

**NEONATE RESERVES, GROWTH AND SURVIVAL OF ROSS' AND  
LESSER SNOW GOOSE GOSLINGS**

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By

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## ABSTRACT

The influence of egg size and brood dispersal on gosling growth and survival was studied in Ross' and Lesser Snow Geese hatched at Karrak Lake, N.W.T. Variation in neonate composition can influence growth, energetics and, possibly, subsequent dispersal patterns of young. Therefore, the relative nutrient profile and physiological development level of neonates in these two dimorphic species were examined by analyzing egg and gosling composition for seasonal, egg size and species-specific effects. Late laid eggs had less yolk protein and, in Ross' Geese, produced goslings with smaller pectoralis muscles. Since skeletal muscles are important for thermogenesis, this seasonal variation in muscle tissue may influence thermoregulatory abilities of late-hatched young. Egg composition varied isometrically with egg size. However, goslings from larger eggs were relatively smaller for their egg size yet contained the same relative nutrient content as goslings from smaller eggs. Because of their higher lipid:body size ratio, goslings from larger eggs were in better condition. Thus larger egg size may give an initial energetic advantage to goslings during periods of nutritional or thermal stress. Although no interspecific variation was observed for egg components, Ross' Goose goslings hatched with more protein for their egg size and larger gizzards for their body size. In addition, Ross' Goose goslings had less water per gram of lean dry mass than did Snow Goose goslings which indicates a greater functional maturity of Ross' Goose neonate tissue. Digestive efficiency, thermoregulatory ability and locomotor capacity may be relatively better in Ross' Geese and these characteristics may represent adaptations to metabolic constraints associated with smaller neonate

body size and foraging requirements.

Resource depletion around large nesting colonies may influence brood movements and subsequent growth and survival of nidifugous young. If per capita food availability increased with distance from the colony, then I predicted that broods settling farther from natal colonies should produce structurally larger and/or relatively heavier goslings than those broods feeding locally. I used radio telemetry to recapture marked broods and found indirect evidence of a nutrient gradient around the Karrak Lake colony. Broods dispersed 8-59 km away from Karrak Lake with Ross' Geese travelling farther than Snow Geese (19-59 km vs 8-21 km, respectively). These dispersal patterns may be a function of parental behavior, body size, bill morphology and nutrient requirements. For known age Ross' Goose goslings, birds reared farther from the colony were heavier for their body size than were goslings raised nearer to Karrak Lake. Body size varied randomly with distance in this sample. Both body size and condition varied positively with distance for Ross' and Snow Goose goslings of unknown age which were measured at marked brood recapture sites. A similar pattern was observed for body size in unmarked adults and this similarity may reflect common environmental effects during the growth period of adults and goslings. Although I found no distance effect on gosling survival, egg size was a significant determinant of within- (Snow and, possibly, Ross' Geese) and among-brood survival (Ross' Geese). Because goslings raised closer to the colony may fledge in poorer condition and thus may have lower first year survival, female philopatry to brood-rearing areas could indirectly influence parental fitness.

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## **LIST OF ABBREVIATIONS**

FRMASS: Fresh egg mass

SHFRMASS: Shell Free Fresh Egg Mass

LDM: Lean Dry Mass

QMGBS: Queen Maud Gulf Bird Sanctuary

## **CHAPTER 1: GENERAL INTRODUCTION**

### **1.1 INTRODUCTION**

Colonial birds that rear their young at the nest usually make daily foraging flights, often over long distances (Harris 1966, Lack 1968, Ashmole 1971, Diamond 1978). Such activity is called central place foraging (Hamilton and Watt 1970). This behavior may reduce potential foraging competition caused by high nesting densities because breeding individuals are not limited to food resources available near the colony. Flightless young of nidifugous colonial species, however, may be restricted to local foraging because movements are limited to walking or swimming. If hatch occurs synchronously throughout the colony, then the resulting foraging competition and/or local food depletion may motivate offspring to disperse long distances. This cost of coloniality could limit nutrient intake and restrict offspring growth and/or survival (Cooch et al. 1991a and b).

### **1.2 OBJECTIVES**

The objective of this research was to examine factors during the brood rearing period that ultimately could affect gosling recruitment into Ross' (*Chen rossii*) and Lesser Snow Goose (*Chen caerulescens*, hereafter referred to as Snow Goose) populations. In particular, I studied nutrient reserves of hatchlings and the effect of brood dispersal on pre-fledging gosling growth and survival. I also examined the potential effect of body size on dispersal-dependent growth by comparing these two

closely related (Awise et al. 1992), but morphometrically distinct species (Trauger et al. 1971).

### **1.3 SPECIES INFORMATION**

Ross' and Lesser Snow Geese are both colonial nesting species. Snow Geese nest in much of Arctic Canada, usually within 100 km of the coast (Bellrose 1980). Ross' Geese, however, breed primarily in the central Canadian Arctic, particularly in the Queen Maud Gulf Bird Sanctuary (QMGBS) where they may nest among Snow Geese. Snow Geese are 1.5 times heavier than Ross' Geese, on average, and are also structurally larger (Trauger et al. 1971, MacInnes et al. 1989). This morphometric difference may have important implications for their energetics and foraging ecology. Within a breeding season, modal clutch size and nest success are similar for both species (McLandress 1983, Slattery and Alisauskas 1993). However, since few data on the life history of Ross' Geese are available, a comparison of lifetime reproductive success is currently difficult to make.

The Arctic environment can severely restrict breeding by these herbivores. Geese arrive at colonies before ice melts and, as a consequence of low food availability during incubation, both sexes metabolize fat reserves as a primary energy source for egg production and incubation (Ankney and MacInnes 1978, Ryder 1970). Breeding adults, however, consume vegetation opportunistically and, by hatch, adults have denuded the colony site of most nutritive plant life (Ryder 1967, pers. obs.).

Little information has been published on the brood ecology of either species. Offspring of Ross' and Snow Geese are precocial, i.e. mobile and self feeding. Eggs (goslings) hatch synchronously within the clutch and throughout the colony, and

broods leave the nest site within 24 hr. (Ryder 1972, Findlay and Cooke 1982, Sedinger and Raveling 1986). Diets of newly hatched goslings consist primarily of vegetation, although absorbed yolk nutrients may serve as an initial energy source for growth and maintenance (Ankney 1980). Offspring remain with their parents during the entire brood-rearing period (Bellrose 1980, Prevett and MacInnes 1980, pers. obs.) and, since incubating geese have consumed virtually all nutritive vegetation in the colony, broods disperse from nesting areas in search of food (Ryder 1967, Findlay and Cooke 1982).

#### **1.4 GENETIC AND ENVIRONMENTAL EFFECTS ON AVIAN GROWTH AND SURVIVAL**

Much of the phenotypic variation in avian body size can be attributed to genotypic variation within populations (Price and Grant 1985, Schuller and Smith 1986, Boag and van Noordwijk 1987). However, growth studies on Starlings (Ricklefs and Peters 1981, Ricklefs 1984a), Great Tits (Gebhardt-Heinrich and van Noordwijk 1991), Song Sparrows (Smith and Arcese 1988), Red-winged Blackbirds (James and NeSmith 1988), Kittiwakes (Johanson 1978), Willow Ptarmigan (Jorgensen and Blix 1985), Barnacle Geese (Larsson and Forslund 1991, 1992), and Snow Geese (Cooch et al. 1991a,b) demonstrate that environmental factors can mask genetic effects.

Environmental effects are particularly strong when rearing conditions are poor (Price and Grant 1985) or when offspring that experience high energy demands are unable to compensate for poor quality forage through increased food intake (Jorgensen and Blix 1985).

Offspring growth and pre-fledging survival are not necessarily independent parameters and environmental factors which contribute to variation in growth rates can also contribute to variation in pre-fledging survival rates (Johanson 1978, Jorgensen and Blix 1985). Young birds growing under conditions of nutrient limitation may die either through starvation (Johanson 1978, Jorgensen and Blix 1985), increased susceptibility to disease/parasites (S. M. Gomis et al., Department of Veterinary Pathology, University of Saskatchewan, unpubl. data), or predation mediated by reduced parental attentiveness (Johanson 1978). For Arctic nesting species that must reproduce in a relatively short breeding season, reduced growth rates can also result in mortality if fledging is delayed until after freeze-up (*sensu* Barry 1962, Ryder 1967).

In geese, little compensatory growth occurs after fledging (Cooch et al. 1991a, Larsson and Forslund 1991) and environmental constraints during brood-rearing may influence future life history characteristics. Slow growth rates and low fledging mass can result in reduced first year survival rates (Sedinger and Raveling 1984, Owen and Black 1989, Francis et al. 1992), reduced recruitment rates (Francis et al. 1992), smaller adult body size (Cooch et al. 1991b), and, potentially, lower reproductive success (Cooch et al. 1989).

## **1.5 VEGETATIONAL RESPONSE TO GRAZING AND SUBSEQUENT FOOD AVAILABILITY.**

Geese are herbivores, so many aspects of their ecology are tied closely to their principal plant foods. Snow Geese grazing at La Perouse Bay, Manitoba, stimulated above-ground primary production of their graminaceous forage plants beyond

ungrazed (control) levels (Jeffries et al. 1979, Cargill and Jeffries 1984, Bazely and Jeffries 1985, Jeffries 1988, Hik and Jeffries 1990). In the Hudson Bay lowlands, tundra soil is nitrogen limited (Cargill and Jeffries 1984) and grazing facilitates nutrient cycling either directly through fecal nitrification or indirectly by preparing the substrate for colonization by nitrogen fixing cyanobacteria (Bazely and Jeffries 1985). The level of compensation achieved by the vegetation, however, is critically dependent on the timing and intensity of grazing (Hik and Jeffries 1990).

This latter relationship has important implications for colonial nesting geese. Intense foraging near the colony may cancel any positive feedback onto above-ground primary production, thus resulting in overgrazing. Habitat degradation accompanying rapid growth in colony size may be additive over several years (Kerbes et al. 1990, Cooch et al. 1991b) and could result in a systematic decline in local food availability, both within and across seasons.

## **1.6 FOOD AVAILABILITY, BROOD DISPERSAL, AND GOSLING GROWTH AND SURVIVAL**

Kerbes et al. (1990) referred to Snow Geese as a keystone species that greatly alter both biotic and abiotic characteristics of their environment. Intense spring grubbing and summer grazing by growing numbers of Snow Geese have led to severe habitat degradation around colonies at McConnell River and La Perouse Bay (Kerbes et al. 1990, Cooch et al. 1991b). Declines in food availability have been implicated as the cause of long-term declines in both adult and juvenile Snow Goose body size (Cooch et al. 1991a, b) and of reductions in prefledging survival (Williams et al. 1993) and gosling recruitment rates (Francis et al. 1992). These results, however,

may not apply to the entire nesting population since they are based on data collected within 20 km of the nesting colony, and broods are capable of dispersing much farther than this (Cooch et al. 1993). Thus Cooch et al.'s (1991a,b), Francis et al.'s (1992) and Williams et al.'s (1993) results may represent an increase in the variance of gosling growth and survival rates, both within and among age cohorts, since growth and survival rates of goslings reared farther from the colony may have been constant during the study period, or at least declined at a slower rate.

In large colonies with very high nest densities and severe local food depletion, gosling growth rates and/or survival rates should vary positively with brood dispersal distance for the following reasons (Figure 1.1). Local variation in above-ground vegetative biomass has been correlated with variation in gosling growth rates (Cooch et al. 1993). Thus any factors which influence nutrient availability could influence gosling growth and, possibly, survival (*sensu* Cooch et al. 1993, Williams et al. 1993). High brood densities could be one such factor. Brood density should vary both spatially and temporally because broods radiate outward from the same central site. Near hatch, brood density, and hence foraging pressure, should be greatest at the colony center and lowest at some distant point. If the tundra vegetation cannot recover from this intense grazing (*sensu* Hik and Jeffries 1990), then forage quality or per capita quantity should increase with distance from the colony center, i.e. a gradient of nutrient availability would exist around the colony. In Figure 1.1, this gradient is represented by the concentric rings of varying in thickness. If broods disperse variable distances (arrows on the nutrient

7

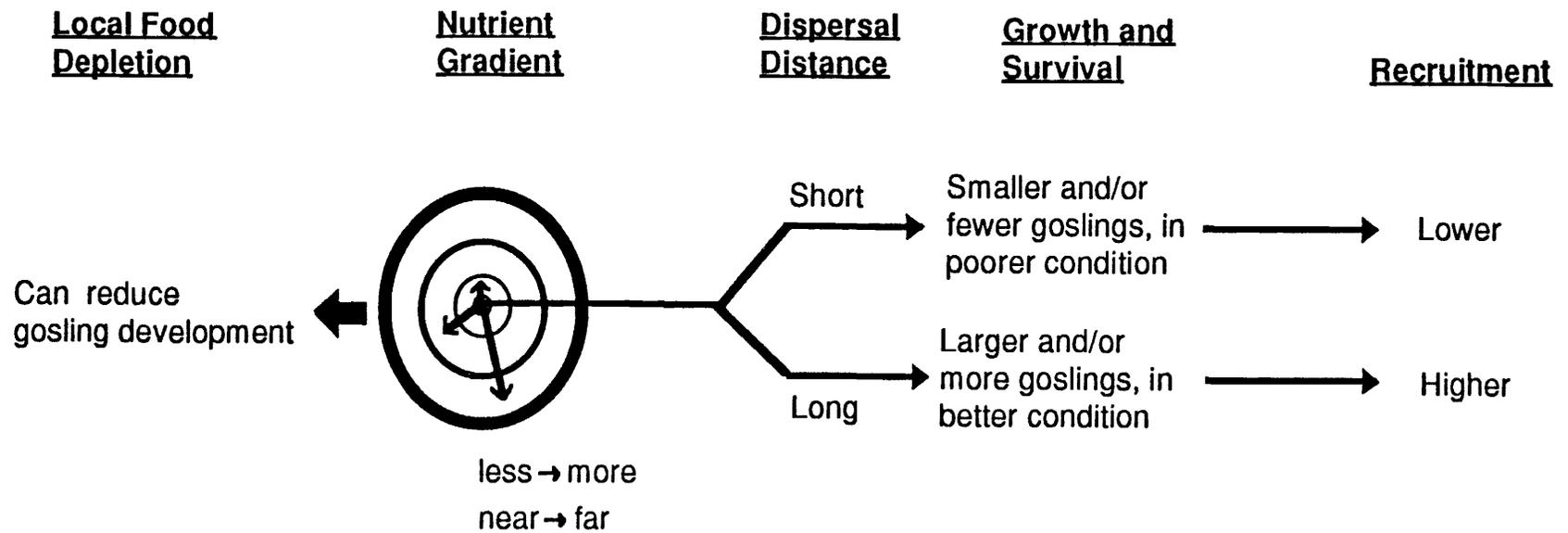


Figure 1.1. The influence of brood dispersal on gosling growth and survival. See section 1.6 for an explanation.

gradient in Figure 1.1), then gosling nutrition and, thus, pre-fledging growth, condition and survival should depend on how far a brood is reared from the poorest foraging habitat located within or near the colony. Broods settling farther from such colonies would experience better foraging conditions and should produce larger and/or more goslings in better condition than those broods settling closer to nesting areas (Figure 1.1). Ultimately, more goslings may be recruited into breeding populations from broods travelling longer distances. Note that this model assumes that the potentially higher energetic costs of long distance dispersal are offset by better foraging conditions on distance brood rearing areas. Unfortunately, little is known about the energetics of brood dispersal.

### **1.7 ROSS' VS. SNOW GOOSE BROOD ECOLOGY: BODY SIZE AND METABOLIC CONSIDERATIONS**

Inventories of Ross' and Snow Geese between 1967 and 1988 indicate that the population of white geese nesting in the QMGBS increased at an exponential rate of 11.3% per year (calculated from Kerbes in press). However, Ross' and Snow Goose populations did not contribute equally to overall population growth rate in the central Arctic; the Ross' Goose population grew at one half the rate of the Snow Goose population ( $r = 7.9\%$  and  $16.2\%$  per year, respectively). Several, non-mutually exclusive explanations exist for this difference, including interspecific differences in annual immigration and emigration of adults and interspecific variation in annual survival of adults. However, local habitat degradation evident at the largest colony (J. P. Ryder, Department of Biology, Lakehead University, pers. comm.) may also exert a stronger influence on the recruitment rate of Ross' Geese

than on that of Snow Geese for reasons outlined below.

Remaining yolk nutrients can be mobilized as an initial energy source for goslings (Ankney 1980, Duncan 1988). Ankney (1980) examined fasting endurance of newly hatched Snow Goose goslings and determined that survival times could be predicted by hatch mass, with heavier goslings surviving longer than lighter goslings. Presumably, lighter goslings had absolutely less yolk reserves. These results were expected since mass-specific resting metabolic rate (kcal/day/kg), and thus relative energy expenditure, increases as body mass declines (Aschoff and Pohl 1970).

Ross' Geese are smaller at hatch than are Snow Geese and may have higher mass-specific resting metabolic rates (Slattery unpubl. data). If Ross' Goose goslings also have proportionally equal or less yolk reserves than do Snow Goose goslings, then energy budget and, hence, the potential ability of Ross' Goose goslings to disperse long distances with minimal nutrient intake could be reduced relative to Snow Geese. Thus Ross' Goose broods may need to begin feeding closer to the natal colony than do Snow Goose broods and may be unable to maintain species-specific growth rates if local habitat quality is poor. Lower food availability and/or inferior food quality near large colonies coupled with the higher mass-specific resting metabolic rate of Ross' Geese, could cause reduced pre-fledging growth and/or brood survival, reduced first year survival, and, ultimately, reduced recruitment of Ross' Goose goslings (*sensu* Figure 1.1). Unfortunately, no literature is available which examines potential adaptations to offset energetic disadvantages of smaller body size in Ross' Geese.

## 1.8 HYPOTHESES

Data from Kerbes (in press) revealed that the Ross' Goose population in QMGBS grew at half the rate of the Snow Goose population between 1967 and 1988.

Reasons for these different gosling recruitment rates are unclear. Factors influencing the number of young recruited into breeding populations can act at various stages in the life cycle of geese (Begon and Mortimer 1986). My project examined factors during the brood-rearing period that could influence productivity, e.g. egg size and brood dispersal, and determined if Ross' Geese are less productive during the pre-fledging period than are Snow Geese.

Before studying the effects of egg size and brood dispersal on subsequent growth and survival in these two closely related species (Avisé et al. 1992), we must first know the nutrient profiles of neonate goslings. Examination of the chemical composition of goslings could reveal adaptations which counteract energetic constraints associated with small body size or which facilitate initial brood movements and thereby influence neonate foraging requirements. With the relative ability of goslings to withstand harsh environmental conditions understood, we can better interpret interspecific variation in patterns of brood dispersal and subsequent effects on gosling growth, body condition and survival. Only then can we begin to understand factors that influence goose demography.

To study factors influencing Ross' and Snow Goose productivity and to examine dispersal-dependent gosling growth and survival, I tested the following null hypotheses:

- a. Relative egg and gosling composition does not vary interspecifically;

- b. Prefledging survival does not differ between Ross' and Snow Geese;
- c. Body condition does not differ interspecifically;
- d. Brood dispersal distance does not differ interspecifically; and,
- e. Gosling growth, condition and survival are independent of egg size and brood dispersal distance;

### **1.9 THESIS FORMAT**

The remainder of this thesis is organized into three chapters. In Chapter 2, I examine egg characteristics and body reserves of neonate Ross' and Snow Geese to determine how egg size influences a gosling's nutrient profile and to compare potential adaptations for thermoregulation or locomotion of neonates. In Chapter 3, I examine the effects of egg size and brood dispersal on gosling growth and survival, then discusses these results in terms of the ecological constraints faced by each species. In Chapter 4, I synthesize my results in terms of how gosling body reserves and physiological characteristics might influence movements, growth and survival of goslings, and how brood dispersal patterns might influence demography in a rapidly growing colony. The literature cited section follows Chapter 4. Section headings and literature citations follow the format of the journal **Condor**.

## **CHAPTER 2. EGG CHARACTERISTICS AND BODY RESERVES OF HATCHLING ROSS' AND LESSER SNOW GEESE**

### **2.1 INTRODUCTION**

Variation in egg size and egg composition has important implications for offspring quality in some species. Egg size can influence neonate mass (Ricklefs et al. 1978, Moss et al. 1981), survival (Parsons 1970, Nisbet 1978, Lundberg and Väisänen 1979), fasting potential (Ankney 1980, Sedinger 1986), thermal resistance (Rhymer 1988, Duncan 1988) and early growth (Schifferli 1973, Ankney 1980, Furness 1983, Peach and Thomas 1986, Larsson and Forslund 1992). Egg size generally is highly heritable (Van Noordwijk et al. 1981, Moss and Watson 1982) and positively correlated with female body size (Newell 1988, Larsson and Forslund 1992) thus genetic factors may be important for determining neonate viability. In geese, the effect of egg size on offspring quality is poorly understood.

Ross' and Lesser Snow Geese breed in the same nesting colonies in the central Canadian Arctic, and therefore likely face very similar environmental constraints when provisioning eggs with nutrients and rearing broods. Females rely on endogenous nutrient reserves for egg production (Ankney and MacInnes 1978) and later nesting females may arrive with smaller reserves (see Alisauskas and Ankney 1992 for a review). If so, then females arriving late must trade-off some aspect(s) of egg production if sufficient reserves are to be spared for fasting during incubation, i.e. reduce clutch size, reduce egg size and/or reduce egg quality

(nutrient composition). Geese appear to use at least one of these strategies: clutch size declines seasonally in both Ross' and Snow Geese (Ryder 1972, Finney and Cooke 1978, R. T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK, unpubl. data). Little to no data are available for the latter two nutrient sparing strategies. In Snow Geese, egg size does not change seasonally (Newell 1988) and this information is unknown for Ross' Geese. In addition, to my knowledge, no one has examined seasonal changes in egg composition. Despite the absence of data, a decline in egg size or quality seems maladaptive because such a trade-off could compromise offspring quality (Ankney and Bissett 1976, Ankney 1980, Lessells et al. 1989). Thus if egg size is heritable, then minimum egg size should be limited by the amount of nutrients needed to produce a viable offspring (Smith and Fretwell 1974, Brockelman 1975). Still, growth in geese declines seasonally (Cooch et al. 1991a, Sedinger and Flint 1991). Although this decline has been attributed to seasonal variation in food availability, egg size and, presumably, composition can influence early growth (Schifferli 1973, Ankney 1980, Furness 1983, Peach and Thomas 1986, Duncan 1988, Larsson and Forslund 1992). Thus the decline in growth rates could be influenced by egg size/composition and the effect of season on egg and gosling composition merits study.

Egg size may play an important role in neonate energetics and, hence, survival during nutritional or thermal stress (Ankney 1980, Alisauskas 1986, Rhymer 1988). Mass-specific metabolic rate and heat loss rate are inversely related to body size (Ricklefs 1974, 1983) thus offspring from smaller eggs should need relatively more energy than those from larger eggs (*sensu* Ankney and Bissett 1976, Ankney 1980, Alisauskas 1988). If true, then viability of neonates during energetic stress

should depend on their relative body condition, i.e. their lipid to body size ratio. Goslings hatching with more endogenous reserves relative to their body size should be at an energetic advantage and thus should survive harsh conditions better than those with poorer body condition. Unfortunately, little is known about how body size and endogenous reserves scale with increasing egg size and one cannot easily predict the effect of egg size on interspecific variation in neonate energetics.

Endogenous reserves available to neonates and ability to withstand energetically stressful conditions could differ between Ross' and Snow Geese. Both species produce precocial young that usually disperse from the nest site within 24 hr. of hatching (Ryder 1972, Findlay and Cooke 1982, Sedinger and Raveling 1986). These initial movements occur rapidly (Chapter 3) and at a time when broods may experience near-freezing temperatures (Ryder 1967, Slattery unpubl. data) and substantial precipitation (pers. obs.). During such energetically stressful weather conditions, goslings may be unable to fully thermoregulate and some may die from hypothermia, particularly goslings from smaller eggs (*sensu* Ankney 1980, Duncan 1988, Rhymer 1988). However, adult Ross' Geese are about 30% smaller than adult Snow Geese (MacInnes et al. 1989) and also lay eggs about 25% smaller than Snow Goose eggs (Ryder 1971). Thus smaller neonate Ross' Geese may be at an energetic disadvantage under poor environmental conditions unless some compensatory adaptation exists to offset smaller egg size, e.g. relatively more egg nutrients or less catabolism of nutrients during embryonic development than Snow Geese. In addition, Ross' Goose egg size could represent another adaptive strategy if Ross' Goose females lay larger eggs relative to their body size than do Snow Geese and thus hatch relatively larger young that need to grow less to reach adult

size.

The objectives of this study were 1) to determine if egg size and egg/gosling quality changes with laying or hatching date, 2) to examine the allometric relationships between egg size and gosling body size/composition and 3) to determine if Ross' Geese compensate for smaller egg size by producing better quality or more developed goslings than do Snow Geese.

## **2.2 STUDY AREA**

Eggs and goslings were collected from Ross' and Snow Geese nesting at Karrak Lake, NWT (66° 15' N, 100° 15' W). This colony is the largest known colony in the Queen Maud Gulf Bird Sanctuary (QMGBS) and contained about 364,000 geese in 1993 (R. T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK, unpubl. data). Data for this paper were collected as part of a long-term monitoring program examining nesting and brood-rearing activities of geese breeding at Karrak Lake. The Karrak Lake region is a heterogenous environment with rock outcrops, sedge meadows and tundra ponds and is described extensively in Ryder (1972).

## **2.3 METHODS**

### **2.3.1 EGG AND GOSLING COLLECTION**

Species of eggs collected for egg and gosling composition analyses was determined using measurements from eggs for which species' identity was positively known. In 1992, 79 Ross' and 83 Snow Goose females observed incubating were flushed from their nests and egg length and breadth measurements were recorded ( $n_{eggs} = 263$  Ross', 318 Snow). Criteria for species identification were then determined using

means and standard deviations (SD) for length and breadth. Collected eggs were identified to species as follows:

1. Ross' Goose- length and/or breadth  $< \bar{x}_{\text{Snow}} - 2\text{SD}_{\text{Snow}}$
2. Snow Goose- length and/or breadth  $> \bar{x}_{\text{Ross}} + 2\text{SD}_{\text{Ross}}$
3. Unknown- either both length and breadth  $\bar{x}_{\text{Snow}} - 2\text{SD}_{\text{Snow}} < X < \bar{x}_{\text{Ross}} + 2\text{SD}_{\text{Ross}}$ , where X equals the egg measurement, or length and breadth yield conflicting species assignments.

Eggs and goslings of unknown species were deleted from analyses ( $n_{\text{eggs}} = 4$ ,  $n_{\text{goslings}} = 2$ ). Length x breadth<sup>2</sup> (LB<sup>2</sup>) was not used because this technique resulted in more unknown eggs and goslings, likely due to the large variation in egg length for both species. Data from known species egg measurements and criteria used to assign species to collected eggs are given in Table 2.1. In this sample, about 53% and 45% of the variation in egg size was due to nest effect for Ross' and Snow Geese, respectively (one-way ANOVA, Ross:  $r^2 = 0.526$ ,  $F = 2.62$ ,  $df = 78$ ,  $P = 0.0001$ , Snow:  $r^2 = 0.450$ ,  $F = 2.34$ ,  $df = 82$ ,  $P = 0.0001$ ).

Fresh eggs were collected during the egg laying period from nests in the central portion of the colony. To reduce possible variation in composition due to position in the laying sequence, only first laid eggs were collected from clutches. When possible, eggs were taken from single egg nests and were assumed to be the first egg laid. However, some eggs (Ross'- 12.9%, Snow- 43.9%) were taken from unincubated two and three egg clutches to better represent colony-wide clutch initiation dates. In these cases, the most heavily stained egg was assumed to have

Table 2.1. Mean (SD) egg measurements (mm) for known species eggs and selection criteria used to assign species to eggs and goslings. Sample sizes are  $n_{Ross'} = 263$  and  $n_{Snow} = 318$ .

Species	Mean (SD)		Selection Criteria	
	Length	Width	Length	Width
Ross'	73.1 (2.7)	48.3 (1.4)	<72.1	<49.4
Snow	78.4 (3.1)	52.6 (1.6)	>78.6	>51.1

been laid first (Williams and Nelson 1943, Cooper 1978, Sedinger and Flint 1991, pers. obs.). Egg length and breadth were measured to the nearest 0.1 mm using dial calipers and eggs were weighed to the nearest gram using a digital Mettler balance. Eggs were then boiled for 20-30 minutes (Montevicchi et al. 1983, Birkhead 1985) and reweighed.

Goslings from pipped eggs were collected from nests in the central portion of the colony. Clutch size was also recorded at this time. Within clutches, the most heavily stained (i.e. the first laid) egg was collected. Length and breadth of pipping eggs were then measured. Goslings were hatched in an incubator and weighed to the nearest gram immediately after clearing the egg. After about 8 hr., dry goslings were reweighed then euthanized using thoracic compression (AOU 1988).

Eggs/goslings were stored unbagged in sealed containers for 45 days at approximately 4° C. Because of this storage technique, water content of egg and gosling components was not examined. After returning from the Arctic, eggs and goslings were frozen at -10° C until further processing occurred.

### 2.3.2 COMPOSITION ANALYSES

After thawing, each egg was separated into shell, albumin and yolk components then weighed to the nearest 0.001 g. Following Dzubin and Cooch (1992), midwing, tarsus, skull and culmen lengths were measured to the nearest 0.1 mm for each gosling and body length was measured to the nearest 1 mm. Down was plucked from goslings and right leg, right pectoralis and gizzard muscles removed and weighed to the nearest 0.001 g. Egg and gosling components were then freeze-dried to constant mass. Dry mass of components was used in subsequent analyses.

Dried albumin mass was assumed to be composed entirely of protein (Montevecchi et al. 1983, C. D. Ankney, Department of Zoology, University of Western Ontario, pers. comm.). Dried yolks and goslings were analyzed for lipid and protein composition. Yolks were ground using a mortar and pestle then redried at 90° C to a constant mass and reweighed. Lipids were extracted using petroleum ether in a modified Soxhlet apparatus. Lipid-free yolk samples were then redried to constant mass and will be referred to as yolk protein. Egg water content was calculated by subtracting freeze-dried egg mass from fresh egg mass. Whole dry goslings were ground using an electric blender. About 10 g of each homogenized dry gosling was redried at 90° C to constant mass. Lipids were extracted with petroleum ether using the modified Soxhlet apparatus. Lean samples were then placed in a muffle furnace for 12 hr. and the remaining ash was redried to constant mass and weighed. Protein was calculated by subtracting the remaining ash mass from the origin lean sample mass. Gosling water content was calculated by subtracting freeze-dried gosling body mass from body mass of the dry, fluffy gosling 8 hr. after clearing the egg.

### 2.3.3 STATISTICAL ANALYSES

In section 2.1, I predicted *a priori* that Ross' Geese would have adaptations to offset potential energetic disadvantages of their smaller body size, i.e. that Ross' Goose goslings would be relatively better quality offspring for their egg/body size than were Snow Goose goslings. In the following interspecific analyses, I use muscular development, body size, and nutrient composition as indices of offspring quality. All interspecific tests are one-tailed and considered significant at  $P < 0.1$ . Where

interspecific trends were opposite than predicted, I considered results significant at  $P = 0.05$ . A significance level of  $P = 0.05$  has been set for all other analyses. Type III sums of squares were used for all linear models.

### 2.3.3.1 EGGS

Unless otherwise noted, egg mass is defined as the shell-free fresh mass (SHFRMASS) of the egg determined by subtracting dried shell mass from egg mass measured before storage. SHFRMASS was used instead of fresh egg mass (FRMASS) since 1) the egg  $LB^2$  explained slightly more variation in SHFRMASS than in FRMASS (because  $LB^2$  marginally described the variation in dry shell mass; Ross':  $r^2_{SHFRMASS} = 0.964$  vs  $r^2_{FRMASS} = 0.951$ ,  $r^2_{dry\ shell} = 0.346$ ; Snow:  $r^2_{SHFRMASS} = 0.949$  vs  $r^2_{FRMASS} = 0.948$ ,  $r^2_{dry\ shell} = 0.481$ ) and 2) I was interested in examining egg nutrients available to the gosling rather than those invested by the female (Williams et al. 1982); about 95% of the egg shell is not used by developing embryos (Carey 1983). Egg components were analyzed for species, lay date and egg size effects using ANCOVA with the last two variables used as covariates. In addition, an ANOVA was used to test for differences in lay dates between species. To examine allometry between egg mass and egg components, I regressed the logarithm of each variable against the logarithm of egg mass (Ricklefs et al. 1978) separately for each species. Slopes ( $b$ ) from log-log regressions equal to 1 indicate isometry. Allometry can be concluded if  $b \neq 1$  (Ricklefs et al. 1978). To test for allometry of egg components, regression slopes were tested against the null hypothesis that  $b = 1$  using the Test statement in Proc Reg (SAS 1985). Slopes were then tested for species effects using a modified Student's t-test (Zar 1984). For all analyses

involving shell, FRMASS was used instead of SHFRMASS.

Interspecific relationships between female body size and egg mass were determined by calculating an egg size index. Females that laid four eggs (modal clutch size, Slattery unpubl. data) were trapped on their nests during incubation. Measurements were recorded for tarsus, skull, culmen and body lengths. At this time, length and breadth were recorded for each egg in the nest. SHFRMASS was estimated from  $LB^2$  using regression equations calculated for each species from the egg composition sample (hence using known egg size) (Table 2.2). I used the first principal component (PC1) from a principal component analysis (PCA) of adult female morphometric measurements as an index of parent female body size (Reyment et al. 1984). Ross' and Snow Goose data were combined in the PCA so that both species were indexed on the same scale. Egg size indices were residuals values calculated from a regression of clutch means for egg mass vs. female body size with data pooled across species. Interspecific variation in relative egg size was then analyzed using these residuals an ANOVA. Because my sample represents only females laying four eggs, I acknowledge the potential problems with generalizing results from this analysis to the entire nesting population. However, in Snow and Barnacle Geese, egg size is highly heritable (Newell 1988, Lessells et al. 1989, Larsson and Forslund 1992). Since clutch size is not heritable (Findlay and Cooke 1983) most of the variation in clutch size is due to female age (Newell 1988) and environmental factors. Therefore, my sample can be used to make cautious inferences about the population.

Table 2.2 Parameters from simple linear regressions used to estimate fresh egg mass (FRMASS) and shell free fresh egg mass (SHFRMASS) using egg measurements ( $LB^2$  in cm).

Species	Category	$r^2$	$F$	$P$	Slope ( $b_1$ )	Intercept ( $b_0$ )
Ross' $n = 31$	SHFRMASS	0.964	866.59	< 0.001	0.524	-1.613
	FRMASS	0.951	613.11	< 0.001	0.561	-2.681
Snow $n = 41$	SHFRMASS	0.949	803.09	< 0.001	0.483	0.223
	FRMASS	0.948	802.30	< 0.001	0.539	0.486

### 2.3.3.2 *GOSLINGS*

The following analyses required the calculation of egg size, body size, and lay date for each gosling. SHFRMASS was estimated from  $LB^2$  for each gosling's egg from species-specific regression equations calculated using egg composition data (Table 2.2). I indexed gosling body size using PC1 calculated from a PCA based on the correlation matrix of midwing, tarsus, skull, culmen and body lengths (Reyment et al. 1984), with data pooled across species. Since hatch date reflects both clutch initiation date and clutch size, I calculated lay date by subtracting 22.3 days for incubation and 1.3 days x clutch size for egg laying from each gosling's hatch date (data on incubation and laying intervals from Ryder 1972). Within each species, Pearson's Correlation analysis was employed to determine the relationship between gosling body size and body mass. Gosling composition was examined relative to species, season, egg size, and body size effects using separate ANCOVA, each with one of the last three variables as the covariate. Where significant interactions existed, separate regression analyses were calculated for each species to further interpret the relationship between the component and the explanatory variable.

I examined relative tissue maturity and body condition for neonate Ross' and Snow Geese by using residuals derived from regression analyses. Researchers have used the ratio of water:lean dry matter to index the functional maturity of tissue (Ricklefs 1983, Ricklefs and Webb 1985, Konarzewski 1988), and the ratio of lipids:protein to index neonate body condition (Alisauskas 1986). Ratios, however, are often not normally distributed (Atchley et al. 1976, Blem 1984). Therefore, I regressed water and lipid content of goslings against lean dry mass (LDM = ash + protein content) and used the residuals in an ANOVA testing for species effects on

neonate tissue maturity and lipid reserves.

Allometry of gosling composition was tested by regressing the logarithm of each component on the logarithm of egg size (Ricklefs et al. 1978). PC1 is a unitless measurement with a mean equal to zero and both positive and negative scores. Since logarithms of negative numbers are not possible, PC1 scores for each gosling were first scaled to become positive. I used the existing eigenvectors to calculate the PC1 score of a theoretical bird with zero size, then added the absolute value of this score to the PC1 score for each gosling (Bortolotti and Iko 1992, G. Bortolotti, Department of Biology, University of Saskatchewan, Saskatoon). Species were analyzed separately.

## 2.4 RESULTS

### 2.4.1 NESTING CHRONOLOGY

In 1992, mean clutch initiation occurred on 13 June  $\pm$  2.9 days and 16 June  $\pm$  1.9 days while mean hatch occurred on 9 July  $\pm$  2.5 days and 12 July  $\pm$  1.9 days for Snow and Ross' Geese, respectively (Slattery and Alisauskas 1993). Except in the sample of Snow Goose goslings, mean laying dates for my egg and gosling samples were about 2 days earlier than mean initiation dates for the colony (Tables 2.3 and 2.4, ANOVA, Ross':  $F_{eggs} = 35.68$ ,  $P_{eggs} < 0.001$ ;  $F_{goslings} = 7.52$ ,  $P_{goslings} = 0.007$ ; Snow:  $F_{eggs} = 9.18$ ,  $P_{eggs} = 0.003$ ;  $F_{goslings} = 1.31$ ,  $P_{goslings} = 0.255$ ). Mean gosling hatch dates in my sample did not differ from those of the colony (Table 2.4,  $F_{Ross'} = 0.00$ ,  $P_{Ross'} = 0.976$ ;  $F_{Snow} = 0.38$ ,  $P_{Snow} = 0.537$ ).

Table 2.3. Egg composition and results of ANCOVA for species and lay date effects. Partial  $F$  values given are under  $F$ .

Component	Mean (SD)		Model	Species Effect		Lay Date Effect	
	Ross' ( $n = 31$ )	Snow ( $n = 41$ )	$r^2$	$F_{1, 70}$	$P$	$F_{1, 70}$	$P$
Shell Free Fresh Egg Mass (g)	84.3 (6.5)	113.1 (7.1)	0.817	262.68	<0.001	0.32	0.571
Yolk Lipid (g)	12.15 (1.12)	15.74 (1.29)	0.694	123.78	<0.001	1.87	0.176
Yolk Protein (g)	6.66 (0.67)	9.11 (0.68)	0.781	84.18	<0.001	4.11	0.046 <sup>1</sup>
Albumin (g)	5.65 (0.63)	7.60 (0.77)	0.653	60.40	<0.001	0.16	0.694
Total Protein (g)	12.30 (1.04)	16.72 (1.02)	0.824	268.82	<0.001	1.06	0.307
Water (g)	59.6 (4.6)	80.5 (5.5)	0.805	246.30	<0.001	0.06	0.804
Shell (g)	7.16 (0.76)	10.46 (1.14)	0.743	159.01	<0.001	2.08	0.154
Size Index <sup>2</sup>	-0.58 (0.64) <sup>3</sup>	-0.88 (0.80)	0.009	2.03	0.156 <sup>4</sup>	-	-
Lay Date (June)	13.4 (2.1)	11.5 (2.8)	0.126	10.23	0.002 <sup>5</sup>	-	-

<sup>1</sup>  $b = -0.065$

<sup>2</sup> Residuals from regression analysis of egg mass on body size of parent female. Data from females that laid four eggs ( $n_{Ross'} = 47$ ,  $n_{Snow} = 24$ )

<sup>3</sup> Least squares means (SE) of residuals

<sup>4</sup>  $F_{1, 60}$

Table 2.4. Gosling composition and laying/hatching data for Ross' and Snow Geese. For simplicity, the only  $F$  and  $P$  values for the species effect presented are from the hatch date ANCOVA. Although values from the lay date ANCOVA are slightly different, patterns of significance for the species effect are similar in the lay date analyses. Degrees of freedom equals 1 for all effects. Error df equals 39 for all test except for SHFRMASS where df equals 33. Partial  $F$  values are given under  $F$ . Table continued on next page.

Component	Ross'		Snow		Species Effect		Lay Date Effect			Hatch Date Effect		
	Mean (SD)	$n$	Mean (SD)	$n$	$F$	$P$	$r^2$	$F$	$P$	$r^2$	$F$	$P$
Shell Free Fresh Mass (g)	89.0 (4.4)	15	109.5 (7.2)	18	88.00	< 0.001	0.758	0.60	0.444	0.761	1.00	0.326
Body Mass (g)	65.2 (5.0)	19	80.9 (5.6)	20	62.25	< 0.001	0.691	0.06	0.801	0.699	0.32	0.574
Body Size	-0.73 (0.46)	19	0.77 (0.64)	20	52.43	< 0.001	0.659	0.39	0.537	0.654	2.23	0.858
Gizzard (g)	0.54 (0.08)	19	0.67 (0.13)	20	16.54	0.001	0.326	3.20	0.082	0.317	0.03	0.144
Leg Muscles (g)	0.72 (0.09)	19	0.89 (0.08)	20	25.56	< 0.001	0.496	0.20	0.659	0.506	0.51	0.480
Pectoralis (g)	0.60 (0.04)	19	0.59 (0.03)	20	9.12	0.005	0.267	10.91	0.002	0.316	11.93	0.002 <sup>1</sup>
Lipid (g)	7.94 (1.13)	19	9.31 (1.02)	20	11.72	0.002	0.285	0.00	0.982	0.294	0.00	0.945

Table 2.4. Continued.

Component	Ross'		Snow		Species Effect		Lay Date Effect			Hatch Date Effect		
	Mean (SD)	<i>n</i>	Mean (SD)	<i>n</i>	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>F</i>	<i>P</i>
Protein (g)	10.02 (1.01)	19	12.33 (1.44)	20	26.34	< 0.001	0.458	0.14	0.714	0.472	0.03	0.865
Ash (g)	1.09 (0.11)	19	1.34 (0.11)	20	39.82	< 0.001	0.565	0.50	0.484	0.572	0.08	0.775
Water (g)	47.2 (3.6)	19	59.3 (3.8)	20	75.90	< 0.001	0.739	0.26	0.614	0.744	0.75	0.393
Lay Date (June)	14.4 (2.0)	18	12.3 (3.1)	20	6.29	0.017	-	-	-	-	-	-
Hatch Date (July)	11.6 (2.1)	19	9.4 (2.4)	20	9.47	0.004	-	-	-	-	-	-
Lipid Index <sup>2</sup>	-0.04 (0.20)	19	0.04 (0.20)	20	0.08	0.785	-	-	-	-	-	-
Water Index <sup>3</sup>	-1.71 (0.63)	19	1.62 (0.62)	20	14.18	< 0.001	-	-	-	-	-	-

<sup>1</sup> Species\*Hatch Date was significant ( $F = 6.57$ ,  $P = 0.015$ ) so separate analyses were run for each species. See text for results

<sup>2</sup> Residuals calculated from a regression of lipid on LDM, Least squares mean (SE)

<sup>3</sup> Residuals calculated from a regression of water on LDM, Least squares mean (SE)

#### 2.4.2 EGG MASS AND COMPOSITION

Snow Geese had absolutely more egg constituents than did Ross' Geese (Table 2.3). However, when controlled for egg size, no species effect was observed for any constituent. These results suggests that Snow and Ross' Geese have the same proportional egg composition (Table 2.5). Note, however, that trends of least squares means for yolk protein and total protein were opposite than predicted and species effects were nearly significant with  $P_{yolk\ protein} = 0.059$  and  $P_{total\ protein} = 0.064$ . Yolk protein also declined seasonally in both species (Table 2.3). Overall, egg size accounted for more than 80% of the constituent variation (Table 2.5). Residuals for the analysis of egg size relative to female body size were derived from a significant interspecific regression of mean egg size on female body size ( $n = 71$ ,  $r^2 = 0.707$ ,  $F = 554.55$ ,  $P = 0.001$ ). No interspecific variation was observed for these residuals (Table 2.3) which suggests that Ross' females do not lay larger eggs for their body size than do Snow Geese.

Egg composition changed isometrically with egg mass because slopes of the log-log regressions were not different from one (Table 2.6). Note, however, that total protein for Snow Geese was almost allometric ( $P = 0.089$ ). I could not conclude that slopes differed between species within any component ( $P > 0.05$ ). However, a species difference in slopes was almost significant ( $P \approx 0.06$ ) for total protein. In Ross' Geese, protein increased relatively faster with egg size than in Snow Geese (Table 2.6).

Table 2.5. Least squares means of egg components and results of ANCOVA for species effects using shell free fresh mass as a covariate. Partial  $F$  values are given under  $F$ .

Component	LS Mean (SE) <sup>1</sup>		Model	Species Effect		Shell Free Fresh Egg Mass	
	Ross' (n = 31)	Snow (n = 41)	r <sup>2</sup>	$F_{1, 71}$	$P$	$F_{1, 71}$	$P$
Yolk Lipid (g)	14.16 (0.30)	14.22 (0.24)	0.834	0.02	0.901	61.98	<0.001
Yolk Protein (g)	7.74 (0.17)	8.29 (0.14)	0.873	3.68	0.059	56.83	<0.001
Albumin (g)	6.82 (0.18)	6.72 (0.14)	0.814	0.12	0.735	60.00	<0.001
Total Protein (g)	14.57 (0.14)	15.01 (0.11)	0.971	3.55	0.064	353.11	<0.001
Water (g)	71.8 (0.3)	71.3 (0.3)	0.993	0.65	0.424	1995.11	<0.001
Shell (g)	8.72 (0.26)	9.28 (0.20)	0.849	1.78	0.186	52.01	<0.001

<sup>1</sup> Least squares means (standard error)

Table 2.6. Allometric relationships of egg components with shell free fresh egg mass. Slopes are calculated from the regression of log egg component on log shell free fresh mass.

Species	Component	b	95% CL (±)	r <sup>2</sup>	t <sub>b=0</sub> <sup>1</sup>	P <sub>b=0</sub>	F <sub>b=1</sub> <sup>2</sup>	P <sub>b=1</sub>	t <sub>b Ross = b Snow</sub> <sup>3</sup>	P <sub>b Ross = b Snow</sub>
Ross'	Yolk Lipid	0.946	0.249	0.675	7.754	< 0.001	0.197	0.660	0.578	> 0.1
(n = 31)	Yolk Protein	0.989	0.311	0.593	6.500	< 0.001	0.005	0.943	1.072	> 0.1
	Albumin	1.145	0.342	0.618	6.846	< 0.001	0.747	0.394	0.421	> 0.1
	Total Protein	1.064	0.132	0.900	16.476	< 0.001	0.985	0.329	1.959	0.05 < P < 0.1
	Water	1.000	0.057	0.978	36.076	< 0.001	0.000	0.999	-1.224	> 0.1
	Shell <sup>4</sup>	0.974	0.361	0.513	5.522	< 0.001	0.021	0.885	0.102	> 0.1
Snow	Yolk Lipid	0.825	0.344	0.377	4.856	< 0.001	1.066	0.308	-	-
(n = 41)	Yolk Protein	0.757	0.314	0.379	4.881	< 0.001	2.461	0.126	-	-
	Albumin	1.033	0.415	0.394	5.039	< 0.001	0.026	0.876	-	-
	Total Protein	0.876	0.143	0.797	12.367	< 0.001	3.041	0.089	-	-
	Water	1.053	0.067	0.962	31.640	< 0.001	0.120	0.120	-	-
	Shell <sup>4</sup>	1.206	0.384	0.553	6.947	< 0.001	2.805	0.102	-	-

<sup>1</sup> Statistics for the null hypothesis: b = 0

<sup>2</sup> Statistics for the null hypothesis: b = 1

<sup>3</sup> Statistics for the null hypothesis: b<sub>Ross'</sub> = b<sub>Snow</sub>

<sup>4</sup> Regressed with log fresh mass as the independent variable

### 2.4.3 GOSLING COMPOSITION

Body size and body mass were not correlated in goslings of either species ( $r_{\text{Ross}'} = 0.347$ ,  $P = 0.159$ ,  $r_{\text{Snow}} = 0.382$ ,  $P = 0.096$ ). All variables were absolutely greater in Snow Geese than in Ross' Geese except for pectoralis muscle which was greater for Ross' Geese (Table 2.4). No seasonal effect was observed for any gosling component except pectoralis muscle (Table 2.4). The species-by-season interaction effect was also significant in the ANCOVA involving pectoralis muscle and separate regression analyses showed that declines in pectoralis muscle mass with lay and hatch date occurred only in Ross' Geese (lay date: Ross',  $n = 18$ ,  $r^2 = 0.429$ ,  $b = -0.013$ ,  $t = -3.470$ ,  $P = 0.003$ ; Snow,  $n = 20$ ,  $r^2 = 0.027$ ,  $b = -0.002$ ,  $t = -0.707$ ,  $P = 0.488$ ; hatch date: Ross',  $n = 18$ ,  $r^2 = 0.523$ ,  $b = -0.015$ ,  $t = -4.176$ ,  $P = < 0.001$ ; Snow,  $n = 20$ ,  $r^2 = 0.016$ ,  $b = -0.002$ ,  $t = -0.539$ ,  $P = 0.597$ ). Interspecific regressions of lipid/water on LDM used to produce residuals for subsequent analyses were significant ( $r^2_{\text{lipid}} = 0.538$ ,  $F = 43.09$ ,  $df = 1$ ,  $P = 0.0001$ ;  $r^2_{\text{water}} = 0.798$ ,  $F = 145.89$ ,  $df = 1$ ,  $P = 0.0001$ ). However, a species effect was only observed for the water index (Ross < Snow, Table 2.4) indicating that Ross' Goose neonate tissue is more functionally mature than that in Snow Geese.

Results from ANCOVA using egg mass showed that all gosling components except leg and pectoralis muscles were correlated with egg mass (Table 2.7). When controlled for differences in egg mass, Ross' Geese had relatively more protein and ash and smaller body size than did Snow Geese. Mass for all other components did not differ interspecifically. In addition, egg mass accounted for more of the variation in body mass than in body size (Table 2.7).

Table 2.7. Interspecific differences in gosling composition using ANCOVA with SHFRMASS as a covariate. Sample sizes:  $n_{\text{Ross}} = 15$ ,  $n_{\text{Snow}} = 18$ . Partial  $F$  values are given under  $F$ .

Component	LS Means (SE) <sup>1</sup>		Model $r^2$	Species Effect		Shell Free Fresh Egg Mass Effect	
	Ross'	Snow		$F_{1, 32}$	$P$	$F_{1, 32}$	$P$
Body Mass	74.3 (0.9)	73.8 (0.8)	0.937	0.11	0.745	120.97	< 0.001
Body Size	-0.22 (0.22)	0.41 (0.19)	0.724	3.08	0.090	8.31	0.007
Gizzard (g)	0.64 (0.04)	0.59 (0.04)	0.415	0.52	0.476	8.59	0.006
Leg Muscles (g)	0.77 (0.03)	0.86 (0.03)	0.538	2.16	0.151	2.63	0.115
Pectoralis (g)	0.60 (0.01)	0.59 (0.01)	0.031	0.59	0.450	0.95	0.337
Lipid (g)	9.01 (0.38)	8.44 (0.34)	0.434	0.80	0.378	9.97	0.004
Protein (g)	12.06 (0.27)	10.73 (0.25)	0.834	8.04	0.008	72.35	< 0.001
Ash (g) <sup>2</sup>	1.28 (0.03)	1.17 (0.02)	0.863	4.07	0.052	72.32	< 0.001
Water (g)	53.2 (0.80)	54.6 (0.73)	0.917	1.03	0.318	68.87	< 0.001

<sup>1</sup> Least squares means (standard error)

<sup>2</sup> Fresh egg mass used for analysis

When controlled for differences in body size, Ross' Geese had relatively lighter body mass and less water, but heavier gizzards than did Snow Geese (Table 2.8). In addition, Snow Geese may have had more lipids but my small sample size could have prevented me from detecting this difference ( $P = 0.069$ , two-tailed since the relationship is opposite than predicted). No other differences between species were observed. Interspecific variation in body mass was likely due to relative differences in water content. All components were positively correlated with body size except pectoralis muscle and lipid content (Table 2.8).

Snow Goose goslings that hatched from heavier eggs were relatively smaller and had relatively less protein than those hatching from lighter eggs (Table 2.9). The log-log regression of body size on egg size was nearly significant in Ross' Geese (Table 2.9,  $0.05 < P_{b=0} < 0.1$ ,  $P_{b=1} < 0.001$ ) and detection of a relationship was likely impaired by small sample size ( $n = 15$ ). No relationship with increasing egg size was observed for leg or pectoralis muscles. All other components varied isometrically with egg size (Table 2.9). Note, however, that the regression line for Ross' Goose gizzard is non-significant ( $P_{b=0} = 0.057$ ) but this lack of significance is likely due to small sample size ( $n = 15$ ). I found no interspecific variation in slopes for any component, although for protein,  $P$  was between 0.05 and 0.1 ( $b_{\text{Ross'}} < b_{\text{Snow}}$ ).

#### 2.4.4 CATABOLISM OF EGG NUTRIENTS DURING EMBRYONIC DEVELOPMENT AND BODY SIZE AT HATCH

Ross' Geese appeared to catabolize fewer egg nutrients during development than did Snow Geese (Table 2.10). Between egg and gosling stage, Ross' Geese lost 6.2%

Table 2.8. Interspecific variation in gosling composition using ANCOVA with body size (PC1) as a covariate. Partial  $F$  values are given under  $F$ . See Table 2.7 for sample sizes.

Component	LS Means (SE) <sup>1</sup>		Model $r^2$	Species Effect		Body Size Effect	
	Ross'	Snow		$F_{1, 32}$	$P$	$F_{1, 32}$	$P$
Body Mass (g)	69.2 (1.72)	78.7 (1.50)	0.724	11.85	< 0.001	4.33	0.046
Gizzard (g)	0.68 (0.03)	0.58 (0.02)	0.660	5.36	0.028	38.21	< 0.001
Leg Muscles (g)	0.79 (0.03)	0.85 (0.02)	0.593	1.53	0.226	8.19	0.008
Pectoralis (g)	0.60 (0.01)	0.59 (0.01)	0.030	0.15	0.697	0.70	0.409
Lipid (g)	8.08 (0.40)	9.27 (0.35)	0.243	3.40	0.075	3.40	0.999
Protein (g)	11.07 (0.41)	11.68 (0.35)	0.553	0.84	0.367	8.06	0.008
Ash (g)	1.22 (0.03)	1.24 (0.03)	0.739	0.48	0.484	24.08	< 0.001
Water (g)	50.0 (1.19)	57.7 (1.04)	0.760	16.19	< 0.001	4.11	0.052

<sup>1</sup> Least squares means (standard error)

Table 2.9. Allometric relationships of gosling composition with shell free fresh egg mass. Slope are calculated from the regression of log component on log shell free fresh mass. Table continued on next page.

Species	Component	b	95% CL (±)	r <sup>2</sup>	t <sub>b=0</sub>	P <sub>b=0</sub>	F <sub>b=1</sub>	P <sub>b=1</sub>	t <sub>b Ross = b Snow</sub>	P <sub>b Ross = b Snow</sub>
Ross'	Body Mass	1.044	0.265	0.848	8.521	< 0.001	0.129	0.726	0.509	> 0.1
(n = 15)	Body Size	0.275	0.331	0.199	1.798	0.095	22.412	< 0.001	-0.172	> 0.1
	Gizzard	1.073	1.116	0.249	2.078	0.058	0.020	0.890	-0.457	> 0.1
	Leg Muscles	0.358	1.411	0.023	0.548	0.593	0.965	0.344	-0.308	> 0.1
	Pectoralis	-0.114	0.750	0.008	-0.328	0.748	10.301	0.007	-1.204	> 0.1
	Lipid	1.484	1.461	0.270	2.194	0.047	0.513	0.487	0.920	> 0.1
	Protein	0.967	0.676	0.424	3.092	0.009	0.011	0.918	-1.756	P < 0.1
	Ash	1.511	0.645	0.663	5.058	< 0.001	2.925	0.111	1.050	> 0.1
	Water	0.986	0.398	0.688	5.350	< 0.001	0.006	0.941	0.696	> 0.1

Table 2.9. Continued.

Species	Component	b	95% CL (±)	r <sup>2</sup>	t <sub>b=0</sub>	P <sub>b=0</sub>	F <sub>b=1</sub>	P <sub>b=1</sub>	t <sub>b Ross = b Snow</sub>	P <sub>b Ross = b Snow</sub>
Snow	Body Mass	0.946	0.267	0.780	7.523	< 0.001	0.182	0.624	-	-
(n = 18)	Body Size	0.313	0.293	0.242	2.263	0.038	24.648	< 0.001	-	-
	Gizzard	1.530	1.474	0.232	2.200	0.043	0.581	0.457	-	-
	Leg Muscles	0.567	0.685	0.161	1.753	0.099	1.797	0.199	-	-
	Pectoralis	0.326	0.378	0.173	1.826	0.087	14.288	0.002	-	-
	Lipid	0.821	0.760	0.247	2.291	0.036	0.249	0.624	-	-
	Protein	1.647	0.480	0.768	7.270	< 0.001	8.161	0.011	-	-
	Ash	1.171	0.350	0.759	7.099	< 0.001	1.072	0.316	-	-
	Water	0.826	0.284	0.704	6.166	< 0.001	1.685	0.213	-	-

less lipids and 7.8% less protein than did Snow Geese (Table 2.10). Water loss from eggs during incubation is in part replaced by metabolic water (Carey 1983) thus the concept of water consumption by the developing embryo does not easily apply. Still, Ross' goslings hatched with a water content more similar to the egg than did Snow Geese.

The ratio of adult size:gosling size can be considered the "growth increment needed to attain adult size" (Alisauskas 1986). When gosling morphometric measurements were compared to a sample of adults (Ross':  $n_{males} = 31$ ,  $n_{females} = 73$ ; Snow:  $n_{males} = 27$ ,  $n_{females} = 36$ ) used in Chapter 3, Ross' Geese needed about 12% less incremental growth to reach adult size than did Snow Geese (Table 2.11). Overall, goslings hatched with small midwings and large tarsi relative to other morphometric features.

## **2.5 DISCUSSION**

### **2.5.1 SEASONAL EFFECTS ON EGG AND GOSLING COMPOSITION**

In both Ross' and Snow Geese, clutch size declines seasonally (Ryder 1972, Finney and Cooke 1978, R.T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK, unpubl. data), presumably because birds nesting later have fewer nutrient reserves to allocate to egg production than do birds nesting earlier (see Alisauskas and Ankney 1992 for a review). Clutch size in Snow Geese shows no heritability (Findlay and Cooke 1983) and thus most variation is environmentally induced. Egg size in geese, however, is both highly heritable and repeatable, and thus is under greater genetic control (Newell 1988, Larsson and Forslund 1992) than clutch size. Ankney and Bissett (1976), Rohwer and Eisenhauer (1989) and Lessells et al. (1989) examined

Table 2.10. Percent change in nutrient composition during embryological development. Values represent the percentage of nutrients catabolized between egg and gosling stages.

Component	Ross'	Snow	Snow-Ross'
Lipid	34.7 <sup>1</sup>	40.9	-6.2
Protein	18.5	26.3	-7.8
Water	20.8	26.3	-5.5

<sup>1</sup> [(Mean egg content - Mean gosling content) / (mean egg content)] x 100%

Table 2.11. Growth increment of morphometric measurements in Ross' and Snow Goose goslings.

Species	Component	Mean Length (mm)		Growth Increment <sup>3</sup>	% Difference <sup>4</sup>
		Goslings <sup>1</sup>	Adults <sup>2</sup>		
Ross'	Midwing	17.4	133.4	7.6	9.5
	Tarsus	29.3	68.7	2.3	8.0
	Skull	38.5	84.9	2.2	15.4
	Culmen	14.6	40.2	2.8	15.2
	Body	149.2	473.6	3.2	11.1
Snow	Midwing	18.6	156.8	8.4	
	Tarsus	32.1	82.7	2.5	
	Skull	43.2	113.6	2.6	
	Culmen	17.1	55.8	3.3	
	Body	163.2	581.2	3.6	

<sup>1</sup> Sample Sizes:  $n_{Ross'}$  = 19,  $n_{Snow}$  = 20

<sup>2</sup> Sample Sizes:  $n_{Ross'}$  = 104,  $n_{Snow}$  = 63

<sup>3</sup> Adult length/Gosling length

<sup>4</sup>  $[(GI_{Snow} - GI_{Ross'}) / (GI_{Snow})] \times 100\%$

the relationship between egg size and clutch size in geese and found no evidence for facultative manipulation of egg size. In this study, about 95% of the population initiated clutches within an 10 day period and egg size did not decline seasonally (Table 2.3). Consequently, later laying geese appear to adjust initial reproductive effort by varying the number, but not size, of young. However, females could further adjust initial reproductive effort by varying egg quality (*sensu* Ricklefs 1984b). In my sample, females nesting later produced eggs with less yolk protein than those laying eggs earlier in the season (Table 2.3). This seasonal decline in yolk protein, however, was insufficient to cause a similar decline in total egg protein (Table 2.3) and, consequently, gosling nutrients did not vary seasonally. During the first week of embryonic development, yolk is the primary source of protein for structural development (Hazelwood 1972). Therefore, the seasonal decline in yolk protein may have influenced how nutrients were allocated to different protein depots within goslings. In Ross' Geese, dry mass of the pectoralis muscle declined seasonally (Table 2.4). Development of skeletal muscles is important for thermoregulation (Ricklefs 1983) and, as a result, survival of later hatched goslings may be compromised under poor environmental conditions.

### 2.5.2 EGG MASS AND OFFSPRING QUALITY

Egg size influenced apparent gosling quality. Goslings from heavier eggs had a relative lipid content similar to goslings from lighter eggs but were proportionately smaller in structural size (Table 2.7). Since egg nutrients varied isometrically with egg size (Table 2.6), goslings from larger eggs catabolized relatively fewer egg nutrients during embryological development and, consequently, hatched in better

condition, i.e. with relatively more nutrient reserves, than goslings from smaller eggs. The potential mechanism for "sparing" nutrients in goslings from larger eggs is unknown but may be related to constraints on embryologic growth and metabolism.

Although goslings from larger eggs appear to have an energetic advantage over goslings from smaller eggs, the relative quality, i.e. viability, of a gosling should be judged on the basis of the ecological constraints faced by offspring. At hatch, inclement weather or poor foraging conditions may preclude feeding by goslings. Those neonates with relatively more lipids may better survive and perhaps continue to grow during periods of thermal and/or nutritional stress. Unfortunately, the lower limit of thermal neutrality is unknown for goslings and specific conclusions about the effect of temperature on gosling growth and survival are difficult to make. In addition to thermal advantages, neonates with greater nutrient reserves could also have lower predation rates than goslings from smaller eggs if they were better able to keep up with dispersing parents (Chapter 3) and thus were less susceptible to avian predation (per. obs.). The hypothesized advantage of larger egg size has been supported by two studies which related egg size to gosling survival. In Snow Geese, Ankney (1980) found that captive goslings hatched from larger eggs had better fasting endurance than those hatched from smaller eggs. In the central Arctic, wild Ross' and Snow Goose goslings hatched from larger eggs had a higher probability of survival (Chapter 3). Thus it appears that under some environmental conditions, a higher lipid:body size ratio in goslings from larger eggs confers an advantage over goslings from smaller eggs. This effect of egg size on survival may be more important for Ross' Goose goslings that travel farther from

the nesting colony and thus may have even higher energetic demands than do Snow Goose goslings (Chapter 3). The potential deleterious effect of small egg size, however, may be diminished farther from the colony if energy/nutrients are more accessible.

Although goslings from larger eggs appear to survive better under some environmental conditions (Ankney 1980, Chapter 3), the evolutionary implication of hatching from a large egg is somewhat unclear. Traits associated with fitness theoretically should have low heritabilities since selection would rapidly lead to genetic fixation (Falconer 1981). However, egg size in geese is highly heritable (Newell 1988, Lessells et al. 1989, Larsson and Forslund 1992) and therefore could respond to selection as defined by Endler (1986). If egg size is positively correlated with gosling survival in the long term, then directional selection should reduce egg size variability and decrease heritability (Boag and Van Noordwijk 1987). Egg size, however, is highly variable in Snow Geese and selective pressures maintaining this variability are unknown (Ankney and Bissett 1976, Newell 1988, Lessells et al. 1989). Ankney and Bissett (1976) hypothesized that egg size was adapted to "average" environmental conditions and that genetic variability was maintained by opposing directional selection for either large or small eggs in some years. By definition, Ankney and Bissett's (1976) hypothesis implies weak stabilizing selection which could also reduce variability in egg size (Grant 1986, Newell 1988). Newell (1988) examined various proximate causes of egg size variation and disagreed with Ankney and Bissett (1976). Because egg size was correlated with female body size, she suggested that selection pressures maintaining variability in body size could also maintain variability in egg size. Evidence from La Perouse Bay supports Newell's

hypothesis. From 1969-1989, Snow Geese have experienced a long-term decline in egg size (Lessells et al. 1989). During the same period, body size also declined and this decline was attributed to environmental degradation (Cooch et al. 1991b and 1993). Thus environmental factors that caused a decline in body size could have indirectly reduced egg size.

Results of Newell (1988) and Lessells et al. (1989) may be important for understanding the evolution of egg size in Ross' and Snow Geese. Egg size is only one life history characteristic that contributes to inclusive fitness. Clutch size, age at first reproduction, survival, and mating success all have a significant influence on the number of offspring an individual contributes to future generations (Price and Boag 1987). Selection on phenotypic correlates of these parameters may occur at different periods of an individual's life and the net result of selection may not be additive (Lande 1982). Thus other factors affecting reproductive performance and, ultimately, survival outside the breeding season could provide antagonistic selection pressure opposing selection for larger egg size. For example, Owen (1976) and Johnson and Raveling (1988) suggested that the ability of geese to exploit habitats during the winter is related to body size and bill morphology. If egg size in Ross' and Snow Geese is correlated with body size (*sensu* Newell 1988), current variation in egg and body size could represent optimization of body size within the constraints of opposing selection pressures. Still, the Ankney and Bissett (1976) hypothesis cannot be readily rejected since opposing directional selection on egg size (Ankney and Bissett 1976) occurring in conjunction with selection on a correlated trait, e.g. body size (Newell 1988), could maintain a high degree of egg size variation (Endler 1986).

### 2.5.3 INTERSPECIFIC VARIATION IN EGG AND GOSLING QUALITY

If egg size influences gosling energetics and subsequent survival under some environmental conditions, then Ross' Geese appear to compensate for smaller egg size by producing goslings with larger protein reserves for their egg size (Table 2.7), heavier gizzards for their body size (Table 2.8) and tissue of greater functional maturity (Table 2.4) than do Snow Geese. In addition, Ross' Goose goslings hatch at a relatively larger size when compared to adult body size (Table 2.11) and thus require less time to reach asymptotic size (MacInnes et al. 1989). Although eggs of Ross' and Snow Geese are laid with the same relative nutrient composition (Table 2.3), during embryological development, Ross' Geese catabolize about 7.8% less egg protein (Table 2.10). Consequently, Ross' Goose neonates hatched with more protein reserves for their egg size than did Snow Goose neonates (Table 2.7). However, the value of protein as an energy source is somewhat limited since protein contains about half the energy of lipids and is not readily mobilized (Blem 1990). Since protein reserves appear to be more important for initial growth than for survival (Duncan 1988), the advantage of larger protein reserves in Ross' Goose goslings may be manifest as relatively faster early growth than Snow Goose goslings.

Interspecific variation in body size may have important implications for neonate energetics and, hence, interpretations of relative offspring quality. Snow Goose goslings are structurally larger and also heavier than Ross' Goose goslings (Table 2.4). Therefore, Ross' Goose neonates should have a higher mass-specific metabolic rate, larger surface:volume ratio, and, consequently, greater mass-specific energy requirements and higher rates of heat loss than do Snow Goose neonates

(Ricklefs 1974 and 1983). Indeed, Balmer and Strobusch (1977) have hypothesized that surface:volume ratios and subsequent heat loss limit minimum body size of precocial neonates and this limit could be higher in Arctic environments (Koskimies and Lahti 1964). Thus under nutritional or thermal stress, smaller Ross' Goose goslings could be energetically disadvantaged compared to larger Snow Goose goslings unless they have adaptations which offset size-related energetic costs. Such adaptations apparently exist. Although I did not examine plumage differences (Ricklefs 1983), Ross' Goose neonates appear to be better adapted for nutrient assimilation and thermogenesis since they have relatively larger gizzards and more functionally mature tissue. Relatively bigger gizzards could be indicative of a more developed digestive system that allows Ross' Goose goslings to process food quicker and thus assimilate nutrients relatively faster than Snow Geese (*sensu* Sibley 1981, Sedinger and Raveling 1984, Manseau and Gauthier 1993). In European Starlings, Ricklefs and Webb (1985) demonstrated that the ability to produce heat was inversely related to the fraction of water in muscle tissue, i.e. the functional maturity of muscles (Ricklefs 1983). If true in precocial species, then Ross' Geese should be able to thermoregulate sooner and produce more heat for their body size than Snow Goose goslings.

These characteristics which could offset size-related energetic costs do not suggest that Ross' Goose goslings can thermoregulate and/or assimilate nutrients more efficiently than Snow Goose goslings. When examining interspecific variation in offspring quality, we must remember that different metabolic constraints likely face each species. Thus when exposed to similar energetically stressful conditions, Ross' Goose neonates may be absolutely disadvantaged compared to Snow Goose

neonates, yet Ross' Goose goslings still may have better physiological abilities to produce heat and acquire nutrients than predicted for their body size. I predict that similar adaptations in digestive efficiency and tissue maturity exist in other Arctic nesting waterfowl, particularly in ducks whose young should be as small as or smaller than Ross' Goose goslings (Koskimies and Lahti 1964, Robertson and Cooke 1993). These adaptations, however, are likely modified by the type of food consumed (animal vs. plant material), brood movement patterns, parental behavior and other energetic considerations.

Relatively greater thermogenic capacity may be one of several advantages associated with more functionally mature tissue in Ross' Goose neonates. Another potential advantage relates to initial brood movements since greater functional maturity of tissues is associated with higher activity levels (King and Farner 1961). Therefore, Ross' Goose goslings should be more active at hatch than are Snow Goose goslings and thus physiologically adapted for travel. Broods disperse rapidly from the colony soon after hatch and within 17 days, some Ross' broods are nearly 60 km away (Chapter 3). Ross' broods, on average, travel about 2.5 times farther from the colony than do Snow Goose broods and these dispersal patterns may be related to different habitat requirements (Chapter 3).

In summary, examination of egg and gosling composition has provided valuable insight into the role of season, egg and body size, and taxonomy on neonate energetics. Composition of eggs and goslings is similar for Ross' and Snow Geese. Although I detected seasonal variation in yolk protein, I found no seasonal variation in overall egg or gosling constituents for either species. Egg size is an important determinant of intraspecific neonate reserves since larger eggs produce goslings with

more lipids for their body size than do smaller eggs. This relationship may explain the higher survival rates observed for goslings from larger eggs (Ankney 1980, Chapter 3). This relationship does not occur at the interspecific level of egg size variation. Although interspecific differences in composition of neonates was minimal, Ross' Geese appear to offset energetic costs associated with smaller body size by producing neonates with relatively larger gizzards and more functionally mature tissue than Snow Geese. The influence of these apparent adaptations for better nutrient assimilation and thermoregulation on survival of hatchling Ross' Geese is unknown.

## **CHAPTER 3: BROOD MOVEMENTS, GROWTH AND SURVIVAL OF ROSS' AND LESSER SNOW GOOSE GOSLINGS**

### **3.1 INTRODUCTION**

Colonial nesting is a dynamic reproductive strategy where costs and benefits accrued by breeding individuals may vary with species, locality, colony size/density, season and year (reviewed by Wittenberger and Hunt 1985). Concentration of birds with similar food requirements increases foraging competition around the colony site (Wittenberger and Hunt 1985) and in many species of birds, especially seabirds, chick growth rates and fledging size/mass are inversely correlated with colony size (Nettleship 1972, Hoogland and Sherman 1976, Hunt et al. 1981, Coulson et al. 1982, Gaston et al. 1983). As colony size increases, per capita forage availability should decline locally (Hamilton and Watt 1970) and, as a result, birds must expend more energy to meet nutrient demands of growing young. In nidicolous species, this expenditure translates into longer range foraging flights (Fry 1972, Diamond 1978, Gaston and Nettleship 1981). In nidifugous species, however, foraging movements are restricted by the ability of young to walk or swim. Therefore, if broods begin foraging soon after hatch, a gradient from low to high resource availability should be expected around the colony since all broods radiate from a central site and little food may be present within the colony (Ryder 1967). The influence of this gradient in nutrient availability on growth and survival of young should depend on how far from the colony a brood settles. Since growth rates can influence first year survival

and subsequent recruitment into breeding populations (Cooke et al. 1984, Owen and Black 1989, Cooch et al. 1991b, Schmutz 1993), brood dispersal decisions could influence parental fitness.

Ross' and Lesser Snow Geese are colonial, nidifugous herbivores whose gosling growth and survival may be influenced by brood dispersal patterns. These species nest in the arctic where breeding seasons are short and, consequently, young must grow rapidly (*sensu* Barry 1962). Nest densities are often high and young hatch synchronously throughout the colony with about 95% of the broods hatching over a 5-10 day period (Ryder 1972, Slattery and Alisauskas 1993, see section 2.4.1 for mean hatch dates in 1991-92). Within about 24 hr. of hatch, broods disperse to foraging areas outside the colony (Ryder 1967, Cooke and Abraham 1980, Slattery unpubl. data). Since growth in geese can be influenced by variation in hatch date, social status or habitat quality (Cooch et al. 1991a, 1991b, Sedinger and Flint 1991, Larsson and Forslund 1991, Cooch et al. 1993), these species are ideal for testing hypotheses about dispersal-dependent growth and survival. I predicted that goslings reared farther from the natal colony would be larger and (or) in better condition than those reared close by. Therefore, the objectives of this paper are to 1) examine brood dispersal patterns in Ross' and Snow Geese, 2) determine if a functional relationship exists between brood dispersal distance and gosling size (condition) and 3) describe factors influencing gosling survival.

## **3.2 STUDY AREA**

Research was conducted in and around the largest known colony of nesting geese in the Queen Maud Gulf Bird Sanctuary (QMGBS) located at Karrak Lake, NWT (66° 15' N, 100° 15' W). During the past five years, the colony population has increased by 71% to about 364,000 Ross' and Snow Geese which nest on over 67 km<sup>2</sup> of land (R. T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK unpubl. data). Data for this paper were collected as part of a long-term monitoring program examining nesting and brood-rearing activities of geese breeding at Karrak Lake. Geese rear goslings in a heterogenous environment composed of rock outcrops, wet sedge meadows, and tundra ponds along 4 river systems and the coast. The Karrak Lake region is described extensively in Ryder (1972). Note, however, that since Ryder's (1972) work in 1966-68, the Karrak Lake colony grew by about 1654% and local habitat degradation may be present (Alisauskas, Canadian Wildlife Service, Saskatoon, SK unpubl. data).

## **3.3 METHODS**

### **3.3.1 RADIO TRACKING AND RECAPTURE OF MARKED BROODS**

I used radio telemetry to follow and recapture marked broods. Because brood size and hatch date influence gosling growth and survival (Cooch et al. 1991, Sedinger and Flint 1991), females selected for radio marking were standardized to control for potential effects of brood size, hatch date and nest site. I chose marked females whose nests 1) had the modal clutch size of four eggs, 2) had eggs which would hatch within one day of predicted peak hatch and 3) were located near the center of the colony. Modal clutch size and peak hatch dates were determined from ongoing

research activities that involved checking nests every third day during the egg laying period (Slattery and Alisauskas 1993). In 1991-1992, 33 Ross' and 22 Snow Goose females were trapped on nests using bow nets (*sensu* Salyer 1962) or snares modified from Cooch (1958), and were fitted with back pack radio transmitters. I assumed that these attachments had no effect on subsequent behavior of females and survival of young. Length and breadth of all four eggs were measured. At hatch, goslings of radio marked females were web-tagged with uniquely coded markers for future identification. Broods were followed intermittently during the brood-rearing period and recaptured after 20-34 days. Initial brood movements (< 5 days after hatch) were monitored daily from radio towers until geese travelled beyond reception range. Subsequent relocations were obtained from a helicopter flying at about 300 m altitude. In 1991, aerial tracking sessions occurred about 17 days and 30 days post-hatch when I searched about 2070 km<sup>2</sup> and 5180 km<sup>2</sup>, respectively (Figure 3.1). Effort was concentrated during the latter period to conserve helicopter time for brood capture. Due to a later breeding season and logistical constraints, the 1992 aerial tracking/banding occurred about 21 days after hatch while searching a 7650 km<sup>2</sup> area surrounding Karrak Lake (Figure 3.1). Marked broods were recaptured during the later tracking periods using the helicopter to corral flightless molting flocks into banding nets. Web-tagged goslings were then sexed, weighed and measured for midwing, tarsus, skull, culmen, and body lengths (see Dzubin and Cooch (1992) for a description of these measurements). All measurements except body length were recorded to the nearest 0.1 mm using dial calipers. Body length was recorded to the nearest 1 mm using a 1 m ruler mounted on a plywood strip for

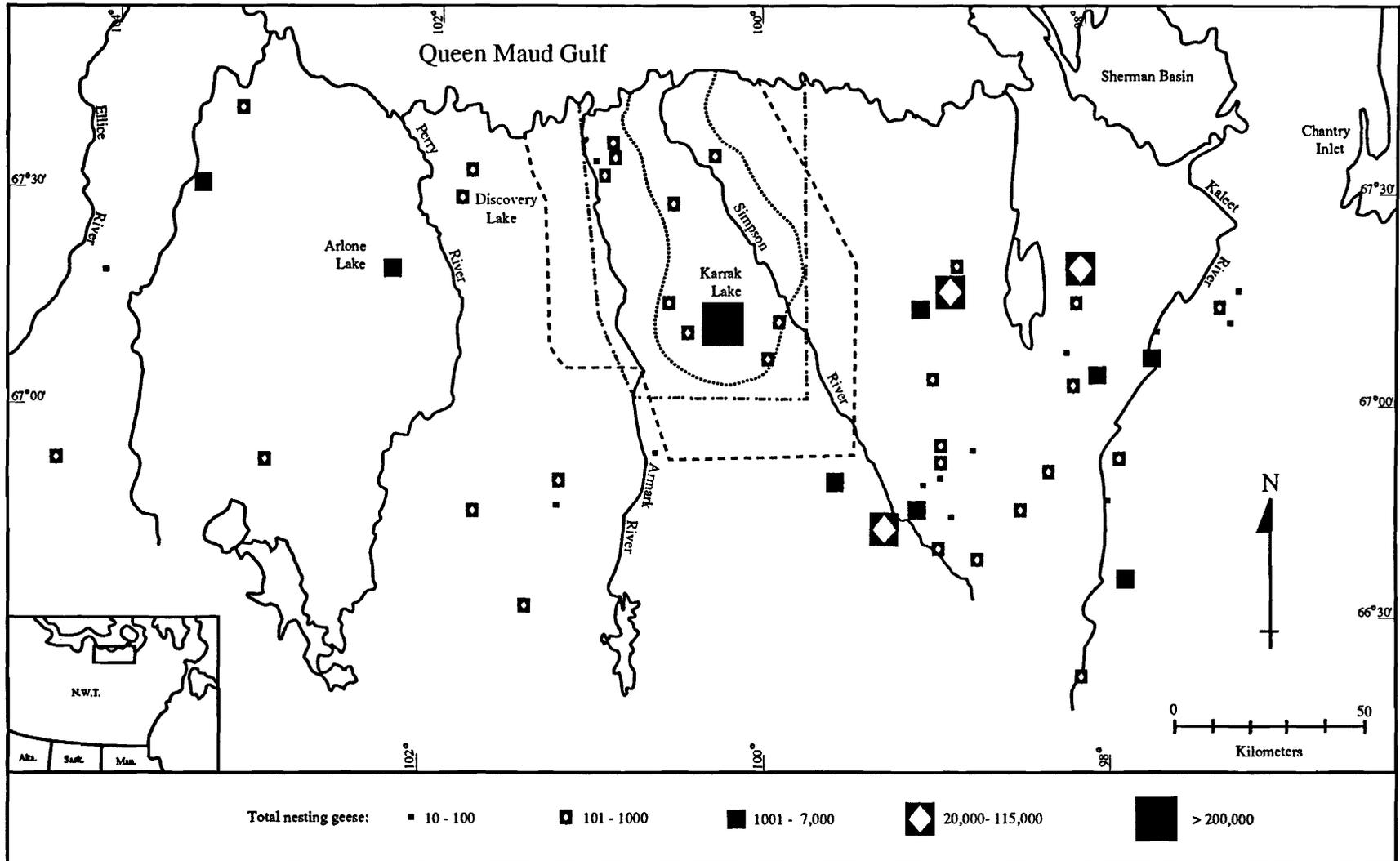


Figure 3.1. Area covered by telemetry flights in 1991 and 1992. Map adapted from Kerbes (in press) and shows colony size and locations in 1988. Legend: 1991  $\cdots$  - 17 days post-hatch,  $\cdots$  - 28-33 days; 1992  $---$  - 22 days.

rigidity. Parent females and a sample of unmarked adults and goslings of each species were also weighed and measured at this time. Unmarked birds were mixed in the banding nets then measured as encountered. In 1991, one adult male, one adult female, and 5 goslings from each species were measured when available at each banding site. In 1992, I measured 5 males, 5 females and 5 goslings of each species when present at each site.

### 3.3.2 STATISTICAL ANALYSES

3.3.2.1 *BROOD DISPERSAL*. In the following analyses of marked brood dispersal, I used only data from females with recaptured goslings since females without goslings could have flown to their retrapping location if brood loss occurred before the onset of wing molt. Annual and interspecific variation in marked brood recapture distances from Karrak Lake were compared using a Wilcoxon Rank-Sum Test. Species composition data from banding drives were used to confirm species distribution patterns observed in marked broods. The percentage of Ross' Goose adults in the total adult sample was determined for each banding site, then results were arcsine transformed to normalize the data (Sokal and Rolf 1981). I then used linear regression to examine the relationship between % Ross' adults and distance from Karrak Lake. I also examined the effect of hatch date, brood age, and egg size on recapture distance of marked broods using linear regression. Species were analyzed separately. Year effects were not significant and were dropped in subsequent analyses. I define egg size as shell-free fresh egg mass (SHFRMASS). SHFRMASS was estimated from length and breadth measurements of eggs laid by marked female using regression equations calculated for each species in Chapter 2.

Brood means of egg size were then used as the data in regression analyses for egg size effects on brood-rearing distance.

### 3.3.2.2 GOSLING RECOVERY.

Effects of egg size, brood age, and recapture distance on probability of gosling recovery were examined using logistic regression (Proc Probit, SAS 1985). Data were pooled across broods and within species for these analyses. The effect of egg size on gosling recovery within broods was determined for each species using a one-tailed Wilcoxon Signed-Ranks Test (Seigel and Castellan 1988). This test is a matched sample analysis and paired samples were the mean egg size of goslings present in or absent from each brood. Data from females with complete brood loss ( $n_{Ross'} = 6$ ;  $n_{Snow} = 2$ ) or complete recovery ( $n_{Ross'} = 1$ ) could not be used for this analysis. Annual and interspecific variation in pooled gosling recovery rates (pooled across broods) were compared using  $\chi^2$  tests. Sample sizes of Snow Geese were small, so a Fisher's Exact Test was used to compare annual variation.

I used the ratio of goslings:adults within each banding drive as an independent assessment of distance-related effects on gosling survival. This age ratio can be considered an index of gosling survival provided several assumptions are met. First, *non-breeders and failed nesters segregate from brood rearing flocks on the foraging areas*. This assumption is likely valid for non-breeders because these geese molt before breeders, regain flight before the banding period, and, therefore, are not caught in brood drives (pers. obs.). The validity of this assumption for failed nesters is unknown but it is probably at least true for pairs failing during clutch initiation and early incubation. These geese probably begin

molting earlier than successful breeders and thus could be flying during the banding period. As further evidence, I relocated two of three marked females in 1992 that had abandoned nests in the last third of incubation, and only one was located in a flock with goslings. Second, *geese with complete brood failure remain in brood-rearing flocks*. My data suggest that this assumption is also valid. I recaptured 6 Ross' and 2 Snow Geese with complete brood loss. All of these geese were caught in flocks containing goslings. Third, *adult mortality from hatch to banding is negligible*. I evaluated gosling survival using this data by analyzing the residuals from a regression using the number of goslings at each site as the dependent variable and the number of adults as the independent variable. Residuals were then used in a linear regression with distance as the explanatory variable. Species were analyzed separately.

3.3.2.3 *BODY SIZE AND BODY CONDITION*. In the following analyses, I examined factors that may affect size and condition of goslings and adults. I define body size as the first principal component (PC1) derived from a Principal Component Analysis (PCA) computed from the correlation matrix of midwing, tarsus, skull, culmen, and body lengths. PC1 is a unitless and dimensionless measure which can be interpreted as an index of structural size (Reyment et al. 1984). Body condition is defined as body mass corrected for PC1 score (body size). Residuals from linear models which included PC1 as a covariate were used in analyses of condition (Proc GLM, SAS 1985). Other variables used to produce residuals are noted where appropriate. In these analyses, negative residual values

indicate lighter body mass for body size and thus poorer body condition than expected from the linear model. Interaction effects were initially considered in all analyses but were dropped from the models during reanalysis when not significant. Type III sums of squares were used for all linear models.

*Marked birds.* I used ANCOVA with sex and age as covariates to compare interspecific variation in body condition of marked goslings. Males and females were not significantly different in condition, so sexes were subsequently pooled before reanalysis. Data were pooled between species and among broods for the PCA and analyses of residuals. ANCOVA were used to analyze residuals of individual goslings while ANOVA were used to analyze brood means. With Snow Geese, interspecific comparisons were not made for body condition of parent females because of small sample size.

Brood dispersal distances were non-overlapping, so species were analyzed separately to calculate size indices (PC1) and to examine effects of egg size and distance moved on gosling growth and condition. Residuals were calculated for size and condition using multiple regression with year and age as explanatory variables. I then used residuals for each gosling in ANCOVA with sex, egg size and distance as main effects. In addition, I analyzed brood means of residuals in multiple regressions with egg size and distance as main effects. Distance effects on condition and size-dependent dispersal of adult females were examined using linear regression. The PCA was calculated using only successful females, i.e. those with at least one recovered gosling. Locations of unsuccessful females may not represent results of brood movements since mortality could have occurred before wing molt. Brood age

(time since hatch) and year did not have significant effects on body condition of adult females and therefore were excluded from analysis. Body size did not vary annually, so data were pooled across years.

*All birds.* The sample of geese considered in the following analyses include both marked and unmarked birds. Separate ANCOVA were used to examine effects of dispersal distance on both goslings and adults. Species were pooled, whereas ages (adults/juveniles) were kept separate, for PCA. Since goslings measured at the beginning of the banding period are not expected to be the same size as those measured at the end, I calculated an index of relative flock age by subtracting the mean hatch date for each year and species from the date of recapture. Number of days since peak hatch, species and sex were then used as covariates with distance as the main effect in the analyses of gosling size and gosling and adult condition. Year and relative flock age were omitted from the model when not significant and the analyses redone.

3.3.2.4 *FEMALE BODY SIZE VS. EGG SIZE.* The relationship between female body size and egg size was examined to better understand maternal influence on gosling growth and survival. PC1 was derived for all recaptured females from the correlation matrix of tarsus, skull, culmen, and body lengths. Midwing was omitted from the PCA since data were missing for one Snow Goose. Clutch means were then calculated for egg size and regressed against PC1 using Proc GLM (SAS 1985). In addition, I used ANOVA to determine the female effect on variation in egg size (*sensu* Ankney and Bissett 1976).

### 3.4 RESULTS

Eggs of radio-marked females hatched at dates similar to the population mean (Table 3.1). Ross' ( $n = 23$ ) and Snow Goose broods ( $n = 10$ ) dispersed rapidly from the colony, and, during the first four days, travelled at a mean ( $\pm 1$  sd) initial rate of  $4.1 \pm 2.1$  and  $4.4 \pm 2.7$  km/ day, respectively. By about 17 days after hatch, I relocated 2 Snow Goose females 8-21 km away from Karrak Lake and 5 Ross' Goose females 19-59 km away. Four of the five Ross' females were found between 55-59 km. Assuming that these broods travelled at a constant rate before relocation, their average dispersal speed was at least 3.4 km per day. These same females appeared to move little during the next 13 days and all were relocated within 3 km of their initial locations (mean  $\pm 1$  sd, Ross:  $2.9 \pm 1.9$  km; Snow:  $2.3 \pm 0.5$  km). Both Snow Geese and four Ross' Geese were subsequently recaptured and only one Snow Goose had complete brood failure. Consequently, in the following analyses, I assume that goslings were reared within 3 km of their banding site.

#### 3.4.1 BROOD DISPERSAL

No annual variation was observed in brood dispersal distances of either species and, consequently, years were pooled for subsequent analyses. Ross' Goose broods dispersed farther from Karrak Lake than did Snow Goose broods (Figure 3.2, Table 3.2,  $Z = -2.832$ ,  $P = 0.005$ ). Although the data were variable, a similar

Table 3.1. Mean July hatch dates (SD in days) for the Karrak Lake colony and for marked broods in 1991 and 1992. Also shown are mean brood ages (in days) at recapture.

Variable	1991				1992			
	Ross'	<i>n</i>	Snow	<i>n</i>	Ross'	<i>n</i>	Snow	<i>n</i>
Colony Hatch	6 (3.1)	89	5 (5.8)	22	12 (1.9)	140	9 (2.5)	112
All Radio Broods	7 (1.4)	7	7 (1.0)	4	12 (1.8)	9	12 (1.0)	3
Successful Radio Broods	7 (1.3)	6	6 (1.2)	3	12 (1.5)	4	12 (0.7)	2
Unsuccessful Radio Broods	9	1	7	1	13 (2.2)	5	13	1
Brood Age at Recapture	30 (2.7)	6	31 (3.5)	3	22 (3.4)	4	21 (0.7)	2

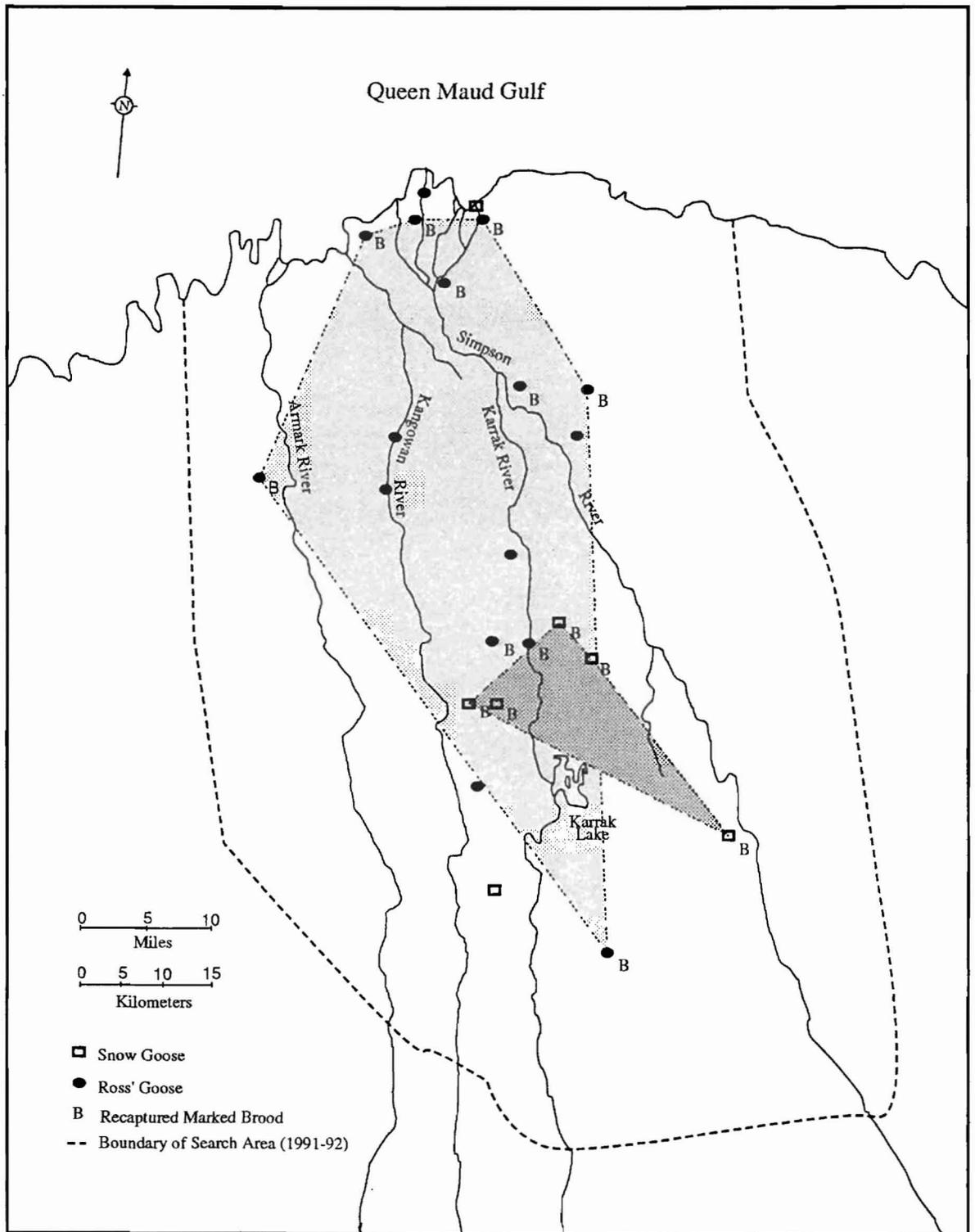


Figure 3.2. Recapture sites of marked female Ross' and Snow Geese. Shaded areas contain the recaptured broods for each species. Note the coastward movement for Ross' broods.

Table 3.2. Brood dispersal distances of Ross' and Snow Geese. Data are pooled across years.

Species	Distance from Karrak Lake (km)				Total	Mean	S.D.
	0-15	16-30	31-45	46-60			
Ross'	0	3	3	5	11	42.1 <sup>a</sup>	15.4
Snow	2	3	0	0	5	16.1 <sup>a</sup>	4.2

<sup>a</sup> Significantly different ( $Z = -2.832$ ,  $P = 0.005$ )

distribution of species was observed in the sample of unmarked adults, with relatively more Ross' Geese captured farther from the colony (Figure 3.3). I could not reject the null hypotheses that dispersal distance was independent of hatch date, egg size, or brood age (Table 3.3). These results suggest that hatch date, brood age and dispersal distance were not correlated and that recaptured goslings hatching from heavier eggs did not travel farther than those hatching from lighter eggs (Table 3.3).

### 3.4.2 GOSLING RECOVERY RATES

Annual variation in gosling recovery rate was not significant and thus years were pooled for subsequent analyses. No interspecific variation was detected for gosling recovery (Table 3.4,  $\chi^2 = 0.200$ ,  $df = 1$ ,  $P = 0.655$ ). Probability of recapture was not related to brood age or dispersal distance so these terms were dropped from the logistic regression model. The independence of recovery rate on distance was supported by age ratio data (residuals) from the sample of geese in banding drives (Figure 3.4). Regressions used to calculate these residuals were significant (Ross:  $n = 16$ ,  $r^2 = 0.847$ ,  $F = 77.65$ ,  $df = 1$ ,  $P < 0.001$ ; Snow:  $n = 16$ ,  $r^2 = 0.845$ ,  $F = 76.23$ ,  $df = 1$ ,  $P < 0.001$ ). Among Ross Goose broods, goslings from heavier eggs were more likely to be recaptured than those from lighter eggs (Figure 3.5). A similar relationship was not observed among Snow Goose broods. Note, however, that the egg size effect on gosling recovery may be less for Snow Geese due to the small variance in egg mass. Snow Goose goslings present in recaptured broods hatched from larger eggs than did siblings that were absent ( $n = 5$ ,  $T^+ = 15$ ,  $P = 0.031$ ).

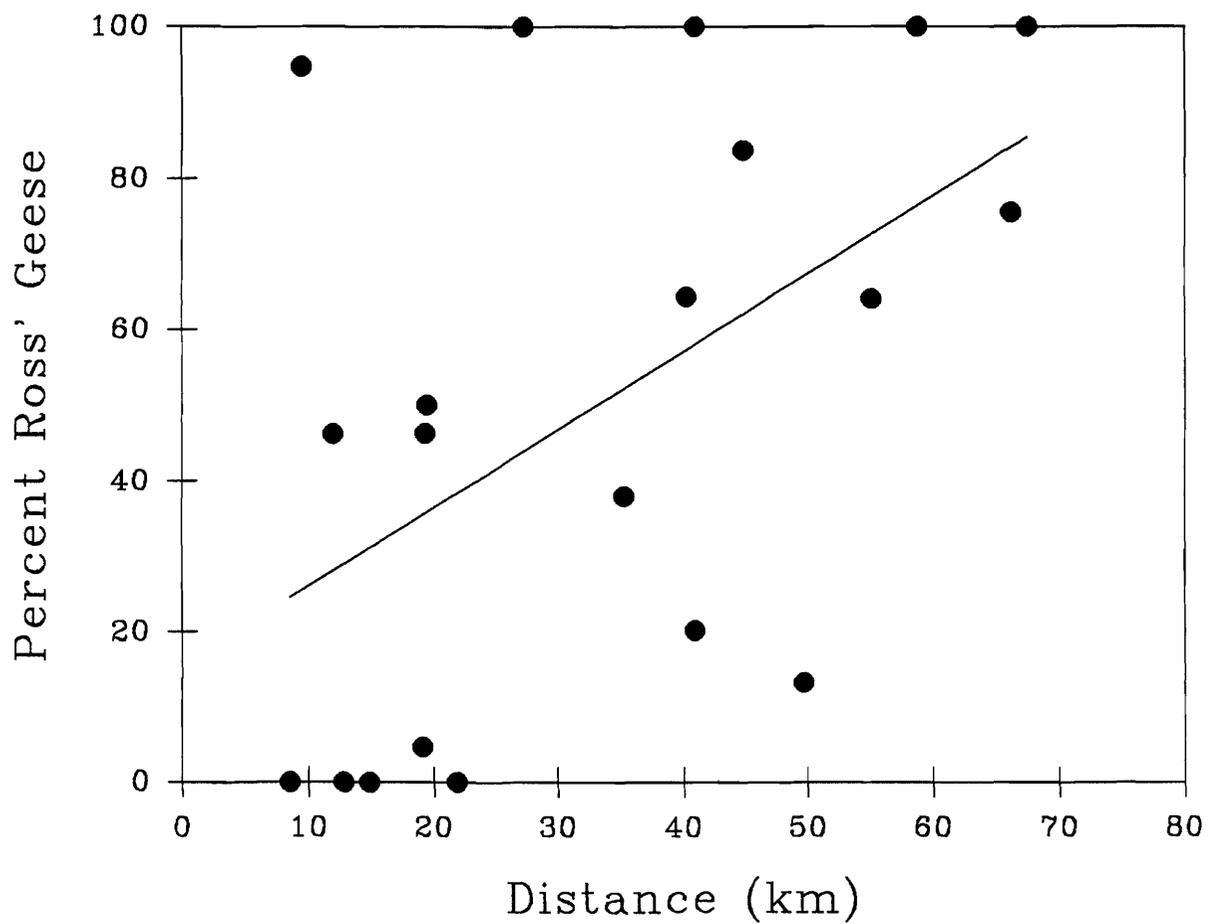


Figure 3.3. Species composition of goose flocks as a function of distance from Karrak Lake. The line is a regression line through percent data to show the trend only. Statistics for the arcsine transformed data:  $n = 20$ ,  $r^2 = 0.285$ ,  $F = 7.18$ ,  $P = 0.015$ .

Table 3.3. Effects of hatch date, mean egg size of recaptured goslings within broods and brood age on dispersal distance of successful females from Karrak Lake. Year effects on dispersal distance were not significant. See Table 3.2 for dispersal distances.

Variable	Ross' ( $n = 10$ )			Snow ( $n = 5$ )		
	$r^2$	$F_{1,9}$	$P$	$r^2$	$F_{1,4}$	$P$
Hatch Date	0.057	0.48	0.506	0.002	0.01	0.939
Egg Size	0.237	2.49	0.153	0.001	0.00	0.958
Brood Age	0.009	0.27	0.794	0.002	0.08	0.943

Table 3.4. Among brood recovery of marked goslings. Variation not significant within or between species.

Year	Ross'	<u>n</u>	Snow	<u>n</u>
1991	44.4 <sup>1</sup>	27	33.3	15
1992	27.8	36	50.0	10
Pooled	34.9	63	40.0	25

<sup>1</sup>Percent of marked goslings recaptured

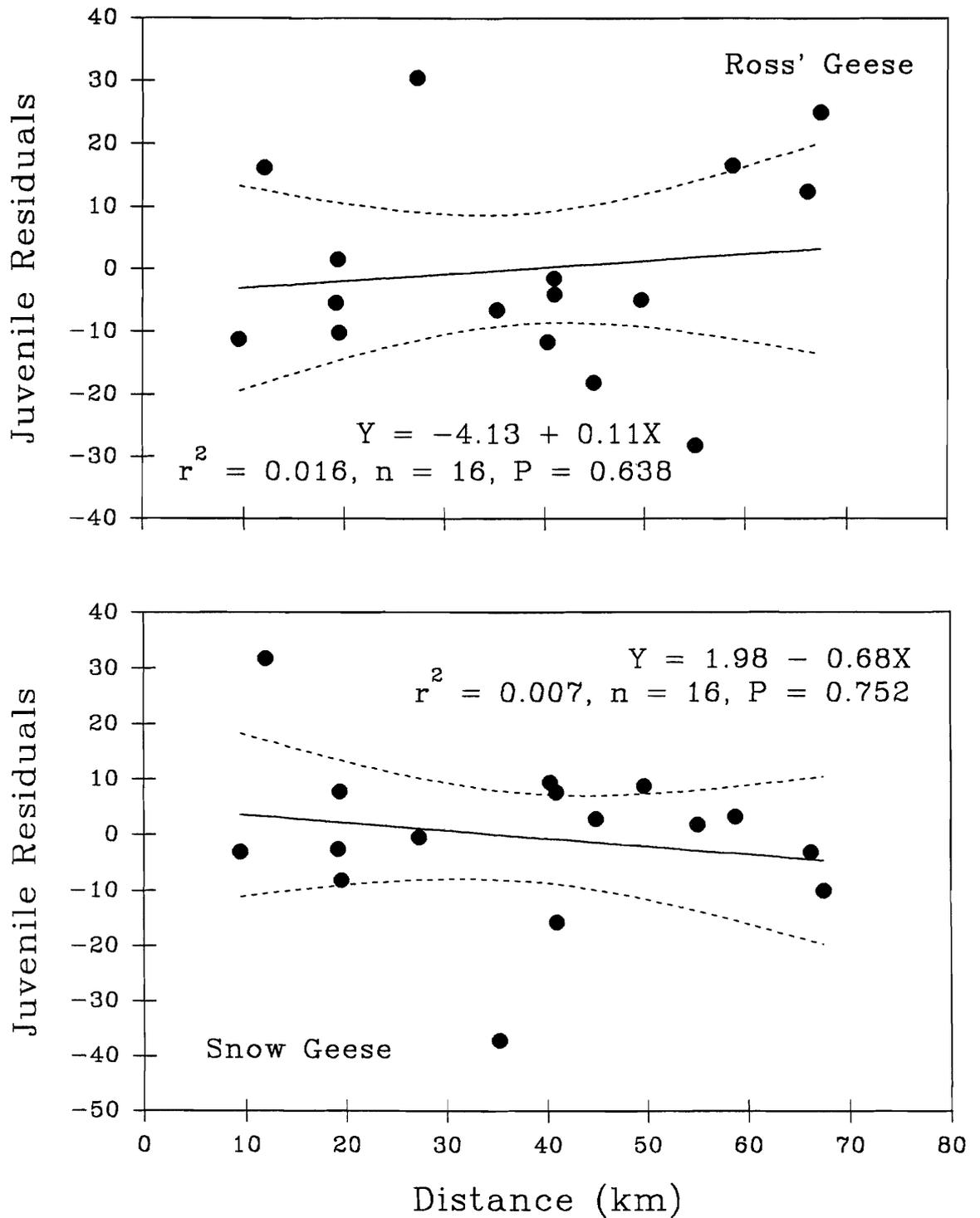


Figure 3.4. Gosling survival in unmarked geese with distance from Karrak Lake. Juvenile residuals were calculated by regressing the number of goslings in each banding drive against the number of adults. See text for assumptions of this analysis. Dotted lines represent 95% confidence intervals.

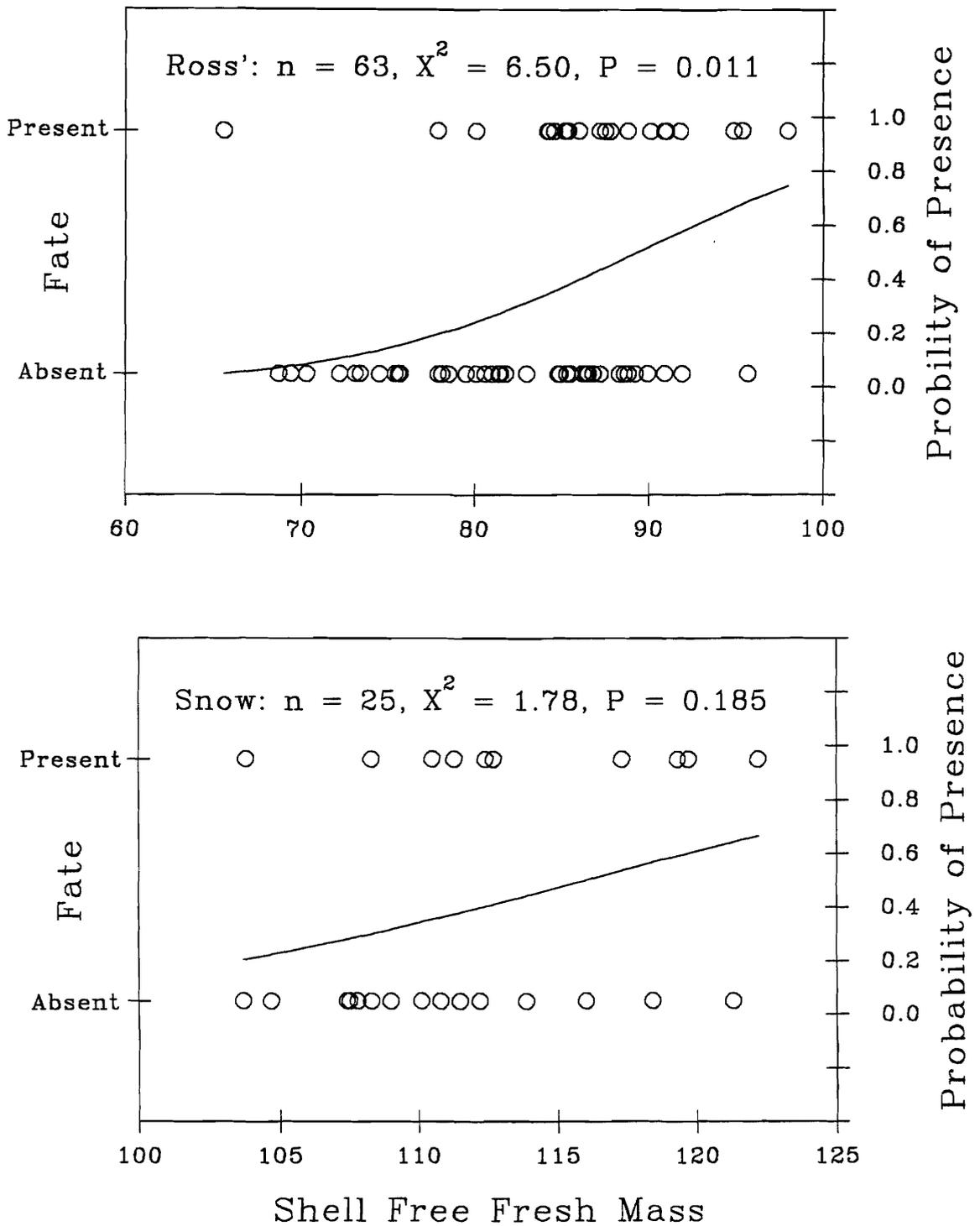


Figure 3.5. Influence of egg size on probability of gosling recovery. Lines represent solutions from logistic regressions.

There was a trend for gosling recovery to be positively related to egg size within Ross' Goose broods (6 of 9 comparisons were in the predicted direction) but this pattern was not significant at the 0.05 level ( $n = 9$ ,  $T^+ = 35$ ,  $P = 0.082$ ). Intra-brood recovery was not related to position in the laying sequence (Logistic regression,  $P > 0.05$  for both species).

### 3.4.3 GOSLING BODY CONDITION AND GROWTH

3.4.3.1 *KNOWN-AGE GOSLINGS*. Residuals used to examine interspecific variation in body condition were derived from a significant interspecific regression ( $n = 32$ ,  $r^2 = 0.762$ ,  $F = 96.13$ ,  $df = 1$ ,  $P < 0.001$ ). Pooled across broods, Ross' Goose goslings were heavier relative to body size than were Snow Goose goslings (Table 3.5).

However, when condition was analyzed using brood means of residuals, no interspecific variation in body condition was detected, possibly due to smaller sample sizes or variable maternal effects within species. Residuals for analyses of distance effects on intraspecific variation in gosling size and condition were derived from significant linear models (size: Ross',  $n = 22$ ,  $r^2 = 0.719$ , model  $F = 24.01$ ,  $df = 2$ ,  $P < 0.001$ , Snow,  $n = 10$ ,  $r^2 = 0.929$ ,  $F = 45.76$ ,  $df = 2$ ,  $P < 0.001$ ; condition: Ross',  $r^2 = 0.904$ , model  $F = 56.76$ ,  $df = 3$ ,  $P < 0.001$ , Snow,  $r^2 = 0.874$ ,  $F = 13.86$ ,  $df = 3$ ,  $P = 0.004$ , same sample sizes). Gosling body condition of Ross' Geese increased with distance from Karrak Lake while body size varied randomly (Table 3.6). In addition, goslings from heavier eggs were structurally larger but in similar condition to goslings from lighter eggs (Table 3.6). No significant relationships of

Table 3.5. Species effect on body condition in marked goslings. A negative residual value indicates that goslings have less mass for their body size. Values listed under  $F$  column are partial  $F$  values for goslings and  $F$  values for brood means.

Category	Effect	Ross'		Snow		$r^2$	$F$	df	$P$
		Residual	$n$	Residual	$n$				
Goslings	Species	17.81 (13.03) <sup>1</sup>	22	-54.18 (19.58) <sup>1</sup>	10	0.401	7.37	1	0.011
	Species* Age	-	-	-	-	-	5.62	2	0.009
Brood Means	Species	13.37 (23.35) <sup>2</sup>	10	-43.32 (33.02) <sup>2</sup>	5	0.131	1.96	1	0.185

<sup>1</sup> Least squares mean (SE)

<sup>2</sup> Mean (SD)

Table 3.6. Effects of egg size, sex and brood dispersal distance on body size and condition of known age Ross' Goose goslings. Residuals controlled for year, age and, for condition, body size effects were used for these analyses. Sample sizes:  $n_{\text{goslings}} = 22$ ,  $n_{\text{brood means}} = 10$ . Values listed under  $F$  are partial  $F$  values.

Category	Effect	Body Size				Body Condition			
		$r^2$	$F$	df	$P$	$r^2$	$F$	df	$P$
Goslings	Egg Mass	0.787	33.66	1	<0.001 <sup>1</sup>	0.475	2.71	1	0.117
	Sex	-	23.85	1	<0.001 <sup>2</sup>	-	0.02	1	0.898
	Distance	-	0.82	1	0.372	-	16.01	1	<0.001 <sup>4</sup>
Brood Means	Egg Mass	0.884	45.27	1	<0.001 <sup>3</sup>	0.734	1.34	1	0.285
	Distance	-	0.65	1	0.447	-	18.23	1	0.004 <sup>5</sup>

<sup>1</sup>  $b_1 = 0.051$

<sup>2</sup> Least squares means (SE): Females = -0.232 (0.070); Males = 0.278 (0.077)

<sup>3</sup>  $b_1 = 0.049$

<sup>4</sup>  $b_1 = 2.570$

<sup>5</sup>  $b_1 = 2.764$

body size or body condition with egg size and distance were detected in Snow Goose goslings (Table 3.7).

3.4.3.2 *ALL GOSLINGS*. Goslings of both species were not only larger farther from Karrak Lake, but also in better condition than goslings measured near the colony (Table 3.8). In addition, females of both species were relatively heavier than males.

#### 3.4.4 ADULT BODY CONDITION AND SIZE DEPENDENT DISPERSAL

Body mass was significantly related to body size in marked females ( $n = 10$ ,  $r^2 = 0.548$ ,  $F = 9.70$ ,  $df = 1$ ,  $P = 0.014$ ). Larger marked Ross' Goose females appeared to travel farther from Karrak Lake and to be in better condition than smaller birds (Figure 3.6). However, these relationships were marginally significant. The small sample size of adult Ross' females may have reduced my ability to detect the positive variation of body size with capture distance observed in my sample of unmarked adults (Table 3.9). Similar trends for larger body size at more distant sites in both the marked (Figure 3.6) and unmarked (Table 3.9) adult samples suggests that the pattern observed for marked adult Ross' Geese was not due to a radio package effect, i.e. radio transmitters probably did not prevent smaller females from dispersing long distances. Body condition varied randomly with distance in the latter sample. In addition, unmarked females of both species were relatively lighter than unmarked males.

Table 3.7. Effects of egg size, sex and brood dispersal distance on body size and condition of known age Snow Goose goslings. Residuals controlled for year, age and, for condition, body size effects were used for these analyses. Sample sizes:  $n_{\text{goslings}} = 10$ ,  $n_{\text{brood means}} = 5$ .

Values listed under  $F$  are partial  $F$  values.

Category	Effect	Body Size				Body Condition			
		$r^2$	$F$	df	$P$	$r^2$	$F$	df	$P$
Goslings	Egg Mass	0.010	0.05	1	0.839	0.716	0.17	1	0.691
	Sex	-	0.00	1	0.978	-	4.97	1	0.067 <sup>1</sup>
	Distance	-	0.03	1	0.872	-	3.56	1	0.108 <sup>2</sup>
Brood Means	Egg Mass	0.022	0.00	1	0.968	0.476	1.03	1	0.417
	Distance	-	0.04	1	0.856	-	0.73	1	0.483

<sup>1</sup> Least squares means (SE): females = 0.004 (0.174); males = -0.003 (0.139)

<sup>2</sup>  $b_1 = 4.59$

Table 3.8. The relationship between body size and condition of all goslings (marked and unmarked) with the distance they were captured from Karrak Lake. Residuals for body condition analyses were calculated from a regression of body mass on body size. Interaction terms were not significant. Sample sizes:  $n_{Ross'} = 137$ ,  $n_{Snow} = 95$ .

Values listed under  $F$  are partial  $F$  values.

Effect	Body Size ( $r^2_{\text{model}} = 0.823$ )			Body Condition ( $r^2_{\text{model}} = 0.254$ )		
	$F$	df	$P$	$F$	df	$P$
Year	8.81	1	0.003 <sup>2</sup>	0.40	1	0.530
Species	347.89	1	< 0.001 <sup>3</sup>	0.51	1	0.478
Sex	29.13	1	< 0.001 <sup>4</sup>	0.89	1	0.346
Day <sup>1</sup>	84.41	1	< 0.001 <sup>5</sup>	0.15	1	0.698
Distance	25.08	1	< 0.001 <sup>6</sup>	65.91	1	< 0.001 <sup>7</sup>

<sup>1</sup> Time since mean hatch date, an index of relative flock age.

<sup>2</sup> Least squares means (SE): 1991 = -0.158 (0.098); 1992 = 0.316 (0.072)

<sup>3</sup> Least squares means (SE): Ross' = -0.520 (0.037), Snow = 0.678 (0.052)

<sup>4</sup> Least squares means (SE): Females' = -0.720 (0.041), Males = 0.230 (0.043)

<sup>5</sup>  $b_1 = 0.162$

<sup>6</sup>  $b_1 = 0.007$

<sup>7</sup>  $b_1 = 1.884$

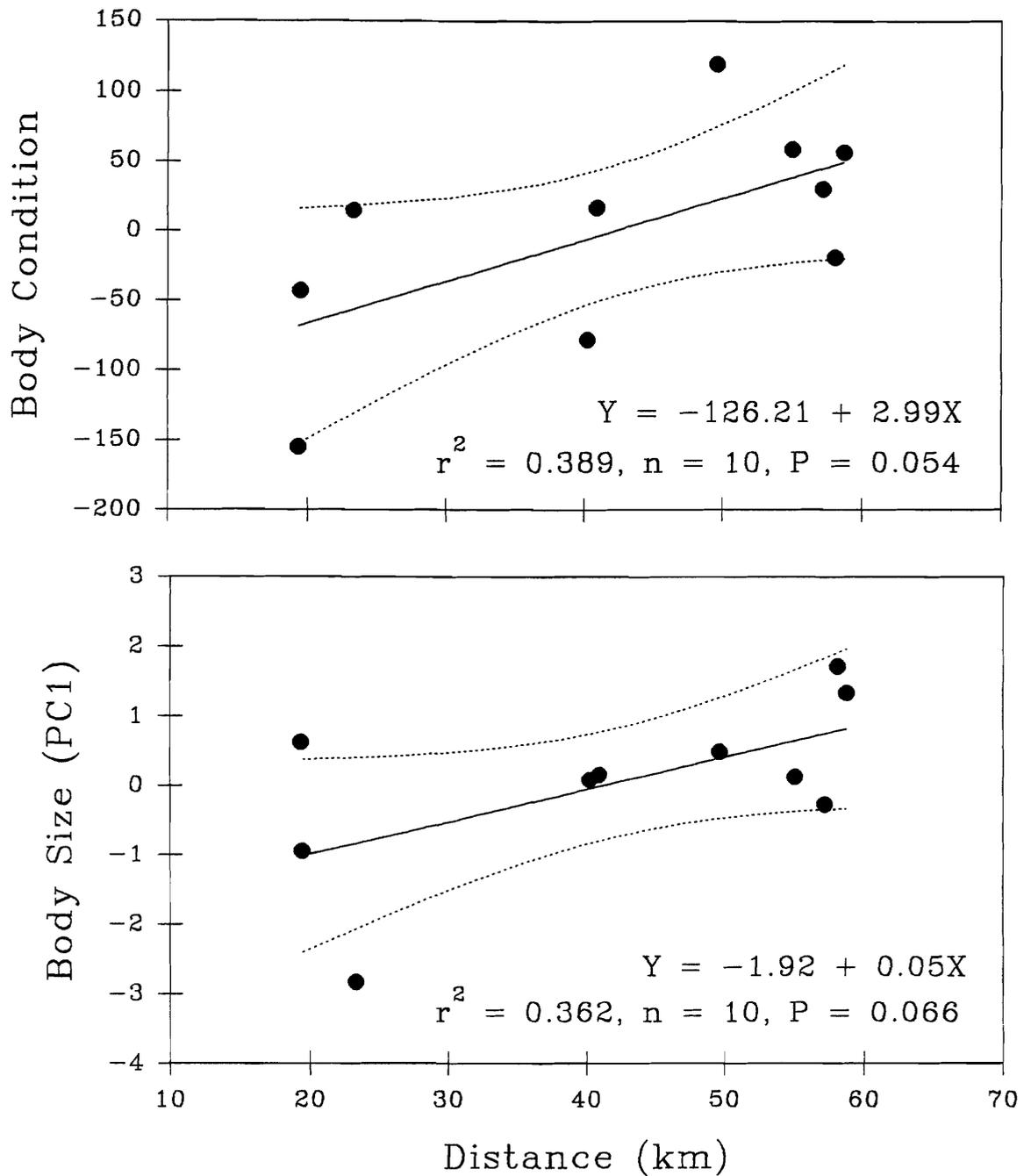


Figure 3.6. Body condition and size distribution for marked adult Ross' Goose females. Body condition was indexed using residuals of body mass on body size and brood age (time since hatch). Snow Goose sample sizes were too small for similar analyses. Dotted lines represent 95% confidence intervals.

Table 3.9. The relationship between body size and condition of marked and unmarked adults with the distance they were captured from Karrak Lake. Residuals for body condition analyses were calculated from a regression of body mass on body size. Interaction terms were not significant. Sample sizes:  $n_{Ross'} = 67$ ,  $n_{Snow} = 55$ . Values listed under  $F$  are partial  $F$  values.

Effect	Body Size ( $r^2_{\text{model}} = 0.937$ )			Body Condition ( $r^2_{\text{model}} = 0.064$ )		
	$F$	df	$P$	$F$	df	$P$
Species	1636.48	1	< 0.001	0.04	1	0.839
Sex	76.05	1	< 0.001	6.88	1	0.010 <sup>4</sup>
Distance	4.02	1	0.047 <sup>1</sup>	1.02	1	0.315

<sup>1</sup> Least squares means (SE): Ross' = -0.836 (0.031); Snow = 1.055 (0.035)

<sup>2</sup> Least squares means (SE): Female = -0.091 (0.032); Male = 0.311 (0.033)

<sup>3</sup>  $b_1 = 0.002$

<sup>4</sup> Least squares means (SE): Female = -24.93 (13.68); Male = 26.63 (14.19)

### 3.4.5 FEMALE EFFECTS ON EGG SIZE

Variation among broods accounted for 74.6% and 26.3% of the variation in egg size for Ross' and Snow Geese, respectively (Ross':  $n = 64$  eggs,  $r^2 = 0.761$ ,  $F = 9.38$ ,  $df = 15$ ,  $P < 0.001$ ; Snow:  $n = 28$  eggs,  $r^2 = 0.263$ ,  $F = 1.25$ ,  $df = 6$ ,  $P = 0.322$ ).

However, egg size was not related to female body size for either species (Figure 3.7).

## 3.5 DISCUSSION

### 3.5.1 BROOD DISPERSAL

A prerequisite for testing my prediction that gosling growth is related to the distance a brood was reared from the natal colony is that broods must disperse over a wide range of distances. Despite interspecific differences, this requirement was met (Figure 3.2). Ross' Goose broods travelled farther from Karrak Lake than did Snow Goose broods (Figure 3.2, Table 3.2) and this dispersal represented a coastward movement for marked Ross' Geese. This pattern was not related to my search method because the search area boundary extended about 7-15 km beyond the closest female locations (Figure 3.2). These differential dispersal patterns may have been related to interspecific differences in body size, bill morphology or habitat requirements. Body size is an important factor determining metabolic rate and energy requirement (Ricklefs 1974). Ross' Geese are smaller than Snow Geese (MacInnes et al. 1989) and thus should have relatively higher metabolic rates and require a diet richer in accessible energy. Since digestion in geese is relatively inefficient when compared to other herbivores (Sibley 1981), geese must consume

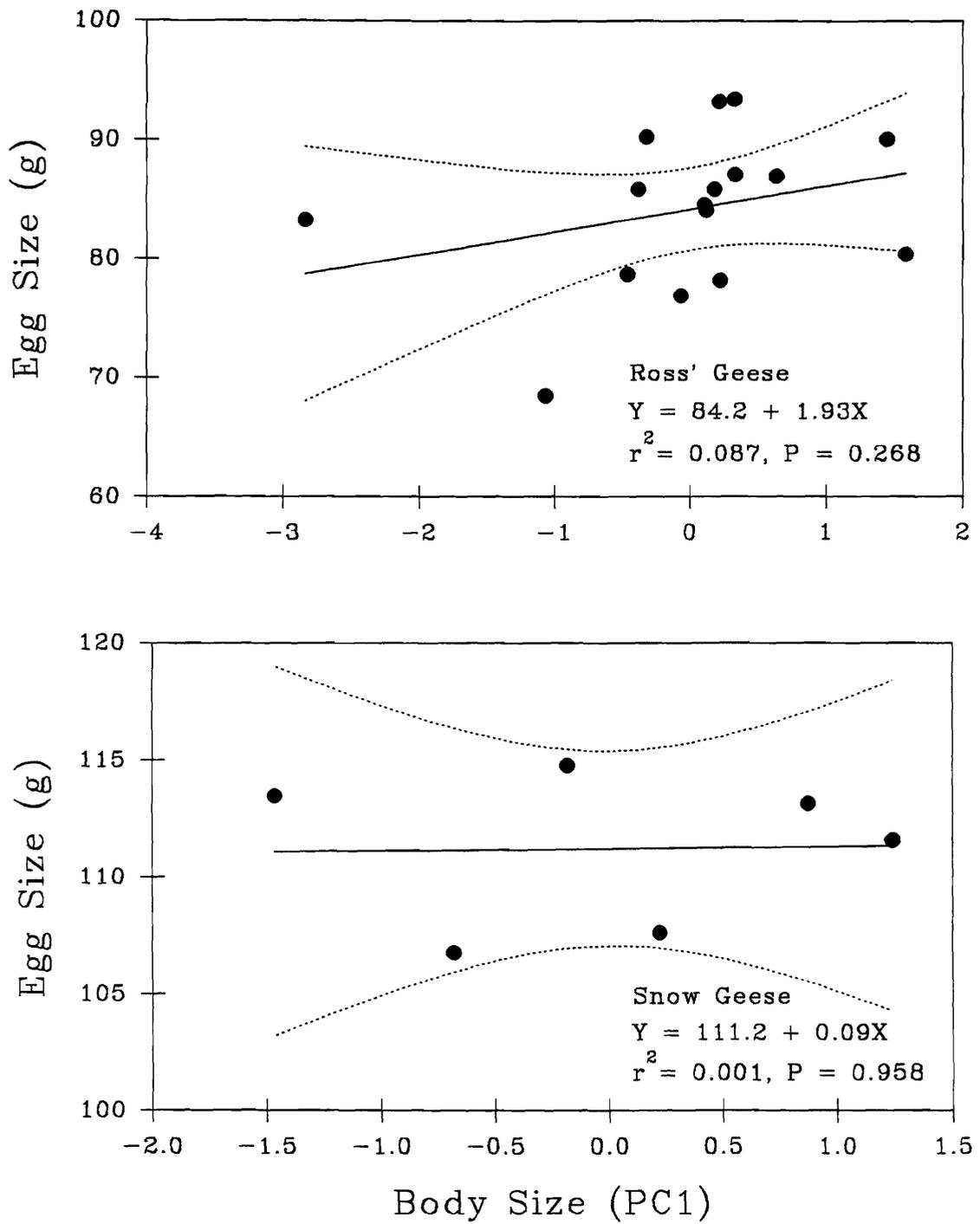


Figure 3.7. Influence of female body size on clutch mean egg size for radio marked geese.

relatively large amounts of food to meet energy demands (Owen 1972 and 1975, Sibley 1981, Buchsbaum et al. 1986, Sedinger et al. 1989). However, forage consumption and nutrient assimilation rates appear to be limited by gut passage times (Sibley 1981, Sedinger and Raveling 1984, Manseau and Gauthier 1993) with the higher retention time of longer guts resulting in greater nutrient assimilation rates (Sibley 1981). Therefore, the gut length of a goose could limit its ability to compensate for poor quality forage through hyperphagy. Ross' Geese have absolutely shorter intestines and caeca than do Snow Geese (R. T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK, unpubl. data) and, therefore, may be less efficient at extracting nutrients from poor quality forage, i.e. Ross' Geese may have to consume vegetation with less fiber to achieve the same nutrient assimilation rate as Snow Geese. During habitat surveys in the QMGBS from 1991-93, A. B. Didiuk (Canadian Wildlife Service, Saskatoon, pers. comm.) noted a change in vegetation communities as he travelled inland from the coast. In particular, plant communities within the first 30 km were dominated by Carex and grasses while those nearer Karrak Lake were dominated by Eriophorum (Ferguson et al. 1992). These communities were associated with differences in hydrology (Ferguson et al. 1992) that may, in part, be due to isostatic rebound. Although little is known about how geese perceive these habitat differences (Manseau and Gauthier 1993), if plant species available near the colony are high in fiber, either due to normal plant composition or selective grazing by dispersing broods, then Ross' Geese may be unable to raise young effectively near the colony. Consequently, broods should disperse to areas with higher quality forage that may be more common near the coast.

Although interspecific competition could have also influenced brood movements, there is some evidence that Ross' Geese have traditionally dispersed long distances to coastal regions. A. Dzubin (formerly with Canadian Wildlife Service, Saskatoon, pers. comm.) working in the QMGBS, noted that in 1959 few white goose broods were located inland around known colonies and that most were within several km of the coast. Few Snow Geese bred in the QMGBS in 1959 and when the Karrak Lake colony was first located circa 1967, Ross' Geese composed about 77% of the 17,000 bird breeding population (Kerbes in press). Thus most of the broods observed by Dzubin were likely Ross' Geese. In addition to requirements based on gut morphology, this apparent traditional habitat use of Ross' Geese may also be related to bill morphology. Acquisition of high quality forage is not only limited by availability of plants within the environment, but also by the ability of the herbivore to effectively manipulate and consume the food resource. Bill morphology may influence which foraging plants are best exploited by a goose species (Owen 1976, Johnson and Raveling 1988) and thus Owen (1976) and Johnson and Raveling (1988) have hypothesized that distributions of wintering geese are related to differences in bill morphology. Bill size and shape are one of the most obvious differences between Ross' and Snow Geese (Trauger et al. 1971). Ross' Geese have absolutely shorter bills, apparently adapted for grazing, while Snow Goose bills are longer, more robust and more suited to rooting tubers (Johnson and Raveling 1988). Thus brood distribution patterns (Figure 3.2) may be related to characteristics of distant vegetation that are more suitable for Ross' Geese to acquire and digest.

Regardless of the reasons for the spatial distribution of species, one cost is apparent: Snow Goose goslings were in poorer condition than were Ross' Goose goslings (Table 3.5) and this observation may be the result of philopatry to brood rearing areas. Since unmarked goslings were not selected randomly with respect to species, I cannot use results in Table 3.8 to address interspecific variation in body condition. To my knowledge, nothing is known about natal philopatry in Ross' Geese. However, Snow Goose females typically return to the brood rearing areas where they foraged as goslings (Cooke and Abraham 1980). This behavior has been observed in at least one other goose species, Barnacle Geese (*Branta leucopsis*, Larsson and Forslund 1991, 1992). If Ross' Geese traditionally dispersed long distances to coastal areas, then regions near the colony would have been available for the growing population of Snow Geese. In the past five years, the breeding population at Karrak Lake has increased by 71% from 213,000 to 364,000 geese (R. T. Alisauskas, Canadian Wildlife Service, Saskatoon, SK, unpubl. data). During this period, the Ross Goose population has grown by 144% while the Snow Goose population only grew by 35% (Chapter 4). These population growth rates were likely not strictly determined by local gosling recruitment. However, if the quality and/or per capita quantity of vegetation declined locally as the colony population grew, then philopatric behavior by Snow Geese may have contributed to poorer gosling condition and, hence, lower first year survival (*sensu* Francis et al. 1992) when parents attempt to rear young in a nutrient limited habitat (Cooch et al. 1993).

### 3.5.2 GOSLING SURVIVAL DURING THE BROOD REARING PERIOD

In marked goslings, recovery is likely equivalent to survival since, at least in Snow Geese, adoption is rare (Prevett and MacInnes 1980). From 1966-1970, Prevett and MacInnes (1980) recaptured 84 of 6,414 web-tagged Snow Goose goslings. Of these, only 4 goslings (~1% per year) were in flocks other than those containing siblings or parents. In addition, these authors began observing 68 marked broods within a few days of hatch and found no change in brood size during the subsequent 4-6 weeks. Therefore, I assume that goslings not recovered during banding activities were dead.

Goslings raised in areas with poor foraging conditions may have poorer pre-fledging survival than those reared on better quality sites. Nutrient limitation near the colony may increase susceptibility to predation by reducing parental attentiveness (Johanson 1978) or increasing the time that goslings remain small enough for predators to catch and consume. In addition, goslings unable to meet energetic demands of growth and maintenance could die of starvation (Johanson 1978, Jorgensen and Blix 1985) or disease/parasites (S. M. Gomis et al., Department of Veterinary Pathology, University of Saskatchewan, unpubl. data). I predicted that gosling survival would be higher farther from the colony but, using logistic regression, I found no evidence of distance effects on gosling survival (see Results).

The most important factor influencing gosling survival appeared to be egg size, both among (Ross' Geese, Figure 3.5) and within broods (Snow and, possibly, Ross' Geese, see Results). The egg size effect on gosling survival may, in part, result from the allometric relationship between neonate body condition and egg size (Chapter 2). Inclement weather or low per capita food availability could limit

nutrient assimilation rates. Goslings unable to feed during initial dispersal must rely on yolk reserves not only for growth and maintenance (Ankney 1980, Sedinger 1986, Duncan 1988) but also for activity. Earlier (Chapter 2), I concluded that larger egg size could confer advantages to goslings under some environmental conditions because goslings from heavy eggs were in absolutely better condition than those from lighter eggs. Ross' and Snow Goose goslings from heavier eggs had relatively similar amounts of lipid and protein reserves, but were structurally smaller relative to egg size than were goslings hatching from lighter eggs (Chapter 2). This allometry of neonate body condition (Chapter 2) explains results of Ankney (1980) who found that goslings from larger eggs survived longer without food than did those from smaller eggs. If goslings from smaller eggs are at an energetic disadvantage, then they may be unable to budget for poor foraging conditions and may have difficulty keeping up with the dispersing brood. This energetic disadvantage and subsequent straggling could result in higher predation rates on goslings from smaller eggs since gulls, which probably are the most important predator of goslings near Karrak Lake, appear to target straggling goslings during initial brood movements (pers. obs.).

In the analyses of egg size effects on gosling survival among broods (Figure 3.5), I recognized the potential bias of parent quality. Effects of parental quality on gosling survival may have both a genetic and an environmental component. For geese, egg size appears to be under strong genetic control (Newell 1988, Lessells et al. 1989). In my sample of marked females, variation among clutches accounted for over 74% of the variation in Ross' Goose egg size and this variation is likely not due to age related factors. In Snow Geese, egg size is highly heritable and is

repeatable within females after 4 years of age (Newell 1988, Lessells et al. 1989). Snow Geese do not breed until at least 2 years of age (Finney and Cooke 1978) and young females tend to lay 2 to 3 egg clutches (Prevett 1973). Since my results were derived from females laying 4 eggs, I believe that my sample contains only a small proportion of young, inexperienced females. In addition, since egg size is highly heritable (Newell 1988, Lessells et al. 1989), I consider egg size variation in my data to reflect the genetic component of parent quality independent of the environmental component. Therefore, I have no *a priori* reason to suspect that females laying smaller eggs are also poorer quality parents and assume that, in this case, parental quality is a function of how far broods are taken from the colony, which habitats are chosen on brood rearing areas, how well parents detect predators, and how well females brood goslings during poor weather.

### 3.5.3 GOSLING GROWTH

Local variation in gosling growth rates has been attributed to environmental variation (Larsson and Forslund 1991 and 1992, Cooch et al. 1993). I predicted that goslings reared farther from a large colony would experience better foraging conditions than those reared nearby and thus should be structurally larger and(or) in better condition. Cooch et al. (1993) described such systematic variation in gosling size and mass, then related these variations to above-ground plant biomass. However, these authors did not examine the relative condition of goslings among recapture sites. My results support the hypothesis that goslings reared farther from Karrak Lake were in better condition, i.e. were heavier for their structural size, than those reared near the colony (Tables 3.6 and 3.8) and thus provide indirect evidence

of a nutrient gradient around this colony. The unpredicted random variation of marked Ross' Goose gosling body size (controlled for age) across recapture distance may reflect selective allocation of nutrients to skeletal growth at the "expense" of body condition. In geese, structural size changes little after fledging (Cooch et al. 1991, Larsson and Forslund 1991) whereas body mass/body condition remains dynamic throughout an individual's life, varying annually, seasonally, and even daily (Raveling 1979, Ankney 1982). Since Arctic nesting geese rely on endogenous nutrient reserves for egg laying and incubation (Ankney and MacInnes 1978), large size may be correlated with greater fecundity (Alisauskas and Ankney 1990). If so, small adult body size may be disadvantageous and goslings growing under conditions of nutrient limitation should not compromise growth of "hard" tissues, i.e. constituents of structural size, which have a finite developmental period.

In the complete sample of goslings, both body size and condition increased with distance from Karrak Lake (Table 3.8). Although these results suggest that nutrient availability improves farther from the natal colony, systematic differences in brood age and size-dependent dispersal of adults may also contribute to my observations. Goose broods do not wander randomly over the entire brood-rearing period. Instead, they appear to travel to a specific area where most of their time is spent growing (see brood dispersal results). Marked broods appeared to have reached their rearing areas before I began recapturing them since broods were found between 8-59 km from Karrak Lake by 17 days post-hatch, yet moved only about 3 km during the next 13 days (see section 3.3). In my sample of marked broods, recapture ages ranged from 22-34 days and brood age was not correlated with distance travelled (Table 3.3). However, an attempt was made to standardized these

broods to peak hatch. If late hatching broods dispersed shorter distances than did those broods hatching at peak, then I might expect to find smaller goslings closer to the colony. Still, regardless of their age and body size, goslings captured farther from Karrak Lake were in better condition than those captured nearby (Table 3.8).

In both species, adults captured farther from the colony were larger (Table 3.9) thereby showing parallel trends with gosling body size (Table 3.8); this may reflect a genetic continuum among adults systematically distributed between Karrak Lake and the coast (*sensu* Cooch et al. 1993). This size-dependent dispersal, however, is observed in two species that vary greatly in body size (MacInnes et al. 1989). If body size of adults or goslings somehow influences a brood's dispersal potential, then I would expect either a reverse pattern of interspecific brood dispersal (Table 3.2, Figure 3.2 and 3.3) or a significant species-by-distance interaction for body size. Since interactions were not significant for either age class (Tables 3.8 and 3.9), my data suggest that either the restriction imposed on brood dispersal by body size acts intraspecifically or that a common environmental effect has acted during the growth of both adults and goslings (Larsson and Forslund 1992, Cooch et al. 1993). Natal philopatry to brood rearing areas seems the most plausible explanation for the parallel patterns in gosling and adult body size with dispersal distance (*sensu* Larsson and Forslund 1992, Cooch et al. 1993) since it is difficult to envision an intraspecific mechanism for sorting broods/adults by body size at the large spatial scale of my study. Alternatively, in my marked sample of goslings, I observed a significant egg size effect on body size (Table 3.6), so the parallel patterns in adult and gosling body size could be explained if egg size and female body size were correlated. However, I found no such relationship (Figure 3.7) nor

did I observe a systematic relationship between egg size of surviving goslings and distance from Karrak Lake (Table 3.3). Thus, if the sample of marked birds adequately represents the population of geese nesting at the colony, then egg size cannot explain similar distance-dependent patterns of body size observed in both age classes.

Body condition of goslings, but not adults, also increased with dispersal distance (Tables 3.8 and 3.9). Goslings are growing during the brood rearing period, possibly balancing competing demands of hard and soft tissue growth (see above), while adults are molting and recuperating from a seasonal low in body condition (Ankney and MacInnes 1978, Ankney 1982). Both must also meet costs of maintenance and activity. If nutrients are more limited closer to the colony, then one might expect both ages to show a functional response in body condition with distance. Body mass of adult females increases 21% from hatching to fledging (calculated from data in Ankney 1982), representing a gain of about 210 g and 350 g for Ross' and Snow Geese, respectively. However, at the same time, goslings are gaining considerably more biomass, increasing from about 70 g at hatch (Chapter 2) to over 800 g 22 days later (Slattery unpubl. data). Because goslings increase weight so rapidly and should have a higher basal metabolic rate than adults (Ricklefs 1974), goslings could be more sensitive to poor foraging conditions.

Goslings raised near Karrak Lake may not be able to compensate for poorer body condition before fledging. If little exchange between brood rearing areas occurs (as observed for both Snow and Barnacle Geese; Healey et al. 1980, Larsson and Forslund 1991), then goslings may experience similar or declining foraging conditions during the remaining prefledging period because above-ground biomass

production and the ability of plants to regrow after grazing declines seasonally (Sedinger and Raveling 1984, Jeffries 1988, Hik and Jeffries 1990). If so, then goslings might not be able to compensate for poor body condition. First year survival and recruitment rates are correlated with fledging body mass in some species of geese (Cooke et al. 1984, Owen and Black 1989, Cooch et al. 1991, Schmutz 1993), so goslings raised farther from the colony may not only fledge larger and in better condition but also may have higher recruitment rates than do goslings raised near the colony. If this occurs with the species I examined, then adults rearing young farther from Karrak Lake should experience greater fitness and selection should occur against philopatry to brood-rearing areas near the colony, i.e. selection for plasticity in dispersal behavior or selection against lineages faithful to local sites (Cooch et al. 1993).

In summary, many factors influence the brood ecology of Ross' and Snow Geese. Brood dispersal patterns differed between these closely related species (Avisé et al. 1992). On average, Ross' Goose broods travelled more than twice the distance away from Karrak Lake than did Snow Goose broods and this pattern may be related to nutrient availability on the landscape modified by interspecific differences in nutrient requirements and/or gut and bill morphology. Nutrient availability may vary systematically with distance from the natal colony because goslings reared farther away were in better condition by 3-4 weeks old than those reared nearby. Although egg size strongly influenced gosling survival in this study, evidence from Williams et al. (1993) suggests that systematic declines in forage quantity can reduce survival during the fifth week of a gosling's life, just before fledging (Bellrose 1980). Thus if a gradient of nutrient availability exists around

Karrak Lake, systematic variation in gosling condition may persist to fledging and could result in lower first year survival for goslings raised nearby (Owen and Black 1989, Francis et al. 1992).

## CHAPTER 4: A SYNTHESIS

### 4.1 DO ANATOMICAL AND PHYSIOLOGICAL ADAPTATIONS

#### COMPENSATE FOR SMALLER EGG SIZE IN ROSS' GEESE?

Under some environmental conditions egg size influences survival in Ross' and Snow Geese (Ankney 1980, Chapter 3). Although Ross' Geese hatch from absolutely smaller eggs than do Snow Geese (Table 2.3), their relatively larger gizzards (Table 2.8) and more functionally mature tissue (Table 2.3) might offset the energetic disadvantages of smaller body size on nutrient assimilation (Sibley 1981) and thermoregulation (Ricklefs 1974). In addition, Ross' Goose goslings appear to be adapted for long range brood dispersal since higher activity levels are typically associated with more functionally mature tissue (King and Farner 1961). Based on these characteristics, Ross' Goose goslings should be able process food quicker, require less brooding and move faster to foraging areas than expected for their body size. Indeed, although Ross' Goose neonates were about 20% smaller than Snow Goose neonates (Table 2.4), Ross' broods travelled at about the same speed during initial movements as did Snow broods ( $4.1 \pm 2.1$  vs.  $4.4 \pm 2.7$ , respectively; Chapter 3). Ultimately, Ross' broods settled farther from the colony (Table 3.2). Thus these adaptations may improve not only the relative but also the absolute ability to disperse.

In Ross' Geese, relatively larger gizzards and more functionally mature tissue may only partially compensate for negative effects of small egg size on gosling

energetics. Probability of gosling survival among broods was related to egg size only in Ross' Geese (Figure 3.5) suggesting that, relative to Snow Geese, smaller Ross' Goose goslings are still somewhat limited by environmental conditions or species-specific foraging requirements. This relationship, however, is confounded by potentially higher energetic demands of broods travelling longer distances. In addition, the causes of gosling mortality are not fully understood and factors such as poor weather or poor foraging conditions could influence gosling mortality directly through hypothermia (*sensu* Rhymer 1988) or indirectly by increasing susceptibility to predation (see Johnson et al. 1992 for a review), disease or parasites (Gomis et al. Department of Veterinary Pathology, University of Saskatchewan, unpubl. data). Clearly, detailed studies are needed to make informed comments on the energetic requirements and adaptations for reducing costs of thermoregulation in Ross' Goose neonates.

#### **4.2 NUTRIENT AVAILABILITY, BROOD DISPERSAL AND GOSLING**

##### **GROWTH: THE IMPLICATIONS FOR A RAPIDLY GROWING COLONY**

Growing Anseriformes are sensitive to variation in forage quality and these variations can influence asymptotic size, mass and, potentially, future reproductive success (see Sedinger 1992 for a review). Therefore, any systematic variation in habitat quality could be reflected as systematic variation in some component of growth (growth rate, asymptotic size or body condition). In my study, gosling size and condition varied positively with distance from the colony and thus my results indirectly suggest that forage quality improves farther from Karrak Lake (Tables 3.6 and 3.8). Cooch et al. (1993) observed similar local variation in gosling growth

around La Perouse Bay and correlated this variation with higher above-ground biomass of vegetation found farther from the colony. If present at Karrak Lake, a gradient in habitat quality could be caused by within-year processes, i.e. simply a functional response of goose density on per capita food availability, and therefore could change if nest density, clutch size, nest success and/or gosling survival varied annually. However, spring grubbing and summer grazing by geese have resulted in cumulative habitat destruction at Snow Goose colonies located on the West Coast of Hudson Bay at McConnell River, NWT, and La Perouse Bay, MB (Jeffries 1988, Kerbes et al. 1990, Cooch et al. 1991b). Researchers have suggested that deteriorating habitat quality on local foraging areas was responsible for long-term declines in gosling growth and survival, adult body size, female fecundity and, possibly, colony population size (Kerbes 1982, Cooch et al. 1989, 1991a and b, Francis et al. 1992, Cooch et al. 1993, Williams 1993) as well as spatial variation in gosling parasite loads and mortality (S. M. Gomis et al., Department of Veterinary Pathology, University of Saskatchewan, unpubl. data). Coincident with this habitat destruction was a rapid increase in breeding populations. Between 1940 and 1974, the McConnell River population grew from about 16,000 to 332,000 geese, a rate of 8.6% per year (calculated from data in MacInnes and Kerbes 1987). The breeding population at McConnell River has declined dramatically since 1974 (R. H. Kerbes, Canadian Wildlife Service, Saskatoon, SK, pers. comm.). Meanwhile, the La Perouse Bay colony grew by 8% per year between 1969-1991, an increase from 4,000 to 20,000 geese (Cooch et al. 1989). The Karrak Lake colony has undergone even faster growth (Figure 4.1), increasing at a rate of 11.3% per year between 1967 and 1993 (Kerbes in press, R. T. Alisauskas, Canadian Wildlife Service, Saskatoon,

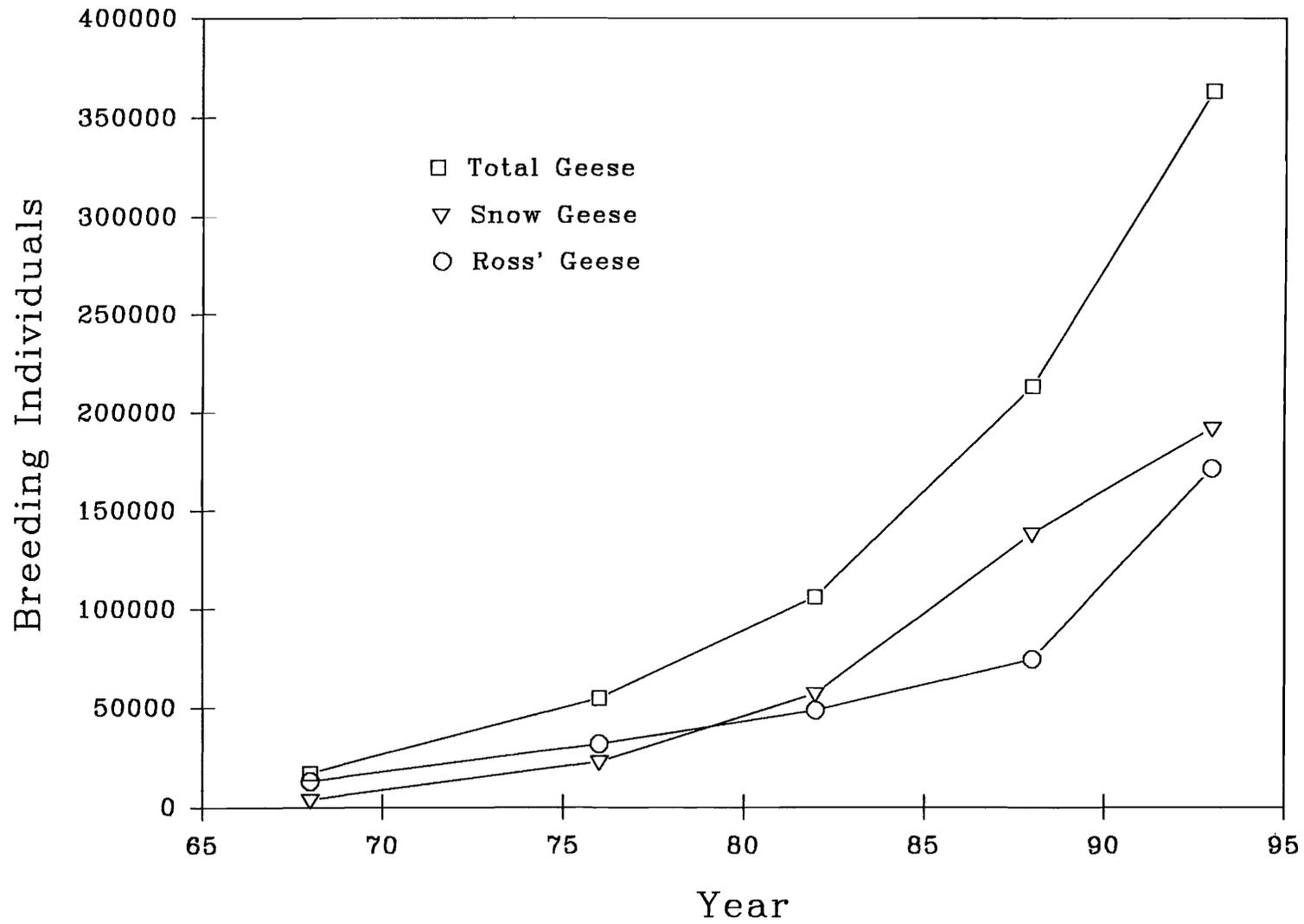


Figure 4.1. Population growth at Karrak Lake, 1968-1993. Data from Kerbes (in press) and Alisauskas (unpubl. data).

SK, unpubl. data), and local habitat degradation is evident (J. P. Ryder, Department of Biology, Lakehead University, pers. comm., A. B. Didiuk, Canadian Wildlife Service, Saskatoon, SK, pers. comm.). John Ryder conducted the earliest scientific research at Karrak Lake circa 1967 (Ryder 1972). He returned to Karrak in 1993 and when asked to provide his historical perspective on local habitat conditions, his response was, "The vegetation has virtually disappeared from overgrazing...efforts to obtain vegetation samples for plots was a meaningful exercise if only to show clearly that none remained anywhere on the colony, hardly a blade of grass" (Slattery and Alisauskas 1993). In addition, during habitat surveys in the Karrak Lake region, Didiuk noted local habitat conditions similar to those attributed to overgrazing near the McConnell River colony (Kerbes et al. 1990). Results from these surveys are currently being analyzed.

The implications of this colony growth at Karrak Lake are clear. The colony cannot continue to grow without negatively affecting the landscape. If habitat degradation accumulates annually, then the effect on gosling growth should become even more evident, possibly influencing demography as has been observed at McConnell River and La Perouse Bay. The current carrying capacity of the Karrak Lake region is unknown, but is likely greater than at either La Perouse Bay or McConnell River. These latter colonies are located on the coast and thus potential goose foraging areas are confined to an inland semicircle, about half the area found at Karrak Lake. The Karrak Lake colony is located about 70 km inland and broods could disperse in all directions. However, movements of radio-marked geese indicate general coastward (northward) movement for both species (Figure 3.2). Carrying capacity of the Karrak Lake region is difficult to measure but it will likely

be influenced by brood movement patterns, the ability of geese to switch from deteriorating habitats, competitive interactions among species, the distribution of suitable foraging sites and the resiliency of tundra vegetation to recover from grazing pressure.

Because distance of brood dispersal varies interspecifically (Table 3.2 and Figure 3.2), continued colony growth could differentially influence local gosling production of each species. Snow Geese tend to raise their young closer to the colony and, as a result, Snow Goose goslings appear to be in poorer condition than are Ross' Goose goslings (Table 3.5). Initially, this dispersal strategy may have favored local recruitment of Snow Geese (1966-1988, Figure 4.1). However, during the past five years, the population has increased by 71% and most of this growth occurred in the Ross' Goose population (1988-1993, Figure 4.1). Although many factors may have influenced these growth rates, e.g. immigration by Ross' Geese and emigration by Snow Geese, local recruitment undoubtedly was an important factor, especially for females who are highly philopatric to natal colonies (Cooke et al. 1975). In addition, between 1966-1988 the Karrak Lake colony contained about one half of the world's Ross' Goose population (Kerbes in press) and thus many returning male Ross' Geese were likely raised locally.

Unless a change in the distribution of Snow Goose broods occurs, either due to reduced fidelity to rearing areas or to greater recruitment of birds raised farther from the colony (Cooch et al. 1993), then the impacts of continued colony growth should be observed first in Snow Geese (*sensu* Rockwell et al. 1993). Per capita food availability should decline throughout the Karrak Lake region as grazing pressure increases. Although increased grazing pressure can stimulate above-ground

primary production due to a positive feedback between herbivores and plants, too much grazing pressure cancels this feedback and results in habitat damage (Jeffries 1988, Hik and Jeffries 1990). Because grazing pressure should be highest near the colony and lowest near the coast, I predict that habitat quality will decline unevenly with distance from Karrak Lake; local conditions should deteriorate faster than those at distant sites. Therefore, the influence of parental brood dispersal decisions on subsequent gosling growth should become even more important as colony size increases. If Snow Goose dispersal patterns do not change, then imminent habitat degradation could result in consumption of poorer quality forage (*sensu* Sedinger and Raveling 1986), slower growth (Cooch et al. 1993), poorer gosling condition, higher pre-fledging mortality (Williams et al. 1993), lower recruitment rates (Francis et al. 1992) and lower productivity in Snow Geese. Similar demographic effects would be observed in Ross' Geese but with a time-lag dependent on how quickly the "biodeterioration zone" (Hamilton and Watt 1970) expands. Future monitoring of brood ecology in the Karrak Lake region should provide valuable insight into the role of brood dispersal and subsequent gosling growth and survival on population dynamics in these two colonial, nidifugous species.

## 5. LITERATURE CITED

- ALISAUSKAS, R. T. 1986. Variation in the composition of the eggs and chicks of American Coots. *Condor* 88:84-90.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1990. Body size and fecundity in Lesser Snow Geese. *Auk* 107:440-443.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl, pp. 30-61. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis.
- AMERICAN ORNITHOLOGIST'S UNION. 1988. Report of committee on use of wild birds in research. *Auk* 105 (Supplement 1):1A-41A.
- ANKNEY, C. D. 1980. Egg weight, survival, and growth of Lesser Snow Goose goslings. *J. Wildl. Manage.* 44:174-192.
- ANKNEY, C. D. 1982. Annual cycle of body weight in Lesser Snow Geese. *Wildl. Soc. Bull.* 10:60-64.
- ANKNEY, C. D., AND A. R. BISSETT. 1976. An explanation of egg-weight variability in the Lesser Snow Goose. *J. Wildl. Manage.* 40:729-734.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.

- ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Amer. Soc. Exp. Biol. 29:1541-1552.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, pp 224-286. In D.S. Farner and J.R. King [eds.]. Avian Biology, Vol 1. Academic Press, NY.
- ATCHELY, W. R., C. T. GASKINS, AND D. ANDERSON. 1976. Statistical properties of ratios. Syst. Zool. 25:137-148.
- AVISE, J. A., R. T. ALISAUSKAS, W. S. NELSON, AND C.D. ANKNEY. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084-1096.
- BALMER, R. T., AND A. D. STROBUSCH. 1977. Critical size of newborn homeotherms. J. Appl. Physiol. 42:571-577.
- BARRY, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. J. Wildl. Manage. 26:19-26.
- BAZELY, D. R., AND R. L. JEFFRIES. 1985. Goose feces: A source of nitrogen for plant growth in a grazed salt marsh. J. Appl. Ecol. 22:693-703.
- BEGON, M., AND M. MORTIMER. 1986. Population Ecology: A Unified Study of Animals and Plants. Blackwell Scientific Publications. Boston, 220 pp.
- BELLROSE, F. C. 1980. Ducks, Geese, and Swans of North America. Stackpole Books. Harrisburg, PA, 549 pp.
- BIRKHEAD, M. 1985. Variation in egg quality and composition in the Mallard (*Anas platyrhynchos*). Ibis 127:467-475.
- BLEM, C. R. 1984. Ratios in avian physiology. Auk 101:153-155.

- BLEM, C. R. 1990. Avian energy storage, pp. 59-113. *In* D. M. Powder [ed.].  
Current Ornithology, Vol 7. Plenum Press, New York.
- BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. The quantitative genetics of  
wild bird populations pp. 45-78. *In* F. Cooke and P. A. Buckley [eds.]. Avian  
Genetics-Its Application to Ecological and Evolutionary Theory. Academic  
Press, London.
- BORTOLOTTI, G. R., AND W. M. IKO. 1992. Non-random pairing in American  
Kestrels: mate choice versus intra-sexual competition. *Anim. Behav.* 44:811-  
821.
- BROCKELMAN, W. Y. 1975. Competition, the fitness of offspring, and optimal  
clutch size. *Am. Nat.* 109:677-699.
- BUSCHBAUM, R., J. WILSON, AND I. VALIELA. 1986. Digestibility of plant  
constituents by Canada Geese and Atlantic Brant. *Ecology* 67:386-393.
- CAREY, C. 1983. Structure and function of avian eggs, pp. 69-103. *In* R. F.  
Johnston [ed.], Current Ornithology. Vol 1. Plenum Press, New York.
- CARGILL, S. M., AND R. L. JEFFRIES. 1984. The effects of grazing by Lesser  
Snow Geese on the vegetation of a subarctic salt marsh. *J. Appl. Ecol.*  
21:669-686.
- COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1989. Long-  
term decline in fecundity in a Snow Goose Population: evidence for density-  
dependence?. *J. Animal Ecol.* 58:711-726.
- COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE.  
1991a. Body size variation in Lesser Snow Geese: Environmental plasticity in  
gosling growth rates. *Ecology* 72:503-512.

- COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1991b. Long-term decline in fecundity in a Snow Goose Population: evidence for environmental degradation? *J. Animal Ecol.* 60: 483-496.
- COOCH, E. G., R. L. JEFFRIES, R. F. ROCKWELL, AND F. COOKE. 1993. Environmental change and the cost of philopatry: An example in the Lesser Snow Goose. *Oecologia* 93:128-139.
- COOCH, F. G. 1958. The breeding biology and management of the blue goose (*Chen caerulescens*). PhD Dissertation, Cornell University.
- COOKE, F., AND K. F. ABRAHAM. 1980. Habitat and locality selection in Lesser Snow Geese: The role of previous experience. *Proc. Int. Ornithol. Congr.* 17:998-1004.
- COOKE, F., C.S. FINDLAY, AND R.F. ROCKWELL. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* 101:451-458.
- COOKE, F., C. D. MACINNES, AND J. P. PREVETT. 1975. Gene flow between breeding populations of Lesser Snow Geese. *Auk* 92:493-510.
- COOPER, J. A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildl. Monogr.* 61:1-87.
- COULSON, J. C., N. DUNCAN, AND C. THOMAS. 1982. Changes in the breeding biology of the herring gull (*Larus argentatus*) induced by reduction in colony size and density of the colony. *J. Animal Ecol.* 51:739-756.
- DAVIES, J. C., R. F. ROCKWELL, AND F. COOKE. 1988. Body size variation and fitness components in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* 105:639-648.

- DIAMOND, A. W. 1978. Feeding strategies and population size in tropical sea birds. *Am. Nat.* 112:215-223.
- DUNCAN, D. C. 1988. Body reserves of neonate Northern Pintails (*Anas acuta*). *Can. J. Zool.* 66:811-816.
- DZUBIN, A., AND E. G. COOCH. 1992. Measurements of geese: general field methods. California Waterfowl Association. Sacramento, CA. 20 pp.
- FALCONER, D. S. 1981. Introduction to quantitative genetics. Longman, London.
- FERGUSON, R. S., A. B. DIDIUK, R. T. ALISAUSKAS, AND G. B. STENHOUSE. 1992. Habitat mapping and inventory of Queen Maud Gulf Bird Sanctuary, Northwest Territories. Progress Report submitted to Ducks Unlimited, Canada.
- FINDLAY, C. S., AND F. COOKE. 1978. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Anser caerulescens caerulescens*). *Evolution* 37:724-734.
- FINDLAY, C. S., AND F. COOKE. 1982. Synchrony in the Lesser Snow Goose: 2. The adaptive value of reproductive synchrony. *Evolution* 36:786-799.
- FINDLAY, C. S., AND F. COOKE. 1983. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Anser caerulescens caerulescens*). *Evolution* 37:724-734.
- FINNEY, G., AND F. COOKE. 1978. Reproductive habits in the Snow Goose: The influence of female age. *Condor* 80:147-158.
- FRANCIS, C. M., M. H. RICHARDS, F. COOKE, AND R. F. ROCKWELL. 1992. Long-term changes in survival rates of Lesser Snow Geese. *Ecology* 73:1346-1362.

- FRY, C. H. 1972. The social organization of bee-eaters (Meropidae) and cooperative breeding in hot climates. *Ibis* 114:1-14.
- FURNESS, R. W. 1983. Variations in size and growth of Great Skua (*Catharacta skua*) chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *J. Zool.* 199:101-116.
- GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick Billed Murre of Prince Leopold Island- a study of colonial, high Arctic seabird. *Can. Wildl. Serv. Monogr.* 6:1-350.
- GASTON, A. J., G. CHAPDELAIN, AND D. G. NOBLE. 1983. The growth of Thick Billed Murre chicks at colonies in Hudson Strait: Inter- and intra-colony variation. *Can J. Zool.* 61:2465-2475.
- GEBHARDT-HEINRICH, S. G., AND A. J. VAN NOORDWIJK. 1991. Nestling growth in the Great Tits I. Heritability estimates under different environmental conditions. *J. Evol. Biol.* 3:341-362.
- HARRIS, M. P. 1966. Breeding biology of the Manx Shearwater (*Puffinus puffinus*). *Ibis* 108:17-33.
- HAMILTON, W. J., III, AND K. E. F. WATT. 1970. Refuging. *Annu. Rev. Ecol. Syst.* 1:263-286.
- HAZELWOOD, R. L. 1972. The intermediate metabolism of birds, pp. 471- 526. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.]. *Avian Biology*, Vol 2. Academic Press, New York.
- HEALY, R. F., F. COOKE, AND P. W. COLGAN. 1980. Demographic consequences of Snow Goose brood-rearing traditions. *J. Wildl. Manage.* 44:900-905.

- HIK, D. S., AND R. L. JEFFRIES. 1990. Increases in the net above-ground production of a salt-marsh forage grass: A test of the prediction of the herbivore-optimization model. *J. Ecol.* 78:180-195.
- HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.* 46:33-58.
- HUNT, G. L., JR., Z. EPPLEY, B. BURGESSON, AND R. SQUIBB. 1981. Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Environmental Assessment of the Alaskan Continental Shelf. Final Reports of Investigators. N.O.A.A. Environmental Research Lab, Boulder, CO. *Biological Studies* 12:1-258.
- JAMES, F. C., AND C. S. NESMITH. 1988. Nongenetic effects in geographic differences among nestling population of Red-winged Blackbirds. *Proc. Int. Ornith. Congr.* 19:1424-1433.
- JEFFRIES, R. L. 1988. Vegetational mosaic, plant-animal interactions, and resources for plant growth, pp. 341-369. *In* L. Gottlieb and S.K. Jain [eds]. *Plant Evolutionary Biology*. Chapman and Hall, New York.
- JEFFRIES, R. L., A. JENSEN, AND K.F. ABRAHAM. 1979. Vegetational development and the effect of geese on vegetation at La Perouse Bay, Manitoba. *Can. J. Bot.* 57:1439-1450.
- JOHANSEN, J. 1978. Reproductive problems of some Laridae species in western Norway. *Ibis* 120:114-115.

- JOHNSON, D. H., J. D. NICHOLS, M. D. SCHWATZ. 1992. population dynamics of breeding waterfowl, pp. 446-485. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis.
- JOHNSON, J. C., AND D. G. RAVELING. 1988. Weak family associations in Cackling Geese during winter: Effects of body size and food resources on goose social organization, pp. 71-90. *In* M. W. Weller [ed.]. Waterfowl in Winter. University of Minnesota Press, Minneapolis.
- JORGENSEN, E., AND A. S. BLIX. 1985. Effects of climate and nutrition on growth and survival of Willow Ptarmigan chick. *Ornis Scand.* 16:99-107.
- KERBES, R. H. in press. Colonies and numbers of Ross' Geese and Lesser Snow Geese in the Queen Maud Gulf Bird Sanctuary. *Can. Wildl. Ser. Occasional Paper No. 81.*
- KERBES, R. H. 1982. Lesser Snow Geese and their habitat on the west Hudson Bay. *Nat. Can.(Rev. Ecol. Syst.)* 109:905-911.
- KERBES, R. H., P. M. KOTANEN, AND R. L. JEFFRIES. 1990. Destruction of wetland habitats by Lesser Snow Geese: A keystone species on the west coast of Hudson Bay. *J. Applied Ecol.* 27: 242-258.
- KERBES, R. H., R. L. MCLANDRESS, G. E. J. SMITH, G. W. BEYERSBERGEN, AND B. GODWIN. 1983. Ross' and Lesser Snow Goose colonies in the central Canadian Arctic. *Can. J. Zool.* 61:168-173.

- KING, J. R., AND D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature, pp. 215-288. *In* A. J. Marshall [ed.]. *Biology and comparative physiology of birds*, Vol 2. Academic Press, New York.
- KONARZEWSKI, M. 1988. A model of growth in altricial birds based on changes in water content of tissues. *Ornis Scand.* 19:290-296.
- KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of european ducks. *Auk* 81:281-307.
- LACK, D. 1968. *Ecological Adaptations for Breeding Birds*. Methuen and Co., Ltd. London. 409 p.
- LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607-615.
- LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose (*Branta leucopsis*). *J. Evol. Biol.* 4:619-636.
- LARSSON, K., AND P. FORSLUND. 1992. Genetic and social inheritance of body and eggs size in the Barnacle Goose (*Branta leucopsis*). *Evolution* 46:235-244.
- LESSELLS, C. M., F. COOKE, AND R. F. ROCKWELL. 1989. Is there a trade-off between egg weight and clutch size in wild Lesser Snow Geese? *J. Evol. Biol.* 2:457-472.
- LUNDBERG, C.-A., AND R. A. VÄISÄNEN. 1979. Selective correlations of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). *Condor* 81:146-156.

- MACINNES, C.D. in press. Growth variations of goslings: Do they have demographic effects? Proc. Int. Canada Goose Symp. 1:000-000.
- MACINNES, C. D., AND R. H. KERBES. 1987. Growth of the Snow Goose (*Chen caerulescens*) colony at McConnell River, Northwest Territories: 1940-1980. Can. Field Nat. 101:33-39.
- MACINNES, C. D., R. K. MISRA, AND J. P. PREVETT. 1989. Differences in growth parameters of Ross' Geese and Snow Geese: evidence from hybrids. Can. J. Zool. 67:286-290.
- MANSEAU, M., AND G. GAUTHIER. 1993. Interactions between Greater Snow Geese and their rearing habitat. Ecology 74:2045-2055.
- MCLANDRESS, M. R. 1983. Population dynamics, behavior, and ecology of Ross' Geese (*Anser rossii*). PhD dissertation, University of California, Davis. 143 pp.
- MONTEVECCHI, W. A., I. R. KIRKMAN, D. D. ROBY, AND K. L. BRINK. 1983. Size, organic composition, and energy content of Leach's Storm Petrel (*Oceanodroma leucohoa*) eggs with reference to position in the precocial-altricial spectrum and breeding ecology. Can. J. Zool. 61:1457-1463.
- MOSS, R. A., AND A. WATSON. 1982. Heritability of egg size, hatch weight, body weight, and viability in Red Grouse (*Lagopus lagopus scoticus*). Auk 99:683-686.
- MOSS, R. A. WATSON, P. ROTHERY, AND W. W. GLENNIE. 1981. Clutch size, egg size, hatch weight and laying date in relation to early mortality in Red Grouse *Lagopus lagopus scoticus* chicks. Ibis 123:450-462.

- NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42:239-268.
- NEWELL, L. C. 1988. Causes and consequences of egg weight variation in the Lesser Snow Goose (*Chen caerulescens caerulescens*). MSc Thesis. Queen's University. 76 p.
- NISBET, I. C. T. 1978. Dependence of fledging success on egg size, parental performance and egg composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougalli*. Ibis 120:207-215.
- NOORDWIJK, A. J. VAN, L. C. P. KEIZER, J. H. VANBALEN, AND W. VAN SCHARLOO. 1981. Genetic variation in egg dimensions in natural populations of the Great Tit. Genetica 55:221-232.
- OWEN, M. 1972. Some factors affecting food intake and selection in Whitefronted Geese. J. Animal Ecol. 41:79-92.
- OWEN, M. 1976. Factors affecting the distribution of geese in the British Isles. Wildfowl 27:143-147.
- OWEN, M., AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. J. Animal Ecol. 58:603-617.
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228:1221-1222.
- PEACH, H. C., AND V. G. THOMAS. 1986. Nutrient composition of yolk in relation to early growth of Canada Geese. Physiol. Zool. 59:344-356.
- PREVETT, J. P. 1973. Familial and age-dependent behaviour of blue geese (*Anser caerulescens*). PhD Dissertation. Univ. Western Ontario, London. 194p.

- PREVETT, J. P., AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. *Wildl. Monogr.* 71:1-46.
- PRICE, T. D., AND P. T. BOAG. 1987. Selection in natural populations of birds, pp. 257-287. *In* F. Cooke and P. A. Buckley [eds.]. *Avian Genetics-Its Application to Ecological and Evolutionary Theory.* Academic Press, London.
- PRICE, T. D., AND P. R. GRANT. 1985. The evolution of ontogeny in Darwin's Finches: A quantitative genetic approach. *Am. Nat.* 125: 169-188.
- RAVELING, D. G. 1979. The annual cycle of body condition of Canada Geese with special reference to control of reproduction. *Auk* 96:234-252.
- REYMENT, R. A., R. E. BLACKITH, AND N. A. CAMPBELL. 1984. *Multivariate Morphometrics.* Academic Press, London.
- RHYMER, J. M. 1988. The effects of egg size variability on thermoregulation of Mallard (*anas platyrhynchos*) offspring and its implications for survival. *Oecologia* 75:20-24.
- RICKLEFS, R. E. 1974. Energetics of reproduction, pp. 152-297. *In* R. Paynter [ed.]. *Avian Energetics.* Nuttall. Ornithol. Club Bull. Vol 15.
- RICKLEFS, R. E. 1983. Avian post-natal development, p. 1-83. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian Biology.* Vol. 7. Academic Press, Inc.
- RICKLEFS, R. E. 1984a. Components of variation in measurements of nestling European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. *Auk* 101:319-333.

- RICKLEFS, R. E. 1984b. Variation in the size and composition of eggs of the European Starling. *Condor* 86:1-6.
- RICKLEFS, R. E., AND S. PETERS. 1981. Parental Components of variance in growth rate and body size of nestling European Starlings (*Sturnus vulgaris*) in eastern Pennsylvania. *Auk* 98:39-48.
- RICKLEFS, R. E., AND T. WEBB. 1985. Water content, thermogenesis, and growth rate of skeletal muscles in the European Starling. *Auk* 102:369-376.
- RICKLEFS, R. E., D. C. HAHN, AND W. A. MONTEVECCHI. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. *Auk* 95:135-144.
- ROBERTSON, G. J., AND F. COOKE. 1993. Intraclutch egg size variation and hatching success in the common eider. *Can. J. Zool.* 71:544-549.
- ROCKWELL, R. F., E. G. COOCH, C. B. THOMPSON, AND F. COOKE. 1993. Age and reproductive success in female Lesser Snow Geese: Experience, senescence and the cost of philopatry. *J. Animal Ecol.* 62:323-333.
- ROHWER, F. C., AND D. I. EISENHAUER. 1989. Egg mass and clutch size relationships in geese, eiders, and swans. *Ornis Scand.* 20:43-48.
- RYDER, J. P. 1967. The breeding biology of Ross' Geese in the Perry River Region, NWT. *Can Wildl. Serv. Rep. Ser.* 3. 56 pp.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Geese. *Wilson Bull.* 82:5-13.
- RYDER, J. P. 1971. Size differences in Ross' and Snow Goose eggs at Karrak Lake in 1968. *Wilson Bull.* 83:438-439.
- RYDER, J. P. 1972. Biology of nesting Ross' Geese. *Ardea* 60:185-215.

- SALYER, J. W. 1962. A bow-net trap for ducks. *J. Wildl. Manage.* 26:219-221.
- SAS INSTITUTE. 1985. SAS user's guide: statistics. Version 5 ed. SAS Institute, Cary, NC.
- SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits (*Parus major*). *Ibis* 115:549-558.
- SCHMUTZ, J. A. 1993. Survival and pre fledging body mass in juvenile Emperor Geese. *Condor* 95:222-225.
- SCHULTER, D., AND J. N. M. SMITH. 1986. Genetic and phenotypic correlations in a natural population of Song Sparrows. *Biol. J. Linn. Soc.* 29:23-26.
- SEDINGER, J. S. 1986. Growth and development of Canada Goose goslings. *Condor* 88:169-180.
- SEDINGER, J. S. 1992. Ecology of pre fledging waterfowl, pp. 109-127. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis.
- SEDINGER, J. S., AND P. L. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. *Ecology* 72:496-502.
- SEDINGER, J. S., AND D. G. RAVELING. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling Canada Geese. *Auk* 101:295-306.
- SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *J. Animal Ecol.* 55:1083-1102.

- SEDINGER, J. S., AND D. G. RAVELING. 1988. Foraging behavior of Cackling Canada Goose goslings: Implications for the roles of food availability and processing rate. *Oecologia* 75:119-124.
- SEDINGER, J. S., R. G. WHITE, F. A. MANN, F. A. BURRIS AND R. A. KEDROWSKI. 1989. Apparent metabolizability of alfalfa components by yearling Black Brant. *J. Wildl. Manage.* 53:726-734.
- SIEGEL, S., AND N. J. CASTELLAN. 1988. *Nonparametric Statistics for Behavioral Sciences*. McGraw-Hill, NY. 399p.
- SIBLEY, R. M. 1981. Strategies of digestion and defecation, pp. 109-139. *In* C. R. Townsend and P. Calow [ed.]. *Physiological Ecology: An Evolutionary Approach to Resource Use*. Sinaur Assoc., Inc. Sunderland, MA.
- SLATTERY, S. M., AND R. T. ALISAUSKAS. 1993. Studies on the nutritional ecology and population biology of Ross' Geese nesting at Karrak Lake, NWT. Progress Report submitted to the California Department of Fish and Game.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *Am Nat.* 108:499-506.
- SMITH, J. N. M., AND C. ARCESE. 1988. Effects of supplemental food on growth and adult size in the Song Sparrow. *Proc. Int. Ornith. Cong.* 19:1416-1423.
- SOKAL, R. R., AND F. J. ROLF. 1981. *Biometry*. W. H. Freeman & Co., New York. 859 p.
- TRAUGER, D. L., A. DZUBIN, AND J. P. RYDER. 1971. White geese intermediate between Ross' and Snow Geese. *Auk* 88:856-875.

- VAN NOORDWIJK, A. J., L. C. P. KEIZER, J. H. VAN BALEN, AND W. SCHARLOO. 1981. Genetic variation in egg dimensions in natural populations of the Great Tit. *Genetica* 55:221-232.
- WILLIAMS, A. J., W. R. SIEGFRIED, AND J. COOPER. 1982. Egg composition and hatchling precocity in seabirds. *Ibis* 124:456-470.
- WILLIAMS, T. D., E. G. COOCH, R. L. JEFFRIES, AND F. COOKE. 1993. Environmental degradation, food limitation and reproductive output: juvenile survival in Lesser Snow Geese. *J. Animal Ecol.* 62: 766-777.
- WILLIAMS, C. S., AND M. C. NELSON. 1943. On Canada Goose nests and eggs. *Auk* 60:341-345.
- WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds, p. 1-78. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.] *Avian Biology*. Academic Press, Inc., London.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Second edition. Prentice Hall, NJ. 718p.