

Circumpolar variation in morphological characteristics of Greater White-fronted Geese *Anser albifrons*

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Capsule Greater White-fronted Geese show significant variation in body size from sampling locations throughout their circumpolar breeding range.

Aims To determine the degree of geographical variation in body size of Greater White-fronted Geese and identify factors contributing to any apparent patterns in variation.

Methods Structural measures of >3000 geese from 16 breeding areas throughout the Holarctic breeding range of the species were compared statistically.

Results Palearctic forms varied clinally, and increased in size from the smallest forms on the Kanin and Taimyr peninsulas in western Eurasia to the largest forms breeding in the Anadyr Lowlands of eastern Chukotka. Clinal variation was less apparent in the Nearctic, as both the smallest form in the Nearctic and the largest form overall (the Tule Goose) were from different breeding areas in Alaska. The Tule Goose was 25% larger than the smallest form. Birds from Greenland (*A. a. flavirostris*) were the second largest, although only slightly larger than geese from several North American populations. Body size was not correlated with breeding latitude but was positively correlated with temperature on the breeding grounds, breeding habitat, and migration distance. Body mass of Greater White-fronted Geese from all populations remained relatively constant during the period of wing moult. Morphological distinctness of eastern and western Palearctic forms concurs with earlier findings of complete range disjunction.

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Conclusions Patterns of morphological variation in Greater White-fronted Geese across the Holarctic can be generally attributed to adaptation to variable breeding environments, migration requirements, and phylo-geographical histories.

Temperate waterfowl (family Anatidae) exhibit relatively few polytypic species compared to many avian families (Delacour 1954, Zink & Remsen 1986). Reasons for a higher degree of monotypism in this group may be related to their generally broad distributions and strong migratory tendencies (Bohning-gaese *et al.* 1998, Bensch 1999), which promote gene flow during evolutionary history and reduce geographical isolation compared to other avian groups. Well-known exceptions to monotypy within Anatidae include the Canada Goose *Branta canadensis* in North America (Bellrose 1980, Dunn & MacInnes 1987) and the Bean Goose complex *Anser fabalis* in Eurasia (Delacour 1954). However, information on the magnitude of intra-specific phenotypic variation is lacking for many other avian species with broad ranges, especially for migratory birds that breed in remote areas, such as much of the arctic.

Greater White-fronted Geese *Anser albifrons* are one of the few waterfowl species, and one of only two goose species (the other being the Brent Goose *Branta bernicla*) with a circum-arctic breeding distribution (Delacour 1954). There is little consensus on the taxonomy and spatial distribution of purported subspecies of Greater White-fronted Geese due largely to the lack of a comprehensive set of morphological data from across the range of the species. For instance, of the four recognized subspecies, there is agreement as to nomenclature and distribution for only the Greenland form, *A. a. flavirostris*. In Eurasia, some consider the nominate form *A. a. albifrons* to breed across the entire continent from the Kanin Peninsula to the Bering Sea (Dement'ev & Gladkov 1967, Owen 1980, Portenko 1989), whereas others have argued that *A. a. albifrons* nests only as far east as the Kolyma River where the nesting distribution of *A. a. frontalis* begins and continues uninterrupted, across the Bering Strait, Alaska and northern Canada to Hudson Bay (Delacour 1954, Philippona 1972, Cramp & Simmons 1977). Mooij (2000) and Mooij & Zockler (2000) have proposed subspecific status for geese breeding in the eastern Palearctic (*A. a. albicans*). In North America there is general agreement that the Tule Greater White-fronted Goose is a distinct subspecies that breeds only in the vicinity of Cook Inlet of south

central Alaska, although two different subspecific designations have been used in the literature: *A. a. gambeli* (American Ornithologists' Union 1957, Timm *et al.* 1982, Ely & Dzubin 1994) and *A. a. elgasi* (Delacour & Ripley 1975). The rest of the White-fronts in North America are thought to be comprised of either a single subspecies (*A. a. frontalis*; American Ornithologists' Union 1957, Timm *et al.* 1982, Ely & Dzubin 1994) or two subspecies: *A. a. frontalis* for White-fronts in the Pacific Flyway and *A. a. gambeli* for White-fronts in the Central Flyway (Delacour & Ripley 1976, R. Banks pers. comm.). Suggestions of the existence of other unique forms from northern Yukon Territory (Elgas 1970), southwestern Alaska (Orthmeyer *et al.* 1995) and the Kava River region of southeastern Siberia (Krechmar 1996) further complicate the taxonomy of the species.

Our intentions here are not to necessarily revise the taxonomy or nomenclature of different breeding populations of Greater White-fronted Geese, although this first comprehensive morphological treatment should provide a strong basis for future taxonomic treatments. Earlier comparisons of morphological variation of Greater White-fronted Geese have generally been restricted to wintering birds (Beer & Boyd 1963, Owen 1980, Takekawa *et al.* 2000) or to forms known to occupy only a limited portion of the breeding range (e.g. southwestern Alaska; Krogman 1979, Orthmeyer *et al.* 1995). Inclusion of wintering birds in morphological analyses has caused confusion, as the breeding ground origin of wintering birds is usually unknown due to population mixing. Long-term marking studies of breeding birds, particularly in North America, have led to a better understanding of geographical affinities of breeding, staging and wintering birds, but population mixing on wintering areas is invariably too pervasive to sample specific populations with any confidence. Only through simultaneous comparisons of morphology and movements (potential gene flow) can we best interpret intraspecific variation and verify or clarify broad biogeographical patterns.

We present the first comprehensive morphological data for a circumpolarly distributed waterfowl species. We examine several factors possibly contributing to geographical variation in morphology of Greater

White-fronted Geese including ecological and life history differences among populations. Our data enables a broad-scale comparison of relationships between morphology and climatic factors on breeding and wintering areas (Zink & Remsen 1986), consequences of variable migration distances (Bohning-gaese *et al.* 1998) and historical distribution.

STUDY AREA AND METHODS

We sampled birds from throughout their known breeding range across northern Asia, Greenland and North America (Owen 1980; Fig. 1). The objective was to sample geese during the summer period when breeding populations are largely segregated. Study sites, and hence inter-sample distances, were dictated by the distribution of established field sites given the limited access to remote arctic breeding locations. As a result, sampling density was greater in North America than in Eurasia.

We obtained linear measurements of standard body parts of adult-plumage birds following the procedures of Dzubin & Cooch (1992). We used the traditional cul-

men measurement referred to by Dzubin & Cooch (1992) as culmen 1. We also measured posterior bill width (widest upper mandible width, at the gape), given the known correlation between bill width and body size in Greater White-fronted Geese (Orthmeyer *et al.* 1995, Schmutz & Ely 1999). Total tarsus was measured for all populations except at the Indigirka River Delta, where a modified diagonal tarsus measurement was used; these measurements were converted to total tarsus based on a ratio developed from a subset of geese with both measurements. Linear measures were obtained to the nearest 0.1 mm with calipers, and body mass was determined from spring or top-loading scales. Ninth primary length was measured to the nearest 1.0 mm with a metric ruler.

Sex was determined in the field by cloacal examination. Geese were classified as breeding if hatching-year birds were present in the capture groups, otherwise they were considered to be pre-breeders or failed/non-breeders. Most geese were captured in moulting flocks on the breeding grounds, except for birds from the Kanin Peninsula of European Russia, the Indigirka and Lena River deltas of Siberia, and MacKenzie River

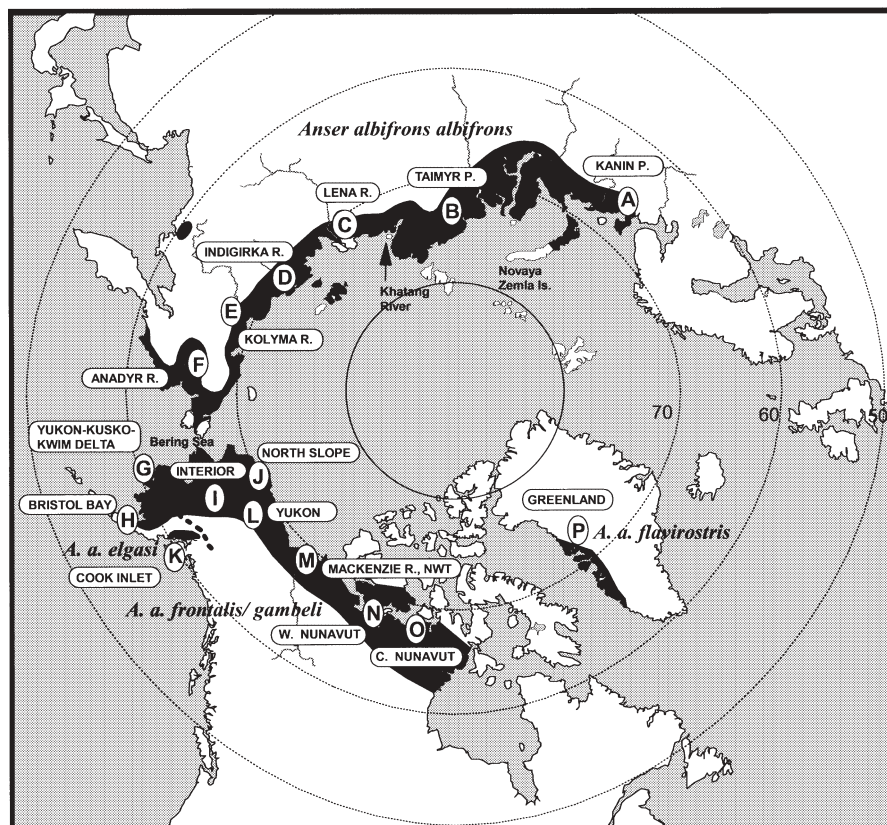


Figure 1. Breeding distribution of Greater White-fronted Geese showing locations where measurements were obtained. The dotted line dividing Alaska shows the approximate boundary between Pacific Flyway and Central Flyway populations.

Delta in Northwest Territories (NWT) Canada, which consisted of birds killed in late spring by indigenous subsistence hunters during the pre-nesting period.

We corrected for seasonal variation in body mass by assuming that late spring birds were 16.1% and 10.1% heavier, females and males respectively, than birds during moult (based on spring and moulting samples of birds from the Yukon-Kuskokwim Delta, Alaska; Budeau *et al.* 1991, this paper). Birds captured in moulting concentrations may have nested at some distance from moulting sites. However, breeding and non-breeding White-fronts from the same population have previously been shown to have similar distributions (Ely & Takekawa 1996) and any discrepancies in breeding ground affiliations are likely to be minor relative to the broad scale (>500 km) of our inter-population comparisons.

Box-plots were constructed of individual measures by sex and location to identify departures from a normal distribution and then tested for constancy of variance using Levene's test in separate one-way analysis of variance (ANOVA) tests for each sex and variable (head, culmen, tarsus, bill width, mass and principal component PC1) using a general linear models procedure (SAS 1989). When variances were not constant (heteroscedastic) we adjusted the ANOVA with a weighted least squares estimate using the reciprocal of the standard deviation (SAS 1989, Timm & Mieczkowski 1997). We constructed 95% confidence intervals (SAS 1989) for making comparisons among population means (Johnson 1999) but also tested for among-population differences in head, culmen, tarsus and bill width using ANOVA (SAS 1989). We used PC1 analysis (SAS 1989) to develop a single variable indicative of overall body size based on head, culmen, tarsus and bill width measurements (Sedinger *et al.* 1995). ANOVA tests were also used to examine differences among populations in body mass but only after testing for effects of moult stage (determined by ninth primary length) on body mass (see below).

Most geese captured were either failed breeders or non-breeders, as moulting flocks of breeding birds (adults with flightless young) are generally small in this dispersed-nesting bird, and difficult to capture in large numbers. In instances where known breeders and non-breeders were sampled from the same area, ANOVA was used to test for differences in measurements between the two groups.

Body mass of Greater White-fronted Geese varies considerably throughout the year (Ely & Raveling 1989). For some species of geese, body mass is known to

vary with stage of wing moult (Ankney 1984, Fox *et al.* 1998), although in one subspecies of Greater White-fronted Goose *A. a. flavirostris*, body mass remains relatively constant throughout the period of wing moult (Fox *et al.* 1998). Before testing for location differences in body mass of moulting geese we first used analysis of covariance (ANCOVA; GLM procedure in SAS 1989) to determine if there was a relationship between body mass and timing of wing moult, as indicated by length of the ninth primary for the 11 populations for which we had data on both body mass and stage of wing moult.

Although all observers followed the measurement instructions and illustrations of Dzubin & Cooch (1992), observer differences in measurement technique may bias the magnitude of observed difference among populations because birds from most populations were measured by different observers (exceptions include locations in western Alaska, where birds were measured by a single observer). By comparing samples from the same geographical area measured by different individuals we were able to test for observer differences using ANOVA techniques.

Environmental variables

Mean temperature during June was calculated from surface air temperature isopleths (Rigor *et al.* 2000) as an index of climate on the breeding grounds. We used mean temperature during January to estimate severity of winters on primary wintering areas (Hansen *et al.* 1999). When possible, estimates of migration distances were based on distribution of recoveries of ringed birds. Recovery data were extensive in the Nearctic, and hence migration patterns and migration distances well understood (Ely & Dzubin 1994). In the western Palearctic, migration distances were obtained from migration pathways described by Fox *et al.* (1999) and Mooij *et al.* (1999). Migration distances of eastern Palearctic populations were inferred from straight-line distances between the few known wintering and staging areas, based on a nominal number of recoveries of ringed or collar-marked birds (Y. Miyabayashi pers. comm., K. Litvin pers. comm.).

Sampling distribution

Geese were sampled from 16 regions, including five areas in Alaska, four in Canada, six across northern Eurasia and one in Greenland (Fig. 1, Table 1). There were no consistent differences in linear or mass mea-

Table 1. Location of capture and breeding site characteristics of Greater White-fronted Geese used in analyses.

Map code	Location	Breeding grounds				Wintering grounds			Staging area
		Latitude	Longitude	Onset of incubation ^a	June temp. ^b	Location ^c	Latitude	January temp. ^d	Location
Palaearctic									
A	Kanin Peninsula, N. Eur. Russia	67°00'N	44°00'E	10 June ¹	2	W. Europe ¹	43–54°	5–10	Estonia, Eur. Russia
B	Taimyr Peninsula, central Siberia	73°40'N	87°00'E	15–20 June ^{2,3}	0	Central Europe ²	43–54°	–1–4	Belarus, Eur. Russia
C	Lena River Delta, E. Siberia	73°30'N	126°30'E	15 June ⁴	2/4	China/Korea ³	28–31°	0–5	Amur River ?
D	Indigirka River, E. Siberia	71°30'N	150°30'E	10–15 June ⁵	2/4	China ³	28–31°	0–5	Amur River ?
E	Kolyma River Delta, E. Siberia	70°23'N	159°50'E	10–15 June ^{2,6}	2/4	China ^{3,4,5}	28–31°	0–5	Amur River ?
F	Anadyr Lowlands, Chukotka	64°10'N	178°20'E	1 June ⁶	4	Japan/Korea/ China ^{4,5,6,7}	28–38°	–6–4	Kamchatka, Amur River
Nearctic									
G	Yukon-Kuskokwim Delta, Alaska	61°20'N	165°30'W	25 May ⁹	6	California ⁹	37–40°	4–10	Klamath Basin, California
H	Bristol Bay Lowlands, Alaska	58°40'N	159°10'W	1–15 May ⁸	8	Mexico ⁹	26°	–1–4	E. Oregon
I	Interior Alaska	65°00'N	156°00'W	1–15 May ¹⁰	10/12	Mexico/Texas ¹⁰	24–27°	–1–4	Alberta, Canada
J	North Slope, Alaska	70°20'N	152°20'W	8–10 June ¹¹	2	Texas ¹¹	26–30°	10–15	Saskatchewan, Canada
K	Cook Inlet, Alaska	62°20'N	151°10'W	12–28 May ⁷	10	California ⁸	39°	4–10	S. Oregon, Gandil R., AK
L	Old Crow, Yukon	68°10'N	140°50'W	25 May ¹²	10	Mexico/Texas ¹⁰	24–30°	10–15	Alberta, Canada
M	Mackenzie River, NWT	69°30'N	123–133°W	1 June ¹³	4	Texas ¹⁰	26–30°	10–15	Saskatchewan, Canada
N	Western Nunavut	68°30'N	105–115°W	10–14 June ¹⁴	4	Texas ¹⁰	26–30°	10–15	Saskatchewan, Canada
O	Central Nunavut	68°00'N	93–101°W	13 June ¹⁵	2	Louisiana/ Arkansas ¹⁰	30–32°	10–15	Canada
P	Greenland	67°30'N	50°30'W	19–26 May ¹⁶	4	Ireland/Scotland ¹²	52–56°	–1–4	Iceland

^aData for incubation from: ¹Litvin *et al.* 1998 (Vayagetch Island); ²Krechmar 1986; ³Mineyev 1995; ⁴D. Solovieva pers. comm.; ⁵Ptushenko 1952, J. Pearce pers. comm.; ⁶Kondratyev 1993; ⁷Bollinger & Ely unpubl. data; ; ⁸Ely & Takekawa 1996; ⁹Ely & Raveling 1984; ¹⁰M. Spindler unpubl. data; ¹¹S. Simpson unpubl. data; ¹²Elgas 1970; ¹³Barry 1967; ¹⁴Carriere *et al.* 1999, R. Bromley unpubl. data; ¹⁵Hanson *et al.* 1956 (based on 1A goslings 20 July); ¹⁶Stroud 1982.

^bTemperature data (°C) from surface air temperature data from Rigor *et al.* 2000.

^cData on wintering area from: ¹Mooij *et al.* 1999; ²Owen 1980; ³Zhang & Yang 1997; ⁴Miyabayashi *et al.* 1994, Miyabayashi & Mundkur 1999; ⁵Kurechi *et al.* 1995; ⁶Pyong-Oh 1990; ⁷Takekawa *et al.* 2000; ⁸Timm *et al.* 1982; ⁹Ely & Takekawa 1996; ¹⁰Ely *et al.* unpubl. data; ¹¹King & Hodges 1979; ¹²Owen 1980.

^dTemperature data (°C) from surface air temperature data from Hansen *et al.* 1999: www.giss.nasa.gov

tures among four boreal forest sites in Alaska (drainages of the Yukon River and in the Kotzebue Sound area) so data from these Interior Alaska sites were pooled for further analysis. Similarly, samples of birds measured near Kugluktuk, Nunavut did not differ in size from birds captured on the Kent Peninsula or Victoria Island, and were pooled as a sample from western Nunavut. Birds measured from the Inglis River (Rasmussen Basin) and the Queen Maud Gulf were combined as a central Nunavut sample.

Measurement data for Greenland White-fronts were obtained from birds wintering in Ireland, with the

exception of body mass, which was collected during summer in Greenland. Sampling of actual Greenland-nesting birds was assured as Greenland White-fronts are often segregated from other White-front populations during winter (Wilson *et al.* 1991) and identification was confirmed by the presence of summer-ringed geese. Diagonal tarsal lengths of geese from the Indigirka River Delta were converted to total tarsal lengths by multiplying by a correction factor of 1.115 for males and 1.142 for females, determined from a sample of museum specimens for which both measurements were obtained.

Samples of geese from the Kanin Peninsula, the Indigirka River Delta, the Northwest Territories and Greenland were missing at least one of the four variables used in the principal components analysis. To include these populations in a more robust (i.e. more variables) treatment, we estimated values for missing variables using multiple regression models (SAS 1989).^a

RESULTS

Observer effects

To assess whether among-population variation could be attributed to differences in how geese were measured (observer effects) we analysed a subset of our data for which birds from a given population were measured by more than one observer. For the two populations with multiple observers measurement error was minimal, as culmen lengths varied little, both for birds from the North Slope of Alaska (mean \pm se of 49.7 ± 0.43 versus 49.5 ± 0.45 and 52.4 ± 1.50 versus 52.7 ± 0.65 for females and males respectively; $F_{1,75} = 0.00$, $P = 0.95$) and from the Taimyr Peninsula, Siberia (mean \pm se of 44.3 ± 1.24 vs. 44.5 ± 0.16 and 45.7 ± 0.84 vs. 46.8 ± 0.19 for females and males respectively; $F_{1,457} = 0.93$, $P = 0.335$), thus verifying that measurement methodology led to repeatable results.

Body size index

The first principal component (PC1) derived from tarsus, culmen, bill width and head measurements appeared to be a good index of overall body size, since the first eigenvector showed approximately equal loadings on all variables (0.544 for head, 0.469 for tarsus, 0.514 for culmen and 0.469 for bill width). PC1 accounted for 77% of the standardized variance suggesting that most covariation in original variables was due to overall size of birds.

Influence of breeding status on morphology

We tested for effects of reproductive status on morphology and body mass to determine whether local successful breeders differed morphologically from failed/non-breeding birds, that could have originally attempted to breed at another locality (i.e. undergone a moult migration). Analyses were restricted to one location in Siberia (Anadyr) and three in North America (Yukon-Kuskokwim Delta, Alaska and Kent Peninsula, and Victoria Island, Nunavut) for which we

had measurements for both successful breeders and failed, or non-breeding geese. In a series of ANOVA models, each with independent factors including reproductive status, sex and location, reproductive status did not significantly contribute to variation in head length ($F_{1,418} = 0.07$, $P = 0.79$), tarsus length ($F_{1,581} = 1.59$, $P = 0.21$), bill width ($F_{1,541} = 0.00$, $P = 0.97$) and body mass ($F_{1,412} = 1.56$, $P = 0.21$) or PC1 ($F_{1,364} = 2.95$, $P = 0.09$), but exhibited some relation with culmen length ($F_{1,588} = 4.10$, $P = 0.04$). However, the importance of the latter relationship is tempered due to interaction of effects between sex, location and reproductive status ($F_{6,588} = 2.02$, $P = 0.06$). Subsequent analyses showed that the significance of reproductive status on culmen lengths was due to longer culmen lengths of failed breeders compared with successful breeders on the Yukon-Kuskokwim Delta, and may be an artefact of small sample size (five female and six male non-breeders, respectively). Given the overall lack of effect of reproductive status on body size (PC1; significant effect of only one of five individual measures for only one out of four populations), we combined birds of different reproductive status for further analyses.

Sexual dimorphism

Males averaged 4.6–5.7% larger than females for all linear measurements and were 10% heavier than females (Fig. 2). Sex effects were more pronounced than location effects for all variables (Table 2). The significant sex*area interaction in three of four linear measures indicates variation in the magnitude of sex-related morphological differences among areas, although the magnitude of the disparities in male size (expressed as male–female/female), was not exceedingly large (Fig. 2; head: mean 5.0%, range 3.4–6.1; culmen: mean 5.7%, range 0.0–8.3; tarsus: mean 5.0%, range 2.6–8.8; bill width: mean 4.6%, range 2.9–8.3; mass; mean 10.2%, range 3.2–16.0). Females were nearly the same size as males on the Kanin Peninsula, with males only 3.4, 0.0 and 3.4% larger than females with respect to length of head, culmen and tarsi, although the result may be somewhat spurious given the difficulty in determining sex of partially frozen hunter-killed birds (K. Litvin pers. comm).

Geographical variation in morphology

Structural measures varied significantly among populations (Table 2). Birds from the Taimyr and Kanin

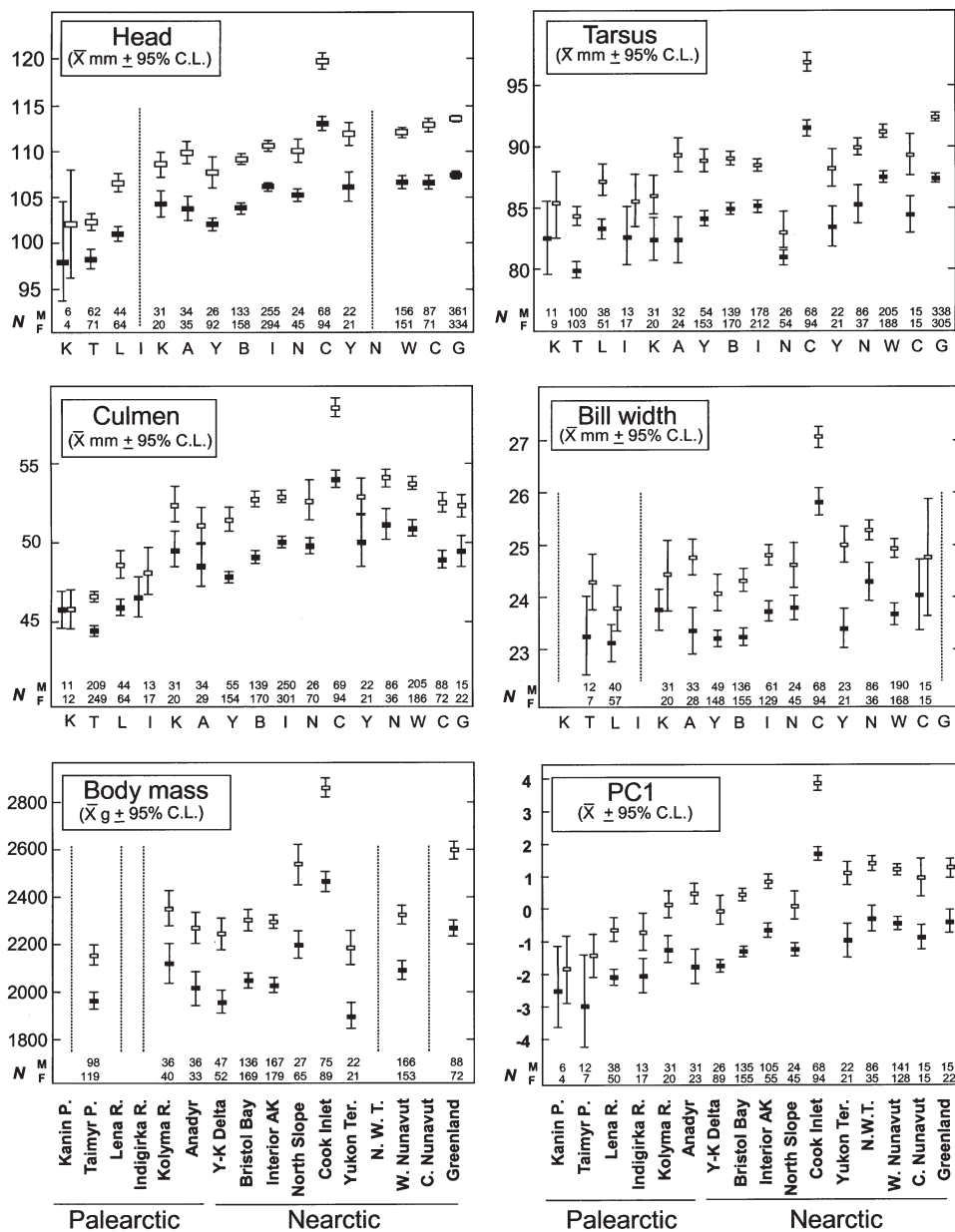


Figure 2. Geographic variation in length of head, tarsus, culmen, width of bill, mass of body and first principal component. □, Males; ■, females. Results are means \pm 95% confidence limits. A vertical line above a location without a value indicates no data available. Locations along the x-axis are listed in order of longitudinal rank. Sample sizes (N) for males (M) and females (F) are shown at the bottom of each panel. K, Kanin Peninsula; T, Taimyr Peninsula; L, Lena River; I, Indigirka River; K, Kolyma River; A, Anadyr; Y, Yukon-Kuskokwim Delta; B, Bristol Bay; I, Interior Alaska; N, North Slope; C, Cook Inlet; Y, Yukon Territory; N, Northwest Territories; W, western Nunavut; C, central Nunavut; G, Greenland.

peninsulas, Siberia were the smallest and geese from Cook Inlet, Alaska were much larger than birds from any other area (Fig. 2). Eurasian populations were generally small in body size (PC1 scores -3.0 to -1.2 for females and -1.8 to 0.5 for males). Taimyr Peninsula birds were smaller than all others, except birds from the Kanin Peninsula, with respect to head, tarsus length

and culmen, but not statistically smaller than other Eurasian populations in bill width and overall body size (PC1) due to a large variance (small sample sizes) in the Taimyr population for these measures (Fig. 2). Sample sizes were small, and variance high, for western-most distributed geese on the Kanin Peninsula. Hence, although mean measures were the second

Table 2. Analysis of variance values for individual morphological variables of Greater White-fronted Geese. Results are of type III sum of squares using weighted least squares analyses – see Methods.

Parameter		Treatment			Total (corrected)
		Sex	Location	Sex*Location	
Head length ^a $r^2 = 0.574$	df	1	13	13	2779
	F	431.8	153.7	2.41	
	P	<0.0001	<0.0001	0.003	
Culmen $r^2 = 0.574$	df	1	15	15	2813
	F	293.6	185.8	2.77	
	P	<0.0001	<0.0001	0.0003	
Tarsus $r^2 = 0.523$	df	1	15	15	2865
	F	391.1	125.2	2.71	
	P	<0.0001	<0.0001	0.0004	
Bill width ^b $r^2 = 0.411$	df	1	12	12	1691
	F	173.1	60.8	1.59	
	P	<0.0001	<0.0001	0.087	
Body mass ^c $r^2 = 0.443$	df	1	10	10	2268
	F	432.9	104.1	2.71	
	P	<0.0001	<0.0001	0.003	
PC1 $r^2 = 0.697$	df	1	15	15	1558
	F	486.4	130.2	1.76	
	P	<0.0001	<0.0001	0.035	

^aNo head length measurements for Mackenzie River, NWT or Indigirka River Delta. ^bNo bill width data for Greenland, Kanin Peninsula or Indigirka River Delta. ^cNo body mass data for central Nunavut, MacKenzie River, NWT, Kanin Peninsula, Indigirka River or Lena River Delta.

smallest of all geese, they were statistically inseparable from all but the largest (most eastern) Eurasian forms.

Too few measurements were obtained from Indigirka River Delta birds to confidently compare PC1 scores with adjacent populations (Lena and Kolyma River deltas). However, Indigirka River Delta birds did not differ in size from birds from the Lena River Delta with respect to culmen length (Fig. 2). In addition, birds in spring near the Indigirka and Lena Rivers were also indistinguishable with respect to both wing length [for females, mean = 393.7 ± 3.0 se ($n = 17$) and 391.5 ± 2.0 ($n = 63$) and for males, mean = 412.1 ± 2.6 ($n = 13$) and 410.9 ± 2.0 ($n = 44$) from the Indigirka and Lena Rivers, respectively ($F_{1,136} = 0.33$, $P = 0.564$ for location effects when controlling for location and sex in ANOVA)] and body mass [for females, mean = 2276 ± 75 se ($n = 17$) and 2206 ± 37 ($n = 63$) and for males, mean = 2509 ± 83 ($n = 13$) and 2478 ± 37 ($n = 44$) from Indigirka and Lena Rivers, respectively ($F_{1,136} = 0.75$, $P = 0.39$ for location effects when controlling for location and sex in ANOVA)]. Populations in eastern Siberia and Chukotka (populations E and F in Fig. 1) were similar in size to birds from the Yukon-Kuskokwim Delta (PC1 = -1.7 for females and -0.1 for males), the latter of which were the smallest in North America. Birds from interior and northern Alaska were similar in size to tundra-nesting birds from across Canada.

Greenland birds, although the second largest geese sampled, were still considerably smaller than geese from Cook Inlet, Alaska.

Body size (mean PC1 score) was positively correlated with breeding area longitude ($r^2 = 0.452$ for females and $r^2 = 0.519$ for males; $P < 0.01$; Table 1, Fig. 2). Within Asia, the west–east increase in body size was driven by the very small body size of geese from the Kanin and Taimyr peninsulas and to a lesser degree, the Lena River Delta, the former being the breeding areas of the smallest Greater White-fronted Geese. The increasing west–east trend in size of morphological characteristics was especially prevalent in culmen and head lengths (Fig. 2).

There was no significant relationship between body size (mean PC1 score) and breeding latitude ($r^2 = 0.141$ for females and $r^2 = 0.176$ for males; $P > 0.05$ for both; Table 1). Mean PC1 scores of each population ($n = 16$) were, however, positively correlated with mean June temperature on the breeding grounds for females ($r^2 = 0.343$, $P < 0.05$) and males ($r^2 = 0.351$, $P < 0.05$; Fig. 3, Table 1). Body size was not related to wintering latitude ($r^2 = 0.028$ for females and $r^2 = 0.031$ for males; $P > 0.05$), or temperature ($r^2 = 0.113$ for females and $r^2 = 0.085$ for males; $P > 0.05$), which is not surprising given that the smallest and largest forms in North America and Eurasia winter sympatrically (see below).

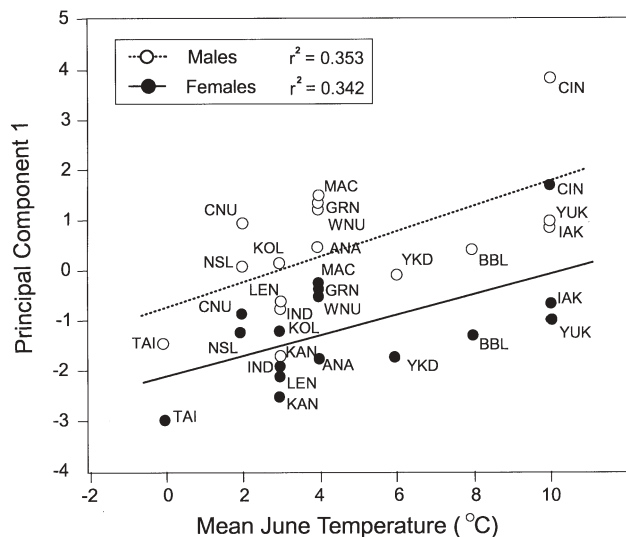


Figure 3. Relationship between body size [PC1] of Greater White-fronted Geese and mean June temperatures (20-year average) on the breeding grounds. Solid regression line, females; dotted line, males.

Body mass

Body mass and stage of wing moult (ninth primary length) were not significantly correlated for the 11 locations for which we had data on body mass and ninth primary (ANCOVA procedure controlling for location and sex effects: $F_{1,617} = 0.44$, $P = 0.510$, with no interaction between primary length and sex or location). Body mass varied significantly among areas in a pattern similar to structural variation, which was not unexpected given that body mass was highly correlated with structural size (PC1 scores: $r^2 = 0.446$ for females and $r^2 = 0.519$ for males; $P < 0.01$; Fig. 4).

Coefficient of variation

Overall (16 populations), the coefficient of variation (CV) was less for head length (CV of 4.55 and 4.45 for females and males, respectively) and tarsi (5.10 and 5.09), than for culmen (7.57 and 7.82) and bill width (5.81 and 5.65), with slightly more variation among females than males for all measurements but culmen. A geographical comparison showed that CV for males and females for all measures was greatest in Pacific Flyway populations (populations G, H, K in Table 1), followed by Eurasia (populations A–F) and mid-continent populations in North America (populations I, J, L–O). Overall variation in mean body size (PC1) across populations was greater for males (range = 5.71 [–1.86 to 3.9]) than females (range = 4.70 [–2.98 to 1.72]).

DISCUSSION

Environmental influences on morphology and mass

Body mass in most waterfowl can vary on a daily, seasonal and annual basis, as mass depends not only on environmental variables such as weather and food availability but also on the stage of the annual reproductive cycle. The relationship between environmental influences and structural characteristics is more complex and has not been completely resolved. In Canada Geese, phenotype can be closely correlated to genotype (VanWagner & Baker 1990). However, environmental factors (specifically food availability) can depress gosling growth rates and subsequent adult body size in several species of colonial and semi-colonial nesting geese (Cooch *et al.* 1991, Larsson & Forslund 1991, Sedinger *et al.* 1995, Reed & Plante 1997, Leafloor *et al.* 1998), although a reduction in size of goslings at fledging does not always result in reduced adult body size (Larsson 1993, Sedinger *et al.* 1998).

One might expect less environmentally induced morphological variation in Greater White-fronted Geese compared to other species, as they nest at generally lower densities than colonially-nesting species. As such they are less likely to suffer impacts of limited food availability during brood rearing. Support for this contention includes lack of temporal variation in morphology of several White-front populations measured over long time periods (e.g. *A. a. frontalis* and *A. a. elgasi* measurements in Krogman 1979 versus Orthmeyer *et al.* 1995 and this study; and *A. a. albifrons* measurements in Beer & Boyd 1963 versus western Palearctic populations in this study). Adult body mass during wing moult is more likely to vary annually than structural characteristics, although even for body mass, variation among populations is probably much higher than temporal variation within populations (Fig. 2).

Geographical variation in morphology

Our analysis of morphological data from across Siberia supports the assertion that geese breeding in European Russia and central Siberia are smaller than geese breeding farther east (Alpherack 1905, Buturlin 1935, Delacour 1954, Cramp & Simmons 1977, Johnsgard 1978, Mooij *et al.* 1999) and also verifies the west–east trend of increasing body size in Asia (Alpherack 1905, Dement'ev & Gladkov 1967). We have no data from the middle reaches of the Anadyr River (Krechmar 1986) or from birds of the Kava River region (Krechmar 1996) but we predict that birds from these

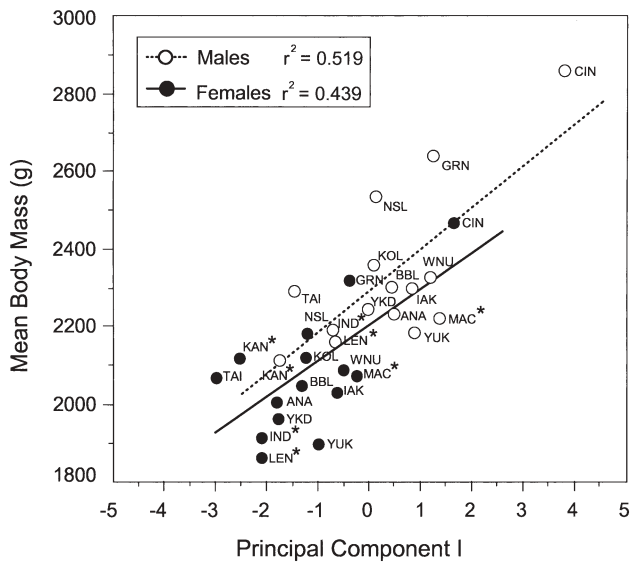


Figure 4. Relationship between body mass and first principal component of linear measures of Greater White-fronted Geese. Letters refer to sampling locations (see Fig. 1, Table 1). *Populations with mass derived from spring weights (see Methods). Solid regression line, females; dotted line, males.

areas would be among the largest in Asia, given their eastern distribution and southern nesting distribution (see below). A west–east increase in size of breeding birds in Asia has been noted for Bean Geese *Anser fabalis* (Cramp & Simmons 1977) and the Bar-tailed Godwit *Limosa lapponica* (McCaffery & Gill 2001), and may be related to a west–east gradient of increasing temperature (Danilov 1966).

Our finding that the Tule Goose is the largest form of Greater White-fronted Goose supports the earlier results of Krogman (1979) and the more detailed analysis of Pacific Flyway geese presented by Orthmeyer *et al.* (1995). The fact that geese breeding in areas from central and northern Alaska across to Hudson Bay varied little morphologically is not surprising given the overlap in migration and winter distribution of these birds (Ely & Dzubin 1994). Some degree of isolation (and possible divergence) of birds from the interior forests of Alaska might be expected, however, given differences in basic nesting ecology and timing of migration compared to other mid-continent populations (populations I, J, L–O in Table 1) of Greater White-fronted Geese (Ely & Dzubin 1994, Ely & Takekawa 1996, C. Ely *et al.* unpubl. data).

Measurements of birds from the Old Crow region, Yukon Territory, were smaller than reported by Elgas (1970), although our sample of non-breeding birds may have been of transients, while Elgas captured breeding

birds. Geographically there is little reason to expect birds from the Old Crow Flats region to differ in size from birds in interior Alaska, as their similar nesting habitat (sparse boreal forest) is <200 km east of the Yukon River drainage where interior Alaska birds nest.

Unlike many other waterfowl species, there has been no reported interchange of Greater White-fronted Geese between Nearctic and eastern Palearctic populations based on ringing recovery data (Ely & Scribner 1994). Thus, the similarity in body size of birds from the Anadyr River region of eastern Siberia and populations near Norton Sound in western Alaska may not be a consequence of gene flow across the Bering Straits, despite the proximity (likely <200 km) of breeding birds from the two continents. Winter allopatry among adjacent breeding populations is also evident within North America, as the distribution of ring recoveries indicates a high degree of isolation between birds of the Pacific Flyway (populations G, H, K in Table 1) and Central Flyway (populations I, J, L–O in Table 1; Lensink unpubl. data, Miller *et al.* 1968, Ely & Dzubin 1994, Ely & Scribner 1994).

Origins of morphological variation

The distribution of breeding White-fronts has changed dramatically since the last glacial maximum (15–21 000 years before present), as most of Canada, all of Alaska south of the Alaska Range, and the Brooks Range, as well as extensive areas in central and western Siberia, were covered with glaciers or polar desert habitats (Ploeger 1968, Pewe 1975, Peltier 1994). Hence, current breeding areas in southwest, south central and the Arctic Sea coast of Alaska, as well as nearly all of the Yukon, Northwest Territories, much of Nunavut and much of northwestern Siberia would have been unavailable for nesting. Birds breeding in the Nearctic would have been restricted to refugia in the Canadian Archipelago, western Greenland, the Queen Charlotte Islands, British Columbia (Warner *et al.* 1982) and west central Alaska, the latter comprising the eastern portion of the Beringia Land Bridge that stretched across the North Pacific and connected Alaska to what is now eastern Siberia (Hopkins 1967, Pewe 1975). In the Palearctic, most of northeastern Europe and western Siberia was completely glaciated except for a refugium in the southeastern portion of the Taimyr Peninsula (Möller *et al.* 1999, Abbott *et al.* 2000). The notion that Pleistocene events may have contributed to species (and subspecies) diversity has

received recent support from genetics research (Lambert *et al.* 2002) in which the timing of species divergence in birds was calculated to be 2–7 times faster than the 200–500 ka bp previously estimated for geese by Shields & Wilson (1987). The much higher rate of evolution re-establishes the potential importance of glacial events in the Pleistocene in leading to allopatric speciation as also purported by Avise *et al.* (1998). While it is impossible to completely resolve the connections between glacial refugia and the distribution of extant breeding populations, the concordance with current patterns of morphology are compelling.

Ecogeographical relationships

The tendency for larger-bodied White-fronts to breed in warmer climates (e.g. Cook Inlet) than smaller forms (e.g. Taimyr Peninsula) is seemingly in conflict with Bergmann's Rule, which purports a negative correlation between body size and temperature and a positive correlation with humidity (Zink & Remsen 1986, James 1991, Ashton 2002). However, as has been shown for Canada Geese (Lefebvre & Raveling 1967), larger-bodied forms generally winter farther north, where climate is more extreme. The correlation between body size of Greater White-fronts and temperature on breeding areas is confounded with a tundra–taiga habitat relationship, with more southerly and continentally situated taiga habitats generally being characterized by longer growing seasons and warmer mid-summer temperatures than more northerly or coastally distributed tundra habitats.

The large size of southern-nesting subspecies may also be related to poorer forage quality at more temperate sites where large body size may be necessary to process higher-fibre diets (Demment & Van Soest 1985). An extended growing season means fewer constraints on time to fledge, but taiga–shrub habitats associated with lower latitudes and elevations have less extensive, and possibly lower nutritional quality, graminoid communities favoured by geese. In Asia, the more southern-nesting (taiga) forms of the Bean Goose (*A. f. fabalis* and *A. f. middendorfi*) are larger than tundra-nesting forms (*A. f. rossicus* and *A. f. serratirostris*), although there is also a west–east cline in size that leads to intermediate forms (Owen 1980). Lesser White-fronted Geese *Anser erythropus* are smaller in body size than Greater White-fronted Geese although they nest at lower latitudes than Greater White-fronts across northern Eurasia, seemingly in conflict with the above

arguments. However, Lesser White-fronts are generally found in mountainous regions characterized by tundra habitats (Owen 1980) or shallow lake systems with modulating water levels that provide abundant forage plants at early successional stages (Romanov 2001). Lesser White-fronts have also been reported to have a unique digestive physiology adapted for feeding on poor quality vegetation (Rosenfeld 2001). Tule Geese may be ecotypal replacements for Bean Geese in the Nearctic, having evolved a larger body size for existence in forested habitats.

Body size relationships in arctic and subarctic Anatidae have also been reported to be related to constraints associated with the energetics of long-distance migration. Rayner (1988) attributed the smaller body size of more northerly breeding waterfowl to specific characteristics of their flight dynamics necessary to make long migrations. Such factors may also be contributing to intra-specific variation in body size of Greater White-fronts, as we found a strong negative correlation between body size (PC1 score) and distance from breeding to wintering areas ($r^2 = 0.53$, $P = 0.001$ for females and $r^2 = 0.52$, $P = 0.002$ for males, $n = 16$; Table 1).

The small size of White-fronts on the Yukon-Kuskokwim Delta is somewhat anomalous given the southern breeding latitude (60°N), although the nesting area is characterized by cool summer temperatures typical of tundra habitats elsewhere (Table 1). The phenomenon of diminution of taxonomic forms on the Yukon-Kuskokwim Delta is also observed in Brant (*Branta bernicla nigricans* is the smallest form, Reed *et al.* 1998) and the Canada Goose complex (*B. c. minima* is the smallest subspecies, Mowbray *et al.* 2002). Small body size of Yukon-Kuskokwim Delta geese may be related to long migration distances due to the longitudinal displacement of western Alaska from staging and wintering areas in the continental United States and Mexico, or possibly food competition due to high densities of four different species of geese during brood rearing (e.g. Schmutz & Laing 2002).

Although morphological variation among the different breeding populations of Greater White-fronted Geese is quite extensive, it is not nearly as pronounced as in Canada Geese, where large-bodied subspecies are nearly three times as large as smaller forms (Bellrose 1980, Mowbray *et al.* 2002). The greater within-species diversity of Canada Geese may be related to species differences in selective environments. Greater White-fronted Geese breed only in tundra or northern taiga habitats whereas Canada Geese are less restrictive in

their habitat requirements and breed from the northern tundra well into the mid-temperate latitudes (Mowbray *et al.* 2002). Southern subspecies of Canada Geese may have evolved large body size in part because morphology has not been constrained by short growing seasons or adaptations to long distance migration.

It seems improbable due to chance alone that, of the nine breeding populations sampled in North America and seven in Greenland and Eurasia, the largest and smallest forms on each continent winter sympatrically. But indeed this is the case: *A. a. frontalis* from the Yukon-Kuskokwim Delta and *A. a. elgasi* from Cook Inlet, Alaska winter together in California; *A. a. flavirostris* from Greenland and *A. a. albifrons* from the Taimyr Peninsula overlap in winter distribution in western Europe (Fox *et al.* 1999). Divergence in structural size in sympatric-wintering forms may be due to resource competition on wintering areas leading to character displacement (Schoener 1974, Schluter 1994). In both subspecies pairs, the larger forms are adapted to aquatic habitats and feed on emergent vegetation or grub on subterranean plant parts, whereas the smaller subspecies are adapted to grazing and feeding on the seed heads of graminoid vegetation (Owen 1980). Similar habitat-related differences in structural size have been noted between wintering populations of Lesser Snow Geese (*Anser caerulescens*, Alisauskas 1998) and among species of geese with respect to robustness of feeding apparatus (Bolen & Rylander 1978).

Sexual variation

Variable degrees of sexual dimorphism have been reported among populations of birds, with some species exhibiting no intra-specific differences across their range (e.g. Hairy Woodpecker *Picoides villosus*; Miller *et al.* 1999) and other species showing widespread patterns of variation (e.g. House Finch *Carpodacus mexicanus*; Badyaev & Hill 2000). Our finding of inter-population differences in sexual dimorphism of *A. albifrons* across its range may be an indication that sex-related selection regimes vary among populations (e.g. mate selection, foraging efficiency, survival benefits), or that differences are dynamic or under loose selection.

The absence of gender differences in the coefficient of variation for morphological features may be related to dispersal rates among populations. In waterfowl, males are much more likely to disperse to new breeding areas than females, while females exhibit strong

breeding site and natal site fidelity (Greenwood 1980). If there is inter-population variation in morphology and males are more likely to disperse than females, then coefficients of variation of morphological attributes should be higher for males than females within a given breeding population, unless: (1) male dispersal is limited to the range of the population; (2) dispersal rates are so low (<1%/year) as to be undetected with relatively small samples such as ours; or (3) phenotypes are solely environmentally driven.

Taxonomic considerations

Our finding of body size variation across the range of the species supports the contentions of Buturlin (1935), Delacour (1954) and Mooij & Zockler (2000) in showing that geese breeding in Chukotka and eastern Siberia are significantly different in size from birds breeding in European Russia and central Siberia. Geese from the Kanin and Taimyr peninsulas were the same size in culmen and tarsal measurements as Greater White-fronted Geese measured during winter in England (Beer & Boyd 1963, Owen 1980) and The Netherlands (Cramp & Simmons 1977) (after converting our total tarsus measurements to diagonal tarsus for comparison to the earlier studies). This supports ringing data showing that these western-breeding birds represent the western Palearctic population (Mooij *et al.* 1996, 1999). Mooij (2000) and Mooij & Zockler (2000) have proposed that the Khatanga River in north central Siberia (Fig. 1) is the dividing line between the two Eurasian stocks, rather than the Kolyma River (Delacour 1954, Philippona 1972). Rogacheva (1992) also considered birds from central Siberia (Taimyr Peninsula) and European Russia (Kanin Peninsula) to migrate only westward, with the watershed of Krasnoyarsk Territory separating them from White-fronts breeding in eastern Siberia and Chukotka. Our finding of a gradual west-east clinal increase in body size of Greater White-fronted Geese across the Eurasian tundra makes designating a specific boundary somewhat subjective. However, the finding that birds from the Lena River Delta and regions further east are significantly larger than birds from the Taimyr (and possibly the Kanin) peninsulas for most structural measures (Fig. 2) is a strong indication of a division somewhere west of the Lena River Delta. Mooij (2000) and Mooij & Zockler (2000) proposed that Greater White-fronted Geese breeding east of the Kahtanga River in eastern Siberia should be considered a distinct subspecies (*A. a. albicans*), based

largely on differences in migration patterns and wintering distribution.

Intra-specific variation, whether the product of natural selection or genetic drift, can be a precursor to speciation (Zink & Remsen 1986), although the process probably varies among species (Grant & Grant 2002). Greater White-fronted Geese have maintained a large degree of morphological variation among populations despite their strong migratory tendencies and dispersal capabilities. It is evident that characteristics promoting gene flow in geese are counteracted by behavioural and life-history traits that maintain phylogeographical structure (Ely & Scribner 1994); more so than in most other groups of waterfowl (Anderson *et al.* 1992). Traits such as natal, breeding, wintering and moulting site fidelity, long-term pair bonds, extended family relationships, delayed maturation and assortative mating, all contribute to steep selection gradients (Endler 1977) and population structuring in geese which, if stable or long-lasting enough, may eventually lead to speciation.

Future research

We hope that our work will serve as a template for more detailed studies of the biogeography of Greater White-fronted Geese and other broadly distributed arctic species. Numerous questions arise from our findings, some of which can be answered with more complete measurement data (such as obtaining a larger sample of measures from birds breeding on the Kanin and Taimyr peninsulas and determining the location of subspecies boundaries in north central Siberia), whereas answers to other questions will require a different research approach. Key tasks include: (1) identifying linkages between breeding, staging and wintering areas, particularly in Eurasia; (2) quantifying population structure; and (3) identifying unique populations across the range of the species, especially populations nesting in the boreal forests of eastern Siberia. Answers to such questions will require extensive fieldwork, mark-recapture studies that measure gene flow and dispersal directly through use of multi-state models (Hestbeck *et al.* 1991) or indirectly through genetic or isotopic studies at breeding, staging and wintering areas across Eurasia. Such tasks will be both logistically and financially daunting.

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ENDNOTE

a. Estimated values for missing variables were determined with the following multiple regression models. Kanin Peninsula: male bill width = $6.382 + 0.099(\text{head}) + 0.039(\text{tarsus}) + 0.074(\text{culmen})$ ($r^2 = 0.334$; $n = 597$); female bill width = $5.354 + 0.107(\text{head}) + 0.044(\text{tarsus}) + 0.067(\text{culmen})$ ($r^2 = 0.352$; $n = 751$). Indigirka River Delta: male head length = $38.875 + 0.292(\text{tarsus}) + 0.864(\text{culmen})$ ($r^2 = 0.636$; $n = 750$); female head length = $33.960 + 0.319(\text{tarsus}) + 0.889(\text{culmen})$ ($r^2 = 0.618$; $n = 892$); male bill width = $10.747 + 0.062(\text{tarsus}) + 0.161(\text{culmen})$ ($r^2 = 0.277$; $n = 762$); female bill width = $9.117 + 0.079(\text{tarsus}) + 0.157(\text{culmen})$ ($r^2 = 0.301$; $n = 893$). Northwest Territories: male head length = $32.783 + 0.742(\text{culmen}) + 0.276(\text{tarsus}) + 0.563(\text{bill width})$ ($r^2 = 0.674$; $n = 597$); female head length = $26.566 + 0.783(\text{culmen}) + 0.275(\text{tarsus}) + 0.693(\text{bill width})$ ($r^2 = 0.659$; $n = 751$). Greenland: male bill width = $5.579 + 0.141(\text{head}) + 0.040(\text{tarsus})$ ($r^2 = 0.320$; $n = 597$); female bill width = $4.926 + 0.141(\text{head}) + 0.046(\text{tarsus})$ ($r^2 = 0.339$; $n = 755$).

REFERENCES

- Abbott, R.J., Smith, L.C., Milne, R.I., Crawford, R.M.M., Wolf, K. & Balfour, J.** 2000. Molecular analysis of plant migration and refugia in the arctic. *Science* **289**: 1343–1346.
- Alisauskas, R.T.** 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent Lesser Snow Geese. *Auk* **115**: 851–862.
- Alpheracky, S.** 1905. *The Geese of Europe and Asia*. Rowland Ward, London.

- American Ornithologists' Union** 1957. *AOU Check-list of North American birds*. Lord Baltimore Press, Baltimore, MD.
- Anderson, M.G., Rhymer, J.M. & Rohwer, F.C.** 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. In Batt, B., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) *Ecology and Management of Breeding Waterfowl*: 365–395. University of Minnesota Press, Minneapolis.
- Ankney, C.D.** 1984. Nutrient reserve dynamics of breeding and moulting Brant. *Auk* **101**: 361–370.
- Ashton, K.G.** 2002. Patterns of within-species body size variation in birds: strong evidence for Bergmann's rule. *Global Ecol. Biogeogr.* **11**: 505–523.
- Avise, J.C., Walker, D. & Brown, G.** 1998. Speciation duration and Pleistocene effects on vertebrate phylogeography. *Proc. R. Soc. Lond. B* **265**: 1707–1712.
- Badyaev, A.V. & Hill, G.E.** 2000. The evolution of sexual dimorphism in the House Finch. I. Population divergence in morphological covariance structure. *Evolution* **54**: 1784–1794.
- Barry, T.W.** 1967. *The Geese of the Anderson River Delta, Northwest Territories*. PhD Dissertation, University of Alberta, Edmonton.
- Beer, J.V. & Boyd, H.** 1963. Measurements of White-fronted Geese wintering at Slimbridge. *Wildfowl Trust Rep.* **14**: 114–119.
- Bellrose, F.C.** 1980. *Ducks, Geese and Swans of North America*, 3rd edn. Stackpole Books, Harrisburg, PA.
- Bensch, S.** 1999. Is the range size of migratory birds constrained by their migratory program? *J. Biogeogr.* **26**: 1225–1235.
- Bohning-gaese, K., Gozalez-guzman, L.I. & Brown, J.H.** 1998. Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evol. Ecol.* **12**: 767–783.
- Bolen, E.G. & Rylander, M.K.** 1978. Feeding adaptations in the Lesser Snow Goose. *Southwest. Nat.* **23**: 158–161.
- Budeau, D.A., Ratti, J.T. & Ely, C.R.** 1991. Energy dynamics, foraging ecology, and behavior of prenesting Greater White-fronted Geese. *J. Wildl. Manage.* **55**: 556–563.
- Buturlin, S.A.** 1935. *The Full Guide Book of Birds of the USSR: Loons, Pelicaniforms, Herons, Anseriformes, Galliformes, Rails and Button-quails*, Vol. 2. KOIZ Publishing House, Moscow-Leningrad.
- Carriere, S., Bromley, R.G. & Gauthier, G.** 1999. Comparative spring habitat and food use by two arctic nesting geese. *Wilson Bull.* **111**: 166–180.
- Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F.** 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. *Ecology* **72**: 503–512.
- Cramp, S. & Simmons, K.E.** 1977. *The Birds of the Western Palearctic*, Vol. 1. Oxford University Press, Oxford.
- Danilov, N.N.** 1966. *Adaptations of Ground-Level Vertebrates to Existence in the Subarctic*. Vol. 2. Birds. Collection of Scientific Issues of the Biological Institute, Sverdlovsk (in Russian).
- Delacour, J.** 1954. *The Waterfowl of the World*, Vol. 1. Country Life Limited, London.
- Delacour, J. & Ripley, S.D.** 1975. Description of a new subspecies of the White-fronted Goose, *Anser albifrons*. *Am. Mus. Novit.* No. 2565.
- Dement'ev, G.P. & Gladkov, N.A. (eds)** 1967. *Birds of the Soviet Union*, Vol. 4. English translation by Israel Program for Scientific Translation, Jerusalem.
- Demment, M.W. & Van Soest, P.J.** 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. *Am. Nat.* **125**: 641–672.
- Dunn, E.H. & MacInnes, C.D.** 1987. Geographic variation in clutch size and body size of Canada Geese. *J. Field Ornithol.* **58**: 355–371.
- Dzubin, A. & Cooch, E.G.** 1992. *Measurements of Geese: General Field Methods*. California Waterfowl Association, Sacramento, California.
- Elgas, B.** 1970. Breeding populations of Tule White-fronted Geese in northwestern Canada. *Wilson Bull.* **82**: 420–426.
- Ely, C.R. & Dzubin, A.** 1994. Greater White-fronted Goose. In Poole, A., Stettenheim, P. & Gill, F. (eds) *The Birds of North America*, No. 131: 1–32. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, DC.
- Ely, C.R. & Raveling, D.G.** 1984. Breeding biology of Pacific White-fronted Geese. *J. Wildl. Manage.* **48**: 823–837.
- Ely, C.R. & Raveling, D.G.** 1989. Body composition and weight dynamics of wintering Greater White-fronted Geese. *J. Wildl. Manage.* **53**: 80–87.
- Ely, C.R. & Scribner, K.T.** 1994. Genetic diversity in arctic nesting geese: implications for management and conservation. *Trans. N. Am. Wildl. Nat. Res. Conf.* **59**: 91–110.
- Ely, C.R. & Takekawa, J.Y.** 1996. Geographic variation in migratory behavior of Greater White-fronted Geese (*Anser albifrons*). *Auk* **113**: 889–901.
- Ender, J.A.** 1977. *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, New Jersey.
- Fox, A.D., Jahlert, J., Walsh, A.J., Stroud, D.A., Mitchell, C., Kristiansen, J.N. & Hansen, E.** 1998. Patterns of body mass change during moult in three different goose populations. *Wildfowl* **49**: 45–56.
- Fox, A.D., Morris, D.W., Wilson, H.J., Merne, O.J., Stroud, D.A., Sigfusson, A. & Glahder, C.** 1999. Greenland White-fronted Goose *Anser albifrons flavirostris*. In Madsen, J., Cracknell, G. & Fox, A.D. (eds) *Goose Populations of the Western Palearctic. A Review of Status and Distribution*: 130–142. Wetlands International Publ. No. 48, Ronde, Denmark.
- Grant, P.R. & Grant, B.R.** 2002. Unpredictable evolution in a 30-year study of Darwin's Finches. *Science* **296**: 707–711.
- Greenwood, P.J.** 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Hansen, J., Ruedy, R., Glascoe, J. & Sato, M.** 1999. GISS analysis of surface temperature change. *J. Geophys. Res.* **104**: 30997–31022.
- Hanson, H.C., Queneau, P. & Scott, P.** 1956. *The Geography, Birds, and Mammals of the Perry River Region*. Special Publication No. 3, Arctic Institute of North America, McGill University, Montreal.
- Hestbeck, J.B., Nichols, J.D. & Malecki, R.A.** 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. *Ecology* **72**: 523–533.
- Hopkins, D.M. (ed.)** 1967. *The Bering Land Bridge*. Stanford University Press, Stanford, CA.
- James, F.C.** 1991. Complementary descriptive and experimental studies of clinal variation in birds. *Am. Zool.* **31**: 694–706.
- Johnsgard, P.A.** 1978. *Ducks, Geese and Swans of the World*. University of Nebraska Press, Lincoln.
- Johnson, D.H.** 1999. The insignificance of statistical significance testing. *J. Wildl. Manage.* **63**: 763–772.
- King, J.G. & Hodges, J.I.** 1979. A preliminary analysis of goose banding on Alaska's Arctic slope. In Jarvis, R.L. & Bartonek, J.C. (eds) *Management and Biology of Pacific Flyway Geese*: 176–188. OSU Book Stores, Inc., Corvallis, OR.
- Kondratyev, A.V.** 1993. Breeding biology, habitat selection, and population number of four geese species in the south-west coast of the Anadyr Bay. *Russ. J. Ornithol.* **2**: 287–302.
- Krechmar, A.V.** 1986. Nesting ecology of the White-fronted Goose (*Anser albifrons*) in different parts of its geographical range. *Zool. Zh.* **65**: 889–900 (in Russian).

- Krechmar, A.V.** 1996. White-fronted Goose (*Anser albifrons*) in the Kava River region, near the northern shores of the Okhotsk Sea. *Casarca* **2**: 52–65.
- Krogman, B.D.** 1979. A systematic study of *Anser albifrons* in California. In Jarvis, R.L. & Bartonek, J.C. (eds) *Management and Biology of Pacific Flyway Geese*: 22–43. OSU Bookstores Inc., Corvallis, OR.
- Kurechi, M., Sabano, Y., Syroechkovsky, E., Baranyuk, V.V., Andreev, A., Kondratyev, A., Takekawa, J.Y. & Mita, N.** 1995. Study on the restoration of Lesser Snow Geese to northeast Asia using miniature satellite transmitters. *Report of Telecommunication Advancement Foundation* **9**: 518–541 (in Japanese).
- Lambert, D.M., Ritchie, P.A., Millar, C.D., Holland, B., Drummond, A.J. & Baroni, C.** 2002. Rates of evolution in ancient DNA from Adelle Penguins. *Science* **295**: 2270–2273.
- Larsson, K.** 1993. Inheritance of body size in the Barnacle Goose under different environmental conditions. *J. Evol. Biol.* **6**: 195–208.
- Larsson, K. & Forslund, P.** 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. *J. Evol. Biol.* **4**: 619–636.
- Leafloor, J., Ankney, C.D. & Rusch, D.H.** 1998. Environmental effects on the body size of Canada Geese. *Auk* **115**: 26–33.
- Lefebvre, E.A. & Raveling, D.G.** 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. *J. Wildl. Manage.* **31**: 538–546.
- Litvin, K.E., Syroechkovsky, E.V. & Gurtovaya, E.N.** 1998. Comparison of breeding of the White-fronted Goose and the Bean Goose in the north-east of the European part of Russia. *Casarca* **4**: 39–55.
- McCaffery B. & Gill, R.G.** 2001. Bar-tailed Godwit. In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 581. The Birds of North America Inc., Philadelphia, PA.
- Miller, H.W., Dzubin, A. & Sweet, J.T.** 1968. Distribution and mortality of Saskatchewan-banded White-fronted Geese. *Trans. N. Am. Wildl. Nat. Res. Conf.* **33**: 101–119.
- Miller, E.H., Walters, E.L. & Ouellet, H.** 1999. Plumage, size, and sexual dimorphism in the Queen Charlotte Islands Hairy Woodpecker. *Condor* **101**: 86–95.
- Mineyev, Y.N.** 1995. White-fronted Goose *Anser albifrons* in the tundra of Nenetskiy autonomous district of Archangelskaya region. *Bull. Geese Study Group of Eastern Europe and Northern Asia* **1**: 121–128.
- Miyabayashi, Y. & Mundkur, T.** 1999. *Atlas of Key Sites for Anatidae in the East Asian Flyway*. Wetlands International – Japan, Tokyo, and Wetlands International – Asia Pacific, Kuala Lumpur. Web-publication: <http://www.jawgp.org/onet/aaa1999/aaaendx.htm> accessed 14 May 1999.
- Miyabayashi, Y., Sugawa, H. & Kurechi, M.** 1994. Inventory of goose habitat in Japan: compilation of inventory and conservation issues identified. In Miyabayashi, Y. (ed.) *Inventory of Goose Habitat in Japan*: 35–65. Japanese Association for Wild Goose Protection, Wakayangagi, Japan.
- Möller, P., Bolshiyarov, D.Yu. & Bergsten, H.** 1999. Weichselian geology and palaeoenvironmental history of the central Taymyr Peninsula, Siberia, indicating no glaciation during the last global glacial maximum. *Boreas* **28**: 92–114.
- Mooij, J.H.** 2000. Population dynamics and migration of White-fronted Geese (*Anser albifrons*) in Eurasia. In Ebbinge, B.S., Mazourov, Yu.L. & Tomkovich, P.S. (eds) *Proceedings of the International Scientific Willem Barents Memorial Arctic Conservation Symposium*: 372–393. Ecopros Publ., Moscow.
- Mooij, J.H. & Zockler, C.** 2000. Reflections on the systematics, distribution and status of *Anser albifrons*. *Casarca* **6**: 92–107.
- Mooij, J.H., Ebbinge, B.S., Kostin, I., Burgers, J. & Spaans, B.** 1996. Panmixia in White-fronted Geese (*Anser a. albifrons*) of the Western Palearctic. PhD dissertation, Wageningen University, The Netherlands.
- Mooij, J.H., Farago, S. & Kirby, J.S.** 1999. White-fronted Goose, *Anser albifrons albifrons*. In Madsen, J., Cracknell, G. & Fox, T. (eds) *Goose Populations of the Western Palearctic. A Review of Status and Distribution*: 94–128. Wetlands International Publication No. 48, Ronde, Denmark.
- Mowbray, T.B., Ely, C.R., Sedinger, J.S. & Trost, R.E.** 2002. Canada Geese (*Branta canadensis*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 682. The Birds of North America Inc., Philadelphia, PA.
- Orthmeyer, D., Takekawa, J.Y., Ely, C.R., Wege, M.L. & Newton, W.E.** 1995. Morphological variation in Greater White-fronted Geese in the Pacific Flyway. *Condor* **97**: 123–132.
- Owen, M.** 1980. *Wild Geese of the World*. B.T. Batsford Ltd, London.
- Peltier, W.R.** 1994. Ice age paleotopography. *Science* **265**: 195–201.
- Pewe, T.L.** 1975. *Quaternary Geology of Alaska*. US Geological Survey Professional Paper No. 835, Reston, Virginia.
- Philippona, J.** 1972. *The White-fronted Goose: Migration and Wintering in Europe and Southwestern Asia*. Ziemsen, Wittenberg-Lutherstadt (in German).
- Ploeger, P.L.** 1968. Geographical differentiation in Arctic Anatidae as a result of isolation during the last glacial period. *Ardea* **56**: 1–159.
- Portenko, L.A.** 1989. *Birds of the Chuckchi Peninsula and Wrangel Island*, Vol. 2, Smithsonian Institution Libraries and National Science Foundation, Washington, DC (translation of Russian text).
- Ptushenko, E.S.** 1952. *White-fronted Goose. Birds of the Soviet Union*, Vol. 4: 301–307. Sovetskaya Nauka Pub., Moscow.
- Pyeong-Oh, W.** 1990. Present status of geese wintering in Korea. *Abstr. Int. Conf. Wild Geese Populations in Northern Asia*, September 1990. Institute of Biological Problems of the North, Magadan, USSR.
- Rayner, J.M.V.** 1988. Form and function in avian flight. In Johnston, R.F. (ed.) *Current Ornithology*, Vol 5: 1–62. Plenum Press, New York.
- Reed, A. & Plante, N.** 1997. Decline in body mass, size, and condition of Greater Snow Geese, 1975–1994. *J. Wildl. Manage.* **61**: 413–419.
- Reed, A., Ward, D.H., Derksen, D.V. & Sedinger, J.S.** 1998. Brant (*Branta bernicla*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 337: 1–32. The Birds of North America, Inc., Philadelphia, PA.
- Rigor, I.A., Colony, R.L. & Martin, S.** 2000. Variations in surface air temperature observations in the arctic, 1979–97. *J. Climate* **13**: 896–914.
- Rogacheva, H.** 1992. *The Birds of Central Siberia*. Husum Druck- und Verlagsgesellschaft mbH & Co., Husum.
- Romanov, A.A.** 2001. Lesser White-fronted Geese on the Putorana Plateau. *Casarca* **7**: 105–115.
- Rosenfeld, S.B.** 2001. Feeding ecology of the Lesser White-fronted Goose in the southern tundra of Yamal in 1998. *Casarca* **7**: 116–129.
- SAS Institute.** 1989. *SAS/STAT User's Guide. Release 6.04*. SAS Institute Inc., Cary, NC.
- Schluter, D.** 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* **266**: 798–801.
- Schmutz, J.A. & Ely, C.R.** 1999. Survival of Greater White-fronted Geese: effects of year, season, sex, and body condition. *J. Wildl. Manage.* **63**: 1239–1249.
- Schmutz, J.A. & Laing, K.K.** 2002. Variation in foraging behavior and body mass in broods of Emperor Geese *Chen canagica*: evi-

- dence for interspecific density dependence. *Auk* **119**: 996–1009.
- Schoener, T.W.** 1974. Resource partitioning in ecological communities. *Science* **185**: 27–39.
- Sedinger, J.S., Flint, P.L. & Lindberg, M.S.** 1995. Environmental influence on life-history traits: growth, survival and fecundity in Black Brant (*Branta bernicla*). *Ecology* **76**: 2404–2414.
- Sedinger, J.S., Lindberg, M.S., Person, B.T., Eicholz, M.W. & Flint, P.L.** 1998. Density-dependent effects on growth, body size, and clutch size in Black Brant. *Auk* **115**: 613–620.
- Shields, G.F. & Wilson, A.C.** 1987. Subspecies of the Canada Goose (*Branta canadensis*) have distinct mitochondrial DNAs. *Evolution* **41**: 662–666.
- Stroud, D.A.** 1982. Observations on the incubation and post-hatching behaviour of the Greenland White-fronted Goose. *Wildfowl* **33**: 63–72.
- Takekawa, J.Y., Kurechi, M., Orthmeyer, D.L., Sabano, Y., Uemura, S., Perry, W.M. & Yee, J.L.** 2000. A Pacific spring migration route and breeding range expansion for Greater White-fronted Geese wintering in Japan. *Global Environ. Res.* **4**: 155–168.
- Timm, D.E., Wege, M.L. & Gilmer, D.S.** 1982. Current status and management challenges for Tule White-fronted Geese. *Trans. Am. Wildl. Nat. Res. Conf.* **47**: 453–463.
- Timm, N.H. & Mieczkowski, T.A.** 1997. *Univariate and Multivariate General Linear Models: Theory and Applications Using SAS software*. SAS Institute, Cary, NC.
- Van Wagner, C.E. & Baker, A.J.** 1990. Association between mitochondrial DNA and morphological evolution in Canada Geese. *J. Mol. Evol.* **31**: 373–382.
- Warner, B.G., Mathewes, R.W. & Clague, J.J.** 1982. Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of Late Wisconsin Glaciation. *Science* **218**: 675–677.
- Wilson, H.J., Norriss, D.W., Walsh, A., Fox, A.D. & Stroud, D.A.** 1991. Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*: implications for conservation and management. *Ardea* **79**: 287–294.
- Zhang, F. & Yang, R.** 1997. *Bird Migration Research of China*. China Forestry Publishing House, Beijing (in Chinese with English summary).
- Zink, R.M. & Remsen, J.V. Jr.** 1986. Evolutionary processes and patterns of geographic variation in birds. In Johnston, R.F. (ed.) *Current Ornithology*, Vol 4: 1–69. Plenum Press, New York.

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