

SURVIVAL AND BROOD REARING ECOLOGY OF EMPEROR GEESE

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SURVIVAL AND BROOD REARING ECOLOGY OF EMPEROR GEESE

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Abstract

Emperor Geese (*Chen canagica*) breed on the Yukon-Kuskokwim Delta in an area inhabited by three other goose species. Whereas populations of other geese increased since the mid 1980s, Emperor Goose numbers remained low. Because survival and habitat selection by broods of Emperor Geese had not been studied previously and numbers of predatory Glaucous Gulls (*Larus hyperboreus*) had recently increased, I studied brood rearing ecology of Emperor Geese during 1993–1996 to assess whether this seasonal period could be limiting population growth.

Survival of goslings to 30 days varied among years from 0.32 to 0.70 and was primarily influenced by mortality during the first five days after hatch. Other goose species with similar rates of gosling survival are increasing rapidly. Survival of Emperor Goose goslings was lowest in 1994, when unusually heavy rainfall occurred during early brood rearing. Using a long-term data set from Izembek National Wildlife Refuge, sizes of families in fall ($n = 23$ years) were related to rainfall during early brood rearing. Gosling survival was lower and gull disturbance of broods greater in 1993–1994 than in 1995–1996. Although goslings were commonly consumed by Glaucous Gulls, gull diets during 1993 were similar to those observed in the 1970s.

Across a broad scale, broods of Emperor Geese ($n = 56$) strongly selected habitats dominated by *Carex subspathaceae*, *Carex ramenskii*, and unvegetated areas interspersed among these forage species, as determined from telemetry. These selected habitats comprised one-third of all available habitat. Habitat selection by the composite goose community (dominated by Cackling Canada Geese [*Branta canadensis minima*]) was assessed by feces collections and differed substantially from that of Emperor Geese.

Broods of Emperor Geese spent more time feeding during 1993–1996 than during an earlier study in 1985–1986. During 1994–1996, feeding rates of gosling and adult females was related more to total goose density than to Emperor Goose density. Although Cackling Canada Geese exhibited strongest selection of other habitats, their

greater overall abundance resulted in numerical equivalence to Emperor Geese in habitats preferred by Emperor Geese. Interspecific competition for food has impacted behavior in Emperor Geese, which may impact growth and survival of juvenile geese.

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Chapter 1

General Introduction

Emperor Geese (*Chen canagica*) are one of four species of geese that nest on the Yukon-Kuskokwim Delta (YKD), Alaska. The YKD is one of the world's most important waterfowl breeding areas, in some years supporting more than half a million geese (Spencer et al. 1951). Geese are an important food resource for local people (Klein 1966, Sedinger 1996) and management of the four species of geese is a high profile and often contentious issue (Mitchell 1986). Emperor Geese are of particular concern because of their stagnantly low population size.

Emperor Geese, Cackling Canada Geese (*Branta canadensis minima*), Greater White-fronted Geese (*Anser albifrons*), and Black Brant (*B. bernicla nigricans*) all declined markedly in numbers between the 1960s and mid 1980s, with harvest on both breeding and wintering areas suspected to have contributed to these trends (Raveling 1984, King and Derksen 1986). Harvest restrictions and agreements between federal, state, and native organizations were implemented in the mid 1980s (Pamplin 1986, Sedinger 1996), and during the next decade numbers of Cackling Canada Geese and Greater White-fronted Geese more than doubled (Bowman et al. 1999). However, numbers of Emperor Geese remained stable at a size well below the population management goal of the U. S. Fish and Wildlife Service. It is unclear what has contributed to persistence of this low population size.

Population trends are a product of the various components of survival and reproduction. For Emperor Geese, some of these demographic components are well studied. For instance, long-term data on clutch size and nest success exists, and these factors have not substantively contributed to observed population trends (Eisenhauer and Kirkpatrick 1977, Petersen 1992, Schmutz unpublished data). More limited information

also exists on adult survival (Schmutz and Morse 2000) and breeding propensity (Schmutz 2000), with no clear indication that patterns in these demographic parameters are responsible for the comparatively low population growth rate of Emperor Geese. In contrast, no prior information exists concerning survival of Emperor Goose goslings, yet survivorship in juvenile geese can be highly variable and sensitive to changes in the breeding environment (Sargeant and Raveling 1992, Sedinger 1992).

The breeding environment has progressively changed for Emperor Geese in that numbers of a primary gosling predator, the Glaucous Gull (*Larus hyperboreus*), approximately doubled between the mid 1980s and mid 1990s (Bowman et al. 1997). Similarly, numbers of potentially competing geese - Cackling Canada and Greater White-fronted Geese - also more than doubled during this same time period (Bowman et al. 1999). These changes could have both direct and indirect effects on juvenile survival of Emperor Geese. Increased numbers of Glaucous Gulls may directly increase gosling mortality through predation. Increased numbers of competing geese may indirectly affect survival by reducing the amount of food available to goslings on a per capita basis. Reduced food availability results in slower growth in goslings (Lindholm et al. 1994, Sedinger et al. 1998), which correspondingly affects late summer - early fall survival of Emperor Geese (Schmutz 1993) and other species of geese (Sedinger et al. 1995, van der Jeugd and Larsson 1998, D. Ward unpublished data). The relevance of such a competitive process depends upon whether Emperor Geese share habitats with other geese during brood rearing. Another environmental change, shifts in long-term summer temperatures and precipitation patterns, may also be relevant for goslings, which are vulnerable to hypothermia, particularly when wet (Poczopko 1968, Beasley and Ankney 1992).

I initiated this study in 1993 to address two broad objectives. My first objective was to document rates of gosling survival and the effects of Glaucous Gulls and precipitation on mortality, and this objective led to several more specific hypotheses.

One hypothesis was whether the mean gosling survival rate (across four years, 1993–1996) differed substantially from other sympatric goose species. A second hypothesis was whether predation rates of Glaucous Gulls during brood rearing affected gosling survival, which I addressed by using a proxy for gull predation - the frequency of gull disturbance of goose broods. By using data from an earlier study (Strang 1976), I also addressed the hypothesis of whether Glaucous Gulls in 1993 relied more on goslings and other birds for food during brood rearing than they did in the 1970s, when goose abundances differed. A fourth hypothesis within this objective was whether the amount of rain during early brood rearing, when goslings are most susceptible to hypothermia, affected survival, which was measured with a long-term index - the size of families during fall migration.

My second broad objective was to ascertain what habitats are used by broods of Emperor Geese and how such use may be affected by other geese, because such patterns may impact the ability of Emperor Goose goslings to acquire adequate food. Although geese are highly selective foragers (Sedinger and Raveling 1984) and captive Emperor Goose goslings selected a small set of plant species (Laing and Raveling 1993), little information existed on what habitats wild Emperor Goose broods used. I therefore used radio-telemetry to assess broad scale habitat use of Emperor Goose broods, with the straw man hypothesis that broods selectively (non-randomly) used habitats. More importantly, I addressed the hypothesis that Emperor Goose broods selected different habitats than broods of Cackling Canada Geese and Greater White-fronted Geese.

At a finer scale of investigation, I examined the behavioral use of the most preferred set of habitats. Specifically, I addressed the hypothesis that time spent feeding by Emperor Goose broods had increased since a similar study 10 years previous. Further, I tested the hypothesis that such behavioral changes were in response to increased numbers of competing geese, principally Cackling Canada Geese.

This set of objectives and hypotheses asks how survival of goslings varies and

whether it is impacted by predatory Glaucous Gulls, what habitats are used by Emperor Geese, how such use differs from other sympatric goose species, and how Emperor Geese behaviorally use these habitats. The behavioral and spatial patterns of habitat use ultimately affect juvenile survival because they affect what plants goslings consume and how rapidly goslings grow. Collectively, this body of work contributes towards an understanding of whether population growth of Emperor Geese is limited by growth and survival of juveniles.

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Chapter 2

Survival Estimation and the Effects of Dependency among Animals

Abstract: Survival models assume that fates of individuals are independent, yet the robustness of this assumption has been poorly quantified. We examined how empirically derived estimates of the variance of survival rates are affected by dependency in survival probability among individuals. We used Monte Carlo simulations to generate known amounts of dependency among pairs of individuals and analyzed these data with Kaplan-Meier and Cormack-Jolly-Seber models. Dependency significantly increased these empirical variances as compared to theoretically derived estimates of variance from the same populations. Using resighting data from 168 pairs of black brant (*Branta bernicla nigricans*), we used a resampling procedure and program RELEASE to estimate empirical and mean theoretical variances. We estimated that the relationship between paired individuals caused the empirical variance of the survival rate to be 155% larger than the empirical variance for unpaired individuals. Monte Carlo simulations and use of this resampling strategy can provide investigators with information on how robust their data are to this common assumption of independent survival probabilities.

INTRODUCTION

Knowledge about patterns of survival rate variation is vital to understanding population processes of animals. Our ability to achieve such knowledge is dependent on the use of an appropriate and accurate statistical model for each ecological study. Over the last 10-15 years there has been a large volume of literature produced concerning appropriate statistical methods for estimating survival rates of animals (Brownie et al.

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1985, McCullough and Barrett 1992, Lebreton and North 1993). For studies where all marked animals can be reliably located, i.e., resighting or recapture parameters are 1.0 and do not need to be estimated, a commonly used survival model is the Kaplan-Meier (KM) Product Limit method (Pollock et al. 1989). Parametric alternatives to the KM estimator exist, but they require more stringent assumptions (Bunck and Pollock 1993). When recapture parameters must be estimated, the Cormack-Jolly-Seber (CJS) models (Pollock et al. 1990, Lebreton et al. 1992) are the most frequently used. These survival models all make a common assumption that survival rates among individuals in a population are independent.

Biological intuition tells us that independence in survival among individuals is not likely to be strictly true. Among social animals, a specific mortality force or factor in a local area (e.g. the attack of a predator, a flood, or perhaps a poor quality habitat patch) that has the capacity to affect more than one animal (e.g., the predator or hunter could kill more than one animal) would more similarly affect the likelihood of survival of animals within that local group than animals of some other group. If a pair of geese fly by a hunter and one goose is killed, its mate is more likely to be killed than are other geese in that population (Prevett and MacInnes 1980).

The presence of dependence in survival probabilities is believed to have no effect on point estimates of survival, but it is expected to result in an underestimation of the true variance (Pollock and Raveling 1982, Nichols et al. 1982, McCullagh and Nelder 1989:124-128). Perhaps because of this expectation of no bias, the assumption of independence among animals has received only perfunctory recognition. However, lack of independence and heterogeneity in survival probabilities are the two main reasons for overdispersion in data which can then lead to poor model selection and model fit (Anderson et al. 1994). Survival estimation of precocial birds prior to fledging is one area of research where investigators have addressed this assumption of independence. Such attention is not surprising given the high mortality rates of these young and the

frequency of observations of predation events affecting multiple members of a given brood (Rotella and Ratti 1992). Winterstein (1992) developed χ^2 procedures to test for lack of independence in survival among broods. Other investigators changed the sampling unit to broods rather than individuals (Savard et al. 1991, Rotella and Ratti 1992). This technique may result in biased estimates of survival when ultimately the number of individuals, not broods, is the population statistic of concern. Flint et al. (1995) modified variances to enable estimation of individual survival rates when dependence among brood mates exists. Essentially, they derived point estimates using individuals as the sampling unit, yet derived estimates of variance by using broods as the sampling unit with a weighting factor based on the number of individuals within a brood. Although their variance equations result in larger, and thus more conservative variances, they are still theoretical variances that are provided with no knowledge of the extent of true variance inflation that occurs due to dependency. Additionally, it should be noted that the procedures used in the above studies of precocial birds would not be readily applicable to CJS models.

Until very recently, the influence of dependency on variance inflation, parameter bias, and model selection remained poorly quantified. Using simulated data and ring recovery models (Brownie et al. 1985), Zablán (1993) found that dependency among survival probabilities of individuals can be an important factor affecting the true variance of a survival estimate. Anderson et al. (1994) conducted extensive simulations of data analyzed with CJS models and found that the ability to select the most appropriate model, as judged by a minimization of residuals, was adversely affected by dependency. Still, the effect of dependent survival probabilities on estimators of survival for real animal populations remains unquantified.

Our objective is to estimate the inflation of variance that occurs when dependency in survival exists. We will use simulated data to demonstrate to what extent known amounts of dependency result in inflation of the estimated variance when using

KM and CJS models. These results should complement existing simulations for ring recovery models (Zablan 1993) and provide investigators a means for evaluating *a priori* how much bias may exist when estimating survival for their particular study. We will then demonstrate a method for detecting variance inflation in real data sets, provided some *a priori* information exists on associative status among individuals. To demonstrate this technique, we will use resampling procedures and CJS models with field data from a study of black brant (*Branta bernicla nigricans*).

METHODS

KM analysis of simulated data

We iteratively created sample populations, each comprised of 100 animals. Within each population, each animal was subjected to a baseline daily survival probability of 0.99 that, for some brief period of time, dropped below 0.99 (Fig. 2.1). For a population where all 100 animals had independent survival probabilities, the timing of this drop in survival probability was randomized among the 75 day survival period for each of the 100 animals. To simulate a population with correlated survival probabilities, the timing of this drop in survival probability was randomized for 50 of the 100 individuals and then each of these 50 animals was "paired" with a second individual with an identical hazard function. By having identical hazard functions, two animals would not necessarily die on the same day, but they were more likely to do so than animals with differing hazard functions. The strength of this correlation in survival probability was affected by altering the depth and breadth of this drop in survival probability.

Each animal within each population had its fate ascertained at 15, 30, 45, 60, and 75 days. We then used a KM estimator (Pollock et al. 1989) to calculate survival to day 75 for each population of 100 animals. By iteratively creating and analyzing data from 1000 such populations (1000 for each of two scenarios - dependent and independent survival probabilities), we could calculate both an empirical variance of the mean estimate of survival and the mean of the 1000 theoretical variances normally calculated

by KM methods. The expectation was that mean theoretical variances would be equivalent for both independent and dependent scenarios, but that the empirical variance for the dependent scenario would be larger than the empirical variance for the independent scenario. The amount of this disparity in empirically derived estimates of variance should be related to the degree of dependency among individuals. We examined correlation coefficients (CVs) to compare these empirical variances from the independent and dependent scenarios.

CJS analysis of simulated data

As with the previous simulations, we again compared empirical variances from sets of 1000 iteratively created populations. However, for these CJS simulations, we used only one level of correlation, a 100% correlation in survival probability. We also incorporated another factor, heterogeneity in survival probabilities, since both heterogeneity and non-independence may be common and can similarly result in overdispersed data sets (Anderson et al. 1994), and thus, their relative contributions to variance inflation may be difficult to detect in real data sets.

We simulated 300 animals per population and 1000 such populations for each of four different scenarios: independence and homogeneity (in survival probability), dependence and homogeneity, independence and heterogeneity, and dependence and heterogeneity. Within a population, we created dependency in survival probability by first creating random capture histories for each of 150 individuals. We then duplicated these 150 histories to arrive at 300 total individuals. These 300 individuals consisted of 150 "pairs" in which survival probability of members of a pair were perfectly correlated. To create the random capture histories, we generated random numbers from a uniform 0-1 distribution and compared them to a mean survival rate of 0.7 and resighting probability of 0.8. We assigned 0s and 1s to an individual's capture history based on whether these random draws were above or below these means. To create heterogeneity in survival within a population, we used this same randomization process except that we

divided individuals into two equal groups - one group with a mean survival probability of 0.9 and the other group using a mean survival probability of 0.5.

We used program RELEASE (Burnham et al. 1987) to estimate survival rates and theoretical variances for each population of 300 animals. From each set of 1000 such populations we computed an empirical variance and a mean theoretical variance, and then we compared these among the four different dependency-heterogeneity scenarios.

CJS analysis of Black Brant data

To examine dependency effects in a real population, we used data from a long-term study of black brant. Black brant have been ringed with metal and plastic tarsal rings each summer since 1985 at the Tutakoke River colony on the Yukon-Kuskokwim Delta, Alaska. During winter 1991-92, 168 uniquely identifiable pairs from the Tutakoke colony were observed in Baja California, Mexico. Brant were again resighted the following two years on the Yukon-Kuskokwim Delta in summer and at Izembek Lagoon, Alaska, in autumn. Using these resighting data, we constructed a 336 x 5 capture history matrix from which to analyze survival rates. For this paper, we present data for only one period - survival from winter in Mexico to summer on the Yukon-Kuskokwim Delta, 1992.

We then analyzed these brant data in two different ways. In one analysis method (SINGLE analysis), we selected only one individual from each pair for each sample population, while in the second analysis method (PAIR), only half the pairs were selected for a given sample population, but both members of each selected pair were included in the analysis for that population. For each analysis method, we iteratively created 1000 populations, each comprised of 168 individuals (half of the 336 brant). As with the previous simulation, we used RELEASE to compute a survival rate and theoretical variance for each population and then calculated empirical means from the sets of 1000 iterations. We also calculated a standard variance inflation factor (VIF) from the analysis of each population. This statistic was simply the chi-squared goodness-of-fit statistic

divided by the degrees of freedom (Lebreton et al. 1992).

For the SINGLE analysis, we randomly selected which member of each known pair to include in a given population. Thus, each population was comprised of 168 birds, none of which were paired (Table 2.1). By repeating this process 1000 times, all 336 birds contributed to the overall analysis, but all birds were likely independent from each other in that none were paired. For the PAIR analysis, we randomly picked which 84 of the 168 pairs to include in a given population and then included both birds from the selected pairs. As with the SINGLE analysis, each population was thus comprised of 168 birds and by creating 1000 such populations, all 336 birds contributed to the overall analysis. By using a resampling method structured relative to pair status, we created two data sets whose only difference was the relative pair status of individuals.

RESULTS AND DISCUSSION

KM analysis of simulated data

Applying the KM estimator to simulated data, we found that empirically estimated CVs were greater than CVs calculated from theoretical estimates of variance for all degrees of correlation simulated. The rate of increase in CV for the dependent case relative to the independent case was 0.76% per 1% increase in correlation of survival times (linear regression, $R^2 = 0.850$, $P = 0.026$) (Fig. 2.2). As expected, empirical variances virtually matched mean theoretical variances for all independent cases.

Analysis of simulated data using KM estimators clearly showed that dependency in survival probabilities results in underestimation of the theoretical variance. The extent of underestimation was determined by the strength of correlation among individual survival probabilities, with even low levels of dependency causing underestimation of variances (Fig. 2.2).

CJS analysis of simulated data

With no dependency or heterogeneity in data, empirical and theoretical variances were identical; however, with imposed dependency, empirical variances exceeded mean

theoretical variances by 35% (Table 2.2). Heterogeneity did not further increase empirical variances.

Our Monte Carlo simulation of dependency and heterogeneity effects on CJS models was simplistic, but provided evidence that dependency can cause substantial underestimation of true variances. These results are consistent with the more extensive simulations done by Zablan (1993) for ring recovery data. The lack of heterogeneity effects on bias should not necessarily be interpreted as robustness to this factor as this simulation over-simplifies real heterogeneity. Unlike this simulation where heterogeneity was induced independently for each sample period, patterns of heterogeneity that persist between multiple sampling periods have greater effects on bias and precision (K. H. Pollock, pers. comm.). Further, models explicitly accounting for heterogeneity would be preferable, but these models are limited in the range of parameters they can consider, e.g., they assume a constant survival rate (Rexstad & Anderson 1992). Additional Monte Carlo simulation of dependency effects can be readily accomplished with the EBV (extra-binomial variation) option within RELEASE.

CJS analysis of Black Bant data

Mean survival rates calculated from resightings of black brant were virtually identical for the PAIR ($\bar{x} = 0.772$) and SINGLE ($\bar{x} = 0.773$) data sets. Using the PAIR data, the empirical estimate of variance (0.00092) was 155% larger than the empirical estimate of variance for the SINGLE data (0.00036). Mean theoretical estimates of variance were essentially identical for the two data sets. These results suggest that theoretically derived variances may strongly underestimate true variances when survival probabilities are not independent.

Examination of VIFs, however, were not entirely consistent with this result and lead us to be cautious in our interpretations. The mean VIF for the SINGLE data set was 2.79 whereas for the PAIR data set it was 3.0. Although the VIF increased between the two data sets, as expected, this represents only a 7% increase in VIF due to dependency;

much smaller than the 155% difference between empirical variances. It is presently unclear why these percent increases are so different, but one possibility is that the standard VIFs do not accurately account for the increase in variation due to dependency.

To further investigate this unexpected result, we randomly split the brant data set into two separate sets of 84 pairs each and then reiterated the analysis procedure for the two different data sets. For the first of these data sets, the difference between empirical variances for the dependent and independent cases was 265%, whereas the difference between VIFs for the two cases was 5%. For the second of these data sets, empirical variances differed by 71% and VIFs differed by 6%. Still, no clear relation existed between percent changes in empirical estimates of variance and VIFs.

The results from this resampling method indicate that pairing in brant is a significant source of overdispersion in data and can result in underestimated variances. However, as indicated by the mean VIF of 2.79 for the SINGLE data, these brant data contain overdispersion beyond what is induced by pairing status. This overdispersion may result from additional dependency in survival rates, possibly among other family members or larger social groupings (Reed et al. 1989, Ely 1993). Alternatively, other sources such as heterogeneity in survival may exist. Not all components of the Tutakoke River colony are equally accessible to hunters during the non-breeding season, which may lead to variable survival probabilities among individuals.

We have applied this resampling method to just one population at one point in time, the Tutakoke River brant colony, 1991-92. This method should be replicated with other data sets to further evaluate its behavior. Although presently suggestive of inadequate variance correction by VIFs, replication is needed as other data sets may have different inherent properties (Hulbert 1984).

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Table 2.1. Example of how individuals were selected for analysis relative to pairing status. Two different scenarios were used: One where individuals were known to be paired (PAIR data, dependent case) and one where individuals were known not to be paired (SINGLE data, independent case). The X denotes that individuals were selected for this particular sample population. For the dependent case, 84 of the 168 pairs were randomly selected and both pair members included in the analysis. For the independent case, one of the two members of each pair was selected thus resulting in 168 individuals in the analysis.

Brant no.	Pair no.	Dependent case	Independent case
1	1		
2	1		X
3	2	X	X
4	2	X	
5	3		
6	3		
7	4	X	
8	4	X	X
9	5	X	
10	5	X	
11	6		X
.	.		
.	.		
.	.		
336	168		

Table 2.2. Analysis with CJS models of simulated data containing heterogeneity. Monte Carlo data were generated under four different scenarios of dependency and heterogeneity in survival probabilities among individuals.

	Mean survival rate	Empirical variance	Mean theoretical variance
No dependence, no heterogeneity	0.7008	0.0013	0.0012
Dependent pairs, no heterogeneity	0.7037	0.0023	0.0012
No dependency, two levels of heterogeneity	0.7026	0.0011	0.0011
Dependent pairs, two levels of heterogeneity	0.7038	0.0021	0.0011

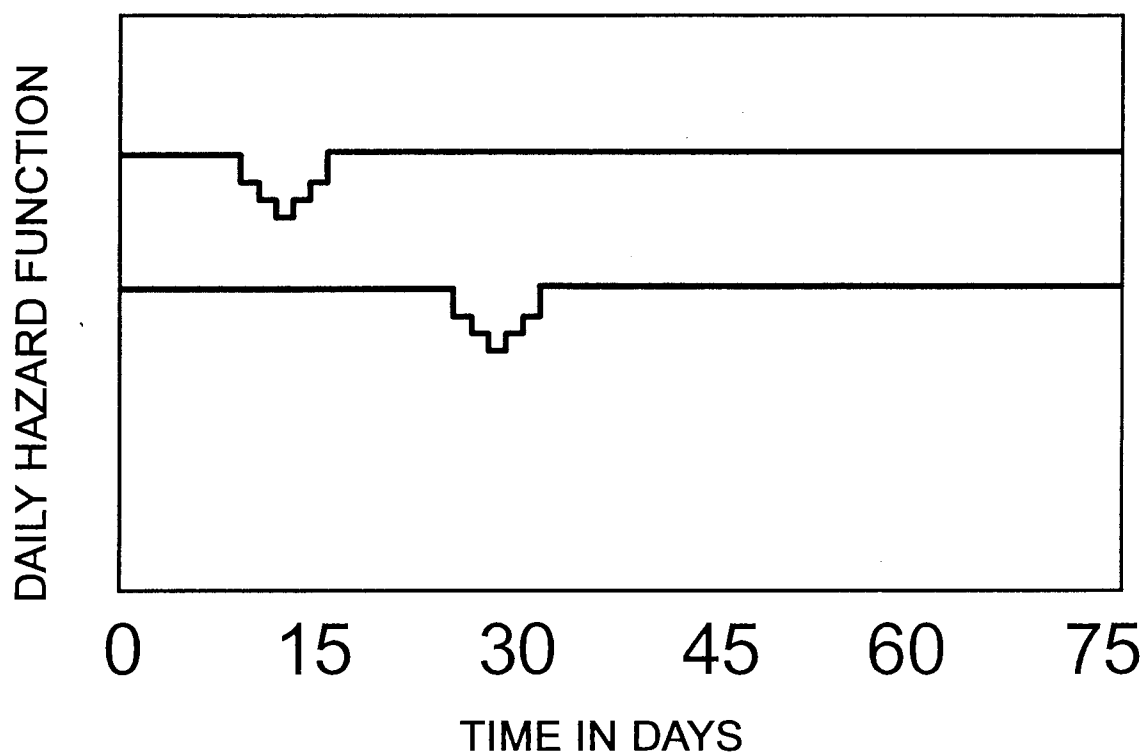


Figure 2.1. Example of daily hazard function for two simulated individuals. Both individuals experience a temporary drop in survival probability during some part of the 75 day period. For populations with dependency, these hazard functions were identical within pairs of individuals. For the independent case, we randomly determined when a temporary drop in survival probability occurred for each hazard function.

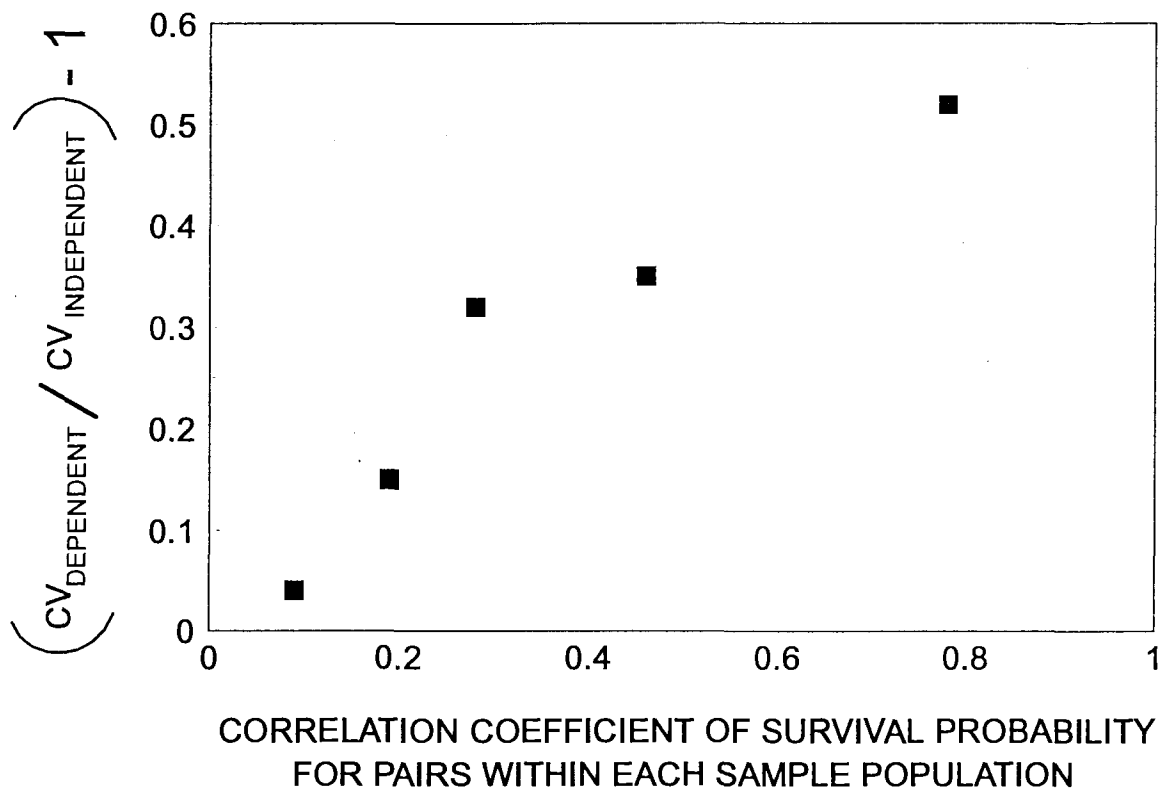


Figure 2.2. Relationship between dependency and variances for survival estimates. We calculated the amount of dependency in survival probability among individuals and the amount of increase observed in the empirical estimate of variance for a survival estimate. Monte Carlo simulations of pairs of individuals were analyzed using Kaplan-Meier estimators.

Chapter 3

Geographic, Temporal, and Age-specific Variation in Diets of Glaucous Gulls in Western Alaska

Abstract. We collected boluses and food remains of adult Glaucous Gulls (*Larus hyperboreus*) at or near nests and chicks, and digestive tracts from adults at three sites on the Yukon-Kuskokwim Delta, Alaska that differed in proximity to marine and terrestrial foods. We observed both geographic and temporal variation in diet; gulls consumed proportionately more terrestrial prey after peak hatch in late June, and gulls near the coast consumed proportionately more marine prey than gulls at two inland areas. Goslings occurred in > 60% of all samples from these inland areas. We compared these data to those from a previous study in western Alaska and found no marked differences. Evidence for similar patterns of geographic and temporal variation in diet was found using measurements of stable-carbon and nitrogen isotopes in gull and prey tissues. Stable isotope analysis further revealed that adult gulls consumed proportionately more marine prey (saffron cod, *Eleginus gracilis*) than they fed to their young. Using isotopic models, we estimated that 7-22% and 10-23% of the diet of adult and juvenile Glaucous Gulls, respectively, was comprised of terrestrial species. In addition to significant age-related variation, dietary estimates varied among geographic areas and between pre- and post-hatch periods. Overall, our isotopic estimates of the contribution of terrestrial prey to the diet of Glaucous Gulls was less than what may be inferred from conventional methods of diet analysis. Our study emphasizes the benefit of combining stable-isotope and conventional analyses to infer temporal and geographic changes in diet of wild birds and

other organisms.

INTRODUCTION

Large gulls (*Larus* spp.) are well documented as opportunistic predators of young birds (Erikstad 1990, Spear 1993, Emslie et al. 1995). In particular, Glaucous Gulls (*L. hyperboreus*) have long been known to commonly prey on young waterfowl (Strang 1976, Swennen 1989, Barry and Barry 1990). However, Glaucous Gulls are coastal marine in distribution (Grant 1986), and in some areas they appear to rely predominantly on a marine diet, notably coastal fish and mollusks (Ingolfsson 1967). Both individual (Pierotti and Annett 1990) and inter-colony (Strang 1976, Barry and Barry 1990) variations among gulls in their prey choice have been documented frequently.

The Yukon-Kuskokwim Delta (YKD), Alaska, is an expansive and important breeding area for waterfowl (Spencer et al. 1951) and shorebirds (Gill and Handel 1990). Glaucous Gulls, along with Arctic foxes (*Alopex lagopus*) and jaegers (*Stecorarius* spp.), are the only significant predators of eggs and young waterfowl on the YKD. Because of concerns about factors affecting the population dynamics of these waterfowl, Strang (1976, 1982) investigated feeding ecology of Glaucous Gulls on the YKD in 1972-1974 and 1979. He assayed the diet spectrum of gulls by examining boluses (regurgitated pellets of indigestible material) and food remains at nests or feeding areas, and digestive tracts of harvested birds. Through studies at two different sites on the YKD in different years, he demonstrated geographic and/or annual variation in diet as well as a within-year seasonal shift. At the more coastal site, Kokechik Bay (Fig. 3.1), where gulls nested in small colonies, Glaucous Gull diets were comprised mostly of fish species, particularly saffron cod (*Eleginus gracilis*). However, after peak hatch of gulls and geese in late June, birds also constituted a significant part of gull diets. At the more inland site, Old Chevak, where gulls nested as isolated pairs, gull diets were more terrestrial-based throughout the season than at Kokechik Bay, but similarly showed an apparent shift towards avian prey after peak hatch (Strang 1976, 1982).

Declines in waterfowl populations on the YKD were first noticed in the late 1960s and early 1970s (Raveling 1984, King and Derksen 1986). Since 1985, populations of Cackling Canada (*B. canadensis minima*) and Greater White-fronted Geese (*Anser albifrons*) have risen steadily. However, Emperor Goose (*Chen canagica*) numbers have remained relatively low (Petersen et al. 1994), and Spectacled Eiders (*Somateria fischeri*) have continued a precipitous drop in numbers (Stehn et al. 1993) and have recently been classified as a threatened species. It is unclear to what extent Glaucous Gulls have contributed to these population changes. No population estimates for Glaucous Gulls exist prior to the mid-1980s. More recently, gull numbers on the YKD in 1993 and 1994 were 45% greater than numbers estimated in 1985-1986 (Bowman et al. 1997). Thus, the ratio of predators to prey probably has varied substantially. It is unknown whether a change in the relative numbers of predator and prey would influence the magnitude of predation on waterfowl, but other studies in multiple-prey systems indicate such potential exists (Sodhi and Oliphant 1993, Dale et al. 1994).

In 1993 we initiated a study on foraging ecology of Glaucous Gulls with one of its objectives being to replicate these aforementioned aspects of Strang's (1976, 1982) work to determine whether the proportional contribution of waterfowl to the diet of Glaucous Gulls had shifted. In particular, we wanted to examine the distribution of taxa represented in boluses, food remains, and stomachs of gulls and do so at multiple areas before and after peak hatch of geese. We thus wanted to test the hypothesis that the taxonomic distributions of prey items were similar during Strang's studies and ours. We chose the same Old Chevak study site used by Strang and also conducted studies at Kigigak Island and Manokinak River (Fig. 3.1). Kigigak Island is a coastal site where gulls nest in small colonies, similar to the Kokechik Bay study area used by Strang. The Manokinak River site is 5-12 km inland where gulls occur in comparatively lower densities and nest as dispersed pairs, thus it is more similar to the Old Chevak site. By examining multiple sites within years, we removed the confounding influences of

geographic and annual variation in diets inherent in Strang's work.

Most previous studies of seabird diets have relied upon examination of boluses, food remains, and stomachs. These conventional methods are useful for identifying specific prey taxa. However, differential digestion and assimilation of various prey species bias quantitative evaluations of how much nutrient uptake gulls derive from their prey (Hyslop 1980, Duffy and Jackson 1986, Erikstad 1990, Brugger 1992, Brekke and Gabrielsen 1994). Additionally, each sample typically constitutes a single meal, resulting in a dietary perspective that may be biased by where samples were collected, e.g., at-sea versus near a nest. A complementary method is to examine the proportional abundance of stable isotopes of various elements in tissues from both predator and prey (Tieszen and Boutton 1989, Hobson and Clark 1992a, 1992b, Michener and Schell 1994, Sydeman et al. 1997). For species with simple, isotopically distinct diets, these methods offer a powerful means for quantifying relative importance of various prey types. For example, the often large difference between marine and terrestrial organisms in $\delta^{13}\text{C}$ values enabled an estimate of the contribution of terrestrial prey to the diet of Western Gulls (*L. occidentalis*) (Hobson 1987), Northern Saw-Whet Owls (*Aegolius acadicus*) (Hobson and Sealy 1991), and Marbled Murrelets (*Brachyramphus marmoratus*) (Hobson 1990). Our objective was to measure stable-nitrogen and carbon isotope ratios in various tissues of gulls and in their prey in order to estimate the numerical importance of terrestrial prey to total nutrient uptake.

METHODS

Study area and species

The YKD is an expansive coastal marsh where salt water influence extends up to 55 km inland (Tande and Jennings 1986) (Fig. 3.1). Distribution of gulls and geese is predominantly coastal with the vast majority within 15 km of the Bering Sea coast and associated bays. Nesting densities of geese at all study sites were > 10 nests km^{-2} , with much higher densities at localized areas, particularly at Kokechik Bay and Kigigak Island

(Bowman et al. 1996). Approximately 140,000 total pairs of the four species of geese nested on the YKD in 1993. At least 17,000 Glaucous Gulls occurred in early June and 12,000 in early July, 1993-1994, on a major portion of the YKD that did not include the Kokechik Bay area (Bowman et al. 1997). Strang (1976) provides a detailed study of the general ecology of Glaucous Gulls on the YKD. Peak hatch of gulls and geese usually occurs in late June; in 1993, peak hatch was approximately 20 June (Bowman et al. 1996).

Conventional methods

We examined diet of Glaucous Gulls from boluses and food remains found at feeding sites near nests or chicks, and from stomach contents of harvested adults. Nests were initially located in late May or early June. Distinct feeding areas were readily found at or near nests or within close proximity to chicks. All boluses and food remains were collected during a nest/chick visit. These collections occurred both pre- and post-hatch at Kigigak Island and Old Chevak, but only post-hatch at Manokinak River. We killed adults by shooting them, immediately removed their entire digestive tracts, and stored them in 70% ethanol. We collected gulls pre- and post-hatch at Kigigak Island and Manokinak River, but only post-hatch at Old Chevak.

Food remains, boluses, and gull stomach contents from Kigigak Island and Old Chevak were examined in the laboratory after the field season. We used reference collections to identify prey and enumerated the minimum number of individuals found within a sample. A sample constituted all boluses and food remains found during one visit or the contents of one digestive tract. Examining frequency of occurrence (Duffy and Jackson 1986), we compared the distribution of prey taxa between sites or time periods (pre- vs. post-hatch) using likelihood ratio chi-square tests. To minimize bias due to small cell frequency counts, we pooled all terrestrial prey types into one category for tests involving Kigigak Island data. To compare our data to that of Strang (1976, 1982), we pooled goslings and shorebirds into a single category and mollusks and other marine

invertebrates into one category. Due to multiple tests (up to three to test for year, site, and within season effects) and some low cell frequencies, we feel a conservative P -value of 0.01 for interpretation of significance is warranted. We did not combine these tests into a single categorical model because comparisons with the less taxon-specific data of Strang (1976) required different pooling. For samples from Manokinak River, we obtained only a field-based and grosser level of taxonomic occurrence of food items. Thus, we did not use data from this area in chi-square analyses.

Stable isotope methods

We collected approximately 1 g of breast muscle and liver, and 1 cc of blood from harvested adult gulls. We collected multiple tissues per individual as variation among tissues in metabolic activity results in different rates of isotopic turnover in those tissues (Tieszen and Boutton 1989). Thus, diet perspectives pertaining to different periods were obtained by sampling several tissue types (Hobson and Clark 1992a). We also obtained approximately 1 cc of blood from gull chicks at about four weeks of age. Tissues were temporarily cold-stored in tundra pits, then frozen until analysis at the laboratory. Prey taxa were harvested opportunistically. We collected fully developed goose embryos from eggs that failed to hatch completely. Samples from older goslings were obtained from capture mortalities during associated studies of geese. Tundra voles (*Microtus oeconomus*) were trapped or found at gull nest sites. Intertidal invertebrates were gathered at low tides in Hazen Bay or found in stomachs of collected gulls. We collected fish using small seines or by rod and reel. We excised muscle tissue from prey for isotope analysis.

All samples were freeze dried and then powdered using an analytical mill. Lipids were extracted from tissues using a chloroform:methanol rinse according to a modification of the method described by Bligh and Dyer (1959). Samples were loaded into vycor tubes together with wire-form CuO, elemental copper and silver wire, and then sealed under vacuum before combustion at 850°C for 2 hr. After cooling overnight,

sample CO₂ and N₂ was separated cryogenically and then introduced into a VG Optima isotope-ratio mass-spectrometer.

Stable isotope values are expressed as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000 \quad (1)$$

where $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$, and $R =$ the corresponding ratio ${}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. R_{standard} for ${}^{15}\text{N}$ and ${}^{13}\text{C}$ is that for atmospheric N₂ (AIR) and the Peedee Belemnite (PDB) standard, respectively. Using hundreds of replicate analyses of an egg albumen laboratory standard, we estimated measurement precision to be $\pm 0.1\text{‰}$ and $\pm 0.3\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively.

We tested whether $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in gulls varied geographically (Kigigak Island versus Manokinak River) and/or temporally (pre- versus post-hatch) using multivariate analysis of variance (MANOVA). We ran separate analyses for muscle and liver tissues, but did not include blood in these analyses because it was not collected at all areas at all times. In addition, we did not include Old Chevak data in the MANOVA because no pre-hatch data were collected there. Because of relatively small sample sizes, we computed significance values for the MANOVAs using randomization tests as described in Manly (1991). F -statistics were computed from the original data and 1,000 randomizations of the data. In each randomization, each pair of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were randomly assigned to a geographic and temporal category. F -statistics from the 1,000 randomizations were numerically ordered and then significance of the MANOVA determined by where within this rank order of F -statistics the F -statistic from the original data laid. For example, if the F -statistic from the original data equaled the F -statistic from the 994th largest F -statistic of the 1,000 randomizations, then $P = 0.006$. We similarly applied a randomization test to results from one-way MANOVAs to test whether stable isotope values in blood samples from chicks differed among the three study sites.

Stable-isotope values of various macronutrients (protein, lipid, carbohydrate) in foods fractionate or change when incorporated into consumer tissues according to the relationship:

$$D_t = D_d + \Delta_{dt} \quad (2)$$

where D_t = the isotope value of the consumer tissue, D_d the isotope value of the diet, and Δ_{dt} the fractionation factor between diet and consumer. Similar to Hobson (1993), we used different $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ fractionation factors for adults and chicks because young birds incorporate a greater proportion of consumed isotopes directly into new somatic tissue and so may exhibit fractionation patterns different from adults. For adults, we used 2.4‰ and 2.3‰ for ^{15}N in muscle and liver tissues, respectively, and 2.1‰ and 1.3‰ for ^{13}C in muscle and liver, respectively, as determined by Mizutani et al. (1991) for an adult Great Cormorant (*Phalacrocorax carbo*). For chicks we used 3.1‰ and -0.3‰ for fractionation of ^{15}N and ^{13}C , respectively, in whole blood as determined by Hobson and Clark (1992b) for captive-raised Ring-billed Gull chicks (*L. delawarensis*).

We used a three-source isotopic mixing model (Ben-David et al. 1997) to estimate what proportion of the Glaucous Gull diet is comprised of each of the major diet categories or sources (marine, intertidal, or terrestrial). Because of the dominance of saffron cod in gull diets (see Results) and its similar isotopic composition to that of other local marine fishes (unpubl. data), we used this species as the sole representation of the marine diet. We considered bivalve species (blue mussel, razor clam, other clam spp.) to be the intertidal prey source. Eggs (full-term embryos), voles, shorebirds, and goslings were collectively considered terrestrial prey. For each gull, we calculated how distant its $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope values in bivariate space were from the mean values for each of the three diet sources after accounting for isotopic fractionation between diet and gull tissue. Proportional diet contributions were inversely related to this distance according to the following equation (Ben-David et al. 1997):

$$P_a = D_{ag}^{-1} / (D_{ag}^{-1} + D_{bg}^{-1} + D_{cg}^{-1}) \quad (3)$$

where P_a = the proportion of the diet derived from source a , and D_{ag} , D_{bg} , and D_{cg} are the Euclidean distances between isotopic values of an individual gull and the mean isotopic values of prey from source a , b , or c . As an estimate of P_a was associated with each gull, we calculated standard errors based on the inherent variation among individuals. We examined variation among study areas and ages in the proportional consumption of prey by post-hatch gulls using a two-way ANOVA.

RESULTS

Boluses, prey remains, and stomach contents

We collected 51, 91, and 58 sets of boluses and food remains from Kigigak Island, Manokinak River, and Old Chevak, respectively. We also obtained 10 gull digestive tracts from each area. Distributions of the frequency of occurrence of various prey taxa at Old Chevak in 1993 were not different from that observed by Strang (1976) in 1974 in either pre-hatch ($\chi^2_4 = 9.3$, $P > 0.05$) or post-hatch periods ($\chi^2_4 = 6.4$, $P > 0.05$). We also compared Strang's (1976) Kokechik Bay samples from 1973 with ours from Kigigak Island in 1993 because these areas were similar in their proximity to the coast and densities of gulls and geese. Prey distributions at Kokechik Bay were not statistically different from those at Kigigak Island post-hatch ($\chi^2_3 = 7.3$, $P > 0.05$). However, pre-hatch samples at these two areas were different ($\chi^2_4 = 13.8$, $P < 0.01$), primarily due to the absence of mammals in the diet of Kigigak Island gulls.

Examining just 1993 data, frequencies of occurrence of various prey taxa were different between pre-hatch and post-hatch periods, both for Old Chevak ($\chi^2_5 = 17.4$, $P < 0.01$) and Kigigak Island ($\chi^2_2 = 12.6$, $P < 0.01$, Table 3.1). Examining prey distributions between sites, Old Chevak and Kigigak Island were different throughout the season, both pre-hatch ($\chi^2_2 = 11.9$, $P < 0.01$) and post-hatch ($\chi^2_5 = 22.3$, $P < 0.01$). The statistical significance of all the above tests remained the same when data from stomach contents (< 20% of all samples) were excluded.

Fish was a dominant component of the diet at all areas for pre- and post-hatch

periods (Table 3.1). Saffron cod occurred in 60% of samples with up to 9 individual fish identified in a given sample. Identified species of fish other than saffron cod occurred in 28% of analyzed sets of boluses and food remains. Mollusks, primarily razor clams (*Siliqua alta*), were rare or absent from the diet prior to hatch at both Old Chevak and Kigigak Island, but were observed in > 20% of all samples after hatch.

Terrestrial mammals, primarily tundra voles, were not recorded in the diet at Kigigak Island, but occurred in 40% of Old Chevak samples prior to hatch and 10% after hatch. Egg remains were rare at Kigigak Island, but occurred in > 20% of samples at Old Chevak and Manokinak River after hatch and nearly 60% of samples at Old Chevak prior to hatch. Goslings and shorebirds were common diet items at both Old Chevak and Manokinak River, with > 60% of post-hatch samples containing goslings. Because the distribution of hatching dates for geese may encompass 10 or more days, some goslings appeared in pre-hatch samples and some eggs in post-hatch samples.

Isotope analyses

Evidence for geographic and temporal variation in diet was found using stable isotope analyses. Stable isotope values in both liver ($P = 0.04$) and muscle tissue ($P < 0.01$) of adult gulls differed between Kigigak Island and Manokinak River (Table 3.2). Stable isotope values in muscle ($P < 0.01$), but not liver ($P > 0.05$), tissue varied between pre- and post-hatch periods. Interactions between study area and time period were not significant for either liver ($P > 0.05$) or muscle ($P > 0.05$) tissue.

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in blood from gull chicks were correlated linearly (Fig. 3.2), and were significantly different among sites ($P < 0.01$). Samples from Kigigak Island differed from Manokinak River and Old Chevak ($P < 0.05$, Tukey's multiple comparison test, Fig. 3.2). Although samples from Old Chevak were more variable than those from Manokinak River, their mean values were not different ($P > 0.05$, Tukey's multiple comparison test).

Mean (\pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for three shorebird species (Black Turnstone

[*Arenaria melanocephala*], Dunlin [*Calidris alpina*], and Semipalmated Sandpiper [*Calidris pusilla*]) were $7.5 \pm 0.5\text{‰}$ and $-25.5 \pm 2.5\text{‰}$, respectively (Fig. 3.3). Isotopic means for embryos of Cackling Canada Geese and Greater White-fronted Geese, 4 to 5 week-old Emperor Goose goslings, and tundra voles were all similar to those for shorebirds (Fig. 3.3). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for full-term embryos from Emperor Geese were more marine than other terrestrial prey, probably as a consequence of the marine diet of Emperor Geese prior to egg laying (Petersen et al. 1994). As Emperor Goose goslings grew, their isotopic signal became similar to that of the other goose species and terrestrial prey (Fig. 3.3, unpubl. data). Generally, $\delta^{15}\text{N}$ was less variable than $\delta^{13}\text{C}$. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of these six terrestrial groups was 7.1 and -25.8, respectively. Means (and SDs) for bivalves and saffron cod also are shown in Fig. 3.3.

Using the three-source isotopic mixing model, we estimated that the contribution of terrestrial foods to the diet of Glaucous Gulls varied from 7 to 23%, depending upon time and area (Table 3.3). Similar to the MANOVAs on the raw isotope values (Table 3.2), the proportional diet contribution of terrestrial prey was greater for Manokinak River and Old Chevak than for Kigigak Island (Table 3.3, $P < 0.01$). Also, chicks at all three study sites consumed a diet less heavily weighted towards saffron cod than did breeding adults from these same areas ($P < 0.01$).

DISCUSSION

Comparison of 1970s and 1993 data with conventional methods

We did not find evidence of any marked change in diet of Glaucous Gulls from that observed by Strang (1976, 1982) in the 1970s. No differences in diet among years were observed at Old Chevak, the only area studied during both the 1970s and 1993. Differences between Kokechik Bay in 1973 and Kigigak Island in 1993 were driven largely by differences in the occurrence of tundra voles. The annual variability in populations of these voles (Stickney 1989) makes it likely that there is annual variability in the frequency of predation on voles by gulls. These findings are similar to what Strang

(1976, 1982) concluded for variation among years in the 1970s. Overall, our observed patterns of geographic and seasonal variation in diet corroborated those of Strang (1982).

Sources of error in using isotope models

Isotopic mixing models require that the different prey sources be isotopically distinct from each other in order to be treated separately (Ben-David 1996), thus the similarity between shorebirds and goslings prohibited examining these two types of prey separately. Also, mixing models are somewhat sensitive to how many different sources are included in the model. For instance, if we had excluded bivalves as a prey source, our estimates of the contribution of terrestrial prey post-hatch (mostly goslings) to chick diets would have changed from 10-23% (the range among areas) to 12-43%. Bivalves are, however, a significant prey item based upon the conventional diet results and therefore we believe our three-source model is appropriate. Incorrect inclusion (or exclusion) of less common diet sources would have less pronounced effects on our results than the above example. More taxon specific prey sources could be modeled if finer isotopic resolution could be achieved. Use of additional stable isotopes, sulfur ($\delta^{34}\text{S}$) in particular, would likely allow greater segregation of the terrestrial and marine signals within foodwebs (Peterson et al. 1985, Hesslein et al. 1991).

Another probable source of error in the isotope models is the use of assumed isotope fractionation factors between diet and gull tissues. Although we used values derived from captive-rearing studies of piscivorous seabirds (Mizutani et al. 1991, Hobson and Clark 1992b), further studies are required to refine these estimates and to establish their general applicability across species. Fractionation values also may vary among individuals within a species (Ben-David 1996), but such differences are expected to be small (Hobson and Schwarcz 1985). Despite these limitations in developing isotopic models to estimate marine, terrestrial, and intertidal inputs to gull diets on the YKD, we are encouraged by the potential of this technique to investigate this and other questions. In particular, the strong correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the blood

of gull chicks with differential access to marine and terrestrial foods indicates that chick diets can be readily ascertained and monitored using routine techniques.

Inferences on feeding ecology of gulls from stable isotope analyses

Analyses of stable isotopes in muscle tissues revealed a pattern of geographic and seasonal differences in diet that was similar to results of the conventional diet analyses. Coastal gulls consumed less terrestrial prey than inland gulls, and the consumption of terrestrial prey was greater post-hatch than pre-hatch. Lack of a seasonal shift in isotope ratios in livers may have been a function of tissue turnover times and short-term (day-to-day or week-to-week) variations in diet. Based on differential turnover rates among tissues, Hobson and Clark (1992a) and Hobson (1993) inferred that isotopic measurement of liver integrated dietary information over a period of about one week, whereas muscle tissue corresponded to four to six weeks. Thus, analysis of muscle tissues from the two seasonal periods in our study reflected integrations of diets throughout most of the pre-hatch and post-hatch periods, whereas liver tissues reflected only small subsets of these time periods and were therefore more sensitive to short term deviations from average diets. Overall, isotope values from Kigigak Island were less variable than those from Manokinak River and Old Chevak (Tables 3.2 and 3.3, Fig. 3.2). Kigigak Island gulls were almost uniformly marine feeders, whereas inland nesting gulls exhibited individual variation in how much they consumed marine prey. This pattern was evident for both adults and chicks (Tables 3.2 and 3.3, Fig. 3.2).

Using isotopic mixing models, estimates of the contribution of terrestrial prey to the diet of Glaucous Gulls varied from 7-22% for adults and 10-23% for chicks. Such estimates are not possible with conventional methods; nevertheless, one may be tempted to form a mental approximation of diet contributions upon examining frequency of occurrence data in Table 1 and in Strang (1976, 1982). The actual contribution of terrestrial prey to diets of adult gulls based upon stable isotope models is lower than what one might infer from frequency of occurrence data (> 60% occurrence of goslings). Such

a different perspective from examination of boluses, food remains, and stomach contents could occur simply by sampling near nests and chicks located near terrestrial prey. Soft-bodied marine prey and bones of small fishes may be completely digested by the strong gastric action in gulls (Barry and Barry 1990) before they return from their marine foraging areas. Additionally, because adults fed their young a smaller proportion of marine prey than they consumed themselves, as demonstrated by the isotopic models (Table 3.3), conventional food habits data collected near nests and chicks resulted in a diet perspective that is not representative of either age class alone, but rather is a composite of both adults and their young.

Dietary differences between adult gulls and their young has not been noted often. However, previous studies have recorded temporal shifts in how much fish are consumed by gulls (Murphy et al. 1984, Pierotti and Annett 1990), and Tinbergen (1960) observed that adult Herring Gulls (*L. argentatus*) consumed bivalves while feeding fish to their young. Using stable isotope techniques, Hobson (1993) determined that while Black-legged Kittiwakes (*Rissa tridactyla*) at a high Arctic colony fed their young primarily Arctic cod (*Boreogadus saida*), they depended themselves more on *Parathemisto* amphipods. These differential feeding patterns were attributed to variability in abundance (Murphy et al. 1984) and quality (Pierotti and Annett 1990) of prey. For gulls on the YKD, it is not clear why inland nesting adults fed more on marine prey than they fed to their young, but energetics of food transport and food quality are two possible contributing factors. For adults to feed marine prey (saffron cod) to their young, they would need to carry a food load farther than if they fed their young terrestrial prey (goslings and young shorebirds) that are common near gull nesting areas. It should be noted, however, that some marine foods may be accessible in and along the tidal rivers that bisect inland study areas, a pattern Strang (1976, 1982) deduced based upon average flight directions of gulls from his inland study site. Fish and gosling prey may differ in nutritive content, which also could lead to age differences in feeding if adults have

different nutritive and energetic needs than their young. Goslings have high lipid content at hatch, but this steadily declines as goslings increase only muscle and skeletal mass during growth (Sedinger 1986). Proximate analyses of saffron cod have not been conducted, but Pacific herring (*Clupea harengus*), the next most common fish species in gull diets (Table 3.1), had high fat contents compared to other Bering sea fishes (Stansby 1976).

Sampling concerns necessitated that we focus this study on breeding gulls. However, a large number of nonbreeding Glaucous Gulls also spend some portion of the summer (mostly pre-hatch) on the YKD (Bowman et al. 1997). Observations of nonbreeders at coastal locations and the pattern of breeding adults favoring marine foods in contrast to what they feed their young both suggest that nonbreeding gulls on the YKD have a largely marine diet that is probably similar to that observed for breeding adults from Kigigak Island.

Our data and those of Strang (1976) indicate that there has been no large change over time in how much individual Glaucous Gulls consume gosling prey. Glaucous Gull numbers have approximately doubled during the past decade (Bowman et al. 1996, 1997). This increase corresponded with large increases in sympatrically nesting Cackling Canada Geese and White-fronted Geese; however, during the same time period numbers of the less abundant Emperor Goose stayed approximately stable (Bowman et al. 1997). It is therefore possible that while Glaucous Gull predation of geese in general has remained the same over time, predation on individual species, such as Emperor Geese, has increased.

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Table 3.1. Taxa found in boluses, food remains, or digestive tracts of Glaucous Gulls. In the second column, n represents the total number of occurrences of a given taxon within all samples. The third through sixth columns refer to Kigigak Island (KI) and Old Chevak (OC) during pre- and post-hatch periods and represent the proportion of samples within a given area and time period that contained at least one occurrence of that particular taxon or taxa. The number of samples contributing to the calculated proportion is given in parentheses. Due to sample size constraints and to enable direct comparison of these 1993 data with Strang's (1976) data, we calculated proportions for broad categories rather than each individual species.

Taxa of prey	n	KI-Pre (13)	KI-Post (48)	OC-Pre (21)	OC-Post (47)
Marine invertebrates		0.08	0.50	0.05	0.23
Mollusks		0.08	0.50	0.00	0.23
<i>Natica</i> spp.	13				
<i>Mytilus edulis</i>	3				
<i>Siliqua alta</i>	101 ⁺ ^a				
Unknown bivalve spp.	2				
Other marine invertebrates		0.00	0.15	0.05	0.00
Isopoda spp.	13				
Ampipoda spp.	3				
Unknown starfish spp.	2 ⁺				
Unknown sea urchin spp.	1 ⁺				
Fish		0.77	0.50	0.76	0.79
<i>Clupea harengus</i>	19 ⁺				
<i>Eleginus gracilis</i>	138				

Unknown Gadidae spp.	22				
<i>Lycodes</i> spp.	2				
<i>Myoxocephalus</i> spp.	4+				
Unknown flatfish spp.	1				
<i>Ammodytes hexapterus</i>	1				
Unknown fish	49+				
Birds		0.15	0.46	0.67	0.72
Geese		0.00	0.27	0.43	0.62
<i>Branta canadensis</i>	5				
<i>Chen canagica</i>	1				
<i>Anser albifrons</i>	2				
Unknown Anserini spp.	121+				
Ducks					
<i>Anas acuta</i>	2				
<i>Somateria mollissima</i>	1				
Unknown Anatini spp.	2				
Shorebirds		0.00	0.06	0.48	0.32
<i>Arenaria melanocephala</i>	7				
<i>Calidris alpina</i>	3				
Unknown <i>Calidris</i> spp.	16				
<i>Limnodromus griseus</i>	11				
Other					
<i>Lagopus lagopus</i>	1				
<i>Larus canus</i>	1				
<i>Xema sabini</i>	1				

Unknown Larini spp.	4				
<i>Catharus</i> spp.	1				
<i>Carduelis</i> spp.	1				
Unknown bird	18+				
Eggs		0.00	0.08	0.62	0.19
Unknown Anserini spp.	11+				
Unknown Anatini spp.	6+				
Unknown Larinae spp.	5+				
Unknown bird	5+				
Mammals		0.00	0.00	0.38	0.08
Terrestrial					
<i>Microtus oeconomus</i>	35				
<i>Sorex</i> spp.	2				
Marine					
Unknown Phocidae	1+				

^a A + indicates a minimum count because in one or more samples it was not possible to determine if there was more than one individual contained within the given sample. This was always the case for eggs.

Table 3.2. Stable-carbon and nitrogen isotope values of adult Glaucous Gull tissues. Estimates presented as mean \pm SE in ‰. Gulls were collected during mid to late incubation (Pre-hatch) and ≥ 4 weeks after peak hatch of geese (Post-hatch)^a. We note that $n = 5$ except for muscle and liver tissues from Old Chevak, where $n = 10$.

Tissue		Kigigak Island		Manokinak River		Old Chevak
		Pre-hatch	Post-hatch	Pre-hatch	Post-hatch	Post-hatch
Muscle	C	-19.3 \pm 0.1	-18.4 \pm 0.3	-20.5 \pm 0.5	-20.6 \pm 0.6	-20.6 \pm 0.2
	N	18.0 \pm 0.1	17.9 \pm 0.2	17.4 \pm 0.3	16.1 \pm 0.6	16.8 \pm 0.3
Liver	C	-19.3 \pm 0.2	-19.0 \pm 0.2	-20.1 \pm 0.6	-21.1 \pm 0.9	-21.1 \pm 0.5
	N	19.1 \pm 0.1	19.7 \pm 0.3	19.1 \pm 0.5	17.7 \pm 1.0	16.8 \pm 0.6
Blood	C	-18.1 \pm 0.1	-17.9 \pm 0.1			-19.8 \pm 0.3
	N	18.2 \pm 0.1	18.9 \pm 0.3			17.5 \pm 0.4

^a Pre-hatch samples were collected 3-13 June and 11-13 June at Kigigak Island and Manokinak River, respectively. Post-hatch samples were collected 17-18 July at Kigigak Island, 16-17 July at Manokinak River, and 12-19 July for five Old Chevak samples and 6 August for the other five samples.

Table 3.3. Isotopic estimation of prey proportions in diets of Glaucous Gulls. We estimated proportions using isotopic mixing models (Ben-David et al. 1997) and measures of ^{13}C and ^{15}N in muscle (adults) and blood (chicks) collected in 1993.

	Goslings/shorebirds/			
	<i>n</i>	eggs/voles	Saffron cod	Bivalves
Adults				
Kigigak Island				
pre-hatch	5	11.8 ± 0.7	70.0 ± 1.8	17.8 ± 1.0
post-hatch	5	6.6 ± 2.1	83.6 ± 5.3	10.0 ± 3.1
Manokinak River				
pre-hatch	5	18.4 ± 4.5	56.4 ± 3.9	25.2 ± 2.0
post-hatch	5	22.0 ± 4.2	48.0 ± 7.5	30.0 ± 3.7
Old Chevak				
post-hatch	10	20.3 ± 1.6	50.9 ± 3.4	28.7 ± 1.8
Chicks				
Kigigak Island	18	9.9 ± 0.3	73.0 ± 0.9	17.0 ± 0.6
Manokinak River	24	19.9 ± 0.7	29.2 ± 2.7	50.9 ± 2.4
Old Chevak	25	22.9 ± 2.8	39.9 ± 4.2	37.4 ± 2.6

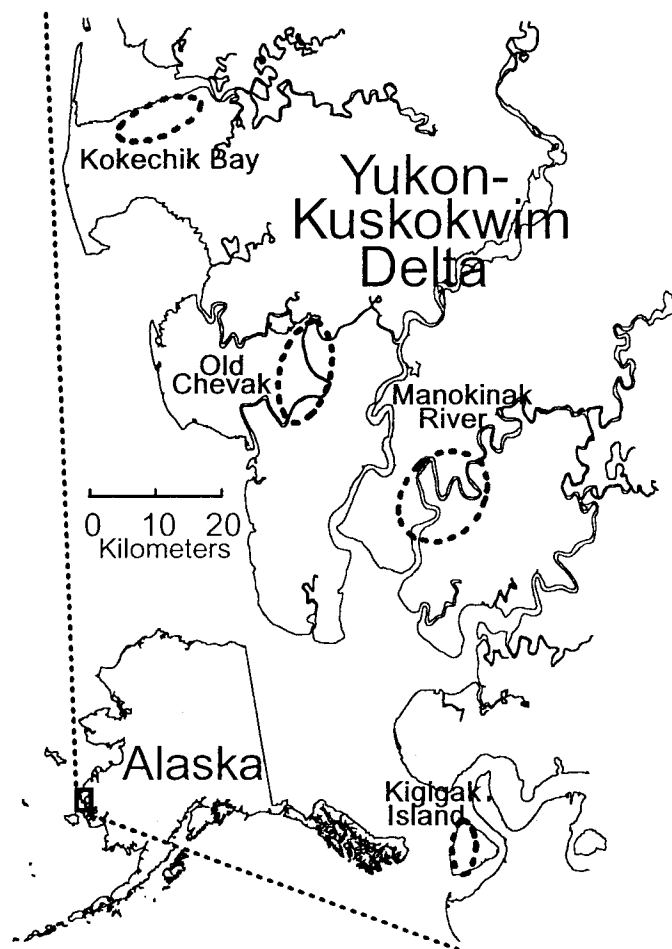


Figure 3.1. Four study sites on the Yukon-Kuskokwim Delta, Alaska. Strang (1976, 1982) studied Glaucous Gull at Kokechik Bay and Old Chevak. Our studies in 1993 occurred at Old Chevak, Manokinak River, and Kigigak Island.

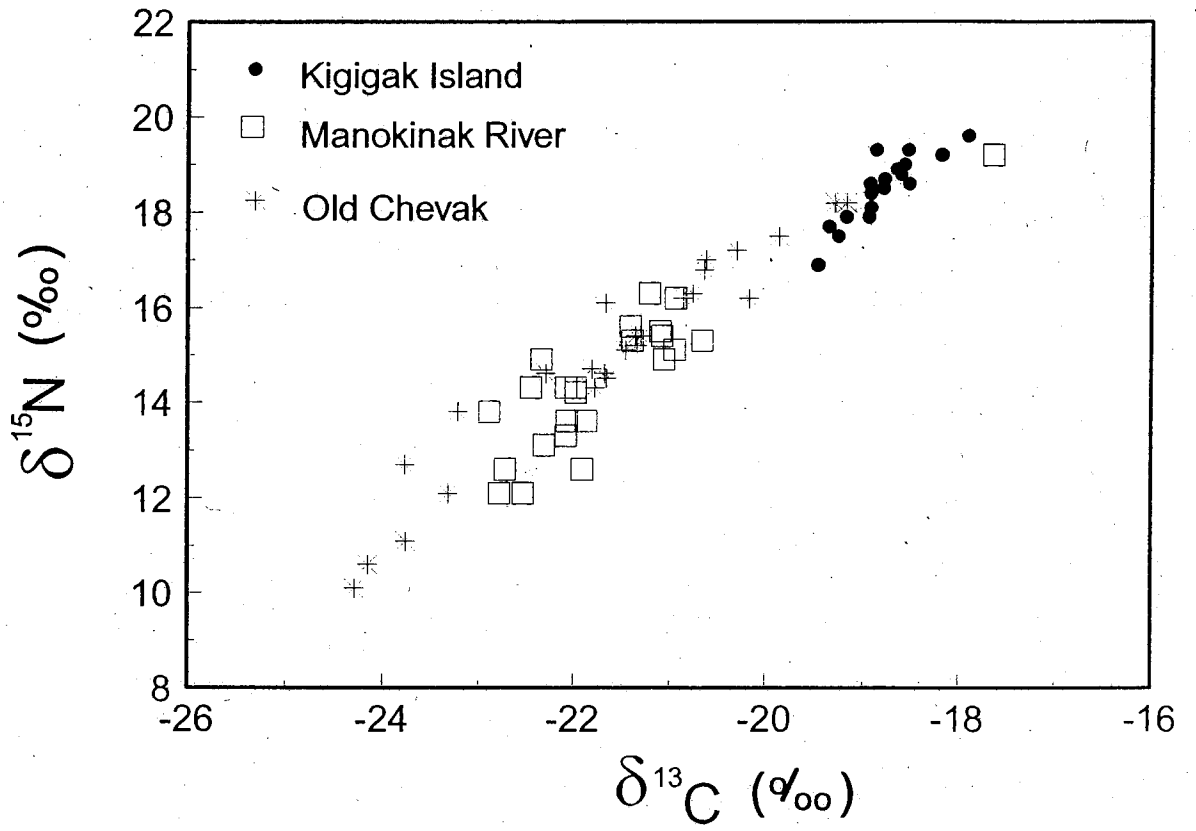


Figure 3.2. Stable-carbon and nitrogen isotope values from chick blood. Blood was drawn when chicks were approximately four weeks of age.

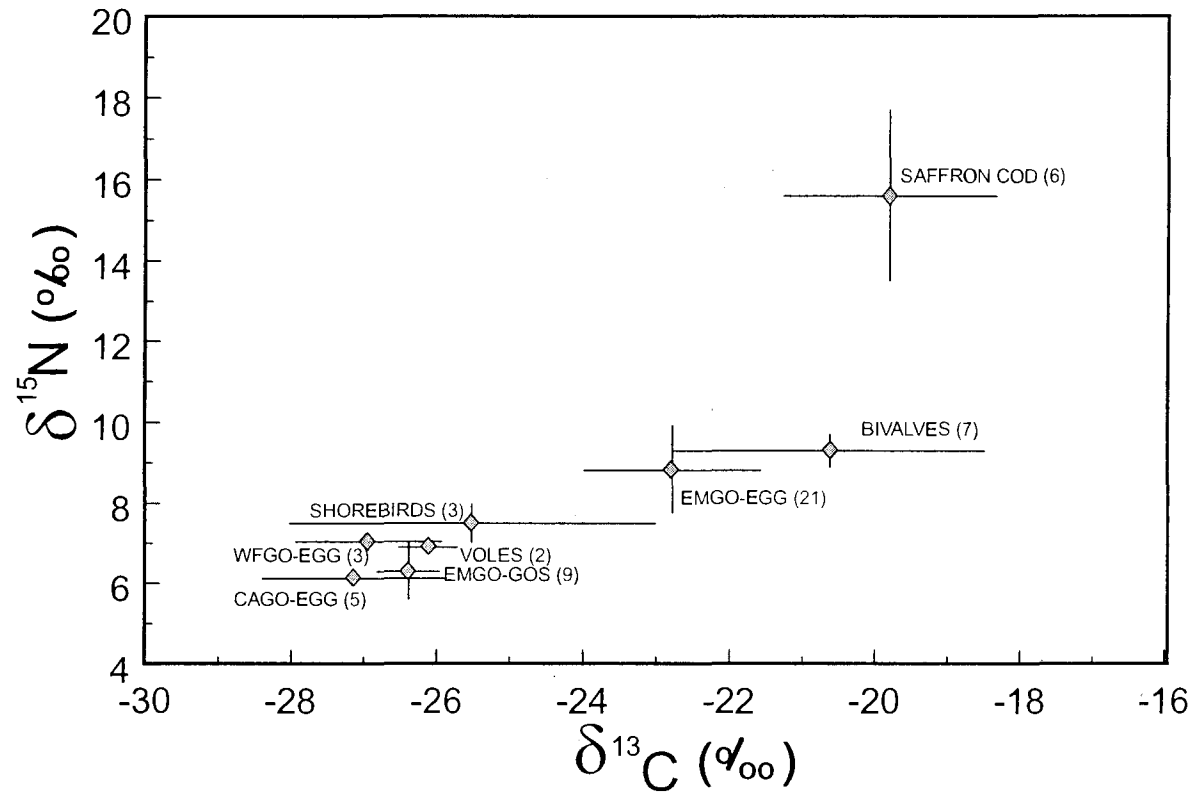


Figure 3.3. Stable-carbon and nitrogen isotope values from prey of Glaucous Gulls. Specific species in each taxonomic grouping are given in the text.

Chapter 4

Effects of Gull Predation and Weather on Survival of Emperor Goose Goslings

Abstract: Numbers of Emperor Geese (*Chen canagica*) have remained depressed since the mid 1980s. Despite increases in a primary predator of goslings, glaucous gulls (*Larus hyperboreus*), little information existed to assess whether recent patterns of gosling survival have been a major factor affecting population dynamics. We used observations of known families of Emperor Geese to estimate rates of gosling survival during 1993–1996 on the Yukon-Kuskokwim Delta, Alaska. Survival of goslings to 30 days of age varied among years from 0.332 in 1994 to 0.708 in 1995. Survival was lowest during 1993–1994, which corresponded with the years of highest frequency of disturbance of goose broods by glaucous gulls. Rainfall during early brood-rearing was much higher in 1994 than other years and this corresponded to low survival among goslings ≤ 5 days of age. Numbers of juveniles in families during fall staging were negatively related to rainfall during early brood-rearing ($n = 23$ years). Although there are no data to assess whether gosling survival in Emperor Geese has declined from some previous level, current survival rates of Emperor Goose goslings are as high or higher as those observed in other goose species that are rapidly increasing. A proposed reduction of glaucous gull numbers by managers may not be the most effective means for increasing population growth in Emperor Geese.

INTRODUCTION

The Emperor Goose population has remained approximately stable since 1985 (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data) and is well below earlier survey counts of population size (Petersen et al. 1994). The unchanging population trend of this

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species, which breeds almost entirely on the Yukon-Kuskokwim Delta (YKD) in western Alaska (Petersen et al. 1994), has occurred despite attempts to limit harvest (Pamplin 1986, Pacific Flyway Council 1994). Gosling survival may have had a large effect on population dynamics if it was highly variable among years compared to other demographic parameters or if there was a shift in the long-term mean rate at which goslings survived (Schmutz et al. 1997).

The brood rearing period for geese, and rates and factors affecting gosling survival in particular, have been poorly studied until recently (Sargeant and Raveling 1992). Prior to our study, there were no data on survival rates of Emperor Goose goslings, although fall population surveys indicated that some aspect of productivity, of which gosling survival is one component, may be low (U.S. Fish and Wildlife Service unpublished data). Factors directly affecting mortality rates of goslings are not well quantified (Sargeant and Raveling 1992). A minor portion of the diet of glaucous gulls on the YKD is goslings, including Emperor Geese but also including sympatrically breeding Cackling Canada Geese (*Branta canadensis minima*), Greater White-fronted Geese (*Anser albifrons*), and Black Brant (*B. bernicla nigricans*) (Strang 1976, Schmutz and Hobson 1998). Following predation, weather factors were identified as the next most common source of mortality for young waterfowl (Johnson et al. 1992). Precipitation has been linked to mortality of precocial young in other species (Marcström 1966, Kostin and Mooij 1995, Vangilder and Kurzejeski 1995, Korschgen et al. 1996), and we hypothesized it may be related to survival of Emperor Goose goslings. Whereas predation and rainfall may directly affect gosling survival, the quality and quantity of foraging habitats also may impact survival (Williams et al. 1993), either directly through starvation or indirectly by weakening goslings and thus predispose them to predation, weather, and other direct mortality factors.

Understanding the effect of predation and amount of rainfall during brood rearing on Emperor Goose goslings is particularly relevant because these 2 factors may be changing in frequency. Glaucous gull numbers on the YKD have increased since 1986 (T. D. Bowman,

U.S. Fish and Wildlife Service, unpublished data), and global climate models predict changes in precipitation for arctic areas (Lynch et al. 1995). Additionally, the Fish and Wildlife Service has proposed reducing the number of glaucous gulls on the YKD as a means of increasing the growth rate of the Emperor Goose population (U.S. Fish and Wildlife Service, unpublished report).

We had 2 primary objectives for this study. First, we estimated the survival rates of Emperor Goose goslings for each year, 1993–1996, and examined whether survival differed among ages or years. We then compared the magnitude and variation in these rates to other species and existing models to evaluate the contribution of gosling survival to current population trends. Secondly, we compared annual variations in estimates or indices of gosling survival to measures of predator disturbance of goose broods and rainfall.

STUDY AREA

We studied survival of Emperor Goose goslings in a 90 km² area along the Manokinak River, which constitutes a portion of the coastal zone of the Yukon-Kuskokwim Delta, Alaska (Fig. 4.1). The vast majority of the world's population of Emperor Geese breeds in this coastal zone (Eisenhauer and Kirkpatrick 1977). Cackling Canada Geese, Greater White-fronted Geese, and Black Brant also nest and raise broods throughout portions of this coastal zone. Populations of all 4 species of geese on the YKD have fluctuated over time (King and Derksen 1986, Sedinger 1996). During field work for this study (1993–1996), numbers of Emperor Geese on the YKD were less than half that of Cackling Canada Geese and Greater White-fronted Geese and comparable to numbers of Black Brant (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data).

The coastal zone of the YKD is flat tundra permeated by many ponds, lakes, and tidally influenced rivers and sloughs. Vegetation in the study area has been described by Tande and Jennings (1986) and Kincheloe and Stehn (1991). Plant communities used by geese are dominated by graminoids (Babcock and Ely 1994). Arctic foxes (*Alopex lagopus*) and jaegers (*Stercorarius* spp.) are the principal predators of goose nests, and foxes and

glaucous gulls commonly hunt goslings (Strang 1976, Stickney 1989, Schmutz and Hobson 1998).

METHODS

Field Methods

We searched for nests to identify marked adults and to locate others for potential trapping and marking. We trapped some adult females with bow traps while they incubated nests; preliminary analyses indicated that gosling survival was similar between broods in which females had or had not been trapped. At each nest, we recorded numbers of eggs and estimated their hatching dates by floating them briefly in water (Westerskov 1950, Walter and Rusch 1997). We revisited many nests at hatch to determine initial family size. For those nests that we did not visit on the day of hatch, we did not necessarily use the clutch size observed on the last nest visit as an estimate of initial family size because some eggs typically do not hatch (≤ 0.5 eggs/clutch; Petersen [1992], Flint et al. [1995]). Instead, we examined egg-specific estimates of hatching dates from the last visit to each nest and excluded eggs that were markedly behind in development. All subsequent observations of families were obtained from a series of 10 elevated observation blinds. These blinds were all placed in similar habitats that were selectively used by Emperor Goose broods - the interface of mudflat and *Carex ramenskii* meadows (Schmutz 2000).

We obtained survival rate data by observing known families opportunistically and recording numbers of goslings. We identified families by reading individually coded tarsal bands or neck collars on 1 or both parents (applied during nest trapping or in previous years during mass banding drives while flightless in late July and early August) and recorded no more than 1 observation per family per day. Observers were in blinds for up to 48 hours at a time and observations were made during late June and July.

If parents that lost all their young behaved differently so that they were less observable from blinds than geese with young, estimates of gosling survival based on these observations would be biased. Such behaviors have been observed for sympatric black brant

and Cackling Canada Geese that fail during nesting or early brood rearing with some leaving local study areas for molting sites (Flint et al. 1995, C. Ely, U.S. Geological Survey, unpublished data). To determine if Emperor Geese also exhibit such behaviors, we attached radio-transmitters to neck collars for a subsample of females trapped on nests. We then monitored these transmitters approximately once per week following hatch from aircraft and determined the presence or absence of a signal within a 1200 km² area. When suitable pilot and aircraft were available, we also flew low enough to verify presence of young if the brood was one not previously seen from our observation blinds. Parents and goslings usually responded to overflights by crouching in tall vegetation - a behavior that did not seem to predispose goslings to additional predation risk. We assumed that a missing signal indicated departure of a female without young because the largest detected movement of a female with a brood was 10 km. Transmitter failure was potentially confounded with female departures.

To evaluate how often glaucous gulls disturbed goose broods, we observed focal goose broods for 1 hr periods (Schmutz 2000) and recorded whether or not focal broods were seen responding to gulls at any time. These 467 focal samples were distributed among all diurnal time periods and among all 10 observation blinds. Because of the large number of goose broods in our study area and our random selection of broods for observation, we believe that few families were sampled multiple times within years (Schmutz 2000). A positive response was considered any alert or aggressive behavior apparently directed towards a gull. We note that during intensive focal observations of glaucous gulls on the YKD, Strang (1976) observed that the number of predation attempts relative to successful predation events was similar when foraging over river versus terrestrial habitats. Therefore, we used our monitoring of behavioral responses of focal goose broods to gulls as an index of gull predation.

Survival Analysis

We used the models of Manly and Schmutz (MS) to estimate rates of gosling survival and variation relative to gosling age and other sources of heterogeneity. We

hypothesized that survival probability may differ among 4 age classes: 0–5 days, 6–10 days, 11–25 days, and > 25 days. These classes were based on changing ecological or physiological states that likely affect gosling vulnerability. The 0–5 day class encompassed loss of young at hatch and the initial transition of goslings from exothermy to endothermy (Marcström 1966, Steen and Gabrielsen 1986). From ages 6–10 days, goslings were largely endothermic but still frequently brooded. From 11–25 days, goslings were endothermic and parents still capable of flight. However, at this age goslings had not yet attained juvenile plumage and thus were relatively vulnerable to hypothermia from excessive wetness. After goslings were about 25 days of age, parental geese began to molt their flight feathers. Flight ability is germane to gosling survival because parental geese sometimes fly upward toward attacking glaucous gulls (Laing 1991).

We used an iterative Mayfield method to estimate age-dependent survival within each year (Manly and Schmutz MS). This method estimates a daily survival rate for a given age class, based on the number of goslings in this class surviving the relevant number of exposure days. Because the original data were observations that were often more than 1 day apart, the number at risk and the number of survivors from age $x-1$ to x days were estimated for $x = 1, 2, 3$, etc. by an iterative calculation that allowed the daily survival rate to vary with age class.

Survival rates may be assumed constant within age classes in two ways. One approach involves estimating the number at risk and the number surviving each day using the iterative calculation, with a different survival rate used for each day of age. The estimated daily survival rate for an age class is then the number surviving divided by the number of exposure days for this class. The estimates obtained in this way are called unsmoothed estimates because the numbers surviving and the numbers at risk are calculated without assuming a constant survival rate within age classes. The other approach involves including the assumption that survival rates are constant within age classes in the iterative process itself, so that the calculation of the number at risk and the number surviving for each

day depends upon the assumption that survival is constant within age classes. The estimates obtained in this way are called smoothed estimates.

Unsmoothed estimates are more robust than smoothed estimates to incorrect assumptions being made about the constancy of survival within age classes. Large systematic deviations between unsmoothed and smoothed estimates therefore indicate that the survival rate is not constant within the assumed age classes, and that 1 or more age classes should be divided into 2 (Manly and Schmutz, MS). Thus, the sum of deviations across days between smoothed and unsmoothed estimates was the statistic we used to select which model best represented these data. For each year, we calculated standard errors with bootstrap resampling of broods. We calculated an annual mean rate of gosling survival weighted by the inverse of the total variance and partitioned the total variance of this mean into the environmental (process) and sampling variances following Burnham et al. (1987).

Rainfall

We were unable to observe goose broods each day; therefore we could not relate the daily pattern of gosling mortality within years to daily variations in rainfall. Instead, we used an index of gosling survival for a whole season as a data point and related annual variation in rainfall to variation in this index. The index we used was the average number of young in families of Emperor Geese observed in fall (September or October) at Izembek Lagoon on the Alaska Peninsula; these data have been collected since 1969. We obtained rainfall data from the Bethel airport, the closest location to our study site with a long-term history of weather data collection. We used rainfall at Bethel as the explanatory variable in a linear regression with size of families in fall as the response variable. We used the cumulative rainfall occurring from 5 days before to 15 days after peak of hatch of geese on the YKD. We chose this time period because most goslings would have been < 3 weeks old and thus at their most vulnerable state relative to rainfall induced hypothermia. We included peak hatch dates, average clutch sizes (C. Dau unpublished data, Mickelson 1973, C. R. Ely unpublished data) and the means of daily minimum temperatures during the same period as

the rainfall measurements as additional explanatory variables. We excluded years with missing data for any of these variables. We then selected among regression models using Akaike's Information Criterion corrected for small sample sizes (AIC_c , Burnham and Anderson 1998). Better fitting models are those with low AIC_c values, indicating models that minimize bias without excessive loss of precision in estimating parameters.

RESULTS

Detecting Females Without Broods

We radio-marked 20 to 28 adult females during each of the 4 years of study. Of these 101 females, 93.3% were known to stay within the Manokinak study area for ≥ 1 week after hatch (Table 4.1). We detected 2 instances of radio failure during visual observation of radio-marked females. We commonly saw adults without broods from our observation blinds as 20.4% of the 220 observed pairs of parental geese of known hatch date were seen at least once without goslings. Adults were known to remain within the observation area for up to 4 weeks after losing all their goslings (Table 4.1).

Survival Rates of Goslings

We observed 83, 71, 73, and 84 broods 2 or more times during 1993–1996. Cumulative survival of goslings to 30 days of age varied among years with point estimates varying from 0.332 (SE = 0.045) in 1994 to 0.708 (SE = 0.049) in 1995 (Fig. 4.2). Daily survival with respect to age was lowest among 0–5 day old goslings in all years; survival of this age class was particularly low in 1994 (Fig. 4.2). The pattern across years in survival of 0–5 day old goslings mirrored the pattern for cumulative survival to 30 days. Daily survival rates among the 3 older age classes varied little. However, in 1993 goslings > 25 days survived less well than those 6–25 days old and in 1996 goslings 6–10 days old had higher survival than older goslings (Fig. 4.2). Mean annual gosling survival to 30 days was 0.534 ($SE_{\text{Total}} = 0.173$, $SE_{\text{Environmental}} = 0.162$).

During 1993 and 1994, 26.2% ($n = 160$, SE = 3.5) and 19.4% ($n = 160$, SE = 3.1) of goose broods were disturbed by glaucous gulls during 1-hour observation periods. These

disturbance rates were higher than in 1995 (8.1%, $n = 99$, $SE = 2.7$) and 1996 (7.4%, $n = 68$, $SE = 3.2$). The 2 years (1995–1996) with greater cumulative gosling survival were the 2 years with lower frequencies of gull disturbance of goose broods (Fig. 4.2).

Rain and Sizes of Families in Fall

Numbers of young were counted during 23 falls in an annual mean of 152 families. We found a negative relationship between cumulative rainfall during brood rearing and subsequent numbers of young in families during fall (0.085 fewer young per cm of rain, $r^2 = 0.282$, $P = 0.009$, Table 4.2, Fig. 4.3).

DISCUSSION

Movements and Detectability of Adults Without Goslings

The vast majority ($\bar{x} = 93\%$) of radio-marked females that hatched young stayed within our study area. The remainder may have departed our study area or their transmitters may have failed. We could not distinguish between these 2 alternatives except for 2 observations of failed transmitters. Frequent observation of marked adults without any young indicated that parents that lost their entire broods did not necessarily depart the study area and were readily detected from observation towers.

This evidence that adults who lost entire broods remained in local areas is corroborated by other observations. In a single season study by Blurton Jones (1972), migrations of Emperor Geese away from the YKD and occurring near hatch did not reflect movements of geese whose reproductive efforts recently failed but rather was largely comprised of 1 yr old geese. In his study, few other migratory movements were noted after this period. During aerial surveys of goose broods on the YKD in late summer of 1993–1994, flocks of adult Emperor Geese with few or no young were frequently observed (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data).

These results and observations suggest that our estimates of gosling survival contain little bias from variation in detection of parents with and without young. Further, accurate approximations of gosling survival might be obtained by less costly and time consuming

methods, such as sampling age ratios just at hatch and during late brood-rearing (Flint et al. 1995).

Comparative Rates of Gosling Survival and Population Dynamics

Goose density must be considered when interpreting patterns of gosling survival (Williams et al. 1993, Loonen et al. 1997). Long-term declines in gosling survival in Snow Geese (*Chen caerulescens*) were coincident with steady increases in goose density, competition for forage, and degradation of habitats available to broods (Williams et al. 1993). In that study, survival at the mid-point of the 12-year decline was approximately equal to our 4-year mean of survival of Emperor Geese to 30 days (0.534). Our estimate for Emperor Geese was also similar to that observed in sympatric Cackling Canada Geese (0.45) during 1986–1990, when density of Cackling Canada Geese had not yet markedly increased and was still similar to that of Emperor Geese (Ely 1998, C. Ely, U.S. Geological Survey, unpublished data). During 1987–1989, 25-day survival of brant goslings at the Tutakoke colony on the YKD was 0.676, about 26% higher than what we documented for Emperor Geese (Flint et al. 1995). However, that colony then substantially increased in size, reduced growth rates of goslings were observed (Sedinger et al. 1998), and preliminary analyses indicated that gosling survival rates declined (J. Sedinger and M. Herzog, University of Alaska, unpublished data). Densities of Emperor Geese have remained stable since the mid 1980s; however, densities of sympatric Cackling Canada Geese increased markedly during the 1990s (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data). Because these 2 species overlap in use of brood habitats (Schmutz 2000), there is potential for survival rates of Emperor Goose goslings to be temporally changing in response to goose densities.

Relating rates of gosling survival to population trends is further complicated by the impact of other demographic parameters on population growth. Variation in adult survival has a comparatively large effect on dynamics of goose populations (Rockwell et al. 1997, Schmutz et al. 1997). Consequently, surging populations of Snow Geese in the Hudson Bay area, coincident with low rates of gosling survival relative to Emperor Geese, may be a

consequence of the changing ecology and survival patterns of adults during non-breeding seasons (Francis et al. 1992, Cooke et al. 1995, Alisauskas 1998).

Sources of Gosling Mortality

To evaluate the extent to which gull predation affects gosling survival, we need to consider other potential mortality factors. Virology and bacteriology surveys of Emperor Geese in 1996 indicated a generally healthy population (Hollmén et al. 1998). Selenium concentrations in the blood of adults were high compared to levels that induce negative effects in Mallards (*Anas platyrhynchos*; Franson et al. 1999). However, there were no conspicuous impacts of this exposure on Emperor Geese. Further, exposure of adults apparently occurred prior to their arrival on the YKD, whereas exposure of goslings to selenium was low (Franson et al. 1999). Ducklings of sympatric Spectacled Eiders (*Somateria fisheri*) were exposed to lead poisoning from spent shot (Flint et al. 1997), and lead exposure reduced survival rates of eiders (Grand et al. 1998). However, exposure of Emperor Geese to lead was negligible, likely due to the differences in feeding ecology between eiders and geese (Franson et al. 1999).

Arctic foxes hunt and consume goslings of all species on the YKD (Stickney 1989). Although we documented 8 disturbances of focal goose broods by foxes, the primarily nocturnal habits of foxes (Anthony 1997) made it impossible to reasonably assess the magnitude of fox predation on goslings. Thompson and Raveling (1987) proposed that the large body size of Emperor Geese made them less vulnerable to fox predation and more susceptible to avian predation than the smaller Cackling Canada Geese. Consequently, nest site selection in Cackling Canada Geese is strongly affected by foxes (Mickelson 1975). These same ecological relations may also exist during brood rearing. The majority of broods of Cackling Canada Geese use habitats immediately adjacent to ponds, and they regularly swim onto ponds to escape foxes (C. R. Ely, U.S. Geological Survey, unpublished data). In contrast, broods of Emperor Geese usually forage along the margin between mudflat vegetation and *Carex ramenskii* meadows (Schmutz 2000), where cover for escape from

foxes is not readily available. Additionally, broods of Emperor Geese have successfully defended their goslings from foxes (Schmutz pers obs).

Young waterfowl are vulnerable to hypothermia. The lower critical temperature of 3-4 day old Barnacle Goose (*B. leucopsis*) goslings was 21° C (Steen and Gabrielsen 1986). Ambient temperatures in our study area in June and July were above this temperature < 5% of the time, and energy expenditure of Snow Goose goslings increased by > 7% for each degree drop below 21° C (Beasley and Ankney 1992). Goslings are vulnerable to energetic stress induced by inclement weather because they have no fat reserves (Sedinger 1986, Lesage and Gauthier 1997). Temperature and wind (Beasley and Ankney 1988) and wet plumage (Poczopko 1968) were factors that most affected the energy budget of captive goslings. In our study, the high rainfall in 1994 (Fig. 4.3) corresponded to the year with the poorest survival of young goslings (Fig. 4.2), which also corresponded to the year with lowest cumulative survival to 30-days. Further, the correlation between rainfall during early brood rearing and size of families in fall suggests that precipitation affected survival of goslings. The large amount of residual variation in this relationship indicates that sampling error and likely other factors also affected this index of gosling survival. Two such factors may be annual variability in gull predation of goslings and survival of juveniles from the YKD to Izembek Lagoon. Survival of juvenile Emperor Geese during this fall migration is related to their pre fledging body mass (Schmutz 1993), which may vary in relation to the quality and availability of habitats for gosling growth (Sedinger et al. 1998).

Predation by Glaucous Gulls

It is not known whether survival rates of Emperor Goose goslings prior to our study were higher than what we observed in 1993–1996. Gull populations on the YKD have increased recently and concurrently with increases in Cackling Canada Geese and white-fronted geese (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data). Because the proportionate contribution of goslings and other birds to the diets of Glaucous Gulls was not markedly different in 1993 from that observed in the 1970s (Strang 1976, Schmutz and

Hobson 1998), individual gulls may have consumed Emperor Geese with similar frequencies during the 2 time periods. Coupled with increased gull numbers and static Emperor Goose numbers, these data suggest that predation rates on Emperor Geese may have increased.

The correspondence of high and low years in gosling survival with low and high years of gull disturbance of Emperor Goose broods suggests that gull predation affected gosling survival. Similarly, in a recent study of Barnacle Geese, gosling survival in an area with a low density of gulls (*L. fuscus*, *L. marinus*, and *L. argentatus*) was much higher than in an area 7 km away with a high gull density (Forsslund 1993). However, it is unclear to what extent the magnitude of predation is independent of limited foraging options for broods and goose density. As brant numbers increased at the Tutakoke colony on the YKD, broods spent more time feeding and parents spent less time alert scanning for predators (Sedinger et al. 1995b). Similarly, parental Emperor Geese during 1994–1996 devoted more time to feeding with increased goose densities, and correspondingly spent less time alert (Schmutz 2000). Irrespective of parental behavior, food limitation may predispose goslings to malnutrition and hypothermia (Swennen 1989).

MANAGEMENT IMPLICATIONS

There are no comparable demographic data from a past period of more rapid population increase to know if gosling survival rates we report here are lower than in the past. Our data strongly suggest that the amount of rainfall occurring during early brood-rearing affects gosling survival. Although Glaucous Gulls consume large numbers of goslings (T. D. Bowman, U.S. Fish and Wildlife Service, unpublished data), it is unclear whether large-scale reductions of Glaucous Gulls would improve gosling survival and population growth rates in Emperor Geese. Competition among geese may lead to density-dependent mortality (Sedinger et al. 1995a, Loonen et al. 1997, van der Jeugd and Larsson 1998) that could partially compensate for the effect of gull removals. Also, because of its dominating effect on population dynamics of geese (Schmutz et al. 1997), future variations in adult survival (Schmutz and Morse 2000) may negate (or augment) the impacts of gull

removals.

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Table 4.1. Detectability of pairs that lost all goslings. We assessed the frequency and detectability of total loss of goslings from broods of Emperor Geese on the Yukon-Kuskokwim Delta, Alaska, 1993-1996.

	Proportion of radio-marked females known to remain within study area for ≥ 1 week after hatch (<i>n</i>)	Proportion of marked females of known hatch date that were seen from observation towers with 0 young (<i>n</i>)	Maximum number of days between first and last observation of a family with 0 young
1993	0.929 (28)	0.262 (80)	21
1994	1.000 (20)	0.286 (56)	29
1995	0.885 (26)	0.058 (52)	9
1996	0.926 (27)	0.156 (32)	20

Table 4.2. Effects of rainfall, clutch size and hatch date on number of young during fall. We present model selection statistics from a multiple regression examining the relation of cumulative rainfall, average clutch size, and peak hatch date to annual variation in average number of young in Emperor Goose families observed in fall at Izembek Lagoon.

Cumulative rainfall was measured at the Bethel airport from 5 days prior to peak hatch to 15 days after peak hatch. The parsimonious model is the one with the lowest AIC_c value (Akaike's information criterion adjusted for small sample size [Burnham and Anderson 1998]). Because AIC_c values within an analysis are only relevant on a relative basis, we present AIC_c values as the amount of difference from the parsimonious model (ΔAIC_c). Only those models with $\Delta AIC_c < 4$ are shown.

Model parameters	r^2	ΔAIC_c
Rainfall	0.282	0.00
Rainfall, Clutch size	0.329	2.33
Rainfall, Peak hatch	0.314	2.85
Rainfall, Min temp	0.294	3.53

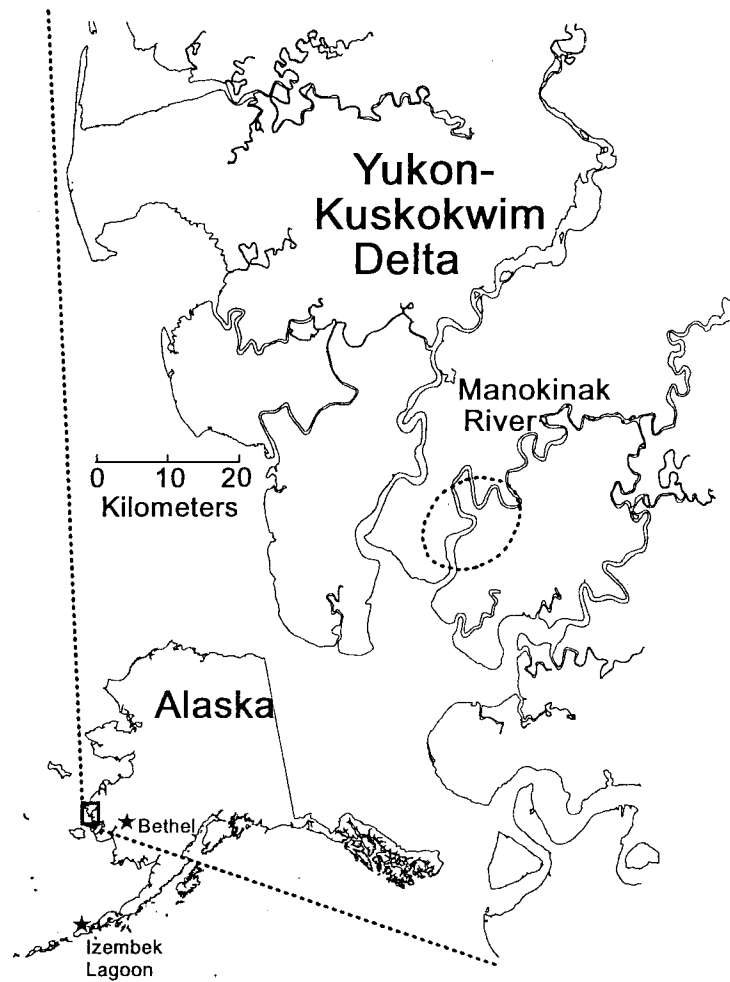


Figure 4.1. Locations for study of gosling survival in Emperor Geese. Observations of marked broods occurred at the Manokinak River on the Yukon-Kuskokwim Delta during 1993–1996. Weather data were obtained at the Bethel airport, and we collected data on sizes of families in fall at Izembek Lagoon.

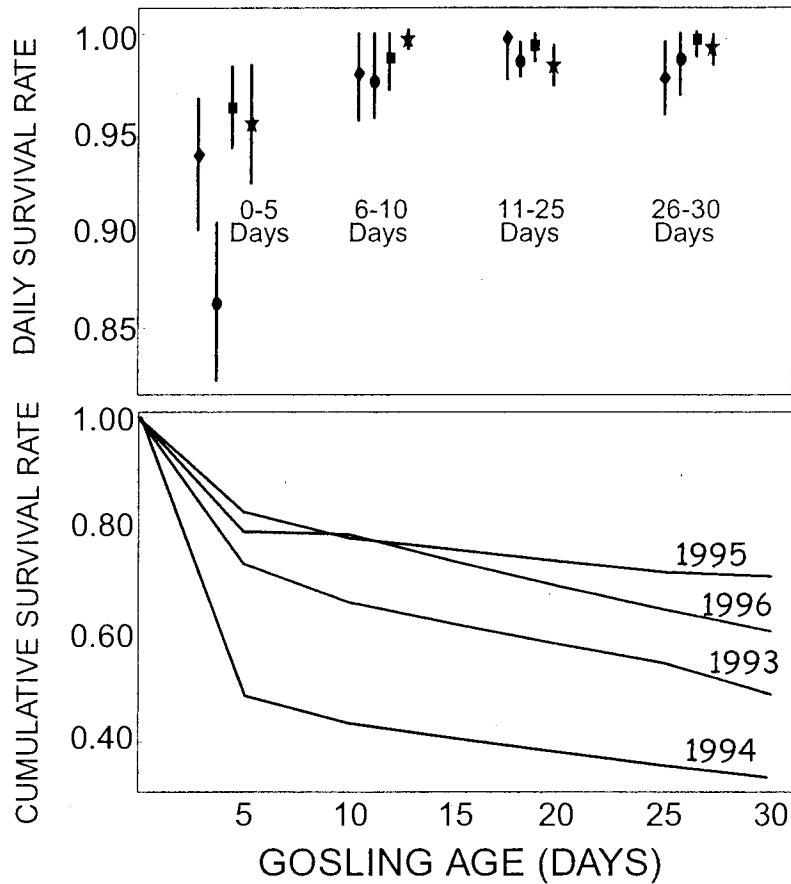


Figure 4.2. Survival of Emperor Goose goslings on the Yukon-Kuskokwim Delta. We estimated survival rates with an iterative Mayfield method (Manly and Schmutz MS), where daily survival rate was constant within each of 4 age classes, but potentially different among age classes. We show daily survival rates of the most general model, i.e., where each age class differed in survival rate, and point estimates in 1993–1996 are respectively represented by diamonds, ovals, squares, and stars. Vertical lines are 95% confidence intervals. We then show the pattern of cumulative survival to 30 days of age, using a parsimonious model where daily survival among some age classes > 5 days of age were constrained equal.

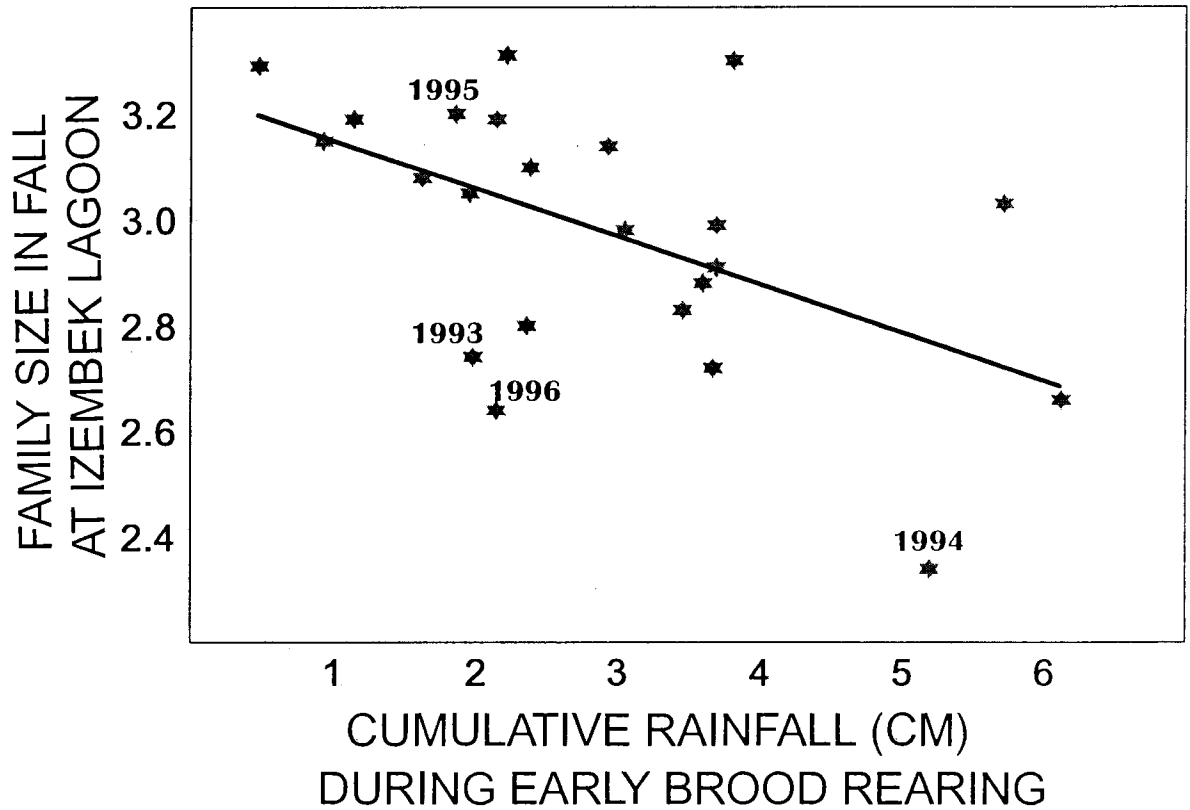


Figure 4.3. Size of families in fall relative to rainfall during brood rearing. Number of young in Emperor Goose families during fall at Izembek Lagoon were counted and related to cumulative rainfall (cm) during early brood rearing, 1969–1996 ($n = 23$ years). Rainfall was measured at the Bethel airport from 5 days prior to peak hatch to 15 days after peak hatch. Linear regression model is: Family Size = $3.239 - 0.085 \times (\text{Rainfall})$.

Chapter 5

Selection of Habitats by Emperor Geese and Other Geese During Brood Rearing

Abstract: Although forage quality strongly affects gosling growth and consequently juvenile survival, the relative use of different plant communities by brood rearing geese has been poorly studied. On the Yukon-Kuskokwim Delta, Alaska, four species of geese nest; however, population growth and juvenile recruitment of Emperor Geese (*Chen canagica*) are comparatively low, and it is unknown whether their selection of habitats during brood rearing differs from other species. I used radio-telemetry to document the use of habitats by 56 families of Emperor Geese in a 70 km² portion of the Yukon-Kuskokwim Delta during brood rearing in 1994–1996. When contrasted with available habitats, as estimated from 398 random sampling locations, Emperor Geese strongly selected Saline Ponds, Mudflat, and *Ramenskii* Meadow habitats and avoided Levee Meadow, Bog Meadow, and Sedge Meadow. The selected habitats were the most saline and comprised one-third of the study area, and 43% of all locations were in *Ramenskii* Meadow. I contrasted these Emperor Goose locations with habitats used by the composite goose community, as discerned from the presence of goose feces at random locations. The marked difference between groups in this comparison implied that Cackling Canada Geese (*Branta canadensis minima*) and Greater White-fronted Geese (*Anser albifrons*) collectively selected much different brood rearing habitats than Emperor Geese.

INTRODUCTION

Geese are important herbivores in their breeding areas in Arctic and subarctic ecosystems (Jefferies et al. 1994). Despite their potential for affecting the composition and

productivity of plant communities (Cargill and Jefferies 1984, Jefferies 1988), selection among habitats at the plant community level by geese raising broods has been comparatively ignored (but see Giroux et al. 1984, Hughes et al. 1994). This paucity of study is partly a consequence of the difficulties of monitoring geese during brood rearing; goslings are precocial, highly mobile, and families are particularly sensitive to human disturbance. Nonetheless, the strong relevance of such habitat selection to goose distribution and fitness is implied by numerous finer-scale studies relating plant nutritional quality to timing of nesting and gosling growth (Sedinger and Raveling 1986, Lindholm et al. 1994, Gadallah and Jefferies 1995), which in turn affects demography (Schmutz 1993, Sedinger et al. 1995a, Van der Jeugd and Larsson 1998). Patterns of habitat selection are also relevant to competition and niche partitioning among geese in multi-species communities, such as the Yukon-Kuskokwim (Y-K) Delta, where four goose species sympatrically nest and raise young.

The Y-K Delta in western Alaska is one of the world's most important breeding areas for geese (Spencer et al. 1951). Virtually all Emperor Geese (*Chen canagica*) and Cackling Canada Geese (*Branta canadensis minima*) breed here as do the majority of Black Brant (*B. bernicla*) and Greater White-fronted Geese (*Anser albifrons*) in the Pacific Flyway, collectively constituting more than half a million geese in some years (King and Derksen 1986, Sedinger 1996). Disparate population trends among species have raised questions from wildlife managers concerning species-specific differences in ecology, including habitat selection. Numbers of Emperor Geese declined by 50% or more between the early 1960s and mid 1980s. Since then, Emperor Goose numbers have remained stationary whereas Cackling Canada Geese and Greater White-fronted Geese have increased at > 10% per year (Bowman et al. 1998a).

Factors contributing to low numbers of juvenile Emperor Geese, as measured from age ratios and counts during fall migration, have been highlighted as a needed area of study (U.S. Fish and Wildlife Service 1994). Because of the aforementioned importance of brood rearing habitats to geese, lack of studies for Emperor Geese, and the existence of on-going

studies of sympatrically breeding Cackling Canada Geese and Black Brant. I studied habitat selection of Emperor Goose broods during 1994–1996. I used radio-telemetry to obtain locations of Emperor Goose broods and then infer selection by comparing the proportionate use of habitats to that available throughout the study area. A second objective was to compare habitat selection of Emperor Geese to that of other sympatric geese, using the distribution of feces as an indicator of habitat use by the composite community of geese. Because Emperor Geese constitute a small percentage of all geese, this distribution of goose feces principally represented use by other species. I also examined whether patterns of habitat use changed across a season, which potentially may occur in response to seasonal declines in plant nutrient quality (Sedinger and Raveling 1986) or reductions in preferred food plants due to grazing.

STUDY AREA AND METHODS

The Y-K Delta is an expansive, coastal wetland where tides extend inward up to 55 km (Tande and Jennings 1986). Plant communities that are flooded annually or more frequently are dominated by graminoids, principally *Carex* species, whereas more elevated habitats are underlain by permafrost and have higher proportions of moss and woody vegetation (Tande and Jennings 1986, Kincheloe and Stehn 1991, Babcock and Ely 1994, Jorgenson 2000). Jorgenson (2000) used vegetative, environmental, and geomorphic characteristics to identify 27 ecotypes, or floristic plant associations, across this deltaic ecosystem. Additionally, he specifically described the relationships among classifications in each of the earlier studies.

I studied habitat selection of Emperor Geese in an approximate 70 km² area along the Manokinak River of the Y-K Delta. My general approach was to use radio-telemetry to remotely monitor locations of goose broods and then subsequently visit used and random sites to classify habitats. Each year I and others thoroughly searched a series of plots to locate nesting Emperor Geese. During 1994–1996 we captured 20, 26, and 27 adult females late in incubation or during early hatching and banded them with neck collars with attached

radio-transmitters. Radio-transmitters weighed 19 g and their antennae were oriented downward along the breast. We then received signals from these radio-transmitters while in observation blinds outfitted with dual four-element antennas mounted 8 - 10 m above ground. To minimize human disturbance of broods, each session in an observation blind lasted for 40 hours and spanned part or all of 3 days. Thus, we gathered once-daily locations of geese in three-day sets when goslings were 0 to 5 weeks of age (24 June - 25 July). Observers arrived at blinds before 1800 hrs on the first day of a 3-day session and began scanning for radio-transmitter signals at 2100 hours. All observers serially scanned through the same numerical order of frequencies to ensure that all bearings on a given goose were gathered nearly simultaneously (Schmutz and White 1990). The next day in a blind, we began telemetry data collection at 1500 hrs, and the following morning, we collected data at 1000 hrs, with each daily collection period lasting approximately 2 hours. Thus, we systematically rotated daily locations among diurnal periods. I note, however, that previous studies have found little variation in behavior of goose broods relative to time of day (Sedinger et al. 1995b, Fowler and Ely 1997).

I estimated the average precision (SD) of our antennae to be 2.4° by placing test transmitters throughout the study area. I then estimated goose locations using simultaneously gathered bearings and the maximum likelihood method described by Lenth (1981). I only used locations that were based on three or more independent bearings and that were not rejected ($P > 0.05$) by a goodness-of-fit test (White and Garrott 1990). In 1997 a team of observers visited each estimated location using GPS receivers (± 5 m) and classified each location to one of Jorgenson's (2000) 27 ecotypes. Similarly, observers visited 398 random locations and categorized each to ecotype. For Emperor Goose brood locations and random locations, observers also recorded whether each location was within 100 m and 250 m of the interface of meadows of *Carex ramenskii* and meadows of mudflat vegetation dominated by *Carex subspathaceae*. Random locations were established by randomly selecting a point within the study area from which a systematic grid of points emanated and encompassed the

distribution of goose locations. These systematically random points, or locations, were approximately 400 m apart. We visited random locations twice. During our first visit, which occurred shortly after peak hatch of geese, we classified each location to an ecotype and also removed all goose feces from a 2 m² area, which was demarcated with a plastic flag to enable relocation. Our second visit occurred about 16 days later when we recorded presence or absence of new goose feces.

Before analysis, I used geomorphic and vegetative attributes noted by Jorgenson (2000) to pool ecotype classes into six composite categories (habitats). A priori, I deemed this pooling necessary to achieve reasonable statistical test power and to reduce misclassification of habitats caused by telemetry error (Pendleton et al. 1998). These six habitats are described in Table 5.1.

I used compositional analysis (Aebischer et al. 1993) to examine proportionate use of habitats by Emperor Geese. Advantages of this method include use of broods, rather than locations, as the sampling unit (Otis and White 1999) and the independence of proportions among habitats (the lack of which is referred to as the unit-sum constraint; Aebischer et al. 1993, Pendleton et al. 1998). For this analysis, one uses the set of i habitats to calculate the proportionate use of each habitat, x_i , for each brood. These proportions are then transformed to log-ratios, y_i , as

$$y_i = \ln (x_i / x_j), \text{ where } i \neq j.$$

For occasions where a brood had no occurrences in a specific habitat, I replaced that value of x with 0.001% (Aebischer et al. 1993). The vectors of y_i for each brood are then combined to form a matrix representing habitats used. A similar matrix is constructed for the proportions of available habitats. In this study, the proportions of habitats available among broods is assumed to be the same. A test for habitat selection is then whether or not the sum of differences between these two matrices is zero. I performed this test using randomization (Aebischer et al. 1993, Pendleton et al. 1998). The selective use of these six habitats was ranked by ordering the habitat-specific differences between these matrices (Aebischer et al.

1993).

I conducted such a compositional analysis to examine whether broods of Emperor Geese used habitats selectively relative to their availability as estimated from the random locations. I also examined whether Emperor Goose broods were close (within 100 m or 250 m) to the interface between Ramenskii Meadows and Mudflat vegetation (Table 5.1) more often than for random locations. To maintain a sample size of 56 broods but account for the fact that some broods were sampled more often than others, I constructed 1000 data sets, each of which contained a randomly selected location for each of the 56 broods. For each of these data sets, I calculated the frequency with which broods were within 100 m and 250 m of this habitat interface, and then I computed the mean of these 1000 frequencies. I compared these mean frequencies with that for the random locations by calculating binomial variances, where $n = 56$ broods, and comparing confidence intervals.

To address the hypothesis of a seasonal (date) change in habitat use, a different analytical approach was required because each brood was located, at most, once per day, and thus documentation of use of one habitat on a given day would result in zero proportionate use for all other habitats. Compositional analyses are robust to some zero values in proportionate use of habitats, but they are not appropriate when all data are of this nature (Aebischer et al. 1993, Pendleton et al. 1998). I therefore used logistic regression analysis, with date as an explanatory variable and a binomial response variable of presence or absence in a given habitat. I conducted three such logistic regressions, one for each of the three most selectively used habitats. I similarly conducted two logistic regressions to examine whether date was an important explanatory variable for whether an Emperor Goose brood was within 100 m or 250 m of the Ramenskii Meadow - Mudflat vegetation interface. For each of these five logistic regression analyses, I maintained a sample size of 56 broods, while still incorporating all data for each brood, by using the resampling procedure described in the previous paragraph for analysis of distance from the habitat interface. Whether or not date affected use of habitats was judged by comparing the Akaike Information Criterion (AIC) for

the model with a date effect (the mean AIC from 1000 iteratively created data sets) to the AIC for a model without this effect. Smaller AIC values indicate a better fitting model (Burnham and Anderson 1998).

I then conducted two analyses concerning use of habitats by the composite goose community, as indicated by goose feces, for which species-specific designations could not be made. First, to contrast habitat use by Emperor Goose broods to that of the composite goose community (which was dominated by other goose species), I conducted a compositional analysis that compared habitats at telemetry-derived locations of Emperor Goose broods to those from the subset of 398 random locations that contained goose feces. Second, to examine whether the composite goose community used habitats selectively, I contrasted habitats for the subset of random locations with goose feces to habitats from the overall set of random locations. In this second analysis, individuals were not known and thus each 2 m² area with feces at a random location was a sample unit. Consequently, I did not use compositional analysis but rather a Chi-square test of homogeneity to examine fecal distribution among habitats (Thomas and Taylor 1990).

For each analysis, I calculated selection ratios to serve as summary measures of the relative use of these six habitats. A selection ratio for a given habitat is simply the observed proportion divided by the used proportion with a value of 1.0 connoting no selection (Manly et al. 1993, Pendleton et al. 1998). For the Emperor Goose data, selection ratios were calculated for each individual and therefore variances of selection ratios were estimable.

RESULTS

The estimated proportionate availability of the six habitats was Wet Sedge Meadow (23.9%), *Ramenskii* Meadow (21.4%), Bog Meadow (20.6%), Levee Meadow (17.1%), Saline Ponds (8.8%), and Mudflat (8.3%) (Fig. 5.1). We obtained a total of 337 acceptable (3 or more bearings, $P > 0.05$ goodness-of-fit) locations from 56 broods in these habitats. Average 95% error ellipse of these locations was 0.075 km². From the compositional analysis, the rank of habitats used by Emperor Geese, from highest to lowest proportionate

use, was Saline Ponds, *Ramenskii* Meadow, Mudflat, Wet Sedge Meadow, Levee Meadow, and Bog Meadow. Selection of the first three habitats was greater than for the latter three habitats ($P \leq 0.001$ all tests). Similarly, selection ratios were > 1 for these first three habitats, which comprised about one-third of all available habitats, and < 1 for the latter three habitats (Fig. 5.1). Emperor Geese spent about 80% of their time in the three selected habitats. *Ramenskii* Meadow was more abundant (21% vs. $< 9\%$) than other selected habitats, and thus was the habitat most used by Emperor Geese (43% of all locations). Randomization tests indicated no marked differences in selection among the three least selected habitats ($P > 0.62$).

Emperor Geese were consistently closer to the interface between Mudflat and *Ramenskii* Meadows than expected by chance. The frequency of Emperor Goose brood locations that were within 100 m of this interface (32%, CI = 20 - 44%) was greater than for random locations (14%, CI = 11 - 18%). Similarly, the frequency of Emperor Goose brood locations that were within 250 m of this interface (48%, CI = 35 - 61%) was greater than for random locations (22%, CI = 18 - 26%).

I detected no seasonal change in habitat use. Models with a date variable had larger AIC values than models without a date effect for each of the logistic regressions concerning the three selected habitats ($\Delta AIC_{\text{Mudflat}} = 1.2$, $\Delta AIC_{\text{Ramenskii Meadow}} = 0.7$, $\Delta AIC_{\text{Saline Ponds}} = 0.2$) and for the two logistic regressions concerning distance from the Mudflat - *Ramenskii* Meadow interface ($\Delta AIC_{100 \text{ m}} = 1.2$, $\Delta AIC_{250 \text{ m}} = 1.2$).

Goose feces was present at 50% of resampled random locations. I then used compositional analysis to compare habitats at locations of Emperor Goose broods with the random locations that contained goose feces. The pattern of habitat rankings and significance tests was identical (Fig. 5.1) to the comparison of Emperor Goose locations with all random locations described above; habitats at Emperor Brood locations differed strongly from habitats at locations containing goose feces. Examining locations of goose feces relative to all random locations, selection ratios were close to one, and differences much less than when

contrasting to locations of Emperor Goose broods (Fig. 5.1).

We were not able to resample 17% of the 398 availability locations to document presence of goose feces. Most failures likely occurred because strong winds tore plastic flags from their thin, wire masts, rendering them difficult to relocate. Such a form of sample loss was likely random with respect to habitat. We were unable to sample 13 sites because they occurred in standing water of the Saline Pond habitat. These unsampled sites had little effect on the results; the distribution of habitats in which goose feces occurred differed from the distribution of available habitats when unsampled sites were either dropped from analysis ($\chi^2 = 14.9, P = 0.011$), recoded as having goose feces present ($\chi^2 = 17.7, P = 0.003$), or recoded as having goose feces absent ($\chi^2 = 21.4, P < 0.001$). Similarly, selection ratios for five of the six habitats were insensitive ($< 10\%$ difference) to which of the three manners were used to treat unsampled sites. The selection ratio for Saline Pond, however, was quite sensitive to method of treatment of unsampled sites. I therefore omitted this habitat from the presentation of selection ratios that utilized fecal data (Fig. 5.1).

DISCUSSION

Saline Pond, Mudflat, and *Ramenskii* Meadow habitats comprised about one-third of all available habitats and were strongly selected by families of Emperor Geese. Selective differences among these three habitats were not discernable. Whereas the compositional analysis ranked *Ramenskii* Meadow as the most preferred habitat, the selection ratio for Saline Pond was highest, although with broadly overlapping confidence intervals. Although selection ratios are subject to the unit-sum constraint and the general correspondence between selection ratios and compositional analyses have not been examined thoroughly (Pendleton et al. 1998), the relative concordance of my results for these two analyses provides confidence in the patterns they depict.

Habitats selected by Emperor Geese differed from those selected by the composite goose community in my study area, as represented by the fecal data. Black Brant were more coastally distributed and were comparatively rare in this study area (Bowman et al. 1998b,

Schmutz and Laing MS), thus my results imply that habitat selection by broods of Emperor Geese differed markedly from that collectively expressed by Cackling Canada Geese and Greater White-fronted Geese. These latter two species collectively selected less saline habitats. Cackling Canada Geese and Greater White-fronted Geese were much more abundant than Emperor Geese (respectively, $2.2 \times$ and $1.8 \times$ Emperor Goose density during 1994–1996; Bowman et al. [1998a]). Schmutz and Laing (MS) observed that during brood rearing Cackling Canada Geese occurred with equal frequency as Emperor Geese in the adjoined habitats dominated by *C. subspathacaea* and *C. ramenskii*, whereas broods of Greater White-fronted Geese were virtually non-existent in these habitats. Thus, despite selection of more inland habitats by most Cackling Canada Geese (Sedinger and Raveling 1984, this study; C. R. Ely, U.S. Geological Survey, unpublished data), these geese may well be a numerically significant competitor to Emperor Geese in habitats selected by Emperor Geese (Schmutz and Laing MS). As populations of Cackling Canada Geese have nearly tripled since the mid 1980s, it is likely that these geese have progressively increased in habitat overlap with Emperor Geese (Schmutz and Laing MS), whose numbers have remained stable. Applying the concept of an ideal free distribution to the selection of these habitats (Fretwell and Lucas 1970), intraspecific competition among Cackling Canada Geese within their most favored habitats may have increased to the point where the fitness value for some geese to use typically less preferred habitats, such as Mudflat and *Ramenskii* Meadows, equilibrated with that experienced by the majority of cackling geese in the preferred habitats.

The importance of Mudflat habitat may be underrepresented in these analyses because this habitat category contained both vegetated and unvegetated mudflat. The vegetated mudflat was predominantly a thin band of *Carex subspathacaea* that bordered the *Ramenskii* Meadow habitat, and direct observations indicated this band was heavily used by foraging geese (Schmutz and Laing MS). The frequent proximity of Emperor Goose broods within 100 m and 250 m of this interface was also indicative of selective use of this band of habitat. Mudflat and Saline Pond were small, patchily distributed, and the least available habitats, and

they consistently shared borders with each other and expansive *Ramenskii* Meadow habitat (Jorgenson 2000). Thus, telemetry error may have caused some bias as to which of these habitats was used most selectively and would tend to underestimate the selectivity of less available habitats (Samuel and Kenow 1992). Because Saline Pond habitat was largely unvegetated, its high use likely resulted from being interspersed between two selected habitats that were heavily used for foraging (Schmutz and Laing MS) and because broods frequently moved into Saline Pond habitat in response to predators. Despite the lack of clear selective differences among Saline Pond, *Ramenskii* Meadow, and Mudflat habitats, Emperor Geese strongly selected these habitats relative to other habitats that comprised the remaining two-thirds of the study area.

The lack of a seasonal change in habitat use corroborates finer scale, direct observations of seasonal use of Mudflat and *Ramenskii* Meadow habitats (Schmutz and Laing MS). These results are consistent with studies of Snow Geese (*Chen caerulescens*; Healy et al. 1980) and Black Brant (Lindberg and Sedinger 1998), in which fidelity to brood rearing sites among seasons was high, and persisted despite long-term reductions in forage abundance (Cooch et al. 1993). Nevertheless, geese may switch among food items within habitats - a scale below that of our observations.

Despite low biomass (< 4%) in most plant communities (Mulder et al. 1996, Jorgenson 2000), *Triglochin palustris* is highly preferred by Cackling Canada Geese as food because of its high nitrogen and low fiber content (Sedinger and Raveling 1984). This forage species is minimally present or absent from habitats that were selected by Emperor Geese in this study (Mulder et al. 1996, Jorgenson 2000, Schmutz unpubl data). Laing and Raveling (1993) noted that captive Emperor Geese preferred *T. palustris* in feeding trials, yet shortly after hatch, wild broods abandoned habitats with comparatively abundant *T. palustris* to feed elsewhere in mudflat habitats. In contrast, Cackling Canada Geese remained during brood rearing in habitats containing *T. palustris* (C. R. Ely and B. T. Person, unpublished data). Emperor Geese are one-third larger than Cackling Canada Geese (Petersen et al. 1994, C. R.

Ely unpublished data), and consequently are expected to have a higher absolute energy and nitrogen demand, but a better ability to utilize low quality diets (Demment and Van Soest 1985). Perhaps these body size-forage relationships allow Emperor Geese greater ability to exploit abundant but poorer quality *C. ramenskii* habitats, whereas Cackling Canada Geese have a comparatively greater ability to exploit habitats where less abundant but highly nutritious *T. palustris* is found. I also note that the highest selection ratio for the collective goose community (in which Cackling Canada Geese are most abundant) was for Wet Sedge Meadow, which was dominated by *C. mackenzii* and *C. rariflora*. Direct observations indicated that *C. mackenzii* was intensively used by Cackling Canada Geese (C. R. Ely and B. T. Person, unpublished data). Interestingly, selection ratios for the composite goose community were close to 1.0 (Fig. 5.1), meaning that collectively, geese in this portion of the Y-K Delta exploited all available habitats (relative to my scale of inquiry).

Identifying which habitats are available to an animal is a subjective process, and the choice made can affect the outcome of analyses of selection (Thomas and Taylor 1990, McClean et al. 1998). By defining availability as the array of habitats within range of our telemetry antennae, I have assumed that geese that moved to habitats outside of this telemetry range did not encounter a different availability of habitats. We did not obtain locations of all radio-marked geese because some families made such movements. During aerial surveys to locate some of these families, I anecdotally observed that their use of habitats was similar to those families that remained in our core study area. For geese, movements of this scale are likely motivated more by patterns of brood site fidelity than by spatial patterns of habitat use (Cooch et al. 1993, Lindberg and Sedinger 1998). Using sighting data from a larger sample of geese marked with neck collars but not transmitters (Schmutz and Morse 2000), we also frequently observed movements in the opposite direction, that is, movements after hatch of young from nesting locations outside of telemetry range into our core study area and within telemetry range. Finally, I note that based on previous vegetative descriptions (Tande and Jennings 1986, Kincheloe and Stehn 1991), substantial change in the proportionate

availability of habitats was unlikely even if we had more than doubled the size of the areas we sampled. In summary, I believe that our set of Emperor Goose locations constituted a random sample of all possible locations with respect to habitat use and that I have defined habitat availability at a biologically meaningful scale.

Emperor geese during brood rearing strongly selected the more saline one-third of habitats in our study area, and this selection differed from Cackling Canada Geese and Greater White-fronted Geese, which used less saline habitats. Despite clear species differences in selectivity of habitats used for brood rearing (this study), there was much overlap and shared used of habitats (Schmutz and Laing MS), thus providing the context for interspecific competition.

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Table 5.1. Habitats available to Emperor Geese along the Manokinak River, Yukon-Kuskokwim Delta.

Habitat	Ecotypes of Jorgenson (2000) that were pooled to create habitat categories ^a .
Saline Ponds	Sloughs (1), Tidal or Brackish Ponds (3, 50) or Ponds with <i>Hippuris tetraphylla</i> (55).
Mudflat	Barren tidal flats (11) and Brackish Fringe Wet Graminoid Meadow, dominated by <i>Carex subspathaceae</i> and <i>Puccinellia phraganoides</i> (13).
<i>Ramenskii</i> Meadow	Brackish Wet Sedge Meadow dominated by <i>Carex ramenskii</i> (15, 21).
Levee Meadow	Brackish Levee Moist Meadows dominated by <i>Elymus arenarius</i> , <i>Salix ovalifolia</i> , <i>Triglochin palustris</i> , or <i>Deschampsia caespitosa</i> (41, 45).
Wet Sedge Meadow	Slightly Brackish Wet Meadow dominated by <i>Carex mackenzii</i> or <i>Carex rariflora</i> and with moderate amounts of <i>Salix fuscencens</i> , <i>Dupontia fischeri</i> , or <i>Carex ramenskii</i> (22, 24, 25).
Bog Meadow	Slightly Brackish Levee Moist Meadow dominated by <i>Carex rariflora</i> , <i>Calimagrostis canadensis</i> , <i>Empetrum nigrum</i> , or <i>Sphagnum</i> spp. (31, 32, 35). Into this habitat category, I also included the few occurrences of Lowland Bog Meadow dominated by <i>Carex aquatilis</i> and <i>Carex lyngbyei</i> (63, 65), and Lowland Moist Low Shrub dominated by <i>Betula nana</i> and <i>Cladina rangiferina</i> (71).

^aJorgenson (2000) contains relationships of ecotypes to previous vegetative classifications (Tande and Jennings 1986, Kincheloe and Stehn 1991, and Babcock and Ely 1994). Numbers in parentheses refer to the ecotype number in Jorgenson (2000).

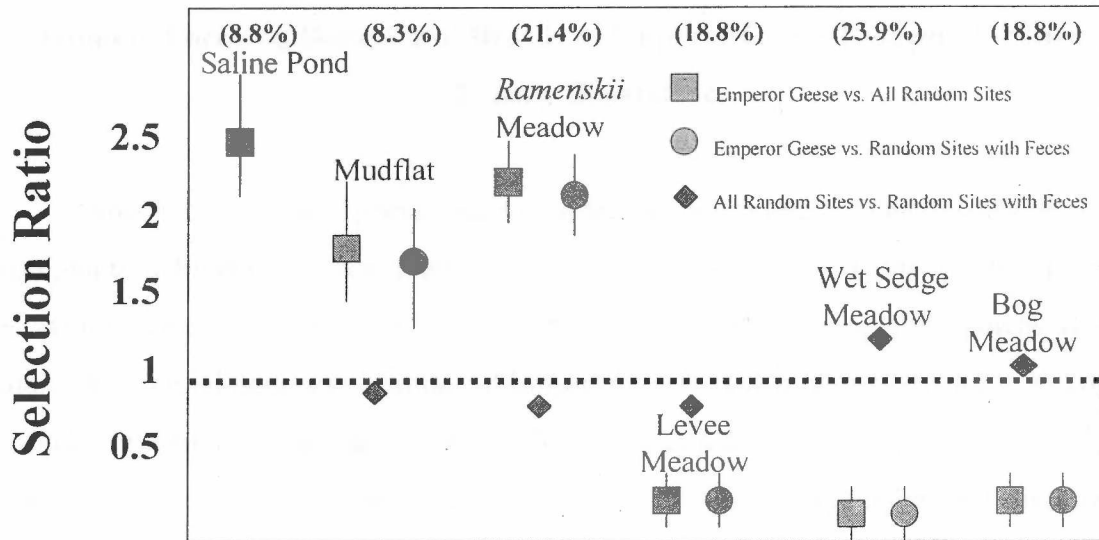


Figure 5.1. Selection ratios for geese using six habitats on the Yukon-Kuskokwim Delta. A selection ratio (proportion observed/proportion available) of 1.0 (dotted line) implies no selection. Three analyses are presented - (1) a comparison of habitats used by Emperor Goose broods relative to habitats deemed available from a series of random locations [squares], (2) a comparison of these same Emperor Goose locations to the subset of random locations where we observed recently deposited goose feces [circles], and (3) a comparison of habitats at random locations with goose feces present relative to habitats at all random locations [diamonds]. In the first two comparisons, selection ratios were calculated for each Emperor Goose brood; thus we estimated standard errors [vertical lines] for the estimated selection ratios from this set of 56 broods. For the latter two analyses, I omitted selection ratios for Saline Pond habitat because this statistic was sensitive to how I treated locations not sampled for fecal deposition. Shown in parentheses is the proportional availability of habitats, as estimated from the set of 398 systematically random locations.

Chapter 6

Variation in Foraging Behavior of Broods of Emperor Geese: Evidence for Interspecific Density Dependence

Abstract: Broods of geese spend time feeding according to availability and quality of food plants, subject to inherent foraging and digestive constraints. Consequently, patterns of behavior serve as a readily measured index to the quality of the local environment. We studied behavioral patterns of broods of Emperor Geese (*Chen canagica*) on the Yukon-Kuskokwim Delta, Alaska, and examined how feeding and alert behavior varied in relation to habitat and goose density. Time spent feeding by goslings, adult females, and adult males were all much higher during 1993–1996 than during an earlier study in 1985–1986. Increased numbers of Cackling Canada Geese (*Branta canadensis minima*) in habitats used by Emperor Geese during 1993–1996 suggest that interspecific competition may account for the increased feeding time. Further evidence of such competition was suggested by variation within 1994–1996 data; feeding by Emperor Goose goslings and adult females was positively related to total goose densities, including Emperor Geese or Black Brant (*B. bernicla nigricans*), and not to just Emperor Geese. Use of meadows of *C. ramenskii* by Emperor Geese was greater than during 1985–1986 and may reflect shifts in habitat selection in response to changes in total goose density.

Feeding behavior of adult male Emperor Geese differed from adult females and goslings and was positively related to just Emperor Goose density and not total goose density. Alert behaviors were significantly and inversely related to these same density factors. We suggest that the age/sex behavioral difference occurred because goslings and

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adult females primarily responded to food limitation, which is proximately affected by all geese, whereas adult males altered their alertness in response to numbers of nearby broods, which were most consistently other Emperor Geese.

These density-dependent changes in foraging behavior indicate that inter-specific competition may affect nutrient acquisition, which can affect growth and survival of juvenile Emperor Geese. Consequently, the dynamics and management of Emperor Goose populations must consider the inter-specific relations and densities of all goose species occurring on the Yukon-Kuskokwim Delta, Alaska.

INTRODUCTION

Intra- and inter-specific densities of geese impact the behavioral use of habitats (Lazarus and Inglis 1978, Williams et al. 1994), which ultimately may affect demographics through changes in recruitment of juveniles. Recruitment of geese into breeding populations is strongly impacted by the environmental conditions experienced by broods before fledging (Cooch et al. 1989, Williams et al. 1993, Sedinger et al. 1995a). Because they are small herbivores (Sedinger 1997), geese must be highly selective foragers and growth rates of goslings are sensitive to changes in the quality and quantity of food plants (Lindholm et al. 1994, Gadallah and Jefferies 1995a, Sedinger et al. 1997, LePage et al. 1998). Reduced nutrient availability and gosling growth rates have demographic consequences because small juvenile body size markedly affects subsequent survival probability and fecundity (Owen and Black 1989, Schmutz 1993, Sedinger et al. 1995a, van der Jeugd and Larsson 1998). The process by which environmental changes in per capita food availability are translated into effects on growth and survival of geese is mediated by foraging behavior during brood rearing. When confronted with low abundance or quality of food, geese compensate by increasing the amount of time devoted to foraging (Sedinger and Raveling 1988, Mulder et al. 1995, Hupp and Robertson 1998). For goslings, such behavioral compensation may ultimately be limited by processing constraints (Sedinger and Raveling 1988), at which point growth rates decline. For adults, increased time spent feeding necessitates a reduction in one

or more other behaviors and may impact the time devoted to protecting their young (Williams et al. 1994).

Emperor Geese (*Chen canagica*) are the least abundant of four species of geese that nest and rear broods sympatrically on the Yukon-Kuskokwim Delta (YKD; King and Derksen 1986, Sedinger 1996). Black Brant (*Branta bernicla nigricans*), Cackling Canada Geese (*B. canadensis minima*), Greater White-fronted Geese (*Anser albifrons*), and Emperor Geese all declined in numbers from the late 1960s to mid 1980s. Since then, numbers of Cackling Canada Geese and Greater White-fronted Geese have increased steadily at greater than 10% per annum (Bowman et al. 1999). Black Brant are the sole colonial nesting goose on the YKD, with dynamics differing among colonies and some colonies increasing recently (Sedinger et al. 1993, Sedinger et al. 1998). In contrast, numbers of Emperor Geese have remained stable since the mid 1980s at a depressed level compared to previous counts (Petersen et al. 1994, Bowman et al. 1999). Such changes in goose abundance provide an important environmental context for how broods may exploit resources.

Habitat selection and foraging behavior of Emperor Goose broods were examined in one prior study during 1985–1986, the nadir of overall goose numbers on the YKD (Laing 1991, Laing and Raveling 1993). In that study, broods quickly departed nesting areas after hatch and populated hypersaline plant communities. Preferred food plants were *Carex subspathaceae* and *Puccinellia phraganoides*, two species that typify short, dense, lawn-like plant communities (Laing and Raveling 1993). Minimal feeding in other plant species and communities was documented, and observations of broods of Cackling Canada Geese were infrequent (Laing, personal observation). During the time since Laing's (1991) study, numbers of Cackling Canada Geese have nearly tripled (Bowman et al. 1999). If this species shares food resources with Emperor Geese during brood rearing, then per capita food availability may have correspondingly declined and caused changes in feeding (and other) behavior of these species.

An understanding of the use of habitats and effects of goose density is necessary to

identify the extent to which sympatric goose populations may impact each other's demographics. In this regard, we observed broods of Emperor Geese during 1993–1996 and addressed two overall objectives. First, we documented the amount of time adults and gosling spent feeding, alert, and in other behaviors, and we compared recent results to similar data collected by Laing (1991) during 1985–1986. Our prediction was that time spent feeding would be similar between studies unless the numbers of Emperor Geese, competing geese, or food availability had changed. We controlled for effects of brood size and date as both have been identified as factors related to variation in goose behavior. Increased time spent feeding as summer progresses may be a function of several factors, including declining nutrient quality (Sedinger and Raveling 1986, Manseau and Gauthier 1993), decreased food abundance due to grazing, and increased foraging capacity as goslings grow (Sedinger and Raveling 1988). Adults with large broods generally spend less time feeding and more time alert than other adults (Williams et al. 1994, Sedinger et al. 1995b, Loonen et al. 1999). For our second objective, we used data from 1994–1996 to examine how feeding and alert behavior were affected by habitat selection, date, and goose density. Our observations focused on the most frequently used habitats (Schmutz MS), and thus habitat-specific behavioral patterns provide a perspective on the functional value of these habitats to broods. To test whether behavior of broods was affected by intra- or inter-specific densities of geese, we compared models of brood behavior that included densities of Emperor Geese with those that included the collective density of Emperor Geese, Cackling Canada Geese, and Black Brant.

STUDY AREA AND METHODS

We studied behavior of Emperor Goose broods during 1993–1996 near the Manokinak River on the Yukon-Kuskokwim Delta, Alaska. This site is 65 km south of the Kokechik Bay area on the Yukon-Kuskokwim Delta where Laing (1991) studied brood behavior of Emperor Geese during 1985–1986. These two sites both lie within the primary nesting distribution of Emperor Geese, which have one of the most geographically restricted

ranges among geese (Owen 1980). Plant communities in the vicinity of observation blinds were similar between these two study sites and were dominated by two adjacent, halophytic communities. The more inland and expansive community was a nearly monospecific meadow of *C. ramenskii*. This community is termed Brackish Fringe Wet Sedge Meadow by Jorgenson (2000), and we refer to it in this paper as meadow habitat. Progressing down in elevation towards tidal waters, there was an abrupt border between *C. ramenskii* meadows and the short, lawn-like community dominated by *C. subspathaceae* that was termed Brackish Fringe Wet Graminoid Meadow by Jorgenson (2000). Minor amounts of *Puccinellia phraganoides* also occurred in this community. This vegetation occurred in a strip along the border with *C. ramenskii* meadows as well as in dispersed patches amongst otherwise primarily barren mudflat. When geese were in this plant community dominated by *C. subspathaceae* or in barren mudflat, we recorded them as being in mudflat habitats. Emperor Geese preferred these meadow and mudflat habitats (Schmutz MS), and our observation blinds were subjectively located at the border between these habitats to maximize numbers of geese observed.

We observed broods of Emperor Geese from a series of 10 elevated blinds distributed across a 70 km² area. We observed broods from a few days after peak hatch of goslings to about 10 days before fledging, an approximate four week period each year. To minimize human-induced alteration of behavior, observers stayed in blinds for two days at a time and no behavior samples were collected during the first three hours of each session in a blind.

A single brood observation consisted of watching a focal brood for up to one hour, and not less than 40 minutes, and each minute recording the instantaneous behavior and habitat of each member of a brood. We distributed these observations throughout diurnal periods. For a given one-hour brood observation, we selected a brood by randomizing which window of the blind we peered from and choosing the first brood we saw that was within approximately 400 m of the blind. The exception to this was if we saw a banded brood from the randomly selected window, then we sampled that brood rather than an unbanded one. We

recorded each instantaneous assessment of behavior into one of the following categories: feeding, alert, locomotion, resting, and comfort. A missing category was also used if broods temporarily disappeared from view. Observations were discontinued if adults disappeared from view for more than five minutes. Feeding was defined as actively grabbing or chewing plants or searching for the next bite with the head held below horizontal. Alert was any posture with the head and neck held in an extended and apparently attentive state. Geese could be classified as alert while either sitting or standing. Locomotion was primarily walking, where broods were moving but not actually engaged in feeding. Geese were classified as resting when they were stationary and not alert nor feeding. Comfort behaviors included preening, bathing, and drinking. We also recorded whether aircraft or Arctic fox were seen during one-hour sampling periods and whether during such samples broods responded in any way (e.g., directed alertness) to the presence of Glaucous Gulls (*Larus hyperboreus*).

We identified sex of adults for some broods by observing brooding behavior (only done by adult females) or by reading individually coded neck collars or tarsal bands worn by a subset of geese (Schmutz and Morse 2000). In the absence of such data, we often were able to classify sex based on the degree of staining of the otherwise white head and neck plumage. These feathers are stained orange during hyperphagic foraging shortly after arrival on the breeding area, and within pairs, the staining is darker for females than males due to greater spring feeding activity by females (Petersen et al. 1994; M. Petersen, U.S. Geological Survey, unpublished data). Because the intensity of this staining diminished as brood-rearing progressed, differential staining could not always be detected. We omitted data for those broods where sex classification of adults was ambiguous. Goslings were not individually identifiable, so we recorded the behavior displayed by the majority of the brood at each instantaneous sample.

We collected two indices of local goose density while in observation blinds. First, once per day the number of Emperor Goose broods were counted in which all goslings could

be observed. We refer to this as a peak count and the timing of this count within a day was subjectively determined to maximize numbers of broods simultaneously seen. Second, every two hours we counted numbers of broods of each goose species that were within the boundaries of a plot or plots within approximately 250 m of each observation blind and delineated with wood lathe. These plots contained approximately equal amounts of meadow and mudflat habitat. Few Greater White-fronted Geese were seen in these plots (< 3% of counts) and are not considered further. We refer to these counts as relative density counts because their primary purpose was to observe enough Emperor Geese, Cackling Canada Geese, and Black Brant in a defined area to provide an estimate of the relative density of the three species around our observation blinds. We enlarged plots multiple times during the course of study to obtain larger samples and exact plot dimensions were not measured. Therefore, these counts only indicated the local density of Emperor Geese relative to Cackling Canada Geese and Black Brant, and they do not address changes in a single species' density over time. During these counts, we also made instantaneous assessments of the dominant habitat and behavior for each brood of each species.

In analyses described below, we use three measures of goose density. First, we used the peak counts as a measure of local Emperor Goose density. We used an analysis of covariance (ANCOVA) model to produce least squares estimates of numbers of Emperor Geese for each blind location and year, after controlling for the covariate date. Second, we used data from relative density counts to calculate the mean number of adult Emperor Geese and Cackling Canada Geese observed at each blind in each year. We then formed a ratio of the two species' densities for each blind and year, and multiplied this ratio by the mean peak count measure for the corresponding blind and year. By adding this product to the peak count, we arrived at a measure of combined Emperor Goose and Cackling Canada Goose density. Our third density measure included Black Brant. Specifically, we used the ratio of Black Brant and Cackling Geese to Emperor Geese in a similar calculation as our previous density measure to arrive at a measure of total goose density that reflected the combined

abundance of Emperor Geese, Cackling Canada Geese, and Black Brant.

We treated each one-hour focal brood observation as an independent sample. Some broods with banded adults were sampled more than once, so we randomly selected one observation per banded brood for inclusion in analyses presented here. The probability of repeated sampling of unidentifiable (not banded) broods was low because of the high number of such broods relative to banded broods (Sedinger and Raveling 1990) and our spatial distribution of sampling among 10 blinds.

We made an a priori decision to analyze goslings, adult females, and adult males separately. Many studies have documented marked differences in behavior among these three classes of geese (Sedinger and Raveling 1990, Sedinger et al. 1995b, Fowler and Ely 1995), and thus it seemed unnecessary to test for the existence of such differences. Similarly, several studies of goose behavior have found time of day to be an unimportant factor (Laing 1991, Sedinger et al. 1995b, Fowler and Ely 1997). We corroborated such findings for our data during preliminary analyses and do not consider this factor further. We also omitted from analysis of focal broods the infrequent observations of pairs that had no young.

Prior to analysis, we applied arcsine transformations to all percentage data to better meet the distributional assumptions of linear models (Sokal and Rohlf 1981). We then back transformed results for presentation in this paper. We treated year as a categorical main effect and brood size and date as continuous covariates in a multivariate analysis of covariance (MANCOVA). When the overall model F test indicated a significant effect for a variable, we used univariate ANCOVAs to assess the importance of the covariates on each behavior. We present least squares estimates of mean behaviors for each year to account for the effects of the covariates.

We compared feeding and alert behaviors of Emperor Goose broods between this study (1993–1996) and one by Laing (1991) during 1985–1986. We calculated mean values across years for each study by weighting annual estimates by the inverse of their variances (Burnham et al. 1987). We then computed the difference between the means of the two study

periods and examined whether confidence intervals on these differences overlapped zero (Johnson 1999).

We then investigated the effects of habitat, date, Emperor Goose density, combined Emperor and Cackling Canada goose density, and total goose density (numbers of Emperor Geese, Cackling Canada Geese, and Black Brant combined) on feeding and alert behavior of Emperor Goose broods during 1994–1996. We did not collect habitat and goose density data in 1993; thus we excluded this year from these analyses. For each age/sex class and behavior, we constructed a set of multiple regression models, which represented different combinations of these independent variables. We identified a parsimonious regression model with Akaike's Information Criterion (AIC), and thus the importance of an independent variable can be judged by its inclusion in the parsimonious model, which is identified by the lowest AIC value (Burnham and Anderson 1998). When models have AIC values within two units of each other, they fit the data nearly equally well and one is not considered clearly superior to the other. In examining the effects of goose density, we did not consider models that included multiple density variables. Instead, we examined which one of the three goose density variables, if any, was included in the parsimonious model, and compared that model's AIC with that of models with one of the other goose density variables (or a model with no goose variable).

Our blind and year specific estimates of goose density serve as specific biological factors hypothesized to cause spatial and temporal variation in behavior. However, other factors may also influence the behavior of geese over space and time. We therefore also constructed ANCOVA models with the generic spatial and temporal factors of blind location and year. We then compared the relative fit of these models with the same models that alternately used goose density to reflect space and time. We used the coefficient of determination (r^2) for this comparison.

Once a parsimonious model had been selected to describe the effects of habitat, goose density, and date, we then constructed two additional models to examine the effects of

disturbance. These models each included a dummy variable that represented the occurrence of either gull or aircraft disturbance during a given time budget sample. We then evaluated whether inclusion of a disturbance term further reduced the AIC. We used a similar modeling approach to evaluate whether the time spent in mudflat versus meadow habitats varied with date.

RESULTS

We obtained 137, 143, 74, and 66 time-budget samples from Emperor Goose broods during 1993–1996. Behavior of goslings, adult females, and adult males varied in relation to year and date ($P < 0.027$ for each MANCOVA). However, behavior appeared unrelated to brood size ($P = 0.239$ for goslings, $P = 0.097$ for adult females, and $P = 0.150$ for adult males). We then further investigated the potential for a brood size effect for adult females by examining the ANCOVA for each behavior. Only time spent resting or missing was related to brood size. Females with large broods appeared to rest more ($\beta_{\text{rest}} = 0.97$, $SE = 0.45$, $P = 0.003$) and be missing less ($\beta_{\text{miss}} = -0.45$, $SE = 0.23$, $P = 0.049$) than females with small broods. Because broods were least observable while resting due to their lower profile and the tall vegetation used for resting, we suspect that large broods were simply easier to see and that most of the actual behavior exhibited while missing was resting. Feeding and alert behaviors dominated the time-budget of adult geese (Table 6.1). For adult females, neither feeding ($\beta_{\text{feed}} = -0.75$, $SE = 0.82$, $P = 0.357$) nor alert behavior ($\beta_{\text{alert}} = 0.12$, $SE = 0.33$, $P = 0.72$) was related to brood size. We therefore conclude that we could detect no effect of brood size on behavior of adults or goslings. We then estimated least squares means of each behavior for each year, adjusting for date (Table 6.1).

Emperor Goose broods spent more time feeding and less time alert during 1993–1996 than during 1985–1986 (Fig. 6.1). The absolute difference in mean percent time spent feeding between the two studies was 17% ($SE = 2.6$) for goslings, 32% ($SE = 2.8$) for adult females, and 28% ($SE = 2.2$) for adult males. The absolute difference in mean time spent alert was 26% ($SE = 6.1$) for adult females and 16% ($SE = 7.5$) for adult males.

Least squares means of peak counts of Emperor Goose broods visible during 1994–1996 from a single tower ranged from 4 to 19 broods. The mean ratio of the number of Cackling Canada Geese to Emperor Geese during relative density counts was 1.02, and the mean ratio of Cackling Canada Geese and Black Brant to Emperor Geese was 1.43. Estimated means of total goose density per tower (all three species combined) ranged from 8 to 38 broods. While in plots around blinds, Black Brant used mudflat habitats more than Emperor Geese and Cackling Canada Geese, and Black Brant spent less of their time in meadow habitats feeding than the other two species (Table 6.2). For data from relative density counts, the mean CV across towers and years for Emperor Geese was 130 (95% CI = 104 - 157), whereas the respective mean CVs for Cackling Canada Geese and Black Brant were 183 (151 - 214) and 291 (233 - 349), thus indicating that Emperor Geese were more consistently in the plots around blinds than the other two species. This explains why, on average, the abundance of Cackling Canada Geese and Emperor Geese was equal (the mean ratio of 1.02), yet many more counts of ≥ 1 broods were obtained for Emperor Geese (Table 6.2).

Habitat strongly affected behavior of Emperor Goose broods. When in mudflat habitat, goslings, adult females, and adult males spent 75, 71, and 46% of their time feeding, whereas they respectively spent 42, 34, and 26% of time feeding when in meadow habitat (Fig. 6.2). Goslings spent more total time (78%) in mudflat habitat than did their parents (64 and 62% for females and males). The relative use of mudflat versus meadow habitat did not markedly change as the season progressed (β_{date} was positive for each age/sex class, but models with a date effect were 0.6 to 1.3 AIC units greater than models without a date effect).

In addition to habitat, goose density and date also affected behavior of goose broods. For goslings, we observed that the best model describing time spent feeding was one incorporating habitat ($\beta_{\text{habitat}} = 0.33$, SE = 0.04, positive values of β_{habitat} indicating increased use of mudflat), date ($\beta_{\text{date}} = 0.53$, SE = 0.19), and total goose density (all three species

combined, $\beta_{\text{density}} = 0.63$, $\text{SE} = 0.31$). A model with combined Emperor and Cackling Canada goose density (but no brant) fit less well ($\Delta\text{AIC} = 0.4$). Models with just Emperor Goose density ($\Delta\text{AIC} = 2.5$) or no goose density variable fit more poorly ($\Delta\text{AIC} = 2.8$). The proportion of variation explained (r^2) by the best model was 0.25, whereas $r^2 = 0.32$ when we modeled time and spatial variation explicitly as year and blind location effects.

Similar to goslings, time spent feeding by adult females was related to habitat ($\beta_{\text{habitat}} = 0.36$, $\text{SE} = 0.03$) and combined Emperor and Cackling Canada goose density ($\beta_{\text{density}} = 0.54$, $\text{SE} = 0.21$). A similar fitting model ($\Delta\text{AIC} = 0.1$) also included a positive effect of date ($\beta_{\text{date}} = 0.18$, $\text{SE} = 0.13$) on female feeding. Models with either Emperor Goose density alone ($\Delta\text{AIC} = 2.9$), total goose density ($\Delta\text{AIC} = 3.2$), or no goose density variable fit poorly ($\Delta\text{AIC} = 5.5$). For the best model, $r^2 = 0.43$ whereas $r^2 = 0.45$ for a model with year and blind location as the variables representing space and time.

For adult males, habitat ($\beta_{\text{habitat}} = 0.20$, $\text{SE} = 0.03$) and date ($\beta_{\text{date}} = 0.28$, $\text{SE} = 0.13$) had similar effects on time spent feeding as seen in goslings and adult females. However, the best model also included Emperor Goose density ($\beta_{\text{density}} = 0.94$, $\text{SE} = 0.35$), which fit markedly better than models with either combined Emperor and Cackling Canada goose density ($\Delta\text{AIC} = 8.2$), total goose density ($\Delta\text{AIC} = 7.4$), or no goose density variable ($\Delta\text{AIC} = 10.0$). For the best model, $r^2 = 0.25$ whereas $r^2 = 0.30$ for a model with year and blind location as the explicit representation of space and time effects.

Time spent alert by adult females was related to habitat ($\beta_{\text{habitat}} = -0.08$, $\text{SE} = 0.03$), date ($\beta_{\text{date}} = 0.11$, $\text{SE} = 0.07$), and combined Emperor and Cackling Canada goose density ($\beta_{\text{density}} = -0.29$, $\text{SE} = 0.01$). However, a model with just Emperor Goose density fit almost as well ($\Delta\text{AIC} = 0.7$). Models with total goose density ($\Delta\text{AIC} = 2.7$) or no goose density variable fit poorly ($\Delta\text{AIC} = 4.5$). For adult males, time spent alert was related to habitat ($\beta_{\text{habitat}} = -0.11$, $\text{SE} = 0.02$) and Emperor Goose density ($\beta_{\text{density}} = -0.94$, $\text{SE} = 0.30$). Models fit poorly that included combined Emperor and Cackling Canada goose density ($\Delta\text{AIC} = 15.2$), total goose density ($\Delta\text{AIC} = 15.8$), or no goose density ($\Delta\text{AIC} = 14.9$). Models describing

alert behavior accounted for less of the variation in the data ($r^2 = 0.12$ for females, $r^2 = 0.13$ for males) as compared to models of feeding behavior.

Adding a gull or aircraft disturbance term to the parsimonious models describing adult feeding behavior did not result in lower AICs for either males or females. Similarly, adding gull or aircraft disturbance terms did not result in better models of alert behavior of adult males. For alert behavior of adult females, adding a gull disturbance term to the best model did not lower the AIC value, but an aircraft disturbance term did ($\Delta\text{AIC} = -1.2$). The negative effect of aircraft disturbance on alert behavior of adult females ($\beta_{\text{alert}} = -3.4\%$, $\text{SE} = 1.9$) was opposite of what we predicted. During 1994–1996, the percent of time budget samples with gull, aircraft, or fox disturbances was 15, 13, and 2%.

In summary, Emperor Goose broods spent more time feeding and less time alert when in mudflat habitat than when in meadow habitat; however, even in meadow habitat geese spent > 20% of their time feeding (Fig. 6.2). As the season progressed, the amount of time spent feeding increased for both adults and goslings. Goose density affected feeding and alert behavior, but the effects differed between adult males and other geese. Adult male behavior was related to densities of Emperor Geese, whereas behavior of adult females and goslings was related to multi-species goose density, which reflected densities of Emperor Geese, Cackling Canada Geese, and, for goslings, Black Brant. Using the regression equations from the best fitting models, time spent feeding by goslings, adult females, and adult males varied positively by an absolute amount of 12, 13, and 16% across the range of densities we observed.

DISCUSSION

The patterns of feeding behavior we documented are indicative of interspecific competition for food. Because growth and survival of juvenile geese are markedly affected by food limitation (Lindholm et al. 1994, Sedinger et al. 1997), these interspecific relationships among geese on the YKD may affect recruitment and demographics of Emperor Geese. This inference of interspecific competition is principally based on (a) the marked

shift in feeding behavior between the mid 1980s and mid 1990s, concurrent with large-scale changes in numbers of competing geese, (b) shared habitats among species, even when species differ in their relative preference for habitats, and (c) the local scale variation in feeding behavior of Emperor Geese during 1994–1996 in relation to densities of total geese.

Comparison of 1985–1986 and 1993–1996 studies

During Laing's (1991) study in 1985–1986, numbers of Cackling Canada Geese and Emperor Geese were similar; however during our study in 1993–1996, numbers of Cackling Canada Geese were nearly three times greater (Bowman et al. 1999). Because of these large changes in goose density between studies, lower per capita food availability is a compelling hypothesis for why feeding rates of Emperor Geese were much greater during the more recent study period than during Laing's (1991) study. Geese spend more time feeding when faced with greater goose densities (Sedinger et al. 1995b, Fowler and Ely 1997) and reduced per capita availability of food (Mulder et al. 1995, Hupp and Robertson 1998). Brood rearing habitats of Snow Geese (*Chen caerulescens*) at La Pérouse Bay were severely degraded from extensive foraging by an increasing population (Kotanen and Jefferies 1997), which corresponded with feeding rates of broods that were much higher than in other studies of goose brood behavior (Mulder et al. 1995).

Because our study and Laing's (1991) occurred at different sites on the YKD, other competing hypotheses include differences in methodology, vegetation or goose abundance, or disturbance of feeding by predators or aircraft. We planned a priori to make this comparison and intentionally replicated Laing's (1991) categorization of behaviors to minimize any methodological influence on results. Plant communities and habitats available to broods around Laing's (1991) observation blind (Laing and Raveling 1993) were similar to those around our observation blinds. We nor Laing (1991) quantified abundance of important forage species, however large reductions of food availability or nutrient quality independent of goose grazing would need to have occurred for this to explain the patterns we documented. Species-specific changes in abundance of geese nesting in the Manokinak study area (M.

Anthony and J. Schmutz, U.S. Geological Survey, unpublished data) mirrored larger scale patterns observed throughout the YKD (Bowman et al. 1999). Hourly rates of fox (3%) and aircraft (9%) observation during Laing's study were similar to our observations. Our rate of gull disturbance (15%) was higher than the hourly rate observed by Laing (7%), but our definition of gull disturbance was more liberal, constituting any alert behavior directed towards gulls and not just the threat displays used by Laing (1991). Further, we note that disturbance of broods by gulls during 1994–1996 did not affect the time Emperor Goose parents spent feeding or alert.

A final alternative explanation for differences between Laing's (1991) and our results is perhaps Laing (1991) sampled an unrepresentative sample of broods, owing to her small sample size. Although she sampled from only one blind and observed just seven individually identifiable broods in each of two years, she collected multiple observations per family and averaged them to get a representative sample per family. Further, the variation we observed among 10 blinds across four years in the 1990s was much less than the behavioral differences observed between studies. Therefore, we believe the most parsimonious explanation for increased time Emperor Geese fed (and reduced time alert) in 1993–1996 versus 1985–1986, a time span when numbers of Emperor Geese remained stable, was due primarily to the increase in density of Cackling Canada Geese, and the associated reduced per capita food availability or quality.

Habitat selection within and among species

Emperor Geese preferentially selected habitats at the interface of mudflat and *C. ramenskii* meadows (Schmutz MS). When in these habitats, Cackling Canada Geese were similar to Emperor Geese in the amount of time feeding and total time spent in meadows versus mudflat. Because of these similar feeding behaviors and the numerical equivalence of these two goose species in these habitats, Cackling Canada Geese compete with Emperor Geese for food in the habitats most used by Emperor Geese, assuming that food is limiting. Growth rates of goslings are sensitive to the quality and quantity of available food (Lindholm

et al. 1994, Gadallah and Jefferies 1995a), and thus food limitation is implied when gosling growth rates decline. Mass of Emperor Goose goslings, adjusted to six weeks following peak hatch, were lower in 1993–1996 than in 1990, the one previous year with mass data on goslings of this species (unpublished data). Similarly, growth rates of Cackling Canada Goose goslings at a nearby study site were lower in 1998–1999 than in the previous four years (C. Ely, U.S. Geological Survey, unpublished data).

Across a larger scale encompassing all habitats, numbers of Cackling Canada Geese during this study were nearly three times those of Emperor Geese (Bowman et al. 1999). Cackling Canada Geese selectively used more inland habitats than what we focused on in this study and appeared to differ from Emperor Geese in selective use of habitats (Sedinger and Raveling 1984, Schmutz MS, C. Ely unpublished data). Thus, use of *C. ramenskii* meadows and the mudflat fringe of *C. subspathaceae* by Cackling Canada Geese, which are one-third smaller than Emperor Geese, may represent density-dependent filling of secondary habitats by this species, sensu an ideal free distribution (Fretwell and Lucas 1970). Use of lower quality habitats as typically higher quality habitats decline in fitness value has been observed in several goose studies (Vickery et al. 1995, Hupp and Robertson 1998). Consistent with this interpretation is that Laing (unpublished data) observed few Cackling Canada Geese in similar mudflat and meadow habitats around her observation blind in 1985–1986, when numbers of Cackling Canada Geese were much lower and similar to that of Emperor Geese (Bowman et al. 1999).

Emperor Geese clearly fed heavily in grazing lawns of *C. subspathaceae*, similar to other species of geese on the YKD (Person et al. 1998) and in other sub-arctic ecosystems (Cargill and Jefferies 1984). We observed a more diverse set of behaviors of Emperor Geese when in meadows of *C. ramenskii*, with less time devoted to feeding. However, the time spent in meadows of *C. ramenskii* (Schmutz MS) and time spent feeding while there (Fig. 6.2) were greater than that observed by Laing and Raveling (1993). We note that the apparent increase in time goslings were missing from view during 1993–1996 (Table 6.1)

relative to that observed by Laing (1991) was likely a consequence of increased use of the much taller (relative to *C. subspathaceae*) *C. ramenskii* meadows.

Carex ramenskii is a poorer quality food than *C. subspathaceae* due to lower total percent nitrogen, yet similar fiber content (Laing and Raveling 1993). With greater densities of geese, the abundance of *C. subspathaceae* may have been reduced enough to cause Emperor Geese to use the more abundant *C. ramenskii* (Schmutz MS) with greater frequency. Geese switch to less preferred habitats when primary habitats become depleted (Sedinger and Raveling 1986, Vickery et al. 1995, Hupp and Robertson 1998).

During 1993–1996, broods of Emperor Geese frequently traveled the abrupt interface between *C. subspathaceae* and *C. ramenskii*. Parents were more often on the *C. ramenskii* side of this border than were goslings (Fig. 6.2). Because of their small size and demands for growth, goslings need to consume less absolute amounts of food but need food of higher nutritional quality (greater nitrogen or less fiber) (Demment and Van Soest 1985, Sedinger 1997). Thus, parents may more ably subsist on *C. ramenskii* than goslings. Further, we note that Emperor Geese clip just the leaf tips of *C. ramenskii* (personal observation). Leaf tips tend to be higher in quality than whole leaves (Gadallah and Jefferies 1995b), and thus the nutritional value of the consumed parts may be more similar between *C. subspathaceae* and *C. ramenskii* than indexed by bulk N content.

Local density effects on behavior

Goose density was an important factor influencing feeding and alert behavior of goslings and adults during 1994–1996. However, the relevance of intra- versus inter-specific density varied among these classes. For goslings and adult females, combined density of Cackling Canada and Emperor Geese better explained feeding (and alert) behavior than did density of Emperor Geese alone. This result further supports the argument that Cackling Canada Geese were competitors for forage. For goslings, a model that also included densities of less abundant Black Brant fit even better. Brant used mudflat habitat disproportionately more than did Emperor and Cackling Canada Geese (Table 6.2). Because Emperor Goose

goslings also used mudflat habitats more than their parents, goslings may have been subjected to more direct competition with Brant.

Adult males differed from females and goslings in that their feeding and alert behavior was related just to conspecific densities. A food-based explanation for this difference would seem to require that male and female Emperor Geese differed in where or what they ate, and that females were more similar than males to the feeding habits of Cackling Canada Geese. We observed no clear habitat or behavioral difference between males and females other than that males fed less often and were alert more often - a pattern evident in virtually all studies of goose brood behavior. Male geese are generally less nutritionally taxed during egg laying and incubation (Ankney 1977, Ankney and MacInnes 1978) and thus would be expected to begin the brood rearing period with less need to feed. We therefore suggest that the behavioral response to goose density in males was primarily with respect to alert behavior, and that relationships between feeding and density were simply correlated responses. Further, we speculate that the lesser rates of alert behavior with greater densities of Emperor Geese were a consequence of a selfish-herd effect (Hamilton 1971), wherein the costs of alert behavior are shared among unrelated members of a group (i.e., other broods) and from which one would predict that time spent alert would be inversely related to the number of broods. During non-breeding seasons, positive relationships between flock size and time spent feeding by Emperor Geese (Schmutz 1994; unpublished data) and other geese (Lazarus 1978) support this hypothesis. To our knowledge, foraging behavior of brood-rearing geese has not previously been related to numbers of nearby or associated broods. The intraspecific but not interspecific nature of this density effect may simply be because Emperor Geese were more consistently around blinds, whereas Cackling Canada Geese and Black Brant were more transient (as indicated by CVs of counts).

Sex-specific behavioral responses to density (feeding by females, alertness by males) are consistent with previous studies that indicated that adult females are in poorer physiological condition than males at hatch (Ankney 1977, Ankney and MacInnes 1978), and

thus have a greater need to feed. In Lesser Snow Geese, experimentally increased food abundance reduced feeding rates of females, but not for males (Mulder et al. 1995). For Emperor Geese, we noted substantial variation in body condition of nesting females (Franson et al. 1999). Further, post-breeding survival of adult female Emperor Geese was lower than adult males, implying a possible cost of reproduction and an inability to recoup adequate condition (Schmutz et al. 1994). Similarly, female Greater White-fronted Geese showed a greater sensitivity of survival to physiological condition than did males (Schmutz and Ely 1999). In contrast, males are the primary aggressor and protector of young (Lazarus and Inglis 1978, Sedinger and Raveling 1990).

We note that models of alert behavior fit less well than models of feeding behavior, which may be a consequence of differing time scales of measurement. Our measures of goose density at each blind location were integrated values across a whole brood rearing season. Similarly, food availability within a season likely changed in a predictable, progressive fashion. However, the numbers of geese present near a blind location during one hour sampling periods, to which alert behavior was likely more directly responsive, was dynamic and highly variable.

We further note that models that incorporated goose density explained similar amounts of variation in the data as did year and blind location, indicating that goose density well represented this particular scale of temporal and spatial variation. However, much variation was left unexplained. Large sampling variability occurred due to the apparent brevity of a one hour sampling period relative to behavior patterns, as evidenced by percent time feeding that ranged from 0 to 100%. Also, for a given plant community, there was likely within-blind location variation in primary productivity irrespective of grazing effects, which consequently may have affected foraging behavior. Significant spatial variation in productivity of *Carex* communities on the YKD has been documented (Person et al. 1998; C. R. Ely, U.S. Geological Survey, unpublished data).

Relevance to population dynamics

Emperor Geese selectively spent the majority of their time in mudflats and *C. ramenskii* meadows (Schmutz MS). In comparison to Cackling Canada Geese, the larger body size of Emperor Geese may allow them to more efficiently exploit abundant, but comparatively low quality *C. ramenskii* (Demment and Van Soest 1985). Nonetheless, the near tripling in size of the Cackling Canada Goose population between the mid 1980s and mid 1990s (Bowman et al. 1999), probably driven by factors not directly related to brood rearing such as harvest management and effects on adult survival (Raveling 1984, Petersen et al. 1994, Sedinger 1996, Schmutz et al. 1997), likely caused increased use of these habitats by Cackling Canada Geese. We believe that changes in feeding behavior of Emperor Geese are indicative of this increased competition. This inference is strengthened by concurrent observations of increased feeding rates of Cackling Canada Geese in relation to goose density (Fowler and Ely 1997).

Several studies have demonstrated inverse relations between goose density and gosling growth and survival (Cooch et al. 1991, LePage et al. 1998, Sedinger et al. 1998). Recent observations of reduced gosling mass (Emperor Geese, Schmutz unpublished data) or growth (Cackling Canada Geese; C. R. Ely, U.S. Geological Survey, unpublished data) suggest that such feedbacks occurred during the 1990s on the YKD. Further, age ratios of Emperor Geese during fall migration were lower during the late 1990s than during the previous 10 years of survey (U.S. Fish and Wildlife Service, unpublished data), which would be expected if rates of gosling growth were less during this later period (Schmutz 1993). We conclude that the patterns of foraging and other behaviors we observed in Emperor Goose broods are indicative of the effects of interspecific competition for food, and that such interspecific relations among geese on the YKD breeding grounds may affect the regulation of population size in Emperor Geese.

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Table 6.1. Mean percent time (\pm SE) spent in various behaviors by broods of Emperor Geese. We sampled focal broods for one-hour periods during which instantaneous assessments of behavior were recorded every minute. We present least squares means, controlling for date effects.

Age/Sex	Year	Behavior						
		Feed	Alert	Maintenance	Brooding	Travel	Rest	Missing
Ad F	1993	59 \pm 2.2	10 \pm 0.9	5 \pm 0.6	4 \pm 1.1	9 \pm 0.7	9 \pm 1.2	5 \pm 0.6
	1994	63 \pm 2.1	9 \pm 0.9	3 \pm 0.6	6 \pm 1.1	10 \pm 0.7	5 \pm 1.2	5 \pm 0.6
	1995	54 \pm 3.0	14 \pm 1.2	3 \pm 0.8	4 \pm 1.5	8 \pm 1.0	13 \pm 1.6	6 \pm 0.9
	1996	55 \pm 3.2	16 \pm 1.3	2 \pm 0.8	4 \pm 1.7	8 \pm 1.0	10 \pm 1.8	6 \pm 0.9
Ad M	1993	42 \pm 1.9	29 \pm 1.5	4 \pm 0.5	0	11 \pm 0.8	11 \pm 1.3	5 \pm 0.8
	1994	43 \pm 1.9	29 \pm 1.5	4 \pm 0.5	0	12 \pm 0.8	9 \pm 1.3	4 \pm 0.8
	1995	37 \pm 2.6	32 \pm 2.0	4 \pm 0.7	0	10 \pm 1.1	14 \pm 1.8	5 \pm 1.1
	1996	36 \pm 2.8	43 \pm 2.2	4 \pm 0.8	0	8 \pm 1.1	7 \pm 1.9	3 \pm 1.2
Gosling	1993	68 \pm 2.8	1 \pm 0.7	2 \pm 0.3	3 \pm 1.1	6 \pm 0.6	8 \pm 1.0	17 \pm 1.9
	1994	73 \pm 2.7	1 \pm 0.7	1 \pm 0.2	6 \pm 1.1	7 \pm 0.6	3 \pm 0.9	14 \pm 1.9
	1995	63 \pm 3.8	0 \pm 0.9	1 \pm 0.3	5 \pm 1.5	6 \pm 0.8	4 \pm 1.3	26 \pm 2.6
	1996	67 \pm 4.0	0 \pm 1.0	1 \pm 0.4	6 \pm 1.6	7 \pm 0.9	5 \pm 1.4	18 \pm 2.8

Table 6.2. Comparison among goose species in time spent in mudflat and meadow habitats. The relative amount of time spent in mudflat versus meadow habitats, and time feeding in these habitats, by Emperor Geese, Cackling Canada Geese, and Black Brant during 1994–1996 on the Yukon-Kuskokwim Delta, Alaska, as discerned from systematic counts. Counts were made from elevated blinds every two hours during diurnal time periods while viewing delimited plots that represented approximately equal proportions of mudflat and meadow habitats. Within each species, only non-zero counts were included. Habitat and behavior was assessed instantaneously according to the categories detailed in the text. Whole broods were the sampling units with the majority habitat and behavior category for a brood being recorded.

	Cackling Canada		
	Emperor Geese (<i>n</i> = 777)	Geese (<i>n</i> = 468)	Black Brant (<i>n</i> = 190)
Percent time in Mudflat	65	66	81
Percent of time feeding while in Mudflat	81	72	72
Percent time in Meadow	35	34	18
Percent of time feeding while in Meadow	47	56	28

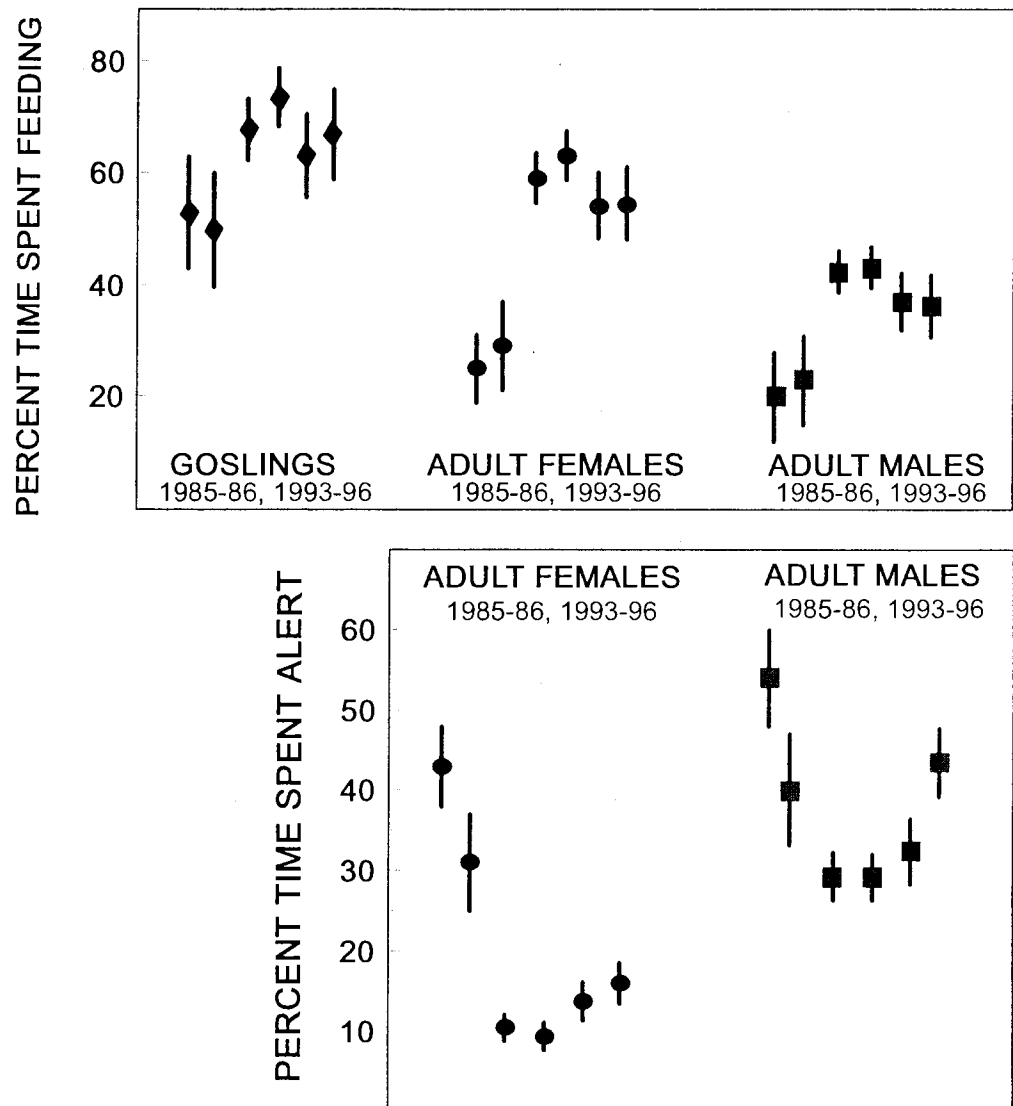


Figure 6.1. Comparison of feeding and alert behaviors between 1985–1986 and 1993–1996. Percent of time spent feeding and alert by broods of Emperor Geese on the Yukon-Kuskokwim Delta, Alaska, was studied during 1985–1986 at Kokechik Bay (Laing 1991) and during 1993–1996 at Manokinak River. Vertical bars are 95% confidence intervals for the estimated mean percentages.

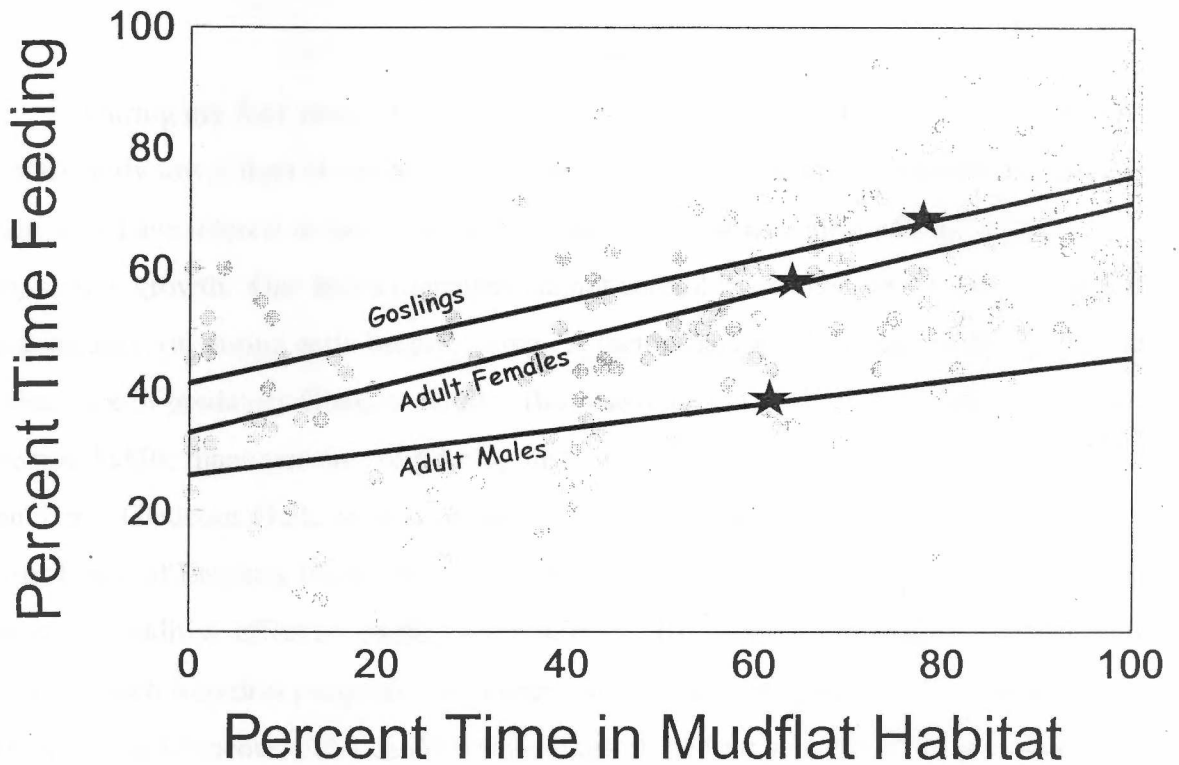


Figure 6.2. Percent time that broods fed in mudflat habitat. We related the percent time that broods of Emperor Goose during 1994–1996 were feeding to the percent time they were in mudflat habitat during one-hour sampling periods. During each instantaneous assessment of behavior, habitat was categorized as mudflat (barren mud or mud vegetated with lawns of *Carex subspathaceae*) or meadow (taller vegetation dominated by *C. ramenskii*). Raw data shown just for adult females. Lines for goslings, adult females, and adult males were derived from parameters from the parsimonious regression models that also considered the effects of date and goose population density. Stars represent the mean time in mudflat habitat for each age/sex class. Left and right intercepts respectively reflect the amount of time spent feeding while in meadow and mudflat habitats.

Chapter 7

Summary

During my four years of study, mortality rates of Emperor Goose goslings were not significantly lower than observed in many other goose populations. Nonetheless, wildlife managers have interest in increasing gosling survival rates as a means for increasing population growth. One factor managers cannot control is weather, which clearly impacted gosling survival during early brood rearing. A factor managers have some effect on is the abundance of predatory Glaucous Gulls. Because numbers of Glaucous Gulls increased since the mid 1980s, managers are considering instituting a control program to reduce gull numbers. Glaucous Gulls consumed many goslings and the correspondence between gull disturbance of Emperor Goose broods and gosling survival suggests that gull predation had an overall additive effect on gosling survival rates. However, one should not infer from these data that such a control program would necessarily achieve its goal. First, evidence to date suggests that Glaucous Gulls consumed goslings of the four goose species in proportion to their availability (Bowman et al. 1997). Such a result is consistent with the increased numbers of Glaucous Gulls responding to the increase in numbers of Cackling Canada Geese and Greater White-fronted Geese, and minimizes the likelihood that survival of Emperor Goose goslings has been impacted by the rise in gull numbers. Second, if removal of Glaucous Gulls led to increased gosling survival, then such increases would be expected for all goose species. Therefore, Emperor Goose goslings would be sharing space with more potentially competing geese, which may ultimately exert a counter-balancing effect to the gull control program. Such a conclusion is premised on the existence of competition among goose broods.

Broods of Emperor Geese spent the majority of their time in the more saline one-third of all available habitats, which were vegetatively dominated by *Carex subspathacaea* and *C. ramenskii*. Although Cackling Canada Geese, which overall were nearly three times more

abundant than Emperor Geese, selectively used a different, more inland array of habitats, they were numerically similar in abundance to Emperor Geese in the *C. subspathacaea* and *C. ramenskii* communities. Further, the time Emperor Geese (goslings and adult females) devoted to feeding increased in relation to total densities of geese, not to densities of just Emperor Geese. Because geese, in general, spend more time searching for and acquiring food when faced with more limited food availability (Mulder et al. 1995, Hupp and Robertson 1998), my observations strongly suggest that broods of Emperor Geese were competing with other nearby geese for food. Feeding rates of Emperor Geese that I observed during 1993–1996 were markedly higher than that observed in broods of Emperor Geese during 1985–1986 (Laing 1991), which is also consistent with interspecific competition as this corresponded to the increase in numbers of Cackling Canada Geese.

The consequence of interspecific competition among broods for food is that goslings may grow more slowly and achieve a smaller body size by late summer. Body mass of Emperor Goose goslings at six weeks of age was less in 1993–1996 than it was in 1990 (Schmutz unpublished), suggesting such competition was occurring. In other portions of the Yukon-Kuskokwim Delta, similar declines in body mass occurred during the early 1990s in Black Brant (Sedinger et al. 1998) and more recently in Cackling Canada Geese (Ely unpublished). Small gosling size in late summer has consistently translated into low juvenile survival prior to or during fall migration, in Emperor Geese (Schmutz 1993) and several other goose species (Sedinger et al. 1995, van der Jeugd and Larsson 1998, Ward unpublished). Reductions in juvenile survival of Emperor Geese during early fall may be occurring; fall age ratios during the late 1990s were significantly lower than during the previous decade, as determined from an annual aerial survey initiated in 1985 (U.S. Fish and Wildlife Service unpublished). These patterns suggest that interspecific competition during brood rearing may be negatively affecting juvenile recruitment in Emperor Geese.

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