TEMPORAL CHANGES IN HABITAT SELECTION AND NEST SPACING IN A COLONY OF ROSS' AND LESSER SNOW GEESE

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ABSTRACT.—I studied the nesting colony of Ross' Geese (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*) at Karrak Lake in the central Arctic of Canada in the summer of 1976. Related studies indicated that this colony had grown from 18,000 birds in 1966–1968 to 54,500 birds in 1976. In 1976, geese nested on islands that were used in the late 1960's and on an island and mainland sites that were previously unoccupied. Average nest density in 1976 was three-fold greater than in the late 1960's. Consequently, the average distance to nearest neighbors of Ross' Geese in 1976 was half the average distance determined 10 yr earlier.

The mean clutch size of Ross' Geese was greater in island habitats where nest densities were high than in less populated island or mainland habitats. The average size of Snow Goose clutches did not differ significantly among island habitats but was larger at island than at mainland sites. Large clutches were most likely attributable to older and/or earlier nesting females. Habitat preferences apparently differed between species. Small clutches presumably indicated that young geese nested in areas where nest densities were low. The establishment of mainland nesting at Karrak Lake probably began with young Snow Geese using peripheral areas of the colony. Young Ross' Geese nested in sparsely populated habitats on islands to a greater extent than did Snow Geese. Ross' Geese also nested on the mainland but in lower densities than Ross' Geese nesting in similar island habitats. Successful nests with the larger clutches had closer conspecific neighbors than did successful nests with smaller clutches. The species composition of nearest neighbors changed significantly with distance from Snow Goose nests but not Ross' Goose nests. Nesting success was not affected by the species of nearest neighbor, however. Because they have complementary antipredator adaptations, Ross' and Snow geese may benefit by nesting together. Received 13 May 1982, accepted 3 January 1983.

MANY Arctic nesting species of geese (Anserini) are sympatric and share numerous lifehistory traits (see Delacour 1954, Johnsgard 1978, Bellrose 1980, Owen 1980 for reviews). Despite these similarities, some species are colonial (see definition in Gochfeld 1980), whereas others are dispersed nesters. Two exclusively colonial species are Ross' Geese (Chen rossii) and Snow Geese (Chen caerulescens). The nesting distribution of Lesser Snow Geese (C. c. caerulescens) is disjunct but includes colonies across most of arctic North America and a colony on Wrangel Island in Siberia (Bellrose 1980). Nearly all Ross' Geese, however, are restricted to the central Arctic of Canada, where they nest in colonies with Lesser Snow Geese (Ryder 1969a, 1971a). Multispecies colonies are fairly common among birds (Burger 1981); these assemblages have been used as a basis for suggesting complex nesting relationships that include both competition and cooperation among species (see Cody 1973, Bedard 1976, Burger 1981 for reviews).

The population of Ross' Geese numbered less than 5,000 in the early 1950's, but by 1976 it had increased to more than 100,000 birds (McLandress 1979). In contrast, there are several million Lesser Snow Geese (Owen 1980), but changes in population sizes have been inadequately measured (see discussion in Kerbes 1975). My objective was to study changes in a nesting colony containing both species, relative to the population expansion of Ross' Geese, and to determine interspecific effects on nesting distribution and success.

STUDY AREA AND RELATED STUDIES

The study was conducted in the summer of 1976 at Karrak Lake (67°15'N, 100°15'W; Fig. 1), the site of the largest goose colony in the Queen Maud Gulf Lowlands of the central Arctic (Ryder 1969a). Based



Fig. 1. The Karrak Lake nesting colony of Ross' and Lesser Snow geese (after Ryder 1972). Black areas were nesting islands used by geese 1966–1968 and 1976, hatched areas were "expansion" sites occupied by 1976, and stippled islands (lower right) were used by nesting geese in 1966–1968 but not in 1976.

on an aerial photographic survey of Karrak Lake, Kerbes et al. (1983) estimated that the colony contained 54,500 nesting geese in 1976. A previous study of the same colony was conducted from 1966 to 1968 (Ryder 1972), when colony size was estimated to be 18,000 birds (visual aerial survey, Ryder 1969a). Although the size of the Karrak Lake colony tripled in this 10-yr interval, species composition changed only slightly (67% Ross', 33% Snow, Ryder 1969a; 60% Ross', 40% Snow, Kerbes et al. 1983). Geese nested only on islands in the mid-1960's, but by 1976 the colony had expanded to include nearby mainland areas and a previously unoccupied large island (Fig. 1).

METHODS

Research commenced on 1 June. Geese had already begun egg laying [the earliest beginning of a nesting season recorded for Ross' and Snow geese in this area (cf. Ryder 1967, 1972)]. Clutch sizes were recorded during nest surveys of the colony. These surveys (23 June–1 July) were conducted during the incubation period after all clutches were completed. Egg size was used to determine species (Ryder 1971b) when nesting birds were not identified by direct observation. Clutches that contained eggs of both Ross' and Snow geese were excluded from analyses. Habitat surrounding each nest site was partitioned into five types, similar to those delineated in Ryder's study (see Ryder 1972 for detailed descriptions). Briefly, these included:

(1) "Rock habitat" was composed of gravel and rocks of various sizes with almost no vegetation apart from a few lichens. Rock habitat occurred along the tops of drumlins (glacial ridges) and was free of snow earlier than other habitats, probably because of exposure to wind.

(2) "Mixed habitat" occurred along lower elevation drumlins and included a scattering of a variety of low-growing vascular plants, lichens, and mosses on a relatively dry, gravel-filled soil. This was the most common upland habitat in the colony.

(3) "Heath patches" occurred in wind sheltered places along the slopes of rock ridges and were characterized by Labrador tea (*Ledum decumbens*) and white heather (*Cassiope tetragona*), as well as a few dwarf birch (*Betula glandulosa*) and willow (*Salix* spp.). Ryder (1972) included heath patches with mixed habitat.

(4) "Sand tussock" was an uncommon habitat of low-lying areas characterized by frost-heaved pingos of sand that were often ringed by sedges (*Carex* spp.) or other vascular plants.

(5) "Moss habitat" predominated in all low-lying areas of the colony and consisted of a wet mat of a variety of mosses overlying 5–10 cm of peat.

I established six 61-m-diameter circle plots (cf. Ryder 1969b) and six $305- \times 6$ -m strip plots (4–19 June) on island and mainland sites of the colony during

				Nests/1,000) m² (tests)ª			
	Sample	ple area (m²) Ross' Geese		′ Geese	Snow Geese			
Habitat (code)) Island ^b Mainland ^b Island		Island	Mainland	Island	M	Mainland	
Rock (A)	2,586	0	16 (BCD) ^a		23 (BCE)			
Heath (B)	1,994	0	64 (ACE)		14 (AE)			
Mixed (C)	9,522	2,629	40 (ABE) P	< 0.01° 3 (D)	14 (AE)	ns^c	16 (0)	
Tussocks (D)	166	2,634	42 (AE)	ns 23 (C)	6 (0)	ns	11 (0)	
Moss (E)	3,462	0	18 (BCD)		2 (ABC)			

TABLE 1. Goose nest densities in different habitats at Karrak Lake in 1976.

^a Habitats (codes) with statistically different nest densities (P < 0.05, χ^2 -tests); 0 = none different.

^b Line plots (6) and circle plots (4) on islands; circle plots (2) on the mainland (0 indicates no habitat in sample plots).

^c Differences between adjacent values, χ^2 -tests; ns = not significant.

the egg-laying period in order to determine nest densities and hatching success. I constructed scale maps of these plots and determined nest locations by "on-site" measurement to the nearest 15 cm. Habitat types were delineated within each plot, and areas were determined from scale maps with a planimeter. Distances of a nest to the next nearest nest and nearest conspecific nest were measured from maps of circle plots (nests that were closer to plot borders than their nearest neighbors were excluded from analyses). I recorded the clutch size of all nests located in circle and strip plots during the incubation period (including nests already abandoned). Hatching success was determined when nests were checked after hatching (9-13 July). I used standard statistical methods, except for the analyses of clutch size, for which I used *t*-tests for unequal variances in test populations (Remington and Schork 1970: 212) because Bartlett's tests for homogeneity (Snedecor and Cochran 1967: 297) revealed significant differences in variance among test populations.

RESULTS

Overall nest densities in circle and strip plots (which included snow-covered areas that were unavailable for nesting) averaged $36/1,000 \text{ m}^2$, significantly greater than the 12 nests/1,000 m²

determined from 11 circle plots measured in 1968 by Ryder (1969b) (t = 3.19, P < 0.05). Nest densities varied greatly among habitats (Table 1). Numbers of nests observed in the various habitats were significantly different from numbers that would be expected if nest sites were distributed independently of habitat types (Ross', $\chi^2 = 212.7$, df = 6, P < 0.001; Snow, $\chi^2 = 54.7$, df = 5, P < 0.001). Highest densities of nesting Ross' Geese occurred in heath patches on islands that had been occupied by geese in the late 1960's, and they were fourfold greater than the lowest densities in rock and moss habitats. Highest densities of Snow Geese occurred in rock habitat on glacial ridge tops, and relatively dispersed nesting occurred in moss habitat. Because Ryder (1969b, 1972) and I probably classified habitats differently, I did not compare our results in detail.

Topographic and habitat features of the largest island at Karrak Lake were more similar to mainland areas than they were to small islands occupied by nesting geese (see also Ryder 1972). Clutch sizes of both Ross' and Snow geese on this island were not significantly different from those of geese nesting in comparable habitats

TABLE 2. Ross' Goose clutch-size variation among island and "expansion" area habitats at Karrak Lake in 1976.

Habitat (code)		Clutch size ($\bar{x} \pm SE$)					
	Islands	n		Expansion	n		
Rock (A)	$3.3 \pm 0.12 (BC)^{a}$	78	ns ^b	$3.1 \pm 0.26 \ (0)^{a}$	9		
Heath (B)	3.6 ± 0.06 (AE)	353		no data			
Mixed (C)	3.5 ± 0.03 (AE)	1,106	$P < 0.05^{\rm b}$	3.3 ± 0.04 (0)	483		
Tussocks (D)	3.5 ± 0.12 (E)	54	P < 0.10	$3.3 \pm 0.05(0)$	399		
Moss (E)	3.2 ± 0.10 (DCB)	110	ns	3.3 ± 0.22 (0)	12		

^a Habitats with statistically different clutch size (P < 0.05, t-tests); 0 = none different.

^b Differences between adjacent means, *t*-tests; ns = not significant.

Habitat (code)	Clutch size ($\bar{x} \pm SE$)					
	Islands	n		Expansion	n	
Rock (A)	$4.2 \pm 0.10 \ (0)^{a}$	146	$P < 0.10^{a}$	4.0 ± 0.12 (E)	153	
Heath (B)	4.5 ± 0.17 (0)	68		no data		
Mixed (C)	$4.4 \pm 0.05(0)$	530	P < 0.05	4.0 ± 0.05 (E)	918	
Tussocks (D)	4.4 ± 0.41 (0)	9	ns	4.0 ± 0.09 (E)	130	
Moss (E)	3.8 ± 0.40 (0)	9	ns	3.4 ± 0.22 (ACD)	28	

TABLE 3.Snow Goose clutch-size variation among island and "expansion" area habitats at Karrak Lake in1976.

^a As in Table 2.

at mainland sites. Therefore, clutch-size data from the large island and mainland (referred to as "expansion" sites) were pooled for further analyses.

The average clutch size of Ross' Geese differed significantly among habitats (Table 2). On islands, clutches were 10% larger in high-density nests in heath patches and intermediatedensity nests in mixed and sand tussock habitats than were clutches in low-density nests in rock and moss habitats. Mean clutch sizes of Ross' Geese nesting in expansion sites were similar to average clutches in island habitats where nest densities were low. Clutch sizes of Snow Geese were not statistically different among island habitats (Table 3). Snow Geese that occupied rock and mixed habitats in expansion areas, however, had significantly smaller clutches than island-nesting Snows in the same habitats.

Nearest neighbors were conspecifics more frequently than would be expected if Snow and Ross' geese were distributed throughout the colony independently of one another ($\chi^2 = 26.25$, df = 1, *P* = 0.001; Table 4). Species composition of nearest neighbors changed sig-

nificantly with distance from nests of Snow Geese. At distances of less than 3 m, nearest neighbors of Snow Geese were Ross' Geese more than twice as often as they were Snow Geese, despite a near equal overall occurrence of either species as nearest neighbors (Table 4). Species composition of nearest neighbors did not change significantly with distance from Ross' Goose nests. Also, as nearest neighbors, twice as many Ross' Geese nested less than 3 m away than at distances exceeding 3 m from both Ross' and Snow goose nests. From these data it appears that Ross' Goose responses to Snow Geese as nearest neighbors were not different from responses to its own species for purposes of spacing.

No clear patterns between clutch size and nearest nest distance were evident when neighbors were considered without respect to species (see also Ryder 1969b, 1972). There was an inverse correlation between clutch size of successful nests and nearest conspecific nest distance for Snow Geese, however (Fig. 2). Successful nests with larger clutches had closer conspecific neighbors than did nests with small clutches. Ross' Geese, on the other hand, did

TABLE 4. Relationship between species of nearest neighbor and internest distance of Ross' and Snow geese in circle plots at Karrak Lake in 1976.

Species/number	Number of		nearest neighbors that were:		
of nests	Distance to nearest neighbor	Snow	Ross'		
Snow Geese $n = 146$	Less than 3 m 6 m or more Total	24 44 68 (47%)	$(\chi^2 = 13.17)^a \begin{array}{c} 51\\ 27\\ 78 \ (53\%) \end{array}$		
Ross' Geese $n = 310$	Less than 3 m 6 m or more Total	40 31 71 (23%)	$(\chi^2 = 2.26)^{\text{b}}$ 158 81 239 (77%)		

P < 0.001.

^b Not significant.

Ross

Snow

76 (68)



Fig. 2. Relationship between clutch size and distance to nearest conspecific nest ($\bar{x} \pm 1$ SE) among successful Ross' and Lesser Snow geese at Karrak Lake in 1976. Numbers beneath bars are sample sizes.

not exhibit a statistically significant relationship, although six-egg nests tended to have closer conspecific neighbors than did nests with smaller clutches. Overall nest success was high (Ross': 84%, n = 692; Snow: 81%, n = 333; excluding one-egg nests; cf. Ryder 1971a, 1972). Nest success did not vary significantly relative to the species of nearest neighbor (Table 5).

DISCUSSION

Variation in average clutch sizes of Ross' and Snow geese among habitats (Tables 2 and 3) was most likely attributable to corresponding differences in age and/or time of laying of nesting geese (see below). Two other factors, nest parasitism (Mineau and Cooke 1979) and egg loss during the period of egg laying and early incubation, may have affected the recorded clutch size of some nests. Parasitic egg laying

geese at Karrak Lake in 1976. Percentage (n) of nests successful Species of nearest neighbor Ross' Geese Snow Geese 80 (239) 81 (78)

80 (71)

TABLE 5. Relationship between species of nearest neighbor and nesting success of Ross' and Snow

by Snow Geese without their own nests is common in some years and results in higher than average recorded clutch sizes (Syroechkovsky 1979). Overall average clutch sizes were not high (cf. Owen 1980), however, and very large clutches (>8 eggs) were extremely rare (3 Snow Geese and 0 Ross' Geese), as were nests containing eggs of both species (n = 5, 0.1%of 4,600 nests). Egg loss was not a major factor affecting average clutch sizes either. Of 379 eggs (94 clutches) that were marked (6 June) during the egg-laying period, only 6 eggs (2%) were lost before the last day of nest surveys on 1 July. Even this low rate of egg loss probably exceeded losses from unmarked nests, because the disturbance of repeated nest checks may have contributed to partial clutch loss to avian predators (MacInnes 1980, Strang 1980).

Colony expansion.—In Snow Geese, older and earlier-nesting females lay the largest clutches (Finney and Cooke 1978), and they tend to be traditional in their nest location (Cooke and Abraham 1980). Thus, many Snow and Ross' geese nesting in the densest island areas of the colony were probably older birds, which initiated nesting early in the season. The recent expansion of the colony to the largest island and mainland areas, coupled with lower average clutch sizes at these locations, probably indicates that a higher proportion of young geese occurred among birds nesting in expansion areas than among island nesting geese (Tables 2 and 3). Recall, however, that mainland nesting Snows had attained densities similar to or even greater than Snow Geese on islands in the same habitat type (Table 1). Presumably, young Ross' Geese utilized the habitats of low-lying areas (moss and tussocks) on islands to a greater extent than did Snow Geese and were present only in low densities on the mainland (relative to similar island habitat). These patterns suggest that young geese were unable to compete with older geese of either species for nest sites and were forced to nest in mainland and less densely occupied island habitats.

Maximum nest densities attainable in a mixed-species colony of Ross' and Snow geese are difficult to predict. Densities of nesting geese reported in other studies are only qualitatively comparable to those at Karrak Lake because of differences in methodologies used and nonuniformity of habitat. Typically, the highest concentrations of Lesser Snow Goose nests reported at other colonies vary from 2 to 6 nests/1,000 m² (Uspenski 1965, Barry 1967, Harvey 1971, Ryder 1972, Kerbes 1975, Finney and Cooke 1978; my calculations). Cooch (1958), however, reported territories of 15-32 m²/nest, indicating densities of 30-66 nests/1,000 m², and found some territories of less than 5 m². Ryder (1967) reported densities of more than 200 Ross' Goose nests/1,000 m² in a colony at Arlone Lake, approximately 50 km west of Karrak Lake. It is possible then, that in the absence of suitable habitat on mainland areas, Snow and/or Ross' geese might have achieved even higher nest densities at Karrak Lake.

Nest spacing and habitat selection.—Snow Geese tend to arrive at colonies a day or two earlier and begin laying eggs sooner than do Ross' Geese (Ryder 1967). Snow Geese appeared to space themselves relative to one another and may have ignored Ross' Geese or, at least, not reacted to them in the same manner as their own species for purposes of spacing. Ross' nested closer to Snow Geese than did other Snow Geese (Table 4), but nest success was not affected by the species of nearest neighbor (Table 5).

Habitat selection by both Ross' and Snow geese was indicated by high nest densities and correspondingly high clutch sizes in preferred habitats. Clutch size and nest densities of Ross' Geese were highest in heath patches. A preference by Ross' Geese for nest sites "next to rocks or birch patches," reported by Ryder (1972: 193), indicated that geese selected habitat features in the late 1960's that were most common in heath patches in 1976. In 1976, highest nest densities of Snow Geese were in the earliest snow-free areas along the tops of the highest drumlins. For both species, nests in rock habitat were little more than scraped depressions in the gravel, but few Ross' Geese nested in rock habitat, and those that did were

probably young or late nesters, based on their small clutches. In other habitats, vegetation was generally used for nest construction, especially for nests in heath patch and moss habitats (see also Ryder 1967). These areas were occupied predominantly by Ross' Geese. Unmelted snow was common in heath patches and moss habitat in early June, indicating that many nest sites in these habitats were unavailable to geese arriving before the study began on 1 June. Perhaps availability of nest material is an important proximate factor in the selection of nest sites by Ross' Geese. Because of their smaller body size, Ross' Geese would be expected to expend relatively more energy for maintenance during the incubation period and should benefit more from a favorable nest microclimate than would Snow Geese.

An important aspect of nest-site selection in colonially nesting birds is safety from predation (Buckley and Buckley 1980). Predation was not a major factor affecting goose nest success in 1976, however. Few avian predators were present during early incubation, probably because of inclement weather from 1 to 15 June. Apart from a few Long-tailed Jaegers (Stercorarius longicaudus), avian predators did not nest successfully. This probably resulted in low food requirements relative to "normal" years. Also, northern red-backed voles (Clethrionomys rutilus) were visibly abundant in early June. This provided a food source other than goose eggs for both avian and mammalian predators. Often, goose nests were abandoned several days before being scavenged by "predators." Nevertheless, predation has been a significant factor affecting nest success at Karrak Lake in the past (Ryder 1972).

Predation may also be an important factor influencing nest-site selection by geese within a colony. Ryder (1972) proposed that Ross' Geese select islands for nesting because they provide safety from predation by arctic foxes (*Alopex lagopus*). Ross' Geese are agile flyers and adept at chasing jaegers (pers. obs.). Snow Geese, on the other hand, are capable of defending against arctic foxes (Barry 1964, Syroechkovsky 1972) and commonly nest on mainland areas at other arctic colonies. Thus, expansion of the Karrak Lake colony to include nearby mainland areas probably began with pioneering by Snow Geese, which predominated in mainland nesting areas.

Nesting territories of colonial geese.-Ryder

Year 1966–1968	Distance (m) to nearest nest $(\bar{x} \pm SE)^a$						
	Successful nests	n U		nsuccessful nests	n		
	$4.7 \pm 0.1^{\rm b}$ P < 0.001	413	$P < 0.01^{\circ}$	4.1 ± 0.2^{b} P < 0.001	114		
1976	3.0 ± 0.1	249	ns	2.7 ± 0.1	59		

 TABLE 6.
 Change in nearest neighbor distances of Ross' Goose nests at Karrak Lake between 1966–68 and 1976.

^a Neighbors were either Ross' or Lesser Snow geese.

^b Source: Ryder (1972).

^c Difference between adjacent means, *t*-tests; ns = not significant.

(1967, 1975) and Inglis (1976) suggested that food was an important attribute of nesting territories of colonial geese. This hypothesis cannot be discounted for Ross' Goose territories despite their small size, because food (vegetation) may be more concentrated in optimal nesting areas (e.g. the heath patches). Snow Geese, however, nested at highest densities in rock habitat, which was almost devoid of vegetation. In addition, Snow Geese should defend food resources from neighboring Ross' as well as neighboring Snows, as it is unlikely that food is in sufficient abundance for the two species to eat different foods when nesting. Interspecific nearest nest distances were smaller than nearest neighbor distances between Snow Geese (Table 4), which suggests that Ross' may be tolerated within intraspecific territories of Snow Geese.

Hypotheses concerning territoriality in colonial geese (Ryder 1975, Inglis 1976, Owen and Wells 1979, Mineau and Cooke 1979) imply that birds in the smallest territories would have less food or more intraspecific strife (rape and/or conflict) than birds in the largest territories. In Ross' Geese, small territories were previously thought to decrease nesting success, because unsuccessful birds tended to have closer neighbors than successful birds (Ryder 1972). A comparison of nearest-neighbor data obtained from 1966 to 1968 (Ryder 1972) with similar data obtained in 1976 (this study) shows that successful nests had closer neighbors in 1976 than either successful or unsuccessful nests 10 yr earlier (Table 6). Despite the decrease in spacing, overall nesting success was high (see above).

For colonial nesting to be successful, any disadvantages of small territories must be offset by advantages of having conspecifics nearby. Syroechkovsky (1972) reported that pre-

dation on Snow Goose nests by foxes on Wrangel Island, Siberia was least where nesting density was highest (see also Cody 1971). At Karrak Lake, Ross' Geese pursued jaegers well beyond the boundaries of their nesting territories. Thus, colonial geese should benefit (perhaps inadvertently) from nest defense by neighbors in high-density areas. If so, selection should favor individuals that tolerate close neighbors. Intraspecific aggression at nesting areas is often interpreted as defense of a "territory" in geese. Aggression among colonial geese, however, may not be related solely to maintenance of a specific area. Mineau and Cooke (1979) argued that male Snow Geese "protect their parenthood" and guard only their mates (from rape) and nests (from parasitism). In addition, or alternatively, these behavioral interactions may be important to assure that conspecific neighbors are in good condition and remain attentive to their nests, thereby increasing the probability of reciprocal nest defense (see discussion of Wasser 1982). Old, experienced birds would be ideal neighbors and expected to predominate in the densest nesting areas. If young and/or late arriving birds are prevented from nesting in established areas of the colony, as suggested from clutch-size distributions at Karrak Lake, then predation should be reduced by enhancement of reproductive synchrony (Darling 1938, Gochfeld 1980).

Competition.—MacInnes and Cooch (1963) suggested competition with Snow Geese may have led to the restricted breeding distribution of Ross' Geese. Ross' do not avoid nesting in colonies with Snow Geese, however, and, at Karrak Lake and other large colonies in the central Arctic, both species have been highly successful in recent years (Kerbes et al. 1983). Further, there was no indication that either species was adversely affected by the other's presence in this study (see also Ryder 1967). Ross' had a high tolerance for crowding and nested close to Snows. Snow Geese were able to nest in areas that Ross' avoided, such as on the mainland or on rock ridges on islands. The two species have different, but complementary, antipredator behavior. This probably accounts for the ability of Ross' to nest successfully on mainland areas when Snow Geese are present for defense of nests against foxes. Reciprocally, close Ross' neighbors may benefit Snow Geese by protecting their nests from avian predators.

If competition with Snow Geese affects the breeding distribution of Ross' Geese, it probably occurs indirectly. For example, interaction at post-hatch feeding sites or on migration and/ or wintering areas may have led to the restricted range of Ross' Geese. Two sympatric species as closely related as Ross' and Snow geese, however, would be expected to avoid competition and probably differ in their use of limited resources (see Lack 1971), at least in areas unaltered by man.

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