from early autumn to late spring (4.5-4.9 hr), except during mid-winter when minimum temperatures were below freezing (3.9 hr), and immediately before migration in spring (6.3 hr). The proportion of time devoted to feeding and alert behavior, the two most dominant activities at field sites, varied significantly among seasons and locations. The amount of time geese were actively engaged in foraging each season was more dependent on feeding intensity than the amount of time spent at foraging sites (fields), and varied almost three-fold, from 1.8 hr during late winter to 5.1 hr during late spring. Geese fed in closer proximity to conspecifics, were more frequently disturbed, and spent less time feeding during the hunting season. Exploitation of high energy foods and catabolism of substantial energy reserves probably enabled geese to minimize foraging time during periods of harsh weather and high predation pressure. Seasonal variation in the proportion of time spent feeding corresponded closely to changes in body mass. Greater White-fronted Geese wintering in the Pacific Flyway spent substantially less time feeding than they do in Europe, as geese in California fed primarily on high energy cereal grains, while in Europe they subsist on green vegetation which has relatively less digestible energy than cereal grains.

**Key words:** Greater White-fronted Goose; time allocation; activity; predation; diet.

## INTRODUCTION

Assessing the proportion of time an animal allocates to different activities during different stages of the annual cycle is a direct method of measuring how animals partition resources, and an indirect means of interpreting intra- and inter-specific variations in life history strategies. Most time allocation studies of wintering waterfowl have focused on ducks (Tribes Anatini and Aythini) (Paulus 1988). The few quantitative studies of the activity of geese wintering in North America generally have been of relatively short duration (Burton and Hudson 1978; Gauthier et al. 1984a, 1988; McLandress and Raveling 1981a), or site-specific (Frederick and Klaas 1982; Davis et al. 1989; but see Gauthier et al. 1984a, 1984b).

Relatively large homeotherms such as geese typically have substantial energy reserves (Pond 1981) which serve to dampen the effects of en-

vironmental perturbations; as such the consequences of particular time allocation "decisions" may not become evident for weeks or even months. Meaningful interpretation of quantitative behavioral investigations of such species thus necessitates relatively long term studies and a knowledge of changes in energy reserves during the period of study.

The objectives of this study were to determine the amount of time Greater White-fronted Geese (*Anser albifrons frontalis*) allotted to various activities in relation to variation in environmental and social factors during winter (September-May). This is the first study to present activity budgets of North American geese throughout winter (including autumn and spring migratory periods), and the first detailed analysis of the activity of Greater White-fronted Geese during winter in North America. The potential consequences of time allocation patterns are interpreted in relation to changes in body condition (Ely and Raveling 1989), and compared to studies of foraging ecology of the European Greater White-fronted Goose (*A. a. albifrons*) (Owen 1971, 1972a, 1972b, 1976).

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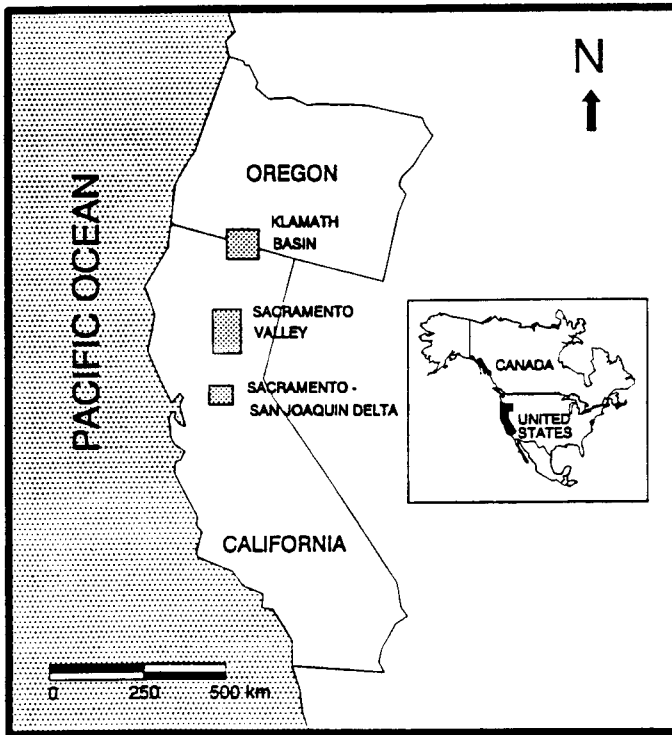


FIGURE 1. Major wintering areas of Greater White-fronted Geese in the Pacific Flyway (except Mexico).

## STUDY AREA AND METHODS

### STUDY AREA

The study was conducted from September to May, 1980–1982, in California and southern Oregon. Observations were made at the three main wintering areas of Greater White-fronted Geese in the Pacific Flyway (Bellrose 1976): (1) The Klamath Basin (KB) of N. California/S. Oregon; (2) the Sacramento Valley (SV), California; and (3) the Sacramento-San Joaquin Delta (SSJD), California (Fig. 1). The SV and the SSJD together comprise the Central Valley (CV). The KB contained most of the geese during early autumn and spring; the SV was most heavily used in late autumn through late winter, and the SSJD was of most importance during early and late winter and early spring.

### SAMPLE PERIODS

The winter was divided into six sampling periods, dictated in part by hunting seasons: (1) Early autumn = time of arrival of geese in early September until the opening of hunting season in

mid-October; (2) Late autumn = mid-October through November; (3) Early winter = 1 December to the end of the hunting season the third week of January; (4) Late winter = the end of hunting season through February; (5) Early spring = March; and (6) Late spring = 1 April until departure of the geese, usually by the first week of May.

### DAILY MOVEMENTS

The amount of time geese spent away from roost sites was determined by recording the time they departed from, or returned to, night-time and mid-day roost sites. Movements to and from roost sites were categorized as first, majority, or last segment of a flock to depart or arrive. The different flight categories gave similar ( $P > 0.05$ ) estimates of the amount of time spent at roost and field sites, so majority out/back was chosen for presentation here. Flight times were analyzed with respect to time of sunrise or sunset. Data on flight times were divided into autumn, winter, and spring periods for analysis of relationships to weather.

## ACTIVITY BUDGETS

I used the flock as the sampling unit to estimate the amount of time an "average" goose allocated to different behaviors. Geese were observed during daylight hours while at roosts and foraging sites. Geese were followed from roost sites to surrounding agricultural fields by motor vehicle. To minimize observer effects, data was not gathered until at least 15 min after a flock was encountered. Scan samples (Altmann 1974) were used to estimate overall behaviors within a flock of geese. If there were fewer than 100 geese in a flock I attempted to record the behavior of all individuals, otherwise the flock was systematically sampled by recording the behavior of geese within the field of a spotting scope (15×, 60). Behaviors were assessed instantaneously as the spotting scope was moved across the width of the flock. If the front and rearward portions of a flock were not in the field of view simultaneously, scans were conducted in a zig-zag manner to sample geese in all parts of the flock. This reduced the potential for sampling error due to influence of location within the flock on behavior (Owen 1972a, Lazarus 1978). Behaviors were assigned to seven categories: (1) feed (head down while stationary or moving), (2) alert (head up, not moving—includes alarm [Lazarus 1978]), (3) motor (walk or swim with head up), (4) fly, (5) comfort (bathing and preening), (6) social (agonistic and intra-family displays), and (7) sleep (head and neck on back, with bill pointing towards tail, or neck coiled on back and eyes closed). Social and fly categories comprised a very small proportion of the overall activity budget, and were combined as "other" for tabular presentation. Behaviors were recorded on a printing calculator (Ely 1987) and later summarized and entered onto a computer.

To analyze for time-of-day differences in behavior, morning and afternoon field times were each divided into three time periods of equal duration and the time spent in various activities transformed into percentages. Analysis of variance tests on transformed data revealed no differences in percent of time engaged in different activities among time periods ( $P > 0.05$ ), or between morning and afternoon periods away from roost sites ( $P > 0.05$ ). Therefore, activity information from field sites was combined into a single daily feeding period.

As social facilitation may lead to lack of in-

dependence of behavior among individuals with a flock (Owen 1972a), each scan was treated as a single data point. Only scans which sampled at least 30 birds were included in data analysis, consequently each scan was given equal weight (Owen 1972a). Daily activity budgets were calculated as the sum of the products of the amount of time geese spent at field and roost sites each season and the proportion of time devoted to each activity at field and roost sites, respectively. Most activity data were collected September to May 1981–1982, with supplemental data in the KB collected from September to November 1982.

## ENVIRONMENTAL AND SOCIAL VARIABLES

Maximum and minimum air temperatures, and times of sunrise and sunset were obtained from the National Weather Service (U.S. Department of Commerce, 1980–1982) and Gale Research Co. (1977), respectively, for Tule Lake (KB), Willows (SV), and Stockton (SSJD), California. Time of sunrise and sunset were adjusted for local variation. Percent cloud cover during observations was ranked in five categories from 0 to 100%. Precipitation was noted and wind speed was estimated as moderate to strong ( $>$  approximately 15 km/hr) or weak or none ( $<$  15 km/hr).

Information on location, habitat use, flock size, associated species, and density was recorded for all flocks encountered from 1979–1982. Disturbance data were collected September–May, 1981–1982. Density of geese in a flock was estimated from inter-goose distances and ranked in 5 categories from highly aggregated to highly dispersed. Disturbances were noted and defined as instances in which the majority of a flock simultaneously became alert, or flew in response to a disturbing stimulus.

## STATISTICAL ANALYSES

Analysis of variance (ANOVA) was used to test for differences in flight times among locations. Activity data were not normally distributed, so they were normalized with an arcsine transformation (Sokal and Rohlf 1981) prior to treatment with ANOVA. ANOVAs were followed with Duncan's multiple-range tests when the overall test was significant. The effects of season, location, and interaction (season  $\times$  location) on behavior of geese at roosting and foraging sites were determined using a two-way ANOVA for data from early and late autumn and early and

TABLE 1. Timing of feeding flights of Greater White-fronted Geese wintering in California and Oregon, 1980-1982.

Season	Morning*				Afternoon*				
	n	Departure Mean	SE	Return Mean	n	Departure Mean	SE	Return Mean	SE
Autumn									
Early	17	-34.8 E <sup>b</sup>	3.5	129.1 CD	38	-103.6 B	5.3	20.5 BC	6.5
Late	16	-14.5 CD	2.5	160.7 BC	10	-85.9 AB	7.6	27.7 ABC	4.8
Winter (E and L)									
Early <sup>c</sup>	9	12.6 A	2.1	107.0 D	6	-63.3 A	38.6	38.3 AB	7.5
Late <sup>c</sup>	9	7.0 AB	7.5	218.9 A	8	-49.5 A	27.0	19.3 BC	4.4
Spring									
Early	14	-12.8 BCD	5.5	153.1 BC	21	-65.7 A	10.8	36.3 AB	9.6
Late	22	-20.6 DE	3.8	160.6 BC	25	-111.9 B	10.8	51.9 A	5.1

\* Time (min) of flight, before (-) or after (+) sunrise (morning) or sunset (afternoon).

<sup>b</sup> Means within a column sharing the same letter are not significantly different, based on Duncan's multiple-range test.<sup>c</sup> Flight times in the Central Valley of California, all others from the Klamath Basin.

late winter (GLM procedure with missing cells—SAS Institute 1988). Seasonal differences in behavior of geese in the KB (the only location with samples during all six time periods), were analyzed with one-way ANOVA. Two-way ANOVA was used to examine the effect of habitat use on behavior in the KB (habitat, season, and habitat  $\times$  season). Stepwise multiple regression (best fit model—SAS Institute 1988) was used to determine relationships between environmental variables and timing of flights to and from feeding areas. Only independent ( $P > 0.05$ ) variables were included in regression analyses. Relationships between percent time spent in various activities and social and environmental factors were tested with Spearman's correlation coefficients (Sokal and Rohlf 1981). Differences in flock densities relative to hunting period and habitat were tested with Wilcoxon's sum of ranks test (ANOVA performed on ranked data—SAS Institute 1988). Chi-square was used to test for differences in the occurrence of disturbances relative to site, hunting season, and associated goose species. Unless noted otherwise, all statistical tests were two-tailed with a significance level of  $P = 0.05$ .

## RESULTS

### DAILY MOVEMENTS

Geese left roost sites morning and evening to feed in nearby agricultural fields. Geese commonly fed in the same areas during morning and afternoon, and used the same roosts during mid-day and at night (C. R. Ely, unpubl. data). The timing of foraging flights in the Sacramento Valley (SV) and the Sacramento-San Joaquin Delta (SSJD) were not significantly different ( $P > 0.05$ , for all flights), so data were combined as Central Valley (CV) for analysis. Data from 1980-1981 and 1981-1982 were also combined, as between-year differences were not significant ( $P > 0.05$  for all tests).

In general, geese departed night roosts within 30 min of sunrise and returned 2-3 hr later (Table 1). There were, however, significant seasonal differences ( $F_{6,98} = 5.89$ ,  $P < 0.0001$ ) in the time of morning departure, with geese leaving earliest (relative to sunrise) in early autumn and late spring and latest during early and late winter. Geese stayed at morning feeding sites for different lengths of time depending on the season ( $F_{6,98} = 7.09$ ,  $P < 0.0001$ ). They remained in fields

TABLE 2. Relationship between environmental variables and timing of feeding flights of Greater White-fronted Geese wintering in southern Oregon and northern California, 1980–1982.<sup>a</sup>

Season/Time of flight	Departure <sup>b</sup>				Return <sup>b</sup>			
	<i>n</i>	<i>r</i> <sup>2</sup>	<i>P</i>	Relationship	<i>n</i>	<i>r</i> <sup>2</sup>	<i>P</i>	Relationship
<b>Autumn</b>								
Morning	33	0.71	0.0001	Y = 149.6 - 0.27D	39	0.34	0.0005	Y = 324.6 - 0.27D
Afternoon	48	0.35	0.0001	Y = 271.0 - 0.53D	19		NS	
<b>Winter</b>								
Morning	27	0.15	0.05	Y = 14.5 - 0.22C	32	0.51	0.0001	Y = 562.8 + 0.82C - 0.63D
Afternoon	28		NS		8		NS	
<b>Spring</b>								
Morning	36	0.11	0.05	Y = 6.28 - 0.81T	37		NS	
Afternoon	46	0.18	0.005	Y = 278.2 - 0.49D	14	0.39	0.0005	Y = 61.1 - 0.35C

<sup>a</sup> Determined from stepwise multiple regression (best fit method—SAS Institute 1988).

<sup>b</sup> Direction of flight from roost.

<sup>c</sup> D = day length, C = cloud cover (0, 25, 50, 75, 100%), T = temperature (minimum daily temperature for morning flights and maximum daily temperature for afternoon flights).

longer ( $P < 0.05$ ) in early winter (CV) than in autumn and spring (Klamath Basin, KB).

Geese left mid-day roost sites earlier with respect to sunset in late spring, early autumn, and late winter than during other seasons ( $F_{6,121} = 4.55$ ,  $P < 0.0005$ ). Geese returned from afternoon foraging latest with respect to sunset during spring and winter in the KB, and earliest during late winter in the CV ( $F_{6,37} = 3.88$ ,  $P < 0.005$ ).

#### FACTORS INFLUENCING TIMING OF FEEDING FLIGHTS

Day length was the single most important factor related to timing of feeding flights, for both departures and returns during autumn, and afternoon departures in spring (Table 2). While temperature and cloud cover contributed significantly to predictive equations of the timing of flights during other time periods, they were not included in the final models because their effects were less significant than day length, and their effects were not independent of day length.

Windy days were prevalent only in the Klamath Basin during spring. Geese departed mid-day roosts earlier when it was windy than when it was calm ( $F_{1,44} = 8.19$ ,  $P < 0.01$ , mean departure =  $-111.7$  [ $n = 22$ ] and  $-71.7$  min [ $n = 24$ ] before sunset for windy vs. calm days, respectively).

#### TOTAL TIME AT ROOSTS AND IN FIELDS

Geese generally remained at field sites 10–30% longer in the morning than in the evening, especially during winter in the Central Valley (Fig.

2;  $P < 0.001$ ,  $F_{1,12} = 10.84$ ,  $\bar{x} = 172.3 \pm 16.3$  SE and  $111.1 \pm 11.8$  for combined seasonal morning and evening sessions, respectively). Geese spent the fewest number (and the smallest proportion) of daylight hours on roosts when day lengths were shortest (late autumn, early and late winter). However, even when days were shortest geese spent more than half of daylight hours on roosts. In the KB, which was the only location where temperatures were commonly below freezing (mean low temperature of  $-12^{\circ}\text{C}$ , December–February), they spent 68% of daylight hours at roost sites.

Greater White-fronted Geese were at field sites for nearly equal amounts of time (268–289 min) during all seasons at all locations, except mid-winter (early and late periods combined) and late spring in the KB, when geese were at field sites for 196 min and 376 min, respectively. A greater proportion of daylight hours was spent at field sites during late autumn and early and late winter than during early autumn, or early or late spring, respectively (44–48% vs. 35–40%).

#### ACTIVITY AT ROOST SITES

Geese spent the majority of time at roost sites either sleeping or alert (Table 3). The amount of time devoted to alert postures varied significantly among locations ( $F_{2,112} = 7.83$ ,  $P < 0.0005$ ; testing all locations during early and late winter); geese in the SSJD and the KB spent more time alert than geese in the SV. The proportion of time allocated to comfort behaviors also varied among locations ( $F_{2,112} = 11.35$ ,  $P < 0.0001$ ), being

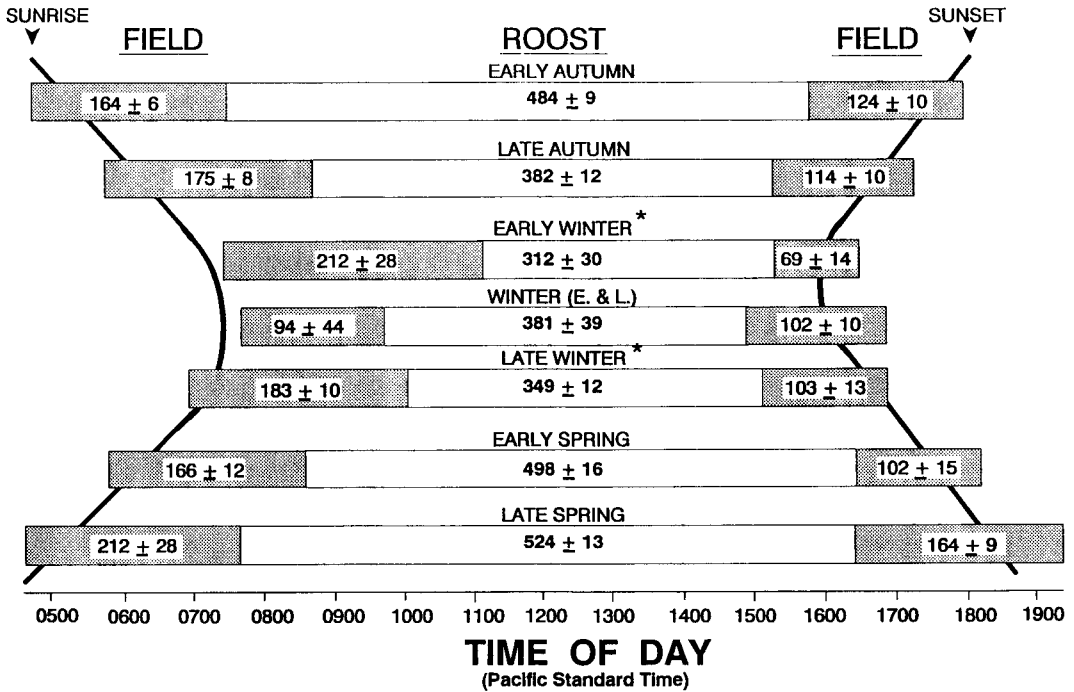


FIGURE 2. Time (minutes) spent at foraging and roosting sites (mean ± SE) by Greater White-fronted Geese wintering in California and S. Oregon, 1980–1982. (\* Denotes samples from the Central Valley, all others from the Klamath Basin).

greatest in the SV during early winter. There was no significant seasonal variation in the proportion of time geese spent in different activities while at roost sites within the KB (only area where data were collected for >2 time periods).

ACTIVITY AT FORAGING SITES

There were no significant differences between years in percent time spent in different behaviors in the KB during autumn or early winter (Tables 3, 4). Data from the two years were combined for analyses (these were the only seasons with more than one year of data).

Feeding was the dominant activity of geese at field sites during all seasons, and at all locations (Table 4). The proportion of time devoted to feeding while at field sites varied significantly, both among locations ( $F_{2,275} = 19.93, P < 0.0001$ ; testing all locations during early and late autumn, and early and late winter), and among seasons ( $F_{3,275} = 4.58, P < 0.005$ , for early and late autumn and early and late winter at all locations;  $F_{3,244} = 7.65, P < 0.0001$ , testing all seasons in the KB). Geese in the KB allocated up to 70% of field time to feeding in late winter, which is

in contrast to the SV or SSJD, where feeding never comprised more than 42% of the activity of geese at field sites. Interpretation of the effects of season and location is complicated, as there was significant interaction between the effects of season and location ( $F_{2,275} = 5.54, P < 0.001$ ).

The proportion of time geese spent in alert postures also varied significantly, both among areas ( $F_{2,275} = 17.99, P < 0.0001$ ), and among seasons ( $F_{3,275} = 4.16, P < 0.01$ , for early and late autumn and winter at all locations;  $F_{3,245} = 7.00, P < 0.0001$ , for all seasons in the KB). Geese at field sites spent the least time alert in the KB ( $P < 0.05$ ), and the most time alert on the SSJD ( $P < 0.05$ ). Geese in the KB spent the most time alert in late autumn and early winter ( $P < 0.05$ ), and the least time alert in late winter. Interaction effects (location × season), however, were also significant ( $F_{2,275} = 6.10, P < 0.0005$ ). The amount of time geese were alert was inversely related to feeding activity ( $r_s = -0.65, P < 0.001, n = 424$ ); these two behaviors constituted 67%–86% of all behaviors at any given location.

The percent of time spent sleeping at field sites

TABLE 3. Proportion of time spent in various activities by Greater White-fronted Geese while at roost sites in three major wintering areas in California and southern Oregon, 1981-1982.

Season/Location	Number of flocks	Number of birds sampled <sup>a</sup>	Percent of time (mean $\pm$ SD) spent in activity <sup>a</sup>					Other	
			Feed	Alert	Motor	Sleep	Comfort		
Autumn									
Klamath Basin <sup>c</sup>	15	207 $\pm$ 31	1.2 $\pm$ 0.4	25.0 $\pm$ 3.7	21.2 $\pm$ 8.2	30.7 $\pm$ 5.8	18.3 $\pm$ 4.0	3.6 $\pm$ 0.7	
Winter									
Early									
Sacramento Valley	14	98 $\pm$ 14	3.8 $\pm$ 2.5	16.9 $\pm$ 3.1	6.4 $\pm$ 1.7	46.0 $\pm$ 5.6	25.3 $\pm$ 4.2	1.6 $\pm$ 0.8	
Sac-San Joaquin Delta	9	170 $\pm$ 18	12.2 $\pm$ 6.3	39.5 $\pm$ 6.9	7.0 $\pm$ 1.3	23.6 $\pm$ 6.3	15.1 $\pm$ 4.1	2.6 $\pm$ 0.6	
Late									
Sacramento Valley	39	182 $\pm$ 107	8.3 $\pm$ 1.7	21.6 $\pm$ 1.9	11.1 $\pm$ 1.7	40.1 $\pm$ 3.7	13.7 $\pm$ 1.5	5.1 $\pm$ 2.1	
Sac-San Joaquin Delta	22	238 $\pm$ 21	12.6 $\pm$ 3.1	38.1 $\pm$ 4.1	12.5 $\pm$ 5.4	29.6 $\pm$ 5.9	5.1 $\pm$ 1.5	2.1 $\pm$ 0.4	
Klamath Basin <sup>c</sup>	34	152 $\pm$ 14	5.7 $\pm$ 2.4	30.9 $\pm$ 4.4	9.9 $\pm$ 3.3	42.6 $\pm$ 6.2	7.4 $\pm$ 1.5	3.4 $\pm$ 0.8	
Spring									
Early									
Klamath Basin <sup>c</sup>	40	403 $\pm$ 51	11.5 $\pm$ 2.9	23.3 $\pm$ 2.5	20.9 $\pm$ 3.2	38.4 $\pm$ 5.0	2.8 $\pm$ 0.5	3.2 $\pm$ 1.3	
Late									
Klamath Basin	16	189 $\pm$ 29	12.8 $\pm$ 6.2	25.8 $\pm$ 5.2	23.7 $\pm$ 6.9	29.4 $\pm$ 7.7	5.8 $\pm$ 2.0	2.4 $\pm$ 1.1	

<sup>a</sup> See methods for description of behavior categories.<sup>b</sup> Mean  $\pm$  SE.<sup>c</sup> Early and late periods combined due to small sample sizes.

TABLE 4. Proportion of time spent in various activities by Greater White-fronted Geese while at foraging sites in three major wintering areas in California and southern Oregon, 1981-1982.

Season/Location	Number of flocks	Number of birds sampled <sup>a</sup>	Percent of time (mean $\pm$ SE) spent in activity <sup>b</sup>							
			Feed	Alert	Minor	Sleep	Comfort	Other		
Autumn										
Early										
Klamath Basin	34	213 $\pm$ 15	58.1 $\pm$ 3.3	25.9 $\pm$ 2.4	6.1 $\pm$ 0.7	4.4 $\pm$ 1.4	2.7 $\pm$ 0.7	3.8 $\pm$ 0.7		
Late										
Klamath Basin	37	250 $\pm$ 18	39.3 $\pm$ 3.8	32.8 $\pm$ 2.7	8.5 $\pm$ 0.8	10.1 $\pm$ 3.4	4.9 $\pm$ 0.8	4.4 $\pm$ 1.1		
Sacramento Valley	22	173 $\pm$ 17	41.0 $\pm$ 4.2	37.1 $\pm$ 2.7	3.7 $\pm$ 0.7	6.1 $\pm$ 1.7	8.3 $\pm$ 2.0	3.5 $\pm$ 0.7		
Winter										
Early										
Klamath Basin	28	190 $\pm$ 19	52.5 $\pm$ 4.7	27.6 $\pm$ 2.8	6.2 $\pm$ 1.1	3.5 $\pm$ 1.8	1.9 $\pm$ 1.0	8.9 $\pm$ 4.0		
Sacramento Valley	42	249 $\pm$ 22	34.4 $\pm$ 3.8	32.8 $\pm$ 2.6	3.9 $\pm$ 0.8	19.9 $\pm$ 3.9	5.5 $\pm$ 0.8	3.4 $\pm$ 0.5		
Sac-San Joaquin Delta	13	201 $\pm$ 24	32.9 $\pm$ 5.0	33.9 $\pm$ 3.4	5.5 $\pm$ 0.7	18.7 $\pm$ 4.5	4.5 $\pm$ 0.9	4.6 $\pm$ 0.8		
Late										
Klamath Basin	17	276 $\pm$ 31	70.4 $\pm$ 3.8	14.4 $\pm$ 2.1	7.5 $\pm$ 1.1	4.0 $\pm$ 1.8	0.3 $\pm$ 0.2	3.3 $\pm$ 1.2		
Sacramento Valley	51	163 $\pm$ 20	42.0 $\pm$ 3.7	29.7 $\pm$ 2.2	4.7 $\pm$ 0.8	12.1 $\pm$ 3.1	7.4 $\pm$ 1.5	4.3 $\pm$ 0.7		
Sac-San Joaquin Delta	40	188 $\pm$ 13	27.5 $\pm$ 3.0	47.7 $\pm$ 2.5	4.1 $\pm$ 0.4	11.9 $\pm$ 2.1	4.7 $\pm$ 0.9	4.1 $\pm$ 0.4		
Spring										
Early										
Klamath Basin	87	256 $\pm$ 22	58.5 $\pm$ 2.3	21.6 $\pm$ 1.2	8.4 $\pm$ 0.7	7.3 $\pm$ 1.6	1.0 $\pm$ 0.2	4.1 $\pm$ 1.0		
Late										
Klamath Basin	48	181 $\pm$ 19	63.1 $\pm$ 2.9	20.9 $\pm$ 1.9	10.7 $\pm$ 2.1	3.2 $\pm$ 0.8	1.3 $\pm$ 0.4	1.2 $\pm$ 0.3		
Sac-San Joaquin Delta	15	174 $\pm$ 16	39.7 $\pm$ 6.1	35.2 $\pm$ 2.4	6.2 $\pm$ 0.9	5.4 $\pm$ 2.1	9.6 $\pm$ 2.5	4.0 $\pm$ 1.0		

<sup>a</sup> See text for description of behavior categories.<sup>b</sup> Mean  $\pm$  SE.



varied significantly among locations ( $F_{2,275} = 3.48$ ,  $P < 0.05$ ). Geese spent the largest proportion of time sleeping (up to 20%) during early winter in the SV, and on the SSJD (Table 4). Walking was the predominant motor activity at foraging sites, as the majority of feeding at all locations was done in unflooded fields. Motor activities were most prevalent in the KB ( $F_{2,275} = 10.47$ ,  $P < 0.0001$ ).

Flying, comfort movements, and social behaviors comprised, on average less than 8% of the total behavior of birds at field sites. The proportion of time devoted to flying while not at roost sites did not vary significantly among locations, but geese in the KB did spend more time in flight in early winter (7.2% of field time) than at other times ( $F_{5,245} = 2.53$ ,  $P < 0.05$ ; maximum of 2.4% of time in flight during other time periods). Geese allocated different amounts of time to comfort behaviors among locations ( $F_{2,275} = 3.90$ ,  $P < 0.001$ ), and seasonal effects were apparent in the KB ( $F_{5,245} = 9.00$ ,  $P < 0.0001$ ). Geese at the SSJD during spring devoted the most time to comfort behaviors (10%), while those at the KB in the winter spent the least amount of time in this activity (0.3%). The frequency of social activities varied among locations ( $F_{2,275} = 12.09$ ,  $P < 0.001$ ), and seasons ( $F_{3,275} = 4.78$ ,  $P < 0.005$ ), being greatest on the SSJD during early and late winter.

#### ENVIRONMENTAL FACTORS RELATED TO ACTIVITY AT FORAGING SITES

Temperature and cloud cover were significantly correlated to day length (and hence season), so data were analyzed by season. Geese in the KB during autumn and winter spent a greater proportion of field time foraging when skies were clear than when cloudy ( $r_s = 0.359$ ,  $P < 0.05$ , and  $r_s = 0.366$ ,  $P < 0.05$ , respectively). During winter in the CV, geese in fields spent more time alert ( $r_s = 0.204$ ,  $P < 0.05$ ), and in comfort behaviors ( $r_s = 0.190$ ,  $P < 0.05$ ), and less time sleeping ( $r_s = -0.199$ ,  $P < 0.05$ ), when skies were cloudy than when they were clear. The proportion of time geese spent alert in the KB during winter was negatively correlated to temperature ( $r_s = -0.490$ ,  $P < 0.01$ ).

Geese during this study fed almost exclusively on agricultural crops. In the KB, their diet consisted largely of seeds (barley, oats and wheat) during early autumn (73% of geese in 592 flocks), seeds (42%) and potatoes (57%) during late au-

tumn and winter ( $n = 408$  flocks), and grasses (53%), seeds (28%) and potatoes (18%) during spring ( $n = 855$  flocks). Geese in the SV fed almost exclusively on rice (98% of geese in 425 flocks), while corn was by far the predominant food source of geese on the SSJD (92% of geese in 266 flocks). The use of multiple food sources in the KB allowed for a comparison of behavior by habitat type.

Behavior data from early and late winter in the KB were combined to increase sample sizes. Overall (two-way ANOVA; 3 habitats  $\times$  4 seasons), there was significant variation in behavior among habitats with respect to time engaged in motor activities ( $F_{2,201} = 9.03$ ,  $P < 0.0001$ ) and feeding ( $F_{2,201} = 6.57$ ,  $P < 0.0001$ ). The variation was largely attributable to activity in potato fields, where geese walked more, and fed less than when on green vegetation or grain fields (13% vs. 7% walking, and 53% vs. 66% feeding, in potato fields vs. seeds/green vegetation, respectively). There was, however, significant interaction (habitat  $\times$  season;  $F_{3,201} = 4.96$ ,  $P < 0.001$ ), as geese in potato fields spent less time feeding than geese on other habitats during late spring, but more time during winter.

#### BIOTIC FACTORS RELATED TO ACTIVITY AT FORAGING SITES

The proportion of time geese in fields spent in various activities was significantly correlated with the number of geese in the flock, and the number of geese other than Greater White-fronted Geese in the flock (Table 5). Greater White-fronted Geese generally spent less time foraging (and more time alert) when flock sizes were large, and when in the presence of other goose species, except during spring when the presence of other geese had little apparent influence on behavior.

The potential influence of interspecific interactions was most apparent during late autumn in the KB when Cackling Canada (*Branta canadensis minima*), Lesser Snow (*Chen c. caerulescens*) and Ross' (*Chen rossii*) Geese (the latter two species referred to collectively as "white geese"; Table 5), were first present in appreciable numbers. In early autumn, when Greater White-fronted Geese had almost sole access to food resources, the number of Greater White-fronted Geese in a flock was positively correlated to the proportion of time geese spent alert ( $r_s = 0.347$ ,  $P < 0.05$ ), and negatively correlated to the amount of time allocated to foraging ( $r_s = -0.400$ ,

TABLE 5. Correlation<sup>a</sup> between the percent of time Greater White-fronted Geese spent feeding and social factors while at field sites in southern Oregon and northern California, 1981–1982.

Attribute	Season and location			
	Autumn	Winter		Spring
	Klamath Basin (n = 71)	Central Valley (n = 146)	Klamath Basin (n = 45)	Klamath Basin (n = 135)
Number of Greater White-fronted Geese	-0.245* (2,857 ± 416) <sup>b</sup>	-0.323*** (1,794 ± 155)	-0.010 (1,549 ± 198)	0.061 (773 ± 56)
Number of white geese <sup>c</sup>	-0.391*** (295 ± 66)	-0.193* (3,842 ± 481)	-0.197 (639 ± 165)	0.014 (848 ± 134)
Number of Cackling Canada Geese	-0.540*** (556 ± 157)	-0.041 (188 ± 25)	-0.461** (929 ± 247)	0.107 (45 ± 12)
Number of associated geese	-0.475*** (851 ± 193)	-0.239** (4,030 ± 480)	-0.334* (1,568 ± 348)	0.011 (893 ± 134)
Proportion of Greater White-fronted Geese <sup>d</sup>	0.526*** (85 ± 3)	0.130 (57 ± 3)	0.341* (63 ± 4.5)	-0.032 (68 ± 2.6)

<sup>a</sup> Spearman's correlation coefficient ( $r_s$ ).

<sup>b</sup> Mean ± SE.

<sup>c</sup> Lesser Snow and Ross' Geese.

<sup>d</sup> Percent of total geese in flock which were Greater White-fronted Geese.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

$P < 0.05$ ). By late autumn, when 81% of Greater White-fronted Goose flocks were associated with white geese (64%) and/or Cackling Canada Geese (60%), the behavior of Greater White-fronted Geese in fields was no longer correlated to the number of conspecifics in a flock, but was significantly related to the presence of other geese. Greater White-fronted Geese spent less time feeding, and more time alert and flying when associated with Cackling Geese during late autumn, than when in monospecific flocks ( $r_s = 0.491$ ,  $P < 0.01$ ,  $r_s = 0.449$ ,  $P < 0.01$  and  $r_s = 0.412$ ,  $P < 0.05$ , for correlation between time spent feeding, alert, and flying, respectively when associated with cackling geese). Greater White-fronted Geese in dense flocks spent more time alert than when they were in more widely dispersed flocks ( $r_s = -0.333$ ,  $P < 0.05$ ).

Interspecific interactions were mediated by habitat selection, at least in the KB where geese fed on several types of foods. Cackling Geese were less often associated with Greater White-fronted Goose flocks in potato fields than on green vegetation or grain ( $\chi^2 = 10.10$ ,  $P < 0.01$ ; 53 of 310 flocks with cackling geese vs. 190 of 724 flocks without cackling geese found on potato fields vs. green vegetation or grain fields). Conversely, white geese were more frequently found with Greater White-fronted Goose flocks in potato or grain fields (64%) than on green vegetation (36%) ( $\chi^2 = 6.87$ ,  $P < 0.01$ ; 344 of 535 flocks with white geese vs. 281 of 499 flocks without

white geese found on potato and grain fields vs. green vegetation). However, Greater White-fronted Geese associated with white goose flocks comprised predominantly of Ross' Geese were usually found on green vegetation (89% of 63 flocks).

Geese were disturbed more frequently while at field sites than when roosting in the KB ( $\chi^2 = 6.07$ ,  $P < 0.01$ ; 0.85 and 0.52 disturbances/hr in 312 and 92 hours of observation at field and roost sites respectively). Geese at field sites were disturbed more often during the hunting season (late autumn and early winter) than immediately before or after (early autumn and late winter) in the KB ( $\chi^2 = 31.55$ ,  $P < 0.001$ ; 1.49 and 0.48 disturbances/hr in 69 and 166 hours of observation during hunting and non-hunting periods, respectively), but not in the CV ( $P > 0.05$ ). Greater White-fronted Geese that associated only with conspecifics before and after the hunting season were less likely to be disturbed than those that associated with white geese ( $\chi^2 = 13.19$ ,  $P < 0.001$ ; 1.02 and 0.43 disturbances/hr in 61 and 141 hr of observation of Greater White-fronted Geese foraging with and without white geese, respectively). During the hunting season monospecific and heterospecific flocks were disturbed at equal rates ( $P > 0.05$ ).

Inter-geese distances between Greater White-fronted Geese at foraging sites in the KB did not vary among habitats in late autumn and winter ( $P > 0.05$ ; testing seeds vs. potatoes), but did in

spring ( $F_{2,807} = 7.11, P < 0.001$ ), when geese in potato fields were significantly more dispersed than geese in grain fields or green vegetation. Greater White-fronted Geese fed in closer proximity to conspecifics during the hunting season in both the KB ( $F_{1,931} = 14.16, P < 0.001$ ), and in the CV ( $F_{1,1240} = 6.16, P < 0.05$ ).

## DISCUSSION

### TIME OF FEEDING FLIGHTS

The pattern of morning and evening foraging flights of Greater White-fronted Geese was similar to that documented for several other species of geese at temperate latitudes (Raveling 1969, Raveling et al. 1972, Newton et al. 1973, Owen 1980, Frederick and Klaas 1982, Alisaukas and Ankney 1992). Timing of flights were related to dawn and dusk periods of rapidly changing light (Raveling et al. 1972) and delayed flights in winter were probably related to cold temperatures as reported for Canada Geese (Raveling et al. 1972, McLandress and Raveling 1981a) and Lesser Snow Geese (Frederick and Klaas 1982). The relatively early departure of geese for evening feeding in the Klamath Basin (cf. Raveling et al. 1972) may have been related to the absence of afternoon hunting.

### FACTORS INFLUENCING TIME ALLOCATION

*Diet.* the amount of time Greater White-fronted Geese spent per day feeding (3.2–6.2 hr at foraging sites but 1.8–5.0 hr actually engaged in feeding; calculated from values in Fig. 2 and Tables 3, 4) was markedly lower than the nearly 10 hr/day reported for Greater White-fronted Geese in Europe (Owen 1972a). Greater White-fronted Geese in California fed predominantly on cereal grains and potatoes, while Greater White-fronted Geese wintering in Great Britain foraged almost exclusively on grasses. Geese can not digest cellulose, and hence grassed have less available energy than cereal grains (McDonald et al. 1973). Energy intake per unit time should, therefore, be greater when geese are feeding on grains and potatoes, provided that food resources are equally available. Similar differences in foraging time related to diet composition have been reported for Cackling Canada Geese (Raveling 1979), Barnacle Geese, *Branta leucopsis*, (Drent et al. 1978), and Pink-footed Geese, *Anser brachyrhynchus* (Madsen 1985a).

*Environmental influences.* Feeding constituted

such a large proportion of the daily activity of Greater White-fronted Geese in Great Britain as to be limited by the short day lengths during winter at 52°N (Owen 1972a). In this study (36°–42°N), geese spent a relatively constant amount of time at foraging areas during winter months, with a concomitant decline in the amount of time at day roosts when there were fewer daylight hours (Fig. 2). Day length thus had little direct effect on the amount of time spent at field sites, but was the major factor limiting the amount of time allocated to sleeping, alert, and comfort activities at roost sites in mid-winter.

Weather apparently had little measurable effect on the behavior of geese in this study, which is a common finding in studies of wintering waterfowl (Baldassarre et al. 1988). Weather conditions during this study were relatively mild compared to many other wintering areas of geese in North America (cf. Lefebvre and Raveling 1967), except during mid-winter in KB, which was the only location where geese were likely to be exposed to temperatures below their lower critical temperature (Williams and Kendigh 1982).

*Body condition.* If daily energy expenditure remains relatively constant over time, then nutrient intake should closely track body mass. Although data on body mass (Ely and Raveling 1989) were not collected the same year as activity data, seasonal changes in body mass of adult geese did correspond closely to the amount of time allocated to feeding ( $r^2 = 0.701, P < 0.05$ ; Table 6).

Gain in body mass associated with increased foraging in geese during autumn and spring is well documented. In autumn, increase in mass replenishes body stores depleted during migration (Wypkema and Ankney 1979), while in spring increase in mass is a result of hyperphagia mediated by hormonal control in response to increasing day length before migration and reproduction (McLandress and Raveling 1981b, Akesson and Raveling 1981, Gauthier et al. 1984b, Alisaukas and Ankney 1992).

Endogenous reserves act as a buffer by enabling geese to forgo or limit feeding during periods of food shortage, severe weather, or high predation. Even during mid-winter, when geese were leanest, lipid levels were still higher than reported for other species of small-bodied geese (Ely and Raveling 1989). Lipid reserves alone (250 g, of which 240 g were probably available

TABLE 6. Change in body mass (g) of adult Greater White-fronted Geese relative to time spent foraging in southern Oregon and northern California, 1979–1982.<sup>a</sup>

Attribute	Time period					
	Early Autumn	Late Autumn	Early Winter	Late Winter	Early Spring	Late Spring
Adult body mass						
Male	2,283	2,368	2,393	2,114	2,351	2,448
Female	2,040	2,130	2,202	2,003	1,999	2,160
Average adult mass <sup>b</sup>	2,162	2,249	2,298	2,059	2,175	2,300
Average change in body mass <sup>c</sup>	+87	+49	-239	+116	+125	+330
Time spent feeding (min) <sup>d</sup>	173	117	109	149	213	304

<sup>a</sup> Body mass data from 1979–1981 (Ely and Raveling 1989). Activity data from this study.

<sup>b</sup> Combined mass of adult males and females.

<sup>c</sup> Difference in body mass between adjacent time periods, except late spring, when change in mass was calculated as difference between mass first week (2,111 g) and last week of April (i.e., late spring—2,441 g).

<sup>d</sup> Data from Figure 2 and Tables 3 and 4. Calculated as [(min at roost)(% time feeding at roost)] + [(min at field)(% time feeding at field)].

as an energy reserve if 0.25% is structural [Wishart 1979]) were probably sufficient to sustain an active goose in the thermoneutral zone for up to six days, assuming a basal metabolic rate (BMR) of 500 kJ/day for a 1950 goose (Aschoff and Pohl 1970) and a daily energy expenditure of 1250 kJ/day ( $2.5 \times \text{BMR}$ —Drent et al. 1978, Nagy 1987), and energy of lipid oxidation of 39.5 kJ/g (Ricklefs 1974). Energy derived from protein oxidation could sustain fasting geese for a few additional days. Body mass has been reported to be positively correlated to survival in several species of ducks (Haramis et al. 1986, Hepp et al. 1986).

**Predation.** Time allocated to various activities also varies with predation risk (Lima 1987), particularly in flocking birds (Caraco et al. 1980, Lendrem 1984). Hunting is the main cause of the 32% annual mortality in Greater White-fronted Geese in the Pacific Flyway (Timm and Dau 1979). Greater White-fronted Geese fed less, spent more time alert, were disturbed more often, and fed closer to conspecifics during the hunting season than before or after. Interpretation of behavior relative to hunting seasons is complicated, as the opening of the hunting season in the Klamath Basin coincided with a switch in habitat use, and an increase in the number of potential competitors. Despite these confounding factors, the immediate switch to foraging almost exclusively within the refuge boundaries upon the opening of hunting season (in the Klamath Basin) made it apparent that hunting significantly influenced the behavior of these geese, as has been reported for several other species of geese (Owen 1973, Owens 1977, Madsen 1985b, Schultz et al. 1988). Greater White-fronted Geese in western North America may be similar to oth-

er species of geese which exploit high energy foods by being less affected by disturbances than species which only graze (Owen 1972a).

**Social factors.** The decrease in foraging rates and increase in time spent alert and flying by Greater White-fronted Geese when associated with other goose species during autumn and winter may be indicative of interspecific competition for food resources. Lesser Snow Geese utilize many of the same food resources as Greater White-fronted Geese, and significantly outnumber them in California. The aggressive nature of Lesser Snow Geese, their tendency to forage in large dense flocks, and their penchant to take flight with little provocation may have reduced food intake by Greater White-fronted Geese. However, the fact that Greater White-fronted Geese associated with white geese when predation pressure was high were not more likely to be disturbed than those not so associated is an indication that some of the added costs of membership in mixed-species foraging groups (e.g., Stinson 1988) are offset by potential benefits of enhanced predator detection (Morse 1977). For species such as Greater White-fronted Geese, which maintain substantial energy reserves during winter, selection may favor individuals minimizing predation exposure over those maximizing food intake.

Although Owen (1972b) asserted that the bill of the European Greater White-fronted Goose was "completely suited to clipping short herbage," Greater White-fronted Geese may be at a competitive disadvantage when foraging on short green vegetation with Cackling or Ross' Geese, as both these species have small, delicate bills and are extremely adept at grazing. In contrast, Lesser Snow Geese have larger, more powerful

bills than Greater White-fronted Geese (Bolen and Rylander 1978), and may be somewhat more proficient than Greater White-fronted Geese at handling and processing large food items such as potatoes.

Greater White-fronted Geese appear to be generalists and suitably preadapted to exploiting a diversity of agricultural crops which are now their staple food during winter in North America. The ability to use a variety of food resources and the maintenance of substantial energy reserves contributes to flexible time allocation patterns, and is a major reason for the success of this species in North America despite significant hunting mortality and tremendous alterations to habitat in the past century.

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