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RELATEDNESS AND NESTING DISPERSION WITHIN BREEDING POPULATIONS OF GREATER WHITE-FRONTED GEESE

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Abstract. We studied patterns of relatedness and nesting dispersion in female Pacific Greater White-fronted Geese (*Anser albifrons frontalis*) in Alaska. Female Greater White-fronted Geese are thought to be strongly philopatric and are often observed nesting in close association with other females. Analysis of the distribution of nests on the Yukon-Kuskokwim Delta in 1998 indicated that nests were significantly clumped. We tested the hypothesis that females in the same nest cluster would be closely related using estimates of genetic relatedness based on six microsatellite DNA loci. There was no difference in the mean relatedness of females in the same cluster compared to females found in different clusters. However, relatedness among females was negatively correlated with distance between their nests, and geese nesting within 50 m of one another tended to be more closely related than those nesting farther apart. Randomization tests revealed that pairs of related individuals ($R > 0.45$) were more likely to occur in the same cluster when analyzed at the scale of the entire study site. However, the pattern did not hold when restricted to pairs found within 500 m of each other. Our results indicate that nest clusters are not composed primarily of closely related females, but Greater White-fronted Geese appear to be sufficiently philopatric to promote nonrandom patterns of relatedness at a local scale.

Key words: Anser albifrons frontalis, *kinship, local population structure, nesting, Pacific Greater White-fronted Goose, philopatry, relatedness.*

Parentesco y Dispersión de Nidos en Poblaciones Reproductivas de *Anser albifrons frontalis*

Resumen. Estudiamos los patrones de parentesco y la dispersión de nidos en hembras de *Anser albifrons frontalis* en Alaska. Se piensa que las hembras de *A. a. frontalis* son fuertemente filopátricas y frecuentemente se las observa nidificando asociadas de modo cercano con otras hembras. El análisis de la distribución de los nidos en el Delta de Yukon-Kuskokwim en 1998 indicó que los nidos estuvieron significativamente agrupados. Evaluamos la hipótesis de que las hembras en el mismo grupo de nidos estarían cercanamente emparentadas usando estimaciones de parentesco genético basadas en seis loci de ADN microsatelital. No hubo diferencias en el promedio de parentesco de hembras en el mismo grupo comparado con hembras que se encontraron en grupos diferentes. Sin embargo, el parentesco entre las hembras se correlacionó negativamente con la distancia entre los nidos, y los gansos que se encontraban nidificando a menos de 50 m unos de otros tendieron a estar más cercanamente emparentadas que aquellos nidificando más lejos. Análisis de aleatorización revelaron que parejas de individuos emparentados ($R > 0.45$) presentaron mayor probabilidad de encontrarse en el mismo grupo cuando los análisis se hicieron a la escala de todo el sitio de estudio. Sin embargo, el patrón no se mantuvo cuando los análisis se restringieron a pares ubicados dentro de 500 m uno de otro. Nuestros resultados indican que los grupos de nidos no están primariamente compuestos por hembras cercanamente emparentadas, pero que *A. a. frontalis* parece ser suficientemente filopátrica como para promover patrones no aleatorios de parentesco a escala local.

INTRODUCTION

Migratory waterfowl, especially geese (tribe Anserini), exhibit strong female-biased philopatry that may affect the magnitude of gene flow across their breeding ranges (Ely and Scribner 1994). Much of the research on patterns of gene flow and genetic differentiation in waterfowl has been conducted at large spatial scales such as entire breeding ranges (Avise et al. 1992, Scribner et al. 2001). Such studies are not designed to detect local groupings of related individuals within populations (Friesen et al. 1996, de Ruiter and Geffen 1998), and we have little information on the degree of population structuring at small spatial scales. Studies of fine-scale population

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structure may provide insight into the mechanisms promoting population differentiation at larger spatial scales (Chesser 1991, Sugg et al. 1996). For example, fine-scale patterns are likely a result of contemporary behavioral processes, such as natal and breeding philopatry, driven by the fitness benefits of site familiarity (Anderson et al. 1992) or proximity to kin (Lessells et al. 1994). Subdivision of populations into kin groups may also play an important role in the evolution of social behavior through kin selection (Hamilton 1964, Friesen et al. 1996).

We examined the genetic structure within a breeding population of Pacific Greater White-fronted Geese (*Anser albifrons frontalis*) nesting on the Yukon-Kuskokwim (Y-K) Delta in western Alaska. White-fronted geese nest in some of their highest densities on the Y-K Delta (Ely and Dzubin 1994). Females show strong natal and breeding philopatry (Ely and Dzubin 1994) and exhibit life-history characteristics, such as long-term family associations (>1 year, Ely 1993) and pair bond stability, which may reinforce philopatric behavior and influence patterns of relatedness among members of a local population (Ely and Scribner 1994). Offspring from the previous year often guard the nest, and pairs with newly hatched young visit other pairs nesting nearby and may move together and jointly defend brood-rearing areas (Ely and Dzubin 1994). During long-term studies of Greater White-fronted Geese on the Y-K Delta, we observed that groups of geese frequently nested in clusters (i.e., internest distances <30 m). Such a pattern could arise through strong fidelity to specific natal and breeding sites, or through preferential nesting associations, possibly among relatives. To evaluate these alternatives, we first examined the dispersion of nests of female Greater White-fronted Geese on the Y-K Delta to test the hypothesis that the distribution of nests was statistically nonrandom. We then examined patterns of genetic relatedness within and among groups of females using six polymorphic microsatellite DNA markers. If nesting associations were based on kinship, we predicted that females nesting within clusters would be more closely related to each other than those nesting in different clusters.

METHODS

The study was conducted in 1998 at the site of a long-term project on the nesting and brood-rearing ecology of subarctic-nesting geese along the Kashunuk River (61°20′N, 165°30′W) on the Y-K Delta (Fig. 1). To find goose nests, long-term study plots were searched intensively and all nests including those that had been depredated before the searches were recorded. Nest locations were plotted on 1:10 000 color-infrared aerial photographs and later digitized into a GIS database. Genetic identity of breeding females was obtained by collecting contour feathers from a subset of Greater White-fronted Goose nests, focusing on natural clusters of nests (usually within 100–150 m) in the north and south sections of the study area (Fig. 1).

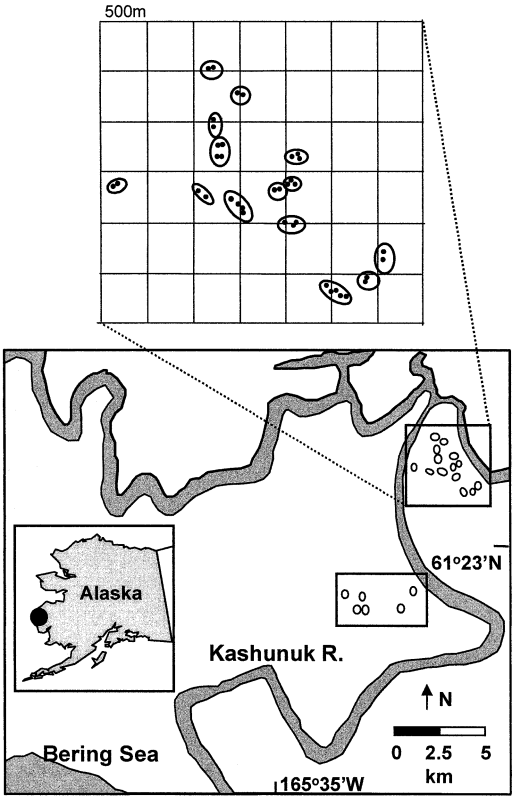

FIGURE 1. Locations of Greater White-fronted Goose nest clusters on the north and south sections of the study area (rectangles) on the Yukon-Kuskokwim Delta, Alaska. Expanded area is a representation of the nests (black dots) and clusters (ovals) on the north section of the study area; each grid section is 500 m.

GENETIC ANALYSES

Template DNA was extracted from the feathers using Puregene DNA Isolation Kits (Gentra Systems, Inc., Minneapolis, Minnesota) and

DNeasy Tissue Extraction Kits (Qiagen, Inc., Valencia, California). Each individual was characterized using six dinucleotide repeat microsatellites (Bcaμ4, Bcaμ6, Bcaμ9, Bcaμ11 and Hhiμ1, Buchholz et al. 1998; Aalμ1, Fields and Scribner 1997). Each locus was amplified in 10-μL reaction volumes using 2.0 μL of template DNA, PCR buffer (20 mM Tris-HCl pH 8.4, 50 mM KCl), 1.5 mM MgCl2, 200 μM dNTPs, 0.4 μM of forward and 5′ fluorescein-labeled reverse primers and 0.5 units Taq DNA polymerase (Invitrogen, Life Technologies, Carlsbad, California). Thermocycler conditions for PCR consisted of one cycle of 94°C denaturation for 2 min and 25–35 cycles of locus-specific annealing temperatures (Aalμ1, 50°C, Bcaμ11, 54°C, Bcaμ4, Bcaμ9 and Hhiμ1, 56°C, Bcaμ6, 60°C) for 45 sec, 72°C extension for 45 sec, and 94°C denaturation for 45 sec, followed by one cycle of locus-specific annealing for 1 min and 72°C extension for 5 min. Amplification products were mixed 1:1.5 with 98% formamide loading dye, denatured for 3–5 min at 95°C and cooled on ice before separating on 5.5% denaturing acrylamide gel at 35 W for about 1 hr. Banding patterns were scanned with a Molecular Dynamics Fluorimager 595 (Molecular Dynamics, Sunnyvale, California) and imaged and archived with Molecular Dynamics ImageQuant software.

STATISTICAL ANALYSES

We used Campbell and Clarke's nearest-neighbor goodness-of-fit (Krebs 1999) to test for nonrandom nest spacing using all Greater White-fronted Goose nests in the north and south sections of the study area. Krebs (1999) suggested that this test is more powerful than other nearest-neighbor methods when samples sizes are large ($n > 50$). Distance classes (the distance between nearest neighbors) were set at 40-m increments so that χ^2 expected cell frequencies were greater than 3. For the subset of nests for which we collected feathers, we used cluster analysis (UPGMA) to define nest clusters (i.e., geese nesting together) objectively. Analyses were performed in STATISTICA (Statsoft 1994). For the above tests, the geometric distances between all pairs of nests were calculated using universal transverse mercator (UTM) coordinates.

Observed heterozygosity (H_o) and deviations from Hardy-Weinberg expectations were calculated using GENEPOP 3.0 (Raymond and Rousset 1995) and FSTAT (Goudet 1995). We calculated an index of relatedness between all pairs of individuals using Program KINSHIP (Queller and Goodnight 1989). KINSHIP estimated relatedness as the proportion of alleles that were shared by two individuals, weighting by the frequency of each allele in the population. The index is the product across all loci and varies between −1 and 1, with average values for full-sibling or parent-offspring comparisons approaching 0.5.

Randomization procedures were used to analyze patterns of relatedness among females due to the lack of independence among samples (i.e., the same individual can occur in more than one pairwise comparison). We used the Simon-Bruce (SB) statistic (Simon 1998, Blank et al. 1999) to compare relatedness of geese nesting in the north and south sections of the study area and to compare relatedness of females in the same and different nesting clusters. Analysis of females in different clusters included only those found in the same section (north or south) of the study area. The SB statistic calculates the sum of absolute differences among groups, $(\Sigma|(\bar{x}_i - \bar{x})|)$ where $\bar{x}_i$ is the mean of each group i and $\bar{x}$ is the grand mean. To determine the significance level of the test statistic, we randomly reshuffled the elements of the groups and recalculated the test statistic and repeated this 10 000 times. The proportion of values that was as large or larger than the original value determined significance. We used Mantel's randomization test to correlate relatedness and nesting proximity. Pairwise matrices of natural logarithms of distance and relatedness values were analyzed by randomly rearranging the elements of one matrix (distance) and recalculating the correlation coefficient. Randomizations were repeated 10 000 times and significance was determined by the proportion of values that was as large or larger than our original value.

We conducted two additional randomization tests to further evaluate the spatial patterns of genetic relatedness. First, using all females on the study area, we classified females as being closely related (top 10% of relatedness values, $R > 0.45$) or unrelated ($R \leq 0.45$). We then counted the number of related females that occurred in the same cluster. We compared this value to that generated from a null model in which pairs were assigned randomly to the same or different cluster, keeping the column and row

totals unchanged (i.e., number of related and unrelated pairs, and number of pairs in the same or different cluster). We repeated this 10 000 times and tallied the proportion of values (number of closely related females in the same cluster) that was as large or larger than the original value to determine significance. (Note that this test is equivalent to assigning individuals randomly among clusters and then calculating relatedness; our method simply determines the relatedness category first, and then randomizes pairs to the same or different cluster).

In the second analysis, we repeated the randomization test after restricting the sample to pairs of females that nested within 500 m of each other. We used a value of 500 m because Ely and Dzubin (1994) reported that radiotracked females generally nested within 500 m of their previous year's nest. If females were preferentially nesting close to relatives, we predicted that related females within 500 m would still be more likely to be found in the same cluster compared to the null distribution. Conversely, if philopatry to a local area alone is sufficient to explain associations among related females at the scale of the entire study site, we predicted that related females would not be more likely to occur in the same cluster when the sample was restricted to females nesting within 500 m.

We calculated 95% CI for estimates of mean pairwise relatedness by resampling with replacement (10 000 times), obtaining a distribution of mean values, and taking the upper 2.5% and lower 97.5% of values as the upper and lower confidence intervals (Blank et al. 1999).

RESULTS

NESTING DISTRIBUTION

Greater White-fronted Geese nesting in the north section of the study area ($n = 69$) were not distributed randomly ($\chi^2_6 = 18.7$, $P < 0.01$); nearest-neighbor distances were shorter than expected, suggesting a clustered distribution (Fig. 2a). Goodness-of-fit tests for nests in the south section ($n = 58$) also rejected the null hypothesis of a random distribution (χ^2_6 19.2, $P < 0.01$); again nests were closer than expected by chance (Fig. 2b).

We collected feathers from 56 nests, 44 nests in the north section and 12 in the south section. The distances between sampled nests within the north and south areas ranged from 12 to 2050 m within areas (mean 1150 m, 95% CI = 1111–1190 m). Cluster analyses defined 20 nest clusters, 14 in the north and 6 in the south. Mean distance between nests in a cluster was 124 m (95% CI = 107–142 m). Average number of nests per cluster was 2.8 ± 0.3 (SE; range 2 to 7). Clusters within an area ranged from 182 to 3041 m apart (mean 1217 m, 95% CI = 1178–1256 m).

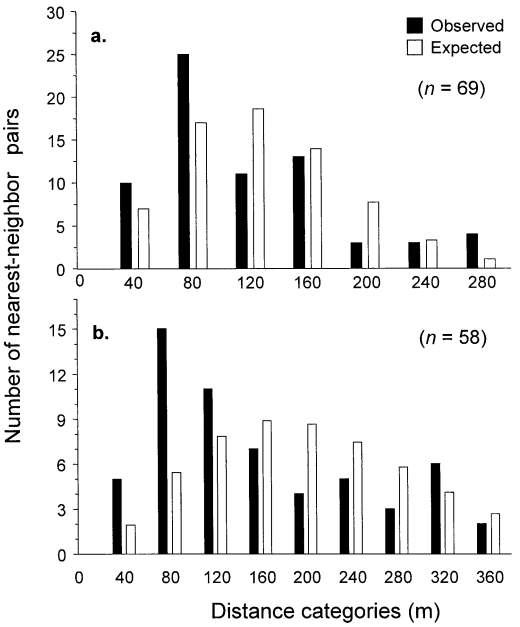

FIGURE 2. Observed (filled) and expected (unfilled) distributions of nearest-neighbor distances for all Greater White-fronted Goose nests in (a) the north ($n = 69$) and (b) south sections ($n = 58$) of the study area. Distances were grouped into 40-m categories.

GENETIC ANALYSES

To insure that we obtained the DNA from only a single female for each nest, we used Bcaμ4, a polymorphic, sex-linked locus with five alleles, as an initial test. No samples exhibited multiple banding patterns for this locus indicating that we extracted DNA from only a single female per nest. Consistent banding patterns (only one or two alleles per sample) across all other loci confirmed this assumption.

The five disomic microsatellite loci were polymorphic, exhibiting two, four, four, eight, and eight alleles at Bcaμ6, Bcaμ9, Bcaμ11, Hhiμ1, and Aalμ1, respectively. Observed heterozygosities of Bcaμ6, Bcaμ9, Bcaμ11, Hhiμ1,

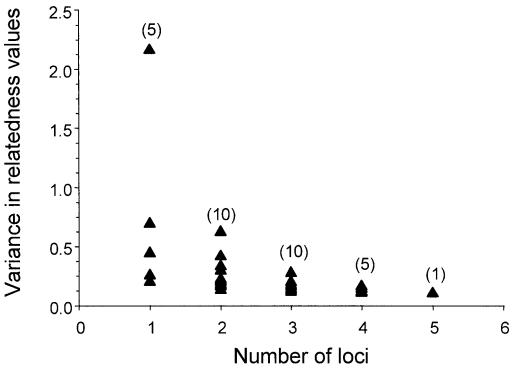

FIGURE 3. Plot of the variance in mean relatedness values using all possible unique combinations of the five loci for Greater White-fronted Goose females nesting on the study area. Sample sizes in parenthesis correspond to the number of unique combinations of different loci.

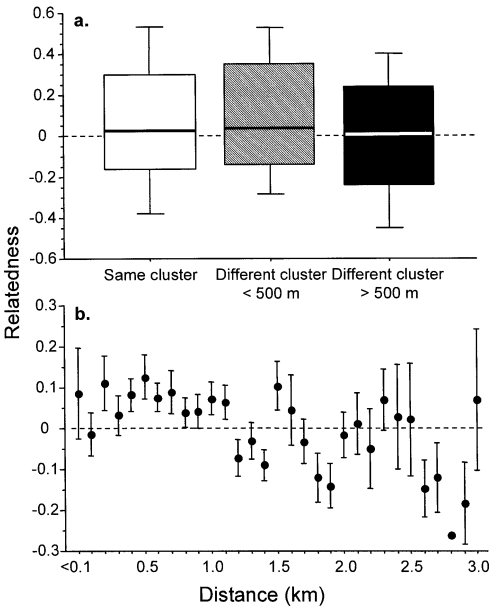

FIGURE 4. (a) Box plots of pairwise relatedness among Greater White-fronted Goose females nesting in the same cluster, in different clusters but within 500 m, and in different clusters >500 m apart but in the same section of the study area (north or south). Boxes represent the 25–75 percentiles, vertical lines represent the 10–90 percentiles, and the horizontal line is the median. (b) Mean (± SE) relatedness as a function of the distance between nesting pairs of Greater White-fronted Geese on the Yukon-Kuskokwim Delta. Only pairs in the same section of the study area (north or south) are included. The relationships shown in these figures were analyzed using randomization tests.

and Aalμ1 were 0.32, 0.55, 0.52, 0.52, and 0.75, respectively, which were not different from Hardy-Weinberg expectations ($P > 0.2$ for all tests). A rarefaction analysis of the relatedness value using all possible combinations of the five loci confirmed that these loci were sufficient to estimate relatedness of individuals with reasonable precision (Fig. 3). As additional loci were included, the variance of mean relatedness decreased and became nearly asymptotic when four or more loci were used. Estimated relatedness values ranged from −0.79 to 0.86 (mean 0.00, 95% CI = −0.01 to +0.02) for all pairwise combinations of individuals (1540 pairs). Relatedness of geese in the north and south sections of the study area did not differ (SB statistic = 0.01, $P > 0.5$).

We compared relatedness of females in the same cluster to that of females in different clusters but in the same study section (north or south) and found no significant difference (females in same cluster: mean $R = 0.05$, 95% CI = −0.01 to +0.09; females in different clusters: mean $R = 0.01$, 95% CI = −0.05 to +0.08; SB statistic = 0.04, $P < 0.35$; Fig. 4a). However, geese that nested very close to one another (within 50 m) tended to be more closely related (mean $R = 0.13$, 95% CI = −0.03 to +0.27) than those that nested farther apart (mean $R = 0.01$, 95% CI = −0.01 to +0.02), although the sample size was small (23 pairs nesting within 50 m; SB statistic = 0.12, $P < 0.07$). Overall, there was a significant negative correlation between relatedness and nesting proximity ($r = -0.09$, $P < 0.02$; Fig. 4b).

Using randomization tests, we found that closely related females ($R > 0.45$) were significantly more likely to occur in the same cluster when samples from the entire study site were considered: 12 of 70 pairs (17%) of females that occurred in the same cluster were related, whereas 98 out of 942 pairs (10%) in different clusters but in the same section of the study area (north or south) were related (randomization test, $P < 0.02$). However, this pattern disappeared when the analysis was restricted to only samples from pairs of females nesting within 500 m of each other (12 of 70 pairs [17%] in the same cluster were related; 32 out of 189 pairs [17%] in different clusters were related; randomization test, $P > 0.9$).

DISCUSSION

We found that the distribution of nests of female Greater White-fronted Geese on the Y-K Delta was clumped; females nested nearer to their neighbors than expected by chance. One possibility for such clustering is that it is simply a result of the availability of suitable nesting habitat. White-fronted geese on the Y-K Delta are flexible in their choice of nest site, nesting along slough levees, on lakeshores and islands, and in meadows and uplands (Ely and Raveling 1984). Nest selection may be more restricted in years of late snowmelt due to limited access to sites (Ely and Raveling 1984), but snowmelt was not late in 1998 (Babcock et al. 2002). Babcock and Ely (1994) estimated the relative area of suitable nesting habitat on the study area and found that about 50% of the area was meadow flats and slough or river levees. Given this abundance of apparently suitable nesting habitat and its intermixture, we believe that neither limitation nor distribution of habitat was responsible for the clustering of nests.

A second possibility is that clusters represent groups of related females, either because of the benefits of associating with kin or because of strong breeding philopatry. Our test of this prediction produced mixed results. On one hand, only a small percentage of females in the same cluster were closely related ($<20\%$) and we found no difference in the average relatedness of females nesting in the same clusters compared to pairs of females nesting in different clusters. These results suggest that kin associations are not the basis for the formation of nesting clusters in Greater White-fronted Geese.

On the other hand, there was a significant negative correlation of genetic relatedness with distance between nests, and clusters were heterogeneous with respect to related and unrelated females. When we considered all nests in each section of the study area, a higher percentage of closely related females occurred in the same cluster (17%) than in different clusters (10%). When we restricted this analysis to include only females nesting within 500 m, the pattern disappeared. This result could be readily explained if females were simply more likely to return to within 0.5 km of their natal site to breed, without regard to the location of relatives. Under this scenario, we would expect nonrandom patterns of association among relatives when examined at the scale of the entire study area, but those patterns would disappear when examined at a more localized scale, as we observed.

A negative correlation between relatedness and distance between nest sites is expected in animals that are philopatric to their natal site, although relatively few studies have investigated such relationships. Relatedness of female grey-sided voles (*Clethrionomys rufocanus*) was negatively correlated with distance between capture sites (Ishibashi et al. 1997). Likewise, a negative correlation between relatedness and distance was found for adult female and juvenile Japanese wood mice (*Apodemus argenteus*), but not for males (Ohnishi et al. 2000). Friesen et al. (1996) reported significant genetic substructuring among Thick-billed Murres (*Uria lomvia*) nesting on different ledges within a breeding colony. More often, however, analyses of genetic structure are based on comparisons of populations, rather than individuals, and usually at larger spatial scales than our study. A significant negative correlation was found between genetic and geographic distance among populations of Red Grouse (*Lagopus lagopus*), but these populations ranged from 1 to 52.5 km apart (Piertney et al. 1998). Likewise, in nonmigratory Blue Ducks (*Hymenolaimus malacorhynchos*), genetic similarity decreased as geographic distance increased among populations that ranged from 7 to >50 km apart (Triggs et al. 1992). Investigations focusing on populations rather than individuals as the units of interest may overlook fine-scale patterns of relatedness among individuals at a local scale (Friesen et al. 1996, de Ruiter and Geffen 1998).

Given that our results do not support the hypothesis that nest clusters of Greater White-fronted Geese are primarily kin-based, why do geese nest in close association? One possibility is that social affiliations improve nesting success by increasing the amount of total vigilance: the more pairs that nest in an area, the greater the chance of detecting a terrestrial predator (e.g. Arctic fox [*Alopex lagopus*]). Nesting associations may also facilitate joint defense or deterrence of predators. Geese often fly and call in alarm over approaching foxes, and this ''tolling'' behavior alerts other geese in the area to the presence of a predator (Barry 1967, Ely and Dzubin 1994, Slattery et al. 1998). Tolling may also distract foxes and cause them to leave an area more quickly (Ely and Dzubin 1994, Slat-

tery et al. 1998). Such behavior might be promoted by kin selection if the nearby recipients of such acts were close relatives. However, tolling does not appear to be risky (the birds fly well out of reach of the predator) and so the benefits need not be directed solely at related individuals (Slattery et al. 1998).

We conclude that clusters of Greater White-fronted Goose females are not composed primarily of close kin. However, our results do indicate that philopatry of female Greater White-fronted Geese is sufficiently strong to promote nonrandom patterns of relatedness at a local scale (i.e., within 10 km). Given that philopatry is female biased, future studies on clusters of birds across a broader geographic range using maternally inherited mtDNA markers in combination with biparentally inherited markers such as microsatellite DNA (e.g., Scribner et al. 2001) would be worthwhile. Such analyses would help to establish whether behavioral processes occurring at a local scale, such as sex-biased natal and breeding philopatry, are sufficient to promote population differentiation at larger spatial scales.

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