



Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum

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We tested the predator protection and similar habitat hypotheses in relation to red-breasted goose, *Branta ruficollis*, nesting associations. Geese began laying 1–3 weeks after all associated species. In almost all cases they nested on the mainland only if raptors were also present and always followed raptors when they changed eyries between years. They selected peregrines, *Falco peregrinus*, and snowy owls, *Nyctea scandiaca*, as associates in preference to rough-legged buzzards, *Buteo lagopus*, even though the latter were several times more abundant along river corridors. Nest defence experiments with a surrogate Arctic fox, *Alopex lagopus*, showed that this could be explained by differences in nest defence intensity, rather than habitat types selected. Similar experiments also suggested that gulls were much less aggressive than owls or falcons. Foxes rarely approached, and were easily repelled from goose colonies associated with owls and peregrines, but gulls were apparently incapable of repelling foxes. Breeding success was much higher for geese nesting with raptors than for those on islands and geese apparently preferred to nest with owls in peak lemming years than to remain on islands. These findings support the hypothesis that red-breasted geese actively choose to nest near raptors; however, they probably associate with gulls primarily because both species select fox-free islands. Compared with other studies, red-breasted geese nesting with raptors and on islands apparently represent two extremes in a continuum of nesting associations generally seen in birds. We discuss why the behaviour might have evolved and argue that this may be the only known bird species whose evolution has been facilitated primarily by the exploitation of the nest defence behaviour of aggressive raptorial hosts.

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Associations between two or more species during nesting have been described in many avian taxa (Durango 1949; Lack 1968; Burger 1981). Usually at least one of the two gains direct fitness benefits from the association, normally through improved reproduction, which can be mediated in several ways, including the predation dilution effect (Clark & Robertson 1979; Burger 1984; Wittenberger & Hunt 1985), increased collective nest defence (Fuchs 1977) and increased vigilance against predators (Nuechterlein 1981; Burger 1984; Blanco & Tella 1997). Most strikingly, birds can reduce nest

predation risk by exploiting the nest defence behaviour of a more aggressive species (Summers et al. 1994; Ueta 1994; Blanco & Tella 1997; Larsen & Grundetjern 1997; Bogliani et al. 1999; Richardson & Bolen 1999).

Associations between relatively timid and aggressive species can be explained by two main hypotheses: (1) the 'predator protection hypothesis', in which an associate chooses to nest with a host specifically to gain protection from predators, and (2) 'the similar habitat hypothesis' (Orians & Wilson 1964), in which both species associate simply because they select similar habitat, although by chance some predator protection may still be gained. The key difference between the two hypotheses is whether the association has evolved specifically because of fitness benefits directly related to protection from predators.

In many parts of the Arctic, lemmings, *Dicrostonyx torquatus* and *Lemmus sibiricus*, form the main food basis for vertebrate predators, and cyclic patterns in their abundance can cause fluctuations in predation pressure

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on other prey species (Chernov 1985). In years when lemmings are scarce, predators switch to feeding on other prey, especially birds, their eggs and young (Lack 1954; Syroechkovskiy et al. 1991; Summers et al. 1998). On the Siberian tundra, red-breasted geese, *Branta ruficollis*, nest in association with peregrine falcons, *Falco peregrinus*, snowy owls, *Nyctea scandiaca*, rough-legged buzzards, *Buteo lagopus* ('buzzards' hereafter) and herring gulls, *Larus argentatus*. It is widely claimed that the geese actively choose to nest near these species specifically because they gain protection from predators, especially from the Arctic fox, *Alopex lagopus* (Dementiev & Gladkov 1952; Krechmar & Leonovich 1967; Quinn & Kokorev 2000, 2002), although the similar habitat hypothesis has never been discounted. We tested several predictions of the predator protection and similar habitat hypotheses for red-breasted goose nesting associations.

If geese actively choose to nest with a host, the following four predictions can be made. First, with regard to nest initiation, geese should wait until the host species has established a nest site. In other words, nesting chronology should indicate that geese join their hosts rather than the other way around. Second, the geese should track changes in the availability and distribution of the host types. Two natural phenomena allowed this to be tested: (1) snowy owls nested only when lemmings were abundant, and (2) peregrines habitually alternated nest attempts between adjacent eyries that were some distance apart within a larger territory (Ratcliffe 1993). Third, the geese should select a host according to the host's ability to provide protection. We made direct observations on the frequency of Arctic fox raids at different colony types. We also experimentally measured nest defence intensity of associated species, using a decoy predator, and tested whether the preferred associate species had the highest nest defence intensity. Fourth, the geese should gain a fitness benefit as a result of the association. More specifically, the geese should suffer lower predation when nesting with species that more actively repel predators.

If the similar habitat hypothesis explains the close proximity of goose colonies and aggressive neighbours, then habitat will be just as likely as raptor presence to predict the location of geese on the landscape. Additional support for the similar habitat hypothesis would also be provided by a lack of evidence for the predator protection hypothesis. We compare our results with those of others and discuss mechanisms generally underlying the evolution of nesting association behaviour.

METHODS

Study Area

We conducted fieldwork along rivers that transect the sparsely vegetated tundra landscape of the Pura and Pyasina basins in the Taymyr Peninsula, Siberia, from 1995 to 1999. The main study area was along 270 km of rivers in the Pura basin (72.5°N, 85.5°E, including the Bystraya, Malaya Bystraya and Buotangkaga tributaries) as well as in 1998 and 1999, along 800 km of the Pyasina

River from its mouth near the Kara Sea (73.8°N, 87°E) to the city of Norilsk.

Timing of Nesting and Distribution

We backdated goose nest initiation dates with reference to published information on incubation periods, assuming a mean clutch size of six (Owen 1980). We aged broods of red-breasted geese on 150–200 km of rivers in the Pura basin from a boat in late July 1996, 1997 and 1999, using Yocom & Harris's (1966) key. We estimated first egg dates for 'raptors' (used here to describe owls and birds of prey) at eyries during or just after the hatching period, and by backdating with reference to published incubation, laying and hatching intervals and chick development (Cramp & Simmons 1980; Cramp 1985; Cade & Enderson 1996). Lay date estimates for gulls were based on the oldest chick seen and were made at one colony in 2 peak lemming years, when there were few signs that repeat clutches had been laid.

A 'colony' describes a location where at least one pair of red-breasted geese nested. A goose nest was said to be in a colony associated with a species if it was within 300 m of the eyrie. Searches for red-breasted goose and gull colonies and for raptor nests were made from a boat and restricted to the edges of river valleys (200–1500 m wide and 5–100 m above the river's water level). In 1999, colonies and eyries were located along the 1400 km river transect between the city of Norilsk near the Pyasina river and the upper reaches of the Pura River, as well as along several tributaries of the Pura in early to mid-July. In other years, searches were restricted to the Pura basin. Female red-breasted geese were generally hidden on their nests, but the males usually conspicuously stood guard on the shoreline. By July, raptors had eggs or small young, so at least one adult was near each nest. Adult snowy owls and herring gulls, and the large nests of buzzards, were highly visible. Finding peregrine nests was aided by their traditional use of territories from year to year.

When examining movements of peregrine eyries and associated goose colonies, we made comparisons between 1995 and 1996, and separately between 1998 and 1999. This approach was taken because twice as many territories were surveyed in 1998 and 1999 as in 1995 and 1996. A similar approach was taken for distributions of red-breasted geese and snowy owls.

Associate Nest Defence Intensity

Arctic fox raids

To determine how effective raptors and gulls were at excluding predators from their nesting areas, we recorded the number of times that Arctic foxes were seen approaching (within 300 m and moving directly towards a colony) or entering colonies with raptors or gulls. Three colonies were watched for a total of 615 h during 1995–1997 and 1999. Observations were always made during the goose's incubation period from a hide at least 100 m from the colony and over a number of days for periods

varying from 4 to 24 h of continuous observation per day. Fox raids at the only herring gull colony not on an island, beside a lake near the research station, were recorded on a casual basis in 1997 and 1999.

Experiment

We determined the nest defence intensity of the associate species to test whether geese selected species by their relative aggressiveness. Trials were conducted (1) to test selection within raptors and (2) to determine how aggressive gulls were compared with raptors. Interpretation of the comparison between raptors and gulls requires some caution, because we measured the response of more than one pair of gulls, but only one pair of raptors, at a time. The response of associates was recorded when a surrogate Arctic fox (German Schnauzer dog) was kept at a set distance (15–20 m, depending on terrain) from the nest. The dog was given a 2-m leash to ensure that it could avoid the stoops easily; it was never hit by the subjects during trials. Given the option to stay in the boat, usually 100 m away from the associates' nest, the dog always freely followed observers. The number of times the associates (both sexes pooled) stooped at the dog during a 2-min trial was recorded, beginning either when the first stoop occurred or when the observer was 200 m from the eyrie after placing the dog, whichever was sooner. The minimum height between the dog and associate during each stoop (stoop height) was estimated with reference to the height of the dog (40 cm). Avian nest defence intensity varies with offspring age and annual environmental conditions (Redondo 1989). Therefore, all experiments were carried out in a single year (1999, a peak lemming year in which all species successfully bred), and only at nests that had young; they had no observable effect on either young or adults.

Differences between species (factor) in stoop heights and stoop frequencies were tested with GLIM (N.A.G. 1993) specifying a normal or Poisson error with a log-link function (Crawley 1993). Three response variables were recorded: (1) stoop height (m), (2) total number of stoops in 2 min and (3) number of stoops in 2 min with a stoop height of ≤ 1 m.

Breeding Success

Clutch sizes were recorded 1–2 weeks after incubation initiation and were not adjusted for partial predation in the intervening period. We considered pairs to have nested successfully when eggshell fragments with internal membranes partly separated from the shell were present, or if only small fragments of shell were in the nest (Weller 1956). Nests were considered predated if the internal membrane on eggshell fragments of sufficient size were obviously not parted from the shell wall, or if no eggshells could be found in the nest. The dependent variables used in analyses were mean proportion (1) hatched or (2) predated per colony per year.

Hunting Arctic foxes and other predators switch their attention to the nests and young of birds when their

preferred prey (usually lemmings) are scarce in the tundra ecosystem (Lack 1954; Syroechkovskiy et al. 1991; Summers et al. 1998). This occurs in a 3-year cycle and is synchronized across large areas (Erlinge et al. 1999). We therefore distinguished between years with high (non-peak lemming year) and low (peak lemming year) predation pressure in analyses of breeding success.

Habitat Selection

Locations where raptors, gulls or red-breasted geese nested were classified into specific habitat types: (1) islands; (2) sandy riverbank cliffs with ridges running perpendicular to the river; (3) low mounds/raised ridges, a collective term for a variety of sandy riverbanks that had a random and disrupted structure, and that sometimes involved subsided ridges that ran parallel to the river; (4) rocky cliffs; (5) flat ground; (6) gently sloping hills. Unless stated otherwise, hereafter the term 'cliffs' is used collectively for types 2–4. To analyse the distribution of red-breasted geese we used general log-linear modelling, which tested for significance of terms in a three-way contingency table with habitat type, association and presence or absence of geese identifying separate cells.

More detailed data were collected for cliffs, the most important habitat for red-breasted geese (Quinn & Kokorev 2002). Cliffs were restricted to discrete lengths of the river and were favoured by raptors and geese. Geese are obligate herbivores (Owen 1980) and vegetation cover on the cliff face was known to influence colony size (Poisson error, correcting for overdispersion with Pearson's chi-square; $\chi^2_1=7.65$, $P<0.001$). If cliffs were occupied by nesting geese or raptors, we visually estimated percentage vegetation cover on the cliff face (or on slopes around) within 200 m of either side of the eyrie. If unoccupied, vegetation was estimated within 200 m of either side of the highest point of the cliff. Mosses and lichens were rarely eaten by red-breasted geese (Quinn 2000) and were ignored in the estimation.

We estimated percentage snow cover remaining in shaded gullies in early to mid-July 1999 as an indicator of relative snow conditions along the cliff face 3 weeks earlier when the geese were laying. The following physical parameters were also recorded: (1) cliff height (m, either from the river's surface to the top of the cliff, or, for slopes, where the tundra levelled off); (2) cliff length; (3) direction cliff was facing (cliff aspect), a measure of microclimate, because south-facing cliffs become snow free earlier than those facing north.

We determined whether physical factors or the presence of raptors predicted cliff selection by red-breasted geese (response variable) with a logistic regression model, using GLIM (N.A.G. 1993) and following the procedures outlined by Crawley (1993). The factor 'raptor present' (three levels: no raptor, peregrine present, buzzard present) was included as a predictor along with the physical variables described above. Snowy owls and gulls generally did not nest on these cliff habitats along the river so were not included as treatments.

Table 1. Lay dates for red-breasted geese and the difference in days from these dates that the four associated species began laying

Species	1996	1997	1999
Red-breasted goose	25 Jun (19)	22 Jun (5)	14 Jun (30)
Peregrine falcon	-13 (8)	-16 (16)	-4 (14)
Rough-legged buzzard	-12 (7)	N/A	-11 (6)
Herring gull	-23 (1)*	N/A	-14 (1)†
Snowy owl	-28 (12)	N/A	-21 (6)

Sample sizes given in parentheses (broods for red-breasted geese, colonies for gulls, pairs for raptors). N/A=not available.

*Of 94 nests, nine were hatching or hatched on 4 July.

†Majority with young on 14 July, largest young were 2 weeks old.

RESULTS

Timing of Nesting

Raptor species and gulls began nesting 4–28 days earlier than red-breasted geese, indicating that the geese established their nests after their associated species (Table 1). Lay date differed between species ($F_{3,117}=108$, $P<0.0001$) and years ($F_{2,117}=38.5$, $P<0.0001$), and the magnitude of the difference between species varied with year ($F_{4,113}=7.1$, $P<0.0001$, gulls excluded owing to small sample sizes).

Distribution

The location of red-breasted goose colonies varied markedly between peak and nonpeak lemming years (Fig. 1). In the 1996 peak lemming year, 14 of 19 locations occupied by nesting snowy owls were also occupied by nesting red-breasted geese. In the previous year, when there were few lemmings and consequently no snowy owls, none of these same locations was occupied by nesting red-breasted geese (binomial test: $Z=7.29$, $N=19$, $P<0.001$). The results were similar for the 1999 peak and 1998 nonpeak lemming year comparison (8/16 versus 0/16 locations, respectively; $Z=4.0$, $N=16$, $P<0.001$).

Red-breasted geese never nested at a cliff traditionally used by falcons unless the falcons were also present ($N=28$ eyries, 71 falcon-nesting attempts). When falcons moved eyries within territories between years, geese always followed ($N=9$; Table 2). Conversely, if falcons stayed in the same location between years, so too did the geese ($N=6$). Red-breasted geese never nested in some occupied falcon territories ($N=7$), clearly because they contained no suitable foraging habitat.

Mean \pm SE distances from goose nests to those of their associates were as follows: with peregrines: 35.4 ± 3.2 m ($N=137$); snowy owls: 92.0 ± 16.6 m ($N=23$); buzzards: 71.3 ± 32.5 m ($N=8$); gulls: 15.7 ± 4.14 m ($N=15$; associate species: $F_{3,175}=7.31$, $P<0.001$; year: $F_{4,175}=3.21$, $P=0.01$; means based on logged values). In 1996 on the Pura River and its tributaries, when the highest density of colonies was found, the straight-line distance between adjacent goose colonies was 10.4 ± 1.35 km ($N=29$ colonies of all types). Thus, intercolony distances were

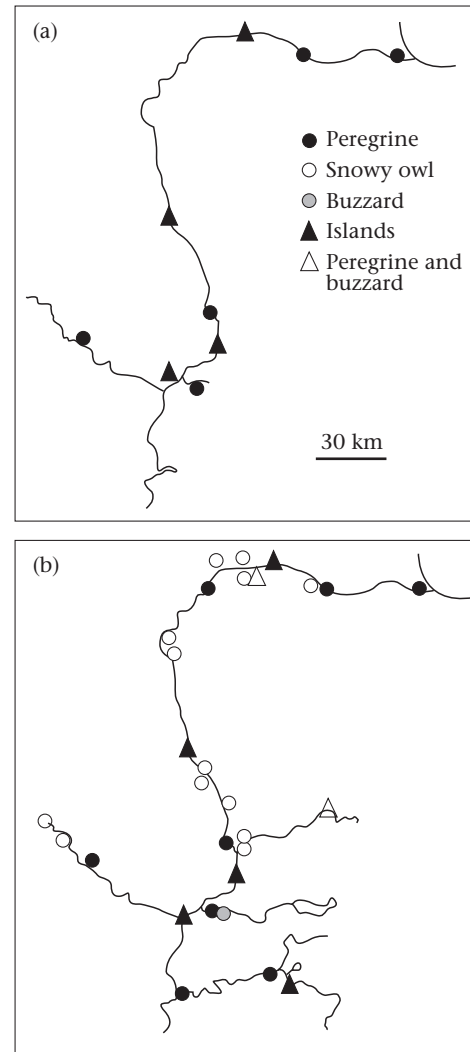


Figure 1. Distribution of red-breasted goose colonies on islands or in association with birds of prey in typical (a) nonpeak (1995) and (b) peak (1996) lemming years in the Pura basin. Colonies on the Pyasina River are not shown. Rivers shown only if surveyed. One colony with owls was outside the core area and is not shown on the map.

almost 300 times greater than distances between goose and raptor nests within colonies.

Including only rivers surveyed in all 3 years, the numbers of goose pairs found in areas that were surveyed intensively from 1995 to 1997 were 97, 105 and 39 pairs, respectively (Fig. 2). In the 1997 nonpeak lemming year, a higher proportion of pairs nested on islands than in the previous peak year (49 versus 13%). The difference (36%) was similar to the proportion with snowy owls and buzzards in 1996 (41% of 105 pairs; $Z=0.56$, $P=0.71$), and the higher proportion with gulls in the 1995 nonpeak year (71–13=+58%) was 17% greater than the proportion with owls and buzzards in 1996 (41%; $Z=-2.42$, $P=0.016$). A similar comparison could not be made for 1998 and 1999, because the timing of surveys differed from 1995–1997, and areas covered were biased against islands. The mean \pm SE number of goose nests per

Table 2. Changes in occupancy of traditional peregrine territories by falcons and red-breasted geese between 1996 and 1997 (11 territories), and between 1998 and 1999 (22 territories)

Number of peregrine territories where	1996 & 1997	1998 & 1999
Both species moved to a new location	2	7
Both species stayed in the same location	3	3
Both species present in one year, neither in the other	2	6
Falcons stayed, geese left territory	0	3
Falcons present, no geese in any year	4	3
Falcons absent or moved, geese present or stayed	0	0

colony varied between colony types (gulls: 7.27 ± 0.59 pairs; peregrines: 3.81 ± 0.29 ; snowy owls: 2.14 ± 0.35 ; buzzards: 1.41 ± 0.39 ; Poisson error, correcting for overdispersion using Pearson's chi-square; associate species: $\chi^2_3=24.5$, $P<0.001$; year: $\chi^2_4=10.3$, $P<0.001$). Mean colony size with gulls was three times higher in years when there were no owls or buzzards, but colony size at peregrine cliffs stayed the same (J. Prop & J. L. Quinn, unpublished data). This result suggests that the majority of those geese nesting with owls in peak lemming years nested with gulls in nonpeak years, and thus that fluctuating patterns in goose distribution were not caused simply by fluctuations in the number of geese breeding.

Associate Selection

Relatively few red-breasted geese nested near the more abundant buzzards, in 1996 (4×2 contingency table, associate species \times occupied/unoccupied by geese: $\chi^2_3=67.5$, $P<0.001$) or in 1999 ($\chi^2_3=60.1$, $P<0.001$). Buzzard eyries were three to eight times more abundant along rivers than were peregrine and owl eyries in 1996 and 1999 (Fig. 3), and geese were associated with only 4.2 and 6.2% of buzzard eyries in those years, respectively. In contrast, in those same years, goose colonies were found at, respectively, 92 and 84% of peregrine eyries and at 74 and 50% of snowy owl eyries. Geese were associated with most gull colonies.

Nest Defence by Associate Species

Observation

Arctic foxes approached a raptor nest only once during 279 observation hours (0.01 visits/h; Table 3). On this occasion, the peregrine stooped five times in 14 s 200 m from its eyrie. The fox was hit once, was repelled easily and appeared extremely distressed. Almost identical responses of raptors to intruders were recorded when (1) two wild dogs approached a peregrine eyrie, and (2) an Arctic fox came to within 300 m of an owl eyrie. In contrast, the probability of a fox raid at the lakeside gull colony was estimated to be 0.12/h (Table 3). Single eggs were taken from gull nests on 33% ($N=33$) of fox raids observed over 24 days. Gulls stooped on the foxes

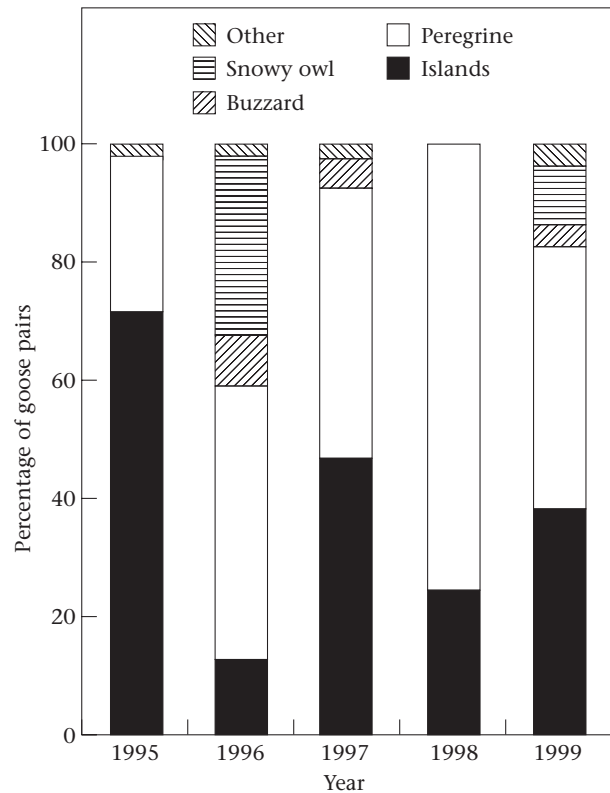


Figure 2. The percentage of red-breasted goose pairs in colonies on islands or in association with birds of prey in the study population in each year, 1995–1999. Numbers of pairs recorded in each year were 97, 105, 39, 50 and 127, respectively. Similar rivers were censused in 1995–1997 (Pura basin), but there was a bias against island colonies in 1998 and 1999 (Pura and Pyasina basins). 1996 and 1999 were low-predation-risk (peak lemming) years. Geese were associated with gulls on most islands (Table 4).

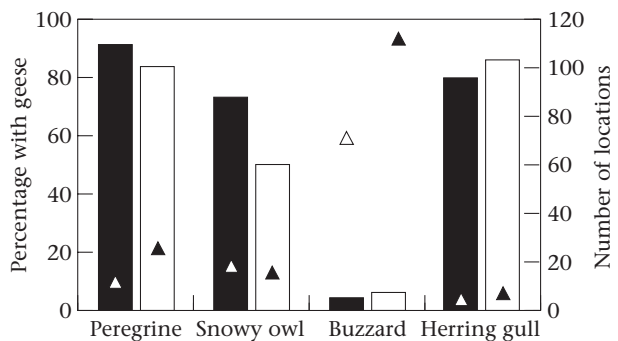


Figure 3. Total number of herring gull colonies and raptor eyries along river valleys in the Pura and Pyasina basins (\triangle : 1996; \blacktriangle : 1999) and the percentage of these with which red-breasted geese were associated (\blacksquare : 1996; \square : 1999).

28.3 ± 3.9 ($\bar{X} \pm SE$) times ($N=26$) per visit. Each visit lasted 3.2 ± 0.3 min ($N=27$), and the foxes seemed unconcerned by the stooping gulls. Foxes did not raid the goose and gull colony on an island that was continuously watched for 48 h in 1995, despite the presence of two occupied fox burrows on the mainland within 500 m of the island and despite lemmings being almost entirely absent in that

Table 3. Number of times that Arctic foxes were seen approaching or entering colonies in the Pyasina basin from 1995 to 1999, based on direct observation

Colony name	No. of RBG pairs	Nesting areas	Year	No. of hours	No. of days observed	No. of fox visits	Probability of fox visits/h
1. Pura Station	0*	Gull, lakeside	97	288†	24	33	0.12
2. Crocodile Is.	37	Gull, island	95	48	2	0	0.00
3. MB	7	Peregrine	96	144	6	0	0.00
4. MB	2	Peregrine	97	41	3	1	0.01‡
5. Japanese	2	Peregrine	97	64	5	0	0.00
6. Byelagorka	6	Snowy owl	99	20	2	0	0.00
7. Near Pura Station	0*	Snowy owl	99	10	2	0	0.00

About 18 and 30 pairs of gulls nested at colonies 1 and 2, respectively. RBG=red-breasted goose. MB=Malaya Bystraya.

*Assumes that absence of geese did not affect the probability of being approached or raided by foxes.

†Assumes 12 h of casual observation per day.

‡Based on the only two colonies with peregrines observed in that year (colonies 4 and 5 combined).

year. Foxes were 12 times more likely to approach the lakeside gull colony than they were the two red-breasted goose colonies associated with peregrines (two-tailed binomial test: $Z = -5.0$, $P < 0.001$; island gull colony excluded owing to different habitat).

Experiment

Stoop height differed significantly between raptor species ($F_{2,18} = 5.72$, $P = 0.012$). Compared to buzzards, both peregrines and snowy owls stooped more than twice as close to the decoy (Fig. 4a). They also stooped more than twice as often as buzzards ($\chi^2_2 = 5.79$, $P = 0.055$) but significantly so only when stoops of < 1 m were counted ($\chi^2_2 = 6.45$, $P = 0.04$; Fig. 4b). These results support the hypothesis that geese selected raptor species according to their nest defence ability.

Stoop height of herring gulls did not differ from that of buzzards ($F_{2,24} = 0.96$, $P = 0.4$; Fig. 4a) but, compared to peregrines and snowy owls, together they stooped only half as close to the decoy ($F_{1,26} = 11.37$, $P = 0.002$). Herring gulls stooped more often than all raptor species, but the difference was not significant ($\chi^2_3 = 7.36$, $P = 0.06$), even when only stoops of < 1 m were included ($\chi^2_3 = 7.05$, $P = 0.07$; Fig. 4b). Thus, nest defence intensity of gulls was similar to that of buzzards, but lower than that of the red-breasted goose's preferred raptor associates. Together with direct observations on fox raids, these data suggest that the predator protection hypothesis is unlikely to explain the red-breasted goose association with gulls.

Breeding Success

In years with low predation pressure, goose clutch sizes in raptor colonies were, on average, 1.8 eggs larger than those with gulls ($F_{1,32} = 8.42$, $P = 0.007$; each observation is a colony mean). Clutch sizes were similar at colonies associated with snowy owls and buzzards, which combined (owing to small N for buzzards, $\bar{X} \pm \text{SE} = 6.94 \pm 0.55$ eggs) were higher than in colonies with peregrines (6.02 ± 0.44 eggs), although not quite significantly so ($F_{1,28} = 4.1$, $P = 0.052$). In years with high predation

pressure, clutch sizes from colonies associated with peregrines were similar to those with gulls ($F_{1,18} = 0.84$, $P = 0.37$). Clutch sizes at peregrine colonies in years with low predation pressure were 1.2 eggs larger than in high-predation years ($F_{1,9} = 8.22$, $P = 0.019$; controlling for colony differences: $F_{17,9} = 2.92$, $P = 0.053$). Clutch sizes on islands were similar in low- and high-predation-pressure years ($F_{1,9} = 0.0$, $P = 1$).

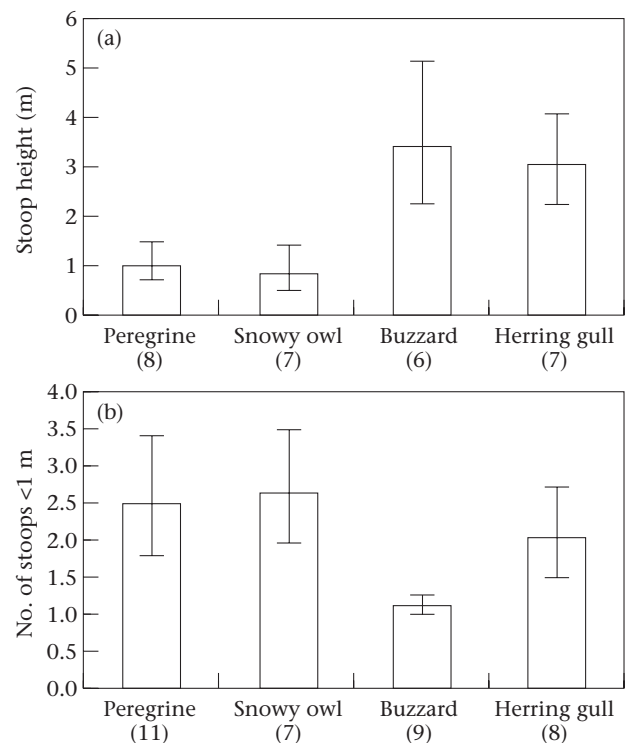


Figure 4. Nest defence intensity of associate species in terms of (a) stoop height and (b) stoop frequency (stoops < 1 m) during 2-min trials on a surrogate Arctic fox in 1999. Numbers in parentheses are sample sizes (colonies for gulls, pairs for raptors). Gull responses are from multiple pairs. Bars are back-transformed SE.

Table 4. Proportion of locations occupied by raptors and gulls that were also occupied by red-breasted geese in each habitat type

Habitat type	Associated species				
	Peregrine	Snowy owl	Buzzard	Herring gull	None
Sandy ridged cliff	19/20	—	1/19	—	—
Rocky cliff	2/7	1/1	1/9	—	—
Low mound/raised ridge	2/2	8/10	0/3	—	—
Sloping hillside	—	7/9	0/8	—	—
Flat ground	—	—	0/13	—	—
Lakeside	—	1/1	—	0/1	2
Island	—	—	0/1	8/8	3*

Data are mainly from 1999 but are supplemented with data from 1996 at locations that were not visited or were not occupied (by geese or raptors) in 1999. —: indicates that the species was not found in that habitat. Log-linear analysis: Habitat×Association: $\chi^2_{20}=123.2$, $P<0.0005$; Red-breasted goose×Association: $\chi^2_4=76.5$, $P<0.0005$; Red-breasted goose×Habitat: $\chi^2_{20}=123.2$, $P<0.05$. 'None' shows the number of locations where geese were not obviously associated with any species.

*Includes an island where Arctic terns, *Sterna paradisaea*, occupied one-half of the island, and another island where geese nested beside gulls on one-half of the island but on their own in the other half.

Geese had a higher nesting success near raptors (76%) than when with gulls (21%) in high-predation-pressure years, but similar nesting success in low-predation-pressure years (lemming abundance × associate species interaction: $F_{1,24}=5.64$, $P=0.026$; controlling for location differences: $F_{37,24}=0.94$, $P=0.58$). In low-predation-pressure years, goose nests with snowy owls had a higher nesting success (93%) than did goose nests with peregrines (72%), although the difference was not significant ($F_{1,24}=3.85$, $P=0.061$). Nesting success of goose nests with buzzards could not be assessed owing to small sample size ($N=2$). In low-predation-pressure years, predation levels at colonies with peregrines and gulls were similar ($F_{1,32}=0.28$, $P=0.6$). In high-predation-pressure years, four times as many nests with gulls than raptor nests were predated ($F_{1,18}=3.25$, $P=0.088$).

Habitat Selection

Red-breasted goose distribution was nonrandom with respect to habitat type and nesting locations of associate species (significant interaction terms in Table 4). In particular, red-breasted geese were associated with more peregrine than buzzard nests on sandy ridged cliffs (two-tailed binomial test: $Z=12.7$, $P<0.001$). The geese associated with similarly low proportions of peregrine and owl (combined) and buzzard eyries on rocky cliffs ($Z=1.32$, $P=0.19$). They were also associated with more (1) peregrine and owl eyries (combined because of small sample sizes) on low mounds ($Z=7.75$, $P<0.001$) and (2) more snowy owl eyries on sloping hillsides ($Z=5.61$, $P<0.001$) than with buzzard eyries in these two habitats. Red-breasted geese nested on islands ($N=11$) regardless of whether gulls were present (Table 4). They nested near the one gull colony that was not on an island just once in five seasons. On two of the eight islands where both gulls and geese occurred, the geese nested adjacent to, but not intermixed with, the gulls. On five of the remaining six

islands, the close association between both species was inevitable because the islands were small.

Several physical features differed between cliffs that were occupied by falcons or buzzards or that remained unoccupied ($F_{4,52}=474.9$, $P<0.0005$). In separate univariate tests, vegetation cover and cliff length did not differ between associate types, but there were differences in cliff height (falcons occupied higher cliffs than buzzards or unoccupied cliffs: $F_{2,55}=10.2$, $P<0.0005$) and in aspect (falcons and buzzards occupied cliffs that were generally facing south: $F_{2,55}=3.7$, $P<0.05$). However, a logistic regression showed that neither cliff height nor cliff aspect affected whether geese nested on cliffs (Table 5). Instead, nest site selection was affected by vegetation cover and largely by the presence or absence of raptor species. Similarly, snow cover at the cliffs did not have an effect on nest site selection by red-breasted geese ($\chi^2_1=0.6$, $N=36$ locations, $P=0.44$), when we controlled for vegetation cover and presence of raptors. We conclude, therefore, that the distribution of red-breasted geese was probably caused by the presence of raptors.

Table 5. Predictors of nest site selection by red-breasted geese on cliffs as shown by a logistic regression GLM

Variable	df	χ^2	P
Raptor species present	2	57.48	<0.0001
% Vegetation	1	13.63	0.0002
Error	54		
Total	57		
Raptor species present×cliff height	2	0.09	0.956
Ln cliff height (m)	1	0.70	0.403
Ln cliff length (m)	1	2.29	0.130
Cliff aspect	3	0.43	0.934

'Raptor species present' and 'Cliff aspect' are factors; all other predictors are continuous. '% Vegetation' was arcsine $\sqrt{}$ transformed.

DISCUSSION

Predator Protection or Similar Habitats?

Red-breasted geese adopted several different strategies when choosing nesting locations safe from predators on the Arctic tundra. Depending on the strategy, the choice was in agreement with the predator protection or similar habitat hypotheses. Evidence for the predator protection hypothesis came from a number of sources. (1) Geese started egg laying later than did all associated species. (2) Without exception, geese followed associates between years when they shifted to new locations, although this could not be tested for gulls, which nested in the same locations every year. (3) Geese showed different preferences for associates, which were at least partly related to the defence abilities of the associates, and to fitness benefits derived from the protective behaviour of their associates. (4) Within colonies associated with peregrines, predation probability and distance of the nests to eyries were positively correlated (Quinn & Kokorev 2002). (5) Preference for individual raptor species was not related to habitat preferences.

We also found support for the similar habitat hypothesis when geese nested in association with gulls. Geese nested on all islands, which were apparently safe from foxes, regardless of whether gulls were present. When geese nested close to gulls on large islands, the association could equally be explained by both species selecting areas that were safest from flooding. In the 5 years of study, only one pair of geese had a single nesting attempt near the only mainland gull colony. It thus seems that geese and gulls shared islands by having similar habitat requirements, that is by selecting fox-free areas. Additional support for the similar habitat hypothesis comes from a lack of evidence for the predator protection hypothesis. There was no evidence that gulls were effective in providing protection for the geese. (1) Direct observations showed that, in contrast to raptors, gulls could not exclude Arctic foxes from the mainland colony, and were generally much less aggressive towards the decoy predator than were snowy owls and peregrines. (2) Geese near gulls on islands had lower reproductive success than those with owls or peregrines. (3) Given the choice, in peak lemming years geese apparently preferred to nest near snowy owls and buzzards than on islands. We cannot completely exclude the possibility that the geese actively chose to nest near gulls for reasons other than sharing the same habitat. However, we believe that an alternative explanation, such as predation risk dilution, (Kruuk 1964) is unlikely, given that gulls are almost certainly the main predators of goose eggs and goslings on islands (Quinn 2000), and given our suspicion that foxes were deterred from islands. Together these results fail to refute the hypothesis that red-breasted geese associate with gulls primarily because they select similar habitat.

Confounding Effects

The synchronized shifts in the distribution of geese and raptors provided strong support for the predator

protection hypothesis. Rather than geese following associates, however, alternative explanations are possible. A shift in potential breeding habitats suitable for all species between years could explain the parallel changes in raptors and geese. Potential features that may cause synchronized movements are (1) snow cover, which can be an important determinant of nest site selection in geese (Ely & Raveling 1984; Petersen 1990), (2) the distribution of lemmings, which are eaten by all three raptor species and which may select similar foraging habitat to geese, and (3) selection for safe nesting sites.

Snow cover was unlikely to be responsible for similar nest site selection by associates and geese. First, snow cover in cliff gullies during incubation was not linked to goose nest site selection. Second, the first areas to become snow free were the cliffs and mounds where falcons and owls nested. In fact, these wind-exposed locations were usually the first to become uncovered by snow in early spring, and it is unlikely that nest site availability for raptors was normally constrained by snow conditions. Similarly, snow conditions did not seem to influence the geese. Red-breasted geese begin nesting relatively late (Dementiev & Gladkov 1952; Quinn 2000), and usually only 50% of the tundra was covered in snow at the start of their incubation period. The likelihood that the only snow-free areas along riverbanks were in the same locations that the raptors had chosen 1–3 weeks earlier must be negligible.

Lemming abundance is also unlikely to explain the association. First, lemmings and red-breasted geese are distributed across entirely different scales. Mean distance between adjacent goose colonies was a minimum of 10.4 km, but in peak lemming years, the two species of lemmings that occur in Taymyr were seen continuously over the tundra in almost all habitat types. Second, raptors forage for their prey up to several kilometres from their eyries (Newton 1979), yet the mean distance between red-breasted goose nests and their associated species' eyries was under 100 m, some pairs nesting just 2 m from the eyrie. Thus, if geese and lemmings did select similar habitat, this would not explain why the geese nest in the immediate vicinity of eyries, rather than at some random location within the raptor's foraging territory. It could be argued that the observed selection by geese against buzzards is also linked to lemming density. There is correlational evidence that snowy owls displace buzzards (Wiklund et al. 1998), and thus that the owls may select the best areas for lemmings, which in turn select the same foraging areas as the geese. In addition to the arguments of spatial scale, our estimates of lay dates suggest that this is unlikely. Snowy owls began laying 2 weeks earlier than buzzards, so the assumed displacement of buzzards by owls may be more related to nesting phenology than to defence of the best areas for lemmings, although the two may be related.

Raptors and geese might have selected similar safe nest sites. However, those sites that are safest for geese are unlikely to be safest for raptors. Like most waterbird nests, those of red-breasted geese are cryptic. In contrast, raptor nests on the tundra are often highly visible and are usually placed on the top of a sandy cliff or raised mound.

This location allows raptors to spot predators from a distance and provides a platform from which to defend their eyries. If the geese did not actively associate with the raptors, they should nest in safe sites (1) away from those of obvious raptor nests, which could attract predators and (2) not along easily accessible riverbank cliffs, but on the open tundra where almost all other geese and waterfowl species nest. In conclusion, the only explanation for the synchronized shifts in the distribution of red-breasted geese and raptors is that the geese follow the raptors.

The comparatively poor nest defence response of gulls to the surrogate fox suggests that the lower breeding success on islands was due to higher predation from foxes compared to when pairs associated with raptors. However, higher predation on islands was also likely to be caused by the gulls (Quinn 2000). To show the specific effect of protection on breeding success, comparisons should ideally be made between goose nests with and without raptors in similar habitat. This was not possible because the geese never nested in similar habitat without raptors. In itself, this means that the comparison with islands is largely unnecessary. Furthermore, within colonies with peregrines, distance of nests to the eyries is negatively correlated with predation risk (Quinn & Kokorev 2002). We conclude that the results support the hypothesis that geese select nesting near raptors in preference to islands because of the higher reproductive success gained, regardless of the mechanisms.

Raptor Host Selection

Nest defence experiments showed that red-breasted geese preferred to nest with the most aggressive associate species, not the most abundant, suggesting that they were choosing the most effective host. This is similar to the finding that wood pigeons, *Columba palumbus*, nest near the most aggressive individual hobbies, *Falco subbuteo* (Bogliani et al. 1999). Stoop height was assumed to be an indicator of relative nest defence ability, yet the true nature of this is likely to be more complex. In the case of peregrines, their speed and agility undoubtedly allow them to stoop closer to intruders without significant risk to themselves. The larger size of snowy owls (1200–2900 g; Snow & Perrins 1998) may also confer an advantage over the smaller buzzards (700–1600 g; Snow & Perrins 1998) and falcons (650–1200 g, J. L. Quinn, unpublished data) when defending against Arctic foxes (mean 3.6 kg; Macdonald & Barrett 1993).

Buzzards must also be able to deter predators from their own nests, but our data suggest that the distance at which they are willing to do so was less than that for both snowy owls and falcons. Furthermore, red-breasted geese are probably not able to adapt simply by nesting closer to buzzards. There is evidence that, when nesting near peregrines, red-breasted geese trade off the risk of being predated by foxes with that of being forced to desert by their aggressive hosts (Quinn & Kokorev 2002). The risk of forced desertion is highest among nests closest to eyries, which may also be the case for snow geese, *Anser caerulescens*, nesting near snowy owls on Wrangel Island, Russia (Menyushina 2000). Unlike peregrines, buzzards

usually take their prey on the ground, which may mean that the geese are particularly at risk of being predated by buzzards. Snowy owls also take prey from the ground, which may explain why geese nested further from snowy owl eyries than from those of peregrines.

Extremes Along a Continuum and Speciation

The red-breasted goose is one of several species that exploit the aggressiveness of raptors. However, the extent to which they do this appears to be unique for two reasons. First, evidence suggests that the majority of the population nests with raptors (Quinn & Kokorev 2000). In all other nesting associations, the behaviour is isolated or restricted to specific habitats. Second, the association appears to be obligatory for successful breeding on the mainland tundra. We have argued here that fitness gained was entirely due to predator protection, because red-breasted geese never nested in similar habitat unless raptors were present, and it seemed unlikely that nests on the tundra could have survived without protection (corresponding to the situation in Brent geese, *Branta bernicla*; Ebbinge 2000). In contrast, evidence suggests that the fitness gained when with gulls was probably entirely due to protection provided by the islands. If anything, the presence of gulls had a negative effect on fitness because of predation on eggs and goslings (Quinn 2000).

For other associations involving aggressive neighbours, we similarly compared reproductive success for individuals under protected and unprotected conditions within similar habitat (Fig. 5). We could find only five studies where reproductive success was measured in both states within similar habitat. In all five cases, the contribution of predator protection to total fitness ranged from low (in greater snow geese with snowy owls) to high (wood pigeons with hobbies). Values never reached 1 (as in red-breasted geese), which means that host presence facilitated but was not obligatory for achieving fitness. Red-breasted goose–raptor associations seem exceptional, because host presence is obligatory for successful reproduction on mainland tundra. We conclude that red-breasted geese nesting with raptors represents the extreme on a continuum of how birds in general limit the effects of predation by associating with aggressive species.

Limiting predation is generally thought to be the main selective force on associating with aggressive partners. However, more fundamentally, nesting associations provide the means for a species to occupy habitats that would otherwise be unavailable. If the behaviour becomes heritable, this could lead to speciation which is hypothesized to have happened in the case of our study species (Quinn 2000). Red-breasted geese appeared to leave river islands in preference for nesting on the mainland near snowy owls in peak lemming years. Although predation pressure was probably important, evidence elsewhere suggests that density dependence was also a major incentive for this preference (J. Prop & J. L. Quinn, unpublished data). This mirrors the hypothesis that ancestral red-breasted geese were restricted to nesting on coastal islands, and that associating with raptors was a means of avoiding density dependence and hence was a

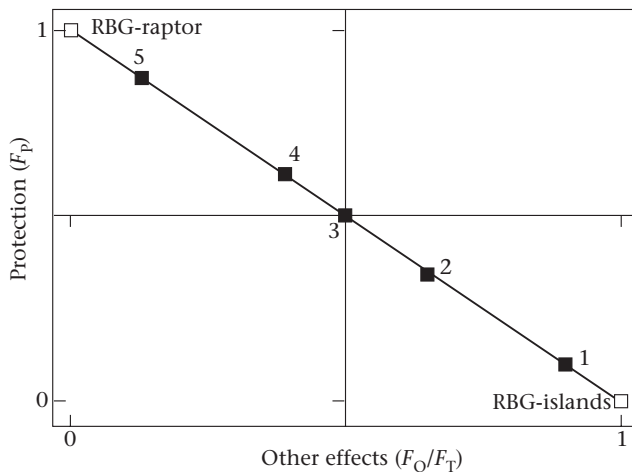


Figure 5. The proportionate contributions of predator protection, F_P and other effects to total fitness gained for different nesting associations. Values for the X axis were calculated as (F_O/F_T) , and for the Y axis as $F_P=1-(F_O/F_T)$, where F_T is the total fitness achieved in the presence of a protector, and F_O is the fitness achieved in the absence of a protector (other effects) but in similar habitat. Fitness measures used differed between studies. Associations are numbered as follows: (1) snow geese and snowy owls, mean percentage of nests that hatched successfully for nests >800 m and <800 m from snowy owls (Figure 5 in Bêty et al. 2001); (2) Bullock's orioles, *Icterus galbula*, 14% nest predation when associated with yellow-billed magpies, *Pica nuttalli*, compared to 43% when not associated (Richardson & Bolen 1999); (3) fieldfares, *Turdus pilaris*, fledge twice as many chicks with merlins, *Falco columbarius*, than when not associated (Wiklund 1982). (4) choughs, *Pyrhcorax pyrrhcorax*, average of 2.8 fledglings/pair inside and 1.1 outside lesser kestrel, *Falco naumanni*, colonies (Blanco & Tella 1997); (5) wood pigeons (73% fledgling success with hobbies, *F. subbuteo*, 9.6% unprotected; Bijlsma 1984).

key factor in their evolution (Quinn 2000). In Taymyr, the brent goose is largely restricted to marine islands, breeds inland only in peak lemming years close to snowy owls and is the principal contender for the red-breasted goose's closest living relative. Although morphometric analysis suggests that the barnacle goose, *B. leucopsis*, is more closely related (Livezy 1996), mtDNA analysis suggests the brent goose is (E. Paxinos & M. Sorenson, personal communication). The finding here that red-breasted geese actively choose to nest near raptors supports the hypothesis that predator protection facilitated their evolution from ancestral geese in an attempt to avoid density dependence. If this is confirmed, the red-breasted goose may be the only known bird species whose evolution has been conditional on predator protection provided by aggressive raptorial hosts.

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