A Pacific Spring Migration Route and Breeding Range Expansion for Greater White-fronted Geese Wintering in Japan

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Abstract

The greater white-fronted goose (Anser albifrons) is a Holarctic species with a wide nesting distribution but only 4 recognized subspecies. The most abundant Nearctic subspecies, the Pacific white-fronted goose (A. a. frontalis) breeds from Hudson Bay, Canada to Alaska and across the Pacific Rim, possibly as far west as the Kolyma River, Russia. Japan is the wintering area for over a third of these white-fronted geese in the eastern Palearctic, but the spring migration route, main breeding area, and morphology of this wintering population had never been documented. On 4 February 1994, we captured 36 white-fronted geese and marked ten adult males with satellite transmitters at Lake Izunuma (38.75°N, 141.12°E), the major wintering area for geese in Japan, 360 km north of Tokyo. Two transmitters failed within a few weeks, but eight of the marked geese migrated 165 km northwest to Hachirogata lagoon in Akita Prefecture (40.04°N, 140.03°E) beginning in late February. After 19 days, they flew 350 km north to Lake Utonai and Miyajimanuma (43.23°N, 141.73°E), Hokkaido. They departed Japan between 5 and 28 May, following a Pacific route along the Kamchatka Peninsula rather than an inland route crossing Sakhalin Island. The last locations for four geese were on the lower Kamchatka Peninsula and were likely during migration since white-fronted geese are not reported to breed there. However, we obtained several locations through the summer from one goose on the Rusakovo River of upper Kamchatka Peninsula which may represent an unconfirmed breeding area, and from three geese at Kharytka and Pekul'ney Lakes (62.60°N, 176.67°E) in the Chukchi Autonomous Region, 250 km south of a previously reported breeding area on the Anadyr River. In 1997, Russian biologists verified that Pekul'ney Lakes supported a breeding population when they found 760 greater white-fronted geese with goslings in aerial surveys. Given the few radio - and collar - marked geese from the Anadyr and Kolyma Rivers that have been resighted in Japan, the coastal region south of the Anadyr River to the Kamchatka Peninsula seems to be the main breeding area for the wintering population in Japan. We also examined the morphological variation of this wintering population compared with European white-fronted goose (A. a. albifrons) and other Pacific Rim populations. We found significant differences in head length separating European white-fronted geese from the wintering population in Japan, and these geese also differed significantly from several other Pacific Rim populations. While European white-fronted geese intermix across their wintering range and have no recognizable subspecies, Pacific white-fronted goose populations seem to exhibit geographic variation.

Key words: Anser albifrons, greater white-fronted goose, Japan, Kamchatka, satellite telemetry, spring migration

1. Introduction

The Arctic nesting greater white-fronted goose (Anser albifrons) has one of the greatest circumpolar breeding ranges of the waterfowl, but only four subspecies are currently recognized (Delaclour 1954, Owen 1980). The two less numerous subspecies include the Greenland white-fronted goose (A. a. flavirostris), consisting of about 33,000 geese (Fox et al. 1999) that breed in Greenland and winter in Great Britain, and the vulnerable (Green 1996) Tule white-fronted goose (A. a. gansbeil) population of less than 8,000 individuals (D. Orthmeyer et al., in prep.) that breeds in central Alaska and winters in the Central Valley of California.

The most numerous subspecies in the Palearctic, the European white-fronted goose (A. a. albifrons) has
shown a marked 10-fold increase from 60,000 to
600,000 individuals following restrictions on hunting
(1991) showed a lower mortality rate after 1970 and
suggested that the restrictions on hunting through
increased adult survival are the cause for the observed
population growth in the western part of Europe.
Mooij et al. (1999) proposed that this increase is
carried by a shift of birds that used to winter in
eastern Europe and has been stable at 1.0–1.5 million
individuals over the past 40 years.

The European white-fronted goose breeds across
the Russian Arctic between 66–77°N from the Kanin
Peninsula (44°E) to the Kolyma River (155°E) and
migrates along 5 major routes to wintering areas
above 35°N in Europe and south to 23°N in southwest
Asia (Mooij et al. 1999). While band recoveries of
birds in the Netherlands and sightings of collar-mar
geese on the Taimyr Peninsula indicate that there is
some exchange between geese in eastern and
western Europe, further research is required to estab
lish whether these stocks should be considered as two
largely separate populations with only a limited
amount of exchange, or as one panmictic population.
In Europe, no subspecies have been described in
greater white-fronted goose, and the observed mixing,
even at a low rate, could have precluded formation of
other subspecies (Mooij et al. 1999; B. Ebbinge, pers.
comm.). However, the eastern geographic range of
the subspecies is not well known, and some have suggest
ed that the distribution of A. a. albifrons extends
across all of Asia (Dement’ev and Gladkov 1968,

The major subspecies in the Nearctic, the Pacific
white-fronted goose (A. a. frontalis) numbering well
over one million geese (Ely and Dzubin 1994), breeds
from Hudson Bay in eastern Canada to the Yukon-
Kuskokwim Delta of western Alaska, across the
Pacific Rim into Siberia as far west as the Kolyma
River (155°E) (Cramp and Simmons 1977, see Mooij et
al. 1999). The three major wintering areas for eastern
Palearctic geese are found in China, South Korea, and
Japan (Miyabayashi and Mundkur 1999).

Greater white-fronted goose, like many other
species of geese, were formerly very abundant in
Japan (Brazil 1993). However, introduction of
firearms during the Meiji Restoration in the late 1800 s
and destruction of wetlands resulted in the decline of
many goose populations in Japan and disappearance
of species such as the lesser snow goose (Anser
cerulascens ceruleascens) (Takekawa et al. 1994).
Since 1971, geese have been protected in Japan as
national cultural treasures and are not hunted (Brazil
1993). Surveys of waterfowl in the Russian Far East in
the past 20 years have indicated alarming declines in
goose populations (Andreev 1994, and see review in
Mooij 1999), but white-fronted geese in Japan have
increased from 3,000 to 50,000 birds in 1998 or one-
third of the 100,000–150,000 in East Asia (Miyabayashi
and Mundkur 1999). The largest concentration in
Japan of up to 30,000 white-fronted geese is found at
Lake Iizumino and Uchinuma, Miyagi Prefecture
(Miyabayashi and Mundkur 1999).

However, the main breeding area for the greater
white-fronted goose wintering in Japan has never been
determined. Earlier reports suggested that geese
migrated to Japan from both west and east of the Sea
of Okhotsk, and that breeding areas included the
Anadyr River lowlands and tundra areas east of the
Kolyma River delta. In the past decade, collar-marking
studies documented that a small proportion (<20%)
of the white-fronted geese marked on the
Anatavool River in the Anadyr Lowlands were
wintering in Japan (Uemura et al. 1996). The spring
migration route and chronology had never been
documented.

In this paper, our objectives were to capture greater
white-fronted goose wintering in Japan, document
their spring migration route and chronology, locate
their breeding areas with satellite telemetry, and
examine their morphology in comparison to other
white-fronted geese. Although preliminary reports of
this study have been presented (Kurechi et al. 1995,
Takeshita and Kurechi 1999), this is the first presenta-

Fig. 1 Major wintering areas (Poyang Lakes, China; Cholwon, South Korea; Central Valley of California, U.S.; Interior Highlands, Mexico) and breeding areas (Anadyr River, Kolyma River, Yukon-Kuskokwim Delta, Bristol Bay Lowlands) for greater white-fronted goose populations on the Pacific Rim.
tion of the complete dataset and comparison of their morphology with other groups on the North Pacific Rim.

2. Study Area and Methods

2.1 Study area

White-fronted geese were captured in the vicinity of the Lake Izunuma and Uchinuma wetland (38.75°N, 141.12°E; hereinafter Izunuma) in northern Japan (Fig. 1). Izunuma is located near Wakayanagi in the state of Miyagi, 860 km north of Tokyo and 100 km north of Sendai, Japan (Fig. 1). In 1989, it was named the second Ramsar wetland of international importance in Japan after Kushiro Marsh, Hokkaido (Finlayson and Moser 1991). The wetland area provides protection for migratory birds and is surrounded by rice fields. The geese also used the Kabukurinuma wetland (38.63°N, 141.10°E) during the winter located 9 km south of Izunuma.

2.2 Capture and marking

Thirty-six geese, from a flock of a few hundred individuals, were trapped under a set of 3 rocket nets (Dill and Thornberry 1950), each 20 m wide, hidden in a rice field southwest of Wakayanagi, Miyagi (Fig. 2). Captured geese were aged, sexed, banded, and measured. We used digital calipers (0.1 mm) to measure head length, culmen, total tarsus, diagonal tarsus, and metric rulers to measure flattened wing chord, 9th primary, and mid tail feathers (see Dzubin and Cooch 1992). Mass was recorded to the nearest 10 g with a spring scale. All geese were marked with plastic neck collars etched with unique 3-digit alphanumeric codes. We marked 10 adult males with 40 g Nippon Telegraph and Telephone (T-2050) satellite transmitters or platform transmitter terminals (PTTs). Half of the transmitters were attached to the geese with backpack harnesses (Dwyer 1972), while half were attached with tail mounts (Giroux et al. 1990, Kurechi et al. 1995). Transmitters duty cycles were set for 6 h on : 72 h off with a pulse interval of 75 s.

2.3 Satellite telemetry locations

U. S. National Oceanic and Atmospheric Adminis-

Fig. 2 Wintering distribution of 4 PTT-marked geese with >11 locations (Argos accuracy class 1-3) captured at Lake Izunuma, Japan on 4 February 1994 and tracked through 19 April. Points of different colors represent the four different individuals and minimum convex polygons indicate their home ranges.
station polar-orbiting weather satellites, circling 850 km overhead about every 100 min, recorded the PTT signals. Service Argos (Toulouse, France), the French aerospace affiliate, estimated PTT locations from Doppler shifts in frequency. We acquired the data from Argos via telnet, and the messages were compiled and concatenated on a Unix workstation and processed into datasets (SAS Inst., 1990) for analysis with customized programs (D. Douglas, unpubl. method). In the tables, coordinates for major use areas were determined from midpoints of the dominant lake or wetland.

Argos provides an estimate of location accuracy (Argos, Inc. 1996) including: a) class 3 (150 m), b) class 2 (350 m), c) class 1 (1,000 m), d) class 0 (> 1,000 m), and e) class Z (unknown). However, some locations with lower Argos accuracy classes (0, Z) may be very accurate (D. Douglas, unpubl. data). For estimating winter minimum convex polygon home ranges and flight distances from Izunuma where the geese roosted, only higher quality (class 1-3: <1,000 m) locations that comprised a single continuous home range were used (n=11). Spatial interpolation was conducted with ArcInfo and Arctview geographic information system software (ESRI, Inc., Redlands, CA, USA). We determined wintering home range size and distances with the animal movement extension to Arctview (Hooge and Eichenlaub 1997).

2.4 Compilation of measurement data

We compared the morphology of geese captured at Izunuma with morphometric datasets from populations on the western Pacific Rim (Fig.1) including geese captured at the Kolyma and Anadyr River deltas of eastern Siberia (M. Kurechi, unpubl. data), and populations on the eastern Pacific Rim (Fig.1) including the Yukon-Kuskokwim Delta (YKD) and the Bristol Bay Lowlands (BBL) of Alaska (see Orthmeyer et al. 1995). We used two-way multivariate analysis of variance (MANOVA: Johnson and Wichern 1988, SAS Institute 1990) to compare differences among sexes, populations, and their interaction. We determined statistical significance by controlling for Type II error at the 0.05 probability level. Univariate analyses of variance (ANOVA) tests were conducted for each measurement. Detection of significant ANOVA differences were followed by pairwise comparisons with Fisher's protected Least Squares Difference tests (Milliken and Johnson 1984) for effects with more than two levels. We conducted a canonical discriminant analysis (Johnson and Wichern 1988, SAS Institute 1990) to examine differences in population centroids for culmen, total tarsus, and bill width. We also compared head length data for Pacific Rim populations with data for A. a. albirostris from the Netherlands (B. Ebbinge and G. Musken, unpubl. data). Confidence intervals for head lengths were calculated using Bonferroni adjustments to ensure the means for sexes of all five groups were simultaneously within their estimation intervals with 95% confidence (Neter et al. 1990).

3. Results

3.1 Transmitter performance

We recorded a total of 987 locations from February through August for the eight working PTT-marked geese (Table 1). We omitted data for one of the tail-mounted transmitters (#5877) that fell off soon after deployment and a backpack transmitter (#7882) that failed after 18 days (although that goose was observed 35 days later at Lake Miyajima, 518 km north of Izunuma with the non-working transmitter still attached). The number of locations obtained from the PTTs was highly variable (2 = 123, 4±72.3), and lifespans ranged from 18 to 208 days. The quality of the locations varied from Argos class Z (16%), 0 (57%), 1 (26%), 2 (1%), and 3 (0%). One transmitter (#7917) had more than twice as many messages as the next best transmitter, but it also had the most low accuracy (class Z) locations.

<table>
<thead>
<tr>
<th>Description</th>
<th>Platform</th>
<th>Transmitter</th>
<th>Terminal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attachment</td>
<td>TM</td>
<td>TM</td>
<td></td>
</tr>
<tr>
<td>Last Message</td>
<td>28 Jun</td>
<td>26 May</td>
<td>14 Jun</td>
</tr>
<tr>
<td>Working Days</td>
<td>145</td>
<td>112</td>
<td>131</td>
</tr>
<tr>
<td>Overpasses</td>
<td>120</td>
<td>60</td>
<td>129</td>
</tr>
<tr>
<td>Total Messages</td>
<td>405</td>
<td>221</td>
<td>499</td>
</tr>
<tr>
<td>Total Locations</td>
<td>119</td>
<td>61</td>
<td>129</td>
</tr>
<tr>
<td>Location Class</td>
<td>8</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>88</td>
<td>38</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>23</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 1 Summary of satellite telemetry data for 8 of 10 greater white-fronted geese marked with tail mount (TM) and backpack (BP) transmitters at Lake Izunuma, Japan, 4 February 1994. Two geese (5877, 7882) lost their transmitters within a few weeks and were excluded from analyses.
**Table 2** Number of locations, total days, minimum convex polygon (MCP) home ranges, and mean distance traveled from the Lake Izunuma roosting area to field feeding areas during the winter for four greater white-fronted geese marked with satellite transmitters at Lake Izunuma, Japan, 4 February 1994.

<table>
<thead>
<tr>
<th>Description</th>
<th>5853</th>
<th>7915</th>
<th>7916</th>
<th>7917</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Locations</td>
<td>20</td>
<td>18</td>
<td>11</td>
<td>23</td>
</tr>
<tr>
<td>Total Days</td>
<td>15</td>
<td>74</td>
<td>15</td>
<td>28</td>
</tr>
<tr>
<td>MCP Home Range (km²)</td>
<td>461</td>
<td>127</td>
<td>410</td>
<td>1073</td>
</tr>
<tr>
<td>Distance Traveled (km)</td>
<td>11.3±7.4</td>
<td>7.8±5.3</td>
<td>10.8±10.0</td>
<td>14.8±9.0</td>
</tr>
<tr>
<td>Range</td>
<td>(1.5-30.2)</td>
<td>(0.9-20.2)</td>
<td>(2.3-35.2)</td>
<td>(1.1-36.1)</td>
</tr>
</tbody>
</table>

![Fig. 3](image) General spring migration route for white-fronted geese marked at Lake Izunuma, Japan on 4 February 1994. Inset boxes indicate map areas shown in detail. The dark line in the Sea of Okhotsk indicates the usual extent of pack ice.

### 3.2 Wintering distribution

We determined minimum convex polygon home ranges (Table 2) from small samples (11–23 locations) for four of the greater white-fronted geese at Izunuma during the late winter (Fig. 2). Home range size varied from 127–1,073 km² and averaged 518 km². Most of the geese fed in rice fields to the north and east of Izunuma, and they flew a mean distance of 11.2±9.9 km (range=0.9–36.1 km) from the lake. We also obtained 18 total locations for four birds (5846, 7623, 7915, 7917) that used the Kabukirinuma wetland.

### 3.3 Staging areas and spring migration chronology

Five of the marked geese (5849, 5853, 7623, 7880, 7916) departed from Izunuma on 17–19 February (Table 3, Fig. 3). Two geese (5846, 7917) migrated on 18–19 March, while 7915 migrated on 19 Apr from Kabukirinuma.

#### 3.3.1 Hachirogata Lagoon, Akita Prefecture

All geese except 5846 staged in Akita Prefecture (Fig. 4) in the vicinity of the Hachirogata Lagoon (40.00°N 140.57°E) including nearby Lake
Table 3  Staging and breeding sites for eight greater white-fronted geese (5846, 5849, 5853, 7623, 7880, 7915, 7916, 7917) marked with platform transmitter terminals (PTTs) in Japan. Total distance (from Lake Izunuma), segment distance (between areas), mean (and range) days of stay (except on the Kamchatka Plain where locations ended for 3 geese), number of birds, and total locations are also reported. Areas include Lake Izunuma, Miyagi Prefecture, Honshu; Hachirogata Lagoon, Aki Prefecture, Honshu; Lake Miyajimunuma, Hokkaido; Kamchatka Plain, southwest Kamchatka, Russia; Rusakovo River, east central Kamchatka, Russia; and Khalyryka and Pekul'yey Lakes, Chukchi Autonomous Region, Russia.

<table>
<thead>
<tr>
<th>Date</th>
<th>Site Name</th>
<th>Type</th>
<th>Coordinates (latitude, longitude)</th>
<th>Total Distance (km)</th>
<th>Segment Distance (km)</th>
<th>Length of Stay (range)</th>
<th>Number of Marked Geese</th>
<th>Total Locations</th>
</tr>
</thead>
<tbody>
<tr>
<td>04 Feb-19 Mar</td>
<td>Izunuma*</td>
<td>Wintering</td>
<td>38.71°N, 141.11°E</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>8</td>
<td>227</td>
</tr>
<tr>
<td>20 Feb-25 Mar</td>
<td>Hachirogata</td>
<td>Staging</td>
<td>40.04°N, 140.03°E</td>
<td>171</td>
<td>171</td>
<td>19.0 (4-26)</td>
<td>7*</td>
<td>126</td>
</tr>
<tr>
<td>16 Mar-07 Apr</td>
<td>Utonai</td>
<td>Staging</td>
<td>42.42°N, 141.42°E</td>
<td>445</td>
<td>227</td>
<td>10.5 (1-22)</td>
<td>6b</td>
<td>54</td>
</tr>
<tr>
<td>31 Mar-06 May</td>
<td>Miyajimunuma</td>
<td>Staging</td>
<td>43.17°N, 141.67°E</td>
<td>518</td>
<td>53</td>
<td>26.5 (4-34)</td>
<td>8</td>
<td>217</td>
</tr>
<tr>
<td>05 May-28 May</td>
<td>Kamchatka Plain</td>
<td>Staging</td>
<td>54.37°N, 155.81°E</td>
<td>1,940</td>
<td>1,521</td>
<td>—</td>
<td>6*</td>
<td>45</td>
</tr>
<tr>
<td>26 May-30 Aug</td>
<td>Rusakovo</td>
<td>Breeding?</td>
<td>58.17°N, 161.29°E</td>
<td>2,649</td>
<td>570</td>
<td>97.0 (1-22)</td>
<td>1*</td>
<td>126</td>
</tr>
<tr>
<td>13 May-22 Aug</td>
<td>Khalyryka/</td>
<td>Breeding</td>
<td>62.86°N, 177.07°E</td>
<td>3,595</td>
<td>1,653</td>
<td>54.0 (32-92)</td>
<td>3*</td>
<td>84</td>
</tr>
</tbody>
</table>

* Includes locations from nearby Kabukurinuma wetland, 9 km south
* All but PTT # 5846
* All but PTT # 7880 and # 7915
* All but PTT # 7623 and # 7915
* PTT # 5849
* Distance from Kamchatka Plain
* PTT # 5846, # 5853, and # 7623

Fig. 4  Early spring staging areas (19 February to 11 May) in northern Japan for white-fronted geese marked with satellite transmitters at Lake Izunuma, Japan on 4 February 1994.
20 km to the north. Five of the geese were first located at Hachiorgata on 20–21 Feb and departed from 14–25 Mar with an average length of stay of 19 days. Goose 7917 spent only 4 days at Hachiorgata (23–27 Mar), while 7915 arrived very late (21 Apr) and departed 12 days later (3 May).

3.3.2 Lake Utonai, Hokkaido
Six geese (5846, 5849, 5853, 7623, 7916, 7917) staged at Lake Utonai, Hokkaido (42.42°N, 141.42°E; Fig. 4). All but 7916 were first located at the lake from 16–29 Mar and were last located from 29 Mar–7 Apr with an average length of stay of 10.5 days. Goose 7916 was only located on a single day (4 Apr) at Lake Utonai.

3.3.3 Lake Miyajimanuma, Hokkaido
All of the geese staged at Lake Miyajimanuma, a small lake (30 ha) on the Ishikari Plain (42.42°N, 141.42°E; Fig. 4). All geese but 7915 were located in the area from 31 Mar–9 Apr and were last located from 30 Apr–6 May with an average length of stay of 26.5 days. Bird 7915 was first located on 7 May and was last located on 11 May.

We observed 34 of the 36 collar-marked geese foraging in the surrounding 5,000 ha of rice and wheat fields. The white-fronted goose population staging at Miyajimanuma in 1994 was estimated to be 33,000 birds, and 20,000 departed on 3 May (Y. Sabano et al., unpubl. data). Goose 5853 was sighted at 1200 h on 2 May near Lake Miyajimanuma, and was later detected on 3 May in the Sea of Okhotsk, flying 995 km in less than 30.5 h (>32.6 km/h).

3.3.4 Kamchatka Peninsula
Seven PTT-marked geese migrated to Kamchatka with six arriving from 5–11 May and one (7880) first located on Kamchatka on 7 June (Fig. 5). Three (5846, 7880, 7916) geese reached the southwest coast of Kamchatka and stopped on the Kamchatka Plain. Goose 5853 reached central Kamchatka (57°N, 161°E) on 5 May, covering 1,988 km in 74.8 h (26.6 km/h).

By 11 May, five geese had migrated farther north on Kamchatka Peninsula. Geese 5846, 7880, 7916, and 7917 migrated to areas near the Moroschechnaya River in western Kamchatka. Goose 7623 continued to stopover sites at Kharchinskoye Lake (56.53°N, 160.18°E), and goose 5853 also stopped there for at least 6 days (5–11 May).

3.4 Final locations and possible breeding areas
Goose 7915 stopped at the limit of the pack ice shown on Department of Defense maps (Fig. 3) in the Sea of Okhotsk east of Sakhalin Island (55.4°N, 145.0°E) on 13 May, where we suspect it perished since it remained there until 14 June. Locations for two geese ended on the lower Kamchatka Peninsula (Fig. 5): 7916 migrated to the southwest coast of
Kamchatka on the Kamchatka Plain near the Bol'shaya River (54.32°N, 155.80°E) where its last location was received on 28 May (Table 2), and 7880 migrated to the southwest coast of Kamchatka on the Kamchatka Plain (55.52°N, 156.79°E) where its last location was received on 7 Jun.

The last locations for two other geese ended on upper Kamchatka Peninsula (Fig. 5). The final location for 5849 was near Ust Kamchatsk at Ozero Nerpich'ye (55.64°N, 162.44°E) on 26 May. Goose 7917 was located at the Rusakovo River (58.17°N, 161.97°E) from 26 May through 30 August. Three geese (5846, 5853, 7623) moved northeast from Kamchatka to the southern Chukchi Autonomous Region at Khatyryka Lake (62.25°N 175.17°E) and Pekul'ney Lakes near Melynpi'l'gyno (62.60°N 176.01°E), 3,600 km from their wintering area (Table 2, Fig. 6). Goose 5846 arrived at Khatyryka Lake on 21 May and remained in the area 38 days providing 21 locations until the PTT quit transmitting on 28 June. Goose 5853 reached the Pekul'ney Lakes area on 13 May and provided 22 locations through 14 June over 32 days, and 7623 arrived at Pekul'ney Lakes on 22 May and provided 27 locations in 92 days through 22 August.

In the winter of 1994–1995, 26 of the 36 geese (72%) were resighted in Japan at Lake Miyajimamoura or Izunuma. These included 4 radio-marked geese, including 5877 which lost its transmitter soon after marking, 5853 and 7623 returning from the Pekul'ney Lakes, and 5849 last located at Ozero Nerpich'ye. All of the resighted radio-marked geese and those which migrated farthest to the Chukchi Autonomous Region had tail mounts, which may indicate that it was a better attachment method (see Kurechi et al. 1995).

### 3.5 Comparison of morphological measurements for Pacific rim populations

Our MANOVA analysis of morphological variation comparing the wintering population at Izunuma with other white-fronted geese from the Pacific Rim showed significant differences. As expected, males were larger than females (Wilks' $\lambda=0.8915$; $F=9.48, df=12, 2564; P<0.0001$). However, the interaction of sex and population was significant (Wilks' $\lambda=0.9779$; $F=1.81, df=12, 2564; P=0.0413$). Females from Bristol Bay differed from Anadyr (Wilks' $\lambda=0.9917$; $F=2.11, df=3, 469; P=0.0445$), Kolyma (Wilks' $\lambda=0.9821$; $F=5.88, df=3, 469; P=0.0006$), and the Yukon–Kuskokwim Delta (Wilks' $\lambda=0.9716$; $F=9.42, df=3, 469; P<0.0001$). Females from Kolyma differed from Izunuma (Wilks' $\lambda=0.9871$; $F=4.21, df=3, 469; P=0.057$) and the Yukon–Kuskokwim Delta (Wilks' $\lambda=0.9901$; $F=3.22, df=3, 469; P=0.022$). Anadyr and Izunuma males were similar (Wilks' $\lambda=0.9942$; $F=1.88, df=3, 469; P=0.13$), but morphology of males from all other populations...
Table 4  Morphological measurements (mm) and mass (g) of adult male and female greater white-fronted geese from five Pacific Rim populations: Anadyr River, Russia; Kolyma River, Russia; Lake Izunuma, Japan; Yukon Kuskokwim, Alaska, USA; and Bristol Bay Lowlands, Alaska, USA. For multivariate analysis of culmen, total tarsus, and bill width, superscript letters following variable names report results of the ANOVA on species effect, sex effect, and their interaction, where A indicates a significant difference (p≤0.05), and B represents a nonsignificant difference (p>0.05). Letters (a,b,c) following means indicate significant differences (p≤0.05) among populations. If the letters are the same no statistical difference was found according to Fisher's protected Least Significant Difference tests.

<table>
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<th>Population</th>
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<th></th>
<th>Izunuma</th>
<th></th>
<th>Kolyma</th>
<th></th>
<th>Yukon-Kuskokwim</th>
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<td>n</td>
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were significantly different.

The canonical discriminant analysis further supported our findings of significant differences among populations. Morphological measurements were linearly transformed into canonical vectors which successively captured the greatest separation between population centroids in 95% ellipsoids (Fig. 7). The first canonical vector was significantly associated with population for females ($F=4.62$, $df=12,1344; P<0.0001$) and males ($F=7.86$, $df=12,1214; P<0.0001$), and explained 80% and 56% of the total separation, respectively.

When we examined the head length of these Pacific Rim populations and European white-fronted geese combined (Fig. 8), we found significant differences in sex ($F=185.7$, $df=1,815; P<0.0001$) and population ($F=237.9$, $df=1,815; P<0.0001$), but their interaction was not significant ($F=2.04$, $df=5,815; P=0.0710$).

4. Discussion

4.1 Winter distribution at Izunuma

Most European and central Asian wintering sites are located between the 0 EC and 10 EC January isotherms (Mooij et al. 1999) in river valleys, estuaries, or deltas. However, the Siberian air mass makes East Asia considerably colder than similar latitudes in Europe (Brazill 1993). The Sea of Okhotsk freezes during the winter, and ice extends to the coast of Hokkaido toward the end of December, remaining until late March. Izunuma is situated relatively far north in comparison to other wintering areas in East Asia, but temperatures are mediated by ocean currents and snow cover is not as heavy as other northern areas in Japan. Most of the marked geese remained in the vicinity of Izunuma through late February. Until migration occurred, we found few locations more than 22 km from the wetland. Numbers of white-fronted geese in Japan have increased from over 3,000 in 1971 to nearly 48,000 in 1998 (Brazill 1993, Miyabayashi and Mundkur 1999, Takeshita and Kurechi 1999), and Izunuma now supports the largest wintering aggregation of geese in Japan.
4.2 Early spring migration in Japan

If the geese we captured and marked at Izunuma from one flock were intermixed as we have documented in lesser snow and white-fronted geese in California (J. Takekawa, unpubl. data), then migration of the PTT-marked geese may represent most of the wintering population. We documented differences in both migration areas and chronology of the PTT-marked geese, which also supports our contention that they were thoroughly intermixed and representative of the wintering population. Of the 5 major staging areas (Hachirogata, Akita; Lake Ogawara, Aomori; Lake Utonai, Oikamanai-numa, Lake Seika and the Ishikari Plain, Hokkaido) white-fronted geese have been reported to use in Japan (Brazil 1993), the PTT-marked geese used three of these areas including Hachirogata, Utonai, and the Ishikari Plain (Miyajimanuma).

Up to 10,000 geese have been counted at Lake Utonai in March and April (Brazil 1993), but we found that the primary staging area for the PTT-marked geese was Miyajimanuma. Similarly, Ely et al. (1993) found that lesser snow geese from Wrangel Island, Russia seemed to follow a single route to a major staging area on the Yukon–Kuskokwim Delta of Alaska during the fall migration. Maisonneuve and Bedard (1993) found greater snow geese (Anser caerulescens atlantica) used the same primary staging areas from year to year, and we suspect the same faithfulness to major sites (Brazil 1993) by white-fronted geese. Migrations along a narrow route are often in response to limited food resources (Welty 2000). Unlike spring staging areas in North America where there is abundant agriculture (Krapu et al. 1995), there is little arable land in East Asia north of 50° N.

4.3 Late spring migration to Kamchatka

Brazil (1993) and Andreev (1994) suggested that most white–fronted geese had a route similar to bean geese (Anser fabalis), migrating to and from Japan across Sakhalin Island following an inland migration route. Although 7915 may have been following the Sakhalin Island interior migration route from Lake Miyajimanuma, it was last recorded east of that area (Fig. 3). We found that all of the other PTT-marked geese flew to Kamchatka and suspect that it is the primary spring migration route for the wintering population from Japan.

Gerasimov et al. (1997) observed geese migrating from the sea to the Vachil River (53.25°N, 159.57°E) and Opala Rivers (52.00°N, 156.50°E) of southeast Kamchatka, and the Bol’shaya River of southwest Kamchatka (52.52°N, 156.28°E) between 29 Apr and 7 May 1994. Our PTT-marked geese were first located in southwest Kamchatka overlapping that period (5–28 May; Table 2), suggesting that their migration chronology was normal. One of the PTT-marked geese (7916) was located at the Bol’shaya River mouth (Fig. 3) during nearly the same period as the survey by Gerasimov et al. (1997).

Gerasimov and Gerasimov (1997) identified Kharchinskoye Lake (Fig. 5) as the most important Kamchatka staging area for greater white-fronted geese during the spring where they counted up to 10,000 there in 1983. We located two geese (5853, 7623) in the vicinity of that area, and staging locations for three other geese (5849, 7880, 7917) were nearby. Thus, our telemetry findings confirmed the importance of this area for geese from Japan, as well as documenting the importance of the Kamchatka Plain to the southwest.

4.4 Breeding areas

Before this study, the migration of greater white-fronted geese along the Pacific Rim in the eastern Palearctic was thought to end at the Anadyr River. In the lower Anadyr (64° N), greater white-fronted geese arrived from 13–16 May, and goslings hatch from 28 June to 5 July (Kondratyev 1992, cited in Andreev 1994). However, we found greater white-fronted geese arrived between 13–22 May at Khatyryk and Pekul’ney Lakes, 250 km south of Anadyr. These lakes comprise part of a coastal plain isolated from the Anadyr River across a mountain range, and Kistchnikli (1980) reported a few goslings in the Khatyryk River area in the mid-1970s. On the basis of these findings, Russian biologists conducted aerial surveys in 1997 at Pekul’ney Lakes in the Koryak lowlands (A. V. Kondratyev, pers. comm.). They found molting flocks and 1,650 greater white-fronted geese, of which 760 were in family groups of adults and goslings. Thus, this survey confirmed a southern breeding range expansion for white-fronted geese in East Asia.

One goose (7917) continued to provide locations on the Russakovo River on the east coast of the upper Kamchatka Peninsula through late August. If geese were breeding in this area, it may represent the southernmost breeding area in East Asia at 58° N latitude. However, the presence of breeding geese has not yet been confirmed through surveys of that region. We found that the last locations of three geese (7916, 7880, 5849) were on the lower Kamchatka Peninsula. Their transmitters ceased transmitting from 26 May to 7 June (Table 1) which may have been prior to reaching their final destination, or these geese were nonbreeding birds because this area is not known to have any breeding white-fronted geese.

4.5 Geographic variation of Pacific Rim populations

On the western Pacific Rim, Ely and Takekawa (1996) have described geographic variation of greater white-fronted goose populations breeding in Alaska. Tule white-fronted geese have been recognized as a distinct subspecies that breed in a different region than most Pacific white-fronted geese. In addition, geese radio-marked in the Bristol Bay lowlands, only 300 km south of the major Pacific coast breeding area on the Yukon–Kuskokwim Delta (a similar distance as the Pekul’ney Lakes region is from Anadyr), had a different migration chronology and separate wintering area. We suspect that population differences also may occur on the west side of the Pacific Rim.

South of Anadyr on the west side of the Sea of Okhotsk, Krechmar (1996) documented an isolated population of white-fronted geese breeding in forest-
tundra on the Kava River, the southernmost (60°N) known breeding population in Eurasia. He found that
goose arrived from 6–11 May and chicks hatched from
21–28 June, a phenology within 5–7 days of the Anadyr
populations. Krecmar (1996) suggested that greater
white-fronted geese may have formerly bred in sev-
eral areas along the Sea of Okhotsk but disappeared
in the past 100 years because of anthropogenic distur-
bances. Even farther south at Ulbansky Bay (53°N,
138°E), Andreev (1994) reported that an unconfirmed
resident breeding population may exist. We suspect
that the PTQ-marked goose (7917) located repeatedly
at the Rusakovo River (38°N) may have been breed-
ing, although our findings have not been verified with
a survey.
A proportion of greater white-fronted geese
marked with collars and transmitters in the Anadyr
region have been resighted in Japan (Shimada et al.
1995). Of 145 geese marked with collars along the
Anadyr River, only 26 (18%) have been resighted in
Japan (Uemura et al. 1996) and many were initially
marked in molting flocks of unknown origin. Resight-
ing rates in Japan are generally high because most
goose are concentrated near Izunuma during the
winter and are easily observed. Most geese from
Anadyr may spend the winter in South Korea or
China. Three geese collar-marked from a non-breeding
flock in Anadyr migrated to the Junam Reservoir
(35.33°N, 128.67°E) and two were located in the
Cholwon Basin (38.25°N, 127.22°E) of South Korea.
In 1993, a goose marked with a satellite transmitter
with a breeding flock on the Avtakool River (64.22°N
178.03°E) migrated over the Sea of Okhotsk and
followed the Amur River to the Naoli River of China
(46.07°N 132.50°E).
It is likely that the Kolyma region includes
goose flocks migrating to wintering areas other than
Japan. Fifty-six of 68 (82%) of the remnant group of
lesser snow goose marked at the Kolyma River were
resighted in North America (Uemura et al. 1998). Of
49 white-fronted goose marked with collars on the
Kolyma River, 11 (22%) were resighted in South
Korea and none were seen in Japan. Thus, similar to
the Bristol Bay population in Alaska which winters in
Mexico separately from the Yukon–Kuskokwim
Delta population (Ely and Takekawa 1996), geese
wintering in Japan may be primarily from breeding
areas from Pekul’ney Lakes to northern Kamchatka
in the west coastal lowlands of the Chukchi and
Koryak Autonomous Regions.
4.6 Comparing the wintering population in Japan
with other Pacific Rim populations
Austin and Kuroda (1953) examined the morphol-
ogy of specimens from Japan and concluded that
white-fronted geese in east Asia were identical to
goose from northwestern North America in size and
color. Our morphological analysis (Fig. 8) is the first
to use live geese to verify that the population winter-
ing in Japan are A. a. frontalis rather than A. a.
albifrons (Dement’ev and Gladkov 1968, Owen 1980,
Portenko 1989), but we found significant differences
in their morphological compared with other Pacific Rim
populations.
Orthmeyer et al. (1995) were able to separate 75%
of the geese from Bristol Bay and the Yukon–
Kuskokwim Delta of Alaska on the basis of their
morphology, which is a level of separation that has
been used to define subspecies (Amadon 1949).
Although we lack the sample size to conduct that
detailed discriminant function analysis, centroid
means for the females (considered to have greater site
faithfulness), are farther apart for Japan and Kolyma
than are the western Alaska populations (Fig. 7). The
populations with the most similar morphology on the
Pacific Rim seem to be those from Anadyr and the
Yukon–Kuskokwim Delta. This would suggest ex-
change of individuals between these populations,
but Ely and Scribben (1994) found that of >14,000
recoveries of geese banded in North America, no cross
-continental recoveries were ever reported, suggest-
ing little opportunity for gene flow between Nearctic
and Palearctic populations. Unlike the western
Palearctic populations which exhibit panmixia during
the winter (see Mooij et al. 1999), our evidence sup-
ports the contention that some of the white-fronted
geese on the Pacific Rim represent distinct popula-
tions (Ely and Takekawa 1996).
4.7 Conservation issues
While goose populations in the eastern Palearctic
have declined precipitously over the past two decades
(Andreev 1994, Mooij 1999), the white-fronted goose
wintering population in Japan has increased. Winter-
ing population indices of white-fronted geese in Japan
were as low as 3,000 individuals prior to the hunting
ban in 1971, but populations increased gradually
through the 1980s, with a much more rapid expansion
in the 1990s (Takeshita and Kurechi 1999). Takeshita
and Kurechi (1999) suggest that the wintering popula-
tion may have increased because of the hunting ban,
but some of the hunting areas outside Japan are more
than others result in improved breeding conditions and
productivity.
4.7.1 Hunting
Hunting may negatively affect goose breeding popu-
lations in the Far East. The white-fronted goose is
the most hunted goose species in the western Palearctic
with up to 25% of the population harvested each year
(Mooij et al. 1999). Similar mortality likely occurs in
the eastern Palearctic although zavpovedniks and zak-
azniki provide some protection for geese in Russia,
but there is a traditional spring hunt for 10 days and
a daily bag limit of two geese in the Russian Federa-
tion (Mooij et al. 1999). Since 1988, native people have
been allowed to subsistence hunt all unprotected
waterfowl without a permit in Russia. In addition,
hunting is suspected to occur through the wintering
range of white-fronted geese in China.
4.7.2 Habitat loss and degradation
Greater white-fronted goose populations in the
eastern Palearctic face threats from loss and degrada-
tion of wetlands and exposure to contaminants. Multi-
national corporations from East Asia and the United
States are pursuing plans to extract resources from
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many areas within eastern Russia. Loss of lesser snow geese in East Asia likely occurred in the early 1900s because of wintering habitat loss combined with over-harvesting (see Takekawa et al. 1994). Disease, primarily avian cholera (Pasteurella multocida) has killed greater white-fronted geese in some crowded staging areas of North America such as the Rainwater Basin of Nebraska (Krapu et al. 1995). Threats to the wintering grounds for Tule white-fronted geese include loss of habitat to human development (Wege 1984).

Recently, management of migratory birds in the Central Valley of California has included working with farmers to modify farming practices and provide flooded rice habitat which seems to improve habitat suitability for many species (Elphick 1998). A similar approach has also begun in Japan at Kabukurinuma (Iwabuchi 2000). These efforts to improve wintering habitats may help to stabilize the existing populations.

4.7.3 Research needs

Management of greater white-fronted geese could be greatly improved through identification of geographic and morphological variation of their populations. Conservation of the intraspecific variation will likely provide the best opportunity for their long-term survival in a rapidly changing environment. However, a detailed genetic analysis will be required to confirm the level of separation of these geographically and morphologically distinct populations.

Acknowledgments

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