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Comparative foraging behavior of sympatric Snow Geese, Greater White-fronted Geese, and Canada Geese during the non-breeding season.—Interspecific comparisons of behavior provide a way to organize information for several species that can lead to hypotheses regarding the functional significance of observed interspecific differences (Clutton-Brock and Harvey 1984). Previous studies of goose time-activity budgets (e.g., Frederick and Klaas 1982, Giroux and Bédard 1990, Black et al. 1991, Ely 1992) have focused on single species and collectively were conducted under widely differing environmental conditions. Certain environmental factors are known to affect goose behavioral patterns and may confound direct interpretation of interspecific comparisons (Table 1). These environmental factors include geographic region, weather, presence of heterospecifics, group size, habitat and vegetation type, year, season, age, social status, and gender. We are aware of no studies that have controlled for environmental variation and examined differences in time-budgets solely as a function of species membership. The objective of this study was to identify interspecies differences (and similarities) in foraging behavior of geese during the non-breeding season, while accounting for sources of environmental variation.

Study area and methods.—This study was conducted from November 1991 to February 1992 and October 1992 to February 1993 southwest of Houston, Texas. The area, known as the rice-prairie region of Texas, lies inland from the coastal marshes and extends from Port Lavaca, Texas, eastward to the Louisiana border (Hobaugh et al. 1989, Gawlik 1994). We studied Snow Geese (*Chen caerulescens*), Greater White-fronted Geese (*Anser albifrons*), and Canada Geese (*Branta canadensis*; small races), the three most abundant species of geese wintering in the mid-continental United States (Haskins 1993). A fourth species, the Ross' Goose (*C. rossii*), also occurred in the study area but was much less common than the other three species (Harpole et al., in press).

We selected four groups of agricultural fields as sample sites, two each in Colorado and Wharton counties. Each site was approximately 2000 ha in size and contained the three most common types of ground cover (i.e., plowed soil, rice stubble, and annual plants) (Gawlik 1994). The sequence of visitation to sites was chosen randomly to reduce biases. Each site was observed from a vehicle driven along a pre-established route starting within one hour of sunrise, except when postponed by heavy rain, and ending by early to mid afternoon. Because we were interested in the foraging behavior of geese, we selected for behavior quantification only those flocks in which >50% of individuals were feeding. To reduce the chance of missing rare behavior or losing sight of individuals altogether, we selected only those flocks that provided reasonable visibility (<300 m). Flocks were characterized with regard to their species composition and relative abundances. After a 10-min settling period, flocks were filmed with a high-resolution 8-mm video camera and telephoto lens for about 15 min. Video tapes were later analyzed to construct 5–12 min continuous time budgets for one focal bird (Altmann 1974) of each species visible in mixed-species flocks and two focal birds of the same species for single-species flocks. If a focal bird became obscured during an observation period, the next closest individual of the same species exhibiting the same behavior was chosen to complete the focal sample. Behavioral categories included feeding stationary, feeding locomotion, non-feeding locomotion, resting (head pulled close to body or tucked under wing), comfort (preening and wing stretches), alert (head up), and aggression.

We quantified interspecies differences in the percentage of time spent on each behavior for each of the species-pairs (i.e., Snow and Greater White-fronted, Snow and Canada, and Greater White-fronted and Canada) with paired *t*-tests. We assessed individual variation in

TABLE 1
FACTORS AFFECTING TIME-ACTIVITY BUDGETS OF GESE DURING THE NON-BREEDING SEASON

Study	Species	Source of variation ^a													
		Geographic region	Habitat or vegetation	Weather	Tide	Year	Season	Time of day	Group size	Presence of hetero-specifics	Position within flock	Social status	Age	Gender	
Frederick and Klaas 1982	Snow Goose		S	S, ns ^b		ns		S							
Ydenberg et al. 1983	Barnacle Goose (<i>Branta leucopsis</i>)			S					S						
Black and Owen 1988	Barnacle Goose					S		S							
Gauthier et al. 1988	Snow Goose	S	S	S	S		S								
Black and Owen 1989	Barnacle Goose					S								S	
Davis et al. 1989	Snow Goose		S			ns	S	S						S	
Turcotte and Bédard 1989	Snow Goose														
Ciroux and Bédard 1990	Snow Goose	S				S		S							
Amat et al. 1991	Graylag Goose (<i>Anser anser</i>)			S											
Black et al. 1991	Barnacle Goose		S						S						
Bélanger and Bédard 1992	Snow Goose		S												
Black et al. 1992	Barnacle Goose														
Ely 1992	Greater White-fronted Goose	S	S	S		ns	S	S	S			S, ns ^c			
Schmutz 1994	Emperor Goose (<i>Chen canagica</i>)		S			S									

^a S: statistically significant or used as a classification category; ns: statistically non-significant.
^b Cloud cover was statistically significant, other weather variables were not.
^c Some age and gender classes were statistically significant, others were not.

time budgets within a species by assigning members of single-species pairs randomly to one of two groups for subsequent analyses with paired *t*-tests as outlined above.

Because our sampling framework provided paired data on individuals foraging in the same location at the same time, we were able to control for sources of environmental variation, as identified in other studies (Table 1), such as geographic region, weather, presence of heterospecifics, group size, habitat and vegetation type, year, and season. We accounted for age differences by selecting only adults as focal birds for Snow Geese and Greater White-fronted Geese based on plumage differences. We could not, however, distinguish between adult and juvenile Canada Geese because both age classes have similar plumages. Gender was a potential source of variation we could not control because differences in body size or plumage were not discernable at the distances we viewed the geese. However, gender does not appear to influence significantly time-activity budgets of Snow Geese (Frederick and Klaas 1982, Bélanger and Bédard 1992) and we do not believe it had an effect on our analysis. Finally, our sampling scheme precluded our identifying social status of individuals. We assume that this potential source of variation was distributed randomly among the individuals we examined.

Results and discussion.—The Greater White-fronted Goose was the only species we observed in single-species flocks often enough to analyze the degree to which individual differences in behavior within a species affect time-activity budgets. Time spent on any behavior by Greater White-fronted Geese differed less than 2% among individuals (all tests, $df = 44$, $P > 0.05$). These data provide quantitative support for the notion that individuals of the same species within a flock behave similarly and thus are not completely independent (Gauthier et al. 1988, Giroux and Bédard 1990, Ely 1992). We suggest that individual differences within age and species classes are not a significant source of variation in time-activity budgets of wintering geese.

All three species spent most of their time feeding or in alert behavior, with substantially less time in other behavior (Fig. 1). The large amount of time spent feeding was not unexpected because we restricted our analysis to observations of flocks engaged primarily in feeding, and feeding has been reported as the primary activity for non-breeding geese in other areas (Gauthier et al. 1988, Bélanger and Bédard 1992, Ely 1992). Alert behavior is also a common activity in social birds, and indeed, most explanations of why birds forage in flocks are based on benefits from group feeding or antipredator behavior (Barnard and Thompson 1985). For many species of geese, the greatest cause of direct mortality is hunting (Boyd 1957, Owen 1980, Francis et al. 1992). In our study sites, hunting pressure was heavy and geese were frequently disturbed by nearby shooting; thus we viewed hunters as the main predator on geese. Another potential predator that frequently disturbed feeding geese was the Bald Eagle (*Haliaeetus leucocephalus*). This species is known to prey on geese in other areas (McWilliams et al. 1994) and it occurred regularly at our sites. However, during two years of study in which we recorded 122 eagle sightings, we observed only two attempts by eagles to capture living geese, and neither was successful. We observed coyotes (*Canus latrans*) in the same field with feeding geese only three times, out of 22 total coyote sightings, and they did not attempt to capture the geese.

Interspecific comparisons showed that time spent feeding differed among species by less than 11%, time spent resting differed by less than 8%, time spent alert differed by less than 4%, and other behavior collectively differed by less than 1%. None of these differences was statistically significant for Snow Geese and Greater White-fronted Geese (all tests, $df = 56$, $P > 0.05$) and Canada Geese differed only in the manner in which they fed (Fig. 1). Canada Geese spent more time in feeding locomotion than did Snow Geese ($df = 15$, $P = 0.007$) and Greater White-fronted Geese ($df = 28$, $P = 0.0001$) and less time feeding stationary than did Snow Geese ($df = 15$, $P = 0.059$) and Greater White-fronted Geese ($df = 28$, P

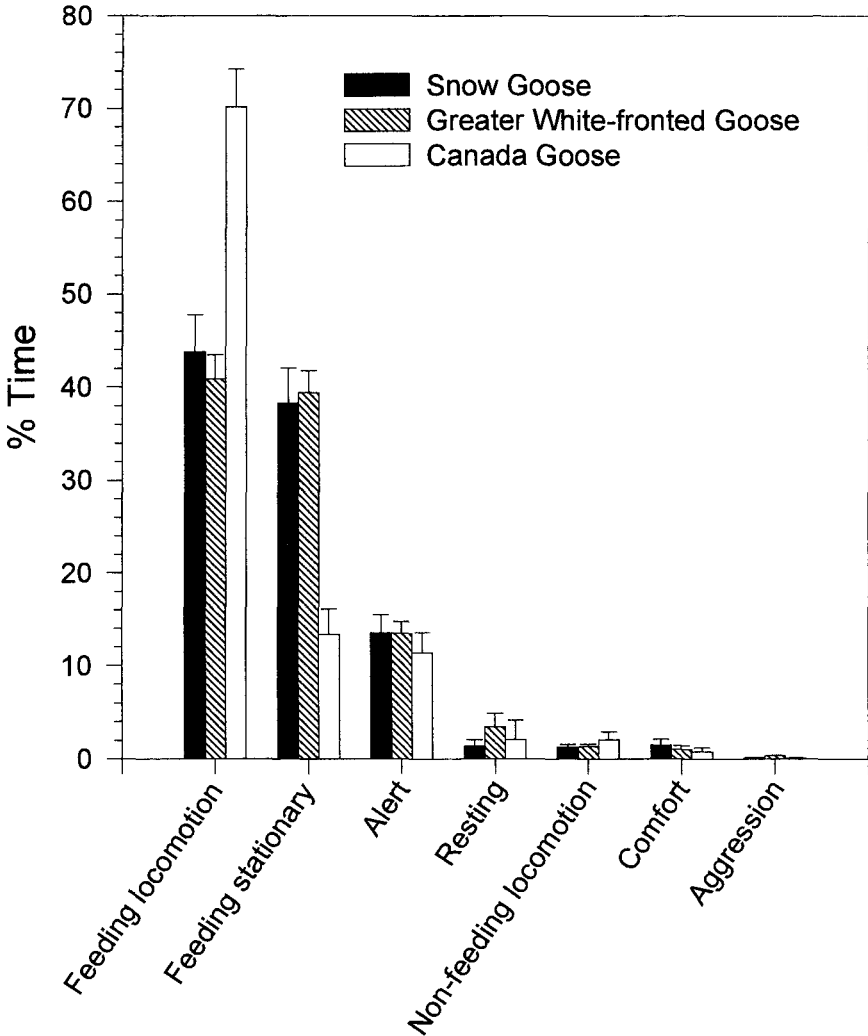


FIG. 1. Time spent on various activities by Snow Geese ($N = 65$), Greater White-fronted Geese ($N = 122$), and Canada Geese ($N = 38$) during the non-breeding season. Bars indicate the mean ± 1 SE. Means represent percentages pooled within a species using one focal bird/species/flock.

= 0.004). These differences in feeding behavior corresponded to differences in diet and morphology. Diet analysis of 16 geese collected by DEG in fields of plowed soil and annual plants within the same study area, showed that subterranean portions of plants made up 27% and 17% of esophageal and proventriculi contents for Snow Geese and Greater White-fronted Geese respectively, whereas Canada Geese contained no subterranean material

(Gawlik 1994). White-fronted Geese and Snow Geese are larger than Canada Geese and more similar to each other in bill morphology. Overall, the smaller-bodied Canada Geese spent a greater proportion of their time walking and feeding on exposed portions of plants, whereas Snow Geese and Greater White-fronted Geese spent more time feeding in one location and consuming underground plant parts. Thus, although the type of feeding behavior exhibited by geese was related to morphology and diet, our results suggest that the overall time devoted to basic daily requirements such as consuming food and avoiding predation was similar for all members of a flock regardless of species.

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DALE E. GAWLIK AND R. DOUGLAS SLACK, *Dept. of Wildlife and Fisheries Sciences, Texas A & M Univ., College Station, Texas 77843-2258.* (Present address DEG: *Everglades Systems Research Division, South Florida Water Management District, P.O. Box 24680, West Palm Beach, Florida 33416-4680.*) Received 7 March 1995, accepted 1 Sept. 1995.

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Survival of radio-collared nestling Puerto Rican Parrots.—A remnant population of the critically endangered Puerto Rican Parrot (*Amazona vittata*) survives in the Luquillo Mountains of northeastern Puerto Rico (Snyder et al. 1987). During the last three decades, intensive research and management have reversed a precipitous population decline to one of continual population growth (Wiley 1980, Snyder et al. 1987, Lindsey et al. 1989, Lindsey 1992). Prior to Hurricane Hugo in 1989, the wild population had grown from 14 birds during the mid-1970s to 47 (Meyers 1995). The hurricane reduced the population to about 22–24 birds; however, by early 1994, the population was estimated at 38–39 individuals (Meyers 1995). Population surveys for late 1994 (post-breeding) and early 1995 were 42 and 33, respectively (F. J. Vilella and F. Núñez, pers. comm.). These data invite optimism for the full recovery of the population because the species has shown the ability to recuperate about 83% of its pre-disturbance numbers within five years following a major disturbance.