

EFFECTS OF BODY SIZE ON GOOSE BEHAVIOR:
LESSER SNOW GOOSE AND ROSS'S GOOSE

A Dissertation

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DEDICATION

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ABSTRACT

Body size is highly variable among geese, both at intra- and interspecific levels. Interspecific variation in several behaviors has been attributed to differences in body size in geese: incubation constancy, tendency to maintain family units, and time spent foraging. Body size has important physiological implications for birds, mostly because mass-specific metabolic rate is greater for birds of smaller mass. The Body-size Hypothesis predicts that smaller species deplete their energy reserves at relatively faster rates than do larger species.

Hypotheses and conclusions concerning effects of body size on waterfowl behavior often are based on comparisons of species that confront different climates, habitat types, and food resources, and migrate variable distances with different energetic costs. Accordingly, I controlled for such variation by comparing the behavior and physiology of lesser snow geese (hereafter snow geese) and Ross's geese, which are closely related and highly sympatric throughout the annual cycle.

I found that incubation constancies of both species averaged 99%. The defeathered ventral area was positively related to clutch volume and inversely related to prolactin levels in female Ross's geese, but not in female snow geese; moreover, prolactin levels and body condition were inversely related in Ross's geese, but not in snow geese. I documented that 5 of 5 female snow geese and 1 of 5 female Ross's geese possessed fully-developed brood patches. In winter, I documented that Ross's geese spent more time feeding than did snow geese. All these findings, except that for incubation constancy, were consistent with predictions of the Body-size Hypothesis.

Finally, I studied effects of intraspecific body size variation on goose behavior by studying movements and behavior of snow geese in southwest Louisiana. I found that both adult and juvenile snow geese from coastal marshes had larger bodies and bills than did those from

rice-prairie habitats. Adult snow geese from coastal marshes spent more time feeding than did those in rice-prairies, whereas the opposite was true for juveniles. I conclude that snow geese in southwest Louisiana segregate into coastal marsh and rice-prairie habitats by body morphometrics, but move too frequently between the 2 habitats to be considered separate populations.

CHAPTER 1: GENERAL INTRODUCTION

THE BODY-SIZE HYPOTHESIS

Body size is highly variable among geese, both at intra- and interspecific levels (Owen 1980, Alisauskas 1998, Madsen et al. 1999, Dickson 2000). Body size has important physiological implications for birds: (1) rate of heat loss increases with decreasing body size and, thus, increasing surface to volume ratio (Schmidt-Nielsen 1997); (2) mass-specific metabolic rate is greater for birds of smaller mass (Kendeigh 1970); (3) gut size scales linearly with body size, and gut size partly determines the rate of energy extraction from food (Demment and Van Soest 1985, Mayhew and Houston 1993); and (4) during incubation, larger species generally have a greater fasting endurance than do smaller species, which compensate by relying more on foraging opportunities (The Body-size Hypothesis: Skutch 1962; Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992). The Body-size Hypothesis predicts that smaller species deplete their energy reserves relatively faster and reach starvation thresholds before larger species (Aldrich and Raveling 1983, Johnson and Raveling 1988, Afton and Paulus 1992).

Interspecific variation in several behaviors has been attributed to differences in body size in waterfowl: incubation constancy, tendency to maintain family units, timing of pair formation, and time spent foraging (Skutch 1962, Afton 1980, Rohwer and Anderson 1988, Johnson and Raveling 1988, Mayhew 1988, Afton and Paulus 1992). Most hypotheses and conclusions concerning effects of body size on waterfowl behavior are based on comparisons of species that confront different climates, habitat types, and food availability, and migrate variable distances with different energetic costs (see Bromley and Jarvis 1993, Gauthier 1993). Among geese, smaller species are: (1) relatively more vulnerable to avian predators (Johnson and Raveling 1988, McWilliams and Raveling 1998); and (2) more likely to be displaced in competition with co-existing larger species (Madsen and Mortensen 1987, Gawlik 1994).

Many bird species develop brood patches before incubation (Jones 1971, Drent 1975, Lea and Klandorf 2002). Body size has implications for brood patch development because heat loss through brood patches can be energetically costly, which may explain absence of brood patch development in certain smaller birds (Payne 1966, Haftorn and Reinertsen 1985, Midtgård 1989, Brummermann and Reinertsen 1991). Furthermore, current dogma states that waterfowl do not fully-develop brood patches, although evidence of brood patch development was reported in black-bellied whistling ducks (Rylander et al. 1980).

STUDY SPECIES

Lesser snow geese (*Chen caerulescens caerulescens*; hereafter called snow geese) and Ross's geese (*Chen rossii*) are closely related, nest within the same colonies, and flock together on wintering areas (Alisauskas and Boyd 1994, Ryder and Alisauskas 1995, Batt et al. 1997, Mowbray et al. 2000, Weckstein et al. 2002, Helm 2003). Ross's geese are approximately two-thirds the size of snow geese; thus, these species often are used in comparative studies on effects of body size on behavior and physiology (MacInnes et al. 1989, Slattery and Alisauskas 1995, McCracken et al. 1997, Gloutney et al. 1999; 2001, Craig 2000, Jónsson et al. 2006). I chose to study snow geese and Ross's geese because comparisons of these species within the same nesting colony and/or wintering area allow observation of a natural experiment (Krebs and Davies 1993), in which phylogeny and temporal and environmental effects are controlled (Gloutney et al. 2001). I tested predictions of the Body-Size Hypothesis with these species by comparing incubation constancy, recess frequency, and recess duration between incubating hens of both species, nesting at Karrak Lake, Nunavut, Canada (Chapter 2).

Body size potentially affects the size of the defeathered brood patch area in geese because a large, bare area of skin can lead to heat loss and increased energy expenditure (Payne 1966, Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991). Thus, I determined which

physiological traits of individuals, including body condition, affect size of the defeathered brood patch area in snow geese and Ross's geese (Chapter 3). Furthermore, incubation periods of snow geese and Ross's geese are 2-6 days shorter than those of other geese; thus, I hypothesized that snow geese and Ross's geese maintained such short incubation periods by fully developing brood patches. I tested this hypothesis by analyzing skin histology of appropriate ventral regions of snow geese and Ross's geese, collected at Karrak Lake (Chapter 4).

The mid-continent population of snow geese has increased markedly during the past 40 years, while their wintering range expanded simultaneously from natural wetlands into agricultural habitats (Cooke et al. 1988, Batt et al. 1997). The continental population of Ross's geese increased during the same period and their wintering range concurrently expanded eastward into Texas and Louisiana (Alisauskas and Boyd 1994, Batt et al. 1997, Helm 2003). The increased grazing pressure from these expanded goose populations has led to vegetation degradation on nesting areas, particularly at Karrak Lake (Batt et al. 1997, Gloutney et al. 1999, Alisauskas et al. 2005). Hunting regulations have been liberalized in attempt to reduce and stabilize the snow goose population and to stabilize the Ross's goose population (U.S. Fish and Wildlife Service 2001).

Both species accumulate endogenous reserves on migration stopover areas in spring (Alisauskas 2002). Snow geese and Ross's geese at Karrak Lake rely entirely on endogenous reserves from early nesting until brood rearing (Gloutney et al. 1999). Ross's geese breeding at Karrak Lake spent more time feeding than did snow geese (Gloutney et al. 2001). However, total food consumption was similar between species, probably because food availability was severely limited due to excessive grazing by geese (Gloutney et al. 2001, see also Alisauskas et al. 2005). This situation contrasts the generally abundant food supply in Louisiana, where breeding stress also is absent (Batt et al. 1997). These different situations might lead to different

behaviors and consequently different energy budgets within each species. Thus, I compared time-budgets of snow geese and Ross's geese in Louisiana (Chapter 5).

INTRASPECIFIC BODY SIZE VARIATION IN SNOW GEESE

Coastal marshes comprised the historical wintering habitat of snow geese in Louisiana, whereas snow geese began utilizing rice-prairies in the 1940s (Bellrose 1980, Bateman et al. 1988, Cooke et al. 1988). Snow geese in coastal marshes forage primarily by digging marshgrass rhizomes from the ground (hereafter grubbing; Alisauskas et al. 1988, Batt et al. 1997). By contrast, snow geese in rice-prairies feed mostly on agricultural plants, which they graze on by removing leaves, flowers and stems of aboveground vegetation (hereafter grazing; Alisauskas et al. 1988, Batt et al. 1997).

Snow geese using rice-prairies and coastal marshes differ in that: (1) social interactions are more frequent but less intense in rice-prairies than in coastal marshes (Gregoire and Ankney 1990); and (2) nutritional values of composite diets differ between rice-prairies and coastal marshes (Alisauskas et al. 1988). Different nutritional values of food plants are known to affect behavior of herbivorous waterfowl (Paulus 1984, Prop and Vulink 1992). Thus, I compared time-budgets of snow geese using rice-prairies and coastal marshes (Chapter 6).

The different food habits of snow geese using rice-prairies and coastal marshes led Alisauskas (1998) to compare body morphometrics of snow geese between these habitats. Alisauskas (1998) reported that adult snow geese collected in coastal marshes had larger bodies, thicker bills, longer skulls, and longer culmens than did those collected in rice-prairies. Thus, Alisauskas (1998) hypothesized that small bill size is selected against in coastal marshes because larger bills are best suited for grubbing. By contrast, snow geese seemingly forage successfully in rice-prairies regardless of bill size (Phenotypic Selection Hypothesis; Alisauskas 1998). Alisauskas (1998) also proposed an alternative hypothesis, which posits that snow geese sample

both habitats and settle into the habitat that best suits their bill size (Habitat Selection Hypothesis). I hypothesized that juveniles feeding in coastal marshes become relatively larger adults than do juveniles feeding in rice-prairies because they experience more physical exercise during their first year of life (Feeding-Exercise Hypothesis). I tested these hypotheses by: (1) analyzing the movements of snow geese neck-banded in both habitats (Chapter 7); and (2) comparing bill size, skull size, and muscle size of juvenile snow geese collected in both habitats (Chapter 8).

LITERATURE CITED

- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. *Auk* 100:670-679.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. *Journal of Wildlife Management* 66:181-193.
- Alisauskas, R. T., and H. Boyd. 1994. Previously unrecorded colonies of Ross's and lesser snow geese in the Queen Maud Gulf bird sanctuary. *Arctic* 47:69-73.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.
- Alisauskas, R. T., J. W. Charlwood, and D. K. Kellett. 2005. Vegetation correlates of nesting history and density by Ross's and lesser snow geese at Karrak Lake, Nunavut. *Arctic submitted*.
- Batt, B. D. J., editor. 1997. *Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group*. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.

- Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent snow geese on their Gulf Coast winter range. Pages 495-515 in M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bromley, R. G., and R. L. Jarvis. 1993. The energetics of migration and reproduction in dusky Canada geese. *Condor* 95:193-210.
- Brummermann, M., and R. E. Reinertsen. 1991. Adaptation of homeostatic thermoregulation: comparison of incubating and non-incubating Bantam hens. *Journal of Comparative Physiology B* 161:133-140.
- Cooke, F. D., D. T. Parkin, and R. F. Rockwell. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105:467-479.
- Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. M.S. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641-672.
- Dickson, K. M. 2000. The diversity of Canada geese. Canadian Wildlife Service Occasional Paper 103:11-24.
- Drent, R. H. 1975. Incubation. Pages 333-419 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian Biology*. Volume 5. Academic Press, New York, New York, USA.
- Gauthier, G. 1993. Feeding ecology of nesting greater snow geese. *Journal of Wildlife Management* 57:216-223.
- Gawlik, D. E. 1994. Competition and predation as processes affecting community patterns of geese. Ph.D. thesis, Texas A&M University, College Station, Texas, USA.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:78-86.
- Gloutney, M. L., R. T. Alisauskas, K. A. Hobson, and A. D. Afton. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: evidence for variable anorexia. *Auk* 116:97-108.
- Gregoire, P. E., and C. D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* 107:550-560.
- Haftorn, S., and R. E. Reinertsen. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* 102:470-478.

- Helm, R. N. 2003. Results of January 2003 Ross's goose survey. Memorandum, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana, USA.
- Johnson, J. C., and D. G. Raveling. 1988. Weak family associations in cackling geese during winter: effects of body size and food resources on goose social organization. Pages 71-89 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Jones, R. E. 1971. The incubation patch of birds. *Biological Reviews* 46:315-339.
- Jónsson, J. E. ., A. D. Afton, R. T. Alisauskas, C. K. Bluhm, and M. E. Halawani. 2006. Ecological and physiological factors affecting brood patch area and prolactin levels in arctic-nesting geese. *Auk in press*.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of a bird. *Condor* 72:60-65.
- Krebs, J. R., and N. B. Davies. 1993. *An introduction to behavioral ecology*. Third edition. Blackwell Science, Oxford, United Kingdom.
- Lea, R. W., and H. Klandorf. 2002. The brood patch. Pages 100-118 in D. C. Deeming, editor. *Avian incubation. Behaviour, environment, and evolution*. Oxford University Press, Oxford, United Kingdom.
- MacInnes, C. D., R. K. Misra, and J. P. Prevelt. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. *Canadian Journal of Zoology* 67:286-290.
- McCracken K.G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. *Auk* 114:610-618.
- Madsen, J., and C. E. Mortensen. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. *Ibis* 129:25-44.
- Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. *Goose populations of the Western Palearctic. A review of status and distribution*. Wetlands International Publication, 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute and Wetlands International, Rönne, Denmark.
- Mayhew, P. W. 1988. The daily energy intake rate of European wigeon in winter. *Ornis Scandinavica* 19:217-223.
- Mayhew, P. W., and D. C. Houston. 1993. Food throughput time in European wigeon *Anas penelope* and other grazing waterfowl. *Wildfowl* 44:174-177.
- McWilliams, S. R., and D. G. Raveling. 1998. Habitat use and foraging behavior of cackling Canada and Ross's geese during spring: implications for the analysis of ecological determinants of social behavior. Pages 167-178 in M. D. Samuel, D. D. Humburg, B. D.

- Sullivan, and D.H. Rusch, editors. Biology and management of Canada geese. Proceedings of the International Canada goose symposium, Milwaukee, Wisconsin, USA.
- Midtgård, U. 1989. Circulatory adaptations to cold in birds. Pages 211-222 in C. Bech, and R. E. Reinertsen, editors. Physiology of cold adaptation in birds. Plenum, New York, New York, USA.
- Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Lesser snow goose. In A. Poole, and F. Gill, editors. Birds of North America, No. 514. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Owen, M. 1980. Wild geese of the world: Their life history and ecology. Batsford Ltd, London, United Kingdom.
- Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. Journal of Wildlife Management 48:371-380.
- Payne, R. B. 1966. Absence of brood patch in Cassin's auklets. Condor 68:209-210.
- Prop, J., and T. Vulink. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6:180-189.
- Rohwer, F. C., and M. G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Current Ornithology 5:187-220.
- Ryder, J. P., and R. T. Alisauskas. 1995. Ross's goose (*Chen rossii*). In A. Poole, and F. Gill, editors. Birds of North America, No. 162. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Rylander, M. K., E. G. Bolen, R. E. McCamant. 1980. Evidence of incubation patches in whistling ducks. Southwestern Naturalist 25:126-128.
- Schmidt-Nielsen, K. 1997. Animal physiology: adaptation and environment. Fifth edition. Cambridge University Press, Cambridge, United Kingdom.
- Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross's and lesser snow geese. Condor 97:970-984.
- Skutch, A. F. 1962. The constancy of incubation. Wilson Bulletin 74:115-152.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. Auk 104:707-716.
- U. S. Fish and Wildlife Service. 2001. Draft environmental impact statement: light goose management. Department of the Interior. U. S. Fish and Wildlife Service, Washington, D.C., USA.
- Weckstein, J. D., A. D. Afton, R. M. Zink, and R. T. Alisauskas. 2002. Hybridization and population subdivision within and between Ross's geese and lesser snow geese: a molecular perspective. Condor 104:432-436.

CHAPTER 2: INCUBATION BEHAVIOR OF SYMPATRIC LESSER SNOW GEESE AND ROSS'S GEESE: A TEST OF THE BODY-SIZE HYPOTHESIS

INTRODUCTION

Arctic-nesting geese often arrive in spring when breeding areas are covered with snow, and thus, must depend heavily on endogenous reserves for breeding (e.g., Ankney and MacInnes 1978). Female waterfowl generally feed little and, thus, lose weight during incubation (Ankney and MacInnes 1978, Ankney and Afton 1988, Afton and Paulus 1992, Chapter 3). Females with larger endogenous reserves generally nest earlier, lay larger clutches, are more attentive to their nests, and have higher nest success (Ankney and MacInnes 1978, Aldrich and Raveling 1983, Thompson and Raveling 1987, Lepage et al. 2000).

Body size is highly variable among geese, at both intra- and interspecific levels (Owen 1980, Alisauskas 1998, Madsen et al. 1999, Dickson 2000). Body size has important physiological implications for birds: (1) the rate of heat loss increases with decreasing body size, and, thus, increasing surface to volume ratio (Schmidt-Nielsen 1997); (2) mass-specific metabolic rate is greater for birds of smaller mass (Kendeigh 1970); (3) gut size scales linearly with body size and gut size partly determines the rate of energy extraction from food in the gut (Demment and Van Soest 1985, Mayhew and Houston 1993); and (4) larger species generally have greater fasting endurance than do smaller species, which compensate by relying more on foraging opportunities during incubation (The Body-size Hypothesis: Skutch 1962; Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992).

At some nesting colonies, geese are able to feed upon arrival and do not initiate egg-laying until several days after arrival (Ankney 1984, Bromley and Jarvis 1991, Gauthier 1993). By contrast, increased grazing pressure from rapidly increasing goose populations has led to vegetation degradation in many colonies, including Karrak Lake, Nunavut (Batt et al. 1997,

Gloutney et al. 1999, Gloutney et al. 2001, Alisauskas et al. 2005). Available evidence suggests that lesser snow geese (*Chen caerulescens caerulescens*; hereafter snow geese) and Ross's geese (*C. rossii*) at Karrak Lake rely almost entirely on endogenous reserves from egg-laying until brood rearing (Gloutney et al. 1999, Alisauskas et al. 2005). Thus, energy conservation should be especially important for incubating geese at Karrak Lake, particularly for smaller Ross's geese.

Interestingly, LeSchack et al. (1998) reported that female snow geese and Ross's geese at Karrak lake spent the same amount of time attending their nests; however, estimates of incubation constancy, recess frequency and recess duration were not reported. Recess frequency generally decreases with increased body size in geese and ducks, and recess duration is inversely related to body weight for all species (Afton and Paulus 1992). Ross's geese are approximately two-thirds the size of snow geese (MacInnes et al. 1989); thus, I predicted that female snow geese would have higher incubation constancy, lower recess frequency, and/or shorter recess duration than would female Ross's geese.

Only females incubate among geese (Afton and Paulus 1992). Although males of all northern swans (*Cygnus spp.*) have been observed sitting on nests and possibly retarding egg-cooling during female absences (Afton and Paulus 1992), male nest attendance has not been reported for snow geese or Ross's geese. However, male geese are observed sitting by their mate's nest during incubation (Inglis 1977, Sedinger and Raveling 1990, Afton and Paulus 1992). During early brood-rearing, males assume the primary responsibility for vigilance and brood protection, whereas females spend most of their time feeding to replenish energy reserves expended during egg-laying and incubation (Lazarus and Inglis 1978, Sedinger and Raveling 1990).

Most hypotheses and conclusions concerning effects of body size on waterfowl behavior are based on comparisons of species that confront different locations, climates, habitats, and food resources, and migrate variable distances with different energetic costs (see Bromley and Jarvis 1993, Gauthier 1993). I compared the behavior of two closely related species that are highly sympatric throughout the annual cycle and, thus, controlled for this variation (Gloutney et al. 2001). The two species nest together at Karrak Lake; they generally use the same nesting habitats and have similar nesting chronologies (McLandress 1983, McCracken et al. 1997). I tested predictions of the Body-Size Hypothesis by comparing incubation constancy, recess frequency, and recess duration of female snow geese and Ross's geese nesting at Karrak Lake. I also examined whether male nest attendance, as described for swans (Afton and Paulus 1992), occurred in snow geese and Ross's geese and quantified the amount of time males spent near nests of their mates.

METHODS

STUDY AREA

I studied incubating snow geese and Ross's geese at Karrak Lake, Nunavut, Canada (67° N 15' N, 100° 15' W), which comprises the largest goose colony within the Queen Maud Gulf Bird Sanctuary (Slattery and Alisauskas 1995, McCracken et al. 1997). The landscape at Karrak Lake is comprised of rock outcrops, sedge meadows, and tundra ponds (Slattery and Alisauskas 1995), which generally offer little shelter for incubating females and their nests (McCracken et al. 1997). Karrak Lake and its surroundings were described in detail by Ryder (1972) and McLandress (1983).

DATA COLLECTION

Dr. Alan D. Afton used super-8 mm cameras (2 Minolta XL401 and 2 Minolta XL601; Konica Minolta Photo Imaging U.S.A., Inc., Mahwah, New Jersey) to record presence and absence of 8 pairs of snow geese and 7 pairs of Ross's geese at Karrak Lake from 22 June through 13 July 1993. Each camera was kept in a fixed position throughout the study period and filmed 2-5 nests. The 8 snow goose nests hatched from 4-10 of July, whereas the 7 Ross's goose nests hatched from 8-12 of July. Cameras ran 24 hours/day and recorded images at 1-minute intervals. Camera batteries were changed and film was replenished every 48 hours.

FILM ANALYSIS

I analyzed films with an Elmo 912 film editor (Elmo USA, Planview, New York) and recorded presence/absence of both pair members on each image. Prior to data recording, I placed a plastic transparency on the film editor display, screened each film, and marked the position and number of each nest with a marker.

For analysis, I estimated: (1) incubation constancy for females and presence of males near nests, which I indexed as the percentage of frames individuals were present (frames/day); (2) recess frequency, the number of times females left the nest each day (recesses/day); and (3) recess duration (minutes), estimated from the number of frames each female was absent during each recess.

Films often contained dark periods, where light intensities were too low to accurately determine whether geese were present; these periods occurred during night hours, and/or rain, heavy cloud cover, and fog. The length and frequency of these dark periods varied between nests and could have affected the results. I evaluated this by running 3 repeated analyses, in which: (1) all data points were included; (2) data for a given nest from days with more than 6 of 24 hours missing were excluded; and (3) data for a given nest from days with more than 10 of 24

hours missing were excluded. These analyses yielded the same findings; thus, I present data from the original analysis with all data points included.

STATISTICAL ANALYSIS

I tested predictions of the Body-size Hypothesis using 3 generalized linear models (PROC GENMOD; Agresti 1996, SAS Institute 1999). Response variables in these models were: (1) incubation constancy (% frames/day); (2) recess frequency (per day); and (3) recess duration (minutes). Species and incubation stage were included as explanatory variables in all models; I estimated incubation stage by backdating from hatch dates, assuming a 23-day incubation period for both species (Ryder 1972).

I recorded whether or not males attended nests during female incubation recesses. I also compared male presence near nests between species, which I indexed by the percentage of frames that males were within the camera's field of vision. I analyzed male presence using the same model I used to analyze incubation constancy of females. My films probably underestimated male presence, because males could have been near their nests without entering the camera's field of vision. However, I assumed this potential bias was similar between species and, thus, that the interspecific comparison of male presence was unbiased.

I evaluated the fit of all models by calculating the ratio between deviance and degrees of freedom; a deviance/df ratio close to 1.0 indicates good model fit (cf. Agresti 1996). For all analyses, I compared fit of models based on the normal distribution, and when appropriate, Poisson and binomial distributions. I present least-square mean estimates (hereafter LSMEAN; SAS Institute 1999) for incubation constancy, recess frequency, recess duration, and male presence near nests for both species.

Models for Incubation Constancy and Recess Frequency

For incubation constancy, I compared fit of models based on the normal and binomial distributions, because incubation constancy is a binomial response variable (presence/absence) (cf. Agresti 1996). The normal model for incubation constancy fit well (deviance/df = 1.01), whereas the binomial model displayed signs of overdispersion (deviance/df = 18.20). Accordingly, I used linear models based on the normal distribution for this analysis.

For recess frequency, I compared fit of models based on the normal and Poisson distributions, because number of recesses constitutes count data (cf. Agresti 1996). The normal model for recess frequency fit well (deviance/df = 1.01), and, the Poisson model similarly fit well (deviance/df = 1.20); both models yielded the same findings with subtle differences in numerical values of F and P. Accordingly, I used linear models based on the normal distribution for this analysis.

Generalized Linear Model for Recess Duration

I used a generalized linear model to examine associations between recess frequency, recess duration, species, and incubation stage (Agresti 1996); I was particularly interested in examining whether recess frequency and recess duration were correlated. I compared fit of models based on the normal and Poisson distributions, because recess duration was recorded as the number of whole minutes and, thus, constitutes count data (cf. Agresti 1996). The normal model fit better (deviance/df = 1.04) than the Poisson model (deviance/df = 9.63). Thus, I used the model based on the normal distribution for this analysis. I started with a saturated model, including all interactions, and I determined my final model using backwards stepwise model selection (Agresti 1996).

Models for Male Presence near Nests

The normal model fit well (deviance/df = 1.01), whereas the binomial model displayed signs of overdispersion (deviance/df = 285.3). Thus, I used the linear model based on the normal distribution for this analyses.

RESULTS

FEMALES

Incubation Constancy

Incubation constancy did not differ between species ($\chi^2 = 0.23$, $df = 1$, $P = 0.6292$). Incubation constancy was inversely related to incubation stage ($\chi^2 = 5.06$, $df = 1$, $P = 0.0245$); incubation constancy declined, on average, 0.06% per day of incubation. Incubation constancies of both species averaged 99% and ranged from 89% to 100% (Table 2.1).

Recess Frequency

Snow geese took more recesses/day than did Ross's geese ($\chi^2 = 7.85$, $df = 1$, $P = 0.0051$) (Table 2.1). Recess frequency did not vary with incubation stage ($\chi^2 = 1.39$, $df = 1$, $P = 0.2391$). Recess frequency ranged from 0 to 5 in snow geese and from 0 to 3 in Ross's geese.

Recess Duration

Recess duration did not differ between species ($\chi^2 = 1.49$, $df = 1$, $P = 0.2228$). Recess duration was not correlated with incubation stage ($\chi^2 = 0.59$, $df = 1$, $P = 0.4419$) or recess frequency ($\chi^2 = 0.27$, $df = 2$, $P = 0.8751$). Recess duration ranged from 1 to 78 minutes in snow geese and from 3 to 43 minutes in Ross's geese.

MALES

I never observed male geese walk to or guard nests during female incubation recesses. Males were out of the camera's view during all female incubation recesses with 4 exceptions; in all 4 cases, males never stood on their mate's nest. Overall, male presence near nests did not

Table 2.1. Summary statistics for incubation constancy, recess frequency, recess duration, and male presence near nests of lesser snow geese and Ross's geese, at Karrak Lake, Nunavut, Canada, during summer 1993.

Variable	Lesser snow geese (n = 8 pairs)		Ross's geese (n = 7 pairs)	
	LSMEAN (n)	SE	LSMEAN (n)	SE
Incubation constancy				
(%frames/day/bird)	99.0 (17)	0.002	99.2 (17)	0.002
Recess frequency/day/bird	0.8 (17)	0.077	0.4 (17)	0.082
Recess duration (minutes)	11.5 (91)	1.338	13.8 (48)	1.944
Male presence				
(% frames/day/bird)	61.3 (17)	0.025	61.1 (17)	0.026

differ between species ($\chi^2 = 0.01$, $df = 1$, $P = 0.9494$) and was not correlated with incubation stage ($\chi^2 = 3.31$, $df = 1$, $P = 0.0689$). Male presence averaged 61.1% for both species (Table 2.1), and ranged from 0 to 100% in both species.

DISCUSSION

I found that incubation behavior of snow geese and Ross's geese were similar at Karrak Lake in 1993 and, thus, my results contradicted predictions of the Body-size Hypothesis. Interestingly, both species had higher incubation constancies than that reported for any goose species (see Afton and Paulus 1992). The high incubation constancy documented here for snow geese agrees with earlier findings for this species, but that for Ross's geese is higher than that reported for many other, larger goose species (Afton and Paulus 1992).

My estimates of incubation constancy may be biased; I was unable to observe geese continuously throughout the incubation period. Incubation recesses occur relatively infrequently (cf. Afton and Paulus 1992) and, thus, a high frequency of dark periods could have resulted in some incubation recesses being missed on films. However, most missing values in my dataset were due to dark periods when incubation recesses were less likely to occur. Image quality was particularly good during sunny periods when recesses were most likely to occur. Incubation recesses generally are rare during night or periods of cool ambient temperatures or rain (Afton and Paulus 1992).

Another important caveat is that my analysis was limited to a single breeding season. Time-budgets of geese vary annually and, thus, 1-year studies should be interpreted with caution (Giroux and Bédard 1990, Chapter 5). Nest initiation date for Ross's geese at Karrak Lake was relatively late in 1993, whereas that for snow geese was near the average for 1991-2001 (Alisauskas 2001). Both snow geese and Ross's geese deposit endogenous reserves on spring migration stopover areas prior to arrival to Karrak Lake (Alisauskas 2002), and they may have

arrived in especially good body condition in spring 1993, which in turn would have allowed high incubation constancies.

My results indicate that, at least in some years, Ross's geese are able to incubate at equally high constancies as do larger snow geese. High incubation constancy is beneficial because it minimizes incubation periods (Poussart et al. 2000). Optimal foraging theory predicts that when foraging becomes too costly or non-beneficial, abandoning foraging altogether can be the most beneficial option (Krebs and Davies 1993). I speculate that the high incubation constancies of snow geese and Ross's geese partially are a result of the limited food availability at this colony (Gloutney et al. 1999, Alisauskas et al. 2005) and, thus, incubating females minimize foraging effort, especially in years when geese arrive in good body condition after feeding gluttonously on the spring stopover areas (Alisauskas 2002). Furthermore, the high predation pressures at Karrak Lake (Samelius and Alisauskas 1999, 2000, 2001) probably also select for high incubation constancies because predators are most likely to eat goose eggs during incubation recesses (Afton and Paulus 1992).

Further studies of incubating snow geese and Ross's geese are needed to evaluate potential factors that favor high incubation constancies. Ross's geese possess several adaptations for nesting in the Arctic, which may compensate for their relatively smaller body size (Slattery and Alisauskas 1995, McCracken et al. 1997, Craig 2000). These include: (1) Ross's goose embryos may need relatively less thermal protection during late incubation than do those of snow geese because they are relatively more developed at hatch, as evidenced by their relatively larger pectoralis muscles, larger gizzards, and lower water contents in tissues (Slattery and Alisauskas 1995); (2) Ross's goose embryos grow faster and generate more metabolic heat during early incubation than do snow goose embryos (Craig 2000); thus, Ross's goose embryos may be relatively less dependent on constant heat transfer from their incubating mothers; and (3) Ross's

geese build relatively larger nests than do snow geese (McCracken et al. 1997, Chapter 3), which probably helps reduce energetic costs because of heat loss via thermoregulation.

Male geese never sat or stood on their mate's nests, as previously reported for swans (Afton and Paulus 1992), and male geese were generally out of camera's view during female incubation recesses. Geese generally have higher incubation constancies than do swans (see review by Afton and Paulus 1992); thus, selection for male nest attendance may be weaker in geese than in swans. Male presence near nests was similar for both species; males were out of the camera's view, on average, for 40% of the time. Male geese probably use these absences from their mates to feed, drink, or seek out forced extra-pair copulations (Mineau and Cooke 1979, Afton and Paulus 1992, Oring and Saylor 1992).

LITERATURE CITED

- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Agresti, A. 1996. *An introduction to categorical data analysis*. John Wiley & Sons Inc, New York, New York, USA.
- Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. *Auk* 100:670-679.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T. 2001. Nutritional ecology and population biology of Ross's geese. Unpublished progress report, January 2001, Canadian Wildlife Service, Saskatoon, Saskatchewan, S7N 0X4, Canada.
- Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. *Journal of Wildlife Management* 56:43-54.

- Alisauskas, R. T., J. W. Charlwood, and D. K. Kellett. 2005. Vegetation correlates of nesting history and density by Ross's and lesser snow geese at Karrak Lake, Nunavut. *Arctic submitted*.
- Ankney, C. D. 1984. Nutrient reserve dynamics of breeding and molting brant. *Auk* 101:361-370.
- Ankney, C. D., and A. D. Afton. 1988. Bioenergetics of breeding northern shovelers: diet, nutrient reserves, clutch size, and incubation. *Condor* 90:459-472.
- Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Batt, B. D. J., editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Bromley, R. G., and R. L. Jarvis. 1993. The energetics of migration and reproduction in dusky Canada geese. *Condor* 95:193-210.
- Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. M.S. thesis, University of Saskatchewan, Saskatoon.
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641-672.
- Dickson, K. M. 2000. The diversity of Canada geese. Canadian Wildlife Service Occasional Paper 103:11-24.
- Gauthier, G. 1993. Feeding ecology of nesting greater snow geese. *Journal of Wildlife Management* 57:216-223.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:78-86.
- Gloutney, M. L., R. T. Alisauskas, K. A. Hobson, and A. D. Afton. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: evidence for variable anorexia. *Auk* 116:97-108.
- Inglis, I. R. 1977. The breeding behavior of the pink-footed goose: behavioural correlates of nesting success. *Animal Behaviour* 25:747-764.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of a bird. *Condor* 72:60-65.
- Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioral ecology. Third edition. Blackwell Science, Oxford, United Kingdom.

- Lazarus, J. and I. R. Inglis. 1978. The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62-88.
- Lepage, D., G. Gauthier, and S. Menu. 2000. Reproductive consequences of egg-laying decisions in snow geese. *Journal of Animal Ecology* 69:414-427.
- LeSchack, C. R., A. D. Afton, and R. T. Alisauskas. 1998. Effects of male removal on female reproductive biology in Ross's and lesser snow geese. *Wilson Bulletin* 110:56-64.
- MacInnes, C. D., R. K. Misra, and J. P. Pevett. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. *Canadian Journal of Zoology* 67:286-290.
- Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publication, 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute and Wetlands International, Rønde, Denmark.
- Mayhew, P. W., and D. C. Houston. 1993. Food throughput time in European wigeon *Anas penelope* and other grazing waterfowl. *Wildfowl* 44:174-177.
- McCracken K.G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. *Auk* 114:610-618.
- McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross's and lesser snow geese. *Auk* 100:335-343.
- Mineau, P., and F. Cooke. 1979. Rape in the lesser snow goose. *Behaviour* 70:280-291.
- Oring, L.W., and R. D. Saylor. 1992. The mating systems of waterfowl. Pages 190-213 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Owen, M. 1980. Wild geese of the world: Their life history and ecology. Bt Batsford Ltd, London, United Kingdom.
- Poussart, C., Larochele, J., Gauthier, G. 2000. The thermal regime of eggs during laying and incubation in greater snow geese. *Condor* 102:292-300.
- Ryder, J. P. 1972. Biology of nesting Ross's geese. *Ardea* 60:185-215.
- Samelius, G., and R. T. Alisauskas. 1999. Diet and growth of glaucous gulls at a large Arctic goose colony. *Canadian Journal of Zoology* 77:1327-1331.
- Samelius, G., and R. T. Alisauskas. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. *Arctic* 53:279-288.

- Samelius, G., and R. T. Alisauskas. 2001. Deterring arctic fox predation: the role of parental nest attendance by lesser snow geese. *Canadian Journal of Zoology* 79:861-866.
- SAS Institute. 1999. SAS/SYSTAT User's Guide. Version 6. Fourth edition. SAS Institute. Cary, North Carolina, USA.
- Schmidt-Nielsen, K. 1997. *Animal physiology. Adaptation and environment*. Fifth edition. Cambridge University Press, Cambridge, United Kingdom.
- Sedinger, J. S., and D. G. Raveling. 1990. Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs. *Condor* 92:174-181.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152.
- Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross's and lesser snow geese. *Condor* 97:970-984.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.

CHAPTER 3: ECOLOGICAL AND PHYSIOLOGICAL FACTORS AFFECTING BROOD PATCH AREA AND PROLACTIN LEVELS IN ARCTIC-NESTING GEESE¹

INTRODUCTION

Many birds develop brood patches (also called incubation patches) prior to incubation (see reviews by Drent 1975, Lea and Klandorf 2002). The brood patch is a featherless area on the breast and belly and facilitates heat transfer from parents to eggs (Jones 1971, Drent 1975). Only the incubating sex develops a brood patch (Wiebe and Bortolotti 1993), which is restricted to females among Northern Hemisphere ducks and geese (Kear 1970, Afton and Paulus 1992). Birds generally shed feathers from brood patches during a process similar to molt (Wiebe and Bortolotti 1993). In contrast, female geese and ducks use their bills to pluck down and contour feathers from breast and belly areas and place them in their nests; nest down insulates eggs from ambient air during incubation recesses (Caldwell and Cornwell 1975, Cole 1979, Thompson and Raveling 1988). Breast plucking occurs throughout incubation in some goose species (Hanson 1959, Inglis 1977, Cole 1979); female Canada geese (*Branta canadensis*) pluck new nest down from their belly after wind blows older down from their nests (Cooper 1978).

Female waterfowl generally feed little and thus lose weight during incubation (Ankney and MacInnes 1978, Ankney and Afton 1988, Afton and Paulus 1992). However, smaller goose species generally take more frequent and longer incubation recesses than do larger species; feeding is the primary purpose for incubation recesses (Afton and Paulus 1992). These behavioral differences commonly are linked to the observation that mass specific metabolic rate increases with decreasing body size among birds (Kendeigh 1970). Thus, larger species generally have a higher fasting endurance than do smaller species, which must rely more upon

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foraging opportunities to support their metabolism during incubation (Body-size Hypothesis; Skutch 1962, Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992).

Featherless body parts, such as brood patches, are areas of increased heat loss that can be energetically costly to maintain (Haftorn and Reinertsen 1985, Midtgård 1989), especially for smaller birds (cf. Brummermann and Reinertsen 1991). In Bantam hens (*Gallus domesticus*), smaller females exhibited a stronger decrease in body temperature during experimental cooling of the brood patch, indicating greater sensitivity to heat loss through brood patches in smaller individuals (Brummermann and Reinertsen 1991). Heat loss through the brood patch can induce shivering thermogenesis in muscles (Tøien 1989), which in turn should increase catabolism of energy reserves.

In some bird species, feathers are removed from the breast and belly but no other signs of brood patch formation occur (Hanson 1959, Jones 1971, Gill 1995, Lea and Klandorf 2002, see also review by Jónsson et al. 2005). Some authors have reported a positive relationship between clutch size and the size of this defeathered ventral region (hereafter brood patch area; see review by Wiebe and Bortolotti 1993). Numerous egg addition experiments have tested the assumption that brood patch area has evolved to accommodate clutch size (Beer 1965, Wiebe and Bortolotti 1993). Waterfowl have large, central brood patches and can enlarge them as needed to incubate larger clutches (see review by Wiebe and Bortolotti 1993). Brood patches of lesser snow geese (*Chen caerulescens caerulescens*; hereafter snow geese) and some Ross's geese (*C. rossii*) undergo enhanced vascularization (Jónsson et al. 2005) and the resulting increased blood flow enhances heat transfer from the female to eggs (Midtgård et al. 1985).

Changes in hormone levels and environmental stimuli initiate brood patch formation (Hanson 1959, Jones 1971, Lea and Klandorf 2002). Prolactin is an important hormone associated with reproduction in birds (Goldsmith 1983, 1990; Johnson 2000, Scanes 2000, Vleck

2002). Prolactin in birds has at least 3 possible functions: (1) prolactin stimulates nesting activity and incubation behavior; tactile stimulation of the brood patch stimulates release of prolactin (Kern 1979, Hall and Goldsmith 1983, El Halawani and Rozenboim 1993, Lea and Klandorf 2002), (2) prolactin accelerates gonadal regression at the end of incubation and also is required for inducing postnuptial molt (Dawson and Sharp 1998, Dawson et al. 2001), and (3) prolactin stimulates foraging activity and weight gain in ringed turtle-doves (*Streptopelia risoria*) (Buntin and Figge 1988, Buntin et al. 1999). Although prolactin is established as a stress hormone in mammals, there seems to be little or no direct evidence for such a role in birds (Maney et al. 1999, but see Hazelwood 2000). If the above functions of prolactin are present in incubating geese, they may rival each other; female geese lose weight as incubation progresses (Ankney and MacInnes 1978), while they reduce their sitting behavior (incubation constancy) simultaneously to increasing time spent feeding (Afton and Paulus 1992, Gloutney et al. 2001). Thus, I hypothesized that any relationship between prolactin, brood patch area, incubation stage, and body condition would be stronger in Ross's geese than in snow geese, because female Ross's geese mobilize their energy reserves at a faster rate than do snow geese (cf. Afton and Paulus 1992).

Nest-site selection is an important factor affecting microclimate of parents and eggs, particularly in cold environments (Dawson and O'Connor 1996, Gloutney and Clark 1997, McCracken et al. 1997). Nesting habitats of geese at Karrak Lake, Nunavut, differ in exposure to wind and availability of nest materials; habitats were classified, from the least to the most sheltered, as rock, moss, mixed, and heath (see detailed descriptions in Ryder 1972, McLandress 1983, McCracken et al. 1997). At Karrak Lake, larger nests provide greater insulation for eggs and availability of nest materials within each habitat influences nest size; nests of both species were smallest in rock habitats, intermediate in mixed habitats, and largest in moss habitats

(Ryder 1972, McCracken et al. 1997). Furthermore, McCracken et al. (1997) reported that rim height, wall thickness, circumference, and outer diameter were relatively larger in Ross's goose nests than in those of snow geese. I examined whether brood patch area was related to nest size to determine if a large brood patch area stimulated geese to build larger nests.

I hypothesized that brood patch area of geese is affected by clutch size and clutch volume, but also is limited by energetic needs of incubating females (a possible parent-offspring conflict, Trivers 1974, Clutton-Brock 1991). Specifically, I hypothesized that brood patch area is (1) adapted to accommodate the size and volume of the clutch, as observed in other birds (Beer 1965, Wiebe and Bortolotti 1993), and (2) limited by female body condition (as indexed by size-adjusted body-mass, see methods), prolactin levels, availability of nest materials, and nest size. My hypothesis assumes that (1) the amount of heat loss through the brood patch is positively correlated with brood patch area (after Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991), and (2) selection of a good nest site and nest building can reduce such heat loss (McCracken et al. 1997). My hypothesis predicts that brood patch area is positively correlated with (1) clutch size because larger clutches need larger brood patch areas (Wiebe and Bortolotti 1993), (2) incubation stage because geese will replace older nest down as incubation progresses (Cooper 1978), (3) body condition because birds in poorer condition refrain from plucking their brood patch (after Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991), (4) prolactin levels because prolactin induces sitting behavior in birds and prolactin levels have a positive relationship with tactile stimulus of the brood patch (Lea and Klandorf 2002), (5) nest size because geese that build larger nests are better sheltered from wind chill (McCracken et al. 1997), and (6) nesting habitat; geese that use the more sheltered nest habitats (McLandress 1983, McCracken et al. 1997) are better protected from wind chill, and thus, can pluck a larger

brood patch area. I tested for these relationships in Arctic nesting geese, using specimens of snow geese and Ross's geese, collected at Karrak Lake in 1996.

I studied implications of body size on brood patch formation in two closely-related, free-ranging, arctic-nesting geese because of its perceived importance to fitness in relatively harsh high-latitude environments; Ross's geese are approximately two-thirds the size of snow geese (MacInnes et al. 1989). My first objective was to test the hypothesis that observed brood patch area is an optimum between clutch size and ecological and physiological variables (i.e. body condition, prolactin levels, nest size, and nest habitat), which I measured for individual female snow geese and Ross's geese. My second objective was to determine whether increased circulating levels of prolactin in incubating geese are correlated with female body condition. My third objective was to test the hypothesis that these relationships would be stronger for Ross's geese than for snow geese.

METHODS

DATA COLLECTION

Dr. Alan D. Afton collected 30 female Ross's geese and 30 female snow geese during incubation from 15 to 30 June 1996, at Karrak Lake, Nunavut, (67° N 15' N, 100° 15' W; Ryder 1972, McLandress 1983). Karrak Lake is the largest goose colony in the Queen Maud Gulf Bird Sanctuary (Slattery and Alisauskas 1995, McCracken et al. 1997). Immediately following collections, he collected blood samples and drew outlines of brood patches on Saran Wrap plastic films (Dow Chemical Company, Midland, Michigan) with a permanent marker. In the lab, Dr. Afton later measured ($\pm 0.01 \text{ mm}^2$) brood patch area on films with a leaf area meter (Li-Cor 3100; Li-Cor Incorporated, Lincoln, Nebraska).

Dr. Cynthia Bluhm measured prolactin levels (ng/ml), in a single assay, following methods validated by Bluhm (1983a, b). The prolactin assay RIA for Turkey (*Meleagris gallopavo*) described by Burke and Papkoff (1980) was validated for use with goose serum by comparing the dose-response relationship of serum from incubating snow geese to that of purified Turkey prolactin; both gave parallel slopes (Bluhm et al. 1983a, b). Dr. Bluhm used this type of assay to measure prolactin in the blood samples; the within assay coefficient of variation for the prolactin assay was 7 %. Prolactin levels could not be estimated for 3 snow geese and 6 Ross's geese because their blood samples had insufficient liquid serum for the hormone assay. In my statistical analyses, I only included geese with successful prolactin assays; and thus, all of my results are based on 27 snow goose and 24 Ross's goose females.

Dr. Afton classified specimens to nesting habitat (cf. McCracken et al. 1997). Ross's geese rarely nest in rock (McCracken et al. 1997); he did not find any Ross's geese nesting in rock in 1996. Thus, my analysis of nest habitats for this species included only heather (n=8), mixed (n=9) and moss (n=7) habitats (McLandress 1983, McCracken et al. 1997). For snow geese, nest habitats included rock (n=3), heather (n=8), mixed (n=9) and moss (n=7). Dr. Afton measured outer diameter, wall thickness, circumference, rim height, bowl depth, and inner diameter (± 1 mm) of all nests (McCracken et al. 1997).

Dr. Afton recorded clutch size and measured (± 0.1 mm) maximum length and width of all eggs in each clutch (Slattery and Alisauskas 1995, Alisauskas et al. 1998). I calculated clutch volume by adding volumetric measurements of each egg in a clutch, using the equation given by Hoyt (1979; see also Flint and Sedinger 1992): egg volume = $(0.507 \times \text{length} \times \text{width}^2)$. Dr. Afton estimated incubation stage by candling all eggs in each clutch (Weller 1956); incubation stage ranged 5 to 24 days in snow geese, and 7 to 22 days in Ross's geese. I estimated first egg date by backdating, assuming a laying rate of 1 egg per 1.3 days and a 23-day incubation for both

species (Ryder 1972). Dr. Afton measured fresh body mass (± 1) g, and head length, wing length, culmen length, and tarsus length (± 0.1 mm) (Dzubin and Cooch 1992).

DATA ANALYSIS

Summary Statistics

I used $P = 0.05$ as the critical value (α) in all statistical analyses. I first examined whether explanatory variables other than body size, size-adjusted body mass, incubation stage, and nest habitat differed between female snow geese and Ross's geese. I used analysis of variance (ANOVA; PROC MIXED, SAS Institute 1999) to compare prolactin levels and clutch size between species as a fixed effect in this analysis. I used multivariate analysis of variance (MANOVA; PROC GLM, SAS Institute 1999), with the PDIFF option on LSMEANS, to compare nest size measurements between species (McCracken et al. 1997).

Calculations of Explanatory Variables

I wanted to account for variation in body mass from sources other than body condition (Ankney and Afton 1988, Alisauskas and Ankney 1994). I anticipated that fresh body mass would be affected by (1) incubation stage because females lose weight during incubation (Afton and Paulus 1992), (2) body size, which accounts for a significant proportion of variation in fresh body mass (Ankney and Afton 1988, Alisauskas and Ankney 1994), and (3) prolactin levels because prolactin levels are related to body condition in other birds (Buntin and Figge 1988, Buntin et al. 1999, Hazelwood 2000, Criscuolo et al. 2002). Accordingly, I conducted a Principal Components Analysis (PCA; PROC PRINCOMP, SAS Institute 1999), separately for each species, on the correlation matrix of head length, culmen length, tarsus length, and wing length. I then used PC1 to index body size in subsequent statistical models. PC1 explained 64% and 61% of the body size variation in snow geese and Ross's geese, respectively. I calculated size-adjusted body mass using a multiple regression for each species separately (PROC REG,

SAS Institute 1999), with fresh body mass as the dependent variable and body size indexed by PC1, incubation stage, and prolactin levels as explanatory variables. I used backwards stepwise selection procedure to determine my final regression models (Alisauskas and Ankney 1994, Gloutney et al. 2001). Prolactin levels were not significant in the regression for snow geese ($P = 0.275$). The final regression models were:

$$\text{Size-adjusted body mass}_{\text{snow geese}} = 2111.2 + 69.2(\text{PC1}) - 19.1(\text{incubation stage})$$

$$(r^2 = 0.67, P < 0.001) \tag{1}$$

$$\text{Size-adjusted body mass}_{\text{Ross's geese}} = 1466.5 + 34.6(\text{PC1}) - 11.4(\text{incubation stage})$$

$$- 0.6(\text{prolactin levels})$$

$$(r^2 = 0.70, P < 0.001) \tag{2}$$

I then calculated size-adjusted body mass for each female by adding individual residuals from the multiple regressions above to the mean fresh body mass of each species (see Ankney and Afton 1988).

I divided measurements of each nest with the square root of clutch volume to account for individual variation due to egg size and clutch size (McCracken et al. 1997). McCracken et al. (1997) reported that Ross's geese built proportionately larger nests than did snow geese. Firstly, I confirmed this difference in my data by comparing all 6 nest measurements with a MANOVA (see results). I needed an index of nest size that would include interspecific differences because they also represent the value of nest building as insulation (McCracken et al. 1997). I indexed nest size by (1) reducing dimensionality of nest measurements using PCA on all 6 nest measurements, and then (2) I used MANOVA with LSMEANS to examine which PC scores

differed between snow geese and Ross's geese. MANOVA showed that PC1 ($P = 0.001$) and PC3 ($P = 0.021$) differed between species; thus, I used PC1 and PC3 to index nest size. These cumulatively explained 61% of the nest size variation. In my analysis, nest habitat accounts for insulation properties of nest materials from rock, heather, mixed, and moss habitats, because selection of nest materials reflected nest habitat and did not differ between species within a nest habitat (Ryder 1972, McCracken et al. 1997).

Statistical Tests of Hypotheses

I used analysis of covariance to determine which ecological and physiological variables affected brood patch area (ANCOVA; PROC MIXED, SAS Institute 1999). I ran separate ANCOVAs for each species because they did not overlap in size-adjusted body mass (Table 3.1). For this analysis, nesting habitat was the only categorical variable; covariates were clutch volume, incubation stage, size-adjusted body mass, prolactin levels, nest size (PC1 and PC3), and first egg date. Habitat type was a fixed effect, but all covariates were random effects because they were a sample from a large population (Kuehl 2000). I determined final models by backward stepwise selection procedures (Alisauskas and Ankney 1994, Gloutney et al. 2001).

I tested my hypothesis, that the relationships between size-adjusted body mass, incubation stage, and prolactin levels were stronger in Ross's geese, as follows. I did a multiple regression (PROC MIXED, SAS Institute 1999) for each species, with prolactin levels as a response variable and size-adjusted body mass and incubation stage as explanatory variables. Because prolactin levels was a response variable, I re-calculated size-adjusted body mass of Ross's geese by removing prolactin levels from regression equation (2); this was not necessary for snow geese because prolactin levels were not significant in equation (1). Here I examined whether removing incubation stage would alter final findings because I was concerned that adjusting for incubation stage might overly inflate my estimate of the relationship between

Table 3.1. Summary statistics for female lesser snow geese and Ross's geese, collected at Karrak Lake, Nunavut, in June 1996.

Variable	Lesser snow geese					Ross's geese					p
	n	Mean ^b	SD ^b	Min	Max	n	Mean ^b	SD ^b	Min	Max	
Clutch size	30	4.2	1.0	2	6	30	3.9	0.8	2.0	5.0	0.371 ^c
Clutch volume (mm ³)	30	445.7	103.7	201.7	654.1	30	348.8	62.2	222.1	460.7	NA
Incubation stage (days)	30	15.1	5.6	5	24	30	14.2	5.1	7.0	22.0	NA
Prolactin levels (ng/ml)	27	169.1	67.9	64.3	371.8	24	167.3	54.9	54.8	248.5	0.700 ^c
Size-adjusted body mass (g)	30	1741.8	96.6	1565.1	1914.3	30	1184.7	67.8	1019.7	1311.6	NA
Nest Measurements:											
Outer diameter ^a	30	15.2	2.4	11.6	20.8	30	16.0	1.8	12.7	20.7	0.127 ^d
Inner diameter ^a	30	7.1	0.5	6.2	8.2	30	7.3	0.4	6.5	8.6	0.100 ^d
Wall thickness ^a	30	4.8	1.1	2.8	6.9	30	5.4	1.0	3.7	8.2	0.040 ^d
Rim height ^a	30	2.9	0.8	1.4	4.4	30	4.2	0.9	2.6	6.0	< 0.001 ^d
Bowl depth ^a	30	3.5	0.6	2.6	5.6	30	3.7	0.5	2.3	4.5	0.147 ^d
Circumference ^a	30	89.3	20.0	65.9	147.9	30	96.6	10.8	72.6	120.1	0.082 ^d

(Table continued)

(Table 3.1 continued)

^a Measurements (mm) divided by the square root of clutch volume

^b Means and standard deviations are based on LSMEANS in SAS (SAS Institute 1999)

^c P-values from ANOVA

^d P-values from MANOVA

prolactin levels and incubation stage. However, I obtained the same final models, whether incubation stage was included or not in the regression. Thus, I present only the analysis without incubation stage, and I refer to size-adjusted body mass from equations (3) and (4) as body condition:

$$\text{Body condition}_{\text{snow geese}} = 1842.7 + 82.1(\text{PC1})$$
$$(r^2 = 0.41, P = 0.0002) \tag{3}$$

$$\text{Body condition}_{\text{Ross's geese}} = 1184.7 + 40.0(\text{PC1})$$
$$(r^2 = 0.25, P = 0.0036) \tag{4}$$

I determined final models by backward stepwise selection procedures (Alisauskas and Ankney 1994, Gloutney et al. 2001). Also, I repeated the ANCOVAs for brood patch area with body condition (equations (3) and (4)) replacing size-adjusted body mass (equations (1) and (2)) as an explanatory variable; both these sets of ANCOVAs arrived at the same final models.

I also performed a multiple regression, with brood patch area as the dependent variable and various covariates as explanatory variables (PROC REG, SAS Institute 1999). I used this accompanying regression to examine multicollinearity among covariates, using variance inflation factors (VIF), following Freund and Wilson (1997), who suggested that multicollinearity is present when $VIF \geq 10$. Also, I compared my findings from backward model selections to findings from model selection using Akaike's information criterion (Burnham and Anderson 2002). In all cases, both methods arrived at the same final model; here, I present results from backward model selection.

Visual inspection of the data led me to consider the possibility that the species relationship between incubation stage and prolactin levels were non-linear. Thus, I tested for polynomial relationships between these variables using a *post hoc* polynomial regression (Dowdy et al. 2004). I used PROC REG (SAS Institute 1999), to run linear, quadratic, and cubic models. I performed F-tests on each model and then selected the model with the highest *F*-value for inference, provided the overall F-test for that model was significant at the $P = 0.05$ level (Dowdy et al. 2004).

RESULTS

ANOVA indicated that clutch size ($F = 0.81$, $df = 49$, $P = 0.371$) and prolactin levels ($F = 0.15$, $df = 49$, $P = 0.700$) were similar between species (Table 3.1). Overall nest size differed between snow and Ross's geese (MANOVA: $F = 7.77$, $df = 6$ and 53 ; $P < 0.001$). Comparisons of LSMEANS indicated that Ross's goose nests had higher rims and thicker walls than did those of snow geese (Table 3.1).

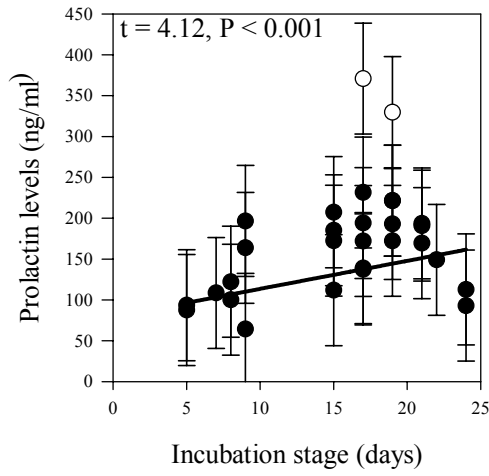
ANCOVA detected no relationships between brood patch area of snow geese and any of the explanatory variables; the accompanying regression confirmed the absence of multicollinearity (all VIFs ≤ 1.1). The final regression model for prolactin in snow geese included only incubation stage ($t = 4.12$, $df = 23$, $P < 0.001$):

$$\text{Prolactin levels}_{\text{snow geese}} = 81.7 + 5.3(\text{incubation stage}) \quad (5)$$

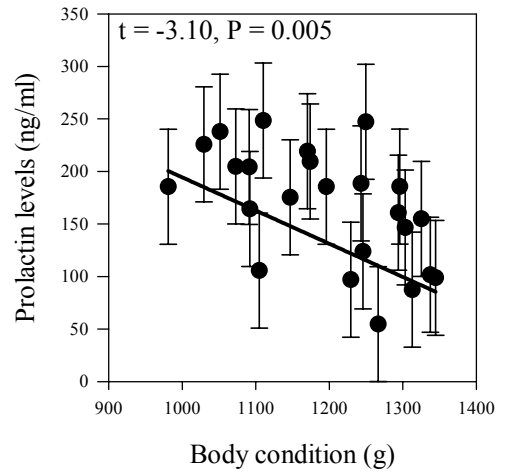
Prolactin levels were positively related to incubation stage in snow geese (Figure 3.1A), although I detected two outliers that had extremely high prolactin levels (unfilled symbols in Figure 3.1A). Nevertheless, I arrived at the same final models for snow geese whether or not these outliers were included. The linear model (equation (5)) had the highest *F*-value in the

Figure 3.1. Relationships between brood patch area and prolactin levels to various explanatory variables in lesser snow geese (hereafter snow geese) and Ross's geese collected at Karrak Lake in June 1996. P and t values are significance levels from final ANCOVA and regression models performed in PROC MIXED. Error bars are 1 standard deviation from the mean of each response variable (see Table 3.1). Unfilled symbols signify suspected outliers (see results for details). Broken line in E indicates that a linear relationship was suggestive but not statistically significant (see text for details).

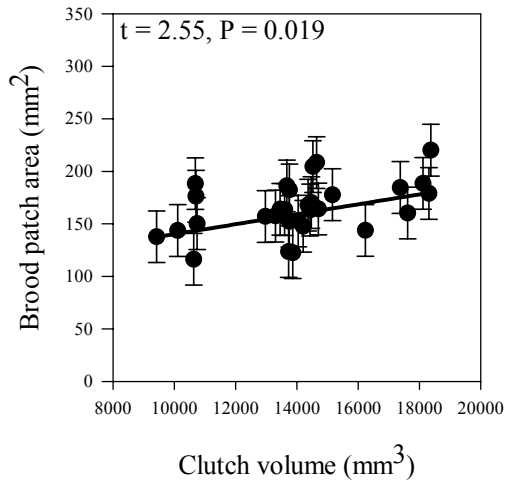
A: Snow geese



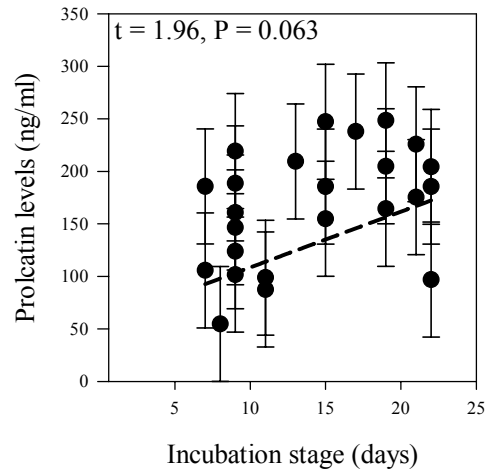
D: Ross's geese



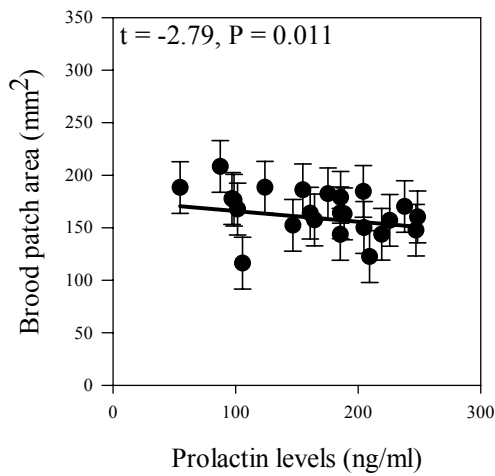
B: Ross's geese



E: Ross's geese



C: Ross's geese



polynomial regression, and thus, was the most appropriate model for the relationship between prolactin levels and incubation stage in snow geese (Table 3.2). The final ANCOVA model for brood patch area in Ross's geese included clutch volume ($t = 2.55$, $df = 21$, $P = 0.019$), and prolactin levels ($t = -2.79$, $df = 21$, $P = 0.011$):

$$\text{Brood patch area}_{\text{Ross's geese}} = 142.3 - 0.2(\text{prolactin levels}) + 0.2(\text{clutch volume}) \quad (6)$$

Brood patch area in Ross's geese was positively related to clutch volume (Figure 3.1B), but inversely related to prolactin levels (Figure 3.1C); the accompanying regression indicated that there was no evidence of multicollinearity between explanatory variables (all VIFs ≤ 1.5). The final regression model for prolactin levels in Ross's geese included only body condition ($t = -3.10$, $df = 22$, $P = 0.005$):

$$\text{Prolactin}_{\text{Ross's geese}} = 312.1 - 0.3(\text{body condition}) \quad (7)$$

Prolactin levels were inversely related to body condition in Ross's geese (Figure 3.1D). A linear relationship was suggestive (Figure 3.1E), but not statistically significant between prolactin levels and incubation stage in Ross's geese ($t = 1.96$, $df = 22$, $P = 0.063$). Linear and quadratic model yielded similar F-values in the polynomial regression analysis; however, F-tests indicated that linear, quadratic, and cubic models were not significant at the $P = 0.05$ level (Table 3.2).

Table 3.2. *Post hoc* polynomial regression for the relationship between prolactin levels (y), and incubation stage (x) for female lesser snow geese and Ross's geese, collected at Karrak Lake, Nunavut, in June 1996.

Lesser snow geese					
Model	Equation	F	R ²	MSE ^a	P
Linear	$y = 77.1 + 5.7(x)$	17.97	0.439	1260.5	0.001
Quadratic	$y = 8.0 + 18.1(x) - 0.5(x^2)$	10.59	0.491	1195.8	0.001
Cubic	$y = 61.6 + 3.5(x) + 0.7(x^2) - 0.1(x^3)$	6.87	0.495	1241.3	0.002
Ross's geese					
Model	Equation	F	R ²	MSE ^a	P
Linear	$y = 115.8 + 3.51(x)$	3.13	0.13	2712.1	0.092
Quadratic	$y = -20.9 + 24.5(x) - 0.70(x^2)$	2.99	0.23	2519.2	0.073
Cubic	$y = 123.2 - 7.9(x) + 1.5(x^2) - 0.05(x^3)$	2.02	0.24	2611.7	0.145

^a MSE = Mean square error

DISCUSSION

None of the factors, that I predicted would limit brood patch area, were statistically significant for snow geese but clutch volume and prolactin levels were significant for Ross's geese. Brood patch area in Ross's geese conformed to their clutch volume (Figure 3.1B). Nest size and nest habitat did not affect brood patch area in either species. Both species lost weight as incubation progressed (equations 1 and 2, see also Ankney and MacInnes 1978, Aldrich and Raveling 1983, Afton and Paulus 1992). Snow geese and Ross's geese differed in that prolactin had significant, inverse relationships with brood patch area (Figure 3.1C) and body condition (Figure 3.1D) in Ross's geese, but not in snow geese. Prolactin levels increased in snow geese as incubation progressed (Figure 3.1A), but although a similar relationship was suggestive; it was not significant in Ross's geese (Figure 3.1E), possibly because during the first half of incubation, prolactin levels in Ross's geese (Figure 3.1E) were variable relative to those of snow geese (Figure 3.1A).

WHAT FACTORS LIMIT BROOD PATCH AREA IN GEESE?

My results indicate that female Ross's geese adjusted brood patch area in relation to clutch volume, as reported for other birds (Beer 1965, Wiebe and Bortolotti 1993). In contrast, my findings on snow geese indicate that they do not limit breast plucking to exposing a bare area of skin that closely conforms their clutch size. Perhaps snow geese that lay smaller clutches (2-4 eggs) pluck a larger brood patch area than needed to warm the clutch; thus, female snow geese may be able to warm all their eggs simultaneously, thereby reducing the need to re-arrange eggs. Arguably, some snow geese in my study may have suffered partial clutch loss before collection, which could confound the relationship between brood patch area and clutch volume. However, I have no evidence that such egg loss was more likely among snow geese than among Ross's geese at Karrak Lake in 1996.

Brood patch area was not related to incubation stage in either species, perhaps because replacement down was unnecessary as incubation progressed (see Cooper 1978). Wind frequently blew down from nests at Karrak Lake, and geese salvaged wind-blown down to use for lining of nests (A. D. Afton personal observation). Snow geese and Ross's geese may supplement lost nest down by breast plucking if wind-blown down is scarce. Alternatively, breast plucking during incubation may have been of feathers grown after the initial breast plucking at the start of incubation (i.e., "trimming" of brood patch). I suspect that breast plucking occurs throughout incubation in snow geese and Ross's geese, as observed in Canada geese (Cooper 1978), although observational studies are needed to confirm this behavior.

The absence of a relationship between brood patch area and nest habitat or nest size does not indicate that heat loss through brood patches (Haftorn and Reinertsen 1985) is unimportant in snow geese or Ross's geese; instead, I conclude only that nesting in relatively sheltered habitats and the building of larger nests seemingly did not encourage females to pluck larger brood patch areas. My findings on interspecific differences in nest size were similar to those of McCracken et al. (1997); I attribute subtle differences in significance levels between the two studies to (1) my smaller sample size (51 nests vs. 105 of McCracken et al. 1997), and (2) annual variations in nest building and/or availability of nest materials.

THE RELATIONSHIP BETWEEN BODY CONDITION AND PROLACTIN

Circulating prolactin levels increased during late incubation in snow geese (Figure 3.1A) and possibly in Ross's geese (Figure 3.1E). This finding agrees with the generalized effects of prolactin on terminating reproduction as summarized by Dawson and Sharp (1998). This hypothesis posits that a positive relationship between incubation stage and prolactin levels occurs because prolactin triggers gonadal regression and/or brood patch regression, both of which are

part of terminating reproduction and inducing postnuptial molt (Dawson and Sharp 1998, Dawson et al. 2001). Under this hypothesis, the inverse relationships between (1) body condition and prolactin levels (Figure 3.1D), and (2) prolactin levels and brood patch area (Figure 3.1C) in Ross's geese are due to relatively earlier gonadal regression in Ross's geese because of body size constraints and the concomitant lesser ability to maintain endogenous reserves.

Elevated prolactin levels during late incubation also are consistent with a second hypothesis, which posits that high levels of prolactin in late incubation stimulate foraging behavior (Buntin et al. 1999). Waterfowl typically take longer and more frequent incubation recesses during late incubation when females are forced to feed because of weight loss incurred during incubation (Afton and Paulus 1992, Gloutney et al. 2001, Criscuolo et al. 2002). The mechanism involved in snow geese and Ross's geese may be similar to that found in ringed turtle doves, where increased levels of prolactin stimulate an increase in foraging activities (Buntin and Figge 1988, Buntin et al. 1999). Furthermore, this hypothesis (1) explains the inverse relationship between size-adjusted body mass and prolactin in Ross's geese (Figure 3.1D) and its absence in snow geese, and (2) is consistent with the Body-Size Hypothesis, which predicts that Ross's geese mobilize endogenous reserves at faster rates than do snow geese (Afton and Paulus 1992).

A third hypothesis posits that females in poorer body condition have higher prolactin levels because they fed more prior to collection than did females in better body condition. My results are somewhat similar to those found in an experimental study on common eiders (*Somateria mollissima*), where (1) females subjected to shortened incubations had higher body masses and higher prolactin levels than did control birds, (2) females subjected to prolonged incubations started to feed and had lower body masses and higher prolactin levels than did

control birds (Criscuolo et al. 2002). Thus, Criscuolo et al. (2002) hypothesized that feeding during late incubation stimulated prolactin secretion, which in turn stimulated females to continue attending their nests despite being in poor body condition. This third hypothesis is interesting because snow geese and Ross's geese at Karrak Lake feed during late incubation but are unable to ingest much food because the colony area is denuded of food plants (Gloutney et al. 2001, Alisauskas et al. 2005). Gloutney et al. (2001) considered alternatives to explain possible functions of feeding behavior other than nutrient acquisition, such as territorial defense, maintenance of gut flora, and search for egg shells as a calcium source. I suggest that the hypothesis of Criscuolo et al. (2002) also should be considered for Ross's geese at Karrak Lake.

In summary, the relationship between high circulating prolactin levels and deteriorating body condition previously was documented in ringed turtle doves (Buntin et al. 1999), and common eiders (Criscuolo et al. 2002). This relationship is particularly intriguing in species that have little or no feeding opportunities during incubation, such as snow geese and Ross's geese nesting at Karrak Lake. I encourage future studies to differentiate among the three hypotheses proposed here to explain the relationship between body condition and high circulating prolactin levels. Importantly, repeated measurements of prolactin levels from individual females throughout incubation would be useful to further examine this relationship in incubating snow and Ross's geese. The functional significance of high levels of prolactin late in incubation (Criscuolo et al. 2002, this study) may prepare the females for brooding behavior of the young after hatch. Dittami (1981) found that, in female bar-headed geese (*Anser indicus*) the presence of goslings was correlated with elevated prolactin levels posthatch, as compared to prolactin levels maintained in females with no goslings.

EFFECTS OF SMALLER SIZE OF ROSS'S GEESE

I found that the brood patch area of Ross's geese was affected by more variables than that of snow geese (Figure 3.1); thus, I conclude that more factors regulate brood patch area in Ross's geese than in snow geese. This interspecific difference is consistent with the Body-Size Hypothesis (Afton and Paulus 1992), regardless of whether elevated prolactin levels (1) stimulate gonadal regression, feeding behavior, or both, or (2) prolactin levels are stimulated by feeding or other behaviors; all these explanations account for the interplay between body condition and incubation stage. I speculate that the relationship between prolactin levels and body condition observed in Ross's geese also would occur in some snow geese during springs when body condition is poor because incubating snow geese likely would then deplete endogenous reserves earlier and at faster rates than observed in 1996.

My data are consistent with the idea that the smaller Ross's geese are more sensitive to heat loss through brood patches, relative to snow geese (cf. Brummermann and Reinertsen 1991), because (1) clutch volume linearly predicted the brood patch area of Ross's geese but not of snow geese, and (2) Ross's geese built relatively larger nests than did snow geese (McCracken et al. 1997, this study). I argue that the limited food availability at Karrak Lake (cf. Gloutney et al. 2001, Alisauskas et al. 2005) makes energy conservation particularly important for incubating females, and that conservation of energy reserves is relatively more important to Ross's geese than to snow geese. I speculate that Ross's geese conserve endogenous reserves by limiting brood patch area, thereby reducing heat loss through brood patches.

Interestingly, incubation periods of snow geese and Ross's geese (23 days) are shorter than those of other goose species (Ryder 1972, Owen and Black 1990, Afton and Paulus 1992). Presumably, this is an adaptation to accelerate development of embryos and hatchlings during

short Arctic summers (Poussart et al. 2000). A brood patch area larger than the minimum area required by the clutch could allow incubating females to transfer heat more efficiently to eggs, by reducing resettling rate and increasing contact area between brood patch and eggs. However, a larger than minimum brood patch area might not be as beneficial to Ross's geese as it would be to snow geese because: (1) Ross's goose neonates potentially need less thermal protection during late incubation than do snow geese, given Ross's geese are relatively more developed at hatch (Slattery and Alisauskas 1995), and (2) Ross's goose embryos produce more heat and grow faster during early incubation than do those of snow goose (Craig 2000).

LITERATURE CITED

- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, G. L. Krapu, Editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Aldrich, T. W. and D. G. Raveling. 1983. Effects of experience and body weight on incubation behavior of Canada geese. *Auk* 100:670-679.
- Alisauskas, R. T., and C. D. Ankney. 1994. Nutrition of breeding female ruddy ducks: the role of nutrient reserves. *Condor* 96:878-897.
- Alisauskas, R. T., S. M. Slattery, J. P. Ryder, M. L. Gloutney, A. D. Afton, R. H. Kerbes, and M. R. McLandress. 1998. Discrimination of Ross's and lesser snow goose eggs. *Journal of Field Ornithology* 69:647-653.
- Alisauskas, R. T., J. W. Charlwood, and D. K. Kellett. 2005. Vegetation correlates of nesting history and density by Ross's and lesser snow geese at Karrak Lake, Nunavut. *Arctic submitted*.
- Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Ankney, C. D., and A. D. Afton. 1988. Bioenergetics of breeding Northern shovelers: diet, nutrient reserves, clutch size and incubation. *Condor* 90:459-472.
- Beer, C. G. 1965. Clutch size and incubation behavior in black-billed gulls (*Larus bulleri*). *Auk* 82:1-18.

- Burke, W. H., and H. Papkoff. 1980. Purification of turkey prolactin and the development of a homologous radioimmunoassay for its measurement. *General and Comparative Endocrinology* 40:297-307.
- Bluhm, C. K., R.E. Phillips, and W. H. Burke. 1983a. Serum levels of lutenizing hormone, prolactin, estradiol, and progesterone in laying and nonlaying mallards, (*Anas platyrhynchos*). *Biology of Reproduction* 28:295-305.
- Bluhm, C. K., R. E. Phillips, and W.H. Burke. 1983b. Serum levels of lutenizing hormone (LH), prolactin, estradiol, and progesterone in laying and nonlaying canvasback ducks (*Aythya valisineria*). *General and Comparative Endocrinology* 52:1-16.
- Brummermann M., and R. E. Reinertsen. 1991. Adaptation of homeostatic thermoregulation: comparison of incubating and non-incubating Bantam hens. *Journal of Comparative Physiology B* 161:133-140.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and multi-model inference*. Second edition. Springer-Verlag, Berlin.
- Buntin, J.D., and G.R. Figge. 1988. Prolactin and growth hormone stimulate food intake in ring doves. *Pharmacology, Biochemistry, and Behavior* 31: 533-540.
- Buntin, J.D., R.M. Hnasko, and P.H. Zuzick. 1999. Role of the ventromedial hypothalamus in prolactin-induced hyperphagia in ring doves. *Physiology and Behavior* 66:255-261.
- Caldwell, P. J., and G. W. Cornwell. 1975. Incubation behavior and temperatures of the mallard duck. *Auk* 92:706-731.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, Washington D.C.
- Cooper, J. A. 1978. The history and breeding biology of the Canada geese of Marshy Point, Manitoba. *Wildlife Monographs* 61:1-87.
- Cole, J. M. 1979. Canada Goose down pulling behavior and some functional aspects of Canada goose nest down. M.S. thesis, University of Minnesota, St. Paul.
- Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. M.S. Thesis. University of Saskatchewan, Saskatoon, Canada.
- Criscuolo, F., O. Chastel, G.W. Gabrielsen, A. Lacroix, and Y. Le Maho. 2002. Factors affecting plasma concentrations of prolactin in the common eider *Somateria mollissima*. *General and Comparative Endocrinology* 125:399-409.
- Dawson, W. R., and T. P. O'Connor. 1996. Energetic features of avian thermoregulatory responses. Pages 85-124 in C. Carey, Editor. *Avian energetics and nutritional ecology*. Chapman and Hall, New York, USA.

- Dawson A., and P.J. Sharp. 1998. The role of prolactin in the development of reproductive photorefractoriness and postnuptial molt in the European starling (*Sturnus vulgaris*). *Endocrinology* 139:485-490.
- Dawson A., V.M. King, G.E. Bentley, and G.F. Ball. 2001. Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16:365-380.
- Dittami, J. P. 1981. Seasonal changes in the behavior and plasma titer of various hormones in bar-headed geese, *Anser indicus*. *Zeitschrift für Tierpsychologie* 55:289-324.
- Dowdy, S., S. Wearden, and D. Chilko. 2004. *Statistics for research*. Wiley Series in Probability and Statistics. Third Edition. Wiley-Interscience, New York.
- Drent, R. H. 1975. Incubation. Pages 333-419 in D.S. Farner, J.R. King, and K.C. Parkes, Editors. *Avian biology*, Vol. 5. Academic Press, New York, USA.
- Dzubin, A., and E. G. Cooch. 1992. *Measurements of geese: general field methods*. California Waterfowl Association, Sacramento, California, USA.
- El Halawani, M. E., and I. Rozenboim. 1993. Ontogeny and control of incubation behavior in turkeys. *Poultry Science* 72:906-911.
- Freund, R. J., and W. J. Wilson. 1997. *Statistical methods*. Revised edition. Academic Press, San Diego.
- Flint, P. L., and J. S. Sedinger. 1992. Reproductive implications of egg-size variation in the black brant. *Auk* 109:896-903.
- Gloutney, M. L., and R. G. Clark. 1997. Nest-site selection by mallards and blue-winged teal in relation to microclimate. *Auk* 114:381-395.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:78-86.
- Goldsmith, A.R. 1983. Prolactin in avian reproductive cycles. Pages 375-387 in J. Bathazart, E. Prove and R. Gilles, Editors. *Hormones and behaviour in Higher Vertebrates*. Springer-Verlag, New York, USA.
- Goldsmith, A.R. 1990. Prolactin and avian reproductive strategies. *Proceedings of the International Ornithological Congress* 20:2063-2071.
- Haftorn, S., and R. E. Reinertsen. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* 102:470-478.
- Hanson, H. C. 1959. The incubation patch of wild geese: its recognition and significance. *Arctic* 12:139-150.
- Hazelwood, R. L. 2000. Pancreas. Pages 539-555 in G. C. Whittow, Editor. *Sturkie's avian physiology*. Fifth edition. Academic Press. San Diego, California, USA.

- Hall, M.R., and A.R. Goldsmith. 1983. Factors affecting prolactin secretion during breeding and incubation in the domestic duck (*Anas platyrhynchos*). *General and Comparative Endocrinology* 49:270-276.
- Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73-77.
- Inglis, I. R. 1977. The breeding behavior of the pink-footed goose: behavioural correlates of nesting success. *Animal Behaviour* 25:747-764.
- Johnson, A. L. 2000. Reproduction in the female. Pages 569-596 in G. C. Whittow, Editor. *Sturkie's avian physiology*. Fifth edition. Academic Press, San Diego, California, USA.
- Jones, R. E. 1971. The incubation patch of birds. *Biological Reviews* 46:315-339.
- Jónsson, J. E., A. D. Afton, D. G. Homberger, W.G. Henk, and R. T. Alisauskas. 2005. Brood patch histology of lesser snow geese (*Chen caerulescens caerulescens*) and Ross's geese (*C. Rossii*). *Journal of Comparative Physiology B*. *in review*.
- Kear, J. 1970. The adaptive radiation of parental care in waterfowl. Pages 357-392 in J.H. Crook, Editor. *Social Behavior in Birds and Mammals*. Academic Press, New York, USA.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size in a bird. *Condor* 72:60-65.
- Kern, M. D. 1979. Seasonal changes in the reproductive system of the female white-crowned sparrow, *Zonotrichia leucophrys gambelii*, in captivity and the field. *Cell Tissue Research* 202:379-398.
- Kuehl, R. O. 2000. Design of experiments. Statistical principles of research design and analysis. Second edition. Duxbury, Pacific Grove, California, USA.
- Lea, R. W. and H. Klandorf. 2002. The brood patch. Pages 100-118 in D. C. Deeming, Editor. *Avian incubation*. Oxford Ornithology series. Oxford University Press, Oxford, United Kingdom.
- MacInnes, C. D., R. K. Misra, and J. P. Pevett. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. *Canadian Journal of Zoology* 67:286-290.
- Maney, D.L., S. J. Schoech, P.J. Sharp, and J.C. Wingfield. 1999. Effects of vasoactive intestinal peptide on plasma prolactin in passerines. *General and Comparative Endocrinology* 113:323-330.
- McCracken, K. G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. *Auk* 114:610-618.
- McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and snow geese. *Auk* 100:335-343.

- Midtgård, U. 1989. Circulatory adaptations to cold in birds. Pages 211-222 in C. Bech and R.E. Reinertsen, Editors. *Physiology of cold adaptation in birds*. Plenum, New York, USA.
- Midtgård U., P. Sejrsen, and K. Johansen. 1985. Blood flow in the brood patch of Bantam hens: Evidence of cold vasodilation. *Journal of Comparative Physiology B* 155:703-709.
- Owen, M., and J. Black. 1990. *Waterfowl ecology*. Blackie Publishers, Glasgow; Scotland.
- Poussart, C., J. Larochelle, and G. Gauthier. 2000. The thermal regime of eggs during laying and incubation in greater snow geese. *Condor* 102:292-300.
- Ryder, J. P. 1972. Biology of nesting Ross's geese. *Ardea* 60:185-215.
- SAS Institute. 1999. *SAS/STAT user's guide*. Version 8.0. SAS Institute, Cary, North Carolina, USA.
- Scanes, C. G. 2000. Introduction to endocrinology: pituitary gland. Pages 437-461 in G. C. Whittow, Editor. *Sturkie's Avian Physiology*. Fifth edition. Academic Press, San Diego, California, USA.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152.
- Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross' and lesser snow geese. *Condor* 97:970-984.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared to other geese: interactions of predation, body size and energetics. *Auk* 104:707-716.
- Thompson, S. C., and D. G. Raveling. 1988. Nest insulation and incubation constancy of arctic geese. *Wildfowl* 39:124-132.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 11:249-264.
- Tøien, Ø. 1989. Effects of clutch size on efficiency of heat transfer to cold eggs in incubating bantam hens. Pages 305-313 in C. Bech and R.E. Reinertsen, Editors. *Physiology of cold adaptation in birds*. Plenum, New York, USA.
- Vleck, C. M. 2002. Hormonal control of incubation behavior. Pages 54-62 in D. C. Deeming, Editor. *Avian incubation*. Oxford Ornithology series. Oxford University Press. Oxford, United Kingdom.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- Wiebe, K. L., and G. R. Bortolotti. 1993. Brood patches of American kestrels; an ecological and evolutionary perspective. *Ornis Scandinavica* 24:197-20.

CHAPTER 4: DO GEESE FULLY DEVELOP BROOD PATCHES? A HISTOLOGICAL ANALYSIS OF LESSER SNOW GEESE AND ROSS'S GEESE²

INTRODUCTION

In most birds, parents develop brood patches (i.e., incubation patches) in preparation for incubation (Drent 1975, Wiebe and Bortolotti 1993, Lea and Klandorf 2002). The skin (i.e., epidermis, dermis, and subcutis) of brood patches is modified to enhance heat transfer from incubating parents to eggs (Jones 1971, Gill 1995, Lea and Klandorf 2002): (1) the epidermis of the brood patch becomes 2-5x thicker than that in non-breeding birds, which protects the skin from injury, (2) the dermal connective tissue (hereafter called connective tissue) is infiltrated by leukocytes, thickens, and becomes more pliable to enhance contact between skin and eggs, (3) blood vessels in the dermis increase in number and diameter, which improves heat transfer from skin to eggs (see also Midtgård et al. 1985), and (4) dermal fat, dermal musculature, and feather follicles are reduced. Furthermore, feathers are shed from the thoraco-abdominal region (hereafter called brood patch region), resulting in a bare area of skin in direct contact with eggs. However, this *defeathered ventral area* often forms independently of the brood patch development described above (Bailey 1952, Hanson 1959, Jones 1971, Lea and Klandorf 2002).

In this chapter, the term *skin* refers collectively to epidermis, dermis, and subcutaneous fat. I define *fully-developed brood patches* as those that undergo epidermal thickening, enhanced vascularization of the dermis, and thickening of connective tissue with an associated leukocyte infiltration (Jones 1971, Lea and Klandorf 2002). The term *brood patch development* is restricted to processes that involve any of these changes. The formation of a defeathered ventral area is associated with brood patch development, but may occur without other modifications of the brood patch skin and is, thus, distinguished from full brood patch development in the narrow

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sense. The term *variable brood patch development* indicates brood patches that lack one or more of the modifications associated with brood patch development in any combination and to any degree of completion (see reviews by Jones et al. 1971, and Lea and Klandorf 2002).

Ostriches (*Struthio camelus*) and other ratites, some species of alcids (*Alcidae*), and waterfowl (Anseriformes) apparently incubate without some or any histological modifications to their brood patch region (Jones 1971, Gill 1995, Lea and Klandorf 2002, McFarlane Tranquilla et al. 2003). Cassin's auklets (*Ptychoramphus aleuticus*) often incubate with only partially-developed brood patches, which do not consistently show bare skin and thickened epidermis or thickened connective tissue (Manuwal 1974, see also McFarlane Tranquilla et al. 2003). Furthermore, bare-skinned brood patches in Cassin's auklets sometimes are re-feathered at mid-incubation and are not maintained for re-nesting attempts; parents that incubate late in the breeding season often do not develop any brood patches at all (Manuwal 1974). Similar variation in brood patch development was observed in the related marbled murrelet (*Brachyramphus marmoratus*) (McFarlane Tranquilla et al. 2003).

Only females incubate in most waterfowl species (Afton and Paulus 1992). Female ducks and geese pluck feathers from their brood patch regions to line their nests; the formation of this defeathered ventral area does not necessarily entail full brood patch development (Bailey 1952, Hanson 1959, Jones 1971, Cole 1979, Afton and Paulus 1992, Lea and Klandorf 2002, see also Dorst 1975, Welty and Baptista 1988, Gill 1995). Current dogma states that the defeathered ventral area in waterfowl is not otherwise modified to enhance heat transfer before incubation (Bailey 1952, Dorst 1975, Gill 1995, Lea and Klandorf 2002). However, in black-bellied whistling ducks (*Dendrocygna autumnalis*), in which both sexes incubate, vascularization of the brood patch region of both sexes increases in preparation for incubation (Rylander et al. 1980, Afton and Paulus 1992).

The rate of heat loss increases in birds with decreasing body size, because a small animal has a relatively greater surface area facing environmental stressors while having a relatively lower tissue volume generating body heat (Calder 1996, Schmidt-Nielsen 1997). This relationship is not linear throughout all bird families, because heat conductance is not just a function of surface area but also depends on the shape and morphology of animals (Calder 1996, Schmidt-Nielsen 1997). Furthermore, small passerine birds in cold environments compensate for small size by decreasing temperature in peripheral tissues while maintaining a stable core temperature, thereby decreasing heat exchange with ambient air to conserve energy (Schmidt-Nielsen 1997). Some passerines apparently also can conserve energy by dropping core temperature as well as peripheral temperatures (Reinertsen and Haftorn 1986).

Payne (1966) suggested that within alcids, smaller species benefit from not developing a brood patch because the unfeathered brood patch region might cause excessive heat loss during cold weather (see also Midtgård 1989). In Bantam hens (*Gallus domesticus*), smaller females were more sensitive to experimental cooling of their brood patch than were larger females (Brummermann and Reinertsen 1991). Mass-specific metabolic rate is greater in birds of smaller mass (Kendeigh 1970). The Body-size Hypothesis predicts that during incubation, larger species generally have greater fasting endurances than do smaller species, which compensate by relying more on foraging opportunities (Skutch 1962; Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992).

Lesser snow geese (*Chen caerulescens caerulescens*; hereafter called snow geese) and Ross's geese (*Chen rossii*) are closely related and frequently nest within the same colonies (Alisauskas and Boyd 1994, Batt et al. 1997, Weckstein et al. 2002). Ross's geese are approximately two-thirds the body size of snow geese; thus, these species often are used in comparative studies on effects of body size on behavior and physiology (MacInnes et al. 1989,

Slattery and Alisauskas 1995, McCracken et al. 1997, Gloutney et al. 1999; 2001, Craig 2000, Jónsson et al. 2006). Comparisons of the two species within the same nesting colony allow observation of a natural experiment (Krebs and Davies 1993), in which phylogeny, general morphology, and temporal and environmental effects are controlled (Gloutney et al. 2001).

Incubation periods of snow and Ross's geese are 23 days, whereas those of other goose species typically last 25 or more days (Ryder 1972, Afton and Paulus 1992). This relatively short incubation period presumably is an adaptation to short Arctic summers and is achieved by maintaining high, constant egg temperatures and by minimizing temperature decreases during incubation recesses (Poussart et al. 2000). Thus, I hypothesized that snow geese and Ross's geese maintained these short incubation periods by fully developing brood patches; an efficient heat transfer from incubating parents to their eggs would be important for minimizing the incubation period. I tested this hypothesis by comparing the histology of the skin (i.e., epidermis and dermis) in the brood patch regions of both sexes of snow geese and Ross's geese.

The brood patch region in geese is located between the lateral pelvic apertures, caudally to the median pelvic aperture (Hanson 1959). Because only females incubate in Arctic nesting geese (Afton and Paulus 1992), I predicted that only females would develop brood patches (Afton and Paulus 1992, Wiebe and Bortolotti 1993). Specifically, my objectives were to determine whether (1) female geese fully develop brood patches or merely remove the feathers from the brood patch regions, and (2) the development of brood patches or patches of bare skin differ between closely related species of varying body size, as previously suggested for Cassin's Auklets relative to certain larger alcid species, such as Razorbill (*Alca torda*) and Puffin (*Fratercula artica*) (Payne 1966, but see also Manuwal 1974).

MATERIALS AND METHODS

MATERIALS

Dr. Alan D. Afton and Richard E. Olsen (hereafter observers) collected specimens at Karrak Lake, Nunavut, Canada (67° N 15' N, 100° 15' W), from the largest goose colony within the Queen Maud Gulf Bird Sanctuary (Slattery and Alisauskas 1995, McCracken et al. 1997). The landscape at Karrak Lake is comprised of rock outcrops, sedge meadows, and tundra ponds (Slattery and Alisauskas 1995), which generally offer little shelter for incubating females and their nests (McCracken et al. 1997). Karrak Lake and its surroundings were described in detail by Ryder (1972) and McLandress (1983).

Observers used a .22 rifle to collect 5 breeding pairs of snow geese on 26 June 1999, and 5 breeding pairs of Ross's geese on 30 June 1999. Observers collected specimens of the two species four days apart to ensure that all specimens were at about the same incubation stage because, on average, Ross's geese initiate nesting four days later than do snow geese (Ryder 1972). Snow and Ross's goose pairs were shot at their nests to confirm their breeding status; observers candled all eggs and estimated that all specimens were collected on day 18 of incubation (Weller 1956). All females were incubating 4 egg clutches. In 1999, the average nest initiation dates at Karrak Lake were 8 June for snow geese and 11 June for Ross's geese (Alisauskas 2001); thus, the chosen collection dates were appropriate.

Hybrids between snow and Ross's geese are common (MacInnes et al. 1989, Weckstein et al. 2002). Thus, observers measured fresh body mass, culmen length, total tarsus, wing length, and head length of all specimens, as defined by Dzubin and Cooch (1992). Analysis of these measurements helped to ensure that the sample did not contain individuals with phenotypic appearances of snow x Ross's geese hybrids (see MacInnes et al. 1989).

METHODS

Immediately after collecting geese, observers excised 2 x 2 cm patches of skin from the appropriate ventral regions. In females, observers collected skin samples from defeathered ventral areas, identified easily between the lateral pelvic apertia and caudal to the median pelvic apertium (Hanson 1959). Observers collected skin samples from the equivalent region of males to serve as controls. Tissue samples were placed in separate labeled vials and preserved in a solution of 10% formaldehyde for subsequent analysis.

In the lab, Dr. Cheryl Crowder processed tissue samples using the following sequence of steps: (1) feathers were cut off above the surface of skin samples, (2) skin samples were dehydrated through a series of graded alcohols, (3) tissue samples were cleared of alcohol in a solvent (xylene) that is miscible in both alcohol and paraffin wax, and (4) tissue samples were infiltrated and impregnated with paraffin wax prior to the embedding procedure. Tissue samples were embedded with the help of a Leica TP1050 Automated Vacuum Tissue Processor (Leica Microsystems Inc., Bannockburn, Illinois). Dr. Crowder subsequently cut sections on a microtome at the thickness of 3 microns and mounted the sections on glass slides for microscopic examination. Dr. Crowder prepared two transverse sections from each skin sample; sections were taken 1.5 mm from the center of each sample, which is 3 mm apart.

Tissue samples were stained with hematoxylin (Anatech Ltd. #812) for cell nuclei (deep purple) and eosin-Y (Anatech Ltd. #832) for cytoplasm (shades of pink, orange, and red). Tissue samples were stained using the following sequence of steps, where slides were: (1) deparaffinized and hydrated to distilled water, (2) stained in a filtered hematoxylin solution for 6 minutes and rinsed in running tap water to remove excess stain, (3) quickly dipped in acid alcohol 3 times and rinsed in running tap water, (4) slowly dipped in ammonia water 3-5 times and rinsed in running tap water, (5) rinsed in 95% alcohol, (6) stained in eosin-Y solution for 1

minute and rinsed in 95% alcohol for 2 changes, (7) cleared in several changes of xylene, and (8) applied with coverslip with synthetic mounting medium.

I recorded histological skin sections with a SPOT RT digital camera (Diagnostic Instruments, Sterling Heights, Michigan) that was mounted on a Zeiss Axioplan microscope (Carl Zeiss MicroImaging, Thornwood, New York). I measured tissues that become modified during brood patch development (Jones 1971, Rylander et al. 1980, and Lea and Klandorf 2002). Using an objective lens with 10x magnification, I recorded images that I subsequently used to measure (1) epidermis thickness ($\pm 0.1\mu\text{m}$), (2) connective tissue thickness ($\pm 0.1\mu\text{m}$), and (3) thickness of the fat (or adipose) tissue ($\pm 0.1\mu\text{m}$) and musculature ($\pm 0.1\mu\text{m}$); the latter two components subsequently were combined for analysis (hereafter summarized as other tissue).

I digitally imaged the superficial layer of the dermis, using an objective lens with 40x magnification, i.e., the top 150 μm of a transverse section through the connective tissue, and used these images to measure or index (1) degree of vascularization of the dermis by measuring blood vessel area as defined by Rylander et al. (1980), and (2) degree of leukocyte infiltration of the dermis by counting the number of leukocytes present in the connective tissue within a particular section (hereafter leukocyte count).

I started the imaging at one side of a skin section and recorded every other field of vision up to 10 images from each section, which was near the maximum number of images that could be sampled from each slide using the 10x objective lens. I obtained 15-19 images per bird using this method (see Appendix 1). Using the 40x objective lens allowed me to sample more than 20 images per bird (i.e., 10 per section), but I used only 20 images to use a consistent number of measurements for each bird in statistical analyses.

I analyzed images of tissues with Scion Image software (Scion Corporation, Frederick, Maryland). I measured three, 500 μm long transects perpendicular to the plane of the epidermis

in each image and used the mean thickness of these transects within each image as my sampling unit. I used mean thickness from the 3 transects to reduce variation in thickness of skin tissues due to possible skewed angles of cutting when I sectioned the tissue samples. I measured blood vessel area by first tracing the circumference of each blood vessel, then calculating the cross-sectional area of each blood vessel from the tracing, and finally adding the cross-sectional areas of all blood vessels to obtain the total blood vessel area. I counted number of leukocytes in each image obtained using the 40x objective lens.

STATISTICAL ANALYSIS

I used mixed models for all analyses (Littell et al. 1996). All my models included species, sex, and the sex x species interaction as fixed effects, and individual birds as random effects (PROC MIXED; SAS Institute 1999; see also Littell et al. 1996). The sex x species interaction tested for species differences in brood patch histology. Individual variation in brood patch histology was of particular interest to me; thus, I used the solution for random effects in PROC MIXED to test which individual means, if any, differed consistently from others within sex or species. My residual error term in all analyses was image within individual bird (n = 15-20; Appendix 1). Although I collected paired geese, my analyses were not pair-wise contrasts because I had no *a priori* reason to expect variation due to pair number (1-5) to be biologically meaningful; I assumed pair members were unrelated individuals.

I used a multivariate analysis to compare the thickness of the epidermis, connective tissue and other tissues between sexes in PROC MIXED (SAS Institute 1999), by examining interactions between tissue and the explanatory variables sex and species, whereas the thickness of each tissue was the response variable. I used the 2-way interaction, sex x tissue (Num df = 2) to test for effects of sex and the 3-way interaction, sex x species x tissue (Num df = 2) to test for effects of species. In this analysis, bird was nested within the 3-way interaction. I determined

final models using backwards stepwise variable selection (Agresti 1996). In the event that MANOVA detected significant interactions in my analyses, I kept the interactions in the model and used least-square means (LSMEANS; SAS Institute 1999) to test for effects of species or sex.

I used a Type 3 sum of square test of fixed effects (F-test; Littell et al. 1996, SAS Institute 1999) to determine whether tissue thickness (hereafter overall thickness) differed between sexes and/or species. If the F- test reported significant differences in overall thickness, I subsequently used a Type 3 sum of square test of simple effects for effects of sex and species, and report t-values (Littell et al. 1996, SAS Institute 1999) for differences in thicknesses of the epidermis, connective tissue, and other tissue. I used a mixed linear model in PROC MIXED to compare blood vessel area and leukocyte count between sexes and species. For this analysis, bird was nested within the sex x species interaction.

RESULTS

FINAL MODELS

The final model for skin thickness included the species x sex x tissue interaction ($F = 15.16$, Num df = 2, Den df = 45, $P < 0.0001$). The final model for blood vessel area included the species x sex interaction ($F = 26.35$, Num df = 1, Den df = 14, $P = 0.0002$). The final model for leukocyte count included species ($F = 4.76$, Num df = 1, Den df = 14, $P = 0.0300$) and sex ($F = 5.38$, Num df = 1, Den df = 14, $P = 0.0348$) but the species x sex interaction was not significant ($F = 3.51$, Num df = 1, Den df = 14, $P = 0.0820$).

SEX COMPARISONS IN SNOW GEESE

Connective tissue thickness ($t = 5.45$, $df = 45$, $P < 0.0001$) and other tissue thickness ($t = -5.90$, $df = 45$, $P < 0.0001$) were greater for females than for males (Table 4.1). Epidermis

Table 4.1. Least-square mean percentage thicknesses (% of 500 μm transect) (\pm standard error) of 3 skin tissues, blood vessel area (μm^2), and leukocyte count (cells/frame) for brood patch regions of 5 pairs of lesser snow geese and 5 pairs of Ross's geese collected at Karrak Lake, Nunavut, Canada in 1999. See text for descriptions of tissues and statistical tests between sexes within each species.

Skin features	Lesser snow geese		Ross's geese	
	Females (n=5)	Males (n=5)	Females (n=5)	Males (n=5)
Epidermis thickness (μm)	5.4 \pm 5.2	2.2 \pm 5.2	2.8 \pm 5.2	2.8 \pm 5.2
Connective tissue thickness (μm)	78.6 \pm 5.2	35.3 \pm 5.2	22.8 \pm 5.2	19.7 \pm 5.2
Other tissue thickness (μm)	16.0 \pm 5.2	62.5 \pm 5.2	74.3 \pm 5.2	77.5 \pm 5.2
Blood vessel area (μm^2)	2637.2 \pm 220.5	67.4 \pm 286.0	200.9 \pm 213.4	46.9 \pm 213.5
Leukocyte count (cells per frame)	106.0 \pm 16.1	25.7 \pm 20.8	37.8 \pm 16.0	22.5 \pm 16.0

thickness was similar between the sexes ($t = 0.39$, $df = 45$, $P = 0.7017$). Females had larger blood vessel areas than did males ($t = 7.12$, $df = 14$, $P < 0.0001$); blood vessel area in females was, on average, 38.9 times larger than that in males (Table 4.1). Females had higher leukocyte counts than did males ($t = 3.05$, $df = 14$, $P = 0.0086$); leukocyte count was, on average, 4.2 times higher in females than in males (Table 4.1). Figure 4.1 shows a section through the skin in the brood patch of a female snow goose (Figure 4.1A) and contrasts it with a section through the skin of the equivalent abdominal region of a male snow goose (Figure 4.1B).

Individual Variation within Sexes of Snow Geese

Among male snow geese, male #1 had the highest connective tissue thickness ($t = 2.16$, $P = 0.0309$) and the lowest other tissue thickness of all males ($t = -2.23$, $P = 0.0263$) (Appendix 1). Among female snow geese, female #3 ($t = 2.22$, $P = 0.0268$) had the largest and female #4 had the smallest connective tissue layer ($t = -2.83$, $P = 0.0048$). Female #3 ($t = -2.61$, $P = 0.0093$) had the smallest and female #4 had the largest other tissue layer ($t = 2.93$, $P = 0.0034$). Female #2 had the highest blood vessel area, and female #3 had the lowest blood vessel area of all females ($t = 3.84$, $P = 0.0002$; and $t = -4.17$, $P < 0.0001$, respectively) (Appendix 1).

SEX COMPARISONS IN ROSS'S GEESE

Thickness of epidermis ($t = -0.01$, $df = 45$, $P = 0.9927$), connective tissue thickness ($t = 0.43$, $df = 45$, $P = 0.6672$) and other tissue ($t = -0.43$, $df = 45$, $P = 0.9927$) were similar between sexes (Table 4.1). Blood vessel area ($t = 0.51$, $df = 14$, $P = 0.6180$) and leukocyte count were similar between sexes ($t = 0.68$, $df = 14$, $P = 0.5079$). Figure 4.2 shows a section through the skin of abdominal regions representative of 4 of 5 Ross's goose females (Figure 4.2A) and all 5 male Ross's geese (Figure 4.2B); one female differed markedly from the other females (see below and Figure 4.3).

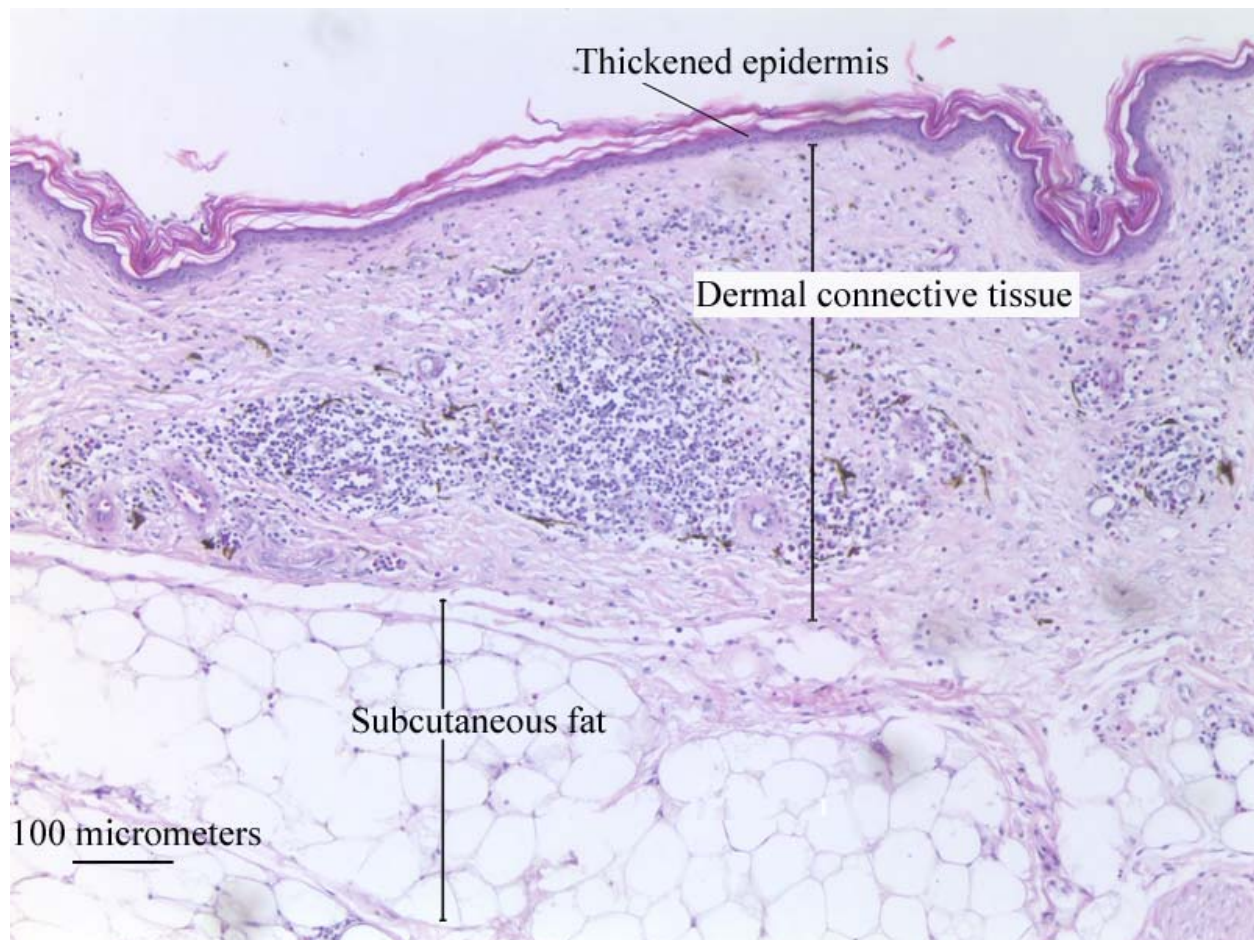


Figure 4.1A. Transverse sections through the skin of the brood patch region of lesser snow geese stained with eosin-hematoxylin. Female snow goose #2: Note the thick layer of dermal connective tissue (purple) in the dermis directly underneath the epidermis. Note also the lumina of blood vessels (white) and the leukocytes (dark purple spots) embedded in the dermal connective tissue (see also inset in Figure 4.3). (Figure continued)

(Figure 4.1, continued)

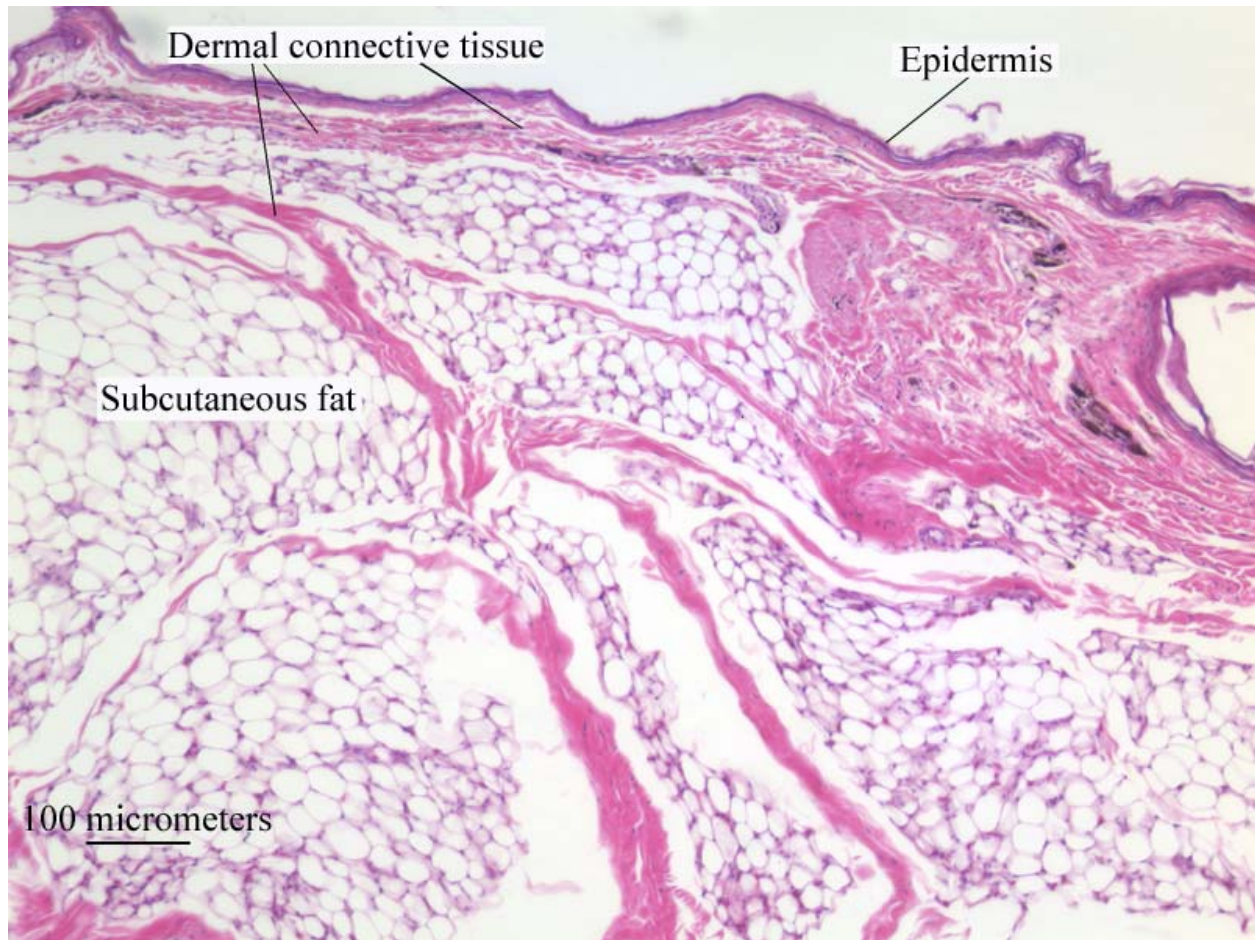


Figure 4.1B. Male snow goose # 5: Note the relatively thin layer of dermal connective tissue (pink) in the dermis directly underneath the epidermis.

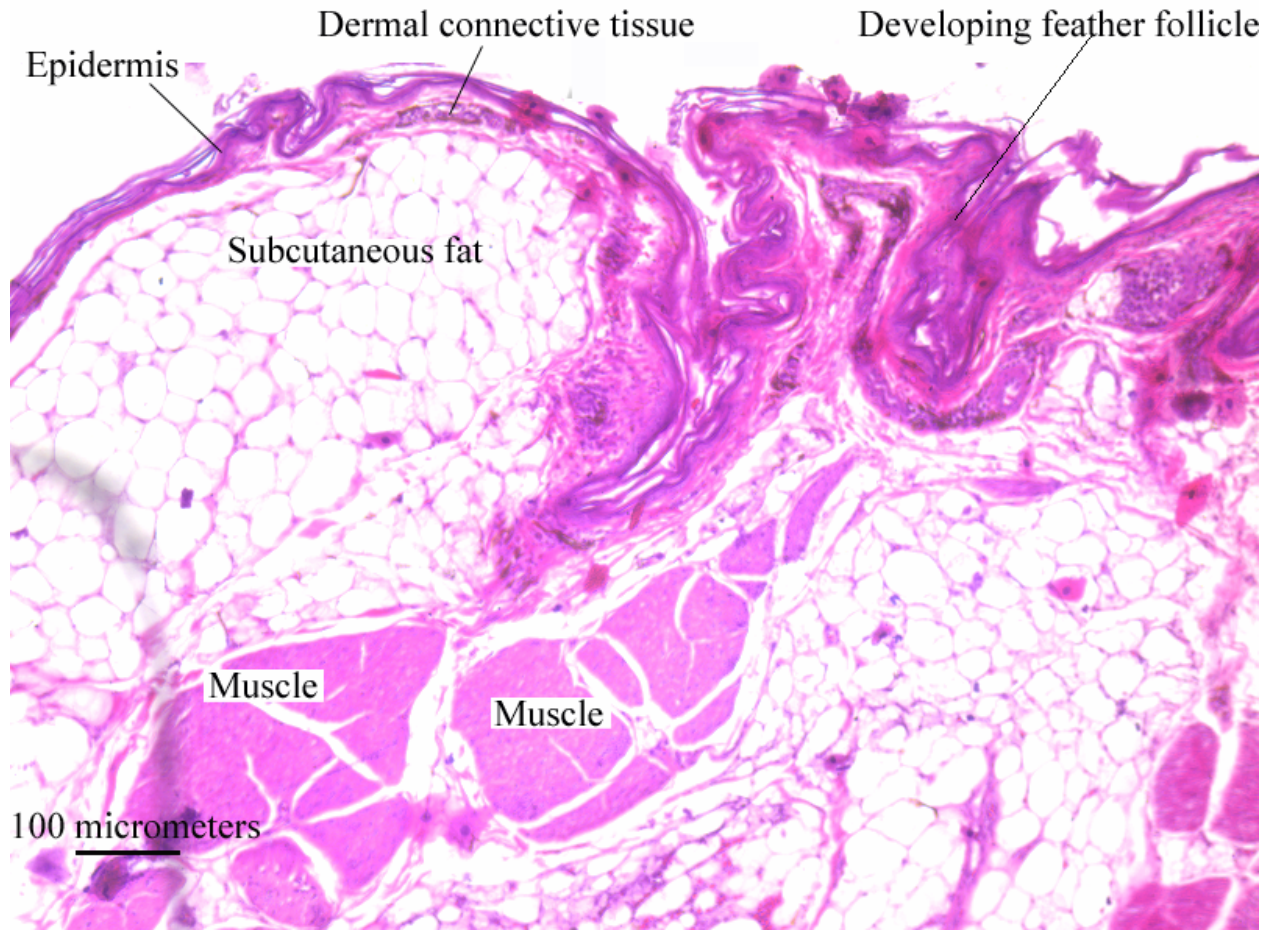


Figure 4.2A. Transverse sections through the skin of the brood patch region of Ross's geese stained with eosin-hematoxylin. Female Ross's goose #2: Note the relatively thin dermal connective tissue layer in the dermis (pink) directly underneath the epidermis. Four of 5 female Ross's geese had brood patches similar to this one; one female Ross's goose (#5) had a brood patch that was similar to that of snow geese and is shown in Figure 4.3. (Figure continued)

(Figure 4.2 continued)

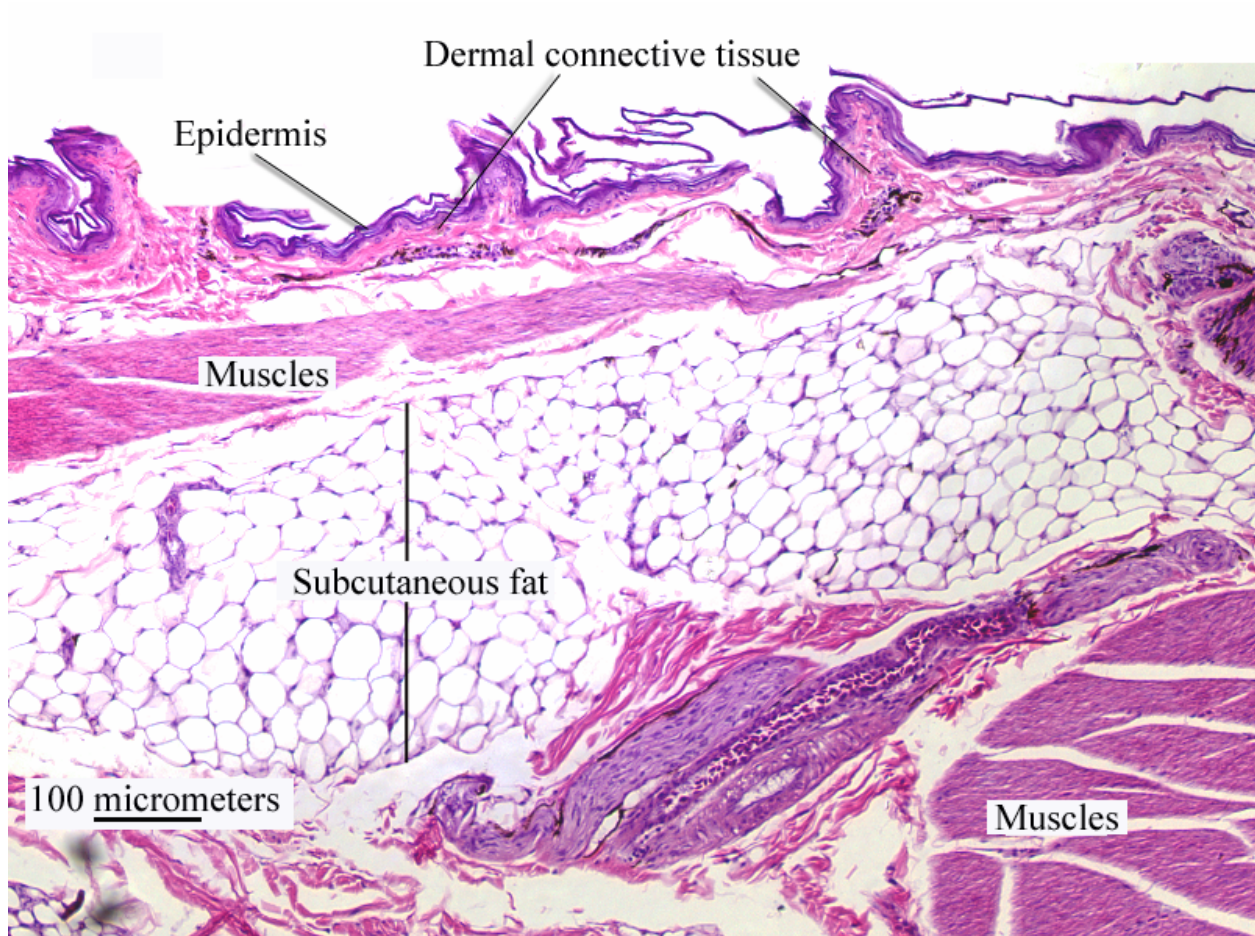


Figure 4.2B. Male Ross's goose #3: Note the relatively thin layer of dermal connective tissue (pink) in the dermis directly underneath the epidermis, and how similar the male is to the female in (A).

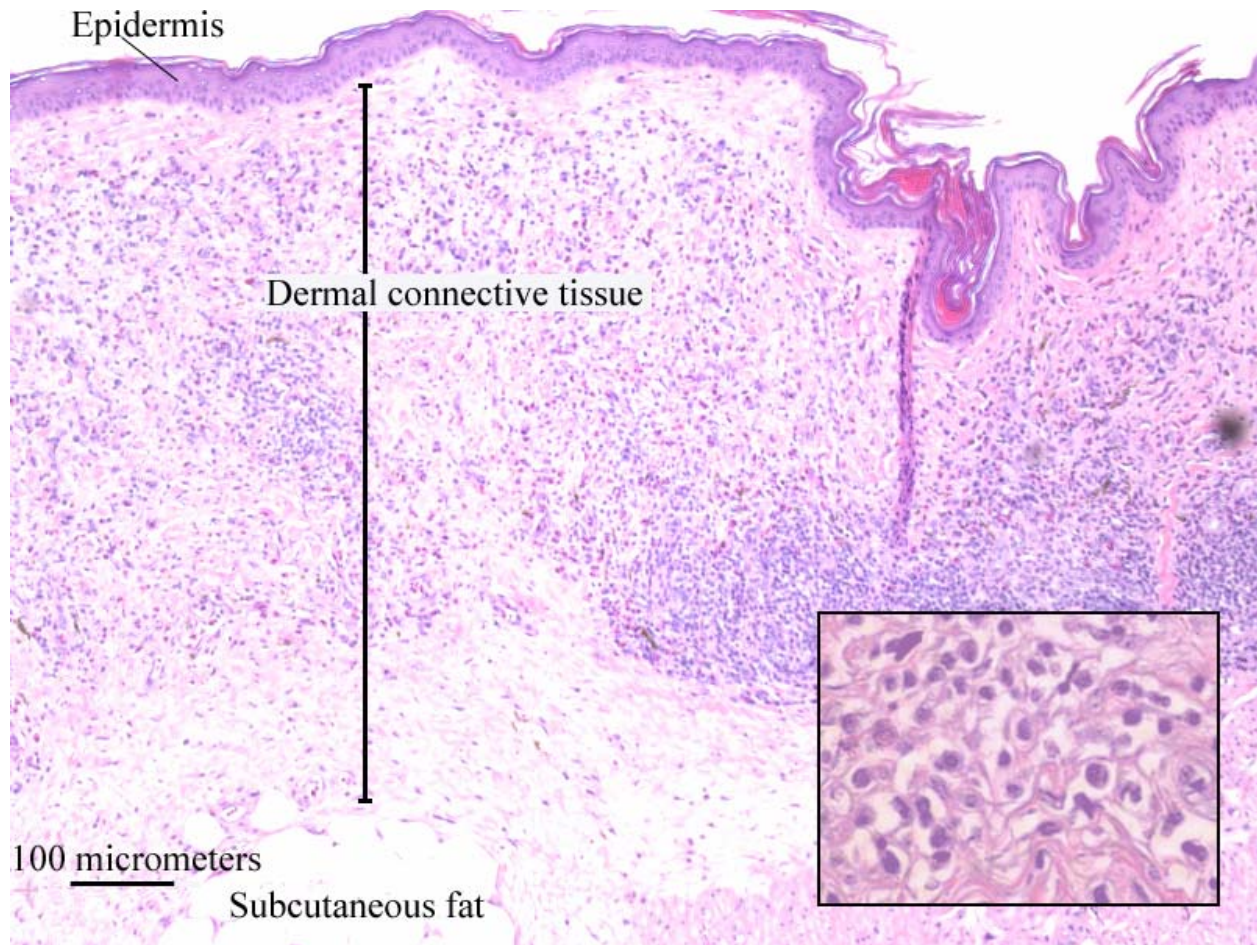


Figure 4.3. A transverse section of brood patch region from female Ross's goose #5 stained with eosin-hematoxylin. Note the similarities with the snow goose brood patch in Figure 4.1A, and compare with the section of the skin through the brood patch of another female Ross's goose in Figure 4.2A. Note: (1) the thick dermal connective tissue (pink) of the dermis directly underneath the epidermis, (2) the lumina of blood vessels (white), and (3) the leukocytes (dark purple) embedded in the dermal connective tissue (see also Figure 4.1A). Inset was imaged using the 40 x objective lens and shows the dermal connective tissue, stained with eosin-hematoxylin, and shows lumina of blood vessels (white) and leukocytes embedded in the dermal connective tissue (dark).

Individual Variation within Sexes of Ross's Geese

Among male Ross's geese, epidermis thickness ($P > 0.94$), connective tissue thickness ($P > 0.46$), other tissue thickness ($P > 0.42$), blood vessel area ($P > 0.75$), and leukocyte count ($P > 0.29$) were similar. Epidermis thickness ($P > 0.85$), connective tissue thickness ($P > 0.06$), other tissue thickness ($P > 0.43$), blood vessel area ($P > 0.05$) and leukocyte count ($P > 0.05$) were similar among females #1, #2, #3, and #4. However, female #5 (Figure 4.3, Appendix 1) had significantly different values for connective tissue thickness ($t = 6.13$, $P < 0.0001$), other tissue thickness ($t = -6.28$, $P < 0.0001$), and leukocyte count ($t = 6.58$, $P < 0.0001$). Female #5 had the thickest connective tissue, the thinnest other tissue, and the highest leukocyte count of all females (Appendix 1).

INTERSPECIFIC COMPARISONS WITHIN SEXES

Female snow geese had thicker connective tissue ($t = -7.68$, $P < 0.0001$) and thinner other tissue ($t = 7.98$, $P < 0.0001$) than did female Ross's geese; thickness of epidermis was similar between females of the two species ($t = -0.36$, $P = 0.7177$) (Table 4.1). Female snow geese had a larger blood vessel area ($t = -7.94$, $P < 0.0001$) than did female Ross's geese (Table 4.1). Female snow geese had a higher leukocyte count ($t = -3.01$, $P = 0.0094$) than did female Ross's geese (Table 4.1). Thicknesses of all 3 tissues, blood vessel area, and leukocyte counts were similar between males of the two species ($P > 0.05$).

DISCUSSION

The observed significant species x interactions indicated that the effects of sex on brood patch histology generally differed between species. In general, brood patch histology differed between sexes of snow geese but not in those of Ross's geese. Brood patch histology differed between female snow geese and Ross's geese, but the histology of the equivalent region in males did not differ between snow geese and Ross's geese.

SKIN HISTOLOGY IN SNOW GEESE

I found histological modifications of the brood patch skin in all 5 female snow geese (Figure 4.1A), relative to skin from equivalent abdominal regions of males (Figure 4.1B). Female snow geese had: (1) thickened connective tissues, (2) an increased blood vessel area, and (3) an increased number of leukocytes in the connective tissue, as described also by Jones (1971), Gill (1995), and Lea and Klandorf (2002). Accordingly, I conclude that brood patches of female snow geese were fully developed to enhance heat transfer to eggs. The only difference between brood patches of snow geese and those of other birds is that feathers are plucked for brood patch development by female snow geese instead of being shed by a hormone-induced process in other birds (Hanson 1959, Jones 1971, Cole 1979). My analysis for snow geese clearly refutes previous broad categorical statements that waterfowl do not fully develop brood patches (see Bailey 1952, Jones 1971, Dorst 1975, Gill 1995, Lea and Klandorf 2002).

SKIN HISTOLOGY IN ROSS'S GEESE

I detected variable brood patch development in female Ross's geese; female #5 (Figure 4.3) had a fully developed brood patch similar to those of the snow geese that I analyzed. Thus, my results suggest that Ross's geese are similar to alcids, wherein some individuals fully develop brood patches and others do so to a lesser degree or not at all (Manuwal 1974, McFarlane Tranquilla et al. 2003).

WHY IS BROOD PATCH DEVELOPMENT VARIABLE IN FEMALE ROSS'S GEESE?

I propose three hypotheses to explain the observed variable brood patch development in female Ross's geese. All three hypotheses posit that the need for a fully developed brood patch in Ross's geese is mitigated by their particular physiology for at least a part of the incubation period. During late incubation, Ross's goose embryos may need relatively less thermal protection than do those of snow geese because they are relatively more developed at hatch, as

evidenced by their relatively larger pectoralis muscles, larger gizzards, and lower water contents in tissues (Slattery and Alisauskas 1995). Ross's goose embryos also grow faster and generate more metabolic heat during early incubation than do snow goose embryos (Craig 2000); thus, Ross's goose embryos may be relatively less dependent on constant heat transfer from their incubating mothers.

My first hypothesis posits that brood patch development is phenotypically fixed by species; female snow geese fully develop brood patches whereas female Ross's geese typically do not develop brood patches. Although analysis of morphometric measurements did not indicate that any specimens were hybrids, Ross's goose female #5 nevertheless could have been of mixed snow goose x Ross's goose ancestry (i.e., F2 or F3 offspring of hybrids). Future tests of this hypothesis will require identification of genetic relationships of specimens when making interspecific comparisons regarding brood patch development.

My second hypothesis posits that (1) females of both species fully developed brood patches, but that most Ross's geese reduce their brood patches earlier in the incubation period than do snow geese, and (2) Ross's geese can incubate successfully without fully developed brood patches during late incubation. Under this hypothesis, most female Ross's geese reduce their brood patches during late incubation, whereas snow geese reduce their brood patches only after eggs hatch. Thus, female #5 could have retained her brood patch relatively longer than did the other four female Ross's geese. Brood patches generally are developed 5-7 days before the onset of incubation (Lea and Klandorf 2002, McFarlane Tranquilla et al. 2003), and it is conceivable that they can regress just as rapidly. This hypothesis could be tested by analyzing skin samples from specimens collected throughout the incubation period.

My third hypothesis posits that variable brood patch development in Ross's geese is the result of a natural polymorphism within this species (hereafter called Polymorphism Hypothesis).

Morphological and physiological characters frequently vary within populations, and I assume that the same would hold true for the expression of brood patches, as is the case in Cassin's auklets (Manuwal 1974). I documented individual variability in skin thickness, blood vessel area, and leukocyte count in both species (see Appendix 1), which indicates possible individual variation in the ability to fully develop brood patches (see McFarlane Tranquilla et al 2003). Such a polymorphic brood patch development could be at least partly under genetic control and partly influenced by biological factors, such as the particular physiology of a species, parental age, nest initiation date, body condition, and breeding experience. All these factors are known to influence the reproductive success of geese (Ankney and MacInnes 1978, Cooke et al. 1995, Lepage et al. 2000).

Environmental conditions, such as weather and food availability, may represent the major selective regime for this polymorphism. In years of harsh weather or low food abundance, Ross's geese that do not develop brood patches may be at a selective advantage, whereas in years of milder weather and abundant food, Ross's geese that develop brood patches fully may be more successful. Polymorphic genes for brood patch development could be maintained within Ross's geese populations because costs and benefits of developing a brood patch are not clear-cut and may depend on the prevailing environmental conditions, in an analogous manner as was shown for bill size and shape in Darwin's finches (*Geospiza fortis* and *G. scandens*) (Grant and Grant 2002), and for the tendency to migrate in blackcaps (*Sylvia atricapilla*) (Berthold 1988, Berthold et al. 1990). Alternatively, this polymorphism also could result from frequent interbreeding between snow geese and Ross's geese (Weckstein et al. 2002) and, hence, the introduction of genes for brood patch development from snow geese into Ross's geese populations as per my first hypothesis. In order to test the Polymorphism Hypothesis, a long-

term study of the occurrence of brood patches within the two goose species is needed, using a larger sample along with genetic analysis of specimens.

Interestingly, the size of the defeathered ventral area is negatively related to body condition in Ross's geese, but not in snow geese (Chapter 3, Jónsson et al. 2006). This difference is consistent with the hypothesis that Ross's geese are more adversely affected by heat loss through the brood patch region than are snow geese because of their smaller size (Brummermann and Reinertsen 1991, Jónsson et al. 2006). Thus, greater susceptibility to cold and wind may select against full brood patch development in most Ross's geese females. A critical assumption here is that snow geese and Ross's geese are exposed to the same microclimate during nesting and both possess the same behaviors and physiological adaptations for thermoregulation and thus, their ability to tolerate heat loss differs only as predicted by their different body sizes.

DO OTHER ANSERIFORMES DEVELOP BROOD PATCHES?

Average incubation periods of geese are positively related to body size (Owen and Black 1990, Afton and Paulus 1992, Figure 4.4). Snow geese, however, have a shorter incubation period than that predicted by their body weight, and this trend also is true for Ross's geese and greater snow geese (*C. c. atlanticus*; Figure 4.4), suggesting that there has been a stronger selection for short incubation periods in these Arctic-nesting species as compared to other geese. In waterfowl, Arctic-nesting species, in particular, should benefit from maximized efficiency of heat transfer provided by fully developed brood patches because they (1) often are exposed to low temperatures and high wind velocities, which cool eggs during incubation recesses (Gloutney et al. 1999), (2) nest in habitats where nesting materials that could be used for thermal insulation often are scarce (McCracken et al. 1997), and (3) practice uniparental incubation

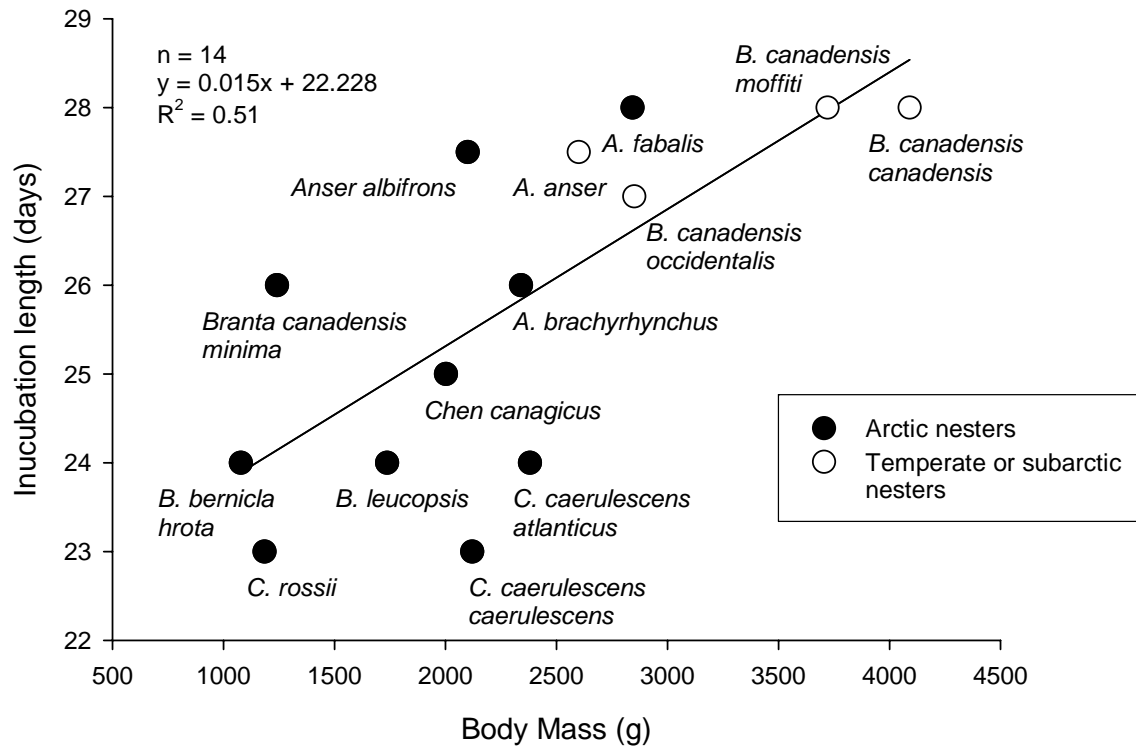


Figure 4.4. The relationship between body mass and incubation period in Northern Hemisphere geese (after Cramp and Simmons 1978, Afton and Paulus 1992; see also Owen and Black (1990).

(Afton and Paulus 1992), which precludes them from alternating incubation sessions between pair members, as reported for whistling ducks (Rylander et al. 1980). Geese and whistling ducks also differ in that female geese remove feathers from their brood patches whereas whistling ducks incubate with fully feathered brood patches (Rylander et al. 1980, Afton and Paulus 1992). Interestingly, whistling ducks and geese are classified among the most ancestral groups of waterfowl (Livezey 1986), which raises the question whether full brood patch development is an ancestral trait among waterfowl. This question perhaps could be answered by studying brood patch development in more derived groups, such as dabbling ducks (Anatini), diving ducks (Aythiini), eiders (Somaterini), and seaducks (Mergini). Species within these groups nest in a broad range of climatic conditions and, thus, may vary in brood patch formation. An investigation of brood patch development in Magpie geese (*Anseranas semipalmata*) would be particularly interesting because (1) they breed in pairs and trios; trios almost always are comprised of 1 male and 2 females, and (2) males participate in incubation duties (Kear 1973, see also Afton and Paulus 1992).

CONCLUSION

I documented that all five female snow geese and one of five female Ross's geese in my sample fully developed brood patches. A fully-developed brood patch may shorten the incubation period, but may not be necessary to incubate a clutch successfully (McFarlane Tranquilla et al. 2003). I argue that, because of their smaller size and concomitant lower fasting endurance compared to those of snow geese (Skutch 1962, Afton 1980, Afton and Paulus 1992), at least some Ross's geese benefit by either not fully developing brood patches or by maintaining them for shorter periods during incubation than do snow geese. I agree with McFarlane Tranquilla et al. (2003) that future studies should examine effects of individual variation on brood patch development and encourage further tests of the three hypotheses proposed here, as

well as comparative histological studies of brood patch development among other waterfowl species. Particularly, future studies should determine when brood patches are formed and regressed in different waterfowl species by collecting tissue samples at different incubation stages.

LITERATURE CITED

- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Agresti, A. 1996. *An introduction to categorical data analysis*. John Wiley & Sons Inc, New York, New York, USA.
- Alisauskas, R. T. 2001. Nutritional ecology and population biology of Ross's geese. Unpublished progress report, January 2001, Canadian Wildlife Service, Saskatoon, Saskatchewan, S7N 0X4, Canada,
- Alisauskas, R. T., and H. Boyd. 1994. Previously unrecorded colonies of Ross's and lesser snow geese in the Queen Maud Gulf bird sanctuary. *Arctic* 47:69-73.
- Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Bailey, R. E. 1952. The incubation patch of passerine birds. *Condor* 54:121-136.
- Batt, B. D. J. Editor. 1997. *Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group*. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, DC, and Canadian Wildlife Service, Ottawa, Canada.
- Berthold, P. 1988. Evolutionary aspects of migratory behavior in European warblers. *Journal of Evolutionary Biology* 1:195-209.
- Berthold, P., W. Wiltschko, M. Miltenberger, and W. Querner. 1990. Genetic transmission of migratory behavior into a non-migrating population. *Experientia* 46:107-108.
- Brummermann, M, and R. E. Reinertsen. 1991. Adaptation of homeostatic thermoregulation: comparison of incubating and non-incubating Bantam hens. *Journal of Comparative Physiology B* 161:133-140.
- Calder, W. A. III. 1996. *Size, function and life history*. Second edition. Dover Publications, Mineola, New York, USA.

- Cole, J. M. 1979. Canada goose down pulling behavior and some functional aspects of Canada goose nest down. M.S. thesis, University of Minnesota, St. Paul, Minnesota, USA.
- Cooke, F., R. F. Rockwell, and D. B. Lank. 1995. The snow geese of LaPerouse Bay. Natural selection in the wild. Oxford University Press, Oxford, United Kingdom.
- Cramp, S., and K. E. L. Simmons. 1978. Handbook of the birds of Europe, the Middle East, and North Africa. Birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. M.S. thesis. University of Saskatchewan, Saskatoon, Canada.
- Dawson, W. R., and T. P. O'Connor. 1996. Energetic features of avian thermoregulatory responses. Pages 85-124 in, Carey C., Editor. Avian energetics and nutritional ecology. Chapman and Hall, New York, New York, USA.
- Dorst, J. D. 1975. The life of birds. Columbia University Press, New York, New York, USA.
- Drent, R. H. 1975. Incubation. Pages 333-419 in D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian Biology. Volume 5. Academic Press, New York, New York, USA.
- Gill, F. B. 1995. Ornithology. Second edition. WH Freeman and Company, New York, New York, USA.
- Gloutney, M. L., R. T. Alisauskas, K. A. Hobson, and A. D. Afton. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: evidence for variable anorexia. *Auk* 116:97-108.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:470-478.
- Grant, P. R., and R. B. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707-711.
- Haftorn, S., and R. E. Reinertsen. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* 102:470-478.
- Hanson, H. C. 1959. The incubation patch of wild geese: its recognition and significance. *Arctic* 12:139-150.
- Jones, R. E. 1971. The incubation patch of birds. *Biological Review* 46:315-339.
- Jónsson, J. E., A. D. Afton, R. T. Alisauskas, C. K. Bluhm, and M. E. El Halawani. 2006. Ecological and physiological factors affecting brood patch area and prolactin levels in arctic-nesting geese. *Auk in press*.
- Kear, J. 1973. The magpie goose in captivity. *International Zoo Yearbook* 13:28-32.

- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72:60-65.
- Krebs, J. R., and N. B. Davies. 1993. *An introduction to behavioral ecology*. Third edition. Blackwell Science, Oxford, United Kingdom.
- Lea, R. W., and H. Klandorf. 2002. The brood patch. Pages 100-118 in: Deeming, D.C., Editor. *Avian incubation*. Oxford ornithology series. Oxford University Press, Oxford, United Kingdom.
- Lepage, D., G. Gauthier, and S. Menu. 2000. Reproductive consequences of egg-laying decisions in snow geese. *Journal of Animal Ecology* 69:414-427.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, North Carolina, USA.
- Livezey, B. C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* 103:737-754.
- MacInnes, C. D., R. K. Misra, and J. P. Pevett. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. *Canadian Journal of Zoology* 67:286-290.
- Manuwal, D. 1974. The incubation patches of Cassin's auklet. *Condor* 76:481-484.
- McCracken, K. G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. *Auk* 114:610-618.
- Mcfarlane Tranquilla, L. A., R. W. Bradley, D. B. Lank, T. D. Williams, L.W. Lougheed, and F. Cooke. 2003. The reliability of brood patches in assessing reproductive status in the marbled murrelet: words of caution. *Waterbirds* 26:108-118.
- McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross's and lesser snow geese. *Auk* 100:335-343.
- Midtgård, U. 1989. Circulatory adaptations to cold in birds. Pages 211-222 in: Bech, C., and R. E. Reinertsen, Editors. *Physiology of cold adaptation in birds*. Plenum, New York, New York, USA.
- Midtgård, U., P. Sejrsen, and K. Johansen. 1985. Blood flow in the brood patch of Bantam hens: evidence of cold vasodilation. *Journal of Comparative Physiology B* 155:703-709.
- Owen, M. and J. Black. 1990. *Waterfowl ecology*. Blackie Publishers, Glasgow, Scotland.
- Payne, R. B. 1966. Absence of brood patch in Cassin auklets. *Condor* 68:209-210.
- Poussart, C., J. Larochelle, and G. Gauthier. 2000. The thermal regime of eggs during laying and incubation in greater snow geese. *Condor* 102:292-300.

- Reinertsen, R. E. and S. Haftorn. 1986. Different metabolic strategies of northern birds for nocturnal survival. *Journal of Comparative Physiology B* 156:655-663.
- Ryder, J. P. 1972. Biology of nesting Ross's geese. *Ardea* 60:185-215.
- Rylander, M. K., E. G., Bolen, and R. E. McCamant. 1980. Evidence of incubation patches in whistling ducks. *Southwestern Naturalist* 25:126-128.
- SAS Institute. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute, Cary, North Carolina, USA.
- Schmidt-Nielsen, K. 1997. *Animal physiology. Adaptation and environment*. Fifth edition. Cambridge University Press, Cambridge, United Kingdom.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152.
- Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross's and lesser snow geese. *Condor* 97:970-984.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared to other geese: interactions of predation, body size and energetics. *Auk* 104:707-716.
- Weckstein, J. D., A. D. Afton, R. M. Zink, and R. T. Alisauskas. 2002. Hybridization and population subdivision within and between Ross's geese and lesser snow geese: a molecular perspective. *Condor* 104:432-436.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- Welty, J. C., and L. Baptista. 1988. *The life of birds*. Fourth edition. Saunders College Publishing, Fort Worth, Texas, USA.
- Wiebe, K. L., and G. R. Bortolotti. 1993. Brood patches of American kestrels; an ecological and evolutionary perspective. *Ornis Scandinavica* 24:197-204.

CHAPTER 5: TIME AND ENERGY BUDGETS, AND THE IMPORTANCE OF FAMILY MAINTENANCE FOR SYMPATRIC, WINTERING LESSER SNOW GEESE AND ROSS'S GEESE

INTRODUCTION

Body size is highly variable among geese at both intra- and interspecific levels (Owen 1980, Alisauskas 1998, Madsen et al. 1999, Dickson 2000). Body size has important physiological implications for birds: (1) the rate of heat loss increases with decreasing body size because of increasing surface to volume ratio (Calder 1996, Schmidt-Nielsen 1997); (2) mass-specific metabolic rate is inversely related to body mass (Kendeigh 1970, Calder 1996); (3) gut size scales linearly with body size and partly determines the rate of energy extraction from food (Demment and Van Soest 1985, Mayhew and Houston 1993); and (4) larger species generally have higher incubation constancies and greater fasting endurance than do smaller species, which compensate by relying more on foraging opportunities (The Body-size Hypothesis: Skutch 1962; Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992). Furthermore, smaller species are: (1) more vulnerable to avian predators (Johnson and Raveling 1988, McWilliams et al. 1994, McWilliams and Raveling 1998); and (2) more likely to be displaced in competition with co-existing larger species (Madsen and Mortensen 1987, Gawlik 1994).

The Body-size Hypothesis predicts that smaller species deplete nutrient reserves at faster rates than do larger species (Afton and Paulus 1992, Calder 1996). In addition to incubation constancy, interspecific variation in other behaviors has been attributed to different body sizes among waterfowl: tendency to maintain family units, timing of pair formation, and time spent foraging (Skutch 1962, Afton 1980, Rohwer and Anderson 1988, Johnson and Raveling 1988, Mayhew 1988, Afton and Paulus 1992, Gloutney et al. 2001). Most hypotheses and conclusions concerning effects of body size on waterfowl behavior are based on comparisons of species that

confront different climates, habitat types, and food availability, and migrate variable distances with different energetic costs (Bromley and Jarvis 1993, Gauthier 1993, Gloutney et al. 2001).

Lesser snow geese (*Chen caerulescens caerulescens*; hereafter called snow geese) and Ross's geese (*C. rossii*) are closely related, nest within the same colonies, and flock together on wintering areas (Alisauskas and Boyd 1994, Ryder and Alisauskas 1995, Batt et al. 1997, Weckstein et al. 2002). Ross's geese are approximately two-thirds the size of snow geese; thus, the two species often are used in comparative studies on effects of body size on behavior and physiology (MacInnes et al. 1989, Slattery and Alisauskas 1995, McCracken et al. 1997, Gloutney et al. 1999; 2001, Craig 2000, Jónsson et al. 2006). I chose to study snow geese and Ross's geese because comparisons of these species within the same wintering area allow observation of a natural experiment (Krebs and Davies 1993), in which phylogeny and temporal and environmental effects are controlled (Gloutney et al. 2001).

During nesting at Karrak Lake Nunavut, Ross's geese spent more time feeding than did snow geese; however, both species ingested little food because the study area was barren of vegetation (Gloutney et al. 2001). In contrast, geese generally have access to abundant food resources while wintering in southwest Louisiana (Bateman et al. 1988, Batt et al. 1997). Based on the Body-size Hypothesis (cf. Afton and Paulus 1992), I predicted that: (1) in order to attain a rate of nutrient intake equal to that of snow geese, Ross's geese compensate for their smaller body size by either increasing time spent feeding and/or increasing food intake rates, i.e. peck rates (Owen 1972, McWilliams and Raveling 1998); and (2) time-budgets of Ross's geese would be affected relatively more by average daily temperature than those of snow geese, because Ross's geese have a higher lower critical temperature (LCT, Owen and Dix 1986). I tested these predictions by comparing time budgets and energy budgets of wintering snow geese and Ross's geese (Afton and Paulus 1992). My study is the first test of the Body-Size Hypothesis on

wintering geese and thus extends testing of this hypothesis to parts of the annual cycle other than the nesting period.

Few studies have reported direct effects of family size on time-budgets of geese (Austin 1990, Bélanger and Bédard 1992). Like most geese, snow geese maintain family units from one breeding season to the beginning of the next (Family Type Social System, Figure 5.1) (Boyd 1953; Raveling 1970; Prevett and MacInnes 1980; Black and Owen 1989a, b; Gregoire and Ankney 1990). Larger goose families generally dominate smaller families, pairs, and lone geese (Black and Owen 1989b, Gregoire and Ankney 1990), although exceptions are known (Lamprecht 1986). Parents apparently profit from juvenile assistance when defending patches of food from other flock members (Contributor Effect Hypothesis, Black and Owen 1989a). Geese in families generally feed longer and are able to use better feeding patches than are lone geese (Black and Owen 1989a), although larger families do not necessarily feed longer than do smaller families (Turcotte and Bédard 1989). When feeding, lone geese spend more time searching, whereas geese in families spend more time ingesting food (grazing or grubbing; Bélanger and Bédard 1992). Parents spend more time alert than do adults in pairs or lone adults (Black and Owen 1989a, Austin 1990). Age also influences time-budgets of geese; adults generally spend more time alert than do juveniles, whereas juveniles spend more time feeding than do adults, presumably because adults are more efficient foragers than are juveniles (Frederick and Klaas 1982, Austin 1990, Bélanger and Bédard 1992).

Consequently, I predicted that: (1) juveniles of both species would spend more time feeding than do adults; (2) parents would spend more time alert than non-parental adults, and adults generally would spend more time alert than do juveniles; and (3) geese in families would spend more time feeding than do lone birds. I estimated and compared energy budgets

Family Type Social System

Gregarious Type Social System

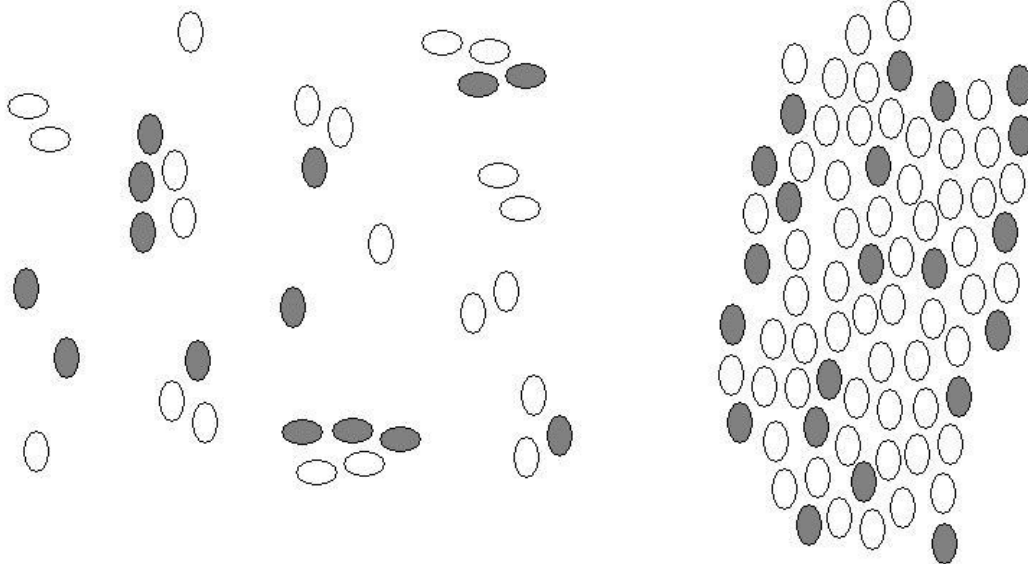


Figure 5.1. Schematic, birds-eye view of two types of social systems observed in lesser snow geese (left) and Ross's geese (right). Shaded ovals represent juvenile geese, whereas white ovals represent adult birds. In the family type system, families defend patches of forage, whereas as no such resource defense occurs in the gregarious type system. The Gregarious Type Social System (right) is effective against predators whereas the Family Type Social System (left) allows families to defend feeding patches against flock-mates.

between geese in families and lone geese, within each age group (adults and juveniles) and species, to test whether snow geese and Ross's geese in families gained more net energy, in accordance with the Contributor Effect Hypothesis (Black and Owen 1989a).

I included age and family size of snow geese and Ross's geese in my analysis because these variables can affect comparisons of time-budgets if their respective frequencies differ markedly between species (Paulus 1988). Interestingly, Ross's geese wintering in California formed denser flocks than do larger species and only a small percentage of individuals were paired or in families (Gregarious Type Social System, see Figure 5.1) (Johnson and Raveling 1988, McWilliams and Raveling 1998). Upon arrival to the wintering areas, parents expel their offspring if the parent-offspring association is non-beneficial or detrimental to parents' future reproductive success (Black and Owen 1989a). This hypothesis posits that (1) Ross's geese in California can not enhance their feeding success by maintaining family units; and (2) the gregarious social system increases foraging efficiency for Ross's geese by maintaining food plants in a low growth status (Johnson and Raveling 1988). Ross's geese in California feed primarily on grass; grass kept in a low growing status has higher nitrogen content and digestibility than does ungrazed grass (Prins et al 1980, Ydenberg and Prins 1981). Rice-plants are more nutritious than are natural grasses (Owen 1980); thus, under the hypothesis of Johnson and Raveling (1988), the constraints of low-quality diet may prevent Ross's geese from maintaining family units. Accordingly, I hypothesized that foraging on rice plants in southwest Louisiana would enable Ross's geese to maintain family units, as has been previously observed for snow geese wintering in the area (Prevett and MacInnes 1980, Gregoire and Ankney 1990). Ross's geese began wintering in Louisiana during the last decade (Helm 2003) and previous studies on social behavior of snow geese in Louisiana pre-date the arrival of Ross's geese to the state (Prevett and MacInnes 1980, Gregoire and Ankney 1990). I compared frequencies of

various social groups between the two species; my study presents the first quantitative analysis of the social system of wintering Ross's geese, that uses a controlled comparison with snow geese. Here, my objective was to determine whether the choice of maintaining families in geese is affected by food quality or body size.

Interspecific competition generally leads to aggressive interactions between individuals (hereafter social encounters) when different goose species use the same feeding habitats simultaneously; interspecific dominance relationships usually are determined by numbers of each species present (Fox and Madsen 1981, Madsen 1985, Gawlik 1994). However, if food is especially abundant, competing species may coexist in feeding patches (Fox and Madsen 1981, Gawlik 1994). I measured frequencies of intra- and interspecific social encounters (after Gregoire and Ankney 1990) to determine if interspecific dominance existed between snow geese and Ross's geese.

Sympatry of snow geese and Ross's geese is beneficial to both species on the breeding areas, where each species uses complementary capabilities to fend off different predators (McLandress 1983). On wintering areas, the smaller Ross's geese are more vulnerable to avian predators, such as bald eagles (*Haliaeetus leucocephalus*), than are snow geese (McWilliams et al. 1994, McWilliams and Raveling 1998); in Louisiana, possible predation threats are red-tailed hawks (*Buteo jamaciensis*) and occasionally bald eagles (Jón Einar Jónsson personal observations; Troy Blair, Louisiana Department of Wildlife and Fisheries, New Iberia, Louisiana, personal observations). Thus, I examined whether Ross's geese contribute equally to flock vigilance relative to snow geese, by comparing time spent alert and the number of times each species assumed the alert position within mixed flocks (as defined by Inglis 1976).

METHODS

STUDY AREA

I observed snow geese and Ross's geese in the rice-prairies in southwest Louisiana during 10 November – 20 February of 2002-2003 and 2003-2004. Rice-prairies are former tall-grass prairies which were extensively cultivated, mostly for rice, but also pasture for cattle (Alisauskas 1988, Alisauskas et al. 1988, Bateman et al. 1988). My study area was previously described in detail by Alisauskas (1988), Alisauskas et al. (1988), and Bateman et al. (1988). I observed mixed white goose (snow geese and Ross's geese combined) flocks that used non-flooded rice-fields almost exclusively, which were either uncut, stubble, tilled, or fallow (see also Alisauskas 1988). I made observations adjacent to and directly north of Lacassine National Wildlife Refuge (NWR; 29°55'N, 92°50'W) and Cameron Prairie NWR (29°57'N, 93° 04'W); this area is bordered from the west, north and east by the towns of Lake Charles (30°13'N, 93° 13'W), Jennings (30°12'N, 92° 40'W), and Lake Arthur (30°05'N, 93° 40'W).

Southwest Louisiana is the historical wintering area of snow geese in the Mississippi Flyway (Bateman et al. 1988, Cooke et al. 1988, Mowbray et al. 2000). In contrast, Ross's geese began wintering in Louisiana only during the last decade (Ryder and Alisauskas 1995, Helm 2003). During my study, Ross's geese comprised 1-15% of observed mixed white goose flocks and Ross's geese rarely were found independent of snow geese (see also Helm 2003). Estimated combined snow goose and Ross's goose numbers in the Midwinter Waterfowl Survey on my study area were 257,119 in 2002-2003 and 360,487 in 2003-2004 (Waterfowl Harvest and Population Survey Data 2004); Ross's geese, on average, comprised 7% of all white geese observed (Helm 2003).

OBSERVATIONS

Sampling of Focal Geese

Three observers and I collected behavioral data in 2002-2003 and 2003-2004; I was the only observer present in both winters. I trained other observers prior to data collection; we simultaneously observed the same focal geese until our independent results were similar (less than 2% difference between percentages of time spent in all activities) for all activities of at least 20 focal birds (Gloutney et al. 2001).

During sampling periods, observers alternated between snow geese and Ross's geese. Observers used spotting scopes with 20x magnification and collected 5 to 10-minute focal sampling observations (Altmann 1974, Black and Owen 1989b). All observations were made from pick-up trucks, either from inside the cab or the bed. Observers recorded data with an Apple Newton Messagepad 2000 (Apple Computer Inc., Cupertino, California) equipped with Ethoscribe software (Tima Scientific, Sackville, New Brunswick, California). Observers selected focal geese within a field of vision by using sequences of 20 random numbers obtained with the Research Randomizer Software (Urbaniak and Plous 2003).

Whenever a flock under observation flushed, observers did not resume sampling for at least 10 minutes. Observers and I did not sample flocks within 150 meters because geese generally remained alert due to observer presence at such close range. Snow geese in southwest Louisiana generally are accustomed to presence of vehicles (Prevett and MacInnes 1980). During the two winters (2002-2003 and 2003-2004), observers and I sampled time-budgets of 703 snow geese and 624 Ross's geese.

Aging and Assigning Social Status of Focal Geese

Prior to each observation, observers and I visually aged snow geese and Ross's geese by plumage color: (1) adult (after-hatch-year) white-phase snow geese and Ross's geese are white

with black wing-tips, whereas juveniles (hatch-year) are pale gray; and (2) adult blue-phase snow geese and Ross's geese have white heads and blue-gray backs and bodies, whereas juveniles have dark heads (Cramp and Simmons 1977, Bellrose 1980, Madge and Burn 1988). Although juveniles have grayish backs and bodies like adults, juvenile plumage is browner above and paler below than that of adults (Cramp and Simmons 1977, Bellrose 1980, Madge and Burn 1988).

Observers and I identified pairs and families based on mutual participation in social encounters, mutual chasing or avoiding other geese, and coordinated directions of locomotion (Raveling 1970, Paulus 1983, Black and Owen 1989b, Gregoire and Ankney 1990). For analysis, I grouped focal individuals into 5 social categories (after Boyd 1953, Raveling 1970, Gregoire and Ankney 1990): (1) *lone adult*, a lone after-hatch-year goose; (2) *parent*, adult goose socially bonded (i.e. paired) with another adult goose, accompanied by at least 1 offspring; (3) *paired non-parent*, adult goose socially bonded with another adult goose without offspring; (4) *juvenile in family*, hatch-year goose accompanied by adult parents; and (5) *lone juvenile*, a lone hatch-year goose. I excluded crippled geese and single-parent families from analysis because their social status is reduced by injury or mate loss (Gregoire and Ankney 1990), which probably affects their time-budgets.

Classifications of Behavioral Activities

I classified behavioral activities as feeding, resting, locomotion (walking or swimming), alert, social interactions, and other activities (Table 5.1). I chose this classification for analysis of time spent feeding, alert, and in locomotion, and for energy budgets calculations (Ganter and Cooke 1996). I further divided feeding into grazing, grubbing, and searching because these activities have different energetic costs which were accounted for in energy budget calculations (cf. Ganter and Cooke 1996).

Table 5.1. Classification and definitions of goose activities (cf. Gauthier et al. 1984, Davies et al. 1989, Black and Owen 1989b, Ganter and Cooke 1996), for lesser snow geese and Ross's geese, observed in southwest Louisiana in winters 2002-2003 and 2003-2004.

Feeding was a combination of 3 types of foraging activities:

Grubbing: goose dug for belowground plant parts, removed mud with bill, softened mud with feet, and ingested bulbs and rhizomes. Food was ingested; thus, time spent grubbing was included in calculations of beginning rates.

Grazing: goose picked up and ingested aboveground plant material, treaded to break water surface with bill, or washed a plant part. Food was ingested; thus, time spent grazing was included in calculations of beginning rates.

Searching: displacements with head lowered and bill pointed toward the ground, looking for digging sites or food. No food was ingested; thus, time spent searching was not included in calculations of beginning rates (see text).

Alert: goose was standing upright with head raised (see Inglis 1976).

Locomotion was a combination of 2 activities:

Walking: goose switched locations on foot with head raised.

Swimming: goose moved on water surface.

Inactive (Reference activities in generalized linear models):

Social interactions: goose directed social displays at other geese.

Resting: goose sat or stood, with bill tucked under wing, or completely still with head upright, not moving, either awake or sleeping.

Other: activities that were not described above, including drinking, preening, and comfort activities.

Indexing Intake Rates and Alert Rates

Grazing geese can compensate for reduced foraging time by increasing intake rates (also termed peck rates; Owen 1972); thus, it is imperative to compare intake rates between groups when studying time spent feeding (see Gloutney et al. 2001). In this study, it was not feasible to directly record peck rates (Owen 1972) because: (1) snow geese feed both by grazing and grubbing (see Alisauskas et al. 1988); and (2) focal geese often were partially covered in vegetation such as rice-stubble or other grasses, which often made observing pecks impossible. Grubbing is particularly difficult to quantify in terms of number of pecks because one “peck” can last for 1 minute or longer (Jón Einar Jónsson personal observation). Thus, I constructed a comparative index for intake rates (hereafter beginning rate); I recorded the number of times each focal bird initiated a foraging bout (bouts/minute), i.e. placed their bill to the ground, and movements of the body indicated that the focal goose bit into plant material.

I counted the number of times focal birds assumed an alert position (hereafter alert rates). I used alert rates (alert positions assumed/minute) and time spent alert to estimate contribution to flock vigilance between species, age groups, and family sizes. I also present descriptions of behavioral responses of goose flocks to avian predators.

Interspecific Social Encounters

Observers and I recorded frequencies of social encounters between focal geese and other geese, scoring wins if opponents responded to interactions by avoiding or fleeing focal geese (Raveling 1970, Gregoire and Ankney 1990). Sampling of social encounters was limited to focal geese for 5-10 minute sampling periods; social encounters other than those directly involving focal geese, their mates, parents or offspring were not recorded.

STATISTICAL ANALYSES

I estimated time-budgets of snow geese and Ross's geese by dividing the time spent on each activity (Table 5.1) by the total time (no. of seconds) each focal goose was observed to obtain percentage (%) of time each focal goose spent on each activity (Paulus 1984). For intake and alert rates, focal geese that were not observed feeding or alert were assigned values of 0. For analysis, all models included species (snow goose or Ross's goose), age (adult or juvenile), family size (1, 2, 3, or 4 and higher), and average daily temperature (°C) as explanatory variables, including all interactions. I included average daily temperature (1) as a covariate in analyses of time-budgets; and (2) to calculate energy expenditure in calculations of energy budgets (see below). I obtained daily minimum, average, and maximum daily temperatures at Lake Charles (Louisiana Office of State Climatology, Louisiana State University 2005).

Calculations of Energy Intake and Energy Expenditure

I derived most estimates for the energy budget analysis from the literature (cf. Owen et al. 1992, Ganter and Cooke 1996). Specifically, these are basal metabolic rate (BMR), energetic costs of each activity expressed as multiples of BMR (Table 5.2), the amount of metabolizable energy obtainable from composite diets from rice-prairies (Alisauskas et al. 1988), average food throughput time as a function of body size, digestion capacity, and energetic costs of thermoregulation (LeFebvre and Raveling 1967, Burton et al. 1979, Gauthier et al. 1984, Alisauskas et al. 1988, Owen et al. 1992, Mayhew and Houston 1993, Ganter and Cooke 1996). I used average body masses from (1) 129 adult female (2008 g) and 105 adult male snow geese (2212 g) caught with rocket-nets and weighed with a pesola scale (± 20 g) in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004 (Chapter 7); and (2) 5 adult female Ross's geese (1305 g) and 8 male Ross's geese (1417 g) shot by hunters in southwest Louisiana (Jón Einar Jónsson unpublished data).

Table 5.2. Estimates of energetic costs of various activities, expressed as multiples of the basal metabolic rate (Wooley and Owen 1978, Gauthier et al. 1984, Owen et al. 1992, Ganter and Cooke 1996), for lesser snow geese and Ross's geese, observed in southwest Louisiana in winters 2002-2003 and 2003-2004.

Activity	Cost	Activity	Cost
Resting	1.3	Walking	2.0
Grazing	2.0	Searching	2.0
Alert	2.1	Social interactions	2.3
Other	2.1 ^a	Swimming	2.8
Grubbing	3.0		

^a average cost for preening and drinking

My estimates of energy intake involved (cf. Ganter and Cooke 1996): (1) the proportion of time spent grazing and grubbing (see Table 5.1); (2) metabolizable energy obtainable from composite diets in the rice-prairies of southwest Louisiana, estimated as 8.5 KJ g/dry weight of food (Alisauskas et al. 1988); and (3) digestive capacity, the amount of food (g) that geese can ingest in 1 hour of constant food intake, estimated as 20 g dry weight/hour for snow geese, assuming food throughput time of 90 minutes (Burton et al. 1979).

Published values on digestive capacity for Ross's geese are not available; thus, I estimated a value for Ross's geese using a regression of body weight on mean food throughput time in grass-eating waterfowl species (Mayhew and Houston 1993):

$$\text{Mean food throughput time (minutes)} = 0.0162(\text{body mass (g)}) + 66.313$$

This regression estimated throughput times of snow geese and Ross's geese as 100.5 and 88.4 minutes, respectively. I used the ratio of these values to adjust the digestion capacity reported by Burton et al (1979) for Ross's geese:

$$\text{Digestive capacity of Ross's geese} = 20 \text{ g} / (100.5/88.4) = 17.6 \text{ g}$$

Thus, I indexed digestive capacities of snow geese and Ross's geese at 20 g dry weight / hour and 17.6 g dry weight / hour, respectively. Digestive capacity scales linearly with body size (Demment and Van Soest 1985), but smaller species have relatively high digestive capacities (Mayhew and Houston 1993, see also Hupp et al. 1995); thus, scaling digestive capacity as a direct function of interspecific differences in body size ($0.68 * 20 \text{ g} = 13.6 \text{ g}$) probably is an underestimate for Ross's geese.

I recorded only diurnal time-budgets, and my calculations assume that geese feed only for 12 hours a day; wintering snow geese generally forage very little during night (McIlhenny 1932, Alisauskas et al. 1988, Davis et al. 1989). The formulas for energy intake were:

$$\text{Energy intake}_{\text{snow geese}} (\text{KJ/day}) = \{(20 \text{ g dry weight food / hour}) \cdot (8.45 \text{ KJ / g dry weight}) \cdot (\text{beginning rate}) \cdot (\text{proportion of time spent grazing} \cdot 12 \text{ hours})\} + \{(20 \text{ g / dry weight food / hour}) \cdot (8.45 \text{ KJ / g dry weight}) \cdot (\text{beginning rate}) \cdot (\text{proportion of time spent grubbing} \cdot 12 \text{ hours})\}$$

$$\text{Energy intake}_{\text{Ross's geese}} (\text{KJ/day}) = \{(17.6 \text{ g / dry weight food / hour}) \cdot (8.45 \text{ KJ / g dry weight}) \cdot (\text{beginning rate}) \cdot (\text{proportion of time spent grazing} \cdot 12 \text{ hours})\} + \{(17.6 \text{ g / dry weight food / hour}) \cdot (8.45 \text{ KJ / g dry weight}) \cdot (\text{beginning rate}) \cdot (\text{proportion of time spent grubbing} \cdot 12 \text{ hours})\}$$

Calculations of energy expenditure (KJ/day) involved: (1) estimated time-budgets; (2) factors of energy expenditure, expressed as multiples of BMR (Table 5.2); (3) estimated basal metabolic rates of snow geese and Ross's geese, using the formula for non-passerine birds from Lasiewski and Dawson (1967; $\text{KJ/day} = 4.184 \times 78.3(\text{kg body weight})^{0.723}$), and body weights (Table 5.3); (4) LCT of snow geese and Ross's geese, estimated by the Ascoff-Pohl Equation ($40 - (4.73 \times \text{bodymass}^{0.274})$; Owen and Dix 1986); and (5) energy costs of thermoregulation, calculated from body mass specific rate of heat loss ($\text{KJ/hour/}^\circ\text{C} (\Delta T)$; after LeFebvre and Raveling 1967, see also Birkebak et al. 1966), and daily minimum, average, and maximum daily temperatures at Lake Charles (Louisiana Office of State Climatology, Louisiana State University 2005).

Table 5.3. Body masses and calculated estimates of heat loss rates (ΔT), lowest critical temperatures (LCT), and basal metabolic rates (BMR) for lesser snow geese and Ross's geese, weighed in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004.

	Body mass			ΔT^a (KJ/Hour/ $^{\circ}C$ Decrease)	LCT ^b ($^{\circ}C$)	BMR ^c (KJ/day)
	males (g)	females (g)	combined (g)			
Lesser snow goose	2212.0	2007.8	2109.9	1.48	1.5	646.7
Ross's goose	1416.7	1305.0	1360.9	1.30	5.8	469.7

^a Heat loss rates calculated after LeFebvre and Raveling (1967)

^b LCT after Ascoff-Pohl Equation (Owen and Dix 1986)

^c BMR after Lasiewski and Dawson (1967)

The temperature at which animals maintain basal metabolic rate during rest (without catabolizing endogenous reserves) is the Lowest Critical Temperature (LCT); I estimated LCTs for snow geese and Ross's geese as 1.5 °C and 5.8 °C, respectively (Table 5.3). I assumed that plumages of the two species have similar insulation qualities. I used a linear regression (PROC REG; SAS Institute 1999) to estimate ΔT for snow geese and Ross's geese by regressing body weight of different-sized races of Canada geese (*Branta canadensis*) (LeFebvre and Raveling 1967) on their reported values for ΔT , and then used the regression equation with body weights of snow geese and Ross's geese (Table 5.3). The regression equation (LeFebvre and Raveling 1967) was:

$$\Delta T = 0.2304 + 0.0584 \times \text{body mass (kg)}$$

$$R^2 = 0.9928, P = 0.0036$$

The residuals from this regression were normally distributed (Shapiro-Wilkes test; $P = 0.98$). The estimated ΔT for snow geese and Ross's geese were 1.48 KJ/hour/° C decrease and 1.30 KJ/hour/° C decrease, respectively (Table 5.3).

My calculations of energy expenditure due to thermoregulation (after Birkebak et al. 1966, Lefebvre and Raveling 1967) required an index of number of hours that geese spent below their LCT during the day they were observed. When compiling an index, I assumed that: (1) LCT minus the minimum daily temperature ($T^{\circ}\text{min}$) each day indexed the number of hours each species spent below its LCT that day; and (2) the maximum daily temperature ($T^{\circ}\text{max}$) minus LCT indexed the number of hours each species spent above its LCT that day. Thus, the formula for energy expenditure due to thermoregulation ($\text{KJ}_{\text{thermoreg}}$) was:

$$(KJ_{\text{thermoreg}}) = \{LCT - T^{\circ}\text{min} / [(LCT - T^{\circ}\text{min}) + (LCT - T^{\circ}\text{max})] * 24\} * \Delta T * \{LCT - T^{\circ}\text{min}\}$$

I set $KJ_{\text{thermoreg}}$ to 0 for focal birds whenever average daily temperature was above LCT.

The calculation of energy expenditure (see also Owen et al. 1992) was:

$$\text{Energy expenditure (KJ/day)} = KJ_{\text{thermoreg}} + \text{BMR} (\text{alert}*2.1 + \text{social}*2.3 + \text{grazing}*2.0 + \text{grubbing}*3.0 + \text{searching}*2.0 + \text{walking}*2.0 + \text{swimming}*2.8 + \text{resting}*1.3 * \text{preening}*2.3)$$

$$(\text{BMR}_{\text{snow geese}} = 646.7 \text{ KJ/day and } \text{BMR}_{\text{Ross's geese}} = 469.7 \text{ KJ/day})$$

Finally, I subtracted energy expenditure from energy intake to obtain net energy intake (i.e. energy budgets, KJ/day) of each focal goose (Ganter and Cooke 1996):

$$\text{Net energy intake (KJ/day)} = \text{Energy intake (KJ/day)} - \text{Energy expenditure (KJ/day)}$$

General Model Building and Model Selection

I used generalized linear models (PROC GENMOD; SAS Institute 1999) to compare (1) time-budgets; (2) beginning rates and alert rates; and (3) net energy intake between snow geese and Ross's geese. My research interests concerned the effects of species, age, family size, and average daily temperature on goose behavior. I ran separate models for each winter because I knew *a priori* that (1) family units were more common in 2003-2004 than in 2002-2003 (see results); (2) winter 2002-2003 was cooler than was the winter 2003-2004 (Louisiana Office of State Climatology, Louisiana State University 2005).

For all analyses, I started with the saturated model and used backwards stepwise model selection to determine the final model (Agresti 1996). Behavioral studies of wintering waterfowl

often include effects of month or period (early, mid- and late winter). However, I did not include such periods in my study; snow geese and Ross's geese stay in Louisiana for 3-4 months, compared to a 6 month wintering period in most other geese (Paulus 1988, Black and Owen 1989b, Ely 1992).

I constructed generalized linear models based on normal and Poisson distributions; in this case, the Poisson log-linear model is equivalent to running a logistic regression based on the multinomial distribution (Agresti 1996). I evaluated goodness of fit for these models by comparing ratios between degrees of freedom (df) and deviance of the models; a ratio of deviance/df close to 1.0 indicates a good model fit (Agresti 1996). In all my analyses, I report least-square means (LSMEANS; $\bar{\chi}$) for all explanatory variables reported as significant by PROC GENMOD (SAS Institute 1999): species, age, family size, and/or average daily temperature.

Generally, normal models fit reasonably well (deviance/df ≤ 1.10), whereas multinomial models fit poorly in all analyses and exhibited signs of overdispersion (deviance/df ≥ 100). Thus, I used models based on the normal distribution for all analyses. Data points with the value 0 can cause bias in estimates of odds ratios and unreliable estimates of goodness-of-fit statistics in generalized linear models (Hosmer and Lemeshow 1989, Agresti 1996). My data on time-budgets and on beginning and alert rates contained numerous zeros; thus I added 0.05 to all data points in to allow models to deal efficiently with values of 0 (Hosmer and Lemeshow 1989, Agresti 1996).

Models for Time-Budgets

I used generalized linear models with a multicategory response (see Agresti 1996; also termed polytomous responses; Stokes et al. 2000), in which significance is tested by examining second-order interactions between activity and explanatory variables (see also Stokes et al.

2000). One activity had to be the reference activity (Agresti 1996); I summed time spent on resting, social interactions, and other activities (Table 5.1) into one reference activity, termed inactive, because my interest was primarily in time spent feeding, alert, and in locomotion. Dependent variables were percentages of time spent alert, feeding, in locomotion, and performing activities classified as inactive (Table 5.1). Explanatory categorical variables were species, age, and family size (1, 2, 3, and 4 or higher); average daily temperature was a covariate, and all interactions were included in the saturated model.

Testing for Effects of Family Size

Generalized linear models with a multcategory response variable require that one level in each category is set as a reference, the choice of which is arbitrary (Agresti 1996). I used lone, adult geese as the reference category in my models when comparing groups of geese. In my statistical analysis, I classified: (1) adults as lone (family size = 1), paired non-parents (family size = 2), or parents (family size ≥ 3); and (2) juveniles as lone (family size = 1) or in family (family size ≥ 3). I treated snow goose families of 4 and higher as one group (family size ≥ 4) because of relatively small sample sizes for families of 5 geese or larger. I combined all Ross's geese in families into one group (Family size ≥ 3).

The number of family sizes differed between (1) species, because Ross's geese in families were 1 group (family size ≥ 3) in contrast to 2 groups in snow geese (family size = 3, and ≥ 4); and (2) age groups, because pairs (family size = 2) were never observed among juveniles of either species. Thus, family size was a nested variable in all my analyses. Firstly, I nested family size within the species x age interaction, to test the hypothesis that family size acted differentially within age groups and/or within each species; if this term was significant, I kept it in the model for interpretation. Otherwise, I nested family size within: (1) species, to test the hypothesis that family size differentially affected time-budgets of the two species,

independent of age; and (2) age group, to test the hypothesis that family size differentially affected time-budgets of age groups, independent of species.

Models for Beginning Rates and Alert Rates

I compared beginning rates between groups in PROC GENMOD; explanatory categorical variables were species, age, and family size, whereas average daily temperature was a covariate, and all interactions were included in the saturated model.

Models for Energy Budgets

I used net energy intake as the response variable in an analysis of variance, using PROC GENMOD (SAS Institute 1999). Explanatory categorical variables were species, age, and family size; all interactions were included in the saturated model. For this analysis, I did not use average daily temperature as a covariate because effects of ambient temperatures were included in calculations of net energy intakes.

Comparison of Social Interactions

I used a generalized linear model in PROC GENMOD (Agresti 1996, SAS Institute 1999) to estimate whether frequencies of social groups (parents, non-parental pairs, and lone geese) differed between species, age groups, and winters. I included the age x social status interaction in this model because pairs without juveniles were, of course, never observed in my juvenile category. A linear model based on the normal distribution fit the data reasonably well (Deviance = 24.0, df = 15). I compared odds of success (O_{success}) in interspecific social encounters vs. intraspecific social encounters for both species using PROC GENMOD (SAS Institute 1999) and calculated odds ratios of winning against the other species over the odds of winning against a conspecific:

$$\{O_{\text{success}} \text{ against other species} = \text{Probability of winning } (P_{\text{other}}) / (1 - P_{\text{other}})\} /$$

$$\{O_{\text{success}} \text{ against own species} = \text{Probability of winning } (P_{\text{own}}) / (1 - P_{\text{own}})\}$$

I assumed that a significant difference in this odds ratio between snow geese and Ross's would indicate that one species plausibly is socially dominant over the other species.

RESULTS

COMPARISON OF TIME-BUDGETS BETWEEN SPECIES

Overall time-budgets differed between species and age groups in both winters (Table 5.4). Average daily temperature and family size influenced time-budgets in 2002-2003 but not in 2003-2004 (Table 5.4).

Time budgets differed between snow geese and Ross's geese for the following activities (see also Table 5.5):

Feeding. Ross's geese ($\bar{\chi} = 53.3\%$) spent more time feeding than did snow geese ($\bar{\chi} = 45.4\%$) in 2002-2003 ($\chi^2 = 11.30$, $df = 1$, $P = 0.0008$) and in 2003-2004 ($\bar{\chi} = 57.1\%$ vs. $\bar{\chi} = 46.3\%$) ($\chi^2 = 14.72$, $df = 1$, $P = 0.0001$).

Alert. In 2002-2003, Ross's geese spent more time alert ($\bar{\chi} = 23.9\%$) than did snow geese ($\bar{\chi} = 20.8\%$) ($\chi^2 = 5.86$, $df = 1$, $P = 0.0155$).

Locomotion. In 2003-2004, Ross's geese spent more time in locomotion ($\bar{\chi} = 7.2\%$) than did snow geese ($\bar{\chi} = 5.6\%$) ($\chi^2 = 5.00$, $df = 1$, $P = 0.0253$).

COMPARISON OF TIME-BUDGETS BETWEEN ADULTS AND JUVENILES

In 2002-2003, overall time-budgets of age groups were dependent on family size nested within age group. In 2003-2004, overall time-budgets differed between adults and juveniles, independent of species or family size, for the following activity:

Table 5.4. Summary of significant effects from final generalized model analysis (PROC GENMOD; SAS Institute 1999) of time-budgets of lesser snow geese and Ross's geese in southwest Louisiana in winters 2002-2003 and 2003-2004. Note that df = 3 for age group (df = 1) and species (df = 1) because in generalized multcategory models, significance is tested on the interaction of these terms with activity (df = 3); thus the df is not 1, as might be expected.

	2002-2003			2003-2004		
	df	χ^2	P	df	χ^2	P
Species	3	11.96	0.0075	3	14.92	0.0019
Age group	3	30.68	<0.0001	3	11.38	0.0098
Average Daily Temperature (°C)	3	49.84	<0.0001	3	4.80	0.1869
Family size nested in age group	20	48.10	0.0004	20	25.50	0.1829

Table 5.5. Least-square mean percentages of time spent alert, feeding, in locomotion, and other activities, by lesser snow geese (hereafter snow geese) and Ross's geese in southwest Louisiana in winters 2002-2003, and 2003-2004. Inactive activities were resting, social displays, preening, and activities classified as other in Table 5.1. ASE indicates asymptotic standard error.

			Alert	Feeding	Locomotion	Inactive	ASE	
Species	2002-2003	Ross's geese	23.9	53.3	2.9	19.5	4.3	
		Snow geese	20.8	45.4	3.6	30.1	2.1	
	2003-2004	Ross's geese	20.0	57.1	7.2	16.0	3.5	
		Snow geese	21.5	46.3	5.6	27.2	2.4	
Age	2002-2003	Adults	28.3	41.1	2.8	27.8	2.9	
		Juveniles	16.4	58.1	3.8	21.3	3.8	
	2003-2004	Adults	26.3	47.5	6.3	20.5	2.4	
		Juveniles	15.2	55.9	6.5	22.7	3.6	
Family size within age group	2002-2003	Ad. lone	1	21.9	50.9	5.1	21.2	3.3
		Ad. pair	2	21.9	49.8	2.1	26.4	3.7
		Ad. parents	3	25.5	34.7	1.3	38.3	6.6
		Ad. parents	4+	43.4	28.9	2.1	25.5	6.5
		Juv. lone	1	17.5	52.3	5.7	23.9	4.3
		Juv. family	3	19.9	51.4	1.5	26.8	6.2
		Juv. family	4+	11.7	72.2	5.1	10.5	5.1

Ad = adults; Juv. = Juveniles

Alert. In 2003-2004, adults spent more time alert ($\bar{\chi} = 26.3\%$) than did juveniles ($\bar{\chi} = 15.2\%$) ($\chi^2 = 5.14$, $df = 1$, $P = 0.0233$).

EFFECTS OF FAMILY SIZE ON TIME-BUDGETS

Overall time-budgets did not differ by family size in 2003-2004. However, overall time-budgets differed by family size in 2002-2003, independent of species, for following behaviors:

Alert. Adults in families of 4 and larger spent more time alert ($\bar{\chi} = 43.4\%$) than did lone adults ($\bar{\chi} = 21.9\%$) ($\chi^2 = 9.27$, $df = 1$, $P = 0.0023$).

Feeding. Adults in families of 3 and 4 spent less time feeding ($\bar{\chi} = 34.7\%$, and $\bar{\chi} = 28.9\%$, respectively) than did lone adults ($\bar{\chi} = 50.9\%$) ($\chi^2 = 5.02$, $df = 1$, $P = 0.0251$; and $\chi^2 = 9.45$, $df = 1$, $P = 0.0021$, respectively). Juveniles in families of 4 or larger spent more time feeding ($\bar{\chi} = 72.2\%$) than did lone juveniles ($\bar{\chi} = 52.3\%$) ($\chi^2 = 7.92$, $df = 1$, $P = 0.0049$).

EFFECTS OF AMBIENT TEMPERATURE ON TIME-BUDGETS

In 2002-2003, time spent feeding had an inverse relationship with average daily temperature ($\chi^2 = 47.36$, $df = 1$, $P < 0.0001$); on average, an 1°C increase in average daily temperature resulted in a 3.8% decrease in time spent feeding. In 2002-2003, time spent in locomotion also had an inverse relationship with average daily temperature ($\chi^2 = 47.36$, $df = 1$, $P = 0.0023$); on average, an 1°C increase in average daily temperature resulted in a decrease of 1.7% in time spent locomotion.

BEGINNING RATES AND ALERT RATES

Final models for beginning rates included only species, which was significant in 2003-2004 ($\chi^2 = 5.70$, $df = 1$, $P = 0.0169$), but not in 2002-2003 ($\chi^2 = 0.75$, $df = 1$, $P = 0.3878$). In

2003-2004, Ross's geese initiated, on average, $\bar{\chi} = 1.4$ feeding bouts/minute as compared to $\bar{\chi} = 1.0$ feeding bouts/minute of snow geese (LSMEANS; Table 5.6).

Final models for alert rates included family size nested within the species x age interaction. Family size was not significant in 2002-2003 ($\chi^2 = 6.68$, $df = 8$, $P = 0.5716$). In 2003-2004, alert rates differed by family size within adults of each species ($\chi^2 = 25.28$, $df = 12$, $P = 0.0135$). In snow geese, alert rates differed between adults in families of 4 and lone adults ($\chi^2 = 5.95$, $P = 0.0147$); adults in families of 4 or larger assumed the alert position $\bar{\chi} = 1.4$ times relative to $\bar{\chi} = 0.9$ times in lone adults (LSMEANS; Table 5.6). In Ross's geese, alert rates differed between pairs and lone adults ($\chi^2 = 5.39$, $P = 0.0203$). Ross's geese pairs, on average, assumed the alert position $\bar{\chi} = 1.7$ times/minute as compared to $\bar{\chi} = 1.3$ times/minute in lone adults (LSMEANS; Table 5.6).

NET ENERGY INTAKE

The final model for energy budgets included family size nested within the age x species interaction ($\chi^2 = 17.76$, $df = 8$, $P = 0.0231$). Adult Ross's geese in families of 3 gained more net energy ($\bar{\chi} = 1044$ KJ/day) than did lone adult Ross's geese ($\bar{\chi} = -66$ KJ/day) ($\chi^2 = 13.06$, $df = 1$, $P = 0.0003$) other family sizes did not differ significantly in net energy intake within either species (Figure 5.2).

SOCIAL STATUS AND INTERSPECIFIC SOCIAL INTERACTIONS

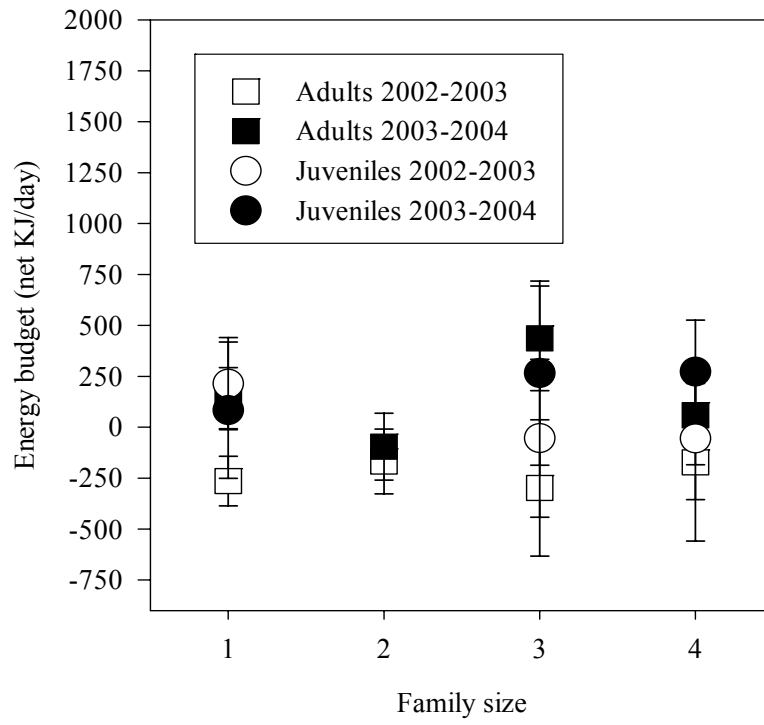
Frequencies of social groups differed significantly between species ($\chi^2 = 6.12$, $P = 0.0134$) and age groups ($\chi^2 = 35.55$, $P < 0.0001$), but not between winters ($\chi^2 = 0.53$, $P = 0.4657$). The ratio of juveniles to adults was higher in snow geese in both winters (Table 5.7). Less than 7% of Ross's geese of either age were in families, whereas over 20% of snow geese of either age were in families (Table 5.7).

Table 5.6. Least-square mean (LSMEAN) beginning rates (bouts/minute) and alert rates (bouts/minute) of lesser snow geese (hereafter snow geese) and Ross's geese in southwest Louisiana in winters 2002-2003, and 2003-2004. SE indicates standard error.

Effect	Species	Age	Family size	Beginning rates		Alert rates	
				LSMEAN	SE	LSMEAN	SE
Species	Snow goose	Both	All	1.00	0.09	1.12	0.08
	Ross's goose	Both	All	1.37	0.11	1.27	0.10
Age	Both	Adults	All	1.09	0.06	1.33	0.05
	Both	Juveniles	All	1.08	0.13	1.06	0.11
Family size	Snow goose	Adults	1	0.80	0.11	0.95	0.10
			2	0.76	0.12	1.05	0.11
			3	1.21	0.20	1.25	0.17
			4	1.12	0.19	1.42	0.16
		Juveniles	1	1.12	0.26	0.89	0.23
			3	0.92	0.34	1.17	0.30
			4	1.05	0.19	1.16	0.17
	Ross's goose	Adults	1	0.90	0.10	1.28	0.08
			2	1.14	0.10	1.70	0.09
			3	1.60	0.23	1.50	0.20
		Juveniles	1	1.20	0.21	0.91	0.18
3			1.06	0.34	1.17	0.30	

Figure 5.2. Least-square mean energy budgets (KJ/day) of lesser snow geese (top) and Ross's geese (bottom) in southwest Louisiana in winters 2002-2003, and 2003-2004. Family size = 2 was only observed among adult geese of both species.

A. Lesser snow geese



B. Ross's geese

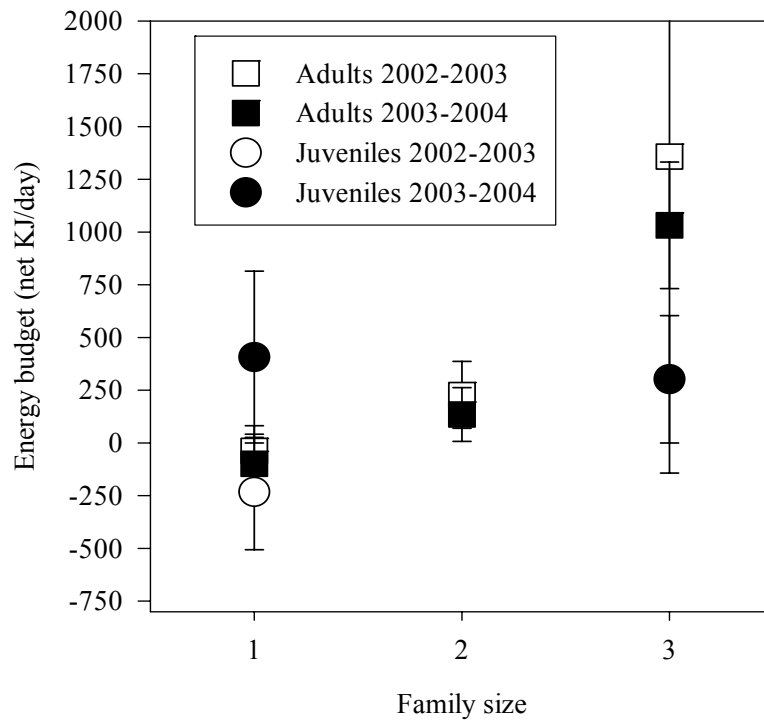


Table 5.7. Percentage frequencies (%) of social classes of lesser snow geese and Ross's geese, observed in the rice-prairies of southwest Louisiana in winters 2002-2003, and 2003-2004.

Age	Social status	Lesser snow geese		Ross's geese	
		2002-2003	2003-2004	2002-2003	2003-2004
Adults	Lone	40.5	31.1	58.9	40.7
	Paired parents	9.8	22.1	0.0	6.9
	Paired non-parents	26.0	25.4	29.5	41.6
Juvenile	Lone	11.7	6.7	11.3	7.2
	In a family	12.1	14.7	0.3	3.6
	Total % juveniles	23.8	21.4	11.6	10.8
	n	405	302	319	305

Snow geese encountered each other more frequently within mixed flocks than did Ross's geese. Ross's geese engaged in intra- and interspecific social encounters with equal frequency in 2003-2004, but had 3 times more interspecific social encounters than intraspecific social encounters in 2002-2003 (Table 5.8). Focal birds of both species were more successful in intraspecific social encounters in 2003-2004 than in 2002-2003 (Table 5.8). Snow geese were more likely to win social encounters with Ross's geese than with other snow geese (Table 5.8). Snow geese were the more successful species in interspecific social encounters; snow geese won 30 out of 52 social encounters in 2002-2003, and 32 of 33 social encounters in 2003-2004 (Table 5.8). When all focal observations of both species are combined, snow geese won 63 out of 87 (72.4%) interspecific social encounters observed.

Overall, I observed focal snow geese lose 10 social encounters against Ross's geese; all Ross's goose wins were against low ranked snow geese (i.e. non-parental pairs and lone birds); 6 were against lone juvenile snow geese, 3 were against lone adult snow geese, and the remaining 1 win was against an adult pair. I never observed Ross's geese win social encounters against snow geese in families.

RESPONSES TO AVIAN PREDATORS

Red-tailed hawks frequently were observed near goose flocks, and geese perceived hawks as threat, became alert, and flushed on at least 10 separate occasions. I observed a pair of red-tailed hawks capture and eat a snow goose in January 2004. In November 2003, I observed snow geese flush when approached by a pair of bald eagles.

Table 5.8. Average frequencies of social encounters (number/hour) of lesser snow geese and Ross's geese, odds of success in social encounters, in the rice-prairies of southwest Louisiana in winters 2002-2003, and 2003-2004.

	Lesser snow geese		Ross's geese	
	2002- 2003	2003- 2004	2002- 2003	2003- 2004
Estimate of social encounters				
Intraspecific social encounters/hour	0.9	1.0	0.2	0.5
Percentage of intraspecific social encounters won	27.8	45.1	50.0	72.0
Interspecific social encounters/hour	0.3	0.1	0.6	0.5
Percentage of interspecific social encounters won	57.6	97.0	42.4	3.0
Odds of winning against other species / Odds of winning against own species	2.1	8120000	0.5	0.01

DISCUSSION

DO TIME-BUDGETS AND ENERGY BUDGETS DIFFER BETWEEN SPECIES?

My findings are consistent with the prediction that Ross's geese compensate for their smaller size by increasing their feeding effort, relative to that of snow geese, as indicated by my findings that: (1) time-budgets differed between snow geese and Ross's geese in both winters (Table 5.4); (2) Ross's geese spent more time feeding than did snow geese in both winters (Table 5.5); and (3) Ross's geese had higher beginning rates than did snow geese in 2003-2004, but not in 2002-2003 (Table 5.6).

Both species seemed to gain approximately enough net energy to meet energy expenditure (Figure 5.2). My findings for both species are consistent with earlier studies that reported that snow geese did not gain weight while wintering in Louisiana (Ankney 1982, see also Owen and Black 1990).

Attempts to quantify energy intake are theoretical tasks that depend on assumptions that must be evaluated critically (Ganter and Cooke 1996). Like previous studies on this subject, I assumed that these values are accurate until better methods become available (Ganter and Cooke 1996). My estimates for energy budgets are crude but should provide a valid, theoretical comparison of net energy intakes of snow geese and Ross's geese (Gauthier et al. 1984). My estimates of digestive capacity were within the range of values reported for other goose species of similar sizes (see Hupp et al. 1996 and citations therein), and my values for average body size from southwest Louisiana had overlapping standard errors to those reported by MacInnes et al. (1989).

The temperature x species interaction was not significant in the time-budget analysis (Table 5.4); thus, my results contradict the prediction that Ross's geese are more sensitive to ambient temperatures than are snow geese. However, the main effect of average daily

temperature was significant and independent of species in 2002-2003. The winter 2002-2003 was cooler than the winter 2003-2004; November, January, and February were below long-term average monthly temperature in 2002-2003, whereas only February was below average in 2003-2004 (Louisiana Office of State Climatology, Louisiana State University 2005). Thus, both species responded similarly to temperature changes in the cooler winter, but apparently neither species was influenced by ambient temperatures in the warmer winter.

Waterfowl will increase time spent feeding with declining ambient temperatures until ambient temperatures drop below 0°C, at which point costs of foraging often are higher than benefits (Paulus 1988, Ely 1992, Newton 1998). Changes in ambient temperature probably affect these species similarly because: (1) the interspecific difference in LCT (4.3°C) is relatively small compared to within-day fluctuations in ambient temperatures during winter in southwest Louisiana; daily minimum and maximum temperatures often differ by 5-15 °C (Louisiana Office of State Climatology, Louisiana State University 2005); and (2) they flock together and activities of flock mates probably are not independent (Owen 1972, Ely 1992, Krause and Ruxton 2002); thus, once declining temperatures facilitate Ross's geese to increase time spent feeding, snow geese might be influenced to do so as well, at least individuals in poorer body condition.

Ross's geese spent slightly more time alert than did snow geese in 2002-2003, and alert rates within each species depended on family size (Table 5.5). However, in Ross's geese, alert behavior also may function to watch out for snow geese, most of which are socially dominant to Ross's geese and can expel them from feeding patches (Table 5.8). Ross's geese spent more time in locomotion than did snow geese in 2003-2004 (Table 5.5); this difference also may reflect the need of Ross's geese to avoid the larger snow geese.

IS FAMILY MAINTENANCE BENEFICIAL TO BOTH SPECIES?

In 2003-2004, adults spent more time alert than did juveniles. In 2002-2003, adult parents spent more time alert than did lone adults. Both findings were independent of species and are consistent with my predictions, which were based on similar findings for parents in other goose studies (Frederick and Klaas 1982, Black and Owen 1989a, b, Austin 1990, Bélanger and Bédard 1992). In Ross's geese, alert rates were higher among pairs than in lone adults; paired non-parents may spend more time alert as a function of their investment in the pair bond, either to watch out for predators or competitors (Paulus 1983, Owen and Black 1989b).

Effects of family size on overall time-budgets were significant only in 2002-2003 and were independent of species (Table 5.4). Parents spent less time feeding and more time alert than did lone adults, as reported for other goose species (Black and Owen 1989b, Austin 1990, Bélanger and Bédard 1992). In contrast, estimated net energy intake of parents was similar to that of lone adults throughout the study period (Figure 5.2); thus, it seems that snow goose parents do not incur a large energetic cost from their parental investment (Trivers 1972, Clutton-Brock 1991). Overall, snow geese in families appeared to gain slightly more net energy in 2003-2004 than did lone snow geese or non-parental pairs, but this difference was not statistically significant (Figure 5.2).

Snow geese do not gain weight while in Louisiana (Ankney 1982), and parents may not ingest markedly more energy because they maintained families in winter. However, parents probably benefit from family maintenance on northern spring staging areas, where adults accumulate reserves for breeding during a period of intense feeding and fat deposition (McLandress and Raveling 1981, Ankney 1982, Alisauskas and Ankney 1992, Alisauskas 2002). Snow geese often do not expel their offspring from the previous year until they are about to initiate breeding (Prevett and MacInnes 1980). During winter, juveniles in families probably

gain experience in foraging and resource defense, and subsequently will assist their parents in monopolizing feeding patches on spring stopover areas (Black and Owen 1989a).

Ross's goose parents had a significantly higher net energy intake than did lone birds and non-parental pairs (Figure 5.2). This finding is based on a small number of individuals, but based on these estimates, it can be inferred that Ross's geese could benefit from maintaining families, provided they are able to tolerate the cost of parental effort (Black and Owen 1989a, McWilliams and Raveling 1998). Families were relatively rare in Ross's geese (Table 5.7); family maintenance in Ross's geese may (1) represent a breeding/foraging strategy that only enhances the fitness of especially healthy individuals within the species; (2) essentially be an alternative strategy (also termed cheating strategy), whereas expelling juveniles represents the evolutionary stable strategy (ESS; Krebs and Davies 1993). Under ESS theory, a stable strategy is a behavioral strategy which can not be replaced by an alternative strategy (Krebs and Davies 1993). Although the family type social system has not replaced the gregarious social system among Ross's geese (Figure 5.1), certain individuals still are successful using the alternative strategy despite the fact it may never become common in the population.

In both species, lone juveniles had similar net energy intakes as did those in families (Figure 5.2). In 2002-2003, juveniles in families spent more time feeding than did lone juveniles, as predicted. Turcotte and Bédard (1989) reported that increased family size did not necessarily mean more time spent foraging in greater snow geese (*C. caerulescens atlanticus*). I found no evidence that juveniles in families contribute to vigilance of the family unit, beyond that done for individual vigilance by lone juveniles; juveniles in families spent the same amount of time alert (Table 5.5) and had similar alert rates as did lone juveniles (Table 5.6). Juveniles also can assist their parents in social interactions; snow geese wintering in Louisiana enhance

their social status by family maintenance (Prevett and MacInnes 1980, Gregoire and Ankney 1990).

Overall time-budgets seemingly differed between winters, as indicated by the different final models for time budgets within each winter (Table 5.4). Similarly, Giroux and Bédard (1990) found that time-budgets of greater snow geese (*C. c. atlanticus*) varied annually and urged caution in interpreting 1-year studies. Annual variation in time-budgets can provide clues about how animals deal with annual variation in environmental factors such as weather events, food availability, and disturbance events such as hunting pressure (Giroux and Bédard 1990). I found that the importance of ambient temperature, success in social interactions, and the relative importance of family maintenance varied annually; future studies should consider annual variation due to these factors. Families were more common in both species in 2003-2004, when family size did not affect time budgets (Table 5.7); thus, benefits of family maintenance and success in social encounters may have an inverse relationship with frequency occurrence of families. Benefits of family maintenance and family size in snow geese probably vary between years, locations, and populations; these variables also probably interact with one another.

SOCIAL HIERARCHIES AND INTER-SPECIFIC SOCIAL INTERACTIONS

My quantitative estimates confirm earlier qualitative observations (Johnson and Raveling 1988, McWilliams and Raveling 1998) that Ross's geese maintain families to a much lesser degree than do snow geese (Table 5.7). For my results, this difference can not be attributed to differences in food quality (Johnson and Raveling 1988) because I observed both species feeding together in mixed flocks. Apparently, few Ross's geese maintain families because (1) costs of parental effort are higher for Ross's geese than for sympatric snow geese; and (2) Ross's geese opt to conserve parental effort for future broods whereas snow geese emphasize their present broods (Black and Owen 1989b). However, Ross's geese are constrained to relatively longer

feeding times than are snow geese (Table 5.5) because of their smaller size and concurrent faster metabolic rates. Thus, I speculate that most adult Ross's geese are unable to devote parental effort at the expense of reduced time spent feeding, unlike larger species such as snow geese.

Snow geese are socially dominant over Ross's geese, as indicated by their differing success against each other relative to that against conspecifics (Table 5.8). This interspecific relationship is somewhat similar to that of a nuclear species (Ross's geese) and satellite species (snow geese); satellite species are socially dominant over nuclear species and increase their foraging success by expelling nuclear species or by local enhancement (Dolby and Grubb 1998, 1999, Krause and Ruxton 2002). However, Ross's geese can opportunistically displace snow geese in social interactions by sneaking behind snow geese and pecking them (this study, Robert McLandress, California Waterfowl Association, Sacramento, California, personal communication). I never saw Ross's geese win social encounters against snow geese in families; Ross's geese probably rarely are successful in social encounters against snow geese with high social ranks.

Recent genetic studies show that gene flow is frequent between snow geese and Ross's geese over historical time, which indicates that the two species probably have associated in the past as they do presently (Weckstein et al. 2002). Ross's geese are more at risk from avian predators than are larger goose species and, thus predation pressure probably influenced the social system of Ross's geese, although predation alone probably is not responsible for the gregarious social system in Ross's geese (McWilliams et al. 1994). I speculate that the long-standing association with snow geese selects against family maintenance in Ross's geese. Under this hypothesis, Ross's geese maintaining family units would not be able to effectively defend resources against the larger and more numerous snow geese. Instead, Ross's geese employ a scramble tactic in their competition for food when flocking with snow geese, whereas

homogenous flocks of Ross's geese form dense bodies (Figure 5.1; Johnson and Raveling 1988), which probably is an antipredator tactic similar to those employed by many mammalian herbivores (Krebs and Davies 1993, Krause and Ruxton 2002).

WHY DO SNOW GEESE AND ROSS'S GEESE FLOCK TOGETHER?

Predator vigilance probably is an important benefit of mixed flocking in both species throughout their range, particularly for the less numerous Ross's geese (i.e. dilution effect, Krebs and Davies 1993, Krause and Ruxton 2002). Red-tailed hawks were the most commonly observed avian predators in my study, although they probably mostly scrounge for injured or sick geese. Any predator-prey system is influenced by performances of individual predators (McWilliams et al. 1994); thus, when red-tailed hawks successfully capture a crippled snow goose or Ross's goose, other geese from that flock learn to be alert against red-tailed hawks.

Snow geese are unlikely to suffer significant costs due to flocking with Ross's geese because most snow geese are socially dominant over Ross's geese (Table 5.8). Ross's geese probably suffer costs from being expelled from feeding patches by snow geese. Foraging success of individual Ross's geese probably depends on avoiding snow geese and dominating other Ross's geese. Both species probably benefit from mixed flocking because of the Dilution Effect (Krebs and Davies 1993, Krause and Ruxton 2002), but further benefits may occur because mixed-species flocks can reduce success of predators to a higher degree than single-species flocks (confusion effect; Sinclair 1985, FitzGibbon 1990, see also Krause and Ruxton 2002). Smaller species particularly can benefit by placing themselves close to larger species, which then also are in the circle of possible predator attacks (Sinclair 1985, FitzGibbon 1990). Interestingly, Ross's geese exhibit this type of behavior, by (1) standing or foraging close to snow geese, rather than standing or foraging alone or with other Ross's geese; and (2) avoiding edges of flocks and remaining noticeably within flock boundaries (Jón Einar Jónsson personal

observation; Rod Drewien, Hornocker Wildlife Research Institute, University of Idaho, Wayan, Idaho, personal communication). Over evolutionary time, Ross's geese in mixed flocks may have had relatively higher fitness by being less likely to be preyed upon by avian predators because they are relatively less likely to attack snow geese (McWilliams et al. 1994).

CONCLUSION

I documented that Ross's geese spent more time feeding than did snow geese, which is consistent with predictions based on the Body-Size Hypothesis (Afton and Paulus 1992). Based on my estimated energy budgets, both species met their energy expenditures, but it is unlikely that they gain weight while in Louisiana (Ankney 1982). Few Ross's geese apparently benefit from family maintenance because most Ross's geese (1) are constrained to relatively longer feeding times than are snow geese, which in turn hinders them from devoting increased time to alert and other forms of parental effort (Black and Owen 1989b); or (2) flock with snow geese, which are socially dominant over Ross's geese, and Ross's goose families would not be any more successful in social encounters with snow geese than are lone and paired Ross's geese. Thus, Ross's geese seemingly employ a sneaking foraging strategy and compete intraspecifically for foraging patches where they are left relatively unharrassed by snow geese. A similar behavioral study of these species on spring stopover areas would be useful to determine if family maintenance leads to higher net energy intake for snow goose parents.

LITERATURE CITED

- Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.
- Afton A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons Inc, New York, New York, USA.
- Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. thesis, University of Western Ontario, London, Ontario, Canada.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. *Journal of Wildlife Management* 66:181-193.
- Alisauskas, R. T., and C. D. Ankney. 1992. Spring habitat use and diets of midcontinent adult lesser snow geese. *Journal of Wildlife Management* 56:43-54.
- Alisauskas, R. T., and H. Boyd. 1994. Previously unrecorded colonies of Ross's and lesser snow geese in the Queen Maud Gulf bird sanctuary. *Arctic* 47:69-73.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-267.
- Ankney, C. D. 1982. Annual cycle of body weight in lesser snow geese. *Wildlife Society Bulletin* 10:60-64.
- Austin, J. 1990. Comparison of activities within families and pairs of wintering Canada geese. *Wilson Bulletin* 102:536-542.
- Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent snow geese on their Gulf Coast winter range. Pages 495-515 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Batt, B. D. J., editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bélanger, L., and J. Bédard. 1992. Flock composition and foraging behavior of greater snow geese (*Chen caerulescens atlantica*). *Canadian Journal of Zoology* 70:2410-2415.
- Birkebak, R. C., C. J. Cremers, and E. A. LeFebvre. 1966. Thermal modeling applied to animal systems. *Journal of Heat Transfer* 88:125-130.
- Black, J. M., and M. Owen. 1989a. Parent-offspring relationships in wintering barnacle geese. *Animal Behaviour* 37:187-198.

- Black, J. M., and M. Owen. 1989b. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37:199-209.
- Boyd, H. 1953. On encounters between wild white-fronted geese in winter flocks. *Behaviour* 5:85-129.
- Bromley, R. G., and R. L. Jarvis. 1993. The energetics of migration and reproduction in dusky Canada geese. *Condor* 95:193-210.
- Burton, B. A., R. J. Hudson, and D. D. Bragg. 1979. Efficiency of utilization of bulrush rhizomes by lesser snow geese. *Journal of Wildlife Management* 43:728-735.
- Calder, W. A. III. 1996. Size, function and life history. Second edition. Dover Publications, Mineola, New York, USA.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Washington, D. C., USA.
- Cooke, F. D., D. T. Parkin, and R. F. Rockwell. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105:467-479.
- Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. M.S. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.
- Cramp, S., and K. E. L. Simmons. 1978. Handbook of the birds of Europe, the Middle East, and North Africa. Birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Davis, S. E., E. E. Klaas, and K. J. Koehler. 1989. Diurnal time-activity budgets and habitat use of lesser snow geese *Anser caerulescens* in the Middle Missouri River Valley during winter and spring. *Wildfowl* 40:45-54.
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641-672.
- Dickson, K. M. 2000. The diversity of Canada geese. Canadian Wildlife Service Occasional Paper 103:11-24.
- Dolby, A. S., and Grubb T. C. Jr. 1998. Benefits to satellite members in mixed species foraging groups: an experimental analysis. *Animal Behaviour* 56:501-509.
- Dolby, A. S., and Grubb T. C. Jr. 1999. Social context affects risk taking by a satellite species in a mixed-species foraging group. *Behavioral Ecology* 11:110-114.
- Ely, C. R. 1992. Time allocation by greater white-fronted geese: influence of diet, energy reserves and predation. *Condor* 94:857-870.

- FitzGibbon, C. D. 1990. Mixed species grouping in Thompson and Grant gazelles - the anti-predator benefits. *Animal Behaviour* 39:1116-1126.
- Fox, A. D., and J. Madsen. 1981. The pre-nesting behaviour of the Greenland white-fronted goose. *Wildfowl* 32:48-54.
- Frederick, R. B., and E. E. Klaas. 1982. Resource use and behavior of migrating snow geese. *Journal of Wildlife Management* 46:601-614.
- Ganter, B., and F. Cooke. 1996. Pre-incubation feeding activities and energy budgets of snow geese: can food on the breeding grounds influence fecundity? *Oecologia* 106:153-165.
- Gauthier, G. 1993. Feeding ecology of nesting greater snow geese. *Journal of Wildlife Management* 57:216-223.
- Gauthier, G., J. Bédard, and Y. Bédard. 1984. Comparison of daily energy expenditure of greater snow geese between two habitats. *Canadian Journal of Zoology* 62:1304-1307.
- Gawlik, D. E. 1994. Competition and predation as processes affecting community patterns of geese. Ph.D. thesis, Texas A&M University, College Station, Texas, USA.
- Giroux, J.-F., and Bédard J. 1990. Activity budgets of greater snow geese in fall. *Canadian Journal of Zoology* 68:2700-2702.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:78-86.
- Gloutney, M. L., R. T. Alisauskas, K. A. Hobson, and A. D. Afton. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: evidence for variable anorexia. *Auk* 116:97-108.
- Gregoire, P. E., and C. D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* 107:550-560.
- Helm, R. N. 2003. Results of January 2003 Ross's goose survey. Memorandum, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana, USA.
- Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York, New York, USA.
- Hupp, J. W., R. G. White, J. S. Sedinger, and D. G. Robertson. 1996. Forage digestibility and intake by lesser snow geese: effects of dominance and resource heterogeneity. *Oecologia* 108:232-240.
- Inglis, I. R. 1976. Agonistic behaviour of breeding pink-footed geese with reference to Ryder's hypothesis. *Wildfowl* 27:95-99.
- Johnson, J. C., and D. G. Raveling. 1988. Weak family associations in cackling geese during winter: effects of body size and food resources on goose social organization. Pages 71-89

- in M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Jónsson, J. E., A. D. Afton, R. T. Alisauskas, C. K. Bluhm, and M. E. Halawani. 2006. Ecological and physiological factors affecting brood patch area and prolactin levels in arctic-nesting geese. *Auk in press*.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of a bird. *Condor* 72:60-65.
- Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford series in ecology and evolution. Oxford University Press, New York, New York, USA.
- Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioral ecology. Third edition. Blackwell Science, Oxford, United Kingdom.
- Lamprecht, J. 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). *Behaviour* 96:28-48.
- Lasiewski, R. C., and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LeFebvre, E., and D. G. Raveling. 1967. Distribution of Canada geese in winter as related to heat loss at varying environmental temperatures. *Journal of Wildlife Management* 31:538-546.
- Louisiana Office of State Climatology. 2005. [Online]. Preliminary Daily summary: Southern Regional Climate Center. Station: Lake Charles. URL: www.Srcc.Lsu.Edu/LOSC/Climate/Lch/.
- MacInnes, C. D., R. K. Misra, and J. P. Prevelt. 1989. Differences in growth parameters of Ross's geese and snow geese: evidence from hybrids. *Canadian Journal of Zoology* 67:286-290.
- Madge, S., and H. Burn. 1988. Wildfowl: an identification guide to the ducks, geese and swans of the World. A & C Black Ltd., London, United Kingdom.
- Madsen, J. 1985. Habitat selection of farmland geese in West Jutland, Denmark: an example of a niche shift. *Ornis Scandinavica* 16:140-144.
- Madsen, J., and C. E. Mortensen. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. *Ibis* 129:25-44.
- Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publication, 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute and Wetlands International, Rønde, Denmark.
- Mayhew, P. W. 1988. The daily energy intake rate of European wigeon in winter. *Ornis Scandinavica* 19:217-223.

- Mayhew, P. W., and D. C. Houston. 1993. Food throughput time in European wigeon *Anas penelope* and other grazing waterfowl. *Wildfowl* 44:174-177.
- McCracken K.G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross's geese and lesser snow geese. *Auk* 114:610-618.
- McIllhenny, E. A. 1932. The blue goose in its winter home. *Auk* 49:279-306.
- McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross's and lesser snow geese. *Auk* 100:335-343.
- McLandress, M. R., and D. G. Raveling. 1981. Hyperphagia and social behavior of Canada geese prior to spring migration. *Wilson Bulletin* 93:310-324.
- McWilliams, S. R., and D. G. Raveling. 1998. Habitat use and foraging behavior of cackling Canada and Ross's geese during spring: implications for the analysis of ecological determinants of social behavior. Pages 167-178 in M. D. Samuel, D. D. Humburg, B. D. Sullivan, and D.H. Rusch, editors. *Biology and management of Canada geese. Proceedings of the International Canada goose symposium, Milwaukee, Wisconsin, USA.*
- McWilliams, S. R., J. P. Dunn, and D. G. Raveling. 1994. Predator-prey interactions between eagles and cackling Canada and Ross's geese during winter in California. *Wilson Bulletin* 106:272-288.
- Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Lesser snow goose. In A. Poole, and F. Gill, editors. *Birds of North America*, No. 514. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Newton, I. 1998. *Population limitation in birds.* Academic Press, San Diego, California, USA.
- Owen, M. 1972. Some factors affecting food intake and selection in white-fronted geese. *Journal of Animal Ecology* 41:79-92.
- Owen, M. 1980. *Wild geese of the world: Their life history and ecology.* Bt Batsford Ltd, London, United Kingdom.
- Owen, M., and M. Dix. 1986. Sex ratios in some common British wintering ducks. *Wildfowl* 37:104-112.
- Owen, M., and J. M. Black. 1990. *Waterfowl ecology.* Blackie Publishers, Glasgow, Scotland.
- Owen, M., R. L. Wells, and J. M. Black. 1992. Energy budgets of wintering barnacle geese: the effects of declining food resources. *Ornis Scandinavica* 23:451-458.
- Paulus, S. L. 1983. Dominance relations, resource use, and pairing chronology of gadwalls in winter. *Auk* 100:947-952.
- Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. *Journal of Wildlife Management* 48:371-380.

- Paulus, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135-152 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Prevett, J. P., and C. D. MacInnes. 1980. Family and other social groups in snow geese. *Wildlife Monographs* 71:6-46.
- Prins, H. H. th., R. C. Ydenberg, and R. H. Drent. 1980. The interaction of brent geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Botanica Neerlanden* 29:585-596.
- Raveling, D. G. 1970. Dominance relationships of agonistic Canada geese in winter. *Behaviour* 37:291-319.
- Rohwer, F. C., and M. G. Anderson. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-220.
- Ryder, J. P., and R. T. Alisauskas. 1995. Ross's goose (*Chen rossii*). In A. Poole, and F. Gill, editors. *Birds of North America*, No. 162. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- SAS Institute. 1999. *SAS/SYSTAT User's Guide*. Version 6. Fourth edition. SAS Institute. Cary, North Carolina, USA.
- Schmidt-Nielsen, K. 1997. *Animal physiology. Adaptation and environment*. Fifth edition. Cambridge University Press, Cambridge, United Kingdom.
- Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology* 54:899-918.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152.
- Slattery, S. M., and R. T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross's and lesser snow geese. *Condor* 97:970-984.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. *Categorical data analysis using the SAS system*. Second edition. SAS Institute Inc., Cary, North Carolina, USA.
- Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 11:249-264.
- Turcotte, Y., and J. Bédard. 1989. Prolonged care and foraging of greater snow goose juveniles. *Wilson Bulletin* 101:500-503.
- Urbaniak, G. C. and S. Plous. 2003. *Research Randomizer*. [Online] Wesleyan University, Connecticut, USA. URL: <http://www.randomizer.org/>.

- Waterfowl Harvest and Population Survey Data. 2004. D. Fronczak compiled. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.
- Weckstein, J. D., A. D. Afton, R. M. Zink, and R. T. Alisauskas. 2002. Hybridization and population subdivision within and between Ross's geese and lesser snow geese: a molecular perspective. *Condor* 104:432-436.
- Wooley, J. B., and R. B. Owen. 1978. Energy costs of activity and daily energy expenditure in the black duck. *Journal of Wildlife Management* 42:739-745.
- Ydenberg, R. C., and H. H. Th. Prins. 1980. Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* 18:443-453.

CHAPTER 6: TIME AND ENERGY BUDGETS OF LESSER SNOW GEESE IN RICE-PRAIRIES AND COASTAL MARSHES IN SOUTHWEST LOUISIANA

INTRODUCTION

Historically, snow geese wintered in coastal marshes in Louisiana but they began using rice-prairies only during the last 60 years (Bateman et al. 1988, Cooke et al. 1988). Snow geese in coastal marshes (hereafter coastal snow geese) forage primarily by digging marshgrass rhizomes from the ground (hereafter grubbing; Alisauskas et al. 1988, Batt et al. 1997). In contrast, snow geese in rice-prairies (hereafter rice snow geese) mostly feed on agricultural plants, which they graze on by removing leaves, flowers and stems of aboveground vegetation (hereafter grazing; Alisauskas et al. 1988, Batt et al. 1997).

Energy content (KJ/g) values of composite snow goose diets differ between rice-prairies and coastal marshes (hereafter rice and coastal diets; Alisauskas et al. 1988). Varying energy contents of food plants affect behavior of herbivorous waterfowl (Paulus 1984, Paulus 1988, Prop and Vulink 1992, Baldassarre and Bolen 1994). Waterfowl which forage on agricultural grains generally spend less time feeding than do conspecifics in natural wetlands because agricultural grain has a higher energy content (KJ/g of food) than do natural foods (Sedinger 1997, Baldassarre and Bolen 1994). In contrast, waterfowl species which forage on aquatic vegetation, such as gadwall (*Anas strepera*), American wigeon (*A. americana*), and Eurasian wigeon (*A. penelope*), spend relatively large amounts of time feeding because of relatively high fiber and water contents and the relatively low energy contents of these plants (Paulus 1984, Mayhew 1988, Baldassarre and Bolen 1994). Water content of food plants generally has an inverse relationship with digestibility and energy content (Alisauskas et al. 1988, Cabrera Estrada et al. 2004). Alisauskas et al. (1988) estimated that rice snow geese had to eat 1.8 times the fresh weight of plant food eaten by coastal snow geese, to acquire their daily energy

requirement (KJ/day), because rice diets had a higher water content than did coastal diets, i.e. coastal diets had higher energy density (KJ/g fresh weight plant material). Thus, I predicted that rice snow geese should compensate for this difference by spending more time feeding and/or have higher intake rates than do coastal snow geese.

Generally, adult geese spend more time alert than do juveniles and juveniles spend more time feeding than do adults (Frederick and Klaas 1982, Austin 1990, Bélanger and Bédard 1992). Adult geese are relatively more efficient foragers because the inexperienced juveniles have yet to fully develop their feeding skills (Frederick and Klaas 1982, Austin 1990, Bélanger and Bédard 1992). Grubbing requires 1.5 times more energy expenditure and more muscular effort than does grazing (Gauthier et al. 1984). Thus, I predicted that juveniles would spend more time feeding than adults, and this age difference would be more pronounced in coastal marshes than in rice-prairies because grubbing probably requires more developed feeding skills than does grazing. I tested my predictions by collecting time-budgets of rice and coastal snow geese in winters 2002-2003 and 2003-2004.

METHODS

STUDY AREA

My assistants (hereafter observers) and I observed snow geese in southwest Louisiana during 10 November – 20 February of 2002-2003 and 2003-2004. My study area (10,764 km²) was bordered by Sabine National Wildlife Refuge (NWR; 29°53'N, 93°23'W) on the west; Lake Charles and Highway 383 on the northwest; Highway 190 on the north; Highway 387 and Interstate 10 to the northeast; Highway 35 on the east, and the Gulf Coast on the south. Rice-prairies and coastal marshes previously were described in detail by Alisauskas (1988), Alisauskas et al. (1988), and Bateman et al. (1988).

The Intracoastal Canal generally separates coastal marsh and rice-prairie habitats in southwest Louisiana (Bateman et al. 1988). Coastal marshes are either fresh, intermediate, brackish, or saline wetlands, but fresh and intermediate marshes are not used frequently by snow geese; snow geese must fly about 32 km between brackish marshes and the rice-prairies (Bateman et al. 1988). Rice-prairies are former tall-grass prairies which have been extensively cultivated, mostly for rice, but also pasture for cattle (Alisauskas 1988, Alisauskas et al. 1988, Bateman et al. 1988).

Snow geese and other waterfowl use several state and federal wildlife refuges in the area, from east to west: Marsh Island State Wildlife Refuge (SWR; 29°36'N, 91°52'W), State Wildlife Refuge (29°40'N, 92°09'W), Rockefeller SWR (29°40'N, 92°55'W), Lacassine NWR (29°55'N, 92°50'W), Cameron Prairie NWR (29°57'N, 93° 04'W), and Sabine NWR (29°53'N, 93° 30'W) (Bateman et al. 1988). In addition, some private lands are managed to attract waterfowl, either as minirefuges or to enhance hunting opportunities (Harris 1990, Cox and Afton 1998).

Southwest Louisiana is the historical wintering area of snow geese within the Mississippi Flyway (Bateman et al. 1988, Cooke et al. 1988, Mowbray et al. 2000). Estimated snow goose numbers within my study area during midwinter were 239,121 in 2002-2003 and 335,253 in 2003-2004 (State Federal Cooperation Information Program 2004). In these midwinter surveys, two-thirds of all snow geese generally were found in the rice-prairies, and 60 to 77% of all snow geese in coastal marshes were found at State Wildlife Refuge and/or Marsh Island SWR (State Federal Cooperation Information Program 2004).

OBSERVATIONS

Sampling of Focal Geese

Observers and I collected behavioral data in 2002-2003 and 2003-2004; I was the only observer present in both winters. I trained other observers prior to data collection; we

simultaneously observed the same focal geese until our independent results were similar (less than 2% difference between percentages of time spent in all activities) for all activities of at least 20 focal birds (Gloutney et al. 2001).

Observers and I used spotting scopes (20x magnification) and recorded 5 to 10-minute focal sampling observations (Altmann 1974, Black and Owen 1989). All observations were made from pick-up trucks, either from inside the cab or from the bed. Observers and I recorded data with an Apple Newton Messagepad 2000 (Apple Computer Inc., Cupertino, California) equipped with Ethoscribe software (Tima Scientific, Sackville, New Brunswick, Canada). Observers and I selected focal geese within a field of vision by using sequences of 20 random numbers, which were obtained using the Research Randomizer Software (Urbaniak and Plous 2003). Whenever a flock under observation flushed, observers and I did not resume sampling for at least 10 minutes. Flocks within 150 meters of observers and I were not sampled because geese generally remained alert due to observer presence at closer range. Snow geese in southwest Louisiana generally become accustomed to presence of vehicles (Prevett and MacInnes 1980).

In the rice-prairies, observers and I sampled time-budgets for at least 3 days each week, from 1 November until 15 February in 2002-2003 and 2003-2004 (see also Chapter 5). However, sampling was less frequent in coastal marshes than in rice-prairies because of weather-related logistical constraints and the more sporadic snow goose presence relative to that in rice-prairies (see Appendix 2). Sampling in coastal marshes was restricted to (1) State Wildlife Refuge, accessible only by boat, which made sampling there heavily dependent on favorable weather conditions for boat use in the Vermillion Bay; and (2) Rockefeller SWR, which generally holds only a few thousand snow geese, usually in only inaccessible parts of the 73,000 ha large refuge. Because of these constraints, I estimated time-budgets of 244 coastal snow geese, and 703 rice snow geese.

Ages of Focal Geese

Observers and I visually aged snow geese by plumage color: (1) adult (after-hatch-year) white-phase snow geese are white with black wing-tips, whereas juveniles (hatch-year) are pale gray; and (2) adult blue-phase snow geese have white heads and blue-gray backs and bodies, whereas juveniles have dark heads. Although juveniles have grayish backs and bodies like adults, juvenile plumage is browner above and paler below than that of adults (Cramp and Simmons 1977, Bellrose 1980, Madge and Burn 1988).

Classifications of Activities

I classified behavioral activities as feeding, resting, locomotion (walking or swimming), alert, social interactions, and other activities (Table 6.1). I chose this classification for analysis of time spent feeding, alert, and in locomotion, and for energy budget calculations (Ganter and Cooke 1996). I further divided feeding into grazing, grubbing, and searching for food because these activities have different energetic costs which I accounted for in the energy budget calculations (cf. Ganter and Cooke 1996).

Indexing Intake Rates for Snow Geese

Grazing geese can compensate for reduced foraging time by increasing rate of food intake (i.e. peck rates; Owen 1972); thus, it was imperative to compare peck rates between groups when studying time spent feeding (see Gloutney et al. 2001). Observers and I were not able to directly record peck rates (Owen 1972) because it was difficult to quantify grubbing in terms of number of pecks because one “peck” can last for 1 minute or longer (Jón Einar Jónsson personal observation). Thus, I used a comparative index for intake rates (hereafter beginning rate); observers and I recorded the number of times each focal bird initiated a foraging bout (bouts/minute), i.e. placed their bill to the ground.

Table 6.1. Classification and definitions of goose behavioral activities (cf. Gauthier et al. 1984, Davis et al. 1989, Black and Owen 1989, Ganter and Cooke 1996), for lesser snow geese observed in southwest Louisiana in winters 2002-2003 and 2003-2004.

Feeding was a combination of 3 types of foraging activities:

Grubbing: goose dug for belowground plant parts, removed mud with bill, softened mud with feet, and ingested bulbs and rhizomes. Food was ingested; thus, time spent grubbing was included in calculations of beginning rates.

Grazing: goose picked up and ingested aboveground plant material, treaded to break water surface with bill, or washed a plant part. Food was ingested; thus, time spent grazing was included in calculations of beginning rates.

Searching: displacements with head lowered and bill pointed toward the ground, looking for digging sites or food. No food was ingested; thus, time spent searching was not included in calculations of beginning rates (see text).

Alert: goose was standing upright with head raised (see Inglis 1976).

Locomotion was a combination of 2 activities:

Walking: goose switched locations on foot with head raised.

Swimming: goose moved on water surface.

Inactive (Reference activities in generalized linear models):

Social interactions: goose directed social displays at other geese.

Resting: goose sat or stood, with bill tucked under wing, or completely still with head upright, not moving, either awake or sleeping.

Other: activities that were not described above, including drinking, preening, and comfort activities.

STATISTICAL ANALYSES

I estimated time-budgets of rice and coastal snow geese by dividing the time spent on each activity (see Table 6.1) by the total time (no. of seconds) each focal goose was observed to obtain percentage (%) of time each focal goose spent on each activity (Paulus 1984). For beginning rates (bouts/minute), focal geese that were not observed feeding were assigned values of 0. For all my analyses, explanatory variables were categorical: habitat (rice-prairies or coastal marshes), age (adult or juvenile), winter (2002-2003 or 2003-2004), and all their interactions. I included winter in my analysis because effects of temperature or family size were not considered in this analysis and, thus, had no *a priori* reason to stratify by winter as in Chapter 5.

Calculations of Energy Intake and Energy Expenditure

I used energetic estimates for various behaviors following Owen et al. (1992) and Ganter and Cooke (1996). Specifically, I used literature-based estimates of basal metabolic rate (BMR), energetic costs of each activity expressed as multiples of BMR (Table 6.2), the amount of metabolizable energy obtainable from composite rice and coastal diets, and digestion capacity (Burton et al. 1979, Gauthier et al. 1984, Alisauskas et al. 1988, Owen et al. 1992, Ganter and Cooke 1996). I used average body masses of 129 adult female (2008 g) and 105 adult male snow geese (2212 g) caught with rocket-nets and weighed in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004 (Chapter 7).

My calculations of energy intake involved (cf. Ganter and Cooke 1996): (1) the estimated proportion of time spent grazing and grubbing (see Table 6.1); (2) metabolizable energy obtainable from composite diets in southwest Louisiana, estimated as 8.5 KJ g/dry weight for rice diets and 7.9 KJ g/dry weight for coastal diets (Alisauskas et al. 1988); and (3) digestive capacity, the amount of food (g) that geese can ingest in 1 hour of constant food intake,

Table 6.2. Estimates of energetic costs (KJ/day) of various activities, expressed as multiples of the basal metabolic rate (Wooley and Owen 1978, Gauthier et al. 1984, Owen et al. 1992, Ganter and Cooke 1996), used for lesser snow geese observed in southwest Louisiana in winters 2002-2003 and 2003-2004.

Activity	Cost	Activity	Cost
Resting	1.3	Walking	2.0
Grazing	2.0	Searching	2.0
Alert	2.1	Social interactions	2.3
Other	2.1 ^a	Swimming	2.8
Grubbing	3.0		

^a average cost for preening and drinking

estimated as 20 g dry weight/hour for snow geese, assuming food throughput time of 90 minutes (Burton et al. 1979).

I estimated only diurnal time-budgets and assumed that snow geese fed for 12 hours a day; wintering snow geese generally forage very little during night (McIlhenny 1932, Alisauskas et al. 1988, Davis et al. 1989). Formulas for energy intake were:

$$\text{Energy intake}_{\text{rice snow geese}} (\text{KJ/day}) = \{(20 \text{ g dry weight food / hour}) * (8.45 \text{ KJ / g dry weight}) * (\text{beginning rate}) * (\text{proportion of time spent grazing} * 12 \text{ hours})\} + \{(20 \text{ g / dry weight food / hour}) * (8.45 \text{ KJ / g dry weight}) * (\text{beginning rate}) * (\text{proportion of time spent grubbing} * 12 \text{ hours})\}$$
$$\text{Energy intake}_{\text{coastal snow geese}} (\text{KJ/day}) = \{(20 \text{ g / dry weight food / hour}) * (7.9 \text{ KJ / g dry weight}) * (\text{beginning rate}) * (\text{proportion of time spent grazing} * 12 \text{ hours})\} + \{(20 \text{ g / dry weight food / hour}) * (7.9 \text{ KJ / g dry weight}) * (\text{beginning rate}) * (\text{proportion of time spent grubbing} * 12 \text{ hours})\}$$

Calculations of energy expenditure (KJ/day) involved: (1) time-budgets; (2) basal metabolic rates of snow geese, using the formula for non-passerine birds from Lasiewski and Dawson (1967; $\text{KJ/day} = 4.184 \times 78.3(\text{kg body weight})^{0.723}$), and body weights from southwest Louisiana; and (3) factors of energy expenditure, expressed as multiples of BMR (see Table 6.2). I assumed equal costs of thermoregulation between rice and coastal snow geese.

The calculation of energy expenditure (see also Owen et al. 1992) was:

Energy expenditure (KJ/day) = BMR (alert*2.1 + social*2.3 + grazing*2.0 + grubbing*3.0 + searching*2.0 + walking*2.0 + swimming*2.8 + resting*1.3 * preening*2.3)

(BMR_{snow geese} = 646.7 KJ/day)

Finally, I subtracted energy expenditure from energy intake to obtain net energy intake (i.e. energy budgets, KJ/day) of each focal goose (Owen et al. 1992, Ganter and Cooke 1996):

Net energy intake (KJ/day) = Energy intake (KJ/day) - Energy expenditure (KJ/day)

Lastly, I performed these calculations a second time; wherein I adjusted net energy intake for the different water content of rice and coastal diets, (cf. Alisauskas et al. 1988), by dividing the digestive capacity of rice snow geese by 1.8 ((20 g / dry weight of food) /1.8), and then subsequently repeated my analysis of energy budgets (see below). Thus, in the unadjusted analysis, food intake was based on dry weight of plant material, whereas in the adjusted analysis, food intake was based on fresh weight of plant material (cf. Alisauskas et al. 1988). The formulas for adjusted energy intake were:

Adjusted energy intake_{rice snow geese} (KJ/day) = {(20 / 1.8) g dry weight food / hour)*(8.45 KJ /g dry weight)*(beginning rate)*(proportion of time spent grazing*12 hours)} + {(20 g / dry weight food / hour)*(8.45 KJ /g dry weight)*(beginning rate)*(proportion of time spent grubbing*12 hours)}

Adjusted energy intake_{coastal snow geese} (KJ/day) = {(20 / 1.0) g dry weight food / hour)*(7.9 KJ /g dry weight)*(beginning rate)*(proportion of time spent grazing*12 hours)} + {(20 g / dry

weight food / hour)*(7.9 KJ /g dry weight)*(beginning rate)*(proportion of time spent grubbing*12 hours)}

General Model Building and Model Selection

I used generalized linear models (PROC GENMOD; SAS Institute 1999) to compare (1) time-budgets; (2) beginning rates; and (3) net energy intake between rice and coastal snow geese. For all analyses, I started with the saturated model and used backwards stepwise model selection to determine final models (Agresti 1996). Explanatory variables in all models were habitat, age, and winter, and all interactions were included in the saturated model. I used Least-square means (LSMEANS; $\bar{\chi}$; SAS Institute 1999) on interactions to test for main effects when my analyses reported significant interactions involving habitat, age, or winter.

I constructed generalized linear models based on normal and Poisson distributions; in this case, the Poisson log-linear model is equivalent to running a logistic regression based on the multinomial distribution (Agresti 1996). I evaluated goodness of fit for these models by comparing ratios between degrees of freedom (df) and deviance of the models; a ratio of deviance/df close to 1.0 indicates a good model fit (Agresti 1996). Normal models generally fit reasonably well (deviance/df ≤ 1.10), whereas multinomial models fit poorly in all analyses and exhibited signs of overdispersion (deviance/df ≥ 100). Thus, I used models based on the normal distribution for all analyses. Data points with the value 0 can cause bias in estimates of odds ratios and unreliable estimates of goodness-of-fit statistics in generalized linear models (Hosmer and Lemeshow 1989, Agresti 1996). My data on time-budgets and beginning rates contained numerous zeros; thus, I added 0.05 to all data points prior to analysis (Hosmer and Lemeshow 1989).

Models for Time-Budgets

I used generalized linear models with a multcategory response variable (see Agresti 1996) to analyze time-budget data, in which significance was tested by examining second-order interactions between activity (response variable) and explanatory variables. One activity had to be the reference activity (Agresti 1996); thus, I summed time spent on resting, social interactions, and other activities (Table 6.1) into one reference activity (hereafter inactive) because my interest primarily was in time spent feeding, alert, and in locomotion. Response variables considered were percentages of time spent alert, feeding, in locomotion, and performing activities classified as inactive (Table 6.1). Explanatory variables were habitat, winter, and age, and all interactions were included in the saturated model.

Models for Beginning Rates and Energy Budgets

Net energy intake was the response variable in an analysis of variance (PROC GENMOD; SAS Institute 1999). Here, I performed my analysis twice: (1) with adjustment (20 g dry weight of food / 1.8) for energy intake in rice-prairies; and (2) without adjustment (20 g dry weight of food / 1.0) for differing water contents of composite diets. Explanatory variables were habitat, age, and winter, and all interactions were included in the saturated model.

RESULTS

TIME-BUDGETS

The final model included the age x habitat interaction ($\chi^2 = 18.59$, $df = 3$, $P = 0.0003$). LSMEANS on habitat within age (Table 6.3) indicated that (1) coastal adults spent more time feeding ($\chi^2 = 6.15$, $df = 1$, $P = 0.0131$) and less time inactive ($\chi^2 = 4.49$, $df = 1$, $P = 0.0340$) than did rice adults; and (2) coastal juveniles spent more time inactive ($\chi^2 = 6.33$, $df = 1$, $P = 0.0119$)

Table 6.3. Least-square mean (LSMEAN) percentages of time spent alert, feeding, in locomotion, and other activities, by lesser snow geese (hereafter snow geese) in southwest Louisiana in winters 2002-2003, and 2003-2004. Inactive activities were combined amounts of time spent in resting, social displays, preening, and activities classified as other in Table 6.1. ASE indicates asymptotic standard error.

Habitat	Age	Alert	Feeding	Locomotion	Inactive	ASE
Rice snow geese	Adult	26.2	40.2	4.2	29.4	2.0
Coastal snow geese	Adult	26.5	52.0	2.2	19.3	4.3
Rice snow geese	Juvenile	14.4	53.9	5.1	26.6	2.7
Coastal snow geese	Juvenile	13.0	41.2	1.2	44.6	6.7

than did rice juveniles. LSMEANS on age within habitat (Table 6.3) indicated that (1) rice adults spent more time alert than did rice juveniles ($\chi^2 = 12.33$, $df = 1$, $P = 0.0004$); (2) rice juveniles spent more time feeding than did rice adults ($\chi^2 = 16.32$, $df = 1$, $P = 0.0001$); and (3) coastal juveniles spent more time inactive than did coastal adults ($\chi^2 = 10.12$, $df = 1$, $P = 0.0015$).

BEGINNING RATES

The final model for beginning rates (bouts/minute) included habitat ($\chi^2 = 14.14$, $df = 1$, $P = 0.0002$) and winter ($\chi^2 = 4.69$, $df = 1$, $P = 0.0303$). Beginning rates for rice and coastal snow geese averaged $\bar{\chi} = 0.8$ (SE = 0.04) and $\bar{\chi} = 0.6$ (SE = 0.06), respectively (LSMEANS).

ENERGY BUDGETS

The final model for unadjusted energy budgets included only habitat ($\chi^2 = 31.02$, $df = 1$, $P < 0.0001$). Rice snow geese gained more net energy (KJ/day) than did coastal snow geese, independent of winter, 95.5 KJ/day (SE = 63.1 KJ/day) and -503.4 KJ (SE = 100.0 KJ/day), respectively. When adjusted for water content of rice diets by a factor 1.8, energy intake did not differ between rice and coastal snow geese ($\chi^2 = 1.53$, $df = 1$, $P = 0.2156$). Rice and coastal snow geese had adjusted net energy intakes of -452.3 KJ/day (SE = 39.1 KJ/day) and -534.0 KJ (SE = 61.8 KJ/day), respectively.

DISCUSSION

COMPARISON BETWEEN RICE-PRAIRIES AND COASTAL MARSHES

Time Spent Feeding and Beginning Rates

My results indicate that water contents of composite diets (Alisauskas et al. 1988) do not predict time spent feeding by adult snow geese in coastal Louisiana. Contrary to my prediction, I found that among adults, coastal snow geese spent more time feeding than did rice snow geese

(Table 6.3). As predicted, I found that rice snow geese had relatively higher beginning rates, independent of age, which may compensate somewhat for their lower time spent feeding.

Geese are highly adapted for herbivory and their digestive systems can adjust morphologically to different diets encountered over the annual cycle (Prop and Vulink 1992). Thus, the relationship between feeding effort and water content of composite diets, as proposed by Alisauskas et al. (1988), may be offset by other, relatively more important differences between composite diets in rice-prairies and coastal marshes. Grubbing in coastal marshes requires more muscular activity and skill than does grazing in rice-prairies; digging and dismantling of tubers and rhizomes is more laborious than is grazing on aboveground vegetation (Gauthier et al. 1984). The additional work needed for grubbing, relative to grazing, probably leads to higher handling times per unit of food (see Keating et al. 1992) for coastal snow geese. The daily food requirement in dry weight is similar for rice and coastal snow geese (Alisauskas 1988). I hypothesize that obtaining sufficient fresh weight of food may be relatively easier for rice snow geese because rice plants probably require relatively lower handling times than do coastal marsh plants. My results offer some support for the hypothesis that rice snow geese have lower handling times than do coastal snow geese, as indicated by relatively lower beginning rates in coastal marshes.

Coastal diets are relatively higher in fiber content than are rice diets (20% and 15%, respectively) and lower in protein content than are rice diets (8% and 27%, respectively), digestibility of foods has an inverse relationship with fiber content and a positive relationship with protein content (Prop and Vulink 1992). The estimates of Alisauskas et al. (1988) accounted for both these properties when estimating fresh weight needs of food for snow geese. However, I suggest that fiber and protein content may be relatively more important determinants of digestibility for snow geese than is water content.

Energy Budgets

My unadjusted estimates of energy budgets were based on energy contents per unit of dry weight. Coastal snow geese had lower unadjusted net energy intake rates than did rice snow geese. This difference mostly was due to lower beginning rates in coastal snow geese. Although dry weight needs are similar in rice-prairies and coastal marshes, Alisauskas et al. (1988) estimated that, to acquire existence energy, rice snow geese had to eat 1.8 times the fresh weight of plant food eaten by coastal snow geese. However, effects of water content of food plants on digestive capacity are not necessarily linear (Cabrera Estrada et al. 2004); thus, the difference in digestibility between composite diets in rice-prairies and coastal marshes may be less than 1.8.

My estimates of unadjusted net energy intake were based on using energy intake based on dry weight of food (cf. Burton et al. 1979). Alisauskas et al. (1988) preferred the use of fresh weight because geese consume fresh plants, not dried plants. Assuming that rice diets have a 1.8 times lower digestibility than do coastal diets (cf. Alisauskas et al. 1988), adjusted net energy intake did not differ between rice and coastal snow geese.

My results raise the question of whether snow geese compensate for higher water content in rice diets (Alisauskas et al. 1988) by prolonging gut retention time. Prolonged gut retention times are achieved by interrupting feeding periods with resting periods (Prop and Vulink 1992). Prolonged gut retention times may enhance water absorption in the colon (Prop and Vulink 1992) and also may allow other parts of the digestive system, such as proventriculus and gizzard, to compensate for relatively high water content of food plants.

Effects of protein content and fiber content on food digestibility are well documented in geese (Prop and Vulink 1992, Sedinger 1997). The suspected negative effect of water content on digestibility was not documented in either of these goose studies; although it has been documented for cows (*Bos taurus*) (Cabrera Estrada et al. 2004). The contention that water

content affects digestive capacity in geese should be re-visited using experiments with captive geese, fed with experimental diets of differing water contents (cf. Cabrera Estrada et al. 2004).

EFFECTS OF AGE ON FORAGING IN THE 2 HABITATS

My findings on effects of age on time spent feeding were consistent with my predictions for rice snow geese, where juveniles spent more time feeding than did adults (Table 6.3). In most geese, juveniles generally spend more time feeding than do adults, presumably because they are inexperienced foragers; thus, they can not attain their daily energy need as quickly as adults (Frederick and Klaas 1982, Austin 1990, Bélanger and Bédard 1992). My findings contradicted my predictions that coastal juveniles would spend more time feeding than coastal adults.

Grubbing requires more skill and muscular activity than does grazing (cf. Gauthier et al. 1984). Thus, grubbing is a more costly foraging method than is grazing, and while this difference will affect both adult and juvenile snow geese, juveniles may incur a relatively greater cost from grubbing because of their undeveloped foraging skills. Although snow geese do not gain weight while in Louisiana (Ankney 1982), juveniles probably need more food per day than do adults because juveniles are not fully grown until they are 1 year old (Cooch et al. 1991).

Feeding in coastal marshes may be particularly challenging for juvenile snow geese. Social interactions among snow geese are more intense in coastal marshes than in rice-prairies, i.e. coastal snow geese frequently fight with physical contact whereas rice snow geese are more likely to use ritualized displays (Gregoire and Ankney 1990). This increased behavioral interference can cause inexperienced social foragers to visit fewer patches, spend more time non-foraging, and spend less time scanning, or peck at a lower rate (Gauvin and Giraldeau 2004). In wintering snow geese, the ability to tolerate behavioral interference may determine how long individuals can stay in a foraging patch. Generally, individuals which are most vulnerable to

behavioral interference spend the least time feeding in socially foraging birds (see review by Gauvin and Giraldeau 2004).

LITERATURE CITED

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons Inc, New York, New York, USA.
- Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. thesis, University of Western Ontario, London, Ontario, Canada.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-267.
- Ankney, C. D. 1982. Annual cycle of body weight in lesser snow geese. *Wildlife Society Bulletin* 10:60-64.
- Austin, J. 1990. Comparison of activities within families and pairs of wintering Canada geese. *Wilson Bulletin* 102:536-542.
- Baldassarre, G. A., and E. G. Bolen. 1994. *Waterfowl ecology and management*. John Wiley and Sons, Inc., New York, New York, USA.
- Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent snow geese on their Gulf Coast winter range. Pages 495-515 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Batt, B. D. J., editor. 1997. *Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group*. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Bellrose, F. C. 1980. *Ducks, geese, and swans of North America*. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bélanger, L., and J. Bédard. 1992. Flock composition and foraging behavior of greater snow geese (*Chen caerulescens atlantica*). *Canadian Journal of Zoology* 70:2410-2415.
- Black, J. M., and M. Owen. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37:199-209.
- Boyd, H. 1953. On encounters between wild white-fronted geese in winter flocks. *Behaviour* 5:85-129.
- Burton, B. A., R. J. Hudson, and D. D. Bragg. 1979. Efficiency of utilization of bulrush rhizomes by lesser snow geese. *Journal of Wildlife Management* 43:728-735.

- Cabrera Estrada, J. I., R. Delagarde, P. Faverdin, and J. L. Peyraud. 2004. Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. *Animal Feed Science and Technology* 114:59-74.
- Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* 72:503-512.
- Cooke, F. D., D. T. Parkin, and R. F. Rockwell. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105:467-479.
- Cox, R. R., Jr., and A. D. Afton. 1998. Use of mini-refuges by female northern pintails wintering in southwestern Louisiana. *Wildlife Society Bulletin* 26:130-137.
- Cramp, S., and K. E. L. Simmons. 1978. Handbook of the birds of Europe, the Middle East, and North Africa. Birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Davis, S. E., E. E. Klaas, and K. J. Koehler. 1989. Diurnal time-activity budgets and habitat use of lesser snow geese *Anser caerulescens* in the Middle Missouri River Valley during winter and spring. *Wildfowl* 40:45-54.
- Ely, C. R. 1992. Time allocation by greater white-fronted geese: influence of diet, energy reserves and predation. *Condor* 94:857-870.
- Frederick, R. B., and E. E. Klaas. 1982. Resource use and behavior of migrating snow geese. *Journal of Wildlife Management* 46:601-614.
- Ganter, B., and F. Cooke. 1996. Pre-incubation feeding activities and energy budgets of snow geese: can food on the breeding grounds influence fecundity? *Oecologia* 106:153-165.
- Gauthier, G., J. Bédard, and Y. Bédard. 1984. Comparison of daily energy expenditure of greater snow geese between two habitats. *Canadian Journal of Zoology* 62:1304-1307.
- Gauvin, S., and L.-A. Giraldeau. 2004. Nutmeg mannikins (*Lonchura punctulata*) reduce their feeding rates in response to simulated competition. *Oecologia* 139:150-156.
- Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. *Oecologia* 127:78-86.
- Gregoire, P. E., and C. D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* 107:550-560.
- Harris, G. A. 1990. Grit site use by wildlife in southwestern Louisiana and southeastern Texas. MS thesis, Louisiana State University, Baton Rouge, Louisiana, USA.
- Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York, New York, USA.

- Inglis, I. R. 1976. Agonistic behaviour of breeding pink-footed geese with reference to Ryder's hypothesis. *Wildfowl* 27:95-99.
- Keating, J. F., R. J. Robel, A. W. Adams, K. C. Behnke, and K. E. Kemp. 1992. Role of handling time in selection of extruded food morsels by two granivorous bird species. *Auk* 109:863-868.
- Lasiewski, R. C., and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- Madge, S., and H. Burn. 1988. *Wildfowl: an identification guide to the ducks, geese and swans of the World*. A & C Black Ltd., London, United Kingdom.
- Mayhew, P. W. 1988. The daily energy intake rate of European wigeon in winter. *Ornis Scandinavica* 19:217-223.
- McIllhenny, E. A. 1932. The blue goose in its winter home. *Auk* 49:279-306.
- Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Lesser snow goose. In A. Poole, and F. Gill, editors. *Birds of North America*, No. 514. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Owen, M. 1972. Some factors affecting food intake and selection in white-fronted geese. *Journal of Animal Ecology* 41:79-92.
- Owen, M., R. L. Wells, and J. M. Black. 1992. Energy budgets of wintering barnacle geese: the effects of declining food resources. *Ornis Scandinavica* 23:451-458.
- Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. *Journal of Wildlife Management* 48:371-380.
- Paulus, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135-152 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Prevett, J. P, and C. D. MacInnes. 1980. Family and other social groups in snow geese. *Wildlife Monographs* 71:6-46.
- Prop, J., and T. Vulink. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* 6:180-189.
- SAS Institute. 1999. *SAS/SYSTAT User's Guide*. Version 6. Fourth edition. SAS Institute. Cary, North Carolina, USA.
- Sedinger, J. S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor* 99:314-326.
- Sedinger, J. S., R. G. White, and J. Hupp. 1995. Metabolizability and partitioning of energy and protein in green plants by yearling lesser snow geese. *Condor* 97:116-122.

Urbaniak, G. C. and S. Plous. 2003. Research Randomizer. [Online] Wesleyan University, Connecticut, USA. URL: <http://www.randomizer.org/>.

Waterfowl Harvest and Population Survey Data. 2004. D. Fronczak compiled. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.

Wooley, J. B., and R. B. Owen. 1978. Energy costs of activity and daily energy expenditure in the black duck. *Journal of Wildlife Management* 42:739-745.

CHAPTER 7: SNOW GEESE FORAGE IN TWO DISTINCT HABITATS IN SOUTHWEST LOUISIANA: IS THERE EVIDENCE FOR SEPARATE POPULATIONS?

INTRODUCTION

Arctic nesting geese (*Anser*, *Branta*, and *Chen* spp.) are among the most thriving herbivores in the Northern Hemisphere because they effectively utilize both natural and anthropogenic food sources (Owen 1980, Madsen et al. 1999, Frederiksen 2004). Body size is highly variable among geese, both at intra- and interspecific levels (Owen 1980, Cooch et al. 1991, Alisauskas 1998, Dickson 2000). The taxonomic significance of closely related, different-sized populations has received considerable discussion (see Avise et al. 1992, Banks et al. 2004). Bill size and shape vary within some goose species and are related to feeding adaptations (Alerstam 1990, Owen and Black 1990, Cooch et al. 1991, Madsen et al. 1999, Alisauskas 1998).

Bill size of lesser snow geese (*Chen caerulescens caerulescens*; hereafter snow geese) varies between feeding habitats in southwest Louisiana (Alisauskas 1998). Historically, snow geese wintered in coastal marshes in Louisiana but the species began inhabiting rice-prairies in the 1940s (Bellrose 1980, Bateman et al. 1988, Cooke et al. 1988). Rice-prairies are located directly north of coastal marshes and comprise former tall-grass prairies, which now is extensively modified by agricultural activity, with rice currently the dominant crop (see Alisauskas 1988, Bateman et al. 1988). Snow geese in rice-prairies feed mostly on agricultural plants, which they graze by removing leaves, flowers and stems of aboveground vegetation (hereafter grazing; Alisauskas et al. 1988, Batt et al. 1997). By contrast, snow geese in coastal marshes forage primarily by digging marshgrass rhizomes from the ground (hereafter grubbing; Alisauskas et al. 1988, Batt et al. 1997). Alisauskas (1998) measured body morphometrics of snow geese wintering in southwest Louisiana and reported that those from coastal marshes had larger bodies, thicker bills, longer skulls, and longer culmen lengths than did those from rice-

prairies. Accordingly, Alisauskas (1998) hypothesized that small bill size is selected against in coastal marshes because larger bills are better suited for grubbing. In contrast, snow geese should be capable of foraging successfully in rice-prairies regardless of bill size (i.e. Phenotypic Selection Hypothesis; Alisauskas 1998). The Phenotypic Selection Hypothesis predicts that snow geese in coastal marshes are isolated from snow geese in rice-prairies (Alisauskas 1998).

Alisauskas (1998) also proposed an alternative hypothesis, which states that snow geese sample both habitats and select the habitat that best suits their bill size (i.e. Habitat Selection Hypothesis). Among geese, individuals select between adjacent feeding habitats in relation to tidal cycles, growth cycles of food plants, disturbance due to varying hunting pressures, age, foraging skills, past experience with areas, and the number of competitors present (Ydenberg and Prins 1980, Sutherland and Allport 1994, Vickery et al. 1995, Sutherland 1996). In Louisiana, availability of foraging patches in coastal marshes also is influenced by the frequency and intensity of marsh burning, which facilitates access to rhizomes for snow geese as well as stimulating growth of young plants (Bellrose 1980, Bateman et al. 1988, Nyman and Chabreck 1995). I conducted a neck-banding study to test the Phenotypic Selection and Habitat Selection Hypotheses, as proposed by Alisauskas (1998). Neck-bands commonly are used in goose research in both North America and Europe to study distributions and movements of geese (Samuel et al. 1990, Hestbeck et al. 1991, Madsen et al. 1999, Menu et al. 2000). I estimated the probability of neck-banded snow geese being sighted in flocks of snow geese banded in the other habitat (hereafter flock mixing).

Since studied by Alisauskas (1988, 1998), snow goose numbers in winter counts have doubled from 1983-1984 to 2001-2003 (Waterfowl Survey Data 2004); in contrast, snow goose numbers in coastal marshes declined during the last decade (Gulf Coast Joint Venture 2001). Snow geese now arrive later (mid-November) in fall and begin to leave earlier in spring (late

January - early February) than that reported by Bateman et al. (1988; U. S. Fish and Wildlife Service 2005). Furthermore, body size has declined in the continental snow goose population over the past few decades (Alisauskas 2002). Thus, movement patterns of snow geese in southwest Louisiana, as well as the overall distribution of morphometrics, possibly has changed during the past 20 years, which in turn could have lead to different relationships between feeding habitat and body morphometrics. Thus, I measured snow geese caught for the banding study to: (1) document whether morphometrics of snow geese presently differ between rice-prairies and coastal marshes (Alisauskas 1998); and (2) determine whether body morphometrics, as a covariate, directly influenced probabilities of moving between rice-prairies and coastal marshes.

METHODS

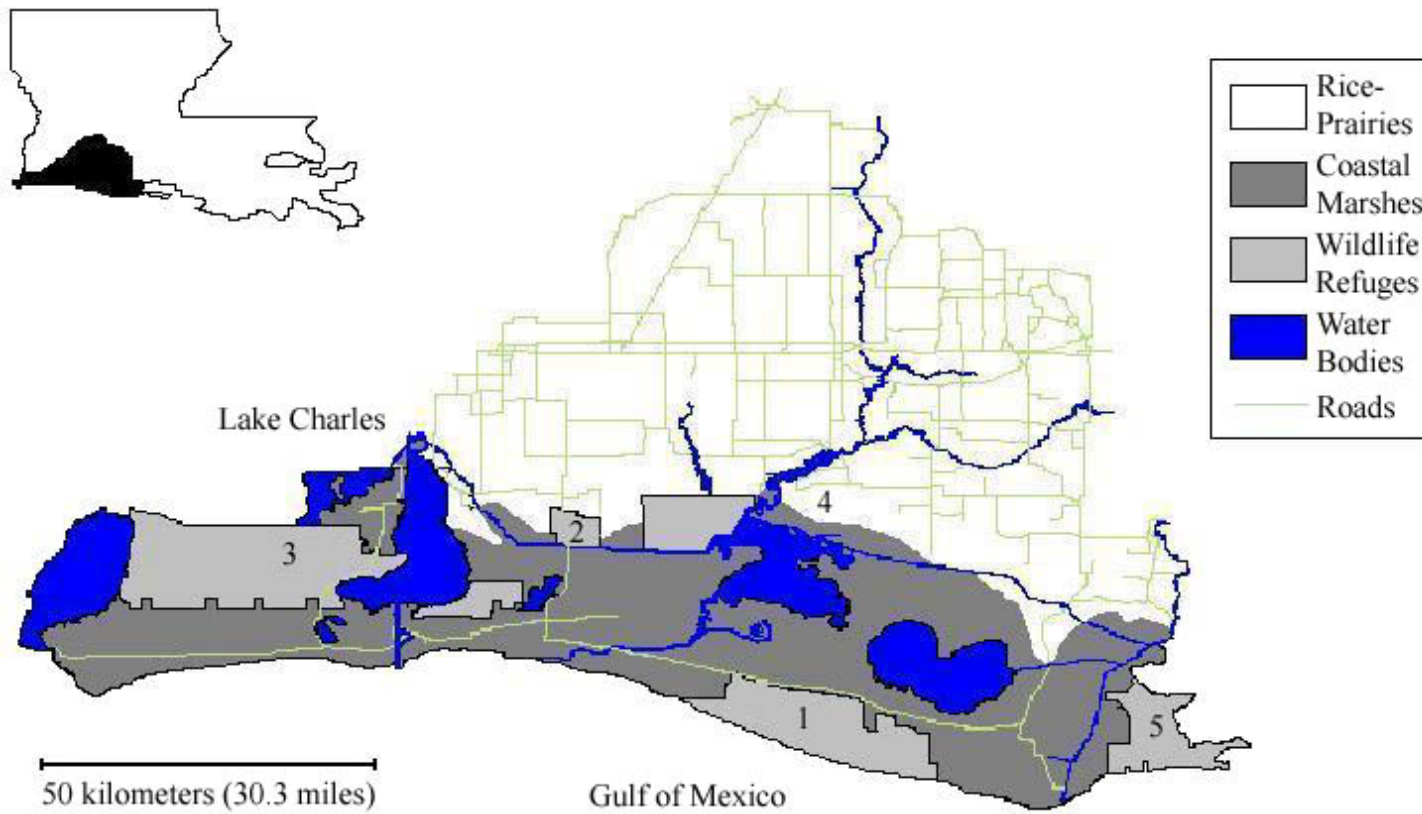
STUDY AREA

My study area (10,764 km²) was bordered by Sabine National Wildlife Refuge (NWR; 29°53'N, 93°23'W) on the west; Lake Charles and Highway 383 on the northwest; Highway 190 on the north; Highway 387 and Interstate 10 on the northeast; Highway 35 on the east, and the Gulf Coast on the south (Figure 7.1). Rice-prairies and coastal marshes were described previously in detail by Alisauskas (1988), Alisauskas et al. (1988), and Bateman et al. (1988).

The Intracoastal Canal approximately separates coastal marshes and rice-prairies in southwest Louisiana (Figure 7.1). Coastal marshes are either fresh, intermediate, brackish, or saline wetlands, but fresh and intermediate marshes are not used frequently by snow geese; snow geese must fly about 32 km between brackish marshes and the rice-prairies (Bateman et al. 1988).

Snow geese and other waterfowl use several state and federal wildlife refuges in the area, from east to west: Marsh Island State Wildlife Refuge (SWR; 29°36'N, 91°52'W), State Wildlife Refuge (29°40'N, 92°09'W), Rockefeller SWR (29°40'N, 92°55'W), Lacassine NWR (29°55'N,

Figure 7.1. Map of the study area in southwest Louisiana during winters 2001-2002, 2002-2003, and 2003-2004. 1: Rockefeller State Wildlife Refuge. 2: Cameron Prairie National Wildlife Refuge (NWR). 3: Sabine NWR. 4: Oak Island (private land). 5: State Wildlife Refuge.



92°50'W), Cameron Prairie NWR (29°57'N, 93° 04'W), and Sabine NWR (29°53'N, 93° 30'W) (Bateman et al. 1988). In addition, a few private lands are managed to attract waterfowl, either as mini-refuges or to enhance hunting opportunities (Harris 1990, Cox and Afton 1998). One such property was used as a banding site in this study; Oak Island (30°00'N, 92° 04'W), 10 miles south of the town of Lake Arthur.

Estimated numbers of snow geese within my study area during mid-winter were 257,290, 239,335, and 335,253 in winters 2001-2002, 2002-2003, and 2003-2004, respectively (Waterfowl Survey Data 2004). In these midwinter surveys, two-thirds of all snow geese generally were found in the rice-prairies, and 60 to 77% of all snow geese in coastal marshes were found at State Wildlife Refuge and/or Marsh Island SWR (Waterfowl Survey Data 2004).

BANDING AND RESIGHTING EFFORT

Many birds ingest hard items such as sand, pebbles, and shells, and maintain a supply in their gizzards (Welty 1982). These articles collectively are termed grit and aid the gizzard in grinding tough food items such as seeds and plant materials (Welty 1982, Harris 1990). The soil in Louisiana contains little grit; thus, artificial grit sites are maintained to benefit waterfowl at several wildlife refuges in southwest Louisiana and southeast Texas (Harris 1990). I caught snow geese using rocket-nets (Dill and Thornsberry 1950) at 4 grit sites: Cameron Prairie NWR and Oak Island in rice-prairies, and Sabine NWR and Rockefeller SWR in coastal marshes (Figure 7.1). The grit site at Oak Island was added to the banding effort in 2002-2003 and 2003-2004. I was unable to capture and neck-band snow geese at Sabine NWR in 2003-2004 due to low numbers of geese using the refuge that year (U.S. Fish and Wildlife Service 2005). I caught and determined sexes of 993 snow geese over the entire study period (Appendix 3).

Weatherhead and Ankney (1984) voiced concerns that baited sites selected for birds in poor body condition; however, an experimental study on greater snow geese (*C. caerulescens*

atlanticus) found no evidence for condition-bias associated with bait use in snow geese captured for banding (Morez et al. 2000). Furthermore, I never baited my capture sites with food. I sexed captured snow geese by cloacal examination (Hochbaum 1942) and aged them by plumage color (Cramp and Simmons 1978, Bellrose 1980, Madge and Burn 1988): (1) adult (after-hatch-year and older) white-phase snow geese are white with black wing-tips, whereas juveniles (hatch-year) are pale gray; and (2) adult blue-phase snow geese have white heads and blue-gray backs and bodies, whereas juveniles have dark heads; although juveniles have grayish backs and bodies like adults, juvenile plumage is browner above and paler below than that of adults. I released catches together, or larger catches in groups so that family units could re-unite more easily; snow goose pairs and families frequently reunite after temporary separations (Prevett and MacInnes 1980, Hill and Frederick 1997).

I recorded morphometrics of 406 captured adult snow geese. Specifically, I measured (± 0.1 mm) total tarsus, head length, bill nares, bill thickness, culmen length, gape length, skull width, skull height, and wing length, using calipers (Alisauskas 1988, Dzubin and Cooch 1992, Alisauskas 1998). Furthermore, I also weighed snow geese to meet other objectives of my study (Chapter 5, Chapter 6). I held captured snow geese for a maximum of 6 hours to avoid capture myopathy (Chalmers and Barrett 1982, Hullan 1985). Most rocket-net catches were too large for measuring all geese caught, but with the exception of 2 occasions at CPNWR, I measured all juveniles (Chapter 8) and at least 30 randomly selected adults from each catch. My primary goal was to determine whether snow geese banded in either habitat moved into the other habitat; thus, obtaining a sufficiently large sample to observe movements had a higher priority than obtaining morphometrics.

Observers and I scanned goose flocks for neck-bands with spotting scopes (20x-60x) and recorded locations of neck-banded individuals with GPS units. In rice-prairies, I surveyed for

neck-banded snow geese at least 4 days each week, from 1 November until 15 February in 2001-2002, 2002-2003, and 2003-2004 (see also Appendix 2). I surveyed less frequently in coastal marshes than rice-prairies (see also Appendix 2) because of logistical constraints, and the fewer snow geese in this habitat.

ANALYSES OF NECK-BANDING DATA

I used multi-strata models for live recaptures (hereafter resightings) to estimate probabilities of snow geese moving between rice-prairies and coastal marshes (movement probability = Ψ) using program MARK (Hestbeck et al. 1991, Brownie et al. 1993, Nichols and Kendall 1995, White and Burnham 1999, Cooch and White 2004). Sampling was done to permit estimation of movement probabilities within winters and between winters (see below).

Hereafter, I refer collectively to rice-prairies and coastal marshes as strata. The model parameters are defined as follows (Hestbeck et al. 1991, Nichols et al. 1993):

Apparent survival (Φ) = the probability that a bird alive and present in stratum j during sample period i survives until sample period $i+1$;

Transition probability (ψ) = the probability that an individual will move from stratum j at time i to stratum j in time period $i+1$; ψ is the product of Ψ and Φ , and program MARK provides estimates of these two parameters separately;

and

Sighting probability (p) = the probability that a bird alive in stratum j during sample period i is sighted during that period.

My models had 2 strata; thus, the likelihood functions were written as the product of two binomial distributions corresponding to birds released in either rice-prairies or coastal marshes (cf. Hestbeck et al. 1991). Each cell of each binomial distribution corresponds to a certain observation history (also termed capture histories). Each observation history describes where each snow goose was sighted in each sampling period, the letter A indicates resightings in rice-prairies, the letter B indicates resightings in coastal marshes, and the letter 0 (zero) indicates that the bird was not sighted during that sampling period. The probability associated with each observation history is then modeled by using the sighting and transition probability parameters of respective models (Hestbeck et al. 1991). I used observed numbers of snow geese displaying each observation history to obtain maximum likelihood estimates under each model, using program MARK (White and Burnham 1999, Cooch and White 2004).

My primary research interest was in Ψ because the Phenotypic Selection and Habitat Selection Hypotheses predict values of this parameter (see below). I attempted to account for variation between strata in p because, *a priori*, I expected this parameter to be higher in rice-prairies than in coastal marshes (see below). Program MARK allows p to differ between strata and time periods; thus, I assume that my models adequately accounted for heterogeneity due to these variables.

Sampling Periods

My analysis spanned 3 winters and I entered my dataset into MARK with each winter divided into early and late winter periods, which yielded 6 sampling periods over the course of my study. I used 2 sampling periods within each winter to include movement events that occurred within winters, and also to examine if parameters differed between periods within winter. The two periods were defined as: (1) early winter, 1 November until 31 December; and (2) late winter, 1 January until 28 February. When individuals were sighted more than once in

one sampling period, I counted it as 1 resighting event; and randomly selected which resighting was kept in the dataset.

Model Assumptions

The assumptions of the multi-strata models include the following (see Pollock et al. 1990 and Hestbeck et al. 1991 for detailed discussions). (1) Time- and stratum specific p and Ψ are equal for all marked birds within a given stratum and within a given sampling period; it should be noted that Φ , p , and Ψ can differ between strata; and Φ and p are conditional on the stratum at the beginning of the sampling period. (2) Behavior of marked birds is independent of sighting probability, survival and movement. (3) Marker loss or marker oversight never occurs. (4) Captures are instantaneous and sampling avoids periods of extensive movements and disturbance such as hunting seasons. (5) Emigration from the population is permanent (Pollock et al. 1990, Hestbeck et al. 1991).

Although mark-recapture models are robust to heterogeneous capture probabilities and no study design can completely avoid such heterogeneity, researchers should always attempt to reduce heterogeneity in survival, transition, and sighting probabilities (Pollock et al. 1990, Lebreton et al. 1992). I included sex in my models because capture and sighting probabilities sometimes differ between males and females (hereafter sex effect; Pollock et al. 1990, Lebreton et al. 1992). I had strong *a priori* reasons to expect Φ , p , and Ψ to differ between rice-prairies and coastal marshes (hereafter stratum effect). Stratum effect represents the different properties of these areas as snow goose habitats and differing sampling intensities within each stratum due to logistical constraints and variable snow goose presence. Sampling effort was regular in rice-prairies, whereas it was more infrequent in coastal marshes (see Appendix 2), thus, I considered it implausible to include the effect of sampling period (time effect) for all parameters. However, I considered the effects of sampling period in my starting model by: (1) including the effect of

sampling period (hereafter season effect; Cooch and White 2004) on p ; and (2) including the effect early and late winter on Φ and Ψ (hereafter within-winter effect).

Banded geese seldom behave completely independently of each other because of their pair bonds and family associations (Sulzbach and Cooke 1978, Hestbeck et al. 1991, Schmutz et al. 1995). Violating this assumption will not bias any estimators, but it will lead to overdispersion, which causes statistical models to underestimate sampling variances (Hestbeck et al. 1991, Anderson et al. 1994, Schmutz et al. 1995). I analyzed adults only because of low sample size (28 resightings) for juveniles; thus, parent-offspring relationships can not bias my results. However, pairs were a possible source of bias in my analysis because movements of mates are not independent of each other (see Hestbeck et al. 1991, Schmutz et al. 1995). Pairs comprised 8.5% (25 pairs total) of resighted neck-collared snow geese. Including both members of pairs in the analysis would cause their respective observation history to be overrepresented by the frequency of one (Schmutz et al. 1995). Thus, I removed one observation history representing one member of each pair from the distribution of observation histories by: (1) assigning random numbers to each pair; (2) then deleting male data from pairs with odd random numbers; and (3) deleting female data from pairs with even random numbers. For this purpose, I used a set of 100 random numbers that I generated using the Research Randomizer software (Urbaniak and Plous 2003).

Studies of neck-banded geese always incur some marker loss and hence violate the third assumption (Alisauskas and Lindberg 2002). Hestbeck et al. (1991) claimed neckband loss did not affect movement probabilities because band loss bias would be associated with the apparent survival component (Φ) of transition probabilities and not the movement component (Ψ). Here, I assumed that marker loss was independent of stratum, period, or sex and, thus, would not bias any estimates in my models.

The fourth assumption of instantaneous sampling can never strictly be met (Hestbeck et al. 1991). It is unrealistic to avoid hunting seasons when studying geese banded in winter (Bell et al. 1993); studying neck-banded snow geese outside hunting seasons is particularly difficult because recent hunting seasons for snow geese last all winter in an attempt to reduce the mid-continent population (U.S. Fish and Wildlife Service 2004). My study avoided extensive migration because southwest Louisiana is the southern terminus of snow geese in the Mississippi Flyway (Mowbray et al. 2000).

The assumption of non-permanent immigration can be important for a study of survival and movement on a small geographic scale (Hestbeck et al. 1991). I received recoveries of 4 neck-banded snow geese (9.8% of recoveries) from outside the study area during the winter period. However, 3 of these occurred after 20 January, at which time my banded birds already were being shot in Arkansas and Missouri (Bird-Banding Lab, Laurel, Maryland, unpublished data). Thus, I assume that 20 January and thereafter is sufficiently late to assume that these birds would have commenced spring migration; and thus, would not have returned to Louisiana that winter.

MODEL SELECTION IN PROGRAM MARK

I tested research hypotheses in program MARK in 3 steps: (1) I predicted ranges for values of Ψ after each hypothesis; (2) I used program MARK to estimate Ψ based on all observation histories (hereafter full dataset analysis) and compared those against my predictions; (3) I ran a second analysis in program MARK (hereafter covariate analysis) to test the effect of body morphometrics on Ψ , in which I analyzed resightings for the 406 snow geese for which morphometrics data were available.

Step 1: Predictions about Ψ based on Research Hypotheses

Currently, established criteria are not available for using Ψ to differentiate two populations, and any such criteria undoubtedly always will be somewhat subjective. Thus, the question of whether 2 populations should be considered separate if movements are completely non-existent, incidental, or “rare” is difficult to answer. A dataset with high probabilities of observation histories AAAA and BBBB arguably will produce low estimates of Ψ in program MARK, whereas high probabilities of observation histories ABAB, ABBB, and ABBA arguably will produce higher estimates of Ψ .

I assumed that some movements could occur incidentally if snow geese in coastal marshes were a separate population from snow geese in rice-prairies; accordingly I predicted $\Psi < 0.1$ if snow geese in the 2 strata represented separate populations. Conversely, I interpreted all $\Psi \geq 0.1$ as too large a movement probability to disregard movements as incidental; thus, I would interpret this result as more consistent with the Habitat Selection Hypothesis than the Phenotypic Selection Hypothesis (Alisauskas 1998).

Step 2: Parameter Estimates from the Full Dataset Analysis

I first identified the most parsimonious models, given my dataset (Burnham and Anderson 2002). In MARK, the general model (also termed global model) is the starting point in AIC model selection, against which other candidate models are tested (White and Burnham 1999, Cooch and White 2004). A fully saturated general model was implausible for my dataset because it had only 41 of 60 parameters fully estimable. Thus, in my general model, I included additive effects of: (1) stratum on all parameters because of the different sampling intensities of rice-prairies and coastal marshes; (2) sampling period for the entire study period on p , and within-winter effect on Φ and Ψ ; and (3) a sex effect on all parameters. Thus, my general model was $\{S_{\text{within-winter, stratum, sex}}; p_{\text{season, stratum, sex}}; \Psi_{\text{within-winter, stratum, sex}}\}$; I believe this general model

provides a reasonable base model for inference. I next considered all simplified versions of my general model, including models with no effect on parameters (null models; $\{\Phi.; p.; \Psi.\}$). I used model averaging in MARK to obtain parameter estimates if 2 or more models were considered equally parsimonious for inference by AIC (Burnham and Anderson 2002).

Testing the goodness-of-fit (GOF) of multi-strata models presently is not established in program MARK; some authors thus have opted not to report GOF statistics such as \hat{c} for their general model (Béchet et al. 2003, Blums et al. 2003). Recently, Pradel et al. (2003) suggested the use of the U-CARE software (Choquet et al. 2002) to assess GOF for multi-strata models (see also Cam et al. 2004). This approach permits the identification of structural failure and the subsequent estimation of \hat{c} in U-CARE; this estimate of \hat{c} is then used in MARK to adjust model selection for overdispersion. I used this approach (Pradel et al. 2003) to obtain \hat{c} for model selection; the \hat{c} estimate was 2.666. General models with \hat{c} lower than 4.0 are suitable for analysis (Cooch and White 2004). Note that I also ran median \hat{c} in MARK although that method is recent but not yet established for multi-strata models, and thus still somewhat experimental (Cooch and White 2004); I did not find reports of others using it in the literature. My median \hat{c} trials yielded estimates that were in agreement ($\hat{c} < 2$) with my estimates from U-CARE.

Finally, I used model selection based on Quasi-likelihood adjusted Akaike's Information Criterion, adjusted for small sample sizes, ($QAIC_c$) to determine which models were most parsimonious for inference, given my dataset (Anderson et al. 1994, Burnham and Anderson 2002). I used $QAIC_c$ to rank candidate models according to $QAIC_c$ differences between models ($\Delta QAIC_c$); the model that had the lowest $QAIC_c$ value was the model deemed most parsimonious for inference (i.e. receive the highest rank), given the dataset at hand (Burnham and Anderson 2002). According to $QAIC_c$ criteria, models with $\Delta QAIC_c < 2$, or $QAIC_c$ weight > 0.05 are

equally well supported, whereas models with $\Delta\text{QAIC}_c > 10$ are essentially not supported (Burnham and Anderson 2002).

Step 3: Analysis of Morphometrics and Covariate Analysis

I performed a Principal Components analysis (PCA) on morphometrics of adult snow geese (SAS Institute 1999, Alisauskas 1998) and used the correlation matrix of measurements to construct 1 index of body size and 8 indexes (PC scores) of shape. I used PC scores as response variables in a multivariate analysis of variance (MANOVA; PROC GLM, SAS Institute 1999) to determine if PC scores differed between rice-prairies and coastal marshes in 2001-2004, as previously observed in 1982-1984 (cf. Alisauskas 1998).

I followed methods of Alisauskas (1998) and considered all PC scores; however, many authors insist that PC scores that explain a small amount of variance in the original data should be discarded (see review by Alisauskas 1998, see also Johnson and Wichern 2002, Stevens 2002). However, these “smaller” PC scores may indicate important linear dependencies in the data (Johnson and Wichern 2002) and/or contain ecologically important information (Ricklefs and Miles 1994, Alisauskas 1998). Accordingly, I retained the number of PC scores that cumulatively explained at least 85% of the variation in the data (cf. Stevens 2002).

In each PCA, I identified measurements that had the highest loadings within eigenvectors for each PC score. Initially, I followed the guidelines for establishing meaningful values of loadings, as a power function of sample size (cf. Stevens 2002; Table 11.1, page 394). For my dataset, this method considers loadings roughly equal to or higher than 0.26 as meaningful. Considering findings of Alisauskas (1998), I believe this value to be too low because of my relatively high sample size ($n=406$) (cf. Stevens 2002), although elsewhere, I find this method useful for smaller sample sizes (Chapter 8). Thus, in this chapter, I interpreted loadings of PC scores more conservatively, following Alisauskas (1998).

Stratum, sex, winter (2001-2002, 2002-2003, and 2003-2004), and all their interactions were explanatory variables in the MANOVA. I determined final models using backward stepwise variable selection, where non-significant interactions were removed one at a time and the analysis subsequently performed again (Agresti 1996). In the event that MANOVA detected stratum in significant interactions with either sex or winter, I kept the interaction in the model and used least-square means (LSMEANS; SAS Institute 1999) to compare PC scores between strata within each winter or sex. All F- and P-values presented from MANOVA are Wilk's Lambda.

I selected PC scores for the covariate analysis based on 2 criteria: (1) PC scores differed between coastal marshes and rice-prairies in the MANOVA; and (2) PC scores represented at least 85% of the cumulative variation in the correlation matrix from the PCA. The covariate analysis had an effective sample size of 525, whereas the full dataset analysis had an effective sample size of 1190. I used the most parsimonious models from step 2 in my model selection as base models in the covariate analysis. I re-calculated \hat{c} for the reduced dataset in U-CARE; the \hat{c} for this reduced dataset was 1.777.

ESTIMATES OF FLOCK MIXING

I calculated the probability of resighting neck-banded snow geese from both strata in the same snow goose flock. This analysis was restricted to all observations of single flocks, where I resighted 2 or more neck-banded snow geese. I used a generalized linear model (PROC GENMOD; SAS Institute 1999) to compare flock mixing between snow geese neck-banded in rice-prairies and coastal marshes. The response variable was a binomial variable: (1) all neck-banded snow geese in the flock were banded in the same stratum (hereafter homogenous flocks); or (2) at least 1 individual in from each stratum was observed in the flock (hereafter mixed flocks). Stratum (rice-prairie or coastal marsh) was the explanatory variable. I used similar

reference values as for Ψ in my interpretation of flock mixing: (1) low flock mixing (< 10%) as consistent with the Phenotypic Selection Hypothesis (Alisauskas 1998); and (2) (>10%) as consistent with the Habitat Selection Hypothesis (Alisauskas 1998).

RESULTS

Overall, I obtained 906 resightings of 295 adults and 30 resightings of 28 juveniles. Forty-one neck-banded snow geese were reported as shot in Louisiana and Texas during winters 2001-2002, 2002-2003, and 2003-2004 (Bird-Banding Lab, Laurel, Maryland, unpublished data).

MOST PARSIMONIOUS MODELS IN FULL DATASET

QAIC_c deemed the 9 highest ranked models equally parsimonious, given the full dataset (Table 7.1); thus, I used model averaging to estimate real parameters based on all 9 models (Table 7.2). Among the 9 most parsimonious models, 3 had no effect on Φ , another 4 models had a within-winter effect on Φ , and remaining 2 models had a stratum effect on Φ ; the highest ranked (rank=11) model with both within-winter and stratum effects had QAIC_c = 3.04 (Table 7.1). All 9 models had both season and stratum effects on p , and models where either effect was removed from p generally performed poorly (Δ QAIC_c > 8, Table 7.1). Among the 9 most parsimonious models, 4 models had no effect on Ψ , another 1 model had a within-winter effect on Ψ , and remaining 4 models had a stratum effect on Ψ ; the highest ranked model (rank=13) with both within-winter and stratum effects had QAIC_c = 3.61 (Table 7.1). None of the most parsimonious models had a sex effect on any parameter; the highest ranked model with a sex effect in it was $\{\Phi_{\text{sex, stratum}; p_{\text{season, stratum}; \Psi_{\text{within-winter, stratum}}}\}$ (Δ QAIC_c = 10.02; Table 7.1).

Table 7.1. Model selection ranks for the most parsimonious models to obtain parameter estimates of apparent survival (Φ), resighting probability (p), and movement probability (Ψ) for lesser snow geese banded in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. QAIC_c is based on $\hat{c} = 2.666$. Only the top 20 models are shown; models with $\Delta\text{QAIC}_c > 10$ have essentially no support. K is the number of parameters in each model.

Rank	Model	ΔQAIC_c	ΔQAIC_c Weight	Model Likelihood	K
1	$\Phi_{.}; p_{\text{season, stratum}}; \Psi_{.}$	0.00	0.157	1.000	12
2	$\Phi_{.}; p_{\text{season, stratum}}; \Psi_{\text{stratum}}$	0.55	0.119	0.760	13
3	$\Phi_{\text{stratum}}; p_{\text{season, stratum}}; \Psi_{.}$	0.63	0.115	0.729	13
4	$\Phi_{\text{within-winter, stratum}}; p_{\text{season, stratum}}; \Psi_{.}$	1.02	0.094	0.601	14
5	$\Phi_{\text{within-winter, stratum}}; p_{\text{season, stratum}};$ Ψ_{stratum}	1.34	0.080	0.511	15
6	$\Phi_{\text{stratum}}; p_{\text{season, stratum}}; \Psi_{\text{stratum}}$	1.49	0.075	0.475	14
7	$\Phi_{\text{within-winter}}; p_{\text{season, stratum}}; \Psi_{.}$	1.55	0.073	0.462	13
8	$\Phi_{\text{within-winter}}; p_{\text{season, stratum}}; \Psi_{\text{stratum}}$	1.87	0.062	0.392	14
9	$\Phi_{.}; p_{\text{season, stratum}}; \Psi_{\text{within-winter}}$	2.03	0.056	0.362	13
10	$\Phi_{\text{stratum}}; p_{\text{season, stratum}}; \Psi_{\text{within-winter}}$	2.67	0.041	0.263	14
11	$\Phi_{\text{within-winter, stratum}}; p_{\text{season, stratum}};$ $\Psi_{\text{within-winter}}$	3.04	0.034	0.218	15
12	$\Phi_{\text{within-winter}}; p_{\text{season, stratum}}; \Psi_{\text{within-winter}}$	3.57	0.026	0.168	14
13	$\Phi_{.}; p_{\text{season, stratum}}; \Psi_{\text{within-winter, stratum}}$	3.61	0.026	0.164	15

(Table continued)

(Table 7.1. continued)

Rank	Model	ΔQAIC_c	ΔQAIC_c Weight	Model Likelihood	K
14	$\Phi_{\text{stratum}; \text{p season, stratum}; \Psi_{\text{within-winter, stratum}}$	5.13	0.012	0.077	16
15	$\Phi_{\text{within-winter}; \text{p season, stratum};$ $\Psi_{\text{within-winter, stratum}}$	5.20	0.012	0.074	16
16	$\Phi_{\text{within-winter, stratum}; \text{p season, stratum};$ $\Psi_{\text{within-winter, stratum}}$	5.38	0.011	0.068	17
17	$\Phi_{\text{within-winter, stratum}; \text{p, stratum}; \Psi.$	8.21	0.003	0.017	6
18	$\Phi_{\text{within-winter, stratum}; \text{p stratum}; \Psi_{\text{within-winter}}$	8.48	0.002	0.014	7
19	$\Phi_{\text{sex, stratum}; \text{p season, stratum};$ $\Psi_{\text{within-winter, stratum}}$	10.02	0.001	0.007	20
20	$\Phi_{\text{stratum}; \text{p stratum}; \Psi_{\text{within-winter}}$	14.15	0.000	0.001	6

Table 7.2. Parameter estimates of Φ , p , and Ψ , based on model averaging of the 9 most parsimonious models in Table 7.1; estimated by program MARK, for adult lesser snow geese neck-banded in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. WASE: Standard Error based on weighted average. %MV: percentage of variation attributable to model variation.

Parameter	Estimate	WASE	95% Confidence Interval		% MV
			Lower	Upper	
Φ early winter, rice-prairies	0.801	0.078	0.582	0.921	19.0
Φ late winter, rice-prairies	0.760	0.083	0.532	0.898	23.6
Φ early winter, coastal marshes	0.875	0.059	0.540	0.976	64.7
Φ late winter, coastal marshes	0.787	0.086	0.514	0.928	35.1
p late winter 2001-2002, rice-prairies	0.514	0.126	0.279	0.742	3.6
p early winter 2002-2003, rice-prairies	0.638	0.133	0.351	0.852	7.7
p late winter 2002- 2003, rice-prairies	0.378	0.072	0.244	0.664	9.2
p early winter 2003-2004, rice-prairies	0.472	0.095	0.288	0.663	11.7
p late winter 2003-2004, rice-prairies	0.278	0.069	0.161	0.435	7.7
p late winter 2001-2002, coast. marsh..	0.260	0.127	0.086	0.574	6.7
p early winter 2002-2003, coast. marsh.	0.023	0.003	0.137	0.022	1.5
p late winter 2002- 2003, coast. marsh.	0.047	0.032	0.011	0.178	6.9
p early winter 2003-2004, coast. marsh.	0.018	0.013	0.004	0.078	4.8
p late winter 2003-2004, coast. marsh.	0.129	0.048	0.055	0.276	22.3
Ψ early winter, rice-prairies	0.161	0.051	0.059	0.370	55.4
Ψ late winter, rice-prairies	0.161	0.051	0.059	0.367	55.5
Ψ early winter, coastal marshes	0.226	0.047	0.138	0.347	23.3
Ψ late winter, coastal marshes	0.226	0.047	0.138	0.346	23.7

SEGREGATION OF SNOW GEESE INTO STRATA BY MORPHOMETRICS

My final MANOVA model (Table 7.3) included stratum ($F = 4.06$, Num df = 9, Den df = 391, $P < 0.0001$), winter ($F = 19.91$, Num df = 18, Den df = 782, $P < 0.0001$), sex ($F = 21.58$, Num df = 9, Den df = 391, $P < 0.0001$), and the stratum x winter interaction ($F = 7.52$, Num df = 18, Den df = 782, $P < 0.0001$). PC5 differed between strata independent of winter, i.e. stratum effect was significant but the stratum x winter interaction was not significant (Table 7.3). The stratum x winter interaction was significant for PC1, PC2, PC3, PC4, and PC7 (Table 7.3). Within winters, PC1, PC2, PC3, PC4, PC5, and PC7 differed between rice-prairies and coastal marshes as follows (LSMEANS on stratum and winter; Figure 7.2; Table 7.4). (1) PC1 (overall body size) was higher in rice-prairies than coastal marshes in 2001-2002 and lower in 2003-2004. (2) PC2 (large skull dimensions relative to bill nares) was higher in rice-prairies than coastal marshes in 2001-2002. (3) PC3 (large bill nares and wide skull, relative to wing length) was higher in rice-prairies than coastal marshes in 2001-2002 but lower in 2002-2003 and 2003-2004. (4) PC4 (large gape length relative to wing length) was higher in rice-prairies than coastal marshes in 2001-2002 and 2002-2003 but lower in 2003-2004. (5) PC5 (relatively small bill thickness) was higher in rice-prairies than coastal marshes, independent of winter. (6) PC7 (relatively small skull height) was higher in rice-prairies than coastal marshes in 2002-2003. PC1 (overall body size), PC2 (skull width and height), and PC3 (bill nares, skull width relative to wing length) differed between sexes ($P < 0.0001$; $P = 0.0138$; and $P = 0.0070$, respectively). Table 7.5 shows which morphological variables covaried the strongest with each PC score. PC1 (overall body size) and PC2 (large skull dimensions relative to bill nares) were higher in males than in females (Figure 7.3). PC3 (large bill nares and wide skull, relative to wing length) was higher in females than in males (Figure 7.3).

Table 7.3. P-values from multivariate (MANOVA) and subsequent univariate analysis of variance (LSMEANS) for 9 morphological variables of 406 adult lesser snow geese captured with rocket-nets in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004.

Explanatory variable	LSMEANS									
	MANOVA	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Sex	<0.0001	<0.0001	0.0138	0.0070	0.1679	0.9941	0.7498	0.0923	0.0799	0.4812
Stratum (S)	<0.0001	0.3238	0.2506	0.0014	0.0248	0.0018	0.8445	0.0642	0.7467	0.2883
Winter (W)	<0.0001	0.2122	<0.0001	<0.0001	<0.0001	0.1761	<0.0001	<0.0001	<0.0001	0.8578
S x W	<0.0001	0.0074	<0.0001	<0.0001	<0.0001	0.0719	0.0717	0.0357	0.3750	0.6498

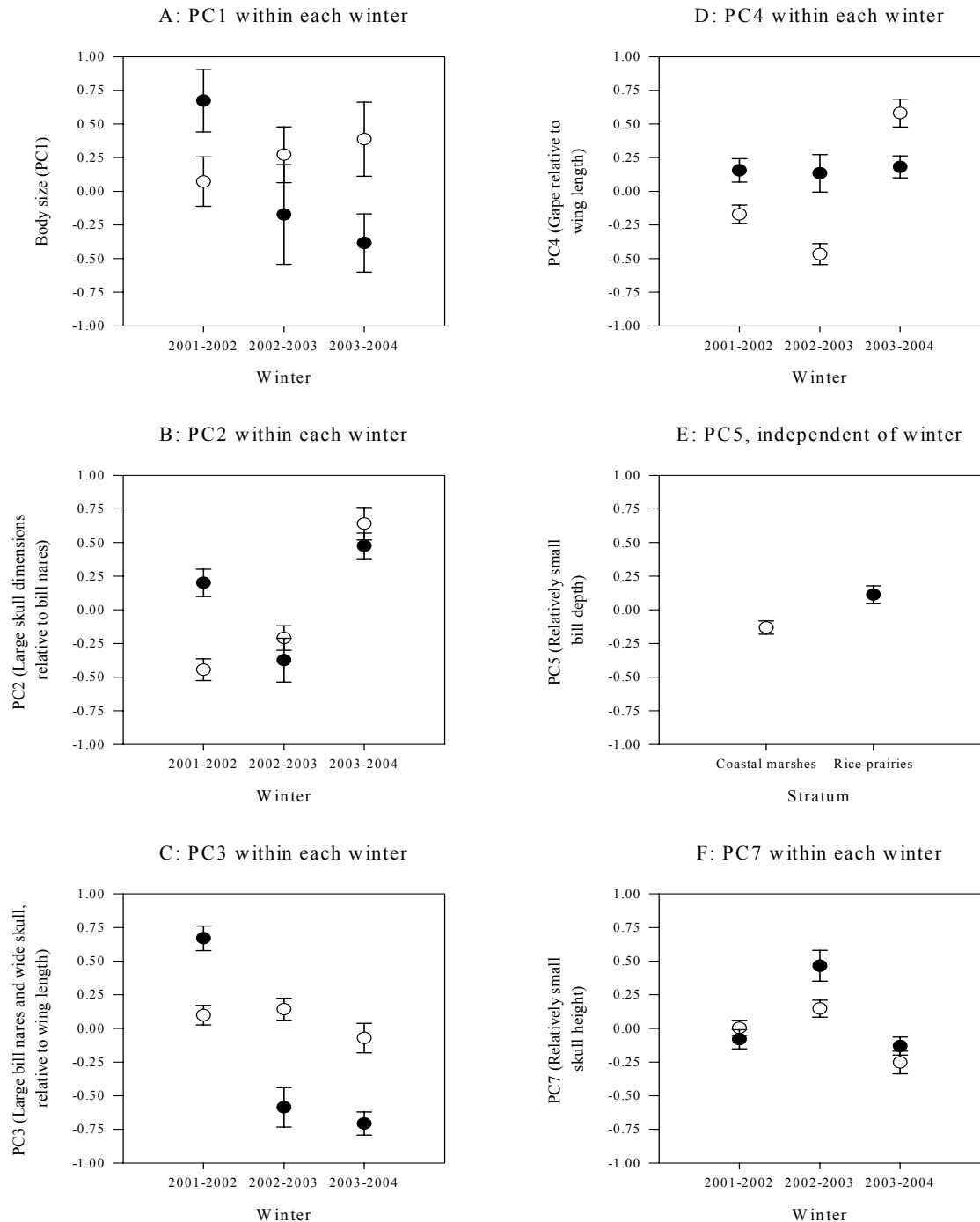


Figure 7.2. PC scores from body morphometrics of lesser snow geese measured in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Only scores that differed between rice-prairies (filled symbols) and coastal marshes (open symbols), as indicated by Least-square means from multivariate analysis of variance (MANOVA), are shown. See text for significance levels from MANOVA. Note that (E) differs from other figures because for PC5, the stratum x winter interaction was not significant; thus, PC5 differed between strata independent of winter.

Table 7.4. P-values from LSMEAN test of significance of stratum effect for 5 PC scores, from morphometrics of adult lesser snow geese in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. All scores presented here had a significant stratum x winter interaction in the LSMEANS in Table 7.3.

Winter	PC1	PC2	PC3	PC4	PC7
2001-2002	0.0428	<0.0001	<0.0001	0.0034	0.3563
2002-2003	0.2953	0.3756	<0.0001	0.0002	0.0151
2003-2004	0.0281	0.2844	<0.0001	0.0025	0.2593

Table 7.5. Principal components analysis of morphological measurements of 406 adult lesser snow geese caught in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Numbers in bold correspond to variables that covaried the strongest with each PC score (have the highest loadings).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Wing length	0.30	0.28	-0.42	-0.58	0.28	0.41	0.27	-0.05	0.04
Culmen length	0.37	-0.33	0.01	-0.05	-0.17	0.13	-0.35	-0.63	0.42
Bill nares	0.30	-0.52	0.45	-0.37	-0.04	0.08	0.10	0.53	0.09
Bill thickness	0.32	0.10	-0.34	0.14	-0.82	0.01	0.16	0.21	-0.04
Gape length	0.30	-0.36	-0.27	0.64	0.37	0.16	0.36	0.06	0.04
Head length	0.40	-0.08	0.02	-0.02	0.08	-0.01	-0.35	-0.10	-0.83
Total tarsus	0.35	0.08	-0.04	-0.15	0.15	-0.86	0.25	-0.11	0.10
Skull width	0.28	0.45	0.66	0.20	-0.06	0.21	0.37	-0.25	-0.03
Skull height	0.35	0.43	0.01	0.21	0.21	0.00	-0.56	0.43	0.33
% variance									
explained	55.5	9.5	8.5	6.7	5.8	4.8	4.1	3.1	2.2

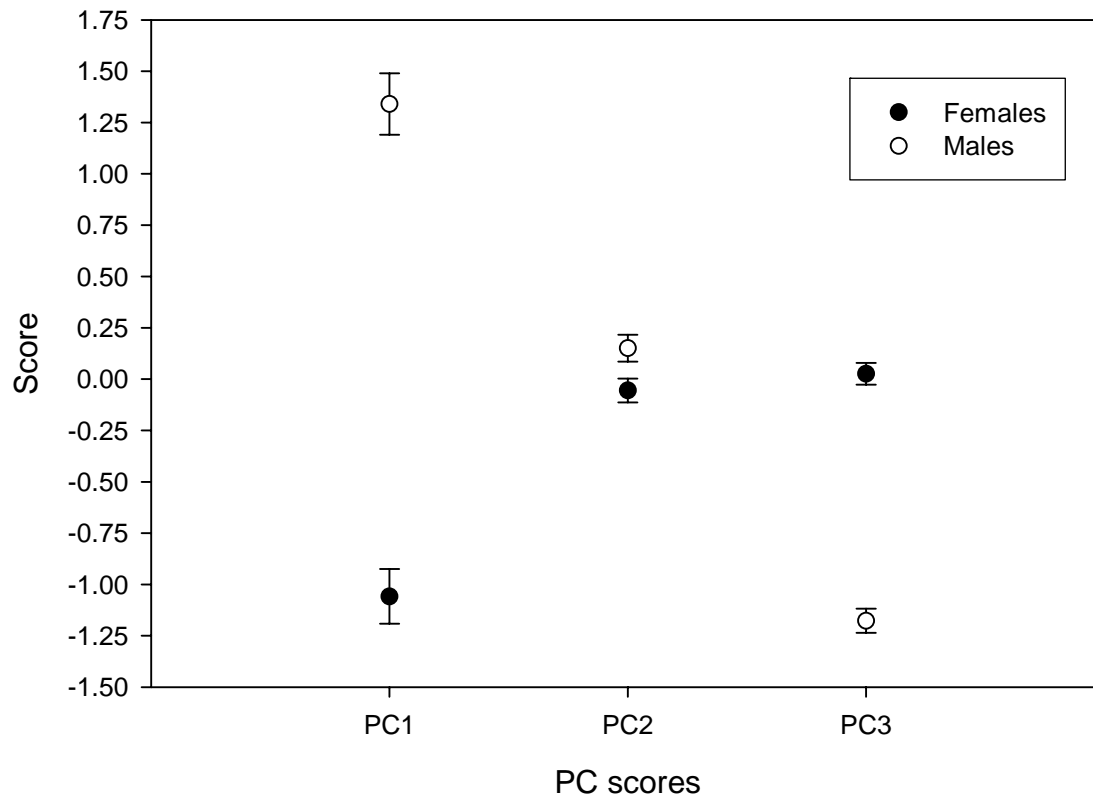


Figure 7.3. PC scores that differed between adult, male and female lesser snow geese, neck-banded in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Only scores that differed between sexes, as indicated by Least-square means from multivariate analysis of variance (MANOVA), are shown. See text for significance levels from MANOVA.

COVARIATE ANALYSIS

The first five PC scores (PC1-PC5) differed between strata and cumulatively represented 86% of the overall variation (Table 7.5); thus, I used all combinations of them in the covariate analysis. I used the 9 most parsimonious models (Table 7.1) as starting models. However, all 9 starting models yielded the same model selection pattern, where QAIC_c deemed the starting models as the most parsimonious model and covariate models ranked increasingly lower as the number of parameters increased. Thus, I present findings only from starting model $\{\Phi; p_{\text{season, stratum}}, \Psi\}$ (Table 7.6).

FLOCK MIXING

The odds of neck-banded snow geese flocking only with those neck-banded in the same stratum were 3.7 times lower for snow geese neck-banded in coastal marshes than rice-prairies ($\chi^2 = 24.80$, $df = 1$, $P < 0.0001$). Snow geese neck-banded in rice-prairies flocked with birds from coastal marshes on 51% of occasions when sighted with ≥ 1 other neck-banded snow goose ($n=163$). Snow geese neck-banded in coastal marshes flocked with birds from rice-prairies on 79% of occasions when sighted with ≥ 1 other neck-banded snow goose ($n=136$). On average, 3.4 (SE = 0.16) and 4.2 (SE = 0.19) neck-banded snow geese comprised each observation of homogenous and mixed flocks, respectively.

DISCUSSION

ESTIMATES OF Ψ AND P

My estimates of Ψ were 0.161 and 0.226, for rice-prairies and coastal marshes, respectively; thus, I conclude that movements are common between rice-prairies and coastal marshes. I indexed the number of snow geese that moved between strata by multiplying Midwinter Survey estimates (Waterfowl Survey Data 2004) with estimated movement probabilities. Midwinter survey numbers of snow geese, averaged for the 3 winters, were

Table 7.6. Model selection ranks, ΔQAIC_c , QAIC_c weights, model likelihoods, and number of parameters (K) for the covariate size analysis of movements of lesser snow geese banded in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Model S_s ; P_s ; Ψ_s was the starting model in this analysis, and covariates were only added to Ψ . QAIC_c based on $\hat{c} = 1.777$.

Rank	{Covariates included}	ΔQAIC_c	QAIC_c Weight	Model Likelihood	K
1	{None}	0.00	0.198	1.000	12
2	{PC1}	1.70	0.084	0.427	13
3	{PC3}	1.83	0.079	0.400	13
4	{PC4}	1.93	0.075	0.381	13
5	{PC5}	2.05	0.071	0.358	13
6	{PC2}	2.08	0.070	0.353	13
7	{PC1 PC3}	3.44	0.035	0.179	14
8	{PC1 PC4}	3.65	0.032	0.161	14
9	{PC1 PC2}	3.79	0.030	0.150	14
10	{PC1 PC5}	3.80	0.030	0.150	14
11	{PC3 PC4}	3.83	0.029	0.147	14
12	{PC3 PC5}	3.92	0.028	0.141	14
13	{PC2 PC3}	3.93	0.028	0.140	14
14	{PC4 PC5}	4.00	0.027	0.135	14
15	{PC2 PC4}	4.02	0.027	0.134	14

(Table continued)

(Table 7.6 continued)

Rank	{Covariates included}	ΔQAIC_c	QAIC _c Weight	Model Likelihood	<i>K</i>
16	{PC2 PC5}	4.14	0.0249	0.126	14
17	{PC1 PC3 PC4}	5.46	0.0128	0.065	15
18	{PC1 PC2 PC3}	5.54	0.0123	0.062	15
19	{PC1 PC3 PC5}	5.55	0.0123	0.062	15
20	{PC1 PC2 PC4}	5.75	0.0112	0.056	15
21	{PC1 PC4 PC5}	5.76	0.0111	0.056	15
22	{PC1 PC2 PC5}	5.89	0.0103	0.052	15
23	{PC3 PC4 PC5}	5.93	0.0102	0.051	15
24	{PC2 PC3 PC4}	5.94	0.0101	0.051	15
25	{PC2 PC3 PC5}	6.02	0.00973	0.049	15
26	{PC2 PC4 PC5}	6.10	0.00936	0.047	15
27	{PC1 PC2 PC3 PC4}	7.58	0.00446	0.023	16
28	{PC1 PC3 PC4 PC5}	7.58	0.00446	0.023	16
29	{PC1 PC2 PC3 PC5}	7.66	0.00428	0.022	16
30	{PC1 PC2 PC4 PC5}	7.86	0.00388	0.020	16
31	{PC2 PC3 PC4 PC5}	8.04	0.00354	0.018	16
32	{PC1 PC2 PC3 PC4 PC5}	9.71	0.00154	0.008	17

210,048 and 88,039 for rice-prairies and coastal marshes, respectively (State Federal Cooperation Information Program 2004). Accordingly, this index estimated that 33,818 snow geese moved from rice-prairies to coastal marshes ($\Psi = 0.161$) and 19,897 snow geese moved from coastal marshes to rice-prairies ($\Psi = 0.226$) during the study period. I conclude that these results are consistent with the Habitat Selection Hypothesis (Alisauskas 1998).

My model selection confirmed my *a priori* suspicions that Φ , p , and Ψ would differ between rice-prairies and coastal marshes (Table 7.2). p was considerably higher in rice-prairies than in coastal marshes (Table 7.2); thus, I had relatively high probabilities of sighting snow geese that (1) were neck-banded in rice-prairies and stayed in that stratum; and (2) were neck-banded in coastal marshes and moved into rice-prairies. Despite this heterogeneity in p , both my starting models (full and covariate analyses) fit reasonably well ($\hat{c} \leq 3$).

EFFECTS OF SEX, SEASON, WITHIN-WINTER AND STRATUM

All models that included a sex effect performed poorly in my analysis. Model averaging of the 9 most parsimonious models (hereafter average model; see Table 7.2) retained separate estimates of Φ for early and later winter, and for rice-prairies and coastal marshes. Φ was slightly higher in coastal marshes than in rice-prairies, and higher in early winter than late winter in both strata; although, neither finding was statistically significant (as indicated by the weighted average standard error, Table 7.2).

All 9 most parsimonious models had effects of season and stratum on p ; thus, retaining these effects on p was well supported in my analysis. p was consistently higher in rice-prairies than coastal marshes throughout the study period, and was higher in 2001-2002 than in the following winters (Table 7.2). It should be noted that sampling effort was relatively consistent over the course of the 3 winters; thus, sampling effort should not have caused higher p in 2001-2002.

Only 1 of the 9 most parsimonious models retained a within-winter effect on Ψ , and thus, Ψ was identical for early and late winter in both strata in the average model. The probability of moving from coastal marshes to rice-prairies was higher than moving in the opposite direction in the average model; however, this finding was marginally significant. The finding of higher Ψ in coastal marshes is reasonable because rice-prairies generally hold twice as many snow geese as do coastal marshes (Waterfowl Survey Data 2004); many animals select habitats that hold the highest number of conspecifics within an area (Sutherland 1996).

DID SNOW GEESE SEGREGATE INTO STRATA BY MORPHOMETRICS?

My results were consistent with those of Alisauskas (1998) in that snow geese in coastal marshes were larger in overall body size, and had thicker bills and skulls than did those in rice-prairies (Figure 7.2). Similarly to that observed by Alisauskas (1998), stratum effect on PC scores was dependent on winter for most PC scores, with only PC5 differing between strata, independent of winter (Table 7.3). I found that snow geese from coastal marshes had larger gape lengths and larger bill nares than did those from rice-prairies; these measurements were not recorded by Alisauskas (1998).

Sex effects were independent of winter or stratum (Table 7.3). My findings on sex differences also were similar to those of Alisauskas (1988); males were structurally larger than females, whereas females seemed to have relatively larger bill nares and wider skulls than did males (PC3; Figure 7.3). Thus, overall findings of both studies are very similar despite subtle differences in measurements used.

COVARIATE ANALYSIS: WHAT AFFECTS Ψ IN SNOW GEESE?

No covariate models ranked higher than the starting models, based on ΔQAIC_c (Table 7.6). Although, the 5 highest ranked covariate models were equally parsimonious ($\Delta\text{QAIC}_c \leq 2$) as the starting model, I consider them to be weakly supported. By adding 1 parameter to a

model, deviance will by definition always decrease (see formulas for AIC estimates in Burnham and Anderson 2002), and, thus, QAIC_c can increase by no more than 2, even if the added covariate adds no new information to the model. Thus, individual morphometrics (see Table 7.5) probably do not significantly influence decisions about moving between rice-prairies and coastal marshes; other factors such as food availability, weather, and behavioral interactions probably are more important (Sutherland 1996, Gauvin and Giraldeau 2004). These environmental variables likely caused snow geese banded in coastal marshes to move into rice-prairies regardless of bill size, i.e. larger snow geese were just as likely to use rice-prairies as were those with smaller bills.

ESTIMATED FLOCK MIXING

The high occurrence of flock mixing (50-70% of all observations) is consistent with the Habitat Selection Hypothesis (Alisauskas 1998). My estimate probably is biased high for snow geese banded in coastal marshes because of differing sampling properties of rice-prairies and coastal marshes, as evidenced by higher odds of flock mixing found for snow geese from coastal marshes. However, this bias should not cause overestimates of flock mixing for snow geese neck-banded in rice-prairies; half of all snow geese banded in rice-prairies flocked with snow geese neck-banded in coastal marshes.

ARE THERE TWO SNOW GOOSE POPULATIONS IN SOUTHWEST LOUISIANA?

My findings generally are consistent with the Habitat Selection Hypothesis (Alisauskas 1998), as indicated by: (1) the estimate of Ψ_{marsh} from the most parsimonious model (Table 7.2); and (2) high frequency occurrence ($\geq 50\%$) of flocks containing snow geese from both strata. I found that snow geese were segregated into rice-prairies and coastal marshes by morphometrics (Table 7.3), as reported 2 decades ago (Alisauskas 1988). In spite of this segregation, I

documented that snow geese banded in coastal marshes commonly move into rice-prairies, where they commonly flocked with snow geese banded in rice-prairies.

Future studies should examine movements of snow geese in southwest Louisiana using radio-tagged individuals to estimate time spent in each stratum, and whether a relationship exists between movement events and frequencies of marsh burns, weather events, and hunting disturbance. Body size in snow geese has declined in recent decades (Cooch et al. 1991, Alisauskas 2002), which could result in fewer snow geese being able to successfully utilize coastal marsh habitats (cf. Alisauskas 1998). Interestingly, snow geese in coastal marshes spent more time feeding than did those in rice-prairies (Chapter 6), which raises the question of whether snow geese are less adept at feeding in coastal marshes than in rice-prairies.

Geese generally are highly site-faithful, both to their breeding and wintering areas (Raveling 1979, Owen 1980, Prevett and MacInnes 1980, Hestbeck et al. 1995, Cooke et al. 1995). I speculate that many snow geese in southwest Louisiana: (1) sampled coastal marshes and rice-prairies in previous winters and used past experiences to select a stratum on arrival to Louisiana, i.e. neck-banded adult snow geese had already selected a stratum when they were banded; and (2) do not need to sample the other stratum because they already forage successfully in the stratum they currently used. Both Alisauskas (1998) and I found significant year-to-year variation in morphometrics which differed between strata, suggesting that body size and bill size strongly influence stratum selection in some years but less so in others. My covariate analysis suggests that morphometrics have little influence on decisions to move between strata (Table 7.6). Large bill size may enhance the competitive ability (Sutherland 1996) of individuals by enhancing their feeding success, but overall competitive ability probably also is influenced by individual traits such as age (i.e. experience with area), family size (Black and Owen 1989b, Gregoire and Ankney 1990), and the ability to tolerate behavioral interference (Gauvin and

Giraldeau 2004). Furthermore, decisions made by individuals invariably will be influenced by those of their flock-mates and their parents, i.e. movements of flock-mates probably are not independent (Prevett and MacInnes 1980, Krebs and Davies 1993, Krause and Ruxton 2002).

LITERATURE CITED

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons Inc, New York, New York, USA.
- Alerstam, T. 1990. Bird migration. Cambridge University Press, Cambridge, United Kingdom.
- Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. thesis, University of Western Ontario, London, Ontario, Canada.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. *Journal of Wildlife Management* 66:181-193.
- Alisauskas, R. T., and M. S. Lindberg. 2002. Effects of neck bands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. *Journal of Applied Statistics* 29:521-537.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 74:1780-1793.
- Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. *Evolution* 46:1084-1096.
- Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, P. C. Rasmussen, J. V. Remsen Jr., J. D. Rising and D. F. Stotz. 2004. Forty-fifth supplement to the American Ornithologists' Union *check-list of North American Birds*. *Auk* 121:985-995.
- Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent snow geese on their Gulf Coast winter range. Pages 495-515 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Batt, B. D. J., editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.

- Bell, M. C., A. D. Fox, M. Owen, J. M. Black, and A. J. Walsh. 1993. Approaches to estimation of survival in two arctic-nesting goose species. Pages 141-155 in J.-D. Lebreton and Ph. M. North, editors. *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland.
- Bellrose, F. C. 1980. *Ducks, geese, and swans of North America*. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Béchet, A., J.-F. Giroux, G. Gauthier, J. D. Nichols, and J. E. Hines. 2003. Spring hunting changes the environmental movements of migrating greater snow geese. *Journal of Applied Ecology* 40:553-564.
- Blums, P., J. D. Nichols, M. S. Lindberg, J. E. Hines, and A. Mednis. 2003. Factors affecting breeding dispersal of European ducks on Engure Marsh, Latvia. *Journal of Animal Ecology* 72:292-307.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference*. Springer-Verlag Telos, Berlin, Germany.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173-1187.
- Cam, E., D. Oro, R. Pradel, and J. Jimenez. 2004. Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *Journal of Animal Ecology* 73:723-736.
- Chalmers, G. A., and M. W. Barrett. 1982. Capture myopathy. Pages 84-94 in G. L. Hoff, and J. W. Davis, editors. *Noninfectious diseases of wildlife*. Iowa State University Press, Ames, Iowa, USA.
- Choquet, R., A.-M. Reboulet, R. Pradel, J. Gimenez, and J.-D. Lebreton. 2002. User's manual for U-CARE, version 2.0. Mimeographed document, CEFE/CNRS, Montpellier ([Ftp://Ftp.Cefe.Cnrs-Mop.Fr/Biom/Soft-CR/](http://Ftp.Cefe.Cnrs-Mop.Fr/Biom/Soft-CR/)).
- Cooch, E. G., and G. C. White. 2004. *Program MARK. Analysis of data from marked individuals. A gentle introduction, Third Edition*. Ithaca, New York, USA.
- Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* 72:503-512.
- Cooke, F. D., D. T. Parkin, and R. F. Rockwell. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105:467-479.
- Cox, R. R., Jr., and A. D. Afton. 1998. Use of mini-refuges by female northern pintails wintering in southwestern Louisiana. *Wildlife Society Bulletin* 26:130-137.

- Cramp, S., and K. E. L. Simmons. 1978. Handbook of the birds of Europe, the Middle East, and North Africa. Birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Dickson, K. M. 2000. The diversity of Canada geese. Canadian Wildlife Service Occasional Paper 103:11-24.
- Dill, H. H., and W. H. Thornsberry. 1950. A cannon-projected net trap for capturing waterfowl. *Journal of Wildlife Management* 14:132-137.
- Dzubin, A., and E. G. Cooch. 1992. Measurements of geese: general field methods. California Waterfowl Association, Sacramento, California, USA.
- Francis, C. M., and F. Cooke. 1993. A comparison of survival rate estimates from live recaptures and dead recoveries of lesser snow geese. Pages 169-83 in J.-D. Lebreton and Ph. M. North, editors. *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland.
- Frederiksen M., R. D. Hearn, C. Mitchell, A. Sigfússon, R. L. Swann, and A. D. Fox. 2004. The dynamics of hunted Icelandic goose populations: a reassessment of the evidence. *Journal of Animal Ecology* 41:315-334.
- Gauvin, S., and L.-A. Giraldeau. 2004. Nutmeg mannikins (*Lonchura punctulata*) reduce their feeding rates in response to simulated competition. *Oecologia* 139:150-156.
- Gulf Coast Joint Venture. 2001. Evaluation plan. Gulf Coast Joint Venture, Lafayette, Louisiana, USA.
- Harris, G. A. 1990. Grit site use by wildlife in southwestern Louisiana and southeastern Texas. MS thesis, Louisiana State University, Baton Rouge, Louisiana, USA.
- Hestbeck, J. B., J. D. Nichols, and R. D. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72:523-533.
- Hill, M. R. J., and R. B. Frederick. 1997. Winter movements and habitat use by greater snow geese. *Journal of Wildlife Management* 61:1213-1221.
- Hochbaum, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. *Transactions of the North American Wildlife Conference* 7:299-307.
- Hulland, T. J. 1985. Muscles and tendons. Pages 139-99 in K. V. F. Jubb, P. C. Kennedy and N. Palmer, editors. *Pathology of domestic animals*. Third edition. Academic Press Inc., New York, New York, USA.
- Johnson, R. A., and D. W. Wichern. 2002. *Applied multivariate statistical analysis*. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford series in ecology and evolution. Oxford University Press, New York, New York, USA.

- Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioral ecology. Third edition. Blackwell Science, Oxford, United Kingdom.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Madge, S., and H. Burn. 1988. Wildfowl: an identification guide to the ducks, geese and swans of the World. A & C Black Ltd., London, United Kingdom.
- Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publication, 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute and Wetlands International, Rönde, Denmark.
- Morez, V., G. Gauthier, and A. Reed. 2000. Effect of body condition on vulnerability of greater snow geese to hunting and capture. *Journal of Wildlife Management* 64:875-886.
- Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Lesser snow goose. In A. Poole, and F. Gill, editors. *Birds of North America*, No. 514. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Menu, S., J. B. Hestbeck, G. Gauthier, and A. Reed. 2000. Effects of neck bands on survival of greater snow geese. *Journal of Wildlife Management* 64:544-552.
- Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* 22:835-846.
- Nichols, J. D., C. Brownie, J. E. Hines, K. H. Pollock, and J. B. Hestbeck. 1993. The estimation of exchanges among populations or subpopulations. Pages 265-279 in J.-D. Lebreton and Ph. M. North, editors. *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland.
- Nyman, J. A., and R. H. Chabreck. 1995. Fire in coastal marshes: history and recent concerns. Pages 134-141 in S. I. Cerulean, and R. T. Engstrom, editors. *Fire in wetlands: a management perspective*. Proceedings of the Tall Timbers Fire Ecology Conference, Tall Timbers Research Station, Tallahassee, Florida, USA.
- Urbaniak, G. C. and S. Plous. 2003. Research Randomizer. [Online] Wesleyan University, Connecticut, USA. URL: <http://www.randomizer.org/>.
- Owen, M. 1980. Wild geese of the world: Their life history and ecology. Bt Batsford Ltd, London, United Kingdom.
- Owen, M. and J. Black. 1990. Waterfowl ecology. Blackie Publishers, Glasgow, Scotland.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1-97.

- Pradel, R., C. M. A. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwartz multisite capture-recapture model. *Biometrics* 59:43-53.
- Prevett, J. P., and C. D. MacInnes. 1980. Family and other social groups in snow geese. *Wildlife Monographs* 71:6-46.
- Raveling, D. G. 1979. Traditional use of migration and winter roost sites by Canada geese. *Journal of Wildlife Management* 43:229-235.
- Ricklefs, R. E., and D. B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pages in 13-41 in Wainwright, P. C., and S. M. Reilly, Editors. *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, Illinois, USA.
- Samuel, M. D., D. H. Rusch, and S. Craven. 1990. Influence of neck bands on recovery and survival rates of Canada geese. *Journal of Wildlife Management* 54:45-54.
- SAS Institute. 1999. *SAS/SYSTAT User's Guide*. Version 6. Fourth edition. SAS Institute. Cary, North Carolina, USA.
- Schmutz, J. A., D. H. Ward, J. S. Sedinger, and E. A. Rexstad. 1995. Survival estimation and the effects of dependency among animals. *Journal of Applied Statistics*. 22:673-681.
- Sulzbach, D. S., and F. Cooke. 1978. Elements of non-randomness in mass-captured samples of snow geese. *Journal of Wildlife Management* 42:437-441.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford, United Kingdom.
- Sutherland, W. J., and G. A. Allport. 1994. A spatial model of the interaction between bean geese and wigeon with the consequences for habitat management. *Journal of Animal Ecology* 63:51-59.
- Stevens, J. P. 2002. *Applied multivariate statistics for the social sciences*. Fourth edition. Lawrence Erlbaum Associates, Publishers, Mahwah, New Jersey, USA.
- Vickery, J. A., W. J. Sutherland, A. R. Watkinson, S. J. Lane, and J. M. Rowcliffe. 1995. Habitat switching by dark bellied brent geese *Branta bernicla bernicla* in relation to food depletion. *Oecologia* 103:499-508.
- U. S. Fish and Wildlife Service. 2004. Draft environmental impact statement: light goose management. Department of the Interior. U. S. Fish and Wildlife Service, Washington, D.C., USA.
- U. S. Fish and Wildlife Service. 2005. Data archived at the Cameron Prairie National Wildlife Refuge, Bell City, Louisiana, USA.
- Ydenberg, R. C., and H. H. Th. Prins. 1980. Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* 18:443-453.

Waterfowl Harvest and Population Survey Data. 2004. D. Fronczak compiled. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.

Weatherhead, P. J., and C. D. Ankney. 1984. A critical assumption of band-recovery models may often be violated. *Wildlife Society Bulletin* 12:198-199.

Welty, J. C. 1982. *The life of birds*. Third edition. Saunders College Publishing, Philadelphia, Ohio, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Supplement):120-139.

CHAPTER 8: MORPHOMETRICS OF JUVENILE SNOW GEESE WITHIN 2 DISTINCT HABITATS: A TEST OF THE FEEDING-EXERCISE HYPOTHESIS

INTRODUCTION

Lesser snow geese (*Chen caerulescens caerulescens*; hereafter snow geese) use rice-prairie and coastal marsh habitats during winter in southwest Louisiana (Alisauskas et al. 1988). Snow geese in coastal marshes forage primarily by digging for belowground parts of vegetation (hereafter grubbing), whereas those in rice-prairies mostly graze on agricultural plants and consume aboveground vegetation (hereafter grazing; Alisauskas et al. 1988, Batt et al. 1997, Alisauskas 1998). Grubbing requires 1.5 times more energy expenditure and more muscular activity than does grazing (Gauthier et al. 1984). Alisauskas (1998) recorded structural measurements in adult snow geese wintering in southwest Louisiana and reported that those from coastal marshes had larger bodies, thicker bills, longer skulls, and longer culmen lengths than did those from rice-prairies. Alisauskas (1998) hypothesized that small bill size was selected against in coastal marshes, because larger bills were better suited for grubbing. Snow geese in rice-prairies were assumed to forage successfully regardless of bill size (Phenotypic Selection Hypothesis; Alisauskas 1998).

Snow geese do not reach full size until they are 1 year old (Cooch et al. 1991, Cooke et al. 1995); thus, relationships between feeding habitat and morphology may differ between juveniles and adults. Foraging methods differ in postures and directional movements of neck, head and bill to grasp different food types (Zweers et al. 1994). Grubbing involves considerably more muscle effort than does grazing (Gauthier et al. 1984), and exercise during growth can contribute significantly to the enrichment of bone mass reached at young adulthood (Bailey et al. 1996, Judex and Zernicke 2000).

I hypothesized that reported differences in bill thickness, culmen length and skull width and height of adults between habitats (Alisauskas 1998) resulted from different exercises of grazing in rice-prairies as compared to grubbing in coastal marshes by juveniles during their first winter (hereafter Feeding-Exercise Hypothesis). Juveniles in rice-prairies (hereafter rice juveniles) probably experience less physical exercise of neck and head musculature than do those in coastal marshes (hereafter coastal juveniles). Thus, bone formation rates of juveniles in rice-prairies should be lower than for those in coastal marshes, leading to smaller-sized bills, skulls, and culmens when they reach adult size. Accordingly, the Feeding-Exercise Hypothesis predicts a relatively greater increase in morphometrics (i.e. greater hypertrophy) in coastal juveniles from early to late winter, relative to that observed in rice juveniles.

Diets of snow geese in coastal marshes (hereafter coastal diets) are relatively higher in fiber content (20% and 15%, respectively) and lower in protein content than are those in the rice-prairies (hereafter rice diets; 8% and 27%, respectively); digestibility of foods has an inverse relationship with fiber content and a positive relationship with protein content (Prop and Vulink 1992). Digestive organs in waterfowl generally increase in size in response to reduced digestibility (Miller 1975, Paulus 1982, Halse 1984, Thompson and Drobney 1996). In contrast, dietary diversity varies inversely with size of digestive organs of waterfowl (Moorman et al. 1992 and citations therein). Thus, I predicted that coastal juveniles would have larger digestive organs than would rice juveniles, to compensate for the lower digestibility of coastal diets, as reported for adult snow geese (cf. Alisauskas et al. 1988).

I tested the Feeding-Exercise Hypothesis by comparing morphometrics between juveniles banded and collected in rice-prairies and coastal marshes throughout winter. Alisauskas (1998) examined adult snow geese only; consequently, I also examined whether structural

measurements of juveniles varied with feeding habitat as previously reported for adults. Finally, I compared gut morphology between juveniles collected in the two habitats.

METHODS

STUDY AREA

My study area (10,764 km²) in southwest Louisiana was bordered by Sabine National Wildlife Refuge (NWR; 29°53'N, 93°23'W) on the west; Lake Charles and Highway 383 on the northwest; Highway 190 on the north; Highway 387 and Interstate 10 on the northeast; Highway 35 on the east, and the Gulf Coast on the south. Rice-prairies and coastal marshes previously were described in detail by Alisauskas (1988), Alisauskas et al. (1988), and Bateman et al. (1988).

Coastal marsh and rice-prairie habitats in southwest Louisiana generally are separated by the Intracoastal Canal (Bateman et al. 1988). Coastal marshes are comprised of fresh, intermediate, brackish, or saline wetlands, but fresh and intermediate marshes are not used frequently by snow geese; snow geese must fly about 32 km between brackish marshes and the rice-prairies (Bateman et al. 1988). Rice-prairies are former tall-grass prairies which have been extensively cultivated, mostly for rice, but also as pasture for cattle (Alisauskas 1988, Alisauskas et al. 1988, Bateman et al. 1988).

Snow geese and other waterfowl use several state and federal wildlife refuges within this area, from east to west: Marsh Island State Wildlife Refuge (SWR; 29°36'N, 91°52'W), State Wildlife Refuge (29°40'N, 92°09'W), Rockefeller SWR (29°40'N, 92°55'W), Lacassine NWR (29°55'N, 92°50'W), Cameron Prairie NWR (29°57'N, 93° 04'W), and Sabine NWR (29°53'N, 93° 30'W) (Bateman et al. 1988). Some private lands within the study area also are managed to attract waterfowl, either as mini-refuges or to enhance hunting opportunities (Harris 1990, Cox and Afton 1998).

Southwest Louisiana is the historical wintering area of snow geese within the Mississippi Flyway (Bateman et al. 1988, Cooke et al. 1988, Mowbray et al. 2000). Estimated snow goose numbers from the Midwinter Waterfowl Survey within my study area were 257,290 in 2001-2002, 239,121 in 2002-2003 and 335,253 in 2003-2004 (Waterfowl Harvest and Population Survey Data 2004). In these midwinter surveys, two-thirds of all snow geese were found in the rice-prairies, and 60 to 77% of all snow geese in coastal marshes were found at State Wildlife Refuge and/or Marsh Island SWR (Waterfowl Harvest and Population Survey Data 2004).

STRUCTURAL MEASUREMENTS OF BANDED JUVENILES

I measured 116 juvenile snow geese that were captured using rocket-nets (Dill and Thornsberry 1950) for banding (Appendix 4A; see Chapter 7). Following capture, I sexed individuals by cloacal examination (Hochbaum 1942) and aged them by plumage color (Cramp and Simmons 1978, Bellrose 1980, Madge and Burn 1988): (1) adult (after-hatch-year and older) white-phase snow geese are white with black wing-tips, whereas juveniles (hatch-year) are pale gray; and (2) adult blue-phase snow geese have white heads and blue-gray backs and bodies, whereas juveniles have dark heads; although juveniles have grayish backs and bodies like adults, juvenile plumage is browner above and paler below than that of adults. I measured total tarsus, head length, bill nares, bill thickness, culmen length, gape length, skull width, skull height, and wing length (± 0.1 mm) with a caliper (hereafter structural measurements; Alisauskas 1988, Dzubin and Cooch 1992, Alisauskas 1998).

COLLECTIONS AND DISSECTIONS OF SPECIMENS

I collected 71 juvenile snow geese from 20 November to 10 February of 2001-2002, 2002-2003, and 2003-2004, using .22 rifles and 12 gauge shotguns (Appendices 4B, 4C, and 4D). I placed collected specimens in plastic bags, froze, and transported them to a lab for further analysis at Louisiana State University.

I thawed collected specimens for 24-48 hours prior to measurements and dissections (Alisauskas 1988). I first aged and sexed each individual and then recorded structural measurements as described for banded juveniles (Alisauskas 1988, Dzubin and Cooch 1992, Alisauskas 1998). I then dissected each collected specimen to measure muscles associated with feeding. I also measured the minor pectoral muscles as a control because they were not expected to be associated with foraging; thus, they should be unaffected by different exercise outputs from different foraging methods. Specifically, I removed: (1) the dorsal neck muscles by rupturing adjoining fascia with a pinsetter; (2) dorsal muscles from the back of the skull (occiput) by rupturing adjoining fascia and excising the muscle by the third vertebrae; (3) jaw muscles by rupturing adjoining fascia and excising muscle from bone as needed; (4) minor pectoral muscles by excision by sternum and humerus, after opening the back; and (5) the 2 outermost muscles (1 from each side) from the tibio-tarsus.

Muscle Measurements from Collected Specimens

I measured the diameter (± 0.1 mm) of skull, neck, pectoral, and leg muscles (hereafter muscle diameter), and the fresh weight (± 0.1 g) of jaw, neck, skull, pectoral, and leg muscles (hereafter muscle weight). Excised jaw muscles were shaped too irregularly for measurements of diameter. I measured muscle diameter at the widest point of each muscle, except in neck and skull muscles, where I used the average from 3 measurements, taken at the two distal ends and at the center of each muscle. I averaged muscle diameters of paired muscles and I summed all fresh weights of paired muscles for subsequent statistical analysis.

Gut Measurements from Collected Specimens

I opened the abdominal cavity on the left side of each collected specimen and then carefully pulled out the alimentary tract and measured the length of upper digestive tract, small intestine, both ceca, and large intestine with a ruler (± 1 mm), and gizzard length with a caliper

(± 0.1 mm) (hereafter gut measurements). In some collected specimens, not all measurements were successful because of shot damage from collections; thus, degrees of freedom varied slightly among various statistical analyses.

STATISTICAL ANALYSIS

Testing of Feeding-Exercise Hypotheses

I classified all juvenile snow geese into 2 groups: (1) rice-prairies, snow geese measured at Cameron Prairie NWR, or collected in the rice-prairies of Sweet Lake, located 8-16 km north of Cameron Prairie NWR; or within 24 km west, or south of the town of Lake Arthur; and (2) coastal marshes, collected or measured at Rockefeller State Wildlife Refuge. I collected juveniles throughout winter; thus, collection date was a covariate in all my analyses in this chapter; 20 November was collection date = 1 and 10 February was collection date = 83.

I used $P = 0.05$ as the critical value (α) in all statistical analyses. I performed 4 multivariate analyses of covariance (MANCOVAs; PROC GLM, SAS Institute 1999) on (1) structural measurements from banded juveniles; (2) structural measurements from collected specimens; (3) muscle measurements from collected specimens; and (4) gut measurements from collected specimens. I ran separate MANCOVAs on structural measurements from banded juveniles and dissected specimens, because collected specimens were stored frozen for more than 3 months prior to dissection and, thus, structural measurements of collected specimens were influenced by the freezing.

Explanatory variables in all MANCOVAs were habitat, sex, collection date as covariate, and all interactions were included in the saturated model. I determined final MANCOVA models using backward stepwise variable selection, where I removed non-significant interactions, one at a time, and proceeded by repeating the analyses (Agresti 1996). A significant collection date x habitat interaction in MANCOVAs would indicate different growth rates (i.e.

different slopes between habitats for the relationship between collection date and morphometrics) between coastal marshes and rice-prairies, as predicted by the Feeding-Exercise Hypothesis. Thus, I always report this interaction regardless of whether it was significant. If the collection date x habitat interaction was significant, I used a *post hoc* analysis of covariance (ANCOVA; SAS Institute 1999) to examine which response variables exhibited different slopes between habitats. I compared differences between LSMEANS in the MANCOVAs (t-test) and I report Least-square means (hereafter LSMEANS; \bar{x} ; SAS Institute 1999) for all significant main effects (habitat, sex).

I also used Principal Components Analysis (PCA) to construct indices of size and shape in my morphological data from juvenile lesser snow geese (cf. Alisauskas 1998). In each PCA, I identified measurements that had the highest loadings within eigenvectors for each PC score. I then used each set of PC scores as response variables in 4 MANCOVAs, all of which had collection habitat (rice-prairies or coastal marshes), sex, collection date, and all their interactions as explanatory variables (Alisauskas 1998). However, using this method yielded exactly the same findings as did the MANCOVAs described above and added no new information to my findings; thus, I present only results from the original MANCOVAs. It should be noted that the two methods are equivalent but the PCA is useful for dimension reduction or identifying relationships between variables (see Alisauskas 1998).

RESULTS

MULTIVARIATE ANALYSES OF MEASUREMENTS

Structural Measurements from banded Juveniles

My final MANCOVA model contained habitat ($F = 3.13$, Num df = 9, Den df = 94, $P < 0.0025$), sex ($F = 3.48$, Num df = 9, Den df = 94, $P = 0.0010$), and collection date ($F = 4.21$,

Num df = 9, Den df = 94, P = 0.0001), and the habitat x collection date interaction (F = 2.23, Num df = 9, Den df = 93, P = 0.0235). The *post hoc* ANCOVAs indicated that the habitat x collection date interaction was not significant for any single response variable (P > 0.08).

LSMEANS from MANCOVA indicated that: (1) bill nares were larger (P < 0.0001) in coastal marshes (\bar{x} = 39.2 mm, SE = 0.4 mm) than in rice-prairies (\bar{x} = 35.6 mm, SE = 0.4 mm); (2) bill thickness was larger (P = 0.0382) in coastal marshes (\bar{x} = 32.7 mm, SE = 0.2 mm) than in rice-prairies (\bar{x} = 32.0 mm, SE = 0.3 mm); (3) bill nares, bill thickness, bill thickness, gape length, wing length, total tarsus, skull width, and skull height were larger in males than in females (Table 8.1); and (4) skull width was larger (P = 0.0003) in early winter (\bar{x} = 36.9 mm, SE = 0.3 mm) than in late winter (\bar{x} = 35.6 mm, SE = 0.3 mm).

Structural Measurements from Collected Specimens

My final MANCOVA included only sex (F = 2.29, Num df = 9, Den df = 59, P = 0.0284); the habitat x collection date interaction was not significant (F = 0.46, Num df = 9, Den df = 58, P = 0.8966). LSMEANS indicated that culmen length, bill nares, bill thickness, bill thickness, gape length, total tarsus, skull width, and skull height were larger in males than in females (Table 8.1).

Muscle Measurements from Collected Specimens

My final MANCOVA model contained habitat (F = 3.52, Num df = 9, Den df = 55, P = 0.0017) and collection date (F = 2.16, Num df = 9, Den df = 55, P = 0.0390); the habitat x collection date interaction was not significant (F = 0.82, Num df = 9, Den df = 54, P = 0.6007). LSMEANS indicated that: (1) jaw muscle mass was higher (P = 0.0063) in coastal marshes (\bar{x} =

Table 8.1. Least-square mean and standard errors (LSMEAN \pm SE) for structural measurements (mm) of 116 banded juvenile lesser snow geese and 71 dissected specimens in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. P-values from comparisons of LSMEANS (t-test) indicate whether these measurements differed significantly ($P < 0.05$) between sexes.

Measurements	Banded juveniles			Dissected specimens		
	Males (n = 58)	Females (n =58)	P	Males (n=34)	Females (n=37)	P
Culmen length	56.9 \pm 6.7	54.2 \pm 7.2	0.2073	56.8 \pm 0.5	54.1 \pm 0.5	0.0002
Bill nares	38.1 \pm 0.4	36.7 \pm 0.4	0.0207	35.6 \pm 0.4	34.5 \pm 0.3	0.0378
Bill thickness	33.0 \pm 0.2	31.9 \pm 0.3	0.0035	32.9 \pm 0.3	31.9 \pm 0.3	0.0256
Gape length	39.6 \pm 0.4	38.2 \pm 0.4	0.0208	38.9 \pm 0.4	37.2 \pm 0.4	0.0018
Head length	114.5 \pm 0.6	110.4 \pm 0.7	0.0001	113.9 \pm 0.7	109.7 \pm 0.7	0.0001
Wing length	400.0 \pm 2.4	388.8 \pm 2.5	0.0019	392.5 \pm 2.9	386.5 \pm 2.9	0.1470
Total tarsus	95.3 \pm 0.6	92.1 \pm 0.7	0.0007	97.1 \pm 0.7	93.5 \pm 0.7	0.0006
Skull width	37.0 \pm 0.3	35.5 \pm 0.3	0.0001	36.3 \pm 0.3	35.8 \pm 0.3	0.0496
Skull height	48.0 \pm 0.3	46.1 \pm 0.3	0.0001	47.8 \pm 0.3	46.4 \pm 0.3	0.0019

7.3 g, SE = 0.3 g) than in rice-prairies (\bar{x} = 6.3 g, SE = 0.3 g); (2) leg muscle mass was higher (P = 0.0331) in rice-prairies (\bar{x} = 15.5 g, SE = 0.4 g) than in coastal marshes (\bar{x} = 14.2 g, SE = 0.4 g); and (3) leg muscle diameter was higher (P = 0.0339) in rice-prairies (\bar{x} = 22.4 mm, SE = 0.42 mm) than in coastal marshes (\bar{x} = 21.2 mm, SE = 0.4 mm).

Gut Measurements from Collected Specimens

My final MANCOVA model contained only habitat (F = 13.91, Num df = 5, Den df = 62, P < 0.0001); the habitat x collection date interaction was not significant (F = 2.05, Num df = 5, Den df = 61, P = 0.0838). LSMEANS indicated that gizzard length was higher (P < 0.0001) in coastal marshes (\bar{x} = 93.3 mm, SE = 1.0 mm) than in rice-prairies (\bar{x} = 81.5 mm, SE = 1.0 mm).

DISCUSSION

FEEDING-EXERCISE HYPOTHESIS

I found little evidence of the Feeding-Exercise Hypothesis in my analysis of structural measurements; although the habitat x collection date interaction was significant in the MANCOVA for structural measurements, the following ANCOVAs detected no significant relationships. I believe this discrepancy between the MANCOVA and ANCOVA probably is explained by collection date being confounded with habitat during collection dates 1-30 (Appendix 4A). Thus, the significant habitat x collection date in the MANCOVA probably was an artifact of my sampling and presents little evidence for the Feeding-Exercise Hypothesis. My analyses of muscle measurements and gut measurements provided no evidence for the Feeding-Exercise Hypothesis; the habitat x collection date interaction was not significant in either MANCOVA model. Sampling effort for dissected specimens was relatively even with respect to

habitat (Appendix 4B-D) and, thus, confounding habitat and collection date was not a concern with data from collected specimens.

I found that juvenile snow geese from coastal marshes had larger culmens, and wider skulls than did those from rice-prairies. Moreover, I found that skull width, relative to other structural measurements, was smaller in early winter than late winter. This latter finding clearly contradicts predictions of the Feeding Exercise Hypothesis; other morphometric axes apparently grow faster than did skull width during the wintering period.

In testing the Feeding-Exercise Hypothesis, I assumed that coastal snow geese feed only by grubbing and rice snow geese feed by grazing (cf. Alisauskas 1998). However, feeding behavior of snow geese was not restricted entirely to grazing in rice-prairies and grubbing in coastal marshes (Appendix 5); snow geese use a combination of grazing and grubbing in both habitats. For example, snow geese in rice-prairies grub for belowground plant parts following intense rain, which softens the substrate sufficiently to allow such excavation (Alisauskas et al. 1998, see also Appendix 5). Thus, many juveniles probably forage by both grubbing and grazing during their first year of life, independent of feeding habitat.

I also assumed that individuals would not move between habitats during winter (cf. Alisauskas 1998). However, in another analysis, I found that snow geese did move between rice-prairies and coastal marshes (Chapter 7), suggesting that snow geese could experience all possible variations of feeding habitats and feeding behavior within a winter. Juvenile snow geese follow their parents or other adults to feeding locations and thus learn locations of feeding areas and migration routes (Raveling 1969, Pevett and MacInnes 1980, Owen 1980).

STRUCTURAL MEASUREMENTS FROM BANDED AND COLLECTED JUVENILES

Body size is heritable in snow geese (Cooke et al. 1995). Thus, I expected juveniles in coastal marshes to have larger structural measurements as previously reported for adults

(Alisauskas 1998). MANCOVA indicated that coastal juveniles had larger bills than did rice juveniles. The early development of large bill nares and bill thickness, observed in my sample of coastal juveniles, may reflect the importance of these adaptations towards feeding in coastal marshes (cf. Alisauskas 1998). Body size did not differ between habitats in juveniles as reported for adults (Alisauskas 1998, Chapter 7). Assuming that large body size and large bill thickness benefit adults feeding in coastal marshes (cf. Alisauskas 1998), juveniles that have not developed these adaptations may be better off foraging in rice-prairies than in coastal marshes.

My analysis indicated that juvenile males were structurally larger than were females, as expected based on the same measurements from adults snow geese (Cooke et al. 1995, Alisauskas 1998, Chapter 7). Fledging weights of goslings at LaPérouse Bay snow goose colony averaged 1600 g and 1500 g for males and females, respectively (Cooke et al. 1995). Thus, it is not surprising to find sexual size dimorphism in juveniles wintering in Louisiana. Sexual dimorphism in body size among birds generally either is due to sexual selection or ecological segregation of the sexes (Webster 1997). Selective mechanisms that maintain sexual size dimorphism in snow geese are not well understood (Cooke et al. 1995).

MUSCLE MEASUREMENTS OF COLLECTED SPECIMENS

My results indicated that rice snow geese had larger leg muscles than did coastal snow geese. Furthermore, coastal juveniles had slightly heavier (1 g, on average) jaw muscles than did rice juveniles, which is consistent with the hypothesis that grazing requires less muscle efforts than does grubbing (cf. Gauthier et al. 1984). I found no sexual differences in muscle measurements, which contrasts my findings of sexual dimorphism in structural measurements.

GUT MEASUREMENTS OF COLLECTED SPECIMENS

As predicted, I found that gut morphology of juveniles differed between habitats as reported for adult snow geese (Alisauskas 1988, Alisauskas et al. 1988). I found that coastal

juveniles had larger gizzards than did rice juveniles. Differences in gut measurements between rice-prairies and coastal marshes may reflect trade-offs in adaptations towards the respective diets in these habitats, and also their differing protein and fiber content and, thus, differences in digestibility (Alisauskas et al. 1988, Prop and Vulink 1992). A large gizzard is advantageous in grinding plant material that is low in digestibility, and adult snow geese in coastal marshes have relatively large gizzards (Alisauskas 1988, Alisauskas et al. 1988).

CONCLUSION

In conclusion, my results mostly generally inconsistent with the Feeding-Exercise Hypothesis. However, I found that rice and coastal juveniles differed in bill size and body size, as previously documented for adults (cf. Alisauskas 1998). My findings indicate that snow geese become sexually dimorphic in body size during their first winter of life. Rice and coastal juveniles differed slightly in morphology of musculature associated with foraging; coastal juveniles had, on average, 1g heavier jaw muscles than did rice juveniles. Finally, coastal juveniles had larger gizzards than did rice juveniles. These observed differences indicate that adaptations towards feeding habitats can influence feeding success of juvenile snow geese, which in turn may determine their probabilities of survival in the long term.

LITERATURE CITED

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons Inc, New York, New York, USA.
- Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Ph.D. thesis, University of Western Ontario, London, Ontario, Canada.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.

- Alisauskas, R. T., E. E. Klaas, K.A. Hobson, and C. D. Ankney. 1998. Stable-carbon isotopes support use of adventitious color to discern winter origins of lesser snow geese. *Journal of Field Ornithology* 69:262-268.
- Bailey, D. A., R. A. Faulkner, and H. A. McKay. 1996. Growth, physical activity, and bone mineral acquisition. *Exercise Sport Science Review* 24:233-266.
- Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent snow geese on their Gulf Coast winter range. Pages 495-515 in M. W. Weller, editor. *Waterfowl in winter*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Batt, B. D. J., editor. 1997. Arctic ecosystems in peril: report of the Arctic Goose Habitat Work Group. Arctic Goose Joint Venture special publication. U.S. Fish and Wildlife Service, Washington, D.C., USA; and the Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* 72:503-512.
- Cooke, F. D., D. T. Parkin, and R. F. Rockwell. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105:467-479.
- Cooke, F. D., R. F. Rockwell, and D. B. Lank. 1995. The snow geese of LaPérouse Bay. Natural selection in the wild. Oxford University Press, Inc., New York, New York, USA.
- Cox, R. R., Jr., and A. D. Afton. 1998. Use of mini-refuges by female northern pintails wintering in southwestern Louisiana. *Wildlife Society Bulletin* 26:130-137.
- Cramp, S., and K. E. L. Simmons. 1978. Handbook of the birds of Europe, the Middle East, and North Africa. Birds of the Western Palearctic. Oxford University Press, Oxford, United Kingdom.
- Dill, H. H., and W. H. Thornsberry. 1950. A cannon-projected net trap for capturing waterfowl. *Journal of Wildlife Management* 14:132-137.
- Dzubin, A., and E. G. Cooch. 1992. Measurements of geese: general field methods. California Waterfowl Association, Sacramento, California, USA.
- Gauthier, G., J. Bédard, and Y. Bédard. 1984. Comparison of daily energy expenditure of greater snow geese between two habitats. *Canadian Journal of Zoology* 62:1304-1307.
- Halse, S. A. 1984. Diet, body condition, and gut size of Egyptian geese. *Journal of Wildlife Management* 48:569-573.
- Harris, G. A. 1990. Grit site use by wildlife in southwestern Louisiana and southeastern Texas. MS thesis, Louisiana State University, Baton Rouge, Louisiana, USA.

- Hochbaum, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. *Transactions of the North American Wildlife Conference* 7:299-307.
- Johnson, R. A., and D. W. Wichern. 2002. *Applied multivariate statistical analysis*. Fifth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Judex, S., and R. F Zernicke. 2000. High-impact exercise and growing bone: relation between high strain rates and enhanced bone formation. *Journal of Applied Physiology* 88:2183-2191.
- Madge, S., and H. Burn. 1988. *Wildfowl: an identification guide to the ducks, geese and swans of the World*. A & C Black Ltd., London, United Kingdom.
- Miller, M. R. 1975. Gut morphology of mallards in relation to diet quality. *Journal of Wildlife Management* 39:168-173.
- Moorman, T. E., G. A. Baldassarre, and D. M. Richard. 1992. Carcass mass, composition and gut morphology dynamics of mottled ducks in fall and winter in Louisiana. *Condor* 94:407-417.
- Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Lesser snow goose. In A. Poole, and F. Gill, editors. *Birds of North America*, No. 514. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C, USA.
- Owen, M. 1980. *Wild geese of the world: Their life history and ecology*. Bt Batsford Ltd, London, United Kingdom.
- Paulus, S. L. 1982. Gut morphology of gadwalls in Louisiana in winter. *Journal of Wildlife Management* 46:483-489.
- Prevett, J. P, and C. D. MacInnes. 1980. Family and other social groups in snow geese. *Wildlife Monographs* 71:6-46.
- Prop, J., and T. Vulink. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* 6:180-189.
- Raveling, D. G. 1969. Social classes of Canada geese in winter. *Journal of Wildlife Management* 33:304-318.
- SAS Institute. 1999. *SAS/SYSTAT User's Guide*. Version 6. Fourth edition. SAS Institute. Cary, North Carolina, USA.
- Stevens, J. P. 2002. *Applied multivariate statistics for the social sciences*. Fourth edition. Lawrence Erlbaum Associates, Publishers, Mahwah, New Jersey, USA.
- Thompson, J. E., and R. D. Drobney. 1996. Nutritional implications of molt in male canvasbacks: variation in nutrient reserves and digestive tract morphology. *Condor* 98:512-526.

Zweers, G. A., H. Berkhoudt, and J. C. Vanden Berge. 1994. Behavioral mechanisms of avian feeding. *Advances in Comparative and Environmental Physiology* 18:241-279.

Waterfowl Harvest and Population Survey Data. 2004. D. Fronczak compiled. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.

Webster, M. S. 1997. Extreme sexual size dimorphism, sexual selection, and the foraging ecology of *Montezuma oropendolas*. *Auk* 114:570-580.

CHAPTER 9: GENERAL CONCLUSIONS

INCUBATION CONSTANCY

I documented that, at least in some years, Ross's geese are able to match the incubation constancy of the larger snow geese, contrary to the predictions of the Body-size Hypothesis (cf. Skutch 1962, Afton 1980, Afton and Paulus 1992). Further long-term comparative studies of incubation constancies of snow geese and Ross's geese are needed to evaluate environmental conditions that favor such high incubation constancies.

BROOD PATCH AREA

I documented that the defeathered ventral (brood patch) area of Ross's geese was positively related to clutch volume and negatively related to prolactin levels, but no such relationships were found in snow geese; thus, I conclude that more factors regulate brood patch area in Ross's geese than for snow geese. Furthermore, prolactin levels and body condition (as indexed by size-adjusted body mass) were inversely related in Ross's geese, but not in snow geese. These documented differences between species are consistent with the Body-Size Hypothesis (Afton and Paulus 1992), regardless of whether elevated prolactin levels (1) stimulate gonadal regression, feeding behavior, or both (Dawson and Sharp 1998, Buntin and Figge 1988), or (2) prolactin levels are stimulated by feeding or other behaviors (Criscuolo et al. 2002); all these explanations account for the interplay between body condition and incubation stage.

BROOD PATCH HISTOLOGY

I documented that 5 of 5 female snow geese and 1 of 5 female Ross's geese had fully developed brood patches. Differential brood patch development in these two closely related species probably is related to different energetic cost-benefit relationships, resulting from differences in incubation constancy, embryonic development, and body size. A fully-developed

brood patch may shorten the incubation period, but may not be necessary to incubate a clutch successfully (McFarlane Tranquilla et al. 2003). I argue that, because of their smaller size and concomitant lower fasting endurance compared to those of snow geese (Skutch 1962, Afton 1980, Afton and Paulus 1992), at least some Ross's geese benefit by either not developing brood patches or by maintaining them for shorter periods during incubation than do snow geese. Future studies should examine effects of individual variation on brood patch development and further test the three hypotheses proposed here, as well as comparing histology of brood patches among other waterfowl species.

BEHAVIOR OF WINTERING SNOW AND ROSS'S GEESE

I documented that Ross's geese spent more time feeding during winter than did snow geese, which is consistent with the Body-Size Hypothesis (Afton and Paulus 1992). Based on my estimated energy budgets, both species met their energy expenditures, but it is unlikely that they gain weight while in Louisiana (see Ankney 1982). Few Ross's geese benefit from family maintenance because most Ross's geese (1) are constrained to relatively longer feeding times than are snow geese, which in turn hinders them from devoting increased time to alert behavior and other forms of parental effort (Black and Owen 1989); or (2) flock with snow geese, which are socially dominant over Ross's geese, and Ross's goose families would not be any more successful in social encounters with snow geese than are lone and paired Ross's geese. Thus, Ross's geese seemingly employ a sneaking foraging strategy and compete intraspecifically for foraging patches where they are left relatively unharrassed by the larger snow geese. A similar behavioral study of the two species on spring stopover areas would be useful to determine if family maintenance leads to higher net energy intake for snow goose parents.

COMPARISON OF SNOW GOOSE BEHAVIOR IN 2 DISTINCT HABITATS

Contrary to my prediction, I found that among adults, snow geese in coastal marshes spent more time feeding than did snow geese in rice-prairies. Thus, my data suggest that water contents of composite diets (Alisauskas et al. 1988) is not an important predictor of time spent feeding in adult snow geese in coastal Louisiana. As predicted, I found that rice snow geese initiated relatively more foraging bouts, independent of age, which may compensate somewhat for their lower time spent feeding. As predicted, I found that juvenile snow geese in rice-prairies would spend more time feeding than would adult snow geese in the same habitat.

THE PHENOTYPIC SELECTION AND HABITAT SELECTION HYPOTHESES

Although many individuals are site-faithful, as indicated by the morphological segregation into rice-prairies and coastal marshes (Alisauskas 1998, this study), my results indicate that snow geese in rice-prairies and coastal marshes are one population and that snow geese commonly move between the two habitats. Finally, my results were more consistent with the Habitat Selection Hypothesis than the Phenotypic Selection Hypothesis in explaining morphological differences in snow geese between rice-prairies and coastal marshes (cf. Alisauskas 1998).

THE FEEDING-EXERCISE HYPOTHESIS

My analyses of structural measurements, muscle measurements, and gut measurements provided little evidence for the Feeding-Exercise Hypothesis. I found that juvenile snow geese from coastal marshes had smaller culmens, wider skulls, and larger tarsi than did those from rice-prairies.

LITERATURE CITED

Afton, A. D. 1980. Factors affecting incubation rhythms of northern shovelers. *Condor* 82:132-137.

- Afton A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851-862.
- Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52:403-414.
- Ankney, C. D. 1982. Annual cycle of body weight in lesser snow geese. *Wildlife Society Bulletin* 10:60-64.
- Black, J. M., and M. Owen. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37:199-209.
- Buntin, J.D., and G.R. Figge. 1988. Prolactin and growth hormone stimulate food intake in ring doves. *Pharmacology, Biochemistry, and Behavior* 31: 533-540.
- Criscuolo, F., O. Chastel, G.W. Gabrielsen, A. Lacroix, and Y. Le Maho. 2002. Factors affecting plasma concentrations of prolactin in the common eider *Somateria mollissima*. *General and Comparative Endocrinology* 125:399-409.
- Dawson A., and P.J. Sharp. 1998. The role of prolactin in the development of reproductive photorefractoriness and postnuptial molt in the European starling (*Sturnus vulgaris*). *Endocrinology* 139:485-490.
- Mcfarlane Tranquilla, L. A., R. W. Bradley, D. B. Lank, T. D. Williams, L.W. Loughheed, and F. Cooke. 2003. The reliability of brood patches in assessing reproductive status in the marbled murrelet: words of caution. *Waterbirds* 26:108-118.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152

APPENDIX 1: SUMMARY OF HISTOLOGICAL MEASUREMENTS OF BROOD PATCHES BY INDIVIDUAL GEESE

Means (mean±SE) from brood patch regions of 5 pairs of lesser snow geese and 5 pairs of Ross's geese, collected at Karrak Lake, Nunavut, Canada, 1999. See chapter 4 for description of tissues and statistical tests for differences between birds within each sex.

	Bird no. (n= no. images obtained for tissue thicknesses)	Dermal connective tissue thickness (µm)	Epidermis thickness (µm)	Other tissue thickness (µm)	Blood vessel area (µm ²) ^a	# Leukocyte count (cells/frame) ^a
Lesser snow geese	male #1 (n=19)	252.0±135.2	10.3±1.8	237.7±135.4	112.2±232.2	41.1±32.6
	male #2 (n=16)	104.6±2.5	10.4±1.8	385.1±0.7	104.1±219.4	39.3±27.8
	male #3 (n=17)	147.4±93.3	12.1±2.1	340.5±93.6	25.5±70.2	31.1±15.5
	male #4 (n=20)	189.3±99.7	11.8±1.9	298.9±99.6	20.6±61.8	13.7±11.4
	male #5 (n=16)	135.0±75.6	13.4±2.6	364.3±89.0	77.3±61.2	24.2±13.5
	female #1 (n=20)	364.6±111.9	22.6±8.1	112.7±114.6	2467.5±1131.8	109.3±45.0
	female #2 (n=19)	415.1±70.8	22.6±6.5	62.3±73.1	3749.3±1059.1	108.7±38.1
	female #3 (n=20)	462.0±6.2	38.0±6.2	0.0±0.0	1429.1±890.0	101.1±25.1
	female #4 (n=20)	309.1±43.9	26.6±7.2	167.8±52.9	3275.2±1473.3	75.3±23.6
	female #5 (n=17)	423.3±75.2	25.0±10.0	51.7±77.2	2264.7±1415.2	135.7±43.6
Ross's geese	male #1 (n=17)	119.7±81.1	16.3±4.1	37.0±83.3	20.3±36.9	18.4±11.7
	male #2 (n=18)	87.1±45.8	13.2±2.5	399.7±43.9	24.9±46.0	12.1±11.8
	male #3 (n=16)	96.4±50.6	15.4±3.2	388.1±52.1	53.2±99.7	39.9±24.0
	male #4 (n=17)	111.4±89.2	11.8±3.0	370.7±90.2	128.3±540.8	25.6±27.0
	male #5 (n=17)	74.8±23.1	13.2±3.7	411.9±24.0	8.0±21.0	16.5±11.6
	female #1 (n=19)	81.1±23.7	13.9±2.4	397.2±36.8	165.7±390.3	14.0±13.4
	female #2 (n=17)	80.2±45.5	11.5±2.7	408.3±46.1	125.7±159.4	13.7±13.3
	female #3 (n=15)	53.4±14.4	11.3±2.6	435.3±14.6	6.9±5.5	4.4±4.6
	female #4 (n=20)	50.6±19.8	11.6±2.8	437.5±21.0	104.8±305.4	9.7±14.7
	female #5 (n=18)	303.0±197.1	19.7±8.3	177.3±202.8	601.4±336.9	147.6±17.4

^a n were always 20 images/bird for blood vessel area and leukocyte count.

APPENDIX 2: SUMMARY OF OBSERVATION EFFORT IN SOUTHWEST LOUISIANA

Number of days spent observing lesser snow geese (hereafter snow geese) in each area during winters 2001-2002, 2002-2003, and 2003-2004 in southwest Louisiana. Effort in coastal marshes mostly was concentrated on Rockefeller State Wildlife Refuge, (hereafter Rockefeller) and State Wildlife Refuge (hereafter State WL). Other indicates days spent in rocket-netting snow geese for neck-banding, equipment maintenance, or days lost due to unfavorable weather conditions. State WL was added to the study area in winter 2002-2003. Snow geese generally were absent from Rockefeller SWR for most of November and late February.

Winter 2001-2002	Rice-prairies	Rockefeller	State WL ^a	Other
1-14 November	7	0	-	7
15-30 November	6	0	-	10
1-14 December	9	1	-	4
14-31 December	10	2	-	5
1-14 January	5	5	-	4
15-31 January	9	3	-	5
1-14 February	5	3	-	6
15-28 February	9	0	-	5

^a this area was not sampled in winter 2001-2002.

(Appendix continued)

(Appendix 2 continued)

Winter 2002-2003	Rice-prairies	Rockefeller	State WL	Other
1-14 November	9	0	0	5
15-30 November	9	0	2	5
1-14 December	8	2	0	4
14-31 December	5	4	1	7
1-14 January	7.5	4.5	0	2
15-31 January	8	6	0	3
1-14 February	7.5	2.5	0	4
15-28 February ^b	0	0	2	0

^b observations were abandoned on 15 February 2004, because snow geese left the study area.

(Appendix continued)

(Appendix 2 continued)

Winter 2002-2003	Rice-prairies	Rockefeller	State WL	Other
1-14 November ^c	6	0	0	3
15-30 November	11	1	0	5
1-14 December	9	0	0	5
14-31 December	5	3	4	5
1-14 January	7	3	0	4
15-31 January	4	2	9	2
1-14 February ^d	2	0	0	8

^c observations began on 10 November 2003, because of later arrival of snow geese this winter.

^d observations ended on 10 February 2004 because snow geese left the study area.

APPENDIX 3: SEX RATIOS AND SAMPLE SIZES AT EACH BANDING LOCATION IN SOUTHWEST LOUISIANA

Percentages of males (n) in neck-banded samples of lesser snow geese captured with rocket-nets at 4 locations in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004.

Winter	Cameron Prairie NWR	Rockefeller State Wild- life Refuge	Sabine ^a NWR	Oak ^b Island	Average ^c
2001-2002	38.8%(67)	41.7%(175)	51.0%(49)	-	42.6%(345)
2002-2003	36.5%(181)	41.1%(207)	46.3%(108)	42.3%(26)	40.6%(522)
2003-2004	49.1%(55)	47.9%(48)	-	56.5(23)	50.0(126)

^a No bandings in 2003-2004

^b No bandings in 2001-2002

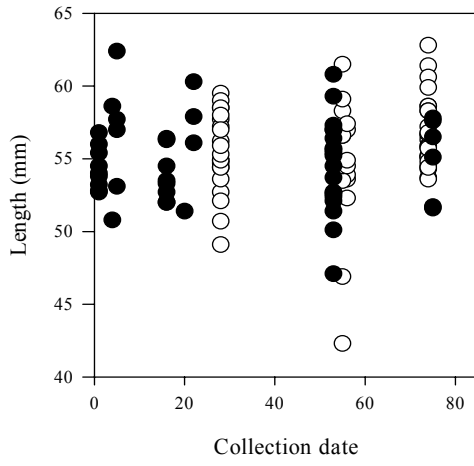
^c Weighted average percentage of males from all banding locations within each winter

APPENDIX 4: RELATIONSHIPS BETWEEN COLLECTION DATE AND MORPHOMETRICS OF JUVENILE LESSER SNOW GEESE

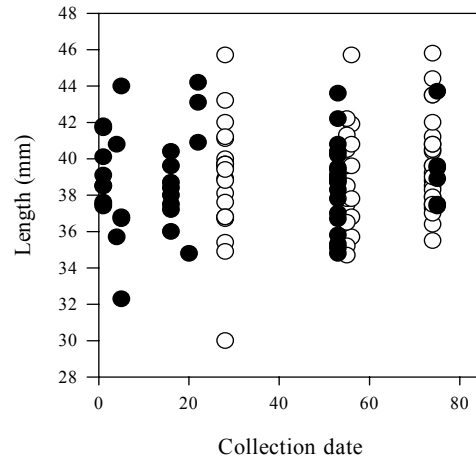
APPENDIX 4A: RELATIONSHIPS BETWEEN COLLECTION DATE AND STRUCTURAL MEASUREMENTS OF BANDED JUVENILE LESSER SNOW GEESE

A total of 116 juveniles were banded and measured in southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Collection date = 1 is 20 November, and Collection date = 83 is 10 February. Solid symbols indicate snow geese from rice-prairies, whereas open symbols indicate snow geese from coastal marshes.

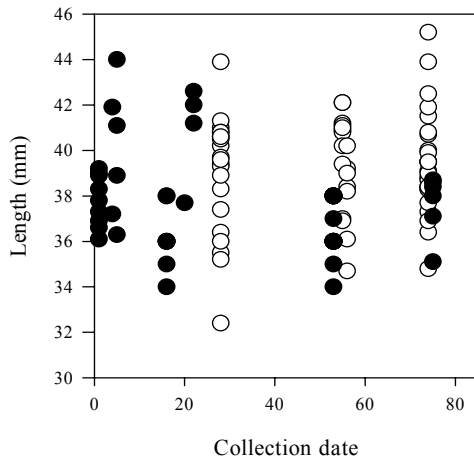
A: Culmen length



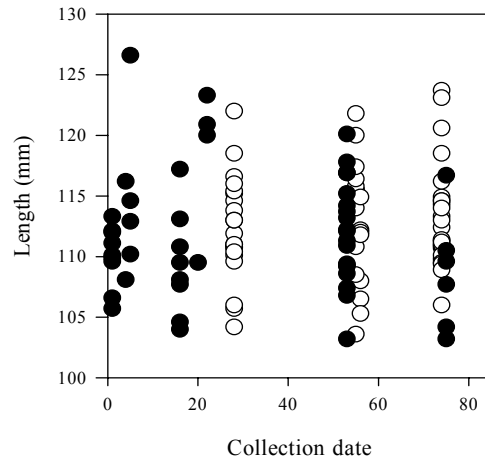
D: Gape length



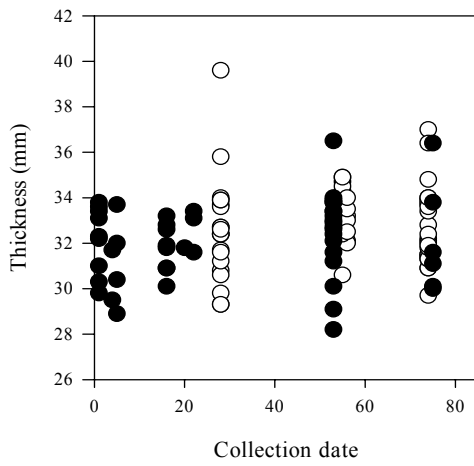
B: Bill nares



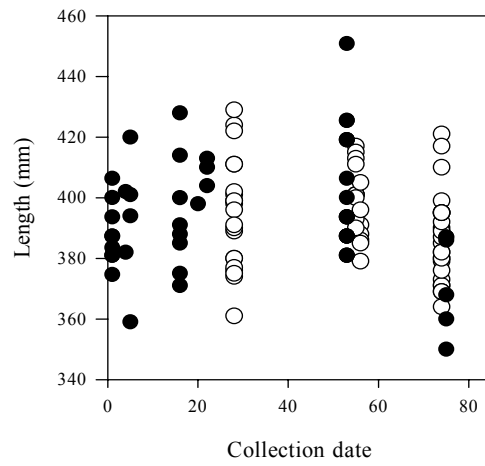
E: Head length



C: Bill thickness



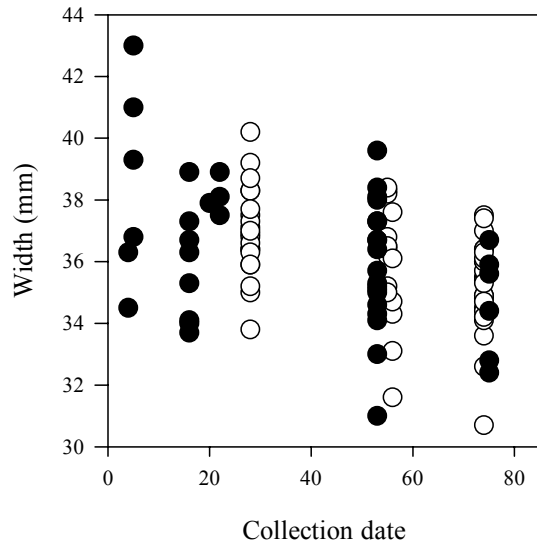
F: Wing length



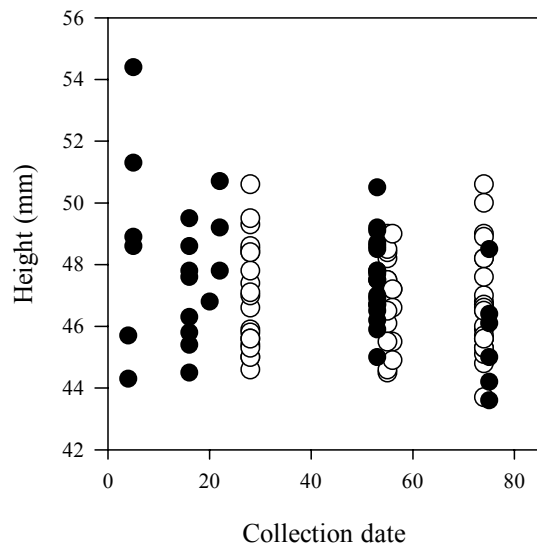
(Appendix continued)

(Appendix 4A continued)

G: Skull width



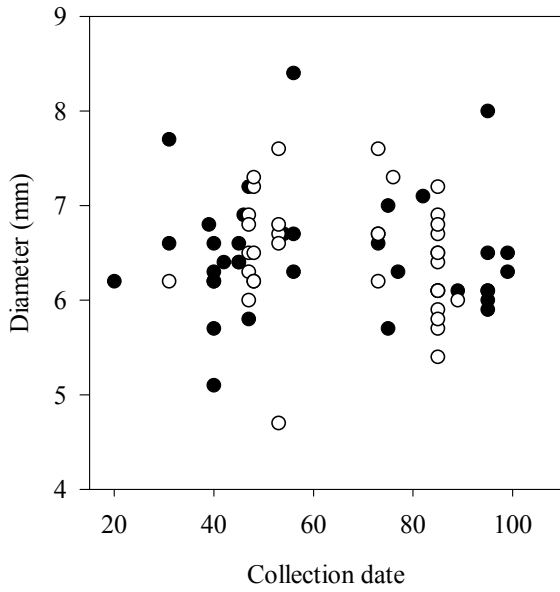
F: Skull height



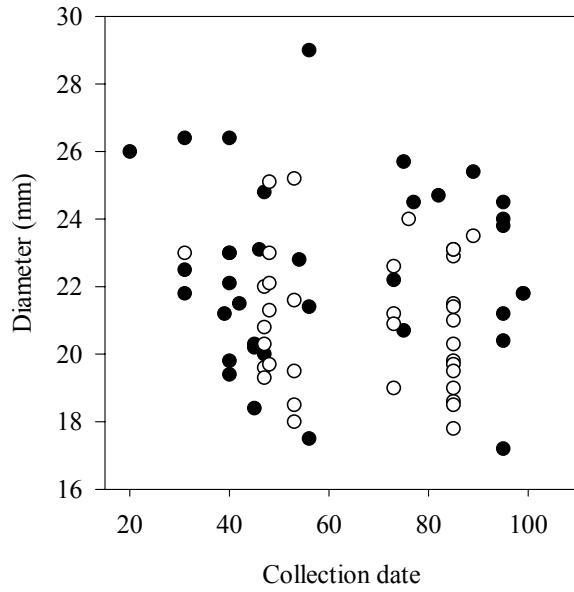
APPENDIX 4B: RELATIONSHIPS BETWEEN COLLECTION DATE AND MUSCLE DIAMETER OF COLLECTED SPECIMENS OF JUVENILE LESSER SNOW GEESE

A total of 71 juveniles were collected, dissected and measured. Specimens were collected from southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Collection date = 1 is 20 November, and Collection date = 83 is 10 February. Solid symbols indicate snow geese from rice-prairies, whereas open symbols indicate snow geese from coastal marshes.

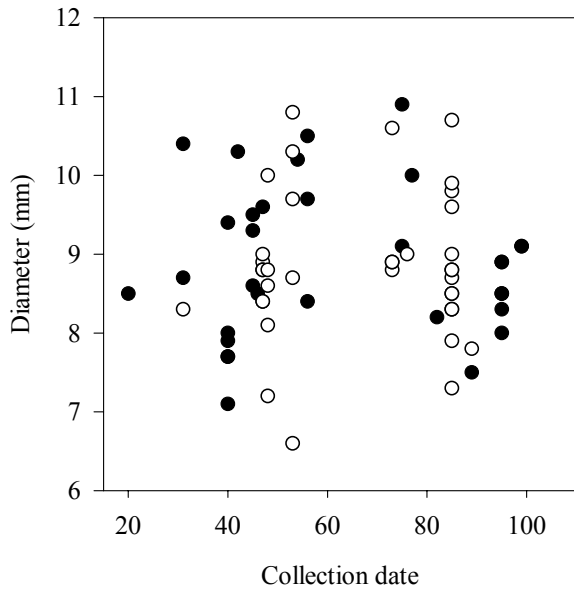
A: Neck muscle diameter



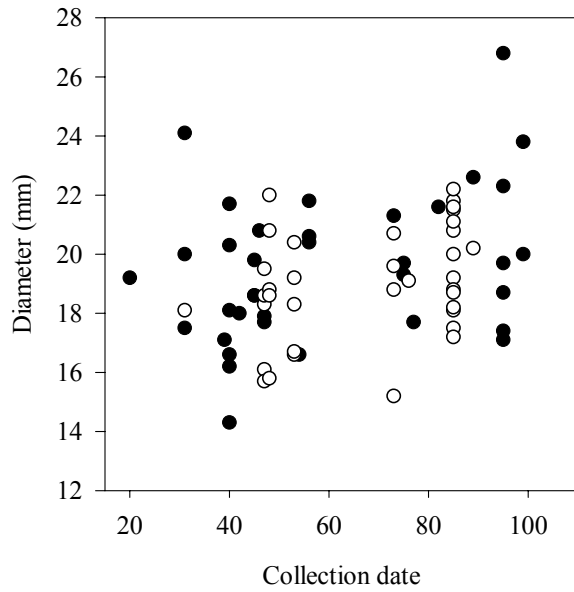
C: Leg muscle diameter



B: Skull muscle diameter



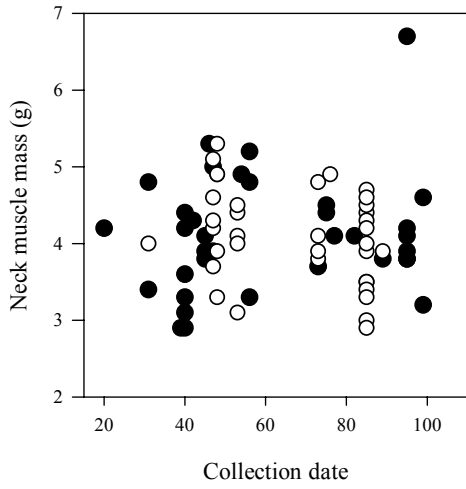
D: Pectoral muscle diameter



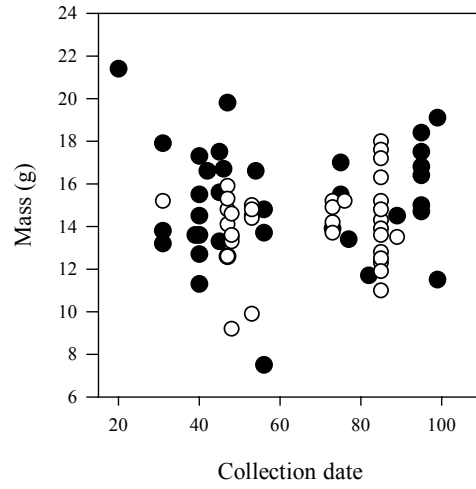
APPENDIX 4C: RELATIONSHIPS BETWEEN COLLECTION DATE AND MUSCLE WEIGHTS OF COLLECTED SPECIMENS OF JUVENILE LESSER SNOW GEESE

A total of 71 juveniles were collected, dissected and measured. Specimens were collected from southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Collection date = 1 is 20 November, and Collection date = 83 is 10 February. Filled symbols indicate snow geese from rice-prairies, whereas open symbols indicate snow geese from coastal marshes.

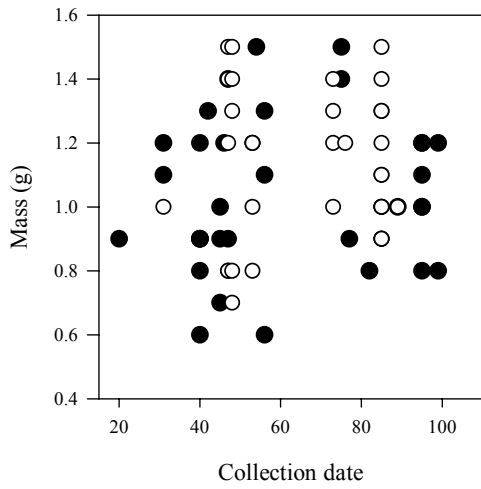
A: Neck muscle mass



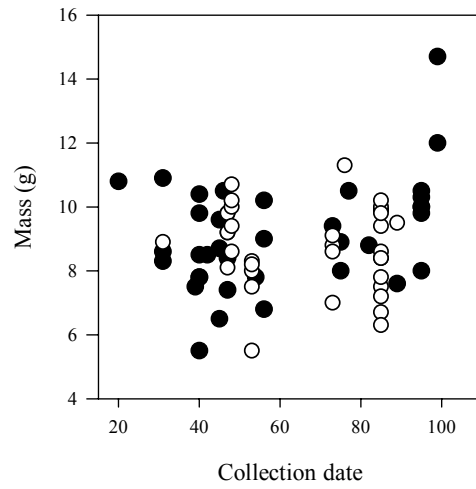
D: Leg muscle mass



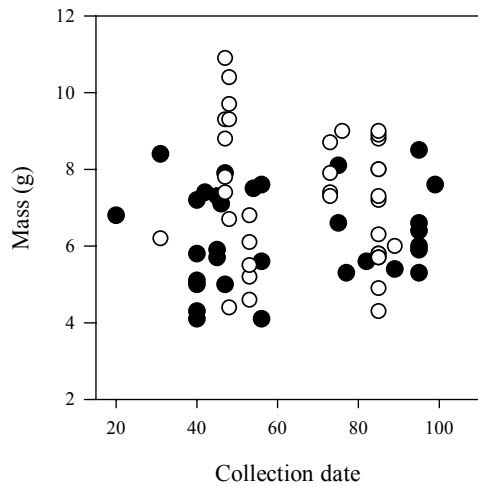
B: Skull muscle mass



E: Pectoral muscle mass



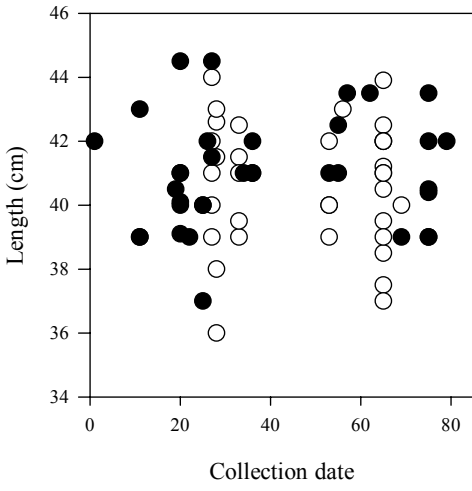
C: Jaw muscle mass



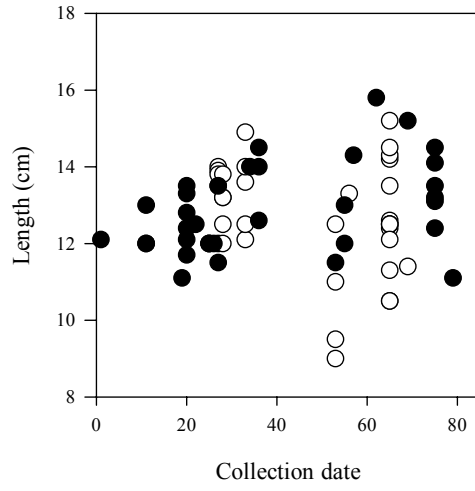
APPENDIX 4D: RELATIONSHIPS BETWEEN COLLECTION DATE AND GUT MEASUREMENTS OF COLLECTED SPECIMENS OF JUVENILE LESSER SNOW GEESE

A total of 71 juveniles were collected, dissected and measured. Specimens were collected from southwest Louisiana in winters 2001-2002, 2002-2003, and 2003-2004. Collection date = 1 is 20 November, and Collection date = 83 is 10 February. Solid symbols indicate snow geese from rice-prairies, whereas open symbols indicate snow geese from coastal marshes.

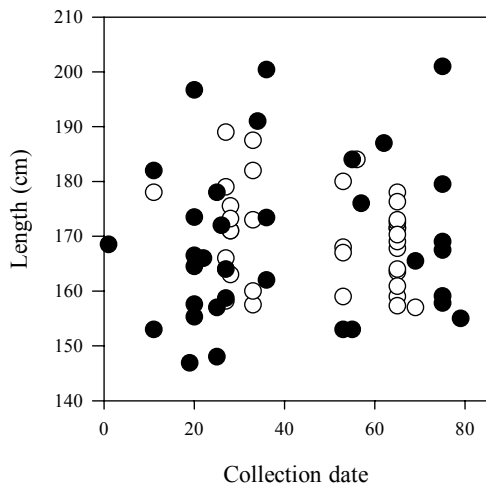
A: Upper digestive tract



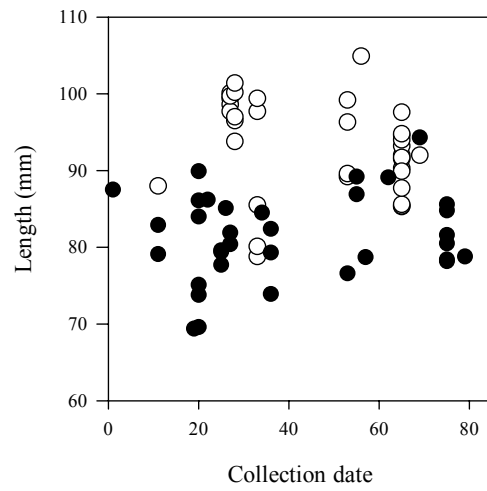
D: Large intestine



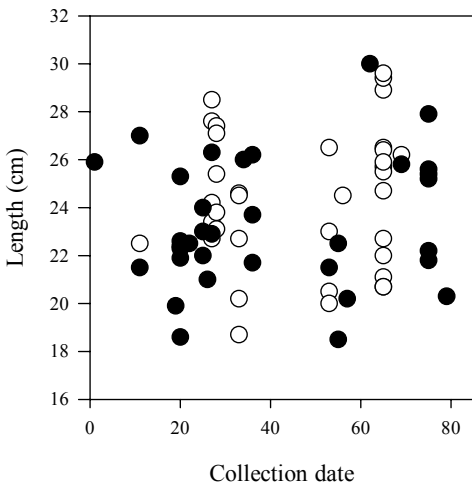
B: Small intestine



E: Gizzard



C: Ceca



APPENDIX 5: SUMMARY OF FEEDING BEHAVIOR BY LESSER SNOW GEESE AND ROSS'S GEESE IN SOUTHWEST LOUISIANA

Least-square mean (LSMEAN) percent time spent in activities by snow geese in rice-prairies, snow geese in coastal marshes, and Ross's geese in southwest Louisiana in winters 2002-2003, and 2003-2004. Note that all types of feeding behavior, i.e. grubbing, searching, and grazing were observed in all groups. Ross's geese never were observed in coastal marshes. ASE indicates asymptotic standard error.

Species/		Adults		Juveniles	
Habitat	Activity	LSMEAN	ASE	LSMEAN	ASE
Snow geese / Rice-prairies	Alert	26.0	1.6	14.3	2.2
	Grubbing	3.5	1.6	2.7	2.2
	Searching	1.1	1.6	2.4	2.2
	Grazing	35.9	1.6	49.3	2.2
	Locomotion	4.2	1.6	5.6	2.2
	Inactive	29.3	1.6	25.6	2.2
Snow geese / Coastal marshes	Alert	27.1	3.4	10.4	5.6
	Grubbing	47.7	3.4	37.0	5.6
	Searching	0.7	3.4	1.9	5.6
	Grazing	3.0	3.4	0.4	5.6
	Locomotion	2.2	3.4	1.2	5.6
	Inactive	19.3	3.4	49.2	5.6

(Appendix continued)

(Appendix 5 continued)

Species/		Adults		Juveniles	
Habitat	Activity	LSMEAN	ASE	LSMEAN	ASE
Ross's geese /	Alert	21.9	2.7	20.5	4.3
Rice-prairies	Grubbing	0.2	2.7	0.4	4.3
	Searching	2.2	2.7	1.7	4.3
	Grazing	52.3	2.7	50.5	4.3
	Locomotion	5.5	2.7	7.2	4.3
	Inactive	17.9	2.7	19.7	4.3

APPENDIX 6: LETTER (E-MAIL) OF PERMISSION FOR REPRINTING FROM *THE AUK*

Mr. Jón Einar Jónsson
School of Renewable Natural Resources
Louisiana State University
Baton Rouge, LA 70803 USA

MS#04-169 Version 3

Dear Mr. Jónsson,

Thank you for submitting your revised manuscript, *ECOLOGICAL AND PHYSIOLOGICAL FACTORS AFFECTING BROOD PATCH AREA AND PROLACTIN LEVELS IN ARCTIC-NESTING GEESE*, for publication in *The Auk*. This version of your manuscript was read by Associate Editor Alfred M. Duffy, Jr. and me. I am pleased to accept your work for publication in the April 2006 issue of *The Auk*. Thank you for your hard work on this manuscript and your serious attempt to shorten it. Your paper will make an important contribution to the literature.

Please e-mail Project Manager Mark Penrose (auk@uark.edu) and indicate your preference of French or Spanish for the second abstract. Also please advise Mark if you plan to be away from your office for an extended period prior to publication as he will be contacting you about final editing.

Finally, your request to include a copy of the manuscript as a portion of your Ph.D. dissertation is hereby granted. Please be sure to acknowledge that the paper has been accepted for publication in an upcoming issue of *The Auk*, in 2006.

Thank you again for submitting your work to *The Auk*. I look forward to seeing your work in print.

Sincerely,

Spencer G. Sealy

APPENDIX 7: LETTER (E-MAIL) OF PERMISSION FOR REPRINTING FROM *THE JOURNAL OF COMPARATIVE PHYSIOLOGY B*

Dear Jón,

I think it would be acceptable to refer to this paper in your thesis, with the citation listed as "in review, Journal of Comparative Physiology B".

I am pleased to hear you will be resubmitting your paper for consideration by the Journal.

Best regards,

Hannah

Hannah V. Carey, Ph.D.
Editor, Journal of Comparative Physiology B
Professor, Department of Comparative Biosciences
School of Veterinary Medicine
University of Wisconsin
2015 Linden Dr Madison, WI 53706
608-263-0418
608-263-3926 (FAX)
careyh@vetmed.wisc.edu
<http://www.vetmed.wisc.edu/people/careyh>

----- Original Message -----

From: "Jón Einar Jónsson" <jjonssl@lsu.edu>
To: "'Hannah Carey'" <careyh@svm.vetmed.wisc.edu>
Cc: <jcpb@uni-marburg.de>
Sent: Tuesday, August 16, 2005 8:42 AM
Subject: RE: Journal of Comparative Physiology - B

Dear Dr. Carey

I received 2 e-mails from you, containing editorial comments from 3 reviewers. I found the feedback very useful and I, of course, plan to re-submit the paper to JCPB as soon as possible.

Best regards

Jón Einar Jónsson

Doctoral Candidate
School of Renewable Natural Resources
Louisiana State University
Baton Rouge
LA 70803

-----Original Message-----

From: Hannah Carey [<mailto:careyh@svm.vetmed.wisc.edu>]
Sent: 15. ágúst 2005 20:57
To: Jón Einar Jónsson
Cc: jcpb@uni-marburg.de

Subject: Re: Journal of Comparative Physiology - B

Dear Dr. Jonsson:

I will check with the journal editorial office to determine whether it is permissible to site this paper in your thesis as "in review" in JCP-B. However, this depends on what you have decided to do based on the decision letter and the comments from the three reviewers that I sent to you in the last 1-2 weeks. Please let me know if you did not receive that information.

Sincerely,

Hannah Carey, Ph.D.
Editor, JCP-B

VITA

Jón Einar Jónsson was born January 5, 1975, in Reykjavík, Iceland. He is the son of Jón Abraham Ólafsson and Sigríður Þorsteinsdóttir. Jón Einar has two older sisters, Ingveldur and Helga Jónsdóttir. Jón Einar resided in Reykjavík until he enrolled at Louisiana State University (LSU) in 2000. Jón Einar graduated from Menntaskólinn við Hamrahlíð, Reykjavík, in May 1994. He graduated with a Bachelor of Science degree in biology from the University of Iceland in June 1997. His undergraduate thesis was titled “Distribution of Eurasian Wigeon on the north basin of Lake Mývatn [Iceland] in 1995-96”, and was directed by Dr. Árni Einarsson. Jón Einar was employed as a graduate student and research technician with Dr. Arnþór Garðarsson at the Institute of Biology, University of Iceland, from June 1997 until December 1999. He graduated with a Master of Science degree from the Biology Department of the University of Iceland in February 2000, under the direction of Dr. Arnþór Garðarsson. His thesis was titled, “The Social System of Dabbling Ducks during Winter”, and dealt with the wintering behavior of mallard, Eurasian wigeon, and Eurasian teal in southwest Iceland. Jón Einar also was involved in monitoring the populations of cormorant and harlequin, as well as participating in various surveys and environmental impact assessments. During January 2000 until July 2000, Jón Einar was an instructor in biology and chemistry at Kvennaskóli Junior College, Reykjavík. In August 2000, he enrolled in the Doctor of Philosophy program at LSU initiating a dissertation titled, “Effects of Body Size on Goose Behavior: Lesser Snow Goose and Ross’s Goose”, under the direction of Dr. Alan D. Afton.