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DIRECT AND INDIRECT ESTIMATES OF PEREGRINE FALCON POPULATION SIZE IN NORTHERN EURASIA

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ABSTRACT.—We used two different methods to estimate the density of nesting Peregrine Falcons (*Falco peregrinus*) across different parts of northern Eurasia. In the "territory-density" method, we extrapolated our density estimate of 406 km² per territory (95% CI = 295 to 650 km² per territory) in a high-density area, the Pyasina basin on the Taymyr Peninsula, to other similar areas across the range defined by published estimates. To estimate numbers in low-density areas, we used published data that suggested that Peregrine Falcon territories occur every 1,000 km². Based on the nesting association between Peregrine Falcons and Red-breasted Geese (*Branta ruficollis*), we used a second, post hoc method to provide a comparative estimate where the ranges of the two species overlap. This model was based primarily on the population ecology of the Red-breasted Goose and included parameters such as the proportion of the goose population nesting with peregrines, the proportion of peregrine pairs associated with geese, goose population size, and three other variables. Some of these variables were already known, whereas others had been estimated as part of another study. The territory-density and nesting-association methods led to estimates of 1,586 (95% CI = 991 to 2,179) and 2,417 (95% CI = 1,306 to 3,528) falcon territories, respectively, across the common range of Peregrine Falcons and Red-breasted Geese; the first method suggested a population of 3,652 falcon territories (95% CI = 2,282 to 5,018) across the entire range *F. p. calidus.* Although both approaches entailed several major assumptions, together they provide the only quantitative estimate of this remote population of Peregrine Falcons. *Received 26 February 1999, accepted 1 October 1999.*

THE REMOTENESS of the breeding grounds of Peregrine Falcons (*Falco peregrinus*) in northern Eurasia means that little is known about their numbers in this region. Even in North America, where Peregrine Falcons are relatively well studied, the continental estimate of 7,000 to 10,000 breeding pairs before the pesticide-induced decline in numbers was extrapolated from suitable information from only a few areas (Kiff 1988). Kolosov (1983) suggested that the Peregrine Falcon population east of the Ural Mountains contained several thousand pairs, but no firm estimate of numbers relates specifically to the range of *F. p. calidus,* which is the most widespread subspecies in the region.

Much of the literature on Peregrine Falcon densities in northern Eurasia relates to a time when the population was severely depressed by pesticides (e.g. Ivanov et al. 1983, Kokorev 1995), but numbers have increased since then (Quinn et al. 2000), as they have in many other parts of the world (Enderson et al. 1995). A current population estimate is needed to help assess the influence that trapping for falconry has on the population as it migrates through Eurasia (Eastham et al. 2000).

Here, we estimate the size of the *F. p. calidus* population by extrapolation using density estimates from our study area in Taymyr and by classifying regions across the entire range into those likely to hold low or high densities. We also use a second method to verify the estimate across part of the range by applying a model that incorporates population parameters linked to the nesting association of Red-breasted Geese (*Branta ruficollis*) with Peregrine Falcons and other birds of prey. The geese are thought to depend heavily on Peregrine Falcons to maintain an area free of terrestrial predators, especially arctic foxes (*Alopex lagopus*), around goose nests (e.g. Dementiev and Gladkov 1951, Kretschmar and Leonovich 1967). Although many nesting associations have been described

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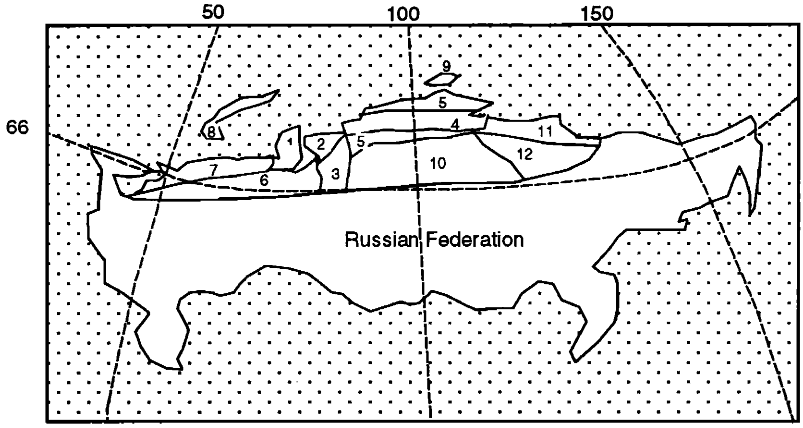

FIG. 1. Map of the Russian Federation showing the breeding range of *Falco peregrinus calidus*. Numbers refer to subdivisions of the range named in Table 1. The Red-breasted Goose's range is limited to areas 1 through 5.

(e.g. Bogliani et al. 1992, Ueta 1994, Larsen and Grundetjern 1997), Red-breasted Geese are possibly unique among bird species in the extent to which this association occurs. Of the 23 Peregrine Falcon nests found by Kretschmar and Leonovich (1967), 19 had Red-breasted Geese nesting next to them. Kostin and Mooiji's (1995) data agree with these findings, as do ours. We suggest that the nesting-association model can provide a useful way to verify the scale of the estimate provided by the first method. Furthermore, it describes an unusual scenario in which the population of one species theoretically can be estimated using parameters based entirely on the population of another species. We do not necessarily suggest that it should become a standard way to monitor the falcon population. In our case, it was possible to do so on a post hoc basis because the parameter estimates were already available or could be easily derived. Some of the parameters can be estimated annually with ease, for example the population size of Red-breasted Geese. Others parameter estimates are more difficult to obtain, however, so the nesting-association method may not always be a cost-effective alternative to the standard territory-density method.

STUDY AREA AND METHODS

The breeding range of *F. p. calidus* stretches eastward from the White Sea near the border of Fennoscandia and Russia (35°E) to the Lena Delta (130°E) and lies above 62°N (White and Boyce 1988, Stepanyan 1995; Fig. 1), but the exact locations of the boundaries are uncertain. Peregrine Falcons in northern Fennoscandia generally are believed to belong to the nominate race, although they may belong to *F. p. calidus* (C. J. Henny pers. comm.). The breeding range of the Red-breasted Goose occurs above 65°N and includes the Yamal (70°E), Gydan (80°E), and Taymyr (100°E) peninsulas (Krivenko 1983, Hunter and Black 1996) and covers approximately 40% of the entire range of *F. p. calidus*. Seventy percent of the Red-breasted Goose population is thought to occur on Taymyr (Kostin 1985), which stretches from 71 to 78°N and 80 to 114°E and is the most northerly part of the Eurasian continent. The data presented in this paper were collected along 823 km of river in the Pura and Pyasina basins in the tundra zone of western Taymyr (Fig. 2) each breeding season from 1995 to 1998.

Territory-density method.—Peregrine Falcons normally nest near water (Ratcliffe 1993), and our experience in Taymyr supports this generalization. Therefore, our searches for occupied territories (hereafter "territories") were limited to the banks of selected rivers and tributaries in the Pyasina and Pura basins. We defined a territory as any location to which one or more Peregrine Falcons were attached, irrespective of whether we found an eyrie.

The distance along a river between territories and the straight-line distance between territories were calculated to facilitate classification of low- and high-density areas across the entire range of *P. p. calidus*. The territory-density estimate for the Pyasina and Pura basins was extrapolated to other high-density areas identified in the literature. Territory density was estimated by assuming that the mean and variance in linear density (territories per linear 100 km) along rivers actually surveyed (823 km) were similar

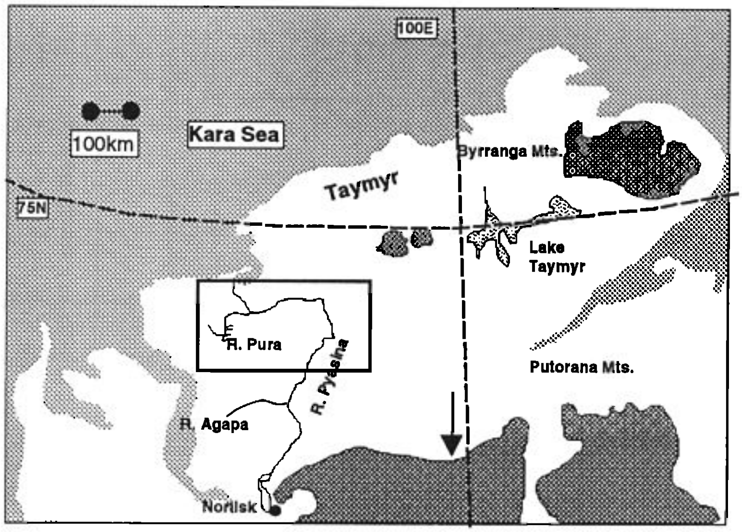

FIG. 2. Map of Taymyr showing the location of the Pura and Pyasina rivers (all other rivers not shown). The square inset shows the area (69,936 km^2) in which all river lengths were measured and used to estimate the density of Peregrine Falcons by extrapolation.

to those along unsurveyed rivers (4,900 km) over a wider sample area of 69,936 km^2 (see Fig. 2). Lengths of rivers were estimated from aeronautical maps (scale 1:1,000,000). Variance was estimated for nine approximately equal river stretches that we surveyed in 1997 (total length 823 km, each corrected to territories per 100 km). The average area per territory was then estimated by dividing the total area by the predicted total number of territories present ($\pm$95% CI). Strictly speaking, this estimate is only an indicator of density because it is expressed as an area per unit rather than vice versa. We took this approach because most of the existing literature is expressed in this manner.

Peregrine densities in the shrub tundra of Yamal and northeastern Europe are thought to be much lower than those on the true tundra, and we have defined shrub-tundra sites as low-density areas for peregrines (Danilov et al. 1984, Morozov 1991). Morozov (1991) found a density of 1,000 km^2 per territory in the shrub tundra of Bolshezemelskaya, which is the only recent published estimate for a low-density area. No dispersion statistics were given, so we used the proportionate CI that we found in the Pyasina basin to construct a "best option" confidence interval around Morozov's estimate.

Nesting-association method.—The nesting-association method assumes that the number of Peregrine Falcon territories (P) is related to the number of Red-breasted Goose colonies (N) associated with them. An explicit model can be derived as follows:

$$P = N/E, \tag{1}$$

where E is the proportion of eyries associated with geese. The number of goose colonies in the population can be predicted from:

$$N = BC/2K, \tag{2}$$

where B is the number of geese that breed in a given year, C is the proportion of B that nest with falcons, and K is the mean colony size converted from birds to pairs. The number of geese that breed in a given year is determined by:

$$B = GDA, \tag{3}$$

where G is the size of the goose population, D is the proportion of G capable of breeding, and A is the proportion of D that attempts to breed in a year. Thus, the final model is:

$$P = \frac{GDAC}{2EK}. \tag{4}$$

The relative contribution each parameter makes to the error of the falcon population estimate can be calculated from:

$$r_P = \left[r_G^2\left(\frac{DAC}{2EK}\right)^2 + r_D^2\left(\frac{GAC}{2EK}\right)^2 + r_A^2\left(\frac{GDC}{2EK}\right)^2 + r_C^2\left(\frac{GDA}{2EK}\right)^2 + r_K^2\left(-\frac{GDAC}{2EK^2}\right)^2 + r_E^2\left(-\frac{GDAC}{2KE^2}\right)^2 \right]^{1/2}, \tag{5}$$

where r is the probable error (half of the total 95% CI) of a given parameter Z. When r_Z is multiplied by the first derivative of the model with respect to Z, and the result is then squared, a relative estimate of

TABLE 1. Estimates of number of pairs of *F. p. calidus* calculated with the territory-density method in different geographic areas that overlapped with nesting Red-breasted Geese and for the remainder of the range, 1995 to 1998. Numbers in the left column refer to locations in Figure 1.

Geographic area	Area (km^2)	Density[a]	Estimated no. of pairs Mean	Minimum	Maximum
Red-breasted Goose range					
(1) Yamal	98,880	High	244	152	335
(2) Gydan	133,488	High	329	205	453
(3) South Gydan	365,856	Low	366	229	501
(4) Central Taymyr	118,656	High	292	183	402
(5) North and South Taymyr	355,968	Low	356	222	488
Subtotal			1,586	991	2,179
Rest of range					
(6) Severodvinsk to Yamal (South)	341,136	Low	341	213	467
(7) Severodvinsk to Yamal (North)	365,836	High	901	563	1,240
(8) Novaya Zemlaya	24,720	High	61	38	84
(9) Severnaya Zemlaya	—	None	0	0	0
(10) Putorana Mountains	—	None	0	0	0
(11) Lower Lena	153,264	High	377	236	520
(12) Upper Lena	385,632	Low	386	241	528
Subtotal			2,066	1,291	2,839
Total	2,343,436		3,652	2,282	5,018

[a] High = 406 km^2 per territory (95% CI = 295 to 650); low = 1,000 km^2 per territory (95% CI = 730 to 1,600).

the contribution of each parameter Z's error to the overall error of P can be made (from Boas 1983). The square root of the sum of these errors gives a 95% CI for P. This is a good estimate if the parameters do not covary, which should be the case because all of the variables were estimated independently.

Estimates and errors for these parameters were taken from our data, the literature, and from unpublished data and are detailed in the Results. We surveyed the Pura River and several of its tributaries (total length 250 km) in the summers of 1995 to 1998 to estimate C and K. Areas where Red-breasted Geese were seen along the rivers one to two weeks after incubation began in early July were searched for nests. These were usually near nests of raptors or on islands. Areas away from riverbanks were not searched intensively because, like Peregrine Falcons in the arctic, Red-breasted Geese are believed to nest exclusively near water. The likelihood that breeding pairs of geese were missed during incubation was tested by comparing the number of broods seen on the rivers in late July with the number of goose pairs found, accounting for nests that did not hatch. Assuming low mortality, as normally happens in a peak lemming year when predation pressure is low, the number of broods seen should be the same as the number of nests found. Predation pressure was very high in 1995 and 1997, when only 30% (n = 67 nests) and 19% (n = 18 nests) of the broods, respectively, that were estimated to have hatched were subsequently seen on the rivers. Therefore, a comparison was possible only in 1996, when lemming abundance was high and predation pressure was very low. Broken eggshells in a nest are a good indicator of hatching success for Barnacle Geese (*Branta leucopsis*; J. Prop pers. comm.) and Brant (*Branta bernicla*; B. Ebbinge pers. comm.) because predators habitually take eggs away from the nests before consumption.

RESULTS

Nest spacing and territory density in the Pyasina basin.—The average distance between falcon territories was 29.2 ± SE of 4.7 km (n = 27) along rivers and 23 ± 4.2 km measured in a straight line. Territories were closer on the Pura River ($\bar{x}$ = 20.7 ± 6.3 km along the river, n = 12) than on the lower and middle reaches of the Pyasina River ($\bar{x}$ = 36.1 ± 6.5 km, n = 15). On one part of the Pura, six territories were only 7.2 ± 2.5 km apart. The mean number of territories per 100 km in the nine river stretches was 3.01 ± 95% CI of 1.13 based on a Poisson distribution (variance and mean test for a Poisson distribution, χ^2 = 10.1, df = 8, $P > 0.25$). This suggests that 172 territories (95% CI = 108 to 237) occurred in the 69,936-km^2 study plot, leading to a density of 406 km^2 per territory (95% CI = 295 to 650 km^2 per territory).

Classifying low- and high-density regions.—We split the range of *F. p. calidus* into 12 geographic areas (Table 1) that we classified as holding either high or low densities of falcons. Among the high-density areas, Kalyakin (1983) estimated a density of 800 km^2 per territory on the Yamal Peninsula, although the population numbers were depressed at the time of the estimate. Subsequently, Mechnikova and Gizzatova (1991) suggested a density of 270 to 416 km^2 per territory. No information is available for the neighboring Gydan Peninsula, but we assume that densities there are similar. Only one detailed study has occurred in the coastal zone from Severodvinsk to Yamal (North). Morozov (1991) estimated one pair of falcons every 592 km^2 in a 41,500-km^2 area. Populations may well have increased since then, so the current density there is likely to be similar to that on Taymyr. Peregrine Falcons are absent from northern Novaya Zemlaya (Snow and Perrins 1998), but coastal populations in the south are also assumed to be of high density. Uspenski et al. (1962) reported that distances between nests along the lower and upper Lena River were 15 to 20 km and 30 to 40 km, respectively. Although the Lena delta itself may hold a higher density than we found in the Pyasina basin, we assumed that densities over the larger region are likely to be more similar to those in central Taymyr.

Morozov's (1991) estimate of 1,000 km^2 per pair of falcons in the area from Severodvinsk to Yamal (South) provides the only data from any of the four low-density regions. Northern Taymyr has an arctic desert landscape, and Peregrine Falcons are thought to occur there in low densities (Y. Kokorev pers. obs.). Peregrine Falcons are said to be effectively absent in the Putorana Mountains (Y. Kokorev pers. obs.) and in Severnaya Zemlaya (Rogacheva 1988).

Population estimate.—The 95% CI for the low-density areas (1,000 km^2 per territory) was taken to be similar to the interval found for high-density areas, i.e. −27% and +60%, or 730 to 1,600 km^2 per territory. Applying this and the high-density values to regions outlined in Table 1 gave an estimated population of 3,652 occupied territories (95% CI = 2,282 to 5,018), of which 1,586 (95% CI = 991 to 2,179) were within the range of the Red-breasted Goose.

Defining parameter values and errors for the nesting-association method.—Parameter values used in the model and their errors are summarized in Table 2. The mean number of Red-breasted Goose pairs nesting with falcons (K) varied from 2.57 ± 0.65 (n = 7) in 1997 to 4.89 ± 1.43

TABLE 2. Parameter values used in the nesting-association model to estimate the number of pairs of *P. p. calidus*, 1995 to 1998.

Parameter	Estimate	Range	n	Error type	Probable 95% error[a]	Contribution[b]
Mean pairs of geese per colony (K)	4.52	0.66[c]	23	Normal	1.29	476,019
Proportion of goose pairs nesting with falcons (C)	0.40	0.38 to 0.43	163	Binomial	0.081	239,638
Proportion of eyries with geese (E)	0.83	0.75 to 0.91	23	Binomial	0.158	210,294
Proportion capable of breeding (D)	0.70	0.63 to 0.77	18,000	Binomial	0.098	114,541
Proportion of D that breed (A)	0.82	0.74 to 0.89	205,231	Binomial	0.117	118,973
Goose population (G)	79,000	70 to 88,000	—	Fixed	9,000	75,847

[a] For a variable with a normal error, this was calculated from 1.96 × SE of 0.66. For estimates following a binomial distribution, the probable error was calculated using half of the interval between the maximum proportion indicated in the binomial confidence limits table (e.g., Steel and Torrie 1981) for the maximum proportions observed from the data, and the minimum proportion indicated in tables for the minimum proportion observed.

[b] Relative contribution of each parameter (r_p) to the error in the estimate of falcon numbers (see equation 5).

[c] Value is SE; all others are range.

($n = 9$) in 1996. The weather was highly unusual in 1997 (early snow melt in spring followed by the return of cold temperatures in June), and only 39 pairs of geese attempted to breed, compared with 93 and 105 pairs in 1995 and 1996, respectively. Only 49 pairs were found in 1998, but this was due to an incomplete survey rather than few pairs attempting to breed. Mean colony size did not differ among the more typical years of 1995, 1996, and 1998 (ANOVA, $F = 0.096$, df = 2 and 20, $P = 0.91$), so we used the combined mean for these three years ($K = 4.52 \pm 0.66$, $n = 23$), which was similar to estimates from other areas. Dementiev and Gladkov (1951) stated that the mean size of goose colonies varied from 4 to 5 pairs, and Kostin and Mooiji (1995) found that annual mean colony size varied from 3.6 to 7.5, although the latter range almost certainly included colonies on islands without raptors (these colony sizes tend to be more variable).

No published data are available on the proportion of goose pairs that nest with Peregrine Falcons, but Kostin and Mooiji (1995) found that in the middle reaches of the Pyasina, 48% of colonies were associated with falcons. Kretschmar and Leonovich (1967) found that 19 out of 23 peregrine eyries were associated with Red-breasted Geese. In our study, 24% of goose pairs in 1995, 47% in 1996, and 46% in 1997 nested with peregrines. The 1995 sample was strongly biased because few falcon eyries were checked, and an unusually large colony of 37 pairs of Red-breasted Geese occurred on an island with no raptors. In 1998, 78% of 49 pairs were associated with falcons, but these data also were biased because we visited goose colonies on islands (away from falcons) only after we suspected they had been flooded and when all traces of failed nests would have disappeared. The number of broods that we saw in 1996 ($n = 83$) exceeded the estimated number of pairs whose eggs hatched successfully ($n = 69$), suggesting that 17% of pairs had not been detected during incubation. Along one small tributary that we observed intensively, eight broods came from nests near falcons, but we found 10 broods in total, suggesting that 20% of the pairs nested away from falcons and were overlooked. For the model, we assumed that 17% of the goose pairs were undetected in 1996 and 1997, which means that on average 40% (C) of the pairs nested near Peregrine Falcons. The 95% CI for a binomial sample with $n = 163$ is 0.321 to 0.483, half of which was taken as the probable error (Steel and Torrie 1981).

From 1960 to 1962, Kretschmar and Leonovich (1967) found that 19 of 23 Peregrine Falcon eyries ($E = 0.83$) in the Pyasina basin were associated with Red-breasted Geese, as were 11 of 12 eyries on the Pura River in 1996 ($E = 0.92$). The association was less marked in 1995 (6 of 11) and 1997 (6 of 10) because several eyries were located in atypical rocky areas where no suitable feeding habitat for geese existed. We used Krechmar and Leonovich's (1967) estimate because it was based on the largest sample size. From the binomial confidence limits tables, the probable error with $n = 23$ is 0.158 (Table 2).

The Red-breasted Goose population (G) in winter was estimated to be about 70,000 individuals (Hunter and Black 1996). Surveys on staging sites in Kazakhstan in autumn 1997 suggest that the population could have been as high as 88,000 (Aarvak et al. 1997). We set the population at the mid-point of these two estimates (79,000) and suggest a conservative probable error of ± 9,000 individuals (Table 2).

Estimates of the proportion of geese nesting in lemming-poor years (6% in 1995, $n = 3,765$; 9% in 1997, $n = 1,008$) do not represent the proportion of potential breeders in the entire population because many geese fail early or do not attempt to breed. Conditions on the Pura River in 1996 were ideal, and 76% of all adults present attempted to breed ($n = 306$). Cramp and Simmons (1977) stated that, based on more extensive surveys undertaken in 1972 and 1973, 60% of 25,000 Red-breasted Geese counted were thought to be breeding adults. Similarly, 70% of the intensively studied Svalbard population of Barnacle Geese (*Branta leucopsis*) were potential breeders in any one year ($D = 0.7$, range 63 to 77%; J. M. Black unpubl. data), and 82% of these attempted to breed ($A = 0.82$, range 74 to 89%; Prop et al. 1984). We used the latter data because they refer to an entire intensively studied population of a closely related goose species.

Population estimate and error from the nesting-association method.—Using the above parameters in the model gave an estimated Peregrine Falcon population across the Red-breasted Goose's range of 2,417 ± 95% CI of 1,111 territories, compared with 1,586 territories from the territory-density method. Fifty-eight percent of the total error was accounted for by two of the parameters: mean colony size of geese and the proportion of geese nesting with falcons (Table 2).

DISCUSSION

Territory-density method.—The bias toward surveying major rivers could be an important source of error in our estimate of 406 km^2 per falcon territory. Tributaries were difficult to survey because they remained frozen longer and often became unnavigable soon after water levels dropped following the snow melt. In Finland, Peregrine Falcons nest primarily on the ground near lakes and boggy pools (Wikman 1990), a habit that also may occur in some parts of Siberia, although we found no evidence for this on the numerous lakes we visited in the Pyasina basin. Peregrine Falcons from recovering populations in arctic and subarctic North America sometimes nest 5 to 10 km from rivers at sites that previously were thought to be suboptimal (C. White pers. comm.). Current evidence from Taymyr indicates that the population has increased substantially since the late 1970s (Quinn et al. 2000). The population is still thought to be below carrying capacity, however, so these peregrines probably are not nesting in suboptimal habitats.

The actual variation in density is likely to be more complex than assumed here. One territory every 17 km^2 has been found in some North American coastal areas (Court et al. 1988), although 2 to 300 km^2 per territory is more usual (Bromley and Matthews 1988, Falk and Moller 1988). Use of the value 1,000 km^2 per territory for low-density areas is based entirely on Morozov's (1991) assertion that this is a typical value for the shrub tundra where most of the low-density areas are likely to be. At low-density areas on the Kolmya peninsula, which is outside the range of *F. p. calidus* but at a similar latitude, the typical density is between 800 and 1,600 km^2 per territory (E. Potapov pers. comm.), supporting Morozov's estimate and our assumption. We found no published data for similar habitats in North America, although in boreal regions Peregrine Falcons occur in densities as low as 5,000 km^2 per pair (Ratcliffe 1993). More data on falcon densities across a wider range of habitat types in Siberia are needed to improve the accuracy of the population estimate for *F. p. calidus.*

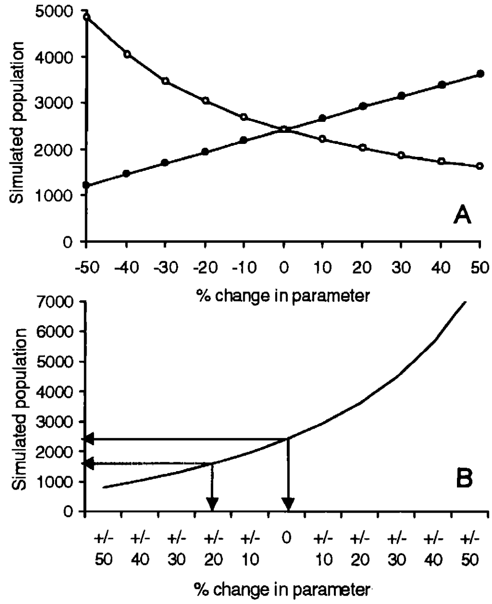

FIG. 3. Simulated population estimates for Peregrine Falcons from the nesting-association model relative to (A) percentage changes in a single numerator (solid circles) or denominator variable (open circles). For some parameters, the maximum percentage change does not reach +50% because the proportion 1 cannot be exceeded. (B) Simulated population estimates for Peregrine Falcons when $C = 0.4$ and $K = 4.52$ (outer set of arrows) compared with a +20% change in K at the same time as a −20% change in C (inner set of arrows). To the left of 0 on the x-axis, values of C are lower than 0.4, and values of K are higher than 4.52 pairs.

Nesting-association method.—Two different methods gave similar estimates for the population of *F. p. calidus* across part of its range. The disparity could be explained by the parameter values not being applicable across the entire range of Red-breasted Geese. The effect on the population estimate of varying individual parameters is simulated in Figure 3A. Fixed variations had the same effect on the population estimate for all numerator and denominator parameters. Varying any one parameter by ±20% resulted in a 16 to 25% change in the predicted population size.

The proportion of geese that nested with Peregrine Falcons (C) and mean colony size (K) were the two most important sources of error in the model. Intuitively, C is unlikely to be

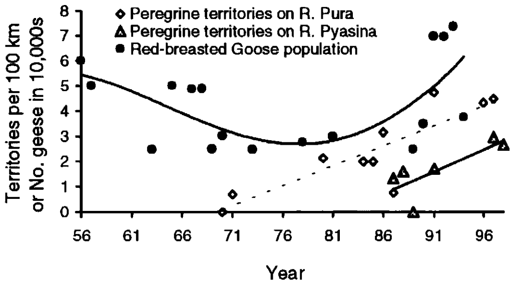

FIG. 4. Counts of the Red-breasted Goose population and trends in Peregrine Falcon density (territories per 100 km) on the Pura and Pyasina rivers in Taymyr (Hunter and Black 1996, Quinn et al. 2000). Lines of best fit were added using a regression-based "trendline" function on a spreadsheet package.

higher than 0.4 at the population level but could be lower. For example, in the Pura basin in 1996, 32% of the Red-breasted Goose pairs that we found (J. Quinn unpubl. data) were associated with Snowy Owls (*Nyctea scandiaca*), a species that may be more important to the geese across their entire range than our data suggest. K also may be higher than our data suggest because most colonies were visited one to two weeks after egg laying began, so we probably missed some early failures. Figure 3B shows the simulated effect on the population estimate of a positive change in K at the same time as a negative change in C. For example, if the true value of C was 0.32 (−20%) and that of K was 5.42 (+20%), this would give a population estimate of 1,612 ± 740 (95% CI using the same probable errors). The proportion of eyries associated with geese (E) contributed the third largest error to r_P (Table 2). Some falcons are likely to nest on the coast where there are few reports of nesting Red-breasted Geese. This is probably the only parameter that currently might lead to an underestimate of the Peregrine Falcon population.

The assumptions that our estimates of the proportion of eyries associated with geese and the proportion of geese that nested with falcons are unbiased can be confirmed only by data collected from other areas. Further evidence supporting the latter assumption is provided by the long-term trends of both species (Fig. 4). Hunter and Black (1996) have summarized data on numbers of Red-breasted Geese, and Quinn et al. (2000) provided information on long-term trends in Peregrine Falcon densities in Siberia. Despite large fluctuations in counts of Red-breasted Geese, their numbers consistently were almost 50% lower in the 1970s and 1980s when the Peregrine Falcon population was depressed. Counts increased in the late 1980s when the falcon population was recovering. Although other factors also may have influenced goose numbers, we believe that our model provides a convincing reason for those interested in monitoring populations of Peregrine Falcons to take note of population trends in Red-breasted Geese and vice versa.

We suggest that future use of the nesting-association method include new estimates for all of the parameters, ideally with information from several parts of the range of the Peregrine Falcon. Admittedly, to do so may require the same effort that would be needed to replicate density estimates across the falcon's range. The population size of Red-breasted Geese, however, is relatively easy to estimate because the geese use a small number of key sites in the nonbreeding season (Hunter and Black 1996, Aarvak et al. 1997). As biologists in the home countries of the Red-breasted Goose begin to study the geese more intensively, it may not be long before a better understanding of the population dynamics of the geese can aid in future attempts to estimate breeding densities of Peregrine Falcons.

Although neither of the two methods provide a statistically rigorous population estimate, the similarity between the results derived from these different approaches strengthens their credibility. Our results suggest that the population of *F. p. calidus* within the range of the Red-breasted Goose is on the order of 1,500 to 2,000 territories and that the entire population contains about 3,580 territories. Referring to the period before the pesticide crash, Kolosov (1983) suggested that a population of several thousand pairs occurred east of the Ural Mountains. Given that most of Russia's Peregrine Falcons occur in the arctic, our estimate of the current population size of *F. p. calidus* supports Kolosov's claim.

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