

AGE, HABITAT AND TIDE EFFECTS ON FEEDING ACTIVITY OF EMPEROR GEESE DURING AUTUMN MIGRATION¹

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Abstract. I studied feeding activity of Emperor Geese (*Chen canagica*) on the Alaska Peninsula during autumn migration, 1991. Scan samples were used to estimate the proportion of birds feeding in flocks as a measure of feeding intensity. Most geese fed during low tides and roosted during high tides. However, flocks with disproportionately more juveniles continued to feed during high tides in either blue mussel (*Mytilus edulis*) beds (during relatively low high tides) or in vegetated habitats. Feeding intensity was higher in mussel habitats than in mud/sand or vegetated habitats, and juveniles fed more than adults. Juvenile geese probably have greater nutritional needs than adults, and feeding during high tide may represent their attempt to satisfy these disproportionate demands. Vegetated habitats may be used when high value bivalve prey are unavailable due to tidal inundation.

Key words: Alaska Peninsula; bivalve; foraging; intertidal; nutrition; staging.

INTRODUCTION

Emperor Geese stage during autumn and spring migrations in large estuaries along the north coast of the Alaska Peninsula (Petersen and Gill 1982). Foraging ecology of Emperor Geese (*Chen canagica*) during migration is poorly understood. In the only study directly addressing this topic, Petersen (1983) observed that Emperor Geese fed principally on blue mussels (*Mytilus edulis*) and macoma clams (*Macoma* spp.) in intertidal areas and roosted on beaches during high tide (Petersen 1983). This carnivorous diet is unique among geese (Owen 1980). Diet choice and patterns of food acquisition on staging areas are important as survival of juvenile Emperor Geese prior to and/or during autumn migration has been linked to body mass (Schmutz 1993). Also, autumn migration is typically a hyperphagic time for geese when large fat reserves are accumulated (Wypkema and Ankney 1979, Sedinger and Bollinger 1987). Given the relatively low survival of Emperor Geese from autumn to spring as compared with other geese (Schmutz et al., in press), foraging patterns and the resultant energy reserves accumulated while at autumn staging areas may have an important influence on future survival. I examined age ratios and feeding activity within flocks of Emperor Geese to further understand how their foraging behavior during autumn mi-

gration is related to age, habitat, and tidal variations.

STUDY AREA AND METHODS

Staging areas along the Alaska Peninsula are typified by extensive intertidal zones with sandy or muddy bottoms. Daily tidal fluctuations range up to 4 m. Mussel beds are conspicuous and sporadically distributed in the intertidal zone. Macoma clams are buried in the intertidal substrate so their distribution is not as obvious, but most apparent feeding on these clams occurs in areas of mixed sand and mud.

Dunes immediately adjacent to the intertidal zone are dominated by lyme grass (*Elymus arrenarius*). Small amounts of beach pea (*Lathyrus maritimus*) and seabeach sandwort (*Honckenya peploides*) are interspersed within this dune community. Beyond the dune community is tundra dominated by willows (*Salix* spp.), crowberry (*Empetrum nigrum*), and graminoids.

We sampled flocks of Emperor Geese at three of the most heavily used staging areas—Cinder Lagoon, Port Heiden Bay, and Nelson Lagoon (Petersen and Gill 1982). Sampling began with arrival of investigators on 12 September 1991 and was truncated on 15 October 1991 when progressive molt of feathers in the head region made age determination uncertain for some geese.

Behavioral sampling was conducted during a related study of survival of neck-collared geese with a sampling protocol to maximize the number of different geese observed within staging ar-

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eas (Schmutz 1993, Schmutz et al., in press). Tide and weather considerations governed the daily activities of observers and affected the spatial distribution of samples. However, observers visited most areas of goose concentration within staging areas multiple times.

Observers first scanned flocks of ≥ 50 geese with telescopes and recorded numbers of juveniles and adults for all geese that could be fully viewed. Smaller flocks were ignored because of their infrequency and their lower observability (see Discussion). Observers ascertained age from an average of 268 geese per flock. Although proportionally fewer geese were sampled in larger flocks, this proportion was probably still large enough to eliminate any bias induced by non-random positioning within flocks (see Discussion). Total flock size was then visually estimated. Flocks were scanned two more times (once for juveniles and once for adults) to estimate the number of geese that were actively feeding. An instantaneous classification of feeding versus not feeding was assigned to each goose during the scan. Feeding was defined as having the head closer to the ground than the base of the neck and engaged in feeding or searching behavior. For each flock observation, habitat and tidal stage also were recorded. Habitats were designated as mussel beds, mud/sand flats, or vegetated areas, and tide stage was simply recorded as high or low.

Flock size was categorized as 50–99, 100–499, 500–999, and $\geq 1,000$. I then used a weighted four-way analysis of variance (ANOVA) to test the effects of habitat, tidal stage, flock size, and staging area on the proportion of juveniles within flocks of Emperor Geese (Type III SS within PROC GLM of SAS, SAS Institute 1988). I weighted each flock observation by the number of geese sampled from that flock. Customized hypothesis tests for differences in mean proportions were performed with CONTRAST statements within PROC GLM. Parametric tests seemed justified as age ratios within $\geq 90\%$ of treatment blocks were normally distributed, and ANOVA is fairly robust to small departures to normality (Sokal and Rohlf 1981).

The proportions of geese feeding within flocks were normally distributed within most habitat-tide combinations. However, as nearly all geese roosted on mud/sand flats at high tide (see Results), the mean proportion of geese feeding within this block was near zero and the distribution

skewed. Thus, nonparametric tests were used whenever this block of data was involved in analyses of feeding proportions.

I tested for age differences in the proportion of geese feeding within flocks by using the non-parametric equivalent to a paired *t*-test (Wilcoxon signed ranks test, Conover [1980]), with the pairs being the two age classes within each flock. Occasionally, only one age class was sampled, such as when the flock flushed prior to counting all feeding proportions. Flocks with a count for only one age class were excluded from this analysis. I also conducted separate nonparametric, four-way ANOVAs (PROC RANK prior to PROC GLM) on data for each age class to determine if the proportion of geese feeding within a flock was related to habitat, tidal stage, flock size, or staging area. Within each age-specific ANOVA, I weighted each flock observation by the number of individuals of that age class that were sampled from that flock. Parametric contrasts among habitats were performed on exclusively low tide data.

RESULTS

Data were collected from 285 flocks with a median flock size of 325; 89% of flocks had $< 1,000$ geese (Fig. 1). Observers obtained age ratio samples from 88, 77, 64, and 32% of geese within flocks of the four respective categories of flock size (from smallest to largest). Forty-two percent of the variation in age ratios was explained by the four-factor model ($F = 4.6$, $P < 0.001$). Age ratios within flocks varied with respect to habitat ($F = 7.8$, $P < 0.001$) and a habitat \times tidal stage interaction ($F = 2.6$, $P = 0.073$). During high tide, most flocks (76%) were observed in mud/sand flats (Fig. 1). Flocks observed in vegetated areas or mussel beds at this tide stage, however, had higher proportions of juveniles (CONTRAST, $P < 0.001$). At low tide, the vast majority of flocks (93%) were located in some type of intertidal habitat, either mussel beds or mud/sand flats, and had similar proportions of young (CONTRAST, $P = 0.633$).

Age ratios were related to flock size ($F = 4.3$, $P = 0.006$), flock size \times habitat \times tide ($F = 2.9$, $P = 0.033$) and flock size \times habitat \times staging area ($F = 6.0$, $P = 0.015$) interactions, and a staging area \times habitat interaction ($F = 5.4$, $P < 0.001$). Small flocks had proportionally more juveniles and were found disproportionately more often in vegetated habitats, especially during high

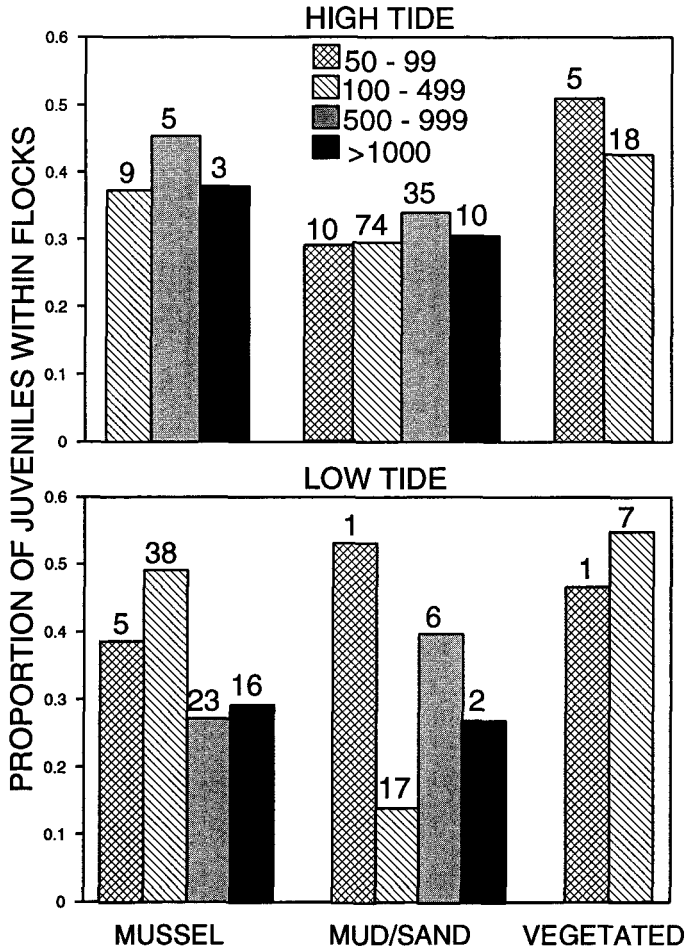


FIGURE 1. Proportions of young within flocks observed during autumn migration on the Alaska Peninsula, 1991. Flocks of four different size categories (50-99, 100-499, 500-999, and >1,000) were sampled at high and low tides in three different habitats. Numbers of flocks sampled per flock size/habitat/tide combination are shown above histogram bars.

tides. Interactions involving staging areas may result from variation in age ratios among staging areas. Aerial photographic surveys of Emperor Geese during autumn indicate variation in age ratios among staging areas, but without a clear annual pattern (W. I. Butler, USFWS, unpubl. data).

The four-factor model explained 60% and 64% of the variation in proportions of geese feeding within flocks for adults and juveniles, respectively ($F = 9.9, P < 0.001$ for adults; $F = 10.0, P < 0.001$ for juveniles). The proportion of geese feeding within each age class was related to the interaction of habitat with tidal stage (Table 1). Most geese roosted on high beaches in mud/sand

habitats during high tide and fed very little (< 3% feeding, Table 2). In contrast, greater feeding activity was observed at low tide, although feeding behavior differed among habitats. During low tide, geese in mussel beds and vegetated areas fed more than geese in mud/sand flats (CONTRAST, $P < 0.001$).

Within flocks of Emperor Geese, the mean proportion of juveniles feeding across all habitat and tide combinations was 6.4% greater than for adults ($P < 0.001$). Mean proportions were similar to those in Table 2, although the number of flocks analyzed ($n = 231$) was somewhat reduced by the exclusion of flocks in which both age classes were not sampled. Juveniles fed at greater in-

TABLE 1. Analysis of variance to test the effects of habitat, tidal stage, flock size, and staging area on the proportions of Emperor Geese observed feeding within flocks.

Source	Adults			Juveniles		
	df ^a	F	P	df ^a	F	P
Habitat	2	1.3	0.262	2	0.2	0.792
Tide	1	0.2	0.689	1	0.1	0.846
Flock size	3	4.5	0.004	3	3.0	0.031
Staging area	2	2.3	0.104	2	4.2	0.016
Habitat × Tide	2	14.1	<0.001	2	12.6	<0.001
Habitat × Flock size	3	1.4	0.240	4	0.9	0.454
Habitat × Staging area	4	1.9	0.117	4	3.9	0.005
Tide × Flock size	2	0.2	0.777	3	0.2	0.897
Tide × Staging area	2	0.8	0.463	2	1.5	0.220
Staging area × Flock size	4	0.8	0.537	4	1.6	0.185
Habitat × Tide × Flock size	2	2.2	0.117	2	2.2	0.112
Habitat × Tide × Staging area	2	0.4	0.686	2	0.1	0.875
Habitat × Flock size × Staging area	1	1.6	0.208	1	3.0	0.084
Tide × Flock size × Staging area	2	0.3	0.759	2	0.1	0.985
Habitat × Tide × Flock size × Staging area	1	0.7	0.402	0		

^a Error degrees of freedom were 232 and 202 for adults and juveniles, respectively.

tensities within all habitat-tide combinations ($P < 0.05$) except for mud/sand flats at low tide ($P = 0.89$).

DISCUSSION

Similar to Petersen (1983), I observed that most Emperor Geese fed intensively on intertidal invertebrates during low tides and roosted during high tides. However, some flocks of geese did not roost at high tide, but, instead, were actively feeding. These flocks were in vegetated areas or in mussel beds during relatively low high tides. Flocks that fed during high tides were disproportionately small, contained proportionately more juveniles, and actively fed on mussels or on beach pea and seabeach sandwort until senescence of these plants in October. This pattern would have been even more apparent if observers could have counted all flocks in vegetated areas. Tall swards of lyme grass often obscured small flocks of families that were feeding in dune habitats and prevented determination of age and feeding activity. Similarly, a failure to sample all geese within flocks probably resulted in more conservative tests. Partial sampling of flocks could be biased towards geese near flock perimeters, which may be disproportionately occupied by family groups (Black et al. 1992). Thus, large flocks would appear in the data as artificially more similar to small flocks as adult geese without young, those near the centers of large flocks, would be under-represented. Overall, while most geese roosted at high tide, flocks with family

groups had a tendency to continue feeding and to use mussel beds or vegetated areas.

During low tides, when most geese were feeding in intertidal areas, geese fed more intensely in mussel beds than in mud/sand flats. Part of this difference may be attributable to habitat-specific foraging behavior relative to how observers defined feeding. Mussel beds were discrete and conspicuous with mussels occurring at fairly high densities, thus geese within mussel beds were able to feed more or less continuously. In contrast, foraging on clams in mud/sand flats required constant movement by geese (behaviors not classified by observers as feeding), which interrupted actual feeding. Geese foraged on clams by repeatedly pumping their feet on recently exposed mud/sand flats, thus creating a slurry of water and sand in which they then performed a tactile sweep for bivalves. Geese followed the

TABLE 2. Proportions of Emperor Geese feeding within flocks observed 12 September–15 October 1991, on the Alaska Peninsula.

Habitat	Age	Tide	
		High	Low
Mussel bed	Adults	0.639 (17 ^a)	0.643 (79)
	Juveniles	0.771 (18)	0.737 (72)
Mud/sand flat	Adults	0.020 (123)	0.244 (22)
	Juveniles	0.024 (104)	0.140 (17)
Vegetated area	Adults	0.367 (20)	0.166 (7)
	Juveniles	0.583 (19)	0.415 (8)

^a Number of flocks sampled.

tide line as it went out, probably because they required a certain level of saturation in the substrate to accomplish this foraging technique. The complexity of this foraging behavior and prior experience also may have contributed to the lower intensity of feeding observed in mud/sand habitats. Bivalves represent a novel food resource to juvenile geese arriving at autumn staging areas, and clams are seemingly more difficult to obtain than mussels due to the complex foot pump and bill sweep foraging method. The lack of age-specific differences in feeding intensity in mud/sand flats, as compared to other habitats, may be due to juvenile inexperience and difficulty in obtaining macoma clams. Indeed, age-specific foraging proficiency has been observed in many bird species (Wunderle 1991) and has been proposed as one of several possible reasons for differences between adult and juvenile foraging behaviors (Marchetti and Price 1989).

Except for in mud/sand flats at low tide (discussed above), juveniles fed more intensely than adults. This disparity may be due to differences in nutritional requirements as has been found for other species (Marchetti and Price 1989). Juvenile geese are smaller than adults during autumn and there is a relationship between body mass and survival among juveniles (Schmutz 1993). Juveniles likely have higher thermoregulatory costs and mass-specific metabolic demands compared to adults and thus may need to feed more to meet their relatively higher energetic needs (Peters 1983). Juveniles of other arctic goose species have smaller pre-migratory lipid reserves than adults (Wypkema and Ankney 1979, Ward and Stehn 1989, Brackney and Hupp, USFWS, unpubl. data). Juvenile Emperor Geese in mid-migration may need to feed more intensively than adults in order to accumulate additional nutrient reserves. Feeding, rather than roosting, during high tide is indicative of these needs. Use of vegetated habitats during high tide probably reflects what is available when intertidal habitats are inundated. However, opportunistic use of mussel beds during certain high tides may reflect the high nutritional quality of mussels. Mussels at Nelson Lagoon were 45–57% protein (dry weight, Petersen 1981), significantly higher than most plants. Although unknown, their lipid content and/or digestibility may be greater than for plants. Autumn staging Emperor Geese may prefer mussels and, for those geese with greater nutritional

demands, they may supplement their diet with plant foods (notably beach pea and seabeach sandwort) when mussels become unavailable.

Greater feeding intensity in juveniles as compared with adults during autumn staging has been observed for other geese including Black Brant (*Branta bernicla nigricans*) (Ward and Stehn 1989), Lesser Snow Geese (*Chen caerulescens caerulescens*) (Frederick and Klaas 1982), and Cackling Canada Geese (*B. canadensis minima*) (Sedinger and Bollinger 1987). Evidence from these studies and mine may reflect a general pattern of disproportionate energetic demands on juvenile arctic geese during autumn migration. Thus, juvenile geese are at greater risk during the energetically demanding period of migration (Owen and Black 1989, Schmutz 1993). Emperor Geese are relatively unique in their use of animal foods to meet these demands. Further study of the availability of staging habitats, diet preference, and the nutritional quality of forage would provide important information on the relative value of staging habitats to Emperor Geese.

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LITERATURE CITED

- BLACK, J. M., 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.
- CONOVER, W. J. 1980. Practical nonparametric statistics. Second edition. John Wiley and Sons, New York.
- FREDERICK, R. B., AND E. E. KLAAS. 1982. Resource use and behavior of migrating Snow Geese. *J. Wildl. Manage.* 46:601–614.
- MARCHETTI, K., AND T. PRICE. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev.* 64:51–70.
- OWEN, M. 1980. Wild geese of the world. Batesford, London.
- OWEN, M., AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *J. Anim. Ecology* 58:603–617.
- PETERS, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, England.
- PETERSEN, M. R. 1981. Populations, feeding ecology and molt of Steller's Eiders. *Condor* 83:256–262.
- PETERSEN, M. R. 1983. Observations of Emperor

- Geese feeding at Nelson Lagoon, Alaska. *Condor* 85:367-368.
- PETERSEN, M. R., AND R. E. GILL, JR. 1982. Population and status of Emperor Geese along the north side of the Alaska Peninsula. *Wildfowl* 33:31-38.
- SAS INSTITUTE, INC. 1988. SAS/STAT user's guide, 6.03 ed. SAS Institute, Cary, NC.
- SCHMUTZ, J. A. 1993. Survival and pre-fledging body mass in juvenile Emperor Geese. *Condor* 95:222-225.
- SCHMUTZ, J. A., S. E. CANTOR, AND M. R. PETERSEN. In press. Seasonal and annual survival of Emperor Geese. *J. Wildl. Manage.* 58.
- SEDINGER, J. S., AND K. S. BOLLINGER. 1987. Autumn staging of Cackling Canada Geese on the Alaska Peninsula. *Wildfowl* 38:13-18.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. Second edition. W. H. Freeman, New York.
- WARD, D. H., AND R. A. STEHN. 1989. Response of Brant and other geese to aircraft disturbance at Izembek Lagoon, Alaska. Final Report, U.S. Fish and Wildl. Serv., Anchorage, AK.
- WUNDERLE, J. M., JR. 1991. Age-specific foraging proficiency in birds. *Current Ornith.* 8:273-324.
- WYPKEMA, R.C.P., AND C. D. ANKNEY. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. *Can. J. Zool.* 57:213-219.