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LESSER SNOW GEESE AND ROSS'S GEESE FORM MIXED FLOCKS DURING WINTER BUT DIFFER IN FAMILY MAINTENANCE AND SOCIAL STATUS

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ABSTRACT.—Smaller species are less likely to maintain families (or other forms of social groups) than larger species and are more likely to be displaced in competition with larger species. We observed mixed-species flocks of geese in southwest Louisiana and compared frequencies of social groups and success in social encounters of Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter Snow Geese) with that of the smaller, closely-related Ross's Geese (*C. rossii*). Less than 7% of adult and <4% of juvenile Ross's Geese were in families, whereas 10–22% of adult and 12–15% of juvenile Snow Geese were in families. Snow Geese won 70% of interspecific social encounters and had higher odds of success against Ross's Geese than against individuals of their own species. The larger Snow Geese maintain families longer than Ross's Geese, which probably contributes to their dominance over Ross's Geese during winter. Predator vigilance probably is an important benefit of mixed flocking for both species. We suggest the long-standing association with Snow Geese (along with associated subordinate social status) has selected against family maintenance in Ross's Geese. Received 23 August 2007. Accepted 27 February 2008.

Body size seemingly influences social behavior and foraging behavior in many animals (Calder 1996). Body size has important physiological implications for birds: (1) rate of heat loss increases with decreasing body size because of increasing surface to volume ratio (Goudie and Ankney 1986, Calder 1996); (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 affects the rate of energy extraction from food (Demment and Van Soest 1985); and (4) larger species generally have greater fasting endurances than smaller species (Goudie and Ankney 1986, Calder 1996, Jónsson et al. 2007). Smaller species are relatively less likely to maintain social groups, generally select more sheltered habitats, and consume more specialized diets (Jarman 1974, Shelley et al. 2004). Smaller species also are more likely to be displaced in competition with larger species, regardless of numbers present (Shelley et al. 2004) and often use scramble tactics in competition for food

(Krause and Ruxton 2002). Smaller species generally are more vulnerable to predator attacks than larger species, but can benefit by forming mixed flocks with larger species, which at times have better predator detection capabilities (McWilliams et al. 1994, Kristiansen et al. 2000, Randler 2004).

Most geese, including Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter Snow Geese) maintain families from one breeding season to the beginning of the next (family social system) (Boyd 1953; Raveling 1970; Prevett and MacInnes 1980; Black and Owen 1989a, b; Gregoire and Ankney 1990; Kalmbach 2006). Larger goose families generally are dominant over smaller families, pairs, and lone geese (Loonen et al. 1999, Stahl et al. 2001, Kalmbach 2006). Parents apparently profit from juvenile assistance when defending patches of food from other flock members (contributor effect hypothesis, Black and Owen 1989b).

Conversely, smaller goose species may not maintain families in winter (McWilliams and Raveling 1998). In California, Ross's Geese (*C. rossii*) form denser flocks than larger goose species when foraging on grasslands where they often associate with Cackling Geese (*Branta hutchinsii*) (Johnson and Raveling 1988, McWilliams and Raveling 1998). Only a small percentage of Ross's Geese in California are paired or in families (dense-flock social system) (Johnson and Raveling

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1988, McWilliams and Raveling 1998). Family maintenance varies in relation to food choices (seeds vs. leafs and tubers) and fine-scale spatial distribution of selected food plants among habitats (McWilliams and Raveling 1998).

Ross's Geese probably are more at risk from avian predators than are larger goose species and predation pressure may have been an important evolutionary factor (albeit not the only factor) influencing their social system during winter (McWilliams et al. 1994). In addition, denser flocks may convey benefits of decreased nearest neighbor distance, i.e., birds in denser flocks are able to spend more time feeding and less time vigilant (Fernandez-Juricic et al. 2004, 2007).

Southwest Louisiana is a historical wintering area for Snow Geese (Jónsson and Afton 2006 and citations therein), but Ross's Geese only began wintering in Louisiana during the last decade (Jónsson 2005). Ross's Geese in Louisiana occur only in rice-prairies (cultivated former tall-grass prairie) where they primarily forage in rice fields in mixed flocks with Snow Geese. Ross's Geese have small bills that are adapted for grazing on grass (Ryder and Alisauskas 1995). Thus, they are rarely found in marshes along the Gulf Coast, which are historical habitats of Snow Geese (which have larger bills adapted for excavation of marsh plants) (Alisauskas 1998).

Dominant goose species can affect feeding behavior, distribution, and food selection of less aggressive species when feeding in mixed flocks (Kristiansen and Jarrett 2002). Interspecific dominance relationships often are affected by the number of individuals present from each species (i.e., the more numerous species is dominant within mixed flocks; Fox and Madsen 1981, Madsen 1985, Gawlik 1994), although exceptions are known (Kristiansen and Jarrett 2002).

We present the first quantitative comparison of (1) frequencies of pairs and families, and (2) frequencies and outcomes of intra- and interspecific social encounters of Ross's Geese and Snow Geese in mixed wintering flocks. Our study provides a comparison of two closely-related species of varying size foraging together on the same plant species and controls for effects of macro habitat, geo-

graphical location, season, and climate (Jónsson et al. 2007).

METHODS

Study Area.—We observed Snow Geese and Ross's Geese in the rice prairie region of southwest Louisiana in winters 2002–2003 and 2003–2004 (Jónsson 2005; Jónsson and Afton 2006, 2008). Rice prairies are former tall-grass prairies which are extensively cultivated and managed, mostly for rice, but also as pasture for cattle (Alisauskas et al. 1988, Bateman et al. 1988). This area has been described by Alisauskas et al. (1988) and Bateman et al. (1988).

We exclusively observed mixed flocks comprised of Snow Geese and Ross's Geese using foraging habitats, i.e., non-flooded rice-fields, which were uncut, stubble, tilled, or fallow (Alisauskas et al. 1988, Jónsson 2005). Ross's Geese comprised, on average, 7% of observed mixed white goose flocks during our study. Estimated combined Snow Goose and Ross's Goose numbers on our study area were 257,119 in 2002–2003 and 360,487 in 2003–2004 (Fronczak 2004).

Sampling of Focal Geese.—Three trained observers and JEJ collected behavioral data in winters 2002–2003 and 2003–2004; JEJ was the only observer present in both winters and trained other observers, until results of observation of the same focal birds were nearly identical among observers (Jónsson and Afton 2006, 2008). We are confident that inter-observer variation between or within years did not bias our results.

We sampled goose behavior 3–4 days/week from 10 November until 10 February each winter. Observations were made during daylight between 0800 and 1700 hrs CST. Mixed flocks were large (a few hundred to a few thousand), mobile, and flushed often; thus, risk of repeated sampling of individuals was minimal.

Observers used 20× spotting scopes and collected 5 to 10-min focal sampling observations of randomly selected individuals (Altmann 1974). We used sequences of 20 random numbers to select focal geese within a field of vision, counting from left or right until a goose was located that corresponded to each random number.

Time of day was not a variable of biological

interest in this study. We attempted *a priori* to control for time of day variation in behavior by alternating between species during field observations to ensure that comparisons between species were unbiased (Jónsson and Afton 2006, 2008). Both species were sampled equally during mid-day (1100–1300 hrs) when geese were relatively prone to cease activities and rest.

We assigned age classes to Snow Geese and Ross's Geese based on plumage color and patterns (Ryder and Alisauskas 1995, Mowbray et al. 2000). We assigned pair and family status to individuals under observation based on mutual participation in social encounters, mutual chasing or avoiding other geese, and coordinated directions of locomotion (Raveling 1970, Black and Owen 1989a, Gregoire and Ankney 1990). We categorized focal individuals into five social groups (after Boyd 1953, Raveling 1970, Gregoire and Ankney 1990): (1) *lone adult*, a lone after-hatch-year goose; (2) *parent*, adult goose bonded (i.e., paired) with another adult goose, accompanied by at least one hatch-year bird; (3) *paired non-parent*, adult goose bonded with another adult goose without hatch-year birds; (4) *juvenile in family*, hatch-year goose accompanied by adult parents; and (5) *lone juvenile*, a lone hatch-year goose.

We recorded frequencies of social encounters between focal geese and other geese, scoring wins if opponents responded to interactions by avoiding or fleeing focal geese; focal birds were assigned a loss if an opponent chased them (Raveling 1970, Gregoire and Ankney 1990). We only recorded social encounters directly involving focal geese, their mates, parents or offspring.

Statistical Analyses.—We 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, which were categorical explanatory variables. Final models were selected using backwards stepwise model selection (Agresti 1996), except the age \times social group interaction was fixed (regardless of significance) in this model because pairs without juveniles were not observed in the juvenile category.

We constructed generalized linear models

based on normal and Poisson distributions; the Poisson log-linear model is equivalent to a logistic regression based on the multinomial distribution (Agresti 1996). We 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). A linear model based on the normal distribution fit the data reasonably well (deviance = 24.0, df = 15), whereas the Poisson model gave a poorer fit (deviance = 149.6, df = 15).

We calculated probabilities of winning encounters against the other species (P_{other}) and compared odds of success (O_{success}) in interspecific social encounters versus intraspecific social encounters for both species. Our goal was to quantify success in interspecific encounters, using success in intraspecific encounters as a baseline value. We calculated odds ratios of winning against the other species over the odds of winning against a conspecific (O_{own}) as:

$$\begin{aligned} & \{O_{\text{success}} \text{ against other species} \\ &= \text{Probability of winning } (P_{\text{other}})/(1 - P_{\text{other}})\} \\ & \div \{O_{\text{success}} \text{ against own species} \\ &= \text{Probability of winning } (P_{\text{own}})/(1 - P_{\text{own}})\}. \end{aligned}$$

We assumed that differing odds of success (unequal odds ratio) between Snow Geese and Ross's Geese indicated that one species was dominant over the other species, whereas odds ratios of ~ 1 indicated equal success in interspecific social encounters and equal social status for the species.

RESULTS

Frequencies of social groups differed between species ($\chi^2 = 6.12$, $P = 0.013$) and age groups ($\chi^2 = 35.55$, $P < 0.001$), but not between winters ($\chi^2 = 0.53$, $P = 0.466$). The ratio of juveniles to adults was relatively higher for Snow Geese in both winters (Table 1). Less than 7% of adult and <4% of juvenile Ross's Geese were in families, whereas 10–22% of adult and 12–15% of juvenile Snow Geese were in families (Table 1).

On average, focal Snow Geese were three to 10 times more likely to have intraspecific encounters than interspecific encounters (Ta-

TABLE 1. Age and social groups (% of observations) of focal Lesser Snow Geese and Ross's Geese in the rice prairies of southwest Louisiana during winters, 2002–2003 and 2003–2004.

Age	Social group	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
Juveniles	Lone	11.7	6.7	11.3	7.2
	In a family	12.1	14.7	0.3	3.6
	Age ratio ^a	23.8	21.4	11.6	10.8
	N ^b	405	302	319	305

^a Percent juveniles within N.^b Number of focal individuals.

ble 2). In contrast, focal 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 2). Focal Snow Geese were more likely to win social encounters with Ross's Geese than with other Snow Geese (Table 2). Focal Snow Geese were relatively more successful in interspecific social encounters; Snow Geese won 30 of 52 social encounters in 2002–2003, and 32 of 33 social encounters in 2003–2004 (Table 2). Snow Geese won 63 of 87 (72.4%) interspecific social encounters observed when all focal observations of both species were combined. Focal birds of both species were more successful in intraspecific social encounters in 2003–2004 than in 2002–2003 (Table 2).

Overall, focal Snow Geese lost only 10 social encounters against Ross's Geese; all Ross's Goose wins were against lower ranked Snow Geese (i.e., non-parental pairs and lone birds); six were against lone juvenile Snow Geese, three were against lone adult Snow

Geese, and one win was against an adult pair. Focal Ross's Geese did not win social encounters against Snow Geese in families.

DISCUSSION

Family Maintenance.—Our data from Louisiana, combined with that from other locations, indicate Ross's Geese maintain families for shorter periods than Snow Geese throughout their current wintering ranges. Timing of family break-up is known to vary among species, individuals, and years (Prevett and MacInnes 1980, Black et al. 2007). Eighty percent of all juvenile Snow Geese wintering in the Mississippi Flyway are in families from 20 December to 15 March, whereas <50% of all goslings are in families on staging areas in late March and early April (Prevett and MacInnes 1980). Generally, over 50% of all gosling Barnacle Geese (*Branta leucopsis*) leave their parents by December and <20% remain with their parents until April; however, this distribution varies among years (Black et al. 2007). We observed more families in winter 2003–2004; family breakup on our study area

TABLE 2. Frequencies of social encounters (n/hr) of focal Lesser Snow Geese and Ross's Geese, and odds of their success in social encounters in the rice prairies of southwest Louisiana during winters, 2002–2003 and 2003–2004.

Types and success of social encounters	Lesser Snow Geese		Ross's Geese	
	2002–2003	2003–2004	2002–2003	2003–2004
Intraspecific social encounters/hr	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/hr	0.3	0.1	0.6	0.5
Percentage of interspecific social encounters won	57.6	97.0	42.4	3.0
Odds of interspecific success ^a	3.53	39.36	0.74	0.01

^a Odds of interspecific success = odds of winning against other species/odds of winning against own species.

may have occurred earlier for both species in winter 2002–2003 than in winter 2003–2004.

Interspecific Dominance and Mixed Flocks.—Snow Geese were dominant over Ross's Geese, as indicated by their relatively higher odds of winning against Ross's Geese. We did not observe a Ross's Goose win a social encounter against a Snow Goose in a family group. The relatively higher success of Snow Geese in interspecific encounters in 2003–2004 corresponded to a higher frequency of families in that year. Effects of species and family maintenance on outcomes of social encounters probably are confounded; Snow Geese may be more successful in interspecific social encounters because they maintain families. Similarly, family maintenance, rather than species or body size may explain different time-budgets of the two species (Jónsson and Afton 2008). Single-species flocks are known for both species in other locations (Johnson and Raveling 1988, Ryder and Alisauskas 1995, Mowbray et al. 2000), but we only observed one single-species flock of Ross's Geese, in winter 2003–2004 (Jónsson 2005).

Predator vigilance (via "many eyes" and dilution effect) probably is an important benefit of mixed flocking in both species (Kristiansen et al. 2000, Krause and Ruxton 2002, Beauchamp 2003, Randler 2004). Predators may find it increasingly difficult to select prey, when prey choice requires choice of differing types and each prey type has differing cost-benefit relationships for the predator (confusion effect; Sinclair 1985, FitzGibbon 1990, Krause and Ruxton 2002). Snow Geese may have relatively better predator detection capacities because they are taller (cf. Randler 2004) and may have greater visual acuity, given acuity is positively correlated with eye size, which scales positively with body size (Fernandez-Juricic et al. 2004). We often observed Red-tailed Hawks (*Buteo jamaicensis*) fly by the geese, causing them to respond by becoming alert. Bald Eagles (*Haliaeetus leucocephalus*) also attacked goose flocks (Jónsson 2005).

Ross's Geese within mixed flocks evade predators by (1) remaining close to Snow Geese, thus, exposing Snow Geese to avian predators potentially chasing Ross's Geese (cf. Sinclair 1985, FitzGibbon 1990), and (2) re-

maining well within flock boundaries (JEJ, pers. obs.; R. C. Drewien, pers. comm.). Thus, dominance of Snow Geese seemingly does not drive Ross's Geese towards flock edges; individuals on flock edges often are subordinates (Black et al. 1992).

Mixed flocks probably have been common throughout evolutionary history of these goose species; recent genetic studies show that gene flow is frequent between Snow Geese and Ross's Geese over historical time (Weckstein et al. 2002). New pairs are formed on wintering grounds or during spring migration (Ganter et al. 2005); thus, the two species exchange genetic material via mutual wintering areas (Mowbray et al. 2000). We suggest that along with predation pressure (cf. McWilliams et al. 1994), the historical association of Ross's Geese with Snow Geese, along with the former's associated subordinate social status, has selected against family maintenance in Ross's Geese. However, we observed a small proportion of Ross's Geese in families each winter. Thus, family maintenance probably represents individual choice within a species, rather than a species-fixed evolutionary constraint (Black et al. 2007).

ACKNOWLEDGMENTS

Our study was funded by the Canadian Wildlife Service, Louisiana Department of Wildlife and Fisheries (LDWF), Delta Waterfowl Foundation, Rockefeller Scholarship program, a Research Partnership Proposal (RPP) Grant from Cameron Prairie National Wildlife Refuge (NWR) and the U.S. Fish and Wildlife Service, and by the U.S. Geological Survey-Louisiana Cooperative Fish and Wildlife Research Unit, Graduate School, School of Renewable Natural Resources at Louisiana State University (LSU), and LSU AgCenter. Rockefeller State Wildlife Refuge, Cameron Prairie NWR, and LDWF provided housing and valuable logistical support. We thank C. J. Michie, Brandt Meixell, M. G. Pollock, T. W. Blair, and J. M. Yurek for help with data collection, and D. C. Blouin and M. D. Kaller for advice on statistical analyses. We thank R. N. Helm, Guthrie Perrie, T. J. Hess, J. T. Linscombe, and Daniel Gary for valuable assistance with our project. We acknowledge D. G. Homberger, W. G. Henk, M. J. Chamberlain, S. R. McWilliams, and an anonymous referee for suggestions that improved this paper.

LITERATURE CITED

- AGRESTI, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, USA.
- ALISAUSKAS, R. T. 1998. Winter range expansion and relationships between landscape and morphomet-

- rics 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.
- ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227–267.
- 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 *Waterfowl in winter* (M. W. Weller, Editor). University of Minnesota Press, Minneapolis, USA.
- BEAUCHAMP, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes* 63:111–121.
- BLACK, J. M. AND M. OWEN. 1989a. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37:199–209.
- BLACK, J. M. AND M. OWEN. 1989b. Parent-offspring relationships in wintering Barnacle Geese. *Animal Behaviour* 37:187–198.
- BLACK, J. M., C. CARBONE, AND M. OWEN. 1992. Foraging dynamics in goose flocks: the cost of living on the edge. *Animal Behaviour* 44:41–50.
- BLACK, J. M., J. PROP, AND K. LARSSON. 2007. Wild goose dilemmas. *Branta Press*, Groningen, The Netherlands.
- BOYD, H. 1953. On encounters between wild White-fronted Geese in winter flocks. *Behaviour* 5:85–129.
- CALDER III, W. A. 1996. Size, function and life history. Second Edition. Dover Publications, Mineola, New York, USA.
- 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.
- FERNANDEZ-JURICIC, E., J. T. ERICHSEN, AND A. KACELNIK. 2004. Visual perception and social foraging in birds. *Trends in Ecology and Evolution* 19:25–31.
- FERNANDEZ-JURICIC, E., G. BEAUCHAMP, AND B. BASTAIN. 2007. Group-size and distance-to-neighbor effects on feeding and vigilance in Brown-headed Cowbirds. *Animal Behaviour* 73:771–778.
- 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.
- FRONCZAK, D. 2004. Waterfowl harvest and population survey data. USDI, Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.
- GANTER, B., W. S. BOYD, V. V. BARANYUK, AND F. COOKE. 2005. First pairing in Snow Geese *Anser caerulescens*: at what age and at what time of year does it occur? *Ibis* 147:57–66.
- GAWLIK, D. E. 1994. Competition and predation as processes affecting community patterns of geese. Dissertation. Texas A&M University, College Station, USA.
- GOUDIE, R. I. AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- 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.
- JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267.
- 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 *Waterfowl in winter* (M. W. Weller, Editor). University of Minnesota Press, Minneapolis, USA.
- JÓNSSON, J. E. 2005. Effects of body size on goose behavior: Lesser Snow Geese and Ross's Geese. Dissertation. Louisiana State University, Baton Rouge, USA.
- JÓNSSON, J. E. AND A. D. AFTON. 2006. Different time and energy budgets of Lesser Snow Geese in rice prairies and coastal marshes in southwest Louisiana. *Waterbirds* 29:451–458.
- JÓNSSON, J. E. AND A. D. AFTON. 2008. Time budgets of Snow Geese and Ross's Geese in mixed flocks: implications of body size, ambient temperature and family associations. *Ibis* 150:In press.
- JÓNSSON, J. E., A. D. AFTON, AND R. T. ALISAUSKAS. 2007. Does body size influence nest attendance? A comparison of Ross's Geese (*Chen rossii*) and the larger, sympatric Lesser Snow Geese (*C. caerulescens caerulescens*). *Journal of Ornithology* 148:549–555.
- KALMBACH, E. 2006. Why do goose parents adopt unrelated goslings? A review of hypotheses and empirical evidence, and new research questions. *Ibis* 148:66–78.
- 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, Oxford, United Kingdom.
- KRISTIANSEN, J. N. AND N. S. JARRETT. 2002. Inter-specific competition between Greenland White-fronted Geese *Anser albifrons flavirostris* and Canada Geese *Branta canadensis interior* moulting in West Greenland: mechanisms and consequences. *Ardea* 90:1–13.
- KRISTIANSEN, J. N., A. D. FOX, H. BOYD, AND D. A. STROUD. 2000. Greenland White-fronted Geese *Anser albifrons flavirostris* benefit from feeding in mixed-species flocks. *Ibis* 142:139–158.
- LOONEN, M. J. J. E., L. W. BRUINZEEL, J. M. BLACK,

- AND R. DRENT. 1999. The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. *Journal of Animal Ecology* 68:753–768.
- MADSEN, J. 1985. Habitat selection of farmland geese in West Jutland, Denmark: an example of a niche shift. *Ornis Scandinavica* 16:140–144.
- 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 *Biology and management of Canada Geese* (M. D. Samuel, Editor) 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. Snow Goose (*Chen caerulescens*). The birds of North America. Number 514.
- PREVETT, J. P. AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. *Wildlife Monographs* 71.
- RANDLER, C. 2004. Coot benefit from feeding in close proximity to geese. *Waterbirds* 27:240–244.
- RAVELING, D. G. 1970. Dominance relationships of agonistic Canada Geese in winter. *Behaviour* 37: 291–319.
- RYDER, J. P. AND R. T. ALISAUSKAS. 1995. Ross's Goose (*Chen rossii*). The birds of North America. Number 162.
- SAS INSTITUTE. 1999. SAS/SYSTAT users guide. Version 8. SAS Institute, Cary, North Carolina, USA.
- SHELLEY, E. L., M. Y. U. TANAKA, A. R. RATNATHICAM, AND D. T. BLUMSTEIN. 2004. Can Lanchester's laws help explain interspecific dominance in birds? *Condor* 106:395–400.
- SINCLAIR, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology* 54:899–918.
- STAHL, J., P. H. TOLSMA, M. J. J. E. LOONEN, AND R. H. DRENT. 2001. Subordinates explore but dominants profit: resource competition in high Arctic Barnacle Goose flocks. *Animal Behaviour* 61: 257–264.
- 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.