

PREDATION AND ANTIPREDATOR TACTICS OF
NESTING BLACK BRANT AND LESSER SNOW GEESE

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By

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ABSTRACT

Adaptive responses to environmental conditions may be constrained by an organism's life-history strategy. When sympatric and ecologically similar species have widely differing reproductive success, they provide an opportunity to study how their adaptive responses to environmental conditions may be constrained by features of their life-history strategies. I examined behavioural adaptations to reduce egg predation in black brant *Branta bernicla nigricans* and lesser snow geese *Chen caerulescens caerulescens* nesting at Anderson River Delta, Northwest Territories, between 1991 and 1993. Nest and egg survival varied both among years and between species. Brant had lower nest and egg survival than snow geese due to greater losses to glaucous gulls *Larus hyperboreus* and parasitic jaegers *Stercorarius parasiticus*. Population projections using estimates of reproductive success suggested that both species declined during this study. Reproductive success was higher in 1993, however, which resulted in projected increases. Estimates of nesting population size suggested that brant had declined little, if at all, from a previous estimate. Estimates of nesting snow geese were consistent with a decline in population size determined from photographic surveys in years before and after this study.

Coloniality has been found to reduce predation on eggs or young in some populations. I tested hypotheses that brant and snow geese benefitted by nesting at high densities, in central positions within the colony, or by nesting farther from shorelines that were commonly travelled by avian egg predators. I also tested the

hypothesis that snow geese had higher reproductive success because they nested at higher densities than brant. Nest density had no effect on nest survival, egg survival, or likelihood of partial clutch predation in snow geese. In brant, nest survival declined as nest density increased in 1992 and with increased distance from shore in 1993. Brant with conspecific nearest neighbours were less likely to suffer partial clutch predation in 1993, but not in 1992. Egg survival in brant increased with nest density in 1993, but decreased as density increased in 1992; however, the decrease occurred only in nests with three or four eggs. Effects of nesting at high densities, in central positions, or far from shorelines, were lacking in snow geese and were inconsistent and contradictory in brant; therefore, I concluded that these features of coloniality did not provide geese with a selective advantage in nest or egg survival. Snow geese nested at higher densities than brant, but this factor was not the cause of higher nest and egg survival in snow geese.

Actions by parent birds that may reduce predation on eggs or young can be taken prior to nesting, e.g. nesting in colonies, or during the nesting period while offspring are at risk. Many nest predators can be deterred if parents guard their offspring; however, nest attendance may be affected by environmental or life-history constraints. The effect of life-history and environmental constraints on nest guarding behaviour was studied by comparing activity budgets of sympatric brant and snow geese during incubation. Brant and snow geese were predicted to have evolved different tactics to resolve the conflicting demands of self-maintenance and nest guarding because they differ in body size and fasting ability. Female snow geese had very high nest attendance and both sexes had high territory attendance so their

nests were rarely unattended during incubation. Brant had lower nest attendance than snow geese. Due to a lack of food near their nests, brant left their territories to feed, so they also had lower territory attendance than snow geese. Although male brant remained on their territories most of the time that their mates were absent, they were less effective when defending the nest from avian predators than were incubating females. Increased vigilance and decreased resting by female brant as incubation progressed provided support for the prediction, from parental investment theory, that nest guarding effort would increase with offspring age, but these behavioural changes did not occur in male brant or in snow geese. However, declining nest and territory attendance by female brant and males of both species contradicted predictions from parental investment theory. Declining nest and territory attendance were consistent with an increased need to forage as nutrient reserves declined through incubation as expected due to energetic constraints.

Nest attendance in female brant was limited by their fasting ability and the effects of this constraint were exacerbated by the lack of food on their territories. These factors made brant nests more vulnerable to avian predators than snow goose nests; nevertheless, brant were able to nest successfully at Anderson River Delta due to a behavioural adaptation whereby male brant guarded their nests while females fed. However, since brant had lower nest and egg survival rates than snow geese, the adaptation to nest guarding behaviour did not compensate completely for the life-history constraint on nest attendance and the environmental constraint that forced brant to forage away from their territories.

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1. GENERAL INTRODUCTION

Reproduction is a key component of life-history strategies, population dynamics, and natural selection. More precisely, the timing and variation in successful reproduction define an organism's life-history strategy (Stearns 1992). Reproductive tactics within a life-history strategy may vary with changes in an individual's age, condition, or environment. When environmental conditions change, adaptive adjustments in reproductive tactics may range from behavioural to genetic (Horn & Rubenstein 1984). However, adaptations to conditions that affect reproductive success within breeding seasons will be constrained by the life-history strategy. Thus, when sympatric species are ecologically similar but their life-history strategies differ, we may expect differences in their reproductive tactics. When those same species differ in reproductive success, they provide an excellent opportunity to study how adaptive responses may be constrained by life-history strategies. An opportunity to do this occurred when two sympatric species of Arctic-nesting geese had a striking difference in reproductive success.

At the Anderson River Delta, black brant *Branta bernicla nigricans* experienced a near reproductive failure while nesting on the same islands as lesser snow geese *Chen caerulescens caerulescens*, which appeared to have high nesting success. The objectives of this study were to examine the effect of life-history

differences between brant and snow geese on their tactics to increase reproductive success.

Before attempting to study interspecific differences, it was necessary to estimate reproductive success in each species in order to determine that apparent differences were real (Chapter 2). In any scientific work, it is incumbent upon researchers to determine how their activities affect phenomena under investigation (Lenington 1979, Huntingford 1984, Knight & Temple 1986). I estimated the effect of disturbance created by my research by comparing clutch sizes in nests visited once and those visited repeatedly, and by comparing nest success in nests that were marked to success in nests left unmarked (Appendix).

In Arctic-nesting geese, reproductive success is influenced by a number of factors. Weather conditions and nutrient reserves can have profound effects on reproduction and have been well studied (Barry 1962, Ryder 1970, Ankney & MacInnes 1978, Ebbinge & Spaans 1995, Lindberg et al. 1997). However, little attention has been paid to the effects of nest predation, which is an important cause of offspring mortality for many species of birds (Nice 1957, Skutch 1966, Ricklefs 1969). Predators take up to 85% of all nests or eggs laid in some species (Klett et al. 1988, Martin 1992), and cause reproductive failure among Arctic geese in some years (Syroechkovskiy et al. 1991, Underhill et al. 1993, Tremblay et al. 1997). Under such intense selection pressure, adaptations to reduce losses of nests or offspring to predators would be expected (Montgomerie & Weatherhead 1988, Martin 1992). Variation in nest predation within or between populations may result from differences in nest vulnerability or detectability due to nest site selection

(Cresswell 1997) or in parents' efforts to defend against predators (Blancher & Robertson 1982, Wiklund 1990).

At Anderson River, brant and snow geese nest in open habitats where nests are easily detected by predators. Detectability is further increased because these geese tend to be both vocal and colonial. Colonies may attract predators resulting in higher predation rates (Clode 1993) or high nest densities may swamp predators resulting in lower predation (Wittenberger & Hunt 1985, Becker 1995) while simultaneously reducing the time each individual must be vigilant (Terhune & Brillant 1996). Nest-site selection within colonies may also influence vulnerability to predators because individuals on the periphery may be more vulnerable than those in central locations (Hamilton 1971). To determine if geese lowered nest vulnerability by nesting colonially, I tested predictions that nest and egg survival would be higher in central nests and at high nest densities (Chapter 3).

Independent of coloniality, parent birds can increase survival of their offspring by defending them from predators (e.g. Wiklund 1990). Even though there may be no conflict between nest guarding and incubation, because both may occur simultaneously (Martin 1992), both may be constrained by species characteristics that influence their life-histories. Brant and snow geese have similar life-history strategies, especially those related to breeding (Bellrose 1980), with one major exception: lesser snow geese are twice as large as brant (Ankney & MacInnes 1978, Ankney 1984). Snow geese have greater absolute nutritional requirements because they are larger than brant but they can survive longer through incubation without feeding since they carry larger nutrient reserves (Ankney & MacInnes 1978, Ankney

1984) and have a lower metabolic rate per gram of body weight (Schmidt-Nielson 1984). Ankney (1984) described brant nesting where food availability was high enough to meet their nutritional requirements without leaving their territories, which enabled brant to feed without leaving their nests exposed to egg predators. Brant territories at Anderson River Delta lacked food (Chapter 2); therefore, I predicted that both male and female brant would adjust their nest guarding tactics to compensate for their need to leave the territory to feed. I tested these predictions by comparing time budgets and nest defence behaviour of brant and snow geese during incubation (Chapter 4).

1.1 References

- Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101:361-370.
- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Barry, T.W. 1962. Effect of late seasons on Atlantic brant reproduction. *J. Wildl. Manage.* 26:19-26.
- Becker, P.H. 1995. Effects of coloniality on gull predation on common tern (*Sterna hirundo*) chicks. *Colonial Waterbirds* 18:11-22.
- Bellrose, F.C. 1980. Ducks, geese and swans of North America, 3rd ed. Harrisburg, Pennsylvania: Stackpole Books.
- Blancher, P.J. & Robertson, R.J. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.* 30:929-945.
- Clode, D. 1993. Colonially breeding seabirds: predators or prey? *Trends Ecol. Evol.* 8:336-338.
- Cresswell, W. 1997. Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* 53:93-103.
- Ebbinge, B.S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26:105-113.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *J. theor. Biol.* 31:295-311.

- Horn, H.S. & Rubenstein, D.I. 1984. Behavioural adaptations and life history. *In* Krebs, J.R. & Davies, N.B. (eds) Behavioural ecology: an evolutionary approach. 2nd ed.: 279-298. Sunderland, Massachusetts: Sinauer Associates.
- Huntingford, F.A. 1984. Some ethical issues raised by studies of predation and aggression. *Anim. Behav.* 32:210-215.
- Klett, A.T., Shaffer, T.L. & Johnson, D.H. 1988. Duck nest success in the prairie pothole region. *J. Wildl. Manage.* 52:431-440.
- Knight, R.L. & Temple, S.A. 1986. Methodological problems in studies of avian nest defence. *Anim. Behav.* 34:561-566.
- Lenington, S. 1979. Predators and blackbirds: the "uncertainty" principle in field biology. *Auk* 96:190-192.
- Lindberg, M.S., Sedinger, J.S. & Flint, P.L. 1997. Effects of spring environment on nesting phenology and clutch size of black brant. *Condor* 99:381-388.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *In* Power, D.M. (ed.) *Curr. Ornithol.*: 9:163-197. New York: Plenum Press.
- Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* 63:167-187.
- Nice, M.M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contr. Zool.* 9:1-48.
- Ryder, J.P. 1970. A possible factor in the evolution of clutch size in Ross' goose. *Wilson Bull.* 82:5-13.

- Schmidt-Nielson, K. 1984. *Scaling: why is animal size so important?* Cambridge: Cambridge University Press.
- Skutch, A.F. 1966. A breeding bird census and nesting success in Central America. *Ibis* 108:1-16.
- Stearns, S.C. 1992. *The evolution of life histories.* Oxford: Oxford University Press.
- Syroechkovskiy, Ye.V., Litvin, K.Ye. & Ebbinge, B.S. 1991. Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988; interplay of weather and Arctic fox predation. *Ardea* 79:373-382.
- Terhune, J.M. & Brilliant, S.W. 1996. Harbour seal vigilance decreases over time since haul out. *Anim. Behav.* 51:757-763.
- Tremblay, J.P., Gauthier, G., Lepage, D. & Desrochers, A. 1997. Factors affecting nesting success in greater snow geese: effects of habitat and association with snowy owls. *Wilson Bull.* 109:449-461.
- Underhill, L.G., Prýs-Jones, R.P., Syroechkovski, E.E. Jr., Groen, N.M., Karpov, V., Lappo, H.G., van Roomen, M.W.J., Rybkin, A., Schekkerman, H., Spiekman, H. & Summers, R.W. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277-292.
- Wiklund, C.G. 1990. The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Anim. Behav.* 40:244-253.
- Wittenberger, J. F. & G. L. Hunt Jr. 1985. The adaptive significance of coloniality in birds. *In* Farner, D.S., King, J.R. & Parkes, K.C. (eds) *Avian Biology*: 8:1-78. Orlando, Florida: Academic Press.

2. NESTING BIOLOGY OF BLACK BRANT AND LESSER SNOW GEESE AT ANDERSON RIVER DELTA, NORTHWEST TERRITORIES

2.1 Introduction

Nesting populations of black brant have declined in recent decades throughout the Arctic (Sedinger et al. 1993, Ward et al. 1993). On Wrangel Island, Russia, the number of nesting brant decreased from "thousands prior to 1940" to fewer than 100 pairs by 1991 (Ward et al. 1993). Following declines that began in the 1960s, three nesting colonies on Alaska's Yukon-Kuskokwim Delta decreased by 60% from 1981 to 1986 (Sedinger et al. 1993). It is not clear what factors caused these population declines, but harvest of both eggs and adults, as well as nest predation are suspected (Anthony et al. 1991, Sedinger et al. 1993, Ward et al. 1993, Ward et al. 1997). Harvesting adults affects population dynamics by reducing survival, whereas egg harvest and nest predation both lower reproductive success. Reducing either adult survival or reproductive success may cause populations to decline.

In Canada, black brant nest along the coast of the Arctic mainland from the Mackenzie River Delta to Queen Maud Gulf in the central Arctic, as well as on Victoria Island and Banks Island (Palmer 1976, Bellrose 1980). One of the largest colonies of black brant in the Canadian Arctic occurs at Anderson River Delta,

Northwest Territories (Sedinger et al. 1993). The number of brant nesting at Anderson River are reported to have declined from as many as 1500 to 400 nesting pairs (Alexander et al. 1988, Sedinger et al. 1993). Even though this colony has been known to biologists for many years, there is no published information on the breeding ecology of brant that nest there, and the cause of any population decline is unknown.

Over much of their nesting range, black brant are sympatric with lesser snow geese (Bellrose 1980). Most lesser snow geese nest in colonies scattered across the Canadian Arctic from Baffin Island to the Mackenzie River Delta. There is also a large colony on Wrangel Island, Russia, and a small colony on Howe Island, Alaska (Bellrose 1980, Johnson 1995). While black brant populations declined over much of their range since the 1960s, lesser snow goose populations increased across most of theirs. Snow goose colonies on Wrangel Island and at Anderson River appear to have declined (Kerbes et al. in prep.) but the midcontinent population has grown steadily since the 1960s (Kerbes 1994, Ankney 1996, Abraham et al. 1996).

Lesser snow geese nesting at Anderson River Delta make up < 5% of the western Canadian Arctic snow goose population, which doubled in size while brant and snow geese at Anderson River declined (Alexander et al. 1988, Sedinger et al. 1993, Kerbes 1986, Kerbes et al. in prep.). Declines in brant and snow goose populations at Anderson River may have been caused by low reproductive success. The first objective in this study was to determine if the number of nesting geese had changed from previous estimates and to assess annual variation in nesting population sizes. The second objective was to estimate reproductive success and relate it to

changes in population size. Reproductive success was measured by clutch size, nest survival, and egg survival rates.

2.2 Study Area

I studied breeding biology of black brant and lesser snow geese from 1991 to 1993 on the outer and middle Anderson River Delta (69°40'N, 129°00'W) where the Anderson River flows into Wood Bay, approximately 160 km east of Tuktoyaktuk, Northwest Territories (Fig. 2.1). The area was described in detail by Mackay (1958) and Barry (1967). The outer and middle delta consist of mud bars and islands up to approximately 1 m elevation. Much of the area is unvegetated mud, but grasses (Graminae) and sedges (*Carex* spp.) dominate parts of the islands. Willows (*Salix* spp.) formerly grew on parts of the study area, but only their dead stems remain. Driftwood accumulates at the high-water line but is scattered across the area by storm tides. Nesting habitat includes bare mud, driftwood, dead willows, and grass and sedge turf. Willow stems are sparse and low (<10 cm) and turf vegetation is <5 cm high.

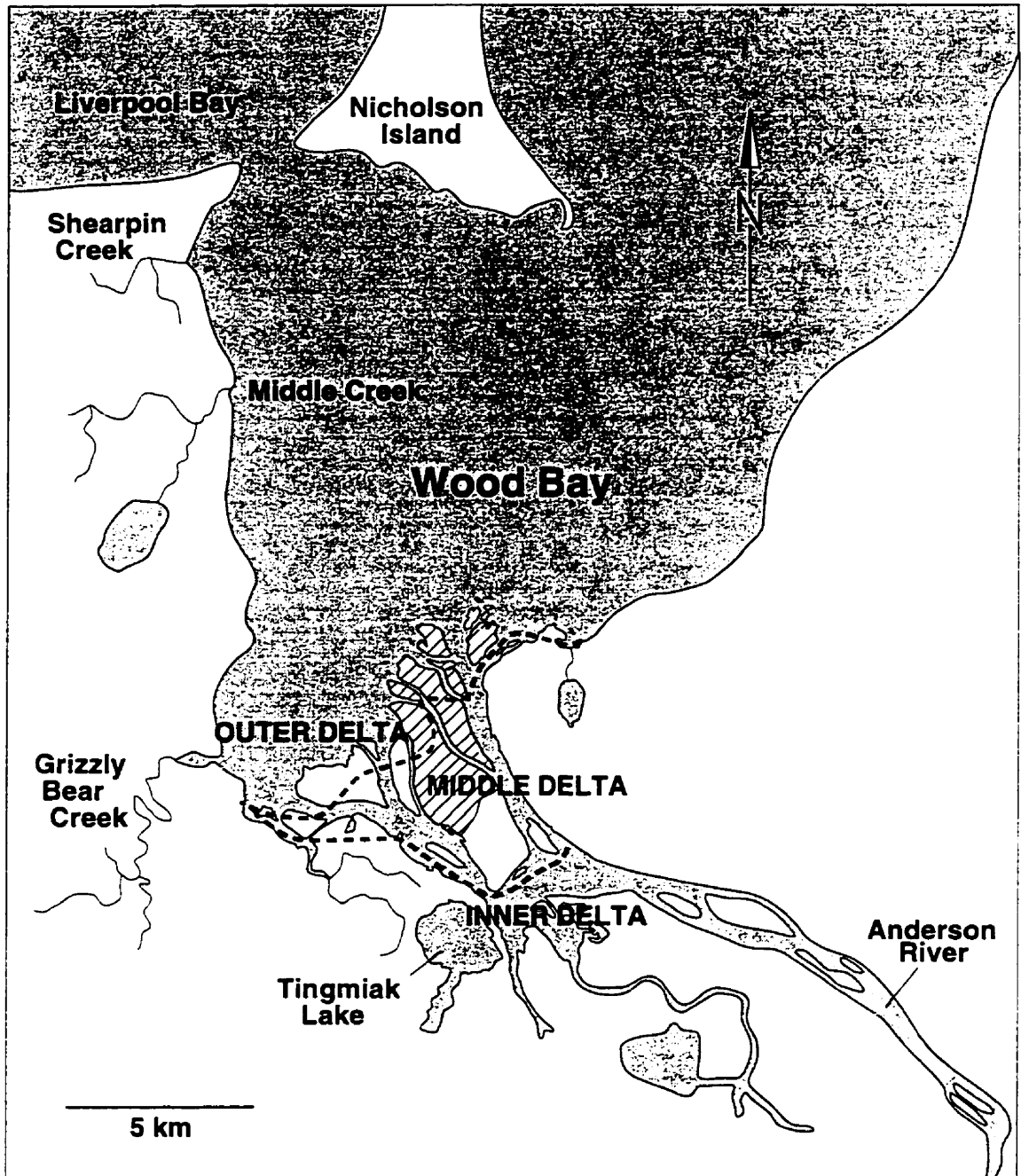


Figure 2.1. Map of the Anderson River Delta, NWT. Outer, middle, and inner Delta areas were delineated after Barry (1967). The hatched area was searched for nests.

2.3 Methods

2.3.1 Population Size and Nesting Distribution

Density of brant and snow goose nests on the Anderson River Delta was estimated by line transect sampling (Burnham et al. 1980). Line transect sampling is distinguished from strip or quadrat sampling methods by two main features. In line transect sampling, it is assumed that some objects will be missed, and the probability that an object (e.g. nest) will be missed increases with its distance from the transect centre line and, second, the distance of each object from the transect centre line is determined (Burnham et al. 1980 p. 10). Line transect sampling requires assumptions that points on the line (i.e. distance equal to zero) will never be missed, points are fixed at the initial sighting position (i.e. do not move away from observers), measurements are made without error or rounding, and sightings are independent events (Burnham et al. 1980 p. 14). These assumptions are reasonable when sampling goose nests whether or not nests are active, unlike the assumption required for quadrat sampling methods (e.g. quadrats or strip transects) where all individuals within the quadrat must be counted, or a correction factor applied to account for individuals missed (Krebs 1989, Walter & Rusch 1997). Density estimates from line transect sampling do not require nests to be randomly or independently distributed in the area of interest (Burnham et al. 1980 p. 14). Sampling results in a sample size and a set of distances from which density is estimated. Since probability of detecting an object is a decreasing function of

distance from the transect centre line, density of objects is estimated by fitting a detection function to the data (Burnham et al. 1980).

All islands in the outer and middle delta (Fig. 2.2) and the mainland area east of Snow Goose Creek and north of Tingmiak Lake were sampled except in 1993, when Canoe Island, Triangle Island, and the mainland area could not be reached. Lines were 500 m apart on an east-west axis which crossed features that affected the distribution of nesting geese. The first line fell on the northern most 1000 m Mercator grid line to cross the Gull Islets on a 1:50,000 scale topographic map. Lines extending across nesting islands and the mainland area were added until the entire length of Fox Den Island was sampled. Transect width was truncated at 50 m because few nests were found >50 m from the line and model fit was improved by excluding them. Line transect sampling was done in July each year, after both brant and snow geese had hatched. Only nests that were active in the current year, based on condition of nest material and disturbance around the bowl, were included in the sample. Nests were identified to species by the size of the nest bowl and colour of feathers. Brant make smaller nest depressions and have dark grey down whereas snow geese create larger nest bowls and have white down (W. T. Armstrong, pers. obs.).

Transect lines were walked by two observers. One remained on the transect centre line at all times to provide the reference point for measuring distances to nests, and to ensure that no nests on the line were missed. Perpendicular distances from the line to nests were measured with a 50 m fibreglass tape. Lengths of transect lines were measured from a 1:50,000 map and areas of each island were

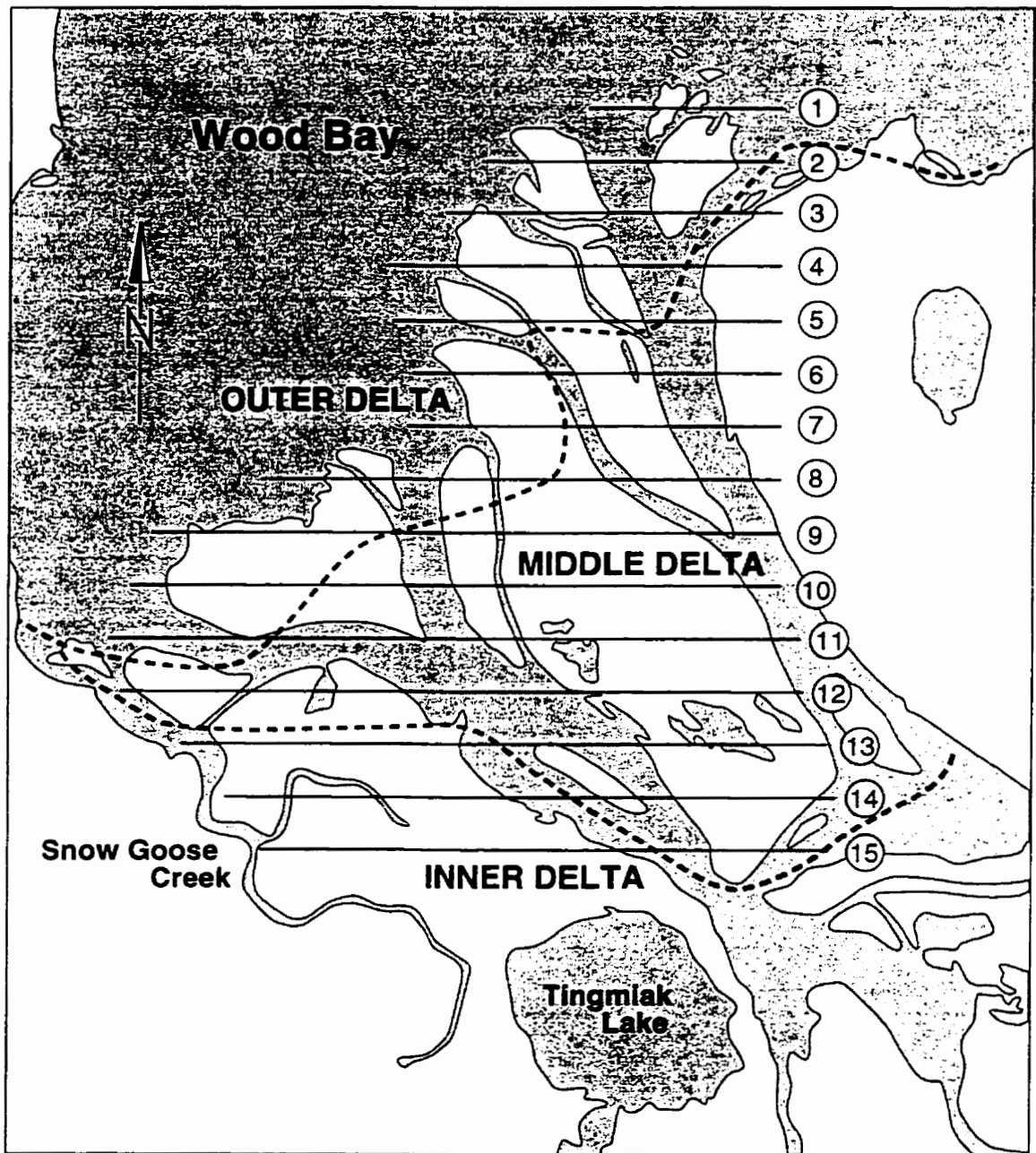


Figure 2.2. Location of transect lines sampled for black brant and lesser snow goose nests at Anderson River Delta, NWT.

calculated from digitized images on aerial photographs. Tundra ponds were included in the measurement of line lengths and island areas. Nest densities were estimated from line transect data using program TRANSECT (Laake et al. 1979).

An estimate of nesting population size based on nests sampled after hatch requires an assumption that the number of nesting pairs equals the number of nests. The population estimate will be biased if this assumption is not valid. If geese continue laying in a new nest after a failed attempt, the number of nests will over estimate the number of breeding pairs. Both brant and snow geese may continue laying in a second nest if their first is destroyed early in egg laying (Barry 1962 p. 22, Ganter & Cooke 1993) and those that lose their eggs to predators "nearly always abandon" their nest site (Cooke et al. 1995 p. 25). Estimated nest densities were adjusted for the proportion of nests estimated to have failed early in egg laying each year. Proportion of nests that failed during laying was estimated from nest survival rates during laying or early incubation (see below). I assumed that females whose nests were destroyed before the third day of egg-laying (brant in 1991 and 1992) or fourth day (brant in 1993, snow geese in all years) completed egg-laying in a new nest. Brant were assumed to lay one egg per day and snow geese to lay one egg every 1.3 days (Ryder 1971, Mickelson 1975, Schubert & Cooke 1993).

2.3.2 Nesting Biology

Nesting biology of brant was studied from 1991 to 1993 and snow geese were studied in 1992 and 1993. The nesting study area (Fig. 2.1) excluded only three

islands (Gull, Canoe, and Triangle) where brant or snow geese regularly nested (Fig. 2.3).

In 1991, the nesting study area was divided in half and each was searched completely for brant nests on alternate days throughout the egg-laying period. Nests were visited on alternate days until egg-laying was completed and were revisited daily beginning two days prior to estimated hatch date. Nests were deemed successful if at least one egg hatched. After 1991, I searched for nests at the end of each species' egg-laying period when nearly all clutches had been completed. Eggs were numbered with waterproof black ink so that I could detect egg losses or additions between visits and were covered with nest material after each visit. Nests were revisited at seven-day intervals in 1992 and at five-day intervals in 1993 to record new or missing eggs and any other evidence of predation. Nests were visited only during incubation in 1992 and 1993 and nests were "successful" if at least one egg remained at the last nest check.

Nest and egg survival rates were estimated using the Mayfield method (Mayfield 1961, 1975, Johnson 1979, Flint et al. 1995b). Daily nest and egg survival rates were estimated for each interval (e.g. early and late incubation) and tested for differences between intervals (Johnson 1979, Sauer & Williams 1989). If nest or egg survival rates differed significantly between intervals, a weighted mean rate over the entire observation period was estimated. The mean was calculated by weighting each rate by the number of nests that contributed to its estimate and interval length. Standard error of the mean was estimated by the standard deviation of 5000 weighted mean survival rates calculated by bootstrap resampling the original

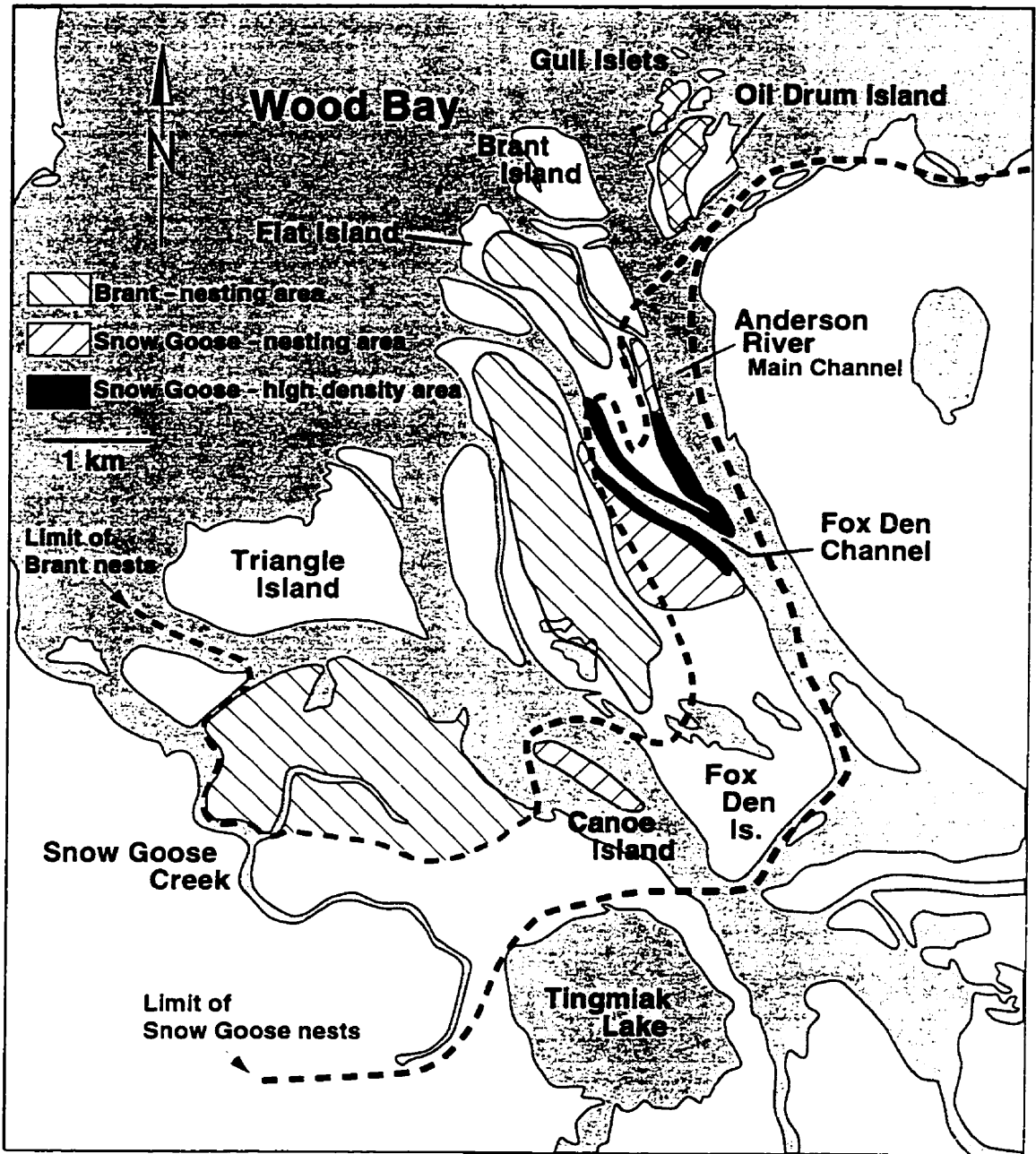


Figure 2.3. Black brant and lesser snow goose nesting areas at Anderson River Delta, NWT, 1991 - 1993. Main nesting areas are hatched. Brant and snow geese nested at low densities outside the hatched areas as far south as the dashed lines.

data (Efron & Tibshirani 1993, Flint et al. 1995b). Season long nest and egg survival rates were calculated by raising daily rates to an exponent equal to the length of laying plus incubation periods.

Clutch size at hatch was recorded when the first egg began to hatch in brant nests in 1991. In 1992 and 1993, clutch size at hatch was estimated by the product of clutch size and mean daily egg survival through incubation, in successful nests, raised to an exponent equal to the length of incubation.

I used simple models to estimate year-specific exponential rates of increase in brant and snow goose populations at Anderson River Delta based on clutch size, nest success, and egg survival in successful nests during this study. Model statements for brant were:

$$N_{a,t+1} = (N_{2,t} + N_{a,t}) \cdot S_a$$

$$N_{2,t+1} = N_{1,t} \cdot S_a$$

$$N_{1,t+1} = \text{Goslings} \cdot S_{juv}$$

$$\text{Goslings} = (N_{2,t} \cdot P_{b2} + N_{a,t}) \cdot (CS \cdot S_{nest} \cdot S_{egg} \cdot S_{hatch} \cdot S_{brood} \cdot SR),$$

and for snow geese:

$$N_{a,t+1} = (N_{3,t} + N_{a,t}) \cdot S_a$$

$$N_{3,t+1} = N_{2,t} \cdot S_a$$

$$N_{2,t+1} = N_{1,t} \cdot S_a$$

$$N_{1,t+1} = \text{Goslings} \cdot S_{juv}$$

$$\text{Goslings} = (N_{2,t} \cdot P_{b2} + N_{3,t} \cdot P_{b3} + N_{a,t}) \cdot (CS \cdot S_{nest} \cdot S_{egg} \cdot S_{hatch} \cdot S_{brood} \cdot SR).$$

Where N_a = number of adult females, N_3 = number of three-year old females, N_2 = number of two-year old females, N_1 = number of yearling females. P_{b2} and P_{b3} =

probability of nesting at age 2 and 3, respectively. P_{b3} and N_3 were used for snow geese only. Probability of breeding as adults was set to 1.0 in both species, and three-year old brant were considered to be adults. *Goslings* = the number of female goslings surviving to fledging. S_a = annual survival of geese over one year of age. S_{juv} is survival rate of juveniles from fledging to beginning of the next nesting season. CS = clutch size, S_{nest} = nest survival through laying and incubation, S_{egg} = egg survival rate in surviving nests, S_{hatch} = survival of goslings from beginning of hatch to leaving the nest, and S_{brood} is survival of goslings from nest exodus to fledging. SR = sex ratio; the models were restricted to females only. For both species, $\lambda = \Sigma N_{i,t+1} / \Sigma N_{i,t}$ and exponential rate of increase, $r = \ln(\lambda)$.

Parameter estimates other than clutch size, nest survival, and egg survival were obtained from other studies (Table 2.1). Annual survival rates of snow geese were taken from geese banded in the western Canadian Arctic, mainly at Anderson River (Hines et al. in prep., J. Hines, Canadian Wildlife Service, Yellowknife, pers. com.). Yearling brant and snow geese were assumed to have the same survival rates as adults (J. Hines, Canadian Wildlife Service, Yellowknife, pers. com.). Estimates were made from initial population sizes of 1000 adult females and annual values of clutch size, nest survival, and egg survival during this study. λ and r were determined after reaching a stable age distribution for each set of starting values. Average rate of change in population size was estimated by the arithmetic mean of annual exponential rates of increase (r).

Statistical tests that had a type I error probability of <0.05 were considered to be statistically significant. All other tests were denoted by n.s.

Table 2.1. Parameter estimates used in population models.

Parameter	Estimate		Sources ^a
	Brant	Snow Geese	
Clutch size (CS)	Table 2.3	Table 2.3	This study
Nest survival (S_{nest})	Table 2.4	Table 2.4	This study
Egg survival (S_{egg})	Table 2.5B	Table 2.5B	This study
Hatching success (S_{hatch})	0.72 ^b , 0.93 ^c	0.93	This study, 1
Gosling survival (S_{brood})	0.68	0.69	1, 2
Sex ratio (SR)	0.50 ^c	0.50	3
Juvenile survival (S_{juv})	0.65 ^d	0.60 ^d	4, 6
Adult survival (S_a)	0.84	0.80	5, 6
Probability of breeding (P_{b2})	0.50 ^c	0.50	1
Probability of breeding (P_{b3})	1.0 ^c	0.86	1

^a Source 1 = Cooke et al. 1995, 2 = Flint et al. 1995a, 3 = Cooke & Harmsen 1983, 4 = Sedinger et al. 1997, 5 = Ward et al. 1997, 6 = Hines et al. in prep.

^b S_{hatch} = 0.72 in 1991 (this study), data from Cooke et al. (1995) used after 1991.

^c Estimate for snow geese used for brant.

^d Survival for 9.5 months estimated from annual survival of juveniles.

^e All female brant assumed to breed at age 3 and older ($P_{b3} = 1.0$).

2.4 Results

2.4.1 Population Size and Nesting Distribution

Total length of transect lines sampled was 38,700 m per year, except in 1993 when 23,920 m were sampled. Snow goose nests were three- to five-times more abundant than brant nests at Anderson River Delta each year and varied more among years (Table 2.2). When the sampled area was expanded from the nesting study islands to include the mainland area east of Snow Goose Creek, the estimated number of brant nests doubled but there was a much smaller increase in snow goose nests (Table 2.2).

The number of nests would have over estimated the nesting population of brant by 17% in 1991 and 1992 due to continuation nesting, but only by 7% in 1993. Assuming half the brant nested on the mainland (Table 2.2), the nesting population in 1993 would have numbered 1600 to 1700 pairs. Continuation nesting by snow geese may have caused their numbers to be over estimated by as much as 37% in 1992, but only 2% in 1993. If 30% of the snow goose population nested on the mainland as in 1992, the total nesting population of snow geese in 1993 would have been 5000 pairs.

Distributions of nesting brant and snow geese overlapped but the main nesting areas of each species were separate. Brant nested on the outer delta and lower parts of the middle delta (Fig. 2.3) usually near shore or next to one of the numerous tundra ponds. Snow geese nested throughout the delta but were concentrated on Flat

Table 2.2. Number (95% C.I.) of black brant and lesser snow goose pairs nesting at Anderson River Delta, NWT. Estimates, adjusted for continuation nests, were made by line transect sampling nests after hatch.

	Brant	Snow Geese
1991		
Study islands	476 (198 - 744)	4,549 (2,489 - 6,611)
Islands + mainland	1,070 (595 - 1,545)	4,955 (2,606 - 7,301)
1992		
Study islands	472 (201 - 744)	1,316 (262 - 2,370)
Islands + mainland	1,039 (520 - 1,557)	1,863 (26 - 3,700)
1993		
Study islands	866 (470 - 1,262)	3,606 (1,813 - 5,400)
Islands + mainland	1,600 - 1,700 ^a	5,000 ^a

^a Mainland area was not sampled in 1993. Total number of nests was estimated by extrapolation assuming 50% of brant nests and 30% of snow goose nests were on the mainland area.

and Fox Den Islands (Fig. 2.3).

2.4.2 Nesting Biology

I found 230 brant nests in 1991, 101 brant and 111 snow goose nests in 1992, and 110 brant and 174 snow goose nests in 1993. Clutch size in brant varied significantly among islands in 1991 ($F_{2,217} = 4.19$, $P < 0.02$) but did not vary among islands in either species in 1992 or 1993 (ANOVA, n.s.). Clutch sizes in brant varied among years and were smaller than snow goose clutches (Table 2.3).

Nest survival varied widely among years in both brant and snow geese (Table 2.4). Nest survival was very low in 1992 due to egg predation by grizzly bears *Ursus arctos*, otherwise the main egg predators each year were glaucous gulls *Larus hyperboreus* and parasitic jaegers *Stercorarius parasiticus*. Nest survival in brant was higher than in snow geese in 1992 but lower in 1993, and both species had higher nest survival in 1993 than 1992 (Table 2.4). In 1991, daily survival of brant nests increased from egg-laying (0.912 ± 0.013 , $\bar{x} \pm SE$, $n = 155$) to incubation (0.954 ± 0.004 , $n = 185$, $\chi^2_1 = 9.62$, $P < 0.01$). Estimated survival of brant nests was 76% (95% C.I. 70 - 82%) through egg-laying and 32% (26 - 39%) through incubation. In 1992, nest survival during incubation increased from the first to the second observation interval in both brant ($\chi^2_1 = 4.73$, $P < 0.05$) and snow geese ($\chi^2_1 = 12.27$, $P < 0.001$), but it did not change during incubation in either species in 1993 (both tests n.s.). Average survival of brant nests through the entire incubation period was 15% (10 - 24%) in 1992 and 70% (60 - 82%) in 1993. Snow

Table 2.3. Mean clutch size (\pm SE (n)) of black brant and lesser snow geese at Anderson River Delta, NWT.

	Brant	Snow Geese	t^a	P
1991	2.8 \pm 0.1 (230)	4.0 \pm 0.1 ^b (70)	-	-
1992	2.9 \pm 0.1 (101)	4.4 \pm 0.2 (111)	6.29 (df = 183 ^c)	0.0001
1993	3.7 \pm 0.1 (110)	4.2 \pm 0.1 (174)	3.50 (df = 282)	0.0001
Test ^d	$F_{2,428} = 18.14$	$t_{283} = 0.94^b$		
P	0.0001	0.31		

^a Comparison of clutch size between species.

^b In 1991, snow goose clutch sizes were sampled at mid-incubation and therefore were excluded from significance tests.

^c Degrees of freedom from t -test using unequal variance model.

^d Comparison of clutch size within species.

Table 2.4. Average Mayfield daily (\pm SE (*n*)) and season long nest survival rates (95% C.I.) of black brant and lesser snow geese at Anderson River Delta, NWT.

	Brant	Snow Geese	Z ^a	P
1991				
Daily	0.950 \pm 0.006 (230)	- ^b	-	-
Seasonal	0.25 (0.18 - 0.35)			
1992				
Daily	0.925 \pm 0.009 (101)	0.881 \pm 0.011 (111)	3.15	0.01
Seasonal	0.15 (0.10 - 0.24)	0.05 (0.03 - 0.09)		
1993				
Daily	0.985 \pm 0.003 (110)	0.993 \pm 0.002 (174)	2.07	0.04
Seasonal	0.70 (0.60 - 0.82)	0.85 (0.79 - 0.92)		
Test ^c	$\chi^2 = 129.49$	Z = 10.10		
P	0.001	0.001		

^a Test of daily nest survival rates between species.

^b Snow goose nest survival was not monitored in 1991.

^c Test of daily nest survival rates within species.

goose nest survival through incubation was 5% (3 - 9%) in 1992 and 85% (79 - 92%) in 1993.

Egg survival rates varied greatly among years and between species (Table 2.5). In nests that survived the observation period, snow geese had higher daily egg survival than brant but annual differences in daily survival rates within species were not significant (Table 2.5). In 1991, daily egg survival in brant increased from 0.895 ± 0.015 ($n = 155$) during egg-laying to 0.948 ± 0.004 ($n = 185$) during incubation ($\chi^2_1 = 12.2$, $P < 0.001$). In successful nests, daily egg survival declined slightly from egg-laying (0.995 ± 0.004 , $n = 40$) to incubation (0.985 ± 0.002 , $n = 63$, $\chi^2_1 = 4.57$, $P < 0.05$). In 1992, overall egg survival during incubation increased from the first to the second observation interval in both brant ($\chi^2_1 = 10.29$, $P < 0.01$) and snow geese ($\chi^2_2 = 5.15$, $P < 0.05$). However, in nests that survived the observation period in 1992, egg survival did not change between intervals in either brant ($\chi^2_1 = 2.45$, n.s.) or snow geese ($\chi^2_1 = 3.17$, n.s.). In 1993, there was no difference in egg survival among intervals (all tests n.s.) so egg survival was calculated assuming a constant daily survival rate for the entire observation period (Table 2.5).

Clutch sizes at hatching mirrored total clutch size variation among years and between species (Table 2.6). In 1991, an average of 1.8 goslings left nests with their parents (95% C.I. 1.5 - 2.1, $n = 60$ nests). The mean difference (0.7) between clutch size at hatch and number of goslings that left nests was due to

Table 2.5. Average Mayfield daily (\pm SE (n)) and season long egg survival rates (95% C.I.) of black brant and lesser snow geese at Anderson River Delta, NWT, in all nests (A) and successful nests only (B).

A: All nests				
	Brant	Snow Geese	Z ^a	P
1991				
Daily	0.942 ^b \pm 0.007 ^c (230)	- ^d	-	-
Seasonal	0.20 (0.13 - 0.30)			
1992				
Daily	0.914 \pm 0.009 (101)	0.873 \pm 0.016 (111)	2.80	0.01
Seasonal	0.08 (0.05 - 0.15)	0.02 (0.01 - 0.06)		
1993				
Daily	0.979 \pm 0.003 (110)	0.991 \pm 0.002 (174)	3.44	0.001
Seasonal	0.55 (0.46 - 0.65)	0.77 (0.69 - 0.87)		
Test ^e	$\chi^2_2 = 63.32$	Z = 10.14		
P	0.001	0.001		

Table 2.5. Continued.

B: Successful nests				
	Brant	Snow Geese	Z ^a	P
1991				
Daily	0.986 ^b ± 0.002 ^c (63)	- ^d	-	-
Seasonal	0.68 (0.61 - 0.76)			
1992				
Daily	0.976 ± 0.005 (39)	0.992 ± 0.003 (25)	3.04	0.01
Seasonal	0.52 (0.39 - 0.68)	0.80 (0.67 - 0.95)		
1993				
Daily	0.989 ± 0.002 (90)	0.997 ± 0.001 (157)	3.79	0.001
Seasonal	0.74 (0.66 - 0.82)	0.92 (0.87 - 0.97)		
Test ^e	$\chi^2_2 = 6.84$	Z = 1.53		
P	0.05	0.06		

^a Test of daily egg survival rates between species.

^b Weighted mean of egg-laying and incubation survival rates. All nests: laying $n = 155$, incubation $n = 185$. Successful nests: laying $n = 40$, incubation $n = 63$.

^c SE estimated from bootstrap resampling procedure repeated 5000 times.

^d Snow goose egg survival was not monitored in 1991.

^e Test of daily egg survival rates within species.

Table 2.6. Mean clutch size at hatching (95% C.I.) (*n*) of black brant and lesser snow geese nesting at Anderson River Delta, NWT.

	Brant	Snow Geese
1991	2.5 (2.2 - 2.7) (230)	- ^a
1992	1.6 ^b (1.2 - 2.2) (101)	3.7 ^b (3.1 - 4.3) (111)
1993	2.8 ^b (2.4 - 3.3) (110)	3.9 ^b (3.6 - 4.3) (174)

^a Not available.

^b Predicted from clutch size and egg survival in successful nests in 1992 and 1993

predation, eggs that failed to hatch, and abandonment. Snow geese had larger estimated clutch size at hatch than brant in both 1992 and 1993 (Table 2.6).

Population models suggested that both brant and snow geese nesting at Anderson River declined during this study. Mean exponential rate of increase for brant was -0.04 and for snow geese it was -0.02. In 1993, when both species had higher reproductive success, $r = 0.10$ for brant $r = 0.15$ for snow geese. Estimates of r were most sensitive to changes in adult survival (W. T. Armstrong, pers. obs.).

2.5 Discussion

2.5.1 Population Size and Nesting Distribution

The nesting population of brant at Anderson River Delta appeared to have declined little if at all from a previous estimate of 1500 pairs (Alexander et al. 1988) but was larger than Sedinger et al.'s (1993) estimate of 400 pairs. Confidence intervals of number of nesting brant included 1500 in both 1991 and 1992, and the point estimate exceeded 1500 in 1993. Estimates of nesting snow geese obtained by line transect sampling were intermediate to counts from photographs covering the entire Anderson River Delta in 1987 and 1995 and were consistent with a decline in numbers between 1981 and 1995 (Kerbes 1986, Kerbes et al. in prep.). Variation in population estimates among years, particularly in snow geese, points to potential concerns with infrequent surveys of nesting colonies. Large annual variation could either mask long term trends in population size, or reveal spurious trends. Numbers

of nesting snow geese counted on photographs of nesting areas during incubation will under estimate the number that initiated egg-laying if nest success is low and failed breeders disperse from nesting areas (Kerbes 1983, 1986). Snow goose nest success was low in 1992 and few failed breeders appeared to remain at Anderson River (Barry 1967, W. T. Armstrong, pers. obs.).

The distribution of both nesting brant and the vegetation communities of the outer and middle delta appear to have changed since the 1960s. Barry (1967 p. 79) reported Brant Island was an important nesting area for brant and described the habitat there as an "interspersed mud flats, grassy clumps or hummocks, small shallow sloughs and puddles and a turf of brant grass (*Carex subspathacea*) and *Puccinellia phryganodes*." By 1991, Brant Island was mostly mud flats with sparse stands of *Carex* and *Puccinellia* on the north and west sides and few brant nested there. Barry's (1967) description of Brant Island more accurately described part of the brant nesting area on Fox Den Island during this study (Fig. 2.3). Much of Flat Island and the north end of Fox Den Island formerly supported stands of low willow (*Salix* spp.) but by 1991 only their dead stems remained. Both vegetation communities and nesting brant appear to have shifted south from the outer to the middle delta between the 1960s and the 1990s. The reason for these changes in distribution of both vegetation and nesting brant are unknown, but may be related to intense herbivory by geese (Srivastava & Jefferies 1996). During this study, many brant nested in mud habitat without *Carex* and *Puccinellia* turf and, unlike other brant on Southampton Island (Ankney 1984), were unable to graze on their territories.

2.5.2 Nesting Biology

Brant clutch sizes were lower than most previous estimates from Anderson River Delta (Barry 1967) as well as other brant nesting areas (Abraham & Ankney 1986, Madsen et al. 1989, Summers et al. 1994, Lindberg et al. 1997) and were consistently smaller than snow goose clutches during this study. Snow goose clutch sizes were similar to those of snow geese nesting at La Pérouse Bay, Manitoba (Cooch et al. 1989). High predation rates likely caused clutch sizes observed in this study to under estimate the number of eggs laid by nesting females. The bias would have been more severe in brant because they suffered greater egg losses, even in successful nests. Predation would result in lower clutch size estimates for two reasons. First, eggs may have been removed during partial clutch predation (Chapter 4) before nests were found, and females whose nests were destroyed before they finished egg laying may have completed their clutch in new nests. Predation during egg laying may have caused inflated estimates of clutch size if failed nesters completed laying their eggs parasitically (Lank et al. 1989). If failed breeders resorbed developing follicles (Hamann et al. 1986) there would be no effect on observed clutch sizes. It is unlikely that clutch size estimates were greatly biased due to intraspecific nest parasitism because clutch sizes were consistently smaller than reported elsewhere.

Nest survival rates of brant and snow geese in 1991 and 1992 were similar to those reported for brant nesting on Svalbard (Madsen et al. 1989) and in Alaska when nesting populations were declining rapidly and nest predation by foxes was

intense (Anthony et al. 1991). Such low nest survival may indicate that in the first two years of this study, geese at Anderson River were suffering reproductive failure that could lead to population declines. However, both species may have experienced population growth in 1993 when nest survival rates were higher than in previous years and similar to those of increasing goose populations elsewhere (Anthony et al. 1991, Rockwell et al. 1993, Bruggink et al. 1994). Egg survival rates in both brant and snow geese at Anderson River were consistently lower than rates reported for other goose populations (Cooke et al. 1985).

Snow geese had consistently larger clutches than brant as well as higher nest and egg survival rates. These results suggest that snow geese had greater reproductive success than brant at Anderson River Delta possibly because they were less vulnerable to egg predation by avian predators. Unless recruitment of brant goslings or adult survival were sufficient to overcome the difference in reproductive success, then snow geese would have increased faster, or declined slower, than brant.

Estimates of r were most sensitive to adult survival (W. T. Armstrong, pers. obs.) unlike Cooke & Rockwell (1988) who found lifetime reproductive success varied most with first-year survival which suggests that r should be influenced by variation in survival rates of adults or juveniles more than variation in reproductive success. However, r would still be influenced greatly by variation in reproduction because reproductive success varied much more (e.g. snow goose nest survival varied from 0.05 to 0.85) than survival estimates (e.g. Kirby et al. 1986, Francis & Cooke 1992, Sedinger et al. 1997, Ward et al. 1997). Population models indicated

that numbers of both brant and snow geese were declining at Anderson River. Model projections indicated that snow geese had higher exponential rates of increase than brant in spite of having lower survival rates. In 1993, reproductive success in both species was sufficient to result in projected increases, although it was greater in snow geese. A projected decline in nesting snow geese and the population estimates were consistent with a decline in snow geese nesting at Anderson River Delta (Kerbes 1986, Kerbes et al. in prep.). Model projections of a declining brant population clearly contradicted my nesting population estimates, which suggested there had been either little change or an increase from previously reported estimates of brant nesting at Anderson River (Alexander et al. 1988, Sedinger et al. 1993). The contradiction between brant population estimates and model projections may be resolved if (1) brant numbers were over estimated even after correcting for bias due to continuation nesting; (2) model projections were inaccurate; (3) brant reproduction from 1991 to 1993 was lower than the long term average; or (4) the nesting population was augmented by immigration.

It is possible that my estimates of nesting brant were too high. However, snow goose estimates were consistent with counts from photographic surveys (Kerbes 1986, Kerbes et al. in prep.) and there is little reason for biases in the technique used to differ between species. It is a near certainty that model projections were inaccurate, and should be viewed with caution, particularly since survival estimates were drawn from other studies. Survival rates can vary greatly among both nesting colonies and years (e.g. Kirby et al. 1986, Francis & Cooke 1992, Francis et al. 1992, Sedinger et al. 1997, Ward et al. 1997), therefore it is likely that survival

rates used differed from those experienced by geese during this study. Geese tend to be highly philopatric to nesting areas (Anderson et al. 1992); however, immigration of nesting females has been documented in snow geese (Geramita & Cooke 1982, Johnson 1995) and barnacle geese *Branta leucopsis* (Larsson et al. 1988). Immigrant pairs of geese were most likely migrants that nested in the new areas instead of continuing on to their traditional areas (Larsson et al. 1988, Johnson 1995).

Migrating brant and snow geese pass through Anderson River Delta in spring (Barry 1967, W. T. Armstrong, pers. obs.), probably on their way to nesting areas on Banks Island. Thus recruitment at some colonies may be augmented by immigrants, and the Anderson River Delta may be a population sink maintained by immigration. However, the most likely cause of disagreement between model projections and population estimates is due to taking a short term snapshot view of reproductive success when long term changes in population size reflect the long term average difference between inputs and losses. There was great variation in reproductive success of both brant and snow geese so average results from 1991 to 1993 may have under estimated long term average reproductive success at Anderson River. High reproductive success in 1993 suggests that populations may increase in some years but decline following failures in others.

Low reproductive success during this study appears to support reports that snow geese (Kerbes 1986, Kerbes et al. in prep.) and brant declined at Anderson River (e.g. Sedinger et al. 1993). However, population estimates suggested that nesting brant had not declined (see Alexander et al. 1988) even though brant had lower reproductive success than snow geese. The discrepancy between reproductive

success and population estimates suggest that immigration may help maintain the nesting population at Anderson River, at least for brant. Even though snow geese declined they had higher reproductive success than brant, in part because brant lost a larger proportion of their eggs to avian predators. However, it is not clear why avian predators took fewer snow goose eggs.

2.6 References

- Abraham, K.F. & Ankney, C.D. 1986. Summer birds of East Bay. Southampton Island, Northwest Territories. *Can. Field-Nat.* 100: 180-185.
- Abraham, K.F., Jefferies, R.L., Rockwell, R.F. & MacInnes, C.D. 1996. Why are there so many white geese in North America? *In* Ratti, J.T. (ed.) Proceedings of 7th International Waterfowl Symposium: 79-92. Memphis, Tennessee: Ducks Unlimited, Institute for Wetland and Waterfowl Research.
- Alexander, S.A., Barry, T.W., Dickson, D.L., Prus, H.D. & Smyth, K.E. 1988. Key areas for birds in coastal regions of the Canadian Beaufort Sea. Edmonton, Alberta: Canadian Wildlife Service.
- Anderson, M.G., Rhymer, J.M. & Rohwer, F.C. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. *In* Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) Ecology and management of breeding waterfowl: 365-395. Minneapolis: University of Minnesota Press.
- Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101:361-370.
- Ankney, C.D. 1996. An embarrassment of riches: too many geese. *J. Wildl. Manage.* 60:217-223.
- Anthony, R.M., Flint, P.L. & Sedinger, J.S. 1991. Arctic fox removal improves nest success of black brant. *Wildl. Soc. Bull.* 19:176-184.

- Barry, T.W. 1962. Effect of late seasons on Atlantic brant reproduction. *J. Wildl. Manage.* 26:19-26.
- Barry, T. W. 1967. Geese of the Anderson River Delta, Northwest Territories. Ph.D. thesis, University of Alberta, Edmonton.
- Bellrose, F.C. 1980. Ducks, geese and swans of North America, 3rd ed. Harrisburg, Pennsylvania: Stackpole Books.
- Bruggink, J.G., Tacha, T.C., Davies, J.C. & Abraham, K.F. 1994. Nesting and brood-rearing ecology of Mississippi Valley population Canada geese. *Wildl. Monogr.* 126:1-39.
- Burnham, K.P., Anderson, D.R. & Laake, J.L. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72:1-202.
- Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. 1989. Long-term decline in fecundity in a snow goose population: evidence for density dependence? *J. Anim. Ecol.* 58:711-726.
- Cooke, F. & Harmsen, R. 1983. Does sex ratio vary with egg sequence in lesser snow geese? *Auk* 100:215-217.
- Cooke, F. & Rockwell, R.F. 1988. Reproductive success in a lesser snow goose population. *In* Clutton-Brock, T.H. (ed.) *Reproductive success*: 237-250. Chicago: University of Chicago Press.
- Cooke, F., Rockwell, R.F. & Lank, D.B. 1995. *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. New York: Oxford University Press Inc.

- Cooke, F., Findlay, C.S., Rockwell, R.F. & Smith, J.A. 1985. Life history studies of the lesser snow goose (*Anser caerulescens caerulescens*). III. The selective value of plumage polymorphism: net fecundity. *Evolution* 39:165-177.
- Efron, B. & Tibshirani, R.J. 1993. An introduction to the bootstrap. New York: Chapman & Hall.
- Flint, P.L., Sedinger, J.S. & Pollock, K.H. 1995a. Survival of juvenile black brant during brood rearing. *J. Wildl. Manage.* 59:455-463.
- Flint, P.L., Pollock, K.H., Thomas, D. & Sedinger, J.S. 1995b. Estimating pre fledging survival: allowing for brood mixing and dependence among brood mates. *J. Wildl. Manage.* 59:448-455.
- Francis, C.M. & Cooke, F. 1992. Sexual differences in survival and recovery rates of lesser snow geese. *J. Wildl. Manage.* 56:287-296.
- Francis, C.M., Richards, M.H. & Cooke, F. & Rockwell, R. F. 1992. Long-term changes in survival rates of lesser snow geese. *Ecology* 73:1346-1362.
- Ganter, B. & Cooke, F. 1993. Reaction of lesser snow geese *Anser caerulescens* to early nest failure. *Wildfowl* 44:170-173.
- Geramita, J.M. & Cooke, F. 1982. Evidence that fidelity to natal breeding colony is not absolute in female snow geese. *Can. J. Zool.* 60:2051-2056.
- Hamann, J., Andrews, B. & Cooke, F. 1986. The role of follicular atresia in inter- and intra-seasonal clutch size variation in lesser snow geese (*Anser caerulescens caerulescens*). *J. Anim. Ecol.* 55:481-489.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.

- Johnson, S.R. 1995. Immigration in a small population of snow geese. *Auk* 112:731-736.
- Kerbes, R.H. 1983. Lesser snow goose colonies in the western Canadian Arctic. *J. Wildl. Manage.* 47:523-526.
- Kerbes, R.H. 1986. Lesser snow geese, *Anser c. caerulescens*, nesting in the western Canadian Arctic in 1981. *Can. Field-Nat.* 100:212-217.
- Kerbes, R.H. 1994. Colonies and numbers of Ross' geese and lesser snow geese in the Queen Maud Gulf Migratory Bird Sanctuary. Ottawa: Canadian Wildlife Service, Occasional Paper No. 81.
- Kirby, R.E., Conroy, M.J., Barry, T.W. & Kerbes, R.H. 1986. Survival estimates for North American Atlantic brant, 1956-75. *J. Wildl. Manage.* 50:29-32.
- Krebs, C.J. 1989. *Ecological methodology*. New York: Harper & Row.
- Laake, J.L., Burnham, K.P. & Anderson, D.R. 1979. User's manual for program TRANSECT. Logan: Utah State University Press.
- Lank, D.B., Cooch, E.G., Rockwell, R.F. & Cooke, F. 1989. Environmental and demographic correlates of intraspecific nest parasitism in lesser snow geese *Chen caerulescens caerulescens*. *J. Anim. Ecol.* 58:29-45.
- Larsson, K., Forslund, P., Gustafsson, L. & Ebbinge, B.S. 1988. From the high Arctic to the Baltic: the successful establishment of a Barnacle Goose *Branta leucopsis* population on Gotland, Sweden. *Ornis Scand.* 19:182-289.
- Lindberg, M.S., Sedinger, J.S. & Flint, P.L. 1997. Effects of spring environment on nesting phenology and clutch size of black brant. *Condor* 99:381-388.

- Mackay, J.R. 1958. The valley of the lower Anderson River, N.W.T. Canada Dept. Mines and Tech. Surv., Geographical Br. Geographical Bull. 11:37-56.
- Madsen, J., Bregnballe, T. & Mehlum, F. 1989. Study of the breeding ecology and behaviour of the Svalbard population of light-bellied brent goose *Branta bernicla hrota*. Polar Research 7:1-21.
- Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.
- Mickelson, P.G. 1975. Breeding biology of cackling geese and associated species on the Yukon-Kuskokwim Delta, Alaska. Wildl. Monogr. 45:1-35.
- Palmer, R.S. 1976. Handbook of North American birds, Vol. 2. New Haven: Yale University Press.
- Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. 1993. Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. J. Anim. Ecol. 62:323-333.
- Ryder, J.P. 1971. Distribution and breeding biology of the lesser snow goose in central Arctic Canada. Wildfowl 22:18-28.
- Sauer, J.R. & Williams, B.K. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. J. Wildl. Manage. 53:137-142.
- Schubert, C.A. & Cooke, F. 1993. Egg-laying interval in the lesser snow goose. Wilson Bull. 105:414-426.

- Sedinger, J.S., Lindberg, M.S., Rexstad, E.A., Chelgren, N. & Ward, D.H. 1997. Testing for handling bias in survival estimation for black brant. *J. Wildl. Manage.* 61:782-791.
- Sedinger, J.S., Lensink, C.J., Ward, D.H., Anthony, R.M., Wege, M.L. & Byrd, G.V. 1993. Current status and recent dynamics of the black brant *Branta bernicla* breeding population. *Wildfowl* 44:49-59.
- Srivastava, D.S. & Jefferies, R.L. 1996. A positive feedback: herbivory, plant growth, salinity and the desertification of an arctic salt marsh. *J. Ecol.* 84:31-42.
- Summers, R.W., Underhill, L.G., Syroechkovski, E.E. Jr., Lappo, H.G., Prýs-Jones, R.P. & Karpov, V. 1994. The breeding biology of dark-bellied brent geese *Branta b. bernicla* and king eiders *Somateria spectabilis* on the northeastern Taimyr Peninsula, especially in relation to snowy owl *Nyctea scandiaca* nests. *Wildfowl* 45:110-118.
- Walter, S.E. & Rusch, D.H. 1997. Visibility bias on counts of nesting Canada geese. *J. Wildl. Manage.* 61:768-772.
- Ward, D.H., Derksen, D.V., Kharitonov, S.P., Stishov, M. & Baranyuk, V.V. 1993. Status of Pacific brant *Branta bernicla nigricans* on Wrangel Island, Russian Federation. *Wildfowl* 44:39-48.
- Ward, D.H., Rexstad, E.A., Sedinger, J.S., Lindberg, M.S. & Dawe, N.K. 1997. Seasonal and annual survival of adult Pacific brant. *J. Wildl. Manage.* 61:773-781.

3. COLONIALITY AND NEST PREDATION IN BLACK BRANT AND LESSER SNOW GEESE

3.1 Introduction

Reduced risk of predation can be a major advantage of group living (Alexander 1974, Wittenberger & Hunt 1985). Predation may be lower in groups because predators are detected earlier (Hoogland & Sherman 1976, Brown & Brown 1987), because of effective group defence (Gross & MacMillan 1981, Tyler 1995), selfish herd effects (Hamilton 1971), or due to predator swamping (Gross & MacMillan 1981). Predator detection occurs earlier, grouped defence tactics are more effective, and predator swamping is more likely to occur as group size increases (Wittenberger & Hunt 1985, Brown & Brown 1987, Tyler 1995). In groups such as nesting colonies, early detection, group defence, and predator swamping should increase with the number of nests and, within colonies, with nest density. Detection and defence may increase with colony density because these effects are related to the number of individuals watching for or defending against predators. Predator swamping will be more effective as the number of nests present in a predator's hunting area increases. A selfish herd is one where survival depends on the proximity of nearest neighbours, or more specifically, the probability that a

neighbour's nest is closer to an attacking predator and therefore more likely to be attacked than one's own (Hamilton 1971).

Proximity of neighbouring nests varies with both local density and position within colonies. Nests in peripheral positions have no neighbours on one side, and are predicted to have lower survival than central nests. Nest survival is predicted to be lower in small colonies, and low density areas within colonies, because there will be fewer parent birds present to be vigilant for and defend against predators. Selfish herd effects are also predicted to increase nest survival in the centre of colonies. The objective of this study was to determine if individuals of two species of Arctic geese gained an adaptive advantage by nesting at high densities or in central positions. Both black brant and lesser snow geese tend to nest in colonies but brant nest at lower densities than snow geese (Mickelson 1975, Bellrose 1980, Sedinger 1990). On the Anderson River Delta, snow geese appeared to have a more clumped distribution and nest more successfully than brant (Chapter 2, W. T. Armstrong, unpubl. data). I hypothesized that individuals of both species, and snow geese in particular, benefitted by nesting colonially. To examine this hypothesis, I tested predictions that nest and egg survival rates would be lower at nests on the colony's periphery, and that survival rates would increase with nest density.

3.2 Methods

I studied 100 snow goose and 95 brant nests in 1992, and 160 snow goose and 103 brant nests in 1993. Nests were found at the end of the egg-laying period in

both years. Brant were much less abundant than snow geese (Chapter 2) so every active brant nest found was recorded but snow goose nests were chosen by randomly selecting 100 of the first 200 active nests encountered in 1992 and 160 of the first 320 in 1993. Snow goose nests were divided equally between two islands that supported the main concentrations of snow goose nests. Local density was measured as nearest neighbour distance, which was calculated as the mean distance from the focal nest to the two nearest goose nests, irrespective of species. Local density was also quantified as the number of each species' nests within a 50 m radius of the focal nest. Combined nest density was the total number of both species' nests within 50 m of each focal nest. Species of the two nearest neighbours was also recorded. Nest position, i.e. peripheral or central, and distance to the nearest shoreline were recorded only in 1993. Distance to the nearest shoreline was measured (± 1 m) to the edge of any large channel, nearest large tundra pond which supported a gull nest, or edge of the island. Central and peripheral positions were classified based on Hamilton's (1971) description of a selfish herd. Central nests were those where a predator approaching from any direction, would pass nearer to at least one other goose nest before reaching the focal nest, i.e. a central nest could not be the first nest encountered by a predator approaching from outside the colony. Peripheral nests were those that a predator could reach without first approaching nearer to any goose nest other than the focal nest. Nest position was determined after mapping nest locations.

Partial clutch predation was defined as the loss, during the time nests were under observation, of at least one egg while the nest remained active. A nest was

deemed to have survived if at least one egg remained when observations ceased. Nests were visited only during incubation to minimize disruption during laying, when geese are sensitive to disturbance, and during hatch, when young goslings are especially vulnerable to gull predation (Barry 1967). Nests were visited at seven-day intervals in 1992 and at five-day intervals in 1993. Nest observations spanned 14 days in 1992 and 15 days in 1993. These were the maximum spans possible between the time when egg-laying was completed in most nests and when the earliest clutches began to hatch.

Egg survival rates were estimated for each nest using Mayfield's method (Mayfield 1961, 1975, Johnson 1979) as modified by Flint et al. (1995) to allow for lack of independence among eggs within nests. This method estimates standard error of egg survival by using nests as the sampling units in a cluster sampling design (Flint et al. 1995).

Effects of nest density and position on nest and egg survival were tested after controlling for the effect of clutch size because it was an important predictor of both egg and nest survival (W. T. Armstrong, unpubl. data). The relationship between nest fate (survive or fail), and nest density and nest position was examined using logistic regression (Hosmer & Lemeshow 1989, LOGISTIC and CATMOD procedures: SAS Institute Inc. 1990a, b). Egg survival rates and all nest density and position data were rank transformed (Conover & Iman 1981) prior to analysis because egg survival data were discontinuous. The rank transformation permits the use of parametric *F* tests and limited analyses of covariance (Conover & Iman 1981). Two-factor ANOVA and analyses of covariance (GLM procedure: SAS Institute Inc.

1990b) were used to control for the effects of clutch size on egg survival in this study. Egg survival rates were compared between species using *Z*-tests (Johnson 1979, Flint et al. 1995).

3.3 Results

In 1992, approximately half of the snow goose nests in the colony, including all of the snow goose study nests on one island ($n = 50$) and 11 brant study nests, were destroyed by grizzly bears in a single day between the time nests were found and the first nest check. Nest density could be calculated for all nests but nest and egg survival in 1992 were analysed using only the remaining sample of 50 snow goose and 84 brant nests since the fates of nests depredated by bears were not independent.

It was not possible to directly examine differences between brant and snow geese for effects of nest density and location on nest and egg survival due to significant interactions between species and density and location variables ($P < 0.05$). Interactions were also present between year and density and location variables within species ($P < 0.05$), therefore species and years were analysed separately.

3.3.1 Brant

Brant nests with two or more neighbours within 50 m were less likely to survive than those with fewer neighbours when both species of neighbouring nests were combined, in 1992 (Fig. 3.1, Table 3.1). Brant nest survival, however, was not influenced by nearest neighbour distance, species of nearest neighbours, nor the number of brant or snow goose nests within 50 m of the focal nest when each neighbouring species was considered separately (Table 3.1). In 1993, brant nests close to shore were more likely to survive than nests farther from water but nest survival was not affected by nest density, species of nearest neighbours, or nest position (Fig. 3.2, Table 3.1).

Partial clutch predation was examined using nests with at least two eggs because, by definition, one-egg clutches can not suffer partial clutch loss. In 1992, partial clutch predation in brant nests was not related to any measure of nest density or to species of neighbouring nests (Table 3.2). In 1993, brant that nested closer to their nearest neighbours were less likely to suffer partial clutch predation (Fig. 3.3, Table 3.2). Partial clutch predation in brant also varied with species of nearest neighbours (Table 3.2). Brant with snow goose neighbours were more likely to experience partial clutch losses than those with two brant as nearest neighbours.

Daily egg survival was examined in all nests, including one-egg clutches. Egg survival in brant was not related to species of the two nearest neighbours, nor to local density of brant or snow geese in 1992 (Table 3.3). There was a significant interaction between the effects of clutch size and nearest neighbour distance on egg

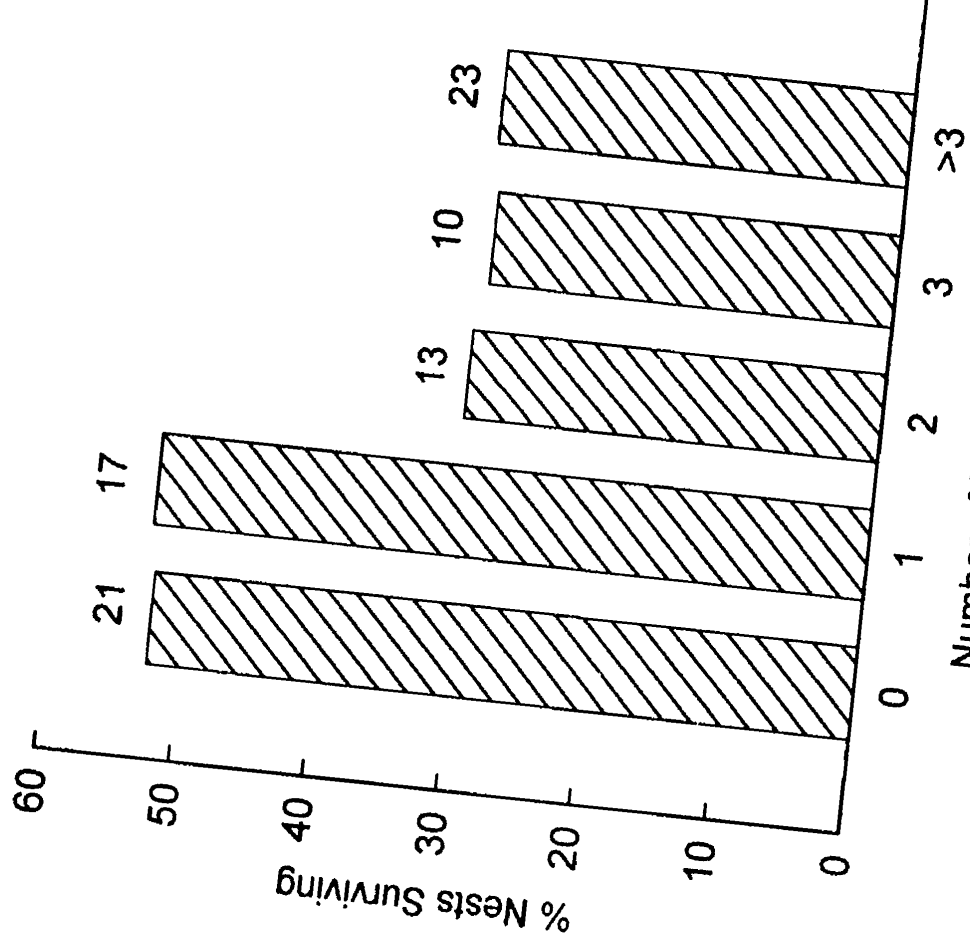


Figure 3.1. Percent of black brant nests that survived relative to the number of black brant and lesser snow goose nests within 50 m, at Anderson River Delta, NWT, in 1992. The number of nests in each category is indicated above the bars.

Table 3.1. Logistic regression analysis of nest survival of black brant at Anderson River Delta, NWT, in relation to nearest neighbour distance^a, nest density, species of neighbouring nests, peripheral or central location, and distance from shore.

Variables	1992			1993		
	df	χ^b	<i>P</i>	df	χ^b	<i>P</i>
Nests within 50 m	1	5.65	0.02	1	1.49	n.s.
Brant within 50 m	1	0.15	n.s.	1	2.38	n.s.
Snow geese within 50 m	1	0.15	n.s.	1	1.49	n.s.
Nearest Neighbour Dist. ^a	1	0.01	n.s.	1	0.06	n.s.
Nearest Neighbour Species ^b	1	0.45	n.s.	1	0.04	n.s.
Nest Location ^c				1	3.35	n.s.
Distance to Shore ^c				1	10.52	0.001

^a Mean distance to two nearest neighbouring nests

^b Conspecific or heterospecific neighbours

^c Measured in 1993 only

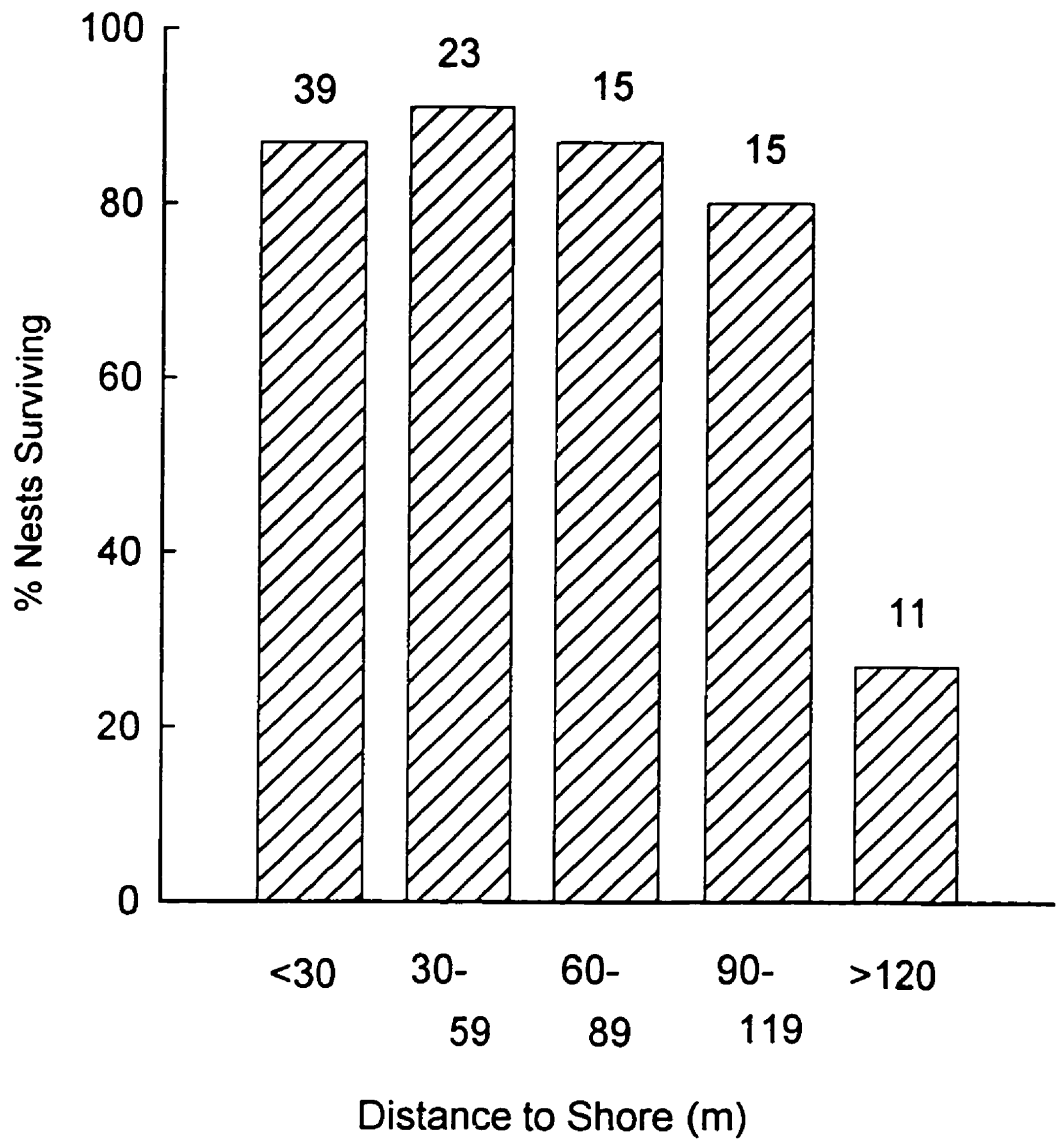


Figure 3.2. Percent of black brant nests that survived relative to distance from shore at Anderson River Delta, NWT, in 1993. The number of nests in each category is indicated above the bars.

Table 3.2. Logistic regression analysis of partial clutch predation in black brant nests at Anderson River Delta, NWT, in relation to nearest neighbour distance^a, nest density, species of neighbouring nests, peripheral or central location, and distance from shore.

Variables	1992			1993		
	df	χ^b	<i>P</i>	df	χ^b	<i>P</i>
Nests within 50 m	1	0.41	n.s.	1	0.86	n.s.
Brant within 50 m	1	1.05	n.s.	1	0.16	n.s.
Snow geese within 50 m	1	0.91	n.s.	1	0.01	n.s.
Nearest Neighbour Dist. ^a	1	0.09	n.s.	1	5.85	0.02
Nearest Neighbour Species ^b	1	0.99	n.s.	1	5.48	0.02
Nest Location ^c				1	0.24	n.s.
Distance to Shore ^c				1	0.00	n.s.

^a Mean distance to two nearest neighbouring nests

^b Conspecific or heterospecific neighbours

^c Measured in 1993 only

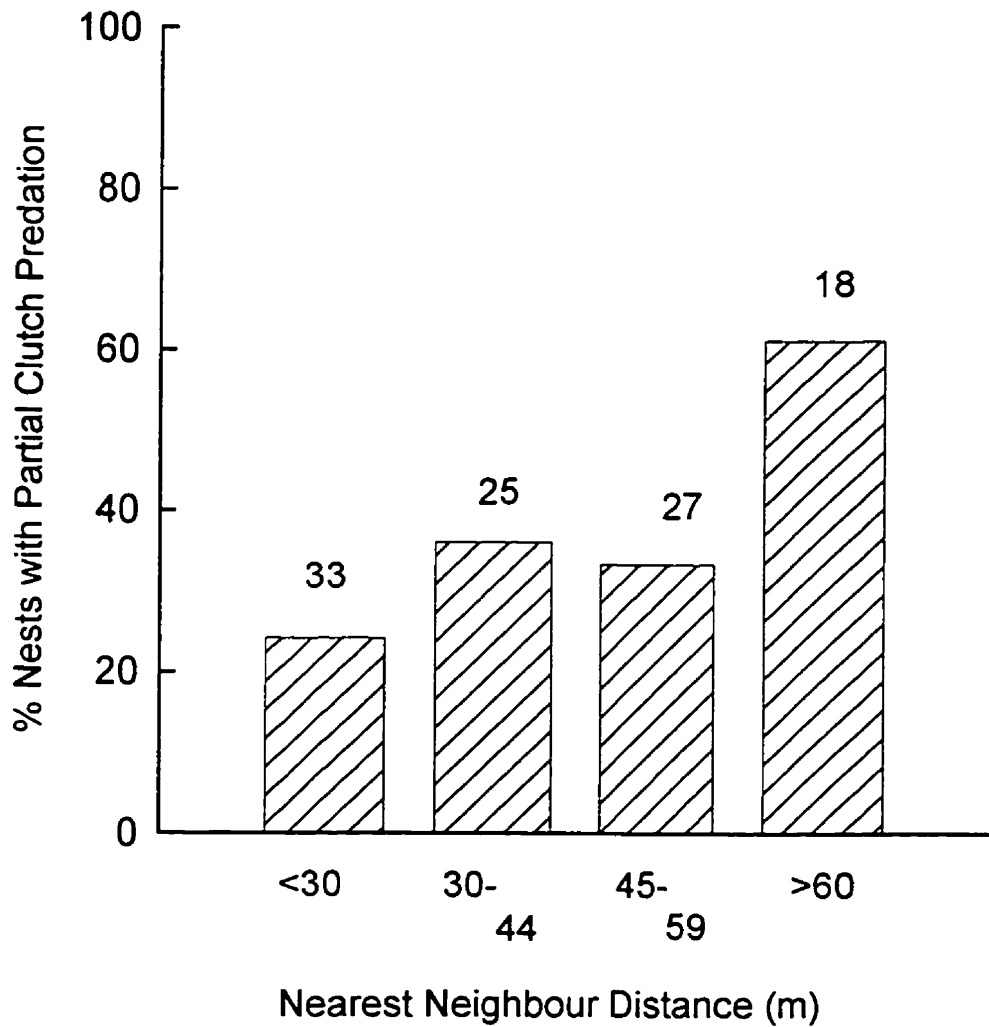


Figure 3.3. Percent of black brant nests that experienced partial clutch predation, relative to mean distance to the two nearest nests at Anderson River Delta, NWT, in 1993. The number of nests in each category is indicated above the bars.

Table 3.3. Egg survival in black brant nests at Anderson River Delta, NWT, in relation to nearest neighbour distance^a, nest density, species of neighbouring nests, peripheral or central location, and distance from shore.

Variables	df	F	P
1992			
Nests within 50 m X Clutch Size	4,74	3.02	0.05
Brant within 50 m	1,78	2.72	n.s.
Snow geese within 50 m	1,78	1.99	n.s.
Nearest Neighbour Dist. ^a X Clutch Size	4,74	3.44	0.02
Nearest Neighbour Species ^b	1,78	3.89	n.s.
1993			
Nests within 50 m	7,91	0.94	n.s.
Brant within 50 m	6,92	0.85	n.s.
Snow geese within 50 m	4,94	0.59	n.s.
Nearest Neighbour Dist. ^a	1,97	7.45	0.01
Nearest Neighbour Species ^b	3,95	0.77	n.s.
Nest Location ^c X Clutch Size	4,93	3.95	0.01
Distance to Shore ^c	1,97	11.78	0.001

^a Mean distance to two nearest neighbouring nests

^b Conspecific or heterospecific neighbours

^c Measured in 1993 only

survival in 1992 (Table 3.3). Egg survival increased with increasing nearest neighbour distance in brant nests with three eggs ($F_{1,21} = 9.60$, $n = 23$, $P < 0.01$) but was not related to nearest neighbour distance in nests with one or two eggs ($F_{1,29} = 0.01$, $n = 31$, n.s.) or nests with four or five eggs ($F_{1,28} = 3.93$, $n = 30$, n.s.). One- and two-egg clutches were pooled, as were four- and five-egg nests, to increase sample sizes. Egg survival in brant was also affected by a significant interaction between the number of nests within 50 m and clutch size in 1992 (Table 3.3). Egg survival decreased with number of nests within 50 m in brant nests with three eggs ($F_{1,21} = 8.41$, $n = 23$, $P < 0.01$) and nests with four or five eggs ($F_{1,28} = 5.58$, $n = 30$, $P < 0.05$), but there was no relationship in nests with one or two eggs ($F_{1,29} = 0.35$, $n = 31$, n.s.). These results indicate that, in nests of certain clutch sizes, egg survival decreased with increasing nest density. In 1993, egg survival in brant declined with nearest neighbour distance (Table 3.3), opposite to the relationship observed in some clutch sizes in 1992. Egg survival, like nest survival, also declined in brant nests that were farther from shore in 1993 (Fig. 3.4, Table 3.3). The interaction between the effects of clutch size and nest position on egg survival was significant (Table 3.3) because brant nests in central positions had higher egg survival than those on the periphery in three-egg ($F_{1,28} = 4.47$, $n = 30$, $P < 0.05$) and four-egg clutches ($F_{1,30} = 7.74$, $n = 32$, $P < 0.01$), but there was no difference in one or two-egg clutches ($F_{1,13} = 2.84$, $n = 15$, n.s.) nor in five-egg clutches ($F_{1,24} = 0.07$, $n = 26$, n.s.).

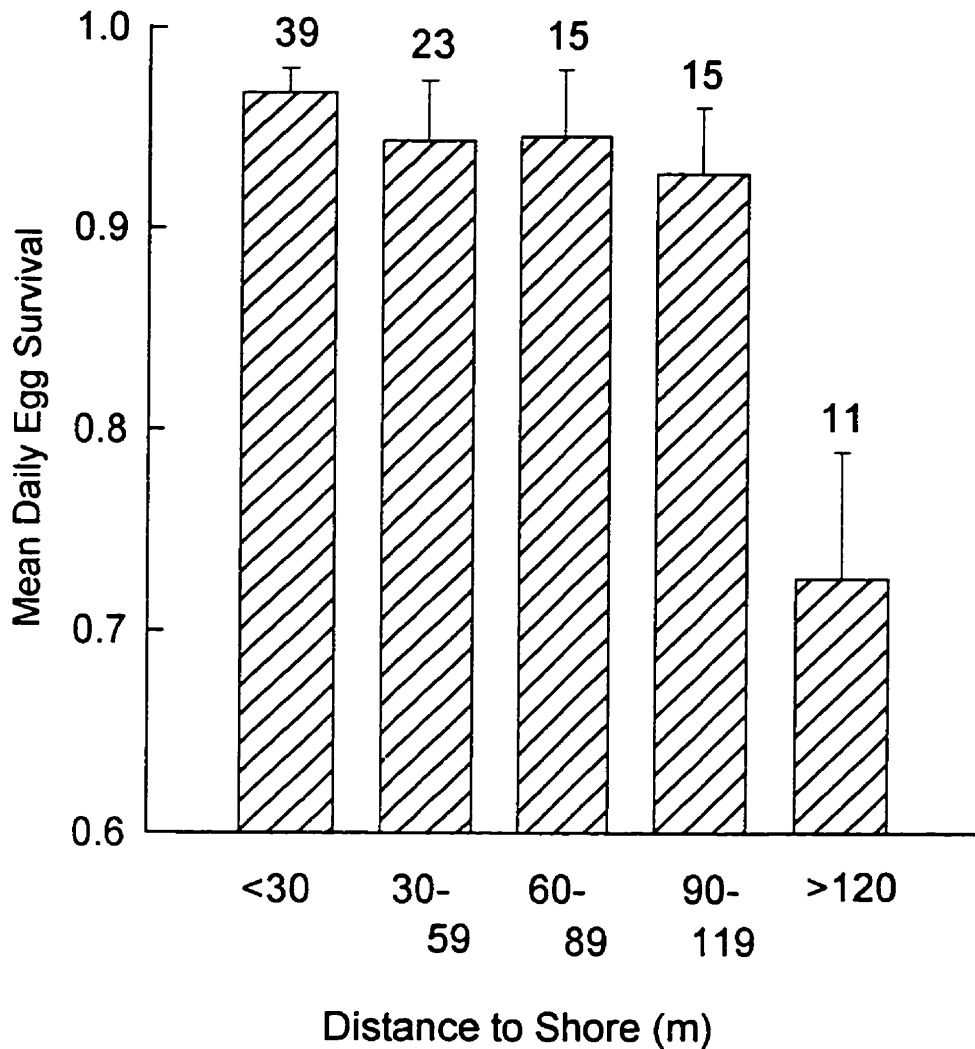


Figure 3.4. Mean (+ SE) daily egg survival rate relative to distance to shore in black brant nests at Anderson River Delta, NWT, in 1993. The number of nests in each category is indicated above the bars.

3.3.2 Snow geese

Snow goose nest survival tended to increase with the number of nests within 50 m in 1992, though this tendency was only marginally significant (logistic regression $\chi^2_1 = 3.87$, $P = 0.05$). However, snow goose nest survival was not related to nearest neighbour distance (logistic regression $\chi^2_1 = 0.46$, n.s.). It was not possible to examine the effects of species composition of neighbouring geese on nest or egg survival in snow geese because no snow goose nest studied had a brant nest as one of its two nearest neighbours or within 50 m in either 1992 or 1993. Snow goose nest survival in 1993 was not related to any measure of nest density or position in this study (logistic regression, all $\chi^2_1 < 1.70$, n.s.).

The likelihood of partial clutch predation at snow goose nests was not related to either measure of nest density in 1992 (logistic regression, all $\chi^2_1 < 0.60$, n.s.) or to any measure of nest density or position in 1993 (logistic regression, all $\chi^2_1 < 3.10$, n.s.).

Egg survival tended to be lower in snow goose nests located farther from their nearest neighbours in 1992; however, this relationship was only marginally significant ($F_{1,43} = 4.03$, $n = 50$, $P = 0.05$). The relationship between egg survival and nearest neighbour distance in snow geese was opposite to that found in three- and four-egg brant nests in the same year. In 1993, egg survival among snow geese was not related to nest density or position (all $F_{1,152} < 1.70$, n.s.).

3.3.3 Interspecific comparisons

Snow geese nested at higher densities and closer to shore than did brant (Table 3.4), but there was no difference between species in the number of nests in peripheral and central positions ($G = 1.0$, $df = 1$, n.s.). Brant (40%, $n = 84$) and snow goose nests (42%, $n = 50$) were equally likely to survive the observation period in 1992 ($G = 0.03$, $df = 1$, n.s.). In 1993, snow goose nests (90%, $n = 160$) were more likely to survive than were brant (81%, $n = 103$, $G = 4.6$, $df = 1$, $P < 0.05$).

Partial clutch predation in clutches larger than one egg occurred in more brant (47%, $n = 72$) than snow goose nests in 1992 (22%, $n = 50$, $G = 8.4$, $df = 1$, $P < 0.01$). The same pattern occurred when only those nests that survived the span of observations were considered. Of surviving nests, 22/33 (67%) brant and 8/21 (38%) snow goose nests suffered partial clutch losses ($G = 4.3$, $df = 1$, $P < 0.05$). In 1993, more brant (37%, $n = 99$) than snow geese (19%, $n = 158$) experienced partial clutch predation ($G = 10.5$, $df = 1$, $P < 0.001$). As in 1992, more brant (39%, $n = 83$) than snow goose nests (18%, $n = 144$) that survived the span of observations suffered partial clutch losses ($G = 11.3$, $df = 1$, $P < 0.001$).

There was no difference in egg survival rate between brant and snow geese in 1992 ($Z = 0.08$, n.s.), but snow geese had higher egg survival than brant in 1993 ($Z = 3.42$, $P < 0.001$).

Table 3.4. Density and location (mean \pm SE, (range)) of black brant and lesser snow goose nests at Anderson River Delta, NWT.

	Brant	Snow Geese	Z	P
1992				
Nests within 50 m	2.2 \pm 0.2 (0 - 7)	7.4 \pm 0.6 (0 - 27)	-6.9	0.001
Nearest Neighbour Distance ^a (m)	45.6 \pm 2.8 (8.2 - 141.0)	24.6 \pm 2.4 (5.4 - 161.5)	7.0	0.001
<i>n</i>	95	100		
1993				
Nests within 50 m	2.2 \pm 0.2 (0 - 7)	16.6 \pm 1.2 (0 - 43)	-8.9	0.001
Nearest Neighbour Distance ^a (m)	42.7 \pm 1.7 (19.2 - 107.4)	21.2 \pm 1.3 (4.8 - 72.8)	9.2	0.001
Distance to shore (m)	57.5 \pm 5.1 (0 - 230)	33.5 \pm 3.5 (0 - 230)	3.8	0.001
<i>n</i>	103	160		

^a Mean distance to two nearest neighbouring nests

3.4 Discussion

Brant that nested at higher densities appeared to be at a selective disadvantage due to reduced nest and egg survival in 1992 (Fig. 3.1, Table 3.3), whereas snow geese tended to have higher nest and egg survival with increased nest density. However, in 1993, partial clutch predation decreased and egg survival rates increased with increasing nest density in brant (Tables 3.2 and 3.3), whereas nest survival was not affected (Table 3.1). The likelihood of partial clutch predation was also higher for brant that had snow geese as their nearest neighbours in 1993, but this did not result in a significant decline in egg survival (Table 3.3). Among snow geese in 1993, nest and egg survival were not related to any measure of nest density or position. These results are unlike those reported in other studies where nesting success or offspring survival increased with nest density or colony size in birds (Berg et al. 1992, Wiklund & Andersson 1994, Becker 1995). However, not all studies reported increased nesting success with nest density. Magellanic penguins *Spheniscus magellanicus* bred more successfully in colonies of intermediate densities rather than at lower or higher densities (Scolaro 1990), and Bellinato & Bogliani (1995) found that predation on artificial nests was higher within than outside heron colonies. Reduced reproductive success was also reported with increasing colony density among lesser frigatebirds *Fregata ariel*; however, chick losses were due to nesting site takeovers by invading males rather than predation (Reville 1991). Densities of nesting geese at Anderson River Delta may have been too low to dilute the combined functional and numerical response of avian predators to increasing nest

densities. Gulls and jaegers may have responded to increased nest densities by concentrating their hunting efforts in those areas (e.g. Velarde 1992, Emslie et al. 1995).

Increased predation with increasing density of brant nests in 1992 is consistent with Ims' (1990) model of predation by a generalist predator. As prey items that are unavailable at certain times of the year (e.g. goose eggs in the Arctic) increase in density, generalist predators will switch from alternate foods to exploit the newly abundant prey. When prey switching occurs at high prey densities or when the number of prey needed to meet the predator's requirements is high relative to the prey's total reproductive output, peak predation rates may occur at high prey densities (Ims 1990). Glaucous gulls and parasitic jaegers at Anderson River are generalist predators (Martin & Barry 1978, Barry & Barry 1990) and nest densities of brant may have been high enough to make egg predation profitable but too low to overwhelm predators' ability to eat eggs. Snow geese nested at higher densities than brant in both years but had higher nest and egg survival only in 1993 (Table 3.4). The lack of an effect of nest density within either species suggests that predators did not switch from other foods to prey on goose nests, but attacked nests in proportion to abundance.

Higher egg survival rates in three- and four-egg brant nests in central positions in 1993 suggest that central nests may have benefitted from selfish herd effects (Hamilton 1971), or from cover provided by other nests (Alexander 1974). However, the effect of nest position on predation was inconsistent because there was no difference in egg survival rates between peripheral and central nests in snow

geese nor in brant nests with one, two, or five eggs. Also, probability of nest survival and partial clutch predation were similar at peripheral and central nests for both species. However, differences in predation between peripheral and central areas of nesting colonies have been reported in other studies. Emslie et al. (1995) noted that predation events were more frequent at peripheral nests and several authors (Anderson & Hodum 1993, Emslie et al. 1995, Gaston & Elliot 1996) have reported that avian predators selectively attacked peripheral nests. In least terns *Sterna antillarum*, central nests suffered higher predation losses (Brunton 1997) but Tyler (1995) found no difference in egg loss between peripheral and central nests in fish (*Abudefduf abdominalis*). Distance of nests from shore also may have influenced predation. Gulls tended to fly along the shores of the river, the islands, and even channels and large ponds on islands where, on windy days, some shorelines created updrafts which gulls frequently used (W. T. Armstrong, pers. obs.). I expected predation to be more frequent near heavily travelled areas but found no such effect. Nest survival and egg survival in brant were higher in nests close to shore and there was no effect of distance from shore on nest or egg survival in snow geese.

There appears to be a threshold relationship between nest or egg survival and nest density or distance from shore in brant (Figs. 3.1, 3.2, and 3.4). The relationship between brant nest survival and density in 1992 (Fig. 3.1) was best described with density either above or below a threshold between one and two nests within 50 m. However, in 1993, brant nest and egg survival in relation to distance from shore (Figs. 3.2 and 3.4) was best described with distance as a continuous

variable. Therefore, number of nests within 50 m, in 1992, was analysed as a categorical variable and distance to shore, in 1993, was analysed as a continuous variable. The appearance of threshold responses were artifacts caused by the distribution of the independent variables (widely spaced nests are rare in a colony) and presenting them in categories.

Brant had little to gain by nesting near or avoiding snow geese. During this study, brant began nesting 5 to 8 days later than snow geese (W. T. Armstrong, unpubl. data) so brant may have been able to nest near or avoid snow goose nests. However, I was unable to test settling patterns for intra- or interspecific attraction or avoidance in nest site selection. Having snow geese as nearest neighbours had no consistent effect on probability of nest survival in brant in either year. Brant with snow goose neighbours had higher egg survival in 1992, but in 1993 they had higher probability of experiencing partial clutch predation. These results suggest that snow geese neither attracted predators to brant nests nor acted as predator buffers.

Snow geese nested at higher densities than brant in both years (Table 3.4) and had higher nest and egg survival rates than brant in 1993, as well as lower probability of suffering partial clutch predation in both years. The lack of differences in nest and egg survival between species in 1992, and the absence of any effects of nest density or position on nest or egg survival in snow geese in either year suggest that snow geese at Anderson River Delta had greater nest success than brant in 1993 for reasons other than nesting at higher densities.

The effects of nest density and position on nest and egg survival in geese at Anderson River Delta were inconsistent. In brant, an apparent disadvantage to

nesting at higher densities in 1992 was contradicted by an apparent advantage of high nest density in 1993. Density and position effects were lacking in snow geese and varied among nests of different clutch sizes as well as between years in brant. If nest density or position resulted in a general selective advantage it is unlikely that the benefits would be seen only in geese with certain clutch sizes, or result in apparent disadvantages in some years. Therefore I rejected the hypothesis that brant and snow geese at Anderson River Delta gained an adaptive advantage by nesting at higher densities or in central positions.

3.5 References

- Alexander, R.D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5:325-383.
- Anderson, D.J. & Hodum, P.J. 1993. Predator behavior favors clumped nesting in an oceanic seabird. *Ecology* 74:2462-2464.
- Barry, S.J. & Barry, T.W. 1990. Food habits of glaucous gulls in the Beaufort Sea. *Arctic* 43:43-49.
- Barry, T.W. 1967. Geese of the Anderson River Delta, Northwest Territories. Ph.D. thesis, University of Alberta, Edmonton.
- Becker, P.H. 1995. Effects of coloniality on gull predation on common tern (*Sterna hirundo*) chicks. *Colonial Waterbirds* 18:11-22.
- Bellinato, F. & Bogliani, G. 1995. Colonial breeding imposes increased predation: experimental studies with herons. *Ethology Ecology & Evolution* 7:347-353.
- Bellrose, F.C. 1980. Ducks, geese and swans of North America, 3rd ed. Harrisburg, Pennsylvania: Stackpole Books.
- Berg, Å., Lindberg, T. & Källénbrink, K.G. 1992. Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. *J. Anim. Ecol.* 61:469-476.
- Brown, C.R. & Brown, M.B. 1987. Group-living in cliff swallows as an advantage in avoiding predators. *Behav. Ecol. Sociobiol.* 21:97-107.
- Brunton, D.H. 1997. Impacts of predators: center nests are less successful than edge nests in a large nesting colony of least terns. *Condor* 99:372-280.

- Conover, W.J. & Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Statistician* 35:124-129.
- Emslie, S.D., Karnovsky, N. & Trivelpiece, W. 1995. Avian predation at penguin colonies on King George Island, Antarctica. *Wilson Bull.* 107:317-327.
- Flint, P.L., Pollock, K.H., Thomas, D. & Sedinger, J.S. 1995. Estimating pre fledging survival: allowing for brood mixing and dependence among brood mates. *J. Wildl. Manage.* 59:448-455.
- Gaston, A.J. & Elliot, R.D. 1996. Predation by ravens *Corvus corax* on Brunnich's guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. *Ibis* 138:742-748.
- Gross, M.R. & MacMillan, A.M. 1981. Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behav. Ecol. Sociobiol.* 8:163-174.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *J. theor. Biol.* 31:295-311.
- Hoogland, J.L. & Sherman, P.W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.* 46: 33-58.
- Hosmer, D.W. & Lemeshow, S. 1989. Applied logistic regression. New York: John Wiley & Sons, Inc.
- Ims, R.A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* 136:485-498.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.

- Martin, M. & Barry, T.W. 1978. Nesting behavior and food habits of parasitic jaegers at Anderson River Delta, Northwest Territories. *Can. Field-Nat.* 92:45-50.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- Mickelson, P.G. 1975. Breeding biology of cackling geese and associated species on the Yukon-Kuskokwim Delta, Alaska. *Wildl. Monogr.* 45:1-35.
- Reville, B.J. 1991. Nest spacing and breeding success in the lesser frigatebird (*Fregata ariel*). *Condor* 93:555-562.
- SAS Institute Inc. 1990a. SAS/STAT User's Guide, Version 6, 4th ed. Vol. 1. Cary, North Carolina: SAS Institute Inc.
- SAS Institute Inc. 1990b. SAS/STAT User's Guide, Version 6, 4th ed. Vol. 2. Cary, North Carolina: SAS Institute Inc.
- Scolaro, J.A. 1990. Effects of nest density on breeding success in a colony of Magellanic penguins (*Spheniscus magellanicus*). *Colonial Waterbirds* 13:41-49.
- Sedinger, J.S. 1990. Effects of visiting black brant nests on egg and nest survival. *J. Wildl. Manage.* 54:437-443.
- Tyler, W.A. III. 1995. The adaptive significance of colonial nesting in a coral-reef fish. *Anim. Behav.* 49:949-966.

- Velarde, E. 1992. Predation of Heermann's gull (*Larus heermanni*) chicks by yellow-footed gulls (*Larus livens*) in dense and scattered nesting sites. Colonial Waterbirds 15:8-13.
- Wiklund, C.G. & Andersson, M. 1994. Natural selection of colony size in a passerine bird. J. Anim. Ecol. 63:765-774.
- Wittenberger, J. F. & G. L. Hunt Jr. 1985. The adaptive significance of coloniality in birds. In Farner, D.S., King, J.R. & Parkes, K.C. (eds) Avian Biology: 8:1-78. Orlando, Florida: Academic Press.

4. INCUBATION BEHAVIOUR AND NEST DEFENCE IN BLACK BRANT AND LESSER SNOW GEESE

4.1 Introduction

Successful reproductive strategies are determined by the allocation of resources, including time, within each breeding episode and over an organism's lifetime (Martin 1992, Stearns 1992). In species that provide care for their young, parental effort devoted to rearing and defending offspring will affect the success of reproductive strategies (Trivers 1974). The optimal allocation of resources, which would maximise lifetime reproductive success, may be constrained by features of an organism's environment or life-history strategy (Drent & Daan 1980). Arctic birds, for example, must nest and rear their young in the typically short northern summer. Large species, such as geese, have a further constraint imposed by their life-history strategy; they can not successfully rear offspring from a second clutch if the first is destroyed. Due to their long juvenile development time (Bellrose 1980), young hatched from late clutches may not be mature enough to migrate south before the onset of inclement weather. Although time and effort spent deterring predators may be small, preventing offspring from being preyed upon is an important aspect of parental care that increases reproductive success (Blancher & Robertson 1982,

Hamer & Furness 1993, Sjöberg 1994). Therefore, parents' ability to defend their nests from predators will be particularly important in large, single-brooded species, such as Arctic-nesting geese.

While life-history constraints frequently require trade-offs between components of fitness (Stearns 1992), there may be no trade-off necessary between incubation and nest guarding because both may be accomplished at the same time (Martin 1992). However, a conflict occurs when parents stop nest guarding in order to forage. Predators may arrive undetected while parents are foraging near the nest, or when parents are too far from the nest to prevent a successful attack (Martin 1992). How parents resolve the conflicting demands of nest guarding and self-maintenance may be constrained by life-history traits. Adaptations to cope with environmental factors under differing life-history constraints may be studied in situations where ecologically similar species co-exist. The breeding biology of black brant is similar to that of lesser snow geese except for differences in body size and nutrient reserves. Snow geese are larger than brant and have greater nutrient reserves at the beginning of incubation, which enable snow geese to survive the incubation period without feeding (Ankney & MacInnes 1978, Ankney 1984). In contrast, brant have lower nest attendance than larger species of geese (Thompson & Raveling 1987, Afton & Paulus 1992) because they have smaller nutrient reserves at the start of incubation and must leave their nests to feed (Ankney 1984). Thus, time available for incubating and nest guarding may be constrained more in brant than snow geese. Based on energetic constraints, brant are predicted to spend more time feeding and less time incubating or nest guarding than snow geese. As nutrient

reserves decline, foraging may increase at the expense of nest attendance in brant but nest attendance should not change in snow geese.

Trade-offs between fitness components for parents that care for their offspring are also predicted by parental investment theory (Trivers 1972, Montgomerie & Weatherhead 1988). Nest defence behaviour is predicted to vary as the fitness value of current offspring changes relative to future offspring (Montgomerie & Weatherhead 1988). As offspring age and grow closer to independence, their probability of surviving increases along with their parents' cost of replacing them. Both increased survival probability and increased replacement costs lead to predictions that nest guarding will increase as the stage of incubation advances (Montgomerie & Weatherhead 1988). Thus, geese should have greater nest attendance, spend more time watching for predators, and spend less time feeding as stage of incubation advances.

I tested the competing predictions from the energetic constraint hypothesis and parental investment theory by comparing activity budgets of nesting brant and snow geese. Black brant and lesser snow geese nest sympatrically at Anderson River Delta, Northwest Territories, where both species suffer high nest and egg predation, primarily due to avian predators (Chapter 2).

4.2 Methods

Geese were observed during incubation in 1993 from blinds elevated 3 m above ground level on towers. Towers and blinds were both in place before geese

began nesting. One blind was located within an area where only snow geese nested and the other was in a mixed nesting area predominated by brant. Nesting habitat in the mixed nesting area was bare mud and in the snow goose nesting area habitat consisted of bare mud, dead willows (*Salix* spp.) and driftwood (Chapter 2). Both areas lacked growing mosses or vascular plants. Observers waited 1 h after entering the blind to allow geese to return to normal activity patterns before beginning observations. Behaviour of nesting geese was sampled using instantaneous, focal-animal sampling (Altmann 1974, Martin & Bateson 1986) at five-minute intervals over 2.5 h per recording session. Recording sessions were distributed evenly through out the 24-h day because the study area is under continuous daylight in the summer. Observers remained in blinds until a series of 10 recording sessions had been completed in order to minimise disturbance to nesting geese. Nests were randomly selected for each session and each nest was sampled only once per series.

At each interval, observers recorded the location and activity of both members of the focal pair of geese. Females' locations were recorded as either on or off the nest, and if off the nest, whether on or off the territory. Males were either on or off their territories. Each pair's territory was defined as the area surrounding the nest that was defended from other geese. Behaviours were recorded as combinations of activities and postures (Lazarus & Inglis 1978). Comfort movements included preening, shaking, scratching, bathing, and for females, adjusting eggs or nest material. Feeding included foraging and drinking. Resting included "head on back" and "head low" positions of the head and neck (Lazarus & Inglis 1978) and could occur while the goose was either sitting or standing.

Vigilance was divided into "head up" and "extreme head up" (Lazarus & Inglis 1978) and either could be recorded when the goose was sitting, standing, or walking. Social interactions included all interactions between members of the pair or with other geese. Nest defence was restricted to interactions with or actions directed toward predators. Locomotion included occurrences of flying, swimming, walking, or running that did not fall into one of the other categories (e.g. walking while grazing was recorded as feeding). When predators attacked a nest, observers recorded species of predator, location and behaviour of the attending pair at the onset of the attack, and their responses to the predator. An attack was successful if the predator pecked at, ate, or removed an egg from a nest.

Time that focal birds were out of sight was excluded from activity budgets. Percentage of time spent in each activity and location was arcsine - square root transformed prior to analyses (Sokal & Rohlf 1981) and data were aggregated by nest except where otherwise noted. When *t*-tests were used to compare means (SAS Institute Inc. 1990), approximate *t* statistics and degrees of freedom were calculated if variances were unequal (Johnson 1995). Tests were considered statistically significant if probability of type I error was less than 0.05.

4.3 Results

Female snow geese had higher nest attendance (98.8% (97.9 - 99.7)) (mean (95% C.I.)), than female brant (83.9% (80.2 - 87.5)), $t = 8.64$, unequal variances $df = 37.2$, $P < 0.0001$). Female snow geese were on their territories more than

female brant both in their overall time budgets ($t = -10.03$, $df = 68$, $P < 0.0001$) and during incubation recesses ($t = -4.41$, $df = 33$, $P < 0.0001$, Table 4.1). Male brant and snow geese spent similar amounts of time on their territories, regardless of whether or not their mates were incubating (Table 4.1). When their mates left the territory, male brant remained 90.0% of the time (85.4 - 94.6, $n = 22$) whereas male snow geese stayed on their territories 36.7% (-21.5 - 94.8, $n = 5$) of the time; however, these differences were not statistically significant (median test, $Z = -1.37$, n.s.).

Territory attendance in male brant was lower when their mates were incubating than during recesses (paired $t = 2.39$, $df = 22$, $P < 0.05$, Table 4.1). In male snow geese, territory attendance did not change when their mates left the nest ($t = -0.23$, $df = 11$, n.s.). During recesses, female brant left their territories more than their mates ($t = 9.33$, $df = 45$, $P < 0.0001$), but in snow geese, females did not leave the territory more than their mates ($t = 0.82$, $df = 20$, n.s., Table 4.1). The combined pattern of male and female territory attendance meant that territories of both species were rarely left unattended. Percent time that at least one member of the pair was on the territory was higher in snow geese (99.8% (99.6 - 100.0)) than in brant (98.6% (97.8 - 99.3)), $t = 4.08$, unequal variances $df = 33.8$, $P < 0.002$).

Changes in behaviour through incubation were examined regressing time spent in different behaviours or locations on observation date. Dependent variables were nest attendance, territory attendance, and percentage of overall time budgets spent feeding or being vigilant. Data were not aggregated by nest for these analyses

Table 4.1. Percentage of time (95% C.I.) black brant and lesser snow geese spent on their territories during incubation when the female was on or off the nest.

Sample size, *n*, is number of nests.

	<i>n</i>	Brant	<i>n</i>	Snow Geese
Females				
Overall	28	85.3 (81.6 - 89.0)	42	99.6 (99.1 - 100.1)
When off nest	24	13.6 (1.9 - 25.3)	11	70.5 (43.4 - 97.5)
Males				
Overall	28	79.6 (73.7 - 85.4)	42	84.5 (78.3 - 90.6)
Female on nest	28	77.7 (70.8 - 84.7)	42	84.5 (78.3 - 90.7)
Female off nest	23	86.7 (79.2 - 94.4)	11	84.6 (65.4 - 104.8)

because variance within individuals exceeded that among individuals. When variance in behaviour within individuals exceeds variance among individuals, including more than one sample per subject does not increase the probability of a type I error (Leger & Didrichsons 1994). Nest attendance among female brant tended to decline as incubation progressed ($r = -0.21$, $n = 84$, $P = 0.05$) but it did not change among female snow geese ($r = -0.14$, $n = 58$, n.s.). Territory attendance declined as incubation advanced in both male and female brant (females: $r = -0.23$, $n = 84$, $P = 0.03$, males: $r = -0.51$, $n = 82$, $P < 0.0001$) and in male snow geese ($r = -0.33$, $n = 56$, $P < 0.02$) but not among female snow geese ($r = -0.24$, $n = 58$, n.s.). As incubation progressed, female brant became more vigilant ($r = 0.26$, $n = 84$, $P < 0.02$) and rested less ($r = -0.38$, $n = 84$, $P < 0.001$) but there was no change in time spent feeding ($r = 0.01$, $n = 84$, n.s.). Male brant and male and female snow geese did not change the percent time spent feeding, resting, or vigilant as incubation progressed.

Female brant and snow geese spent most of their time resting, except while off their nests, when they engaged in comfort movements, feeding, and locomotion (Tables 4.2 and 4.3). Male brant and snow geese also spent most of their time resting, followed by feeding and being vigilant, but spent little time in locomotion or comfort movements (Table 4.2). Nest defence and social interactions occupied very little time of either sex (Table 4.2). Close examination of nesting territories did not reveal what, if anything, geese ingested when they appeared to feed on their territories.

Table 4.2. Time budgets (% of time (95% C.I.)) of nesting black brant and lesser snow geese during incubation. Sample size, *n*, is number of nests.

Activity	Brant			Snow Geese		
	<i>n</i>	Females	Males	<i>n</i>	Females	Males
Vigilance, extreme head up						
Overall	28	0.2 (-0.2 - 0.5)	1.1 (0.4 - 1.7)	42	0.0 (0.0 - 0.1)	2.0 (0.7 - 3.3)
Female on nest	28	0.0	1.0 (0.3 - 1.7)	42	0.0 (0.0 - 0.1)	1.9 (0.7 - 3.2)
Female off nest	24	2.1 (-2.2 - 6.4)	1.4 (0.2 - 2.6)	11	0.0	13.1 (-7.1 - 33.4)
Vigilance, head up						
Overall	28	1.7 (0.4 - 3.0)	19.0 (14.6 - 23.3)	42	0.8 (0.3 - 1.4)	9.4 (6.4 - 12.6)
Female on nest	28	1.6 (0.3 - 2.8)	17.9 (13.1 - 22.7)	42	0.8 (0.2 - 1.4)	9.3 (6.1 - 12.4)
Female off nest	24	3.1 (-1.6 - 7.8)	26.6 (16.4 - 36.9)	11	9.1 (-10.9 - 29.1)	25.3 (-1.4 - 51.9)
Comfort movements						
Overall	28	8.9 (6.7 - 11.0)	3.9 (1.5 - 6.3)	42	6.4 (4.9 - 7.9)	2.0 (0.9 - 3.2)
Female on nest	28	8.2 (6.0 - 10.4)	4.7 (1.4 - 7.9)	42	6.3 (4.8 - 7.8)	2.0 (0.9 - 3.1)
Female off nest	28	31.1 (13.8 - 48.4)	1.8 (0.3 - 3.3)	11	21.2 (-5.5 - 47.9)	1.0 (-1.2 - 3.2)
Feeding						
Overall	28	0.5 (0.1 - 0.9)	12.9 (6.6 - 19.2)	42	0.6 (0.0 - 1.2)	26.3 (20.7 - 32.0)
Female on nest	28	0.1 (0.0 - 0.3)	12.4 (6.1 - 18.7)	42	0.1 (-0.1 - 0.3)	26.1 (20.5 - 31.7)
Female off nest	24	10.8 (0.7 - 20.8)	11.6 (1.5 - 21.7)	11	37.9 (7.4 - 68.4)	42.4 (11.0 - 73.8)
Locomotion						
Overall	28	0.9 (0.4 - 1.4)	7.1 (4.4 - 9.9)	42	0.1 (0.0 - 0.2)	2.2 (1.2 - 3.2)
Female on nest	28	0.3 (0.1 - 0.5)	8.0 (4.8 - 11.3)	42	0.0	2.2 (1.2 - 3.2)
Female off nest	24	20.7 (6.9 - 34.8)	4.3 (1.5 - 7.1)	11	13.6 (-7.8 - 35.1)	0.0
Rest						
Overall	28	87.8 (84.7 - 90.8)	54.5 (46.5 - 62.5)	42	92.1 (90.0 - 94.1)	57.6 (50.6 - 64.6)
Female on nest	28	89.7 (86.9 - 92.6)	54.2 (46.0 - 62.5)	42	92.8 (91.0 - 94.6)	58.2 (51.2 - 65.2)
Female off nest	28	2.9 (-1.4 - 7.2)	49.6 (36.0 - 63.2)	11	0.0	9.1 (-10.9 - 29.1)
Nest Defence						
Overall	28	0.0	0.1 (0.0 - 0.2)	42	0.0	0.0 (0.0 - 0.1)
Female on nest	28	0.0	0.1 (-0.1 - 0.2)	42	0.0	0.0 (0.0 - 0.1)
Female off nest	24	0.0	0.1 (-0.1 - 0.4)	11	0.0	0.0
Social Interactions						
Overall	28	0.1 (0.0 - 0.2)	1.5 (0.6 - 2.3)	42	0.0	0.3 (0.0 - 0.6)
Female on nest	28	0.1 (0.0 - 0.2)	1.8 (0.7 - 2.9)	42	0.0	0.3 (0.0 - 0.7)
Female off nest	24	0.0	0.4 (-0.1 - 0.8)	11	0.0	0.0

Table 4.3. Changes in behaviour when female black brant and lesser snow geese took incubation recesses. Paired *t*-tests of differences between percentage of time spent in each activity while the female incubated and while on recesses. When *t* > 0 the activity occurred more when the female was on the nest.

Activity	Sex	<i>t</i>	<i>P</i>
Brant (df = 23)			
Vigilance, head up	female	0.69	n.s.
	male	-1.01	n.s.
Comfort movements	female	-1.53	n.s.
	male	2.69	0.01
Feeding	female	-2.22	0.04
	male	0.87	n.s.
Rest	female	24.72	0.0001
	male	0.90	n.s.
Snow Geese (df = 10)			
Vigilance, head up	female	-0.44	n.s.
	male	-0.42	n.s.
Comfort movements	female	-0.33	n.s.
	male	-0.13	n.s.
Feeding	female	-2.66	0.02
	male	-1.24	n.s.
Rest	female	30.41	0.0001
	male	4.67	0.001

Male brant spent more time in comfort movements, locomotion, and social interactions when the female was incubating but time spent feeding or resting was unchanged when the female left the nest (Table 4.3). Male snow geese spent less time at rest or in locomotion when their mates were off the nest but time feeding, performing comfort movements, or in social interactions was not related to the female's location (Table 4.3).

Male brant were more vigilant but performed comfort movements and rested less than females regardless of whether the female was on or off the nest (Table 4.4). However, there was no difference between male and female brant in time spent feeding or locomoting during recesses. Male snow geese also spent more time being vigilant and less time resting or performing comfort movements than females when females were on their nests (Table 4.4). Like brant, male and female snow geese spent similar proportions of their time feeding and locomoting when the females took incubation recesses (Table 4.4). Male brant spent more time in head up vigilance and social interactions but less time feeding than male snow geese while their mates incubated (Table 4.5). During recesses, however, male brant and snow geese spent similar percentages of their time being vigilant, feeding, and in social interactions but male brant rested more than male snow geese (Table 4.5).

Glaucous gulls and parasitic jaegers were the only predators observed attacking nests during this study and most of their attacks (82% $n = 28$) occurred during incubation recesses. There was no difference between species in frequency of attacks when the female was on or off the nest ($G = 0.17$, $df = 1$, n.s.). Most attacks were made by single glaucous gulls, but seven gulls were observed attacking

Table 4.4. Comparison of male and female behaviour during incubation in black brant and lesser snow geese. $t > 0$ indicates the female spent more time performing the activity than her mate.

Comparison	Female			
	on/off nest	t	df	P
Brant				
Vigilance, head up	on	-9.13	45.9 ^a	0.0001
	off	-5.21	34.5 ^a	0.0001
Comfort movements	on	2.44	54	0.02
	off	3.27	24.7 ^a	0.003
Feeding	off	-0.16	46	n.s.
Locomotion	off	1.93	28.3 ^a	n.s.
Rest	on	8.50	54	0.0001
	off	-7.09	30 ^a	0.0001
Snow Geese				
Vigilance, head up	on	-6.88	55.8 ^a	0.0001
	off	-1.11	20	n.s.
Comfort movements	on	5.53	82	0.0001
	off	-1.60	10.5 ^a	n.s.
Feeding	off	-0.31	20	n.s.
Locomotion	off	1.40	10 ^a	n.s.
Rest	on	9.63	59 ^a	0.0001
	off	-1.00	10 ^a	n.s.

^a Approximate df assuming unequal variances.

Table 4.5. Comparison of black brant and lesser snow goose behaviour during incubation. $t > 0$ indicates brant spent more time in the activity than snow geese.

Comparison	Female			
	on/off nest	t	df	P
Males				
Vigilance, head up	on	3.61	68	0.001
	off	0.40	13.1 ^a	n.s.
Feeding	on	-3.74	68	0.001
	off	-2.04	12.1 ^a	n.s.
Rest	on	-0.74	68	n.s.
	off	3.68	33	0.001
Social interactions	on	3.32	36.6 ^a	0.001
	off	1.80	23 ^a	n.s.
Females				
Vigilance, head up	on	1.34	68	n.s.
	off	-0.80	11.5 ^a	n.s.
Feeding	on	0.69	68	n.s.
	off	-1.73	12.8 ^a	n.s.
Rest	on	-1.33	68	n.s.
	off	1.43	23	n.s.

^a Approximate df assuming unequal variances.

a snow goose nest on 23 June 1993. If off the nest when an avian predator attacked ($n = 23$), both brant and snow goose females responded by quickly returning to the nest, but they did not always resume incubating. Female brant and snow geese remained on their nests if attacked while incubating ($n = 5$) and all successful attacks ($n = 8$) occurred during recesses. When a predator attacked, males of both species quickly approached the nest regardless of the female's location. Male brant and snow geese also threatened ($n = 5$ occasions in brant, $n = 4$ in snow geese) or chased attackers ($n = 5$ occasions in brant, $n = 7$ in snow geese). On three occasions, male brant stood beside or over the nest to defend against gulls when the female was not present.

4.4 Discussion

Nest attendance by female snow geese was much higher than among female brant, as expected due to energetic constraints (Afton 1979, 1980, Ankney 1984). Female snow geese at Anderson River also had higher nest attendance rates than snow and Ross' geese *Chen rossii* at other nesting colonies (Martin et al. 1985, LeSchack et al. 1998). Like females of other large geese, female snow geese nesting at Anderson River spent nearly all of their time incubating (Cooper 1978, Thompson & Raveling 1987, Afton & Paulus 1992). Nest attendance by female brant at Anderson River was 2% higher than attendance by Atlantic brant *Branta bernicla hrota* (Afton & Paulus 1992), but was lower than black brant nesting on the Yukon-Kuskokwim Delta (89.6%, Thompson & Raveling 1987) and light-bellied

brent geese (also *B. b. hrota*) on Svalbard (90.9%, Madsen et al. 1989). Unlike snow geese at Anderson River and light-bellied brent geese on Svalbard (Madsen et al. 1989), female black brant at Anderson River Delta spent little time on their territories during incubation recesses. However, brant nests were rarely left unattended even though nest and territory attendance in female brant was much lower than in female snow geese because male brant were on the territory most of the time that their mates were absent. Territory attendance by male brant during incubation recesses was not statistically higher than that of male snow geese, but I believe the pattern was biologically meaningful. Instead of accompanying their mates away from the nest, male brant remained on the territory and guarded the eggs. Male snow geese rested less when their females left the nest and tended to increase time spent feeding and being vigilant, but the increases were not significant (Tables 4.2, 4.3). Male brant also tended to be more vigilant during recesses but unlike snow geese, brant did not tend to feed more or spend less time resting (Tables 4.2, 4.3). Male pink-footed geese *Anser brachyrhynchus* were more vigilant during recesses, as were male light-bellied brent geese which also decreased feeding and resting (Inglis 1977, Madsen et al. 1989). Male brant at Anderson River rested on their territories while their mates took incubation recesses but time spent being vigilant did not increase significantly, perhaps because males could not monitor females that were off the territory and "head up" or "extreme head up" postures were generally not required in order to guard nests. Male barnacle geese also appear to guard their nests while their females foraged up to 4 km from their territories (Prop et al. 1984), and Inglis (1977) described three male pink-footed geese that did not accompany

their mates on incubation recesses. Thus male brant tended to rest and guard the eggs during females' recesses whereas male snow geese tended to feed as they accompanied their mates. Division of nest guarding during incubation is analogous to male geese spending more time being vigilant while the female feeds during brood rearing (Sedinger & Raveling 1990). By dividing nest guarding between the sexes, brant were able to compensate for their lower fasting ability and therefore lower nest attendance.

The hypothesis that nest guarding and vigilance would increase and feeding would decrease with stage of incubation as predicted by parental investment theory can be rejected because nest attendance in female brant, and territory attendance in both male and female brant as well as male snow geese, declined through incubation. Even though there was some support for increased parental effort later in incubation because female brant were more vigilant and rested less as incubation progressed there were no changes in behaviour by snow geese or male brant. Nest attendance declined in light-bellied brent geese, barnacle geese, and greater snow geese *Chen caerulescens atlanticus* (Prop et al. 1984, Madsen et al. 1989, Reed et al. 1995), but not in pink-footed geese (Inglis 1977). However, nest attendance increased again immediately before hatch in barnacle and greater snow geese (Prop et al. 1984, Reed et al. 1995) and vigilance increased near hatch in pink-footed geese (Inglis 1977). Reduced time on the nest by females resulted in reduced nest survival in barnacle geese (Prop et al. 1984) as in this study. Mineau & Cooke (1979) noted that male lesser snow geese moved farther from their nests later in incubation and suggested that males guarded their mates and nests less in the latter half of incubation because

threats to their reproductive success due to extra-pair copulations or intraspecific nest parasitism (Lank et al. 1989) were greatly reduced then. However, Mickelson (1975) reported that territory size decreased as incubation progressed in black brant and Canada geese *Branta canadensis minima*. Declining nest attendance through incubation contrasts with increasing nest defence in many species of birds (Forbes et al. 1994, Rytönen et al. 1995, Sjöberg 1994); however, it is consistent with the need to increase food intake (e.g. Reed et al. 1995) as nutrient reserves are depleted.

Feeding was a minor activity in the overall time budget of female snow geese so ingested food probably contributed little to their nutritional requirements during incubation. Brant are unable to survive incubation without feeding (Ankney 1984) yet their territories at Anderson River contained no food (Chapter 2), so they were forced to feed off their territories. Travelling to distant food sources would have further increased energy requirements which could only be met by increased feeding. Although brant have not been previously reported feeding away from their territories, barnacle geese were observed feeding up to 4 km from their territories (Prop et al. 1984). At Anderson River, female brant were absent from their territories 15% of the time and males 20%, values that were higher than in other populations (Thompson & Raveling 1987, Madsen et al. 1989), due to the lack of food on brant territories. Nest attendance rates are influenced by body size and incubation energetics (Afton 1978, 1980, Ankney 1984), but there can be little doubt that nest and territory attendance by brant at Anderson River were also affected by the added energy demand of flying to grazing areas. When brant left their territories they usually flew out of sight in the direction of areas not visible from the tower but

where, on other occasions, brant were observed grazing. On one occasion, a male brant flew 500 m from his territory and joined other brant grazing on *Carex* spp. and *Puccinellia* spp. Both male and female brant probably fed most of the time they were absent from the territory causing their activity budgets while in sight (Table 4.2) to under estimate total time spent feeding. Assuming that female brant fed 88% of the time spent off territory (estimated from percentage of recess time spent feeding reported by Madsen et al. 1989: 85%, Afton & Paulus 1992: 91%, but excluding Thompson & Raveling 1987: 66% because their estimate was based on only three recesses) then feeding off territory would have accounted for 13% of females' total time budget, or slightly more than 3 h per day. Female brant spent only 0.1 h per day feeding on their territories. If males also fed 88% of the time while away from their territory, feeding off territory would have accounted for 18% of their total time budget, and when added to time spent feeding on territory, males would have fed 28% of the time, or over 6.5 h per day. Feeding by male snow geese may also have been under estimated by their observed activity budget (Table 4.2) since males feed during incubation rather than deplete their nutrient reserves (Ankney 1977a, b), and their territories at Anderson River also lacked food. Therefore, declining territory attendance with time suggests that female brant and males of both species spent more time feeding as incubation progressed.

Differences in activity budgets between sexes reflected their roles during incubation. Males spent more time vigilant, travelling, and in social interactions because they defended the territory from intruders, and interactions with intruders were more common in brant than snow geese. Male brant may have been more

vigilant than snow geese due to more frequent territory intrusions and the need to monitor their females' more frequent departures on incubation recesses. Female brant used recesses to drink, feed, bathe, and preen while their mates were vigilant or rested.

Incubation was the most effective means of defending eggs from avian predators in both species of geese at Anderson River Delta, as it was elsewhere (Prop et al. 1984). Predation attempts by gulls or jaegers while females incubated were rare, and none was successful. Avian predators were most successful when the female was absent from the territory and her mate was either inattentive or ineffective at defending the nest. Even though male brant often successfully defended against avian predators, defence by both sexes with the female off the nest was still less effective than incubation at preventing egg predation. Like brant on Svalbard (Madsen et al. 1989), incubating female brant and snow geese rarely responded to the approach of avian predators, although males changed postures to "head up" or "extreme head up", approached the nest and some threatened or chased intruders.

Nest defence by males appeared to be critical to successful reproduction by brant at Anderson River, but it may not have been as important in snow geese. In experiments where male snow and Ross' geese were removed in late egg-laying or early incubation, nest success of widowed females was as high as paired females (Martin et al. 1985, LeSchack et al. 1998). LeSchack et al. (1998) concluded that male removal experiments had demonstrated little effect on female incubation behaviour or nesting success in monogamous, precocial birds, and suggested that

male parental care in Arctic-nesting geese is more important during laying or after hatch than during incubation. Male parental care during incubation (i.e. nest defence) may not be critical where nesting success is generally high or in species where females rarely take incubation recesses, but for species that can not sustain nearly constant incubation when nest predation rates are high, male parental care is probably critical to nesting success.

Variation in reproductive success due to eggs lost to avian predators would select for greater nest attendance by female geese. However, since brant had lower nest attendance than snow geese, as well as brant nesting elsewhere (Thompson & Raveling 1987, Madsen et al. 1989), female brant at Anderson River may have been constrained from increasing nest attendance by life-history traits or environmental factors. The life-history constraint is fasting ability which in turn is related to nutrient reserves and body size (Afton 1979, 1980, Ankney 1984). At Anderson River, an environmental constraint imposed by nesting habitat which lacked food for nesting brant may have resulted in lower nest attendance than at other nesting areas. However, adaptive nest guarding behaviour by brant at least partially compensated for the need to defend their nest even though they could not feed on their territories. By adopting this nest guarding strategy, brant were able to overcome both life-history and environmental constraints to successful reproduction at Anderson River Delta.

4.5 References

- Afton, A.D. 1979. Time budget of breeding Northern Shovelers. *Wilson Bull.* 91:42-49.
- Afton, A.D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton, A.D. & Paulus, S.L. 1992. Incubation and brood care. *In* Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) *Ecology and management of breeding waterfowl*: 62-108. Minneapolis: University of Minnesota Press.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Ankney, C.D. 1977a. The use of nutrient reserves by breeding male lesser snow geese *Chen caerulescens caerulescens*. *Can. J. Zool.* 55:1984-1987.
- Ankney, C.D. 1977b. Feeding and digestive organ size in breeding lesser snow geese. *Auk* 94:275-282.
- Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101:361-370.
- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459- 471.
- Bellrose, F.C. 1980. *Ducks, geese and swans of North America*, 3rd ed. Harrisburg, Pennsylvania: Stackpole Books.

- Blancher, P.J. & Robertson, R.J. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.* 30:929-945.
- Cooper, J.A. 1978. The history and breeding biology of the Canada geese at Marshy Point, Manitoba. *Wildl. Monogr.* 61:1-87.
- Drent, R.H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- Forbes, M.R.L., Clark, R.G., Weatherhead, P.J. & Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behav. Ecol. Sociobiol.* 34:79-85.
- Hamer, K.C. & Furness, R.W. 1993. Parental investment and brood defence by male and female great skuas *Catharacta skua*: the influence of food supply, laying date, body size and body condition. *J. Zool., Lond.* 230:7-18.
- Inglis, I.R. 1977. The breeding behavior of the pink-footed goose: behavioral correlates of nesting success. *Anim. Behav.* 25: 747-764.
- Johnson, D.H. 1995. Statistical sirens: the allure of nonparametrics. *Ecology* 76:1998-2000.
- Lank, D.B., Mineau, P., Rockwell, R.F. & Cooke, F. 1989. Intraspecific nest parasitism and extra-pair copulation in lesser snow geese. *Anim. Behav.* 37:74-89.
- Lazarus, J. & Inglis, I.R. 1978. The breeding behaviour of the pink-footed goose: Parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62-88.

- Leger, D.W. & Didrichsons, I.A. 1994. An assessment of data pooling and some alternatives. *Anim. Behav.* 48:823-832.
- LeSchack, C.R., Afton, A.D. & Alisauskas, R.T. 1998. Effects of male removal on female reproductive biology in Ross' and lesser snow geese. *Wilson Bull.* 110:56-64.
- Madsen, J., Bregnballe, T. & Mehlum, F. 1989. Study of the breeding ecology and behaviour of the Svalbard population of light-bellied brent goose *Branta bernicla hrota*. *Polar Research* 7:1-21.
- Martin, K., Cooch, F.G., Rockwell, R.F. & Cooke, F. 1985. Reproductive performance in lesser snow geese: are two parents essential? *Behav. Ecol. Sociobiol.* 17:257-263.
- Martin, P. & Bateson, P. 1986. *Measuring behaviour*. Cambridge: Cambridge University Press.
- Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *In* Power, D.M. (ed.) *Curr. Ornithol.*: 9:163-197. New York: Plenum Press.
- Mickelson, P.G. 1975. Breeding biology of cackling geese and associated species on the Yukon-Kuskokwim Delta, Alaska. *Wildl. Monogr.* 45:1-35.
- Mineau, P. & Cooke, F. 1979. Territoriality in snow geese or the protection of parenthood - - Ryder's and Inglis's hypotheses reassessed. *Wildfowl* 30:16-19.
- Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* 63:167-187.

- Prop, J., Eerden, M.R. van & Drent, R.H. 1984. Reproductive success of the barnacle goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitzbergen. *Nor. Polarinst. Skr.* 181:87-117.
- Reed, A.H., Hughes, R.J. & Gauthier, G. 1995. Incubation behavior and body mass of female greater snow geese. *Condor* 97:993-1001.
- Rytkönen, S., Orell, M. & Koivula, K. 1995. Pseudo Concorde fallacy in the willow tit? *Anim. Behav.* 94:1017-1028.
- SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, 4th ed. Vol. 2. Cary, North Carolina: SAS Institute Inc.
- Sedinger, J.S. & Raveling, D.G. 1990. Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs. *Condor* 92:174-181.
- Sjöberg, G. 1994. Factors affecting nest defence in female Canada geese *Branta canadensis*. *Ibis* 136:129-135.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*, 2nd ed. San Francisco: W. H. Freeman and Co.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Thompson, S.C. & Raveling, D.G. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- Trivers, R.L. 1972. Parental investment and sexual selection. *In* Campbell, B. (ed.) *Sexual selection and the descent of man 1871-1971*: 136-179. Chicago: Aldine.
- Trivers, R.L. 1974. Parent-offspring conflict. *Amer. Zool.* 14:249-264.

5. GENERAL DISCUSSION

The Arctic habitats where black brant and lesser snow geese nest impose severe constraints on their reproductive strategies. I examined how predation, an important factor influencing reproductive success of birds in many environments, affected reproductive success in sympatric brant and snow geese, their behavioural tactics to reduce egg losses to avian predators, and how those tactics were constrained by life-history traits.

Of all the factors known to influence reproductive success in Arctic geese, predation is probably the least understood, yet it may be one of the most important (Raveling 1989, Anthony et al. 1991, Syroechkovskiy et al. 1991, Tremblay et al. 1997). Other important factors, weather conditions and nutrient reserves, are well known (e.g. Barry 1962, Ryder 1970, Newton 1977, Ankney & MacInnes 1978, Davies & Cooke 1983, Alisauskas & Ankney 1992, Cooke et al. 1995). Egg predation strongly influenced reproductive success of geese at Anderson River Delta; during this study, only 24% of eggs laid by brant and 39% by snow geese remained in nests at hatch (Chapter 2). In the best year, 1993, 78% of snow goose eggs, but only 52% of brant eggs, survived to hatch. In other studies of Arctic geese, foxes were the main egg predators and predation rates varied little among species but greatly among years as fox populations rose and fell following small rodent

abundance (Syroechkovskiy et al. 1991, Underhill et al. 1993, Tremblay et al. 1997). At Anderson River Delta, the main egg predators and their effects differed from other studies. Egg losses in this study were primarily to avian predators and affected brant more than snow geese.

5.1 Coloniality as an Antipredator Strategy

Coloniality would appear to be a simple behavioural adaptation within a reproductive strategy, especially for species that do not need to obtain food from their nesting territories. Snow geese can generally survive incubation without feeding (Ankney 1977, Ankney & MacInnes 1978). Snow geese therefore should have few constraints on minimum territory size beyond that needed by the pair to defend against intraspecific nest parasitism and the male to prevent extra-pair copulations with his mate by neighbouring males (Mineau & Cooke 1979, Lank et al. 1989). However, brant must feed during the nesting period and would benefit by having access to food on their nesting territories (Ankney 1984), so their minimum territory size should be larger. Maximum nest density in brant would then be constrained by a combination of nutrient reserves and food availability (Ryder 1975). Even though snow geese nested at higher densities and had higher nest and egg survival than brant, interspecific differences in reproductive success (Chapter 2) were not related to differences in nest density (Chapter 3).

Geese nesting in the centre of the densest aggregations were as vulnerable to egg predation as the most dispersed nests (Chapter 3). Since nesting at high

densities neither reduced nor increased nest or egg survival, nest densities were too low to induce predators to switch from other prey to goose eggs (Ims 1990) or to overwhelm the killing rate of those that did prey on eggs. Even though there was much intraspecific variation, there was no selection pressure for either increased or decreased nest densities. Coloniality was not a factor in reproductive success of geese at Anderson River Delta, but why it was not is unclear, because reproductive success increased with coloniality in other species, including greater snow geese (Tremblay et al. 1997). Coloniality may be more effective against terrestrial predators like Arctic fox *Alopex lagopus* because they would always encounter defence behaviour at peripheral nests before reaching central nests. Coloniality may be less effective against avian predators because gulls and jaegers were often ignored when they flew over goose nesting areas so central nests could be attacked from overhead without first encountering antipredator behaviour from any other geese.

5.2 Time Constraints on Nest Guarding

The need to prevent egg losses to avian predators is common in Arctic goose nesting areas (Ryder 1970, Harvey 1971, Prop et al. 1984). At Anderson River Delta, the most effective deterrent to egg predation by gulls or jaegers was an incubating goose and female snow geese incubated almost constantly (Chapter 4). Female brant, however, had lower nest attendance than snow geese (Chapter 4), probably due to their lower fasting ability (Ankney 1984). Lack of food forced brant to forage off their territories, which would have increased energy requirements and

caused brant to spend even more time feeding. Even though male brant typically guarded their nests while their mates foraged, this division of labour did not fully compensate for the females' time off the nest because brant had lower nest and egg survival than snow geese (Chapter 2). The behavioural adaptation that resulted in male brant guarding their nests while their mates foraged enabled brant to nest successfully at Anderson River, but greater fasting ability and nest attendance gave snow geese a selective advantage in the presence of avian predators.

Given the time and energy constraints on brant during nesting, it is puzzling why brant spent more time in social interactions (Chapter 4) to defend larger territories than snow geese (Chapter 3). Securing a food supply has been hypothesized as an important function of territoriality in Arctic-nesting geese (Ryder 1975, Inglis 1976) and this would be more important for brant than snow geese, but the brant territories observed in this study lacked food (Chapter 2).

Time and energy constraints on nest attendance may explain more than differences in nest guarding behaviour in brant and snow geese. Brant at Anderson River Delta had smaller clutches than other populations, and I speculated that clutch size estimates may have been biased due to partial clutch predation before nests were found (Chapter 2). However, brant may produce fewer eggs as an adaptive response to nest predation (Martin 1992). By laying fewer eggs, female brant would begin incubation with larger nutrient reserves which would enable them to increase nest attendance (Thompson & Raveling 1987) and by doing so, increase nest survival. Unfortunately, trade-offs between fecundity and nest guarding may be difficult to test in geese because clutch size adjustments due to predation are most likely to be

evolutionary responses. This hypothesis may be tested by manipulating a system with shorter life cycles than geese, e.g. fish, where clutch size and nest guarding are related to nutrient reserves and predation is also an important factor in reproductive success.

5.3 Conclusions

Reproductive success was not related to variables associated with coloniality in either brant or snow geese during this study. Therefore I concluded that variation in dispersion and location of nests at Anderson River did not occur in response to avian predation. Future research on the adaptive significance of coloniality in Arctic-nesting geese should examine how reproductive success varies with nest density and position when the major egg predators are foxes, particularly in colonies with higher densities than at Anderson River Delta.

The most effective adaptation to reduce egg losses, constant nest attendance by the incubating female, was one that brant did not employ. Increasing nest attendance by relying on nutrient reserves, as female snow geese do, would have been the most effective response to avian predators. Female brant may have been constrained from that reproductive strategy by their ability to store or carry endogenous nutrient reserves. The effects of this constraint were exacerbated by the lack of food on brant territories; however, a behavioural adaptation to their reproductive strategy enabled brant to nest successfully in spite of both a life-history and an environmental constraint to nest guarding. The importance of the

environmental constraint, i.e. food supply on nesting territories, could be tested by comparing nest and territory attendance as well as reproductive success of brant with and without food on their territories. Effects of nutrient reserves, the life-history constraint, are difficult to test since manipulating nutrient reserves of female brant may not be possible.

5.4 References

- Alisauskas, R.T. & Ankney, C.D. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. *In* Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) Ecology and management of breeding waterfowl: 30-61. Minneapolis: University of Minnesota Press.
- Ankney, C.D. 1977. The use of nutrient reserves by breeding male lesser snow geese (*Chen caerulescens caerulescens*). *Can. J. Zool.* 55:1984-1987.
- Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101:361-370.
- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459- 471.
- Anthony, R.M., Flint, P.L. & Sedinger, J.S. 1991. Arctic fox removal improves nest success of black brant. *Wildl. Soc. Bull.* 19:176-184.
- Barry, T.W. 1962. Effect of late seasons on Atlantic brant reproduction. *J. Wildl. Manage.* 26:19-26.
- Cooke, F., Rockwell, R.F. & Lank, D.B. 1995. *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. New York: Oxford University Press Inc.
- Davies, J.C. & Cooke, F. 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. *J. Wildl. Manage.* 47:291-296.
- Harvey, J.M. 1971. Factors affecting blue goose nesting success. *Can. J. Zool.* 49:223-224.

- Ims, R.A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* 136:485-498.
- Inglis, I.R. 1976. Agonistic behaviour of breeding Pink-footed geese with references to Ryder's hypothesis. *Wildfowl* 27:95-99.
- Lank, D.B., Mineau, P., Rockwell, R.F. & Cooke, F. 1989. Intraspecific nest parasitism and extra-pair copulation in lesser snow geese. *Anim. Behav.* 37:74-89.
- Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *In* Power, D.M. (ed.) *Curr. Ornithol.*: 9:163-197. New York: Plenum Press.
- Mineau, P. & Cooke, F. 1979. Territoriality in snow geese or the protection of parenthood - - Ryder's and Inglis's hypotheses reassessed. *Wildfowl* 30:16-19.
- Newton, I. 1977. Timing and success of breeding in tundra-nesting geese. *In* Stonehouse, B. & Perrins, C. (eds) *Evolutionary Ecology*: 112-126. Baltimore: University Park Press.
- Prop, J., Eerden, M.R. van & Drent, R.H. 1984. Reproductive success of the barnacle goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitzbergen. *Nor. Polarinst. Skr.* 181:87-117.
- Raveling, D.G. 1989. Nest-predation rates in relation to colony size of black brant. *J. Wildl. Manage.* 53:87-90.
- Ryder, J.P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82:5-13.

- Ryder, J.P. 1975. The significance of territory size in colonial nesting geese - - an hypothesis. *Wildfowl* 26:114-116.
- Syroechkovskiy, Ye.V., Litvin, K.Ye. & Ebbinge, B.S. 1991. Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988; interplay of weather and Arctic fox predation. *Ardea* 79:373-382.
- Thompson, S.C. & Raveling, D.G. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- Tremblay, J.P., Gauthier, G., Lepage, D. & Desrochers, A. 1997. Factors affecting nesting success in greater snow geese: effects of habitat and association with snowy owls. *Wilson Bull.* 109:449-461.
- Underhill, L.G., Prys-Jones, R.P., Syroechkovski, E.E. Jr., Groen, N.M., Karpov, V., Lappo, H.G., van Roomen, M.W.J., Rybkin, A., Schekkerman, H., Spiekman, H. & Summers, R.W. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277-292.

**APPENDIX. EFFECTS OF RESEARCH ACTIVITIES ON NEST
PREDATION IN ARCTIC-NESTING GEESE^a**

Abstract

Effects of researchers' nest visits on nest predation were quantified by comparing clutch sizes between nests visited repeatedly and those visited only once. Marker effects were determined by comparing nest success in marked and unmarked nests. In 1993, clutch size at the end of incubation was 0.6 egg less ($P = 0.02$) at brant nests and 0.4 egg greater ($P = 0.03$) at snow goose nests, visited repeatedly, than at nests visited only once. I found no effect of nest visits on clutch size of brant in 1991. There was weak evidence that nest markers increased nest failure ($P = 0.05$) among snow geese in 1991 but markers did not influence the frequency of complete or partial clutch predation in brant in 1991 or in either species in 1993 (all tests n.s.). Nest markers did not affect clutch size or nest fate in these species, but were useful for identifying nests from a distance.

^a Armstrong, T. 1996. *J. Wildl. Manage.* 60:265-269. Copyright *The Wildlife Society*.

Introduction

Ornithologists have long suspected that their activities affected nest success (Kalmbach 1938, Skutch 1966, MacInnes and Misra 1972). Research activities frequently include visiting nests to record reproductive output and placing markers near them to assist in finding nests on subsequent visits. The suspicion, which motivated this study, is that human activity decreases nest success rates (e.g., Morton et al. 1993).

In a review, Götmark (1992) found that half of the papers that examined the effects of nest visits reported some negative effect on nest success, but conclusions varied from no detectable effect (MacIvor et al. 1990, Sedinger 1990) to potentially severe effects (MacInnes 1980, Strang 1980). In addition to nest visits, markers may have an effect on study populations (Yahner and Wright 1985). Reynolds (1985) reported that some predators learned to search for nests near investigators' markers. Other studies, however, found no detectable effect of markers on nesting success (Galbraith 1987, Vacca and Handel 1988, Hannon et al. 1993).

I assessed the effects of my research activities on partial and complete clutch predation in 2 species of geese, black brant and lesser snow geese. This research was part of a study of predation and antipredator tactics of Arctic-nesting geese and was done to determine how seriously my activities disturbed the system. I placed markers near nests to make it easier to find and identify them on subsequent visits and during behavioral observations. I determined the effect of markers on partial and complete clutch predation, but the effect of visiting nests was determined only

for partial clutch losses. I tested the hypotheses that the presence of nest markers would result in higher partial and complete clutch predation and that nests visited several times would have smaller clutches at the end of incubation than those visited only once.

Methods

Nests were treated in one of two ways. Most were marked with an unpainted, numbered wooden stake (5 x 1 x 50 cm) placed 2 to 5 m from the nest. Remaining nests were not marked, but their locations were recorded relative to a marked nest or other landmark. Identification numbers of unmarked nests were written on driftwood found nearby or were scribed in the mud. Eggs of all nests to be revisited were numbered so I could detect egg losses or additions. Both markers and eggs were numbered with waterproof black ink. Parasitic jaegers and glaucous gulls occasionally followed researchers and attempted, with some success, to take eggs from nests that were left unattended as geese moved away from researchers. Whenever gulls and jaegers followed us, we attempted to frighten them from the goose nests, covered exposed eggs with nest material, and left the area so the geese would return and defend their clutches. Both larids and geese seemed to be less active between 2300 and 0700 hours (pers. obs.) and nest visits were made during those hours in 1993.

In 1991, I recorded clutch sizes of 70 snow goose nests in early incubation. Half of the nests were randomly selected to be marked with stakes and the remainder

were left unmarked. These nests were visited again, about 1 week after hatch, to ascertain their fates based on presence or absence of detached shell-membranes in or beside the nest bowl. I searched for brant nests throughout the egg-laying period. My objectives were to find at least 100 brant nests and randomly select 30 to be left unmarked. Brant nests were revisited every second day during laying to determine clutch sizes and daily during hatch.

In 1993, snow goose and brant nests were found at the end of their egg-laying periods. One hundred and sixty snow goose nests were randomly selected from the first 320 active nests found, and were divided equally between the 2 islands that supported the main snow goose nesting concentrations. My objective was to find at least 100 brant nests. Most nests were marked with a stake except 30 brant and 31 snow goose nests, randomly selected from the larger sample. In 1993, I visited nests at 5-day intervals and recorded missing eggs or any other evidence of predation.

The effects of markers on the fate of nests (survive or fail) and on partial clutch loss were analysed using tests of independence (Sokal and Rohlf 1981:731). To analyse the effect of markers on partial clutch loss, nests were divided into two classes: those with no partial clutch loss and those that lost ≥ 1 eggs. Nests with only 1 egg were excluded from analysis of partial clutch loss because removal of the only egg constitutes complete nest failure. Tests of interest in contingency analyses are for the presence of interactions. In this study the interactions of interest were between marker and fate or marker and partial clutch loss.

The effect of nest visits on partial clutch predation was assessed by comparing mean clutch size of control nests with intensively studied conspecific nests, described above, that had been visited 5.4 ± 1.0 times. Control nests were previously undisturbed and >200 m from any place that we had been during the nesting period. For this test, clutch sizes of intensively studied and control nests were sampled near the end of incubation. For snow geese, control nests were divided between the 2 islands where the intensively studied nests were found. Control nests for brant were found on the same island that supported most of the intensively studied nests. Spatial variation in clutch size, if present, could cause spurious results due to the distance between intensively studied nests and controls. In 1993, nests were mapped and tested for spatial variation in clutch size using a runs test (Siegel and Castellan 1988:58). Clutch sizes of multiple-visit and control groups were compared using Wilcoxon's rank sum test (Siegel and Castellan 1988:128) because they were not normally distributed. Assuming that nests in the control and multiple-visit treatment had the same initial mean clutch sizes, this comparison enabled me to determine if repeated visits increased partial clutch losses.

Results

In 1991, I found 70 snow goose nests on 29 May; 35 were left unmarked, and their fates were recorded on 25 June. I began searching for brant nests on 4 June; found 229 brant nests, and left 33 unmarked. In 1993, I found 103 brant nests and 30 were left unmarked; 31 of the 160 snow goose nests were left unmarked.

Clutch sizes of controls for the nest visit tests were recorded at 31 brant nests on 27 and 28 June 1991; at 68 snow goose nests on 21 June 1993, and 39 brant nests on 27 June 1993.

Markers

In 1991, unmarked brant nests were 35.4 ± 3.8 m ($\bar{x} \pm$ SE, range 5 to 100 m) from the nearest marked nest. In 1993, unmarked snow goose nests were 25.8 ± 3.6 m (range 5 to 81 m) and unmarked brant nests were 46.9 ± 4.1 m (range 15 to 96 m) from the nearest marked nest.

In 1991, 26 of 35 snow goose nests (74%) with markers and 32 of 35 (91%) without markers hatched ($G = 3.76$, $df = 1$, $P = 0.05$, power = 0.48). There was no evidence that the proportion of brant nests that hatched differed between those with (53/196, 27%) and without (10/33, 30%) a marker ($G = 0.15$, $df = 1$, $P = 0.70$, power = 0.09). Nor was there evidence that markers near nests affected the proportion of nests that experienced partial clutch loss (with marker 96/169, 57%, without marker 12/27, 44%, $G = 1.43$, $df = 1$, $P = 0.23$, power = 0.26).

In 1993, markers did not affect nest fate in either snow geese (with marker 15/129, 12% failed, without marker 1/31, 3% failed, $G = 2.45$, $df = 1$, $P = 0.12$) or brant (with marker 13/73, 18% failed, without marker 7/30, 23% failed, $G = 0.40$, $df = 1$, $P = 0.53$). The proportion of nests that suffered partial clutch loss was not influenced by the presence of a marker in either snow geese (with marker 24/129, 19%, without marker 6/31, 19% $G = 0.01$, $df = 1$, $P = 0.92$) or brant

(with marker 25/73, 34%, without marker 12/30, 40%, $G = 0.30$, $df = 1$, $P = 0.58$). Power was < 0.29 in all tests (Cohen 1988).

Nest Visits

Marked and unmarked nests were combined for the following tests because there was no evidence that markers affected partial or complete clutch loss in brant in 1991 or in either species in 1993. In 1991, average clutch size of intensively studied brant nests declined from 3.3 ± 0.1 eggs ($\bar{x} \pm SE$, $n = 103$) early in incubation to 2.5 ± 0.1 eggs ($n = 103$) by late incubation ($Z = 5.04$, $P < 0.001$). Average clutch size of control nests (2.4 ± 0.2 , $n = 31$ eggs) was smaller than that of intensively studied nests early in incubation ($Z = -3.99$, $P < 0.001$). Clutch size at the end of incubation did not differ between intensively studied nests and control nests ($Z = -0.67$, $P = 0.500$). The power of this test approaches that of Student's *t*-test (Siegel and Castellan 1988:137) and would be < 0.20 .

In 1993, there was no evidence that the spatial distribution of clutch sizes differed from random in either brant ($Z = 0.80$, $P = 0.426$) or snow geese ($Z = -1.05$, $P = 0.295$). Clutch size of intensively studied snow goose nests did not decline from early (4.3 ± 0.1 eggs, $n = 143$, first nest visit) to late incubation (4.2 ± 0.1 eggs, fourth nest visit, $Z = 1.38$, $P = 0.167$). Nests visited only once, late in incubation, had a mean clutch of 3.8 ± 0.2 eggs ($n = 68$) which was smaller than that of intensively studied nests ($Z = -2.15$, $P = 0.032$). Among brant, mean clutch size declined from early (3.7 ± 0.1 , $n = 83$) to late incubation (3.2 ± 0.1 , n

= 83, $Z = 2.55$, $P = 0.011$). Mean clutch size of intensively studied nests in early incubation was not significantly different than that of control nests (3.8 ± 0.2 , $n = 39$) found in late incubation ($Z = 0.35$, $P = 0.724$), but by late incubation average clutch size of intensively studied nests was smaller than that of control nests ($Z = 2.32$, $P = 0.020$).

Discussion

The 1991 snow goose data provided only weak evidence that nest markers resulted in increased nest failure in this study. These data however, may have underestimated hatch success because nest fates were determined after hatch. By that time, evidence of successful hatch may have disappeared due to wind or scavengers (pers. obs.). The 1991 brant data should have been more reliable regarding the effects of nest markers because brant nests were visited more frequently and the sample size was much larger. These data however, did not support the hypothesis that markers affected partial or complete clutch loss.

There was no evidence that markers affected partial or complete clutch failure in either brant or snow geese in 1993. I conclude that markers had little effect on partial or complete clutch loss because the data suggest a weak marker effect in only 1 of 4 situations. My results are similar to those reported by others (Galbraith 1987, Vacca and Handel 1988, Hannon et al. 1993). In this study, nesting geese were conspicuous, both visually and audibly, and it is unlikely that marker stakes made

them any easier for predators to find, unlike situations where effects of markers have been reported (Picozzi 1975, Reynolds 1985, Yahner and Wright 1985).

Tests of the effects of markers on both partial and complete clutch predation had low power even though sample sizes were adequate except among snow geese in 1991. Low power was due to the small differences observed between marked and unmarked nests. Had the differences been as large as that observed between marked and unmarked snow geese in 1991, power would have exceeded 0.75 in most tests.

The apparent lack of an effect of nest visits on partial clutch predation among brant in 1991 was surprising because gulls and jaegers were particularly noticeable as they followed researchers that year. Repeated visits to nests in 1993 may have caused higher partial clutch losses among brant but not among snow geese. Average clutch size in snow geese did not decline during incubation whereas it declined in brant in both years due to partial clutch predation. It is unlikely that nest visits caused partial clutch loss to increase among brant, but to decrease among snow geese. Even though there was no evidence of spatial variation in clutch sizes sampling error is a more likely explanation for control nests having smaller clutches than intensively studied snow geese.

Gulls and jaegers probably accounted for all of the predation recorded in this study because no sign of bears was found in the area during the study period. Bears were observed nearby, however, where they destroyed virtually every nest. Human activity caused bears to flee and our presence may have deterred them from entering the study area.

Inconsistent effects of visits to nests were consistent with the findings of other studies, including those of colonial waterfowl (Götmark 1992). Observer-induced predation on eggs has been reported (MacInnes and Misra 1972, MacInnes 1980, Esler and Grand 1993) but others found no effect of nest visits on egg or nest survival (Sedinger 1990, Hannon et al. 1993).

Management Implications

Placing wooden stakes near nests had no overall effect on clutch size or fate of nests in conspicuous, colonial nesting geese. Researchers concerned with potential biases caused by markers have few options. They can use inconspicuous markers or avoid them entirely. Assessing the effects of markers by comparing marked and unmarked samples, as in this study, is a useful technique.

Researchers concerned with potential effects of visiting nests have a problem. It is difficult to collect some types of data without visiting nests, but steps often can be taken to minimize the effect of visits. I found that visiting nests at night reduced the accompaniment of avian predators. Also, after 1991, I avoided visiting nests during laying or hatch, times when eggs or goslings were particularly vulnerable to predation. Ornithologists may believe their activities reduce nest or egg survival because they observe predators following them, and assume they have no effect when such predator activity is absent. However, predators may avoid human activity (e.g., crows (Götmark and Åhlund 1984) and bears during most of this study) which may increase reproductive success of study populations. Researchers should be alert

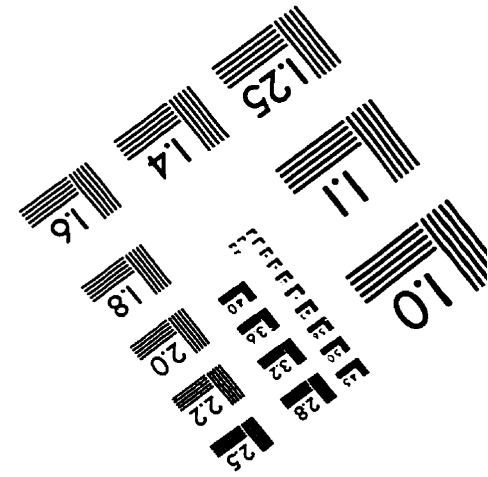
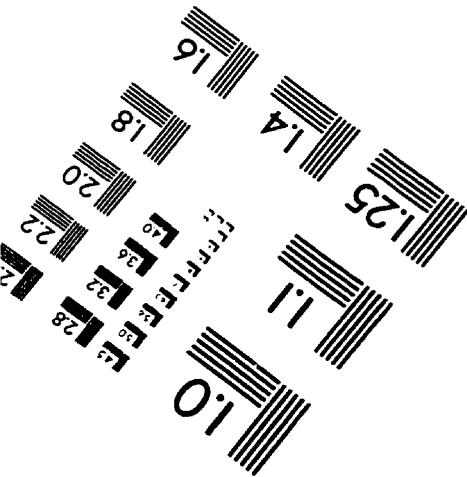
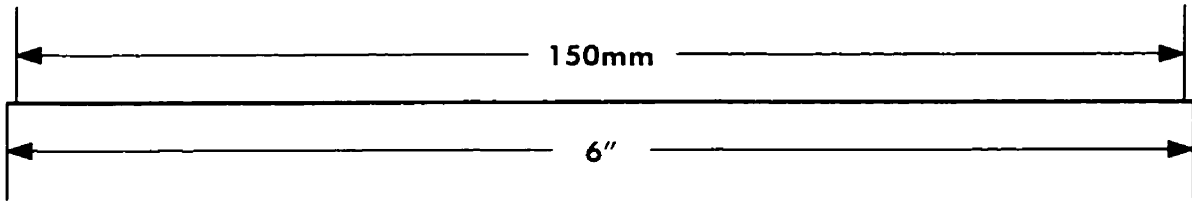
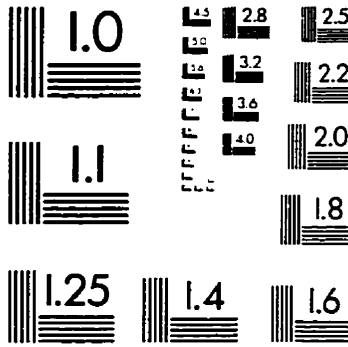
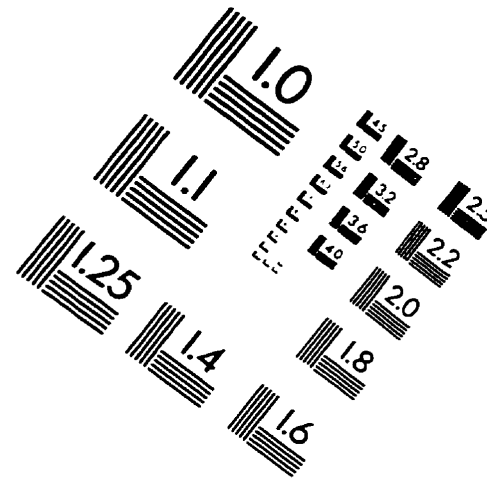
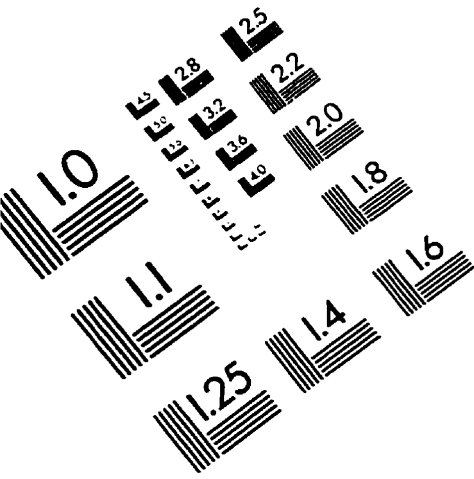
to both types of effects and avoid unidirectional alternate hypotheses (i.e., one-tailed tests).

References

- Cohen, J. 1988. Statistical power analysis for the behavioral sciences, 2nd ed. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Esler, D. & Grand, J.B. 1993. Factors influencing depredation of artificial duck nests. *J. Wildl. Manage.* 57:244-248.
- Galbraith, H. 1987. Marking and visiting lapwing *Vanellus vanellus* nests does not affect clutch survival. *Bird Study* 34: 137-138.
- Götmark, F. 1992. The effects of investigator disturbance on nesting birds. *In* Power, D.M. (ed.) *Curr. Ornithol.*: 9:63-104. New York: Plenum Press.
- Götmark, F. & Åhlund, M. 1984. Do field observers attract nest predators and influence nesting success of common eiders? *J. Wildl. Manage.* 48:381-387.
- Hannon, S.J., Martin, K., Thomas, L. & Schieck, J. 1993. Investigator disturbance and clutch predation in willow ptarmigan: methods for evaluating impact. *J. Field Ornithol.* 64: 575-586.
- Kalmbach, E.R. 1938. A comparative study of nesting waterfowl on the lower Souris refuge: 1936-1937. *Trans. N. A. Wildl. Conf.* 3: 610-623.
- MacInnes, C.D. 1980. Comment: observer-induced predation is real. *J. Wildl. Manage.* 44:222-224.
- MacInnes, C.D. & Misra, R.K. 1972. Predation on Canada goose nests at McConnell River, Northwest Territories. *J. Wildl. Manage.* 36:414-422.
- MacIvor, L.H., Melvin, S.M. & Griffin, C.R. 1990. Effects of research activity on piping plover nest predation. *J. Wildl. Manage.* 54:443-447.

- Morton, M.L., Sockman, K.W. & Peterson, L.E. 1993. Nest predation in the mountain white-crowned sparrow. *Condor* 95:72-82.
- Picozzi, N. 1975. Crow predation on marked nests. *J. Wildl. Manage.* 39:151-155.
- Reynolds, J.D. 1985. Sandhill crane use of nest markers as cues for predation. *Wilson Bull.* 97:106-108.
- Sedinger, J.S. 1990. Effects of visiting black brant nests on egg and nest survival. *J. Wildl. Manage.* 54:437-443.
- Siegel, S. & Castellan, N.J. Jr. 1988. *Nonparametric statistics for the behavioral sciences*, 2nd ed. New York: McGraw-Hill Book Co.
- Skutch, A.F. 1966. A breeding bird census and nesting success in Central America. *Ibis* 108:1-16.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*, 2nd ed. San Francisco: W. H. Freeman and Co.
- Strang, C.A. 1980. Incidence of avian predators near people searching for waterfowl nests. *J. Wildl. Manage.* 44:220-222.
- Vacca, M.M. & Handel, C.M. 1988. Factors influencing predation associated with visits to artificial goose nests. *J. Field Ornithol.* 59:215-223.
- Yahner, R.H. & Wright, A.L. 1985. Depredation on artificial ground nests: effects of edge and plot age. *J. Wildl. Manage.* 49: 508-513.

IMAGE EVALUATION TEST TARGET (QA-3)



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