RESEARCH ARTICLE

Geographic variation in morphometrics, molt, and migration suggests ongoing subspeciation in Pacific Golden-Plovers (*Pluvialis fulva*)

Joop Jukema,[1] Johan G. van Rhijn,[2]* and Theunis Piersma[3,4]

[1] Haerdawei 62, 8854 AC Oosterbierum, The Netherlands
[2] Slochterweg 3, 9635 TA Noordbroek, The Netherlands
[3] Animal Ecology Group, University of Groningen, Groningen, The Netherlands
[4] Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands
* Corresponding author: johan-van-rhijn@wxs.nl

ABSTRACT

Breeding Pacific Golden-Plovers (*Pluvialis fulva*) cover 140 longitudinal degrees of Arctic tundra. Having examined 557 museum skins from across this huge distributional range, we conclude that Pacific Golden-Plovers breeding in Alaska are structurally larger than those breeding in Siberia, especially in wing length. Birds from Alaska also have more pointed wings and almost always postpone the initiation of primary molt until they reach their winter quarters, whereas many Siberian birds start primary molt in the breeding areas. These differences could have been favored by the longer transoceanic flights followed by the Alaskan populations to nonbreeding destinations in the Pacific Islands. We propose that the Alaskan and Siberian breeding birds be distinguished as distinct flyway populations to be used in conservation assessments by the international conservation community.

Keywords: geographic variation, migration, molt, Pacific Golden-Plover, *Pluvialis fulva*, subspeciation, wing length, wing pointedness

Географическая Изменчивость Морфометрии, Линьки и Миграций Предполагает Продолжающееся Видообразование у Бурокрылой Ржанки *Pluvialis fulva*

РЕЗЮМЕ

Гнездовой ареал бурокрылых ржанок (*Pluvialis fulva*) охватывает 140 градусов по долготе в тундрах Арктики. Основываясь на изучении 557 музейных экземпляров в пределах этого огромного пространства, сделано заключение о том, что бурокрылые ржанки, размножающиеся на Аляске, структурно более крупные (особенно по длине крыла) по сравнению с теми, которые гнездятся в Сибири. Птицы Аляски имеют также более заостренные крылья и почти всегда начинают линьку первостепенных маховых перьев лишь после прилёта на зимовку, тогда как многие сибирские птицы приступают к линьке маховых ещё на местах размножения. Формированию этих различий могли способствовать более протяженные трансокеанские перелёты ржанок с Аляски на зимовки, расположенные на островах Тихого океана. Мы предлагаем различать ржанок, гнездящихся на Аляске и в Сибири, в качестве географических популяций разных пролётных путей для природоохранных задач международного сообщества.

Ключевые слова: Pluvialis fulva, бурокрылая ржанка, длина крыла, заостренность крыла, миграции, линька, географическая изменчивость, видообразование.

INTRODUCTION

The breeding and nonbreeding ranges of the Pacific Golden-Plover (Figure 1) are enormous (Figure 2). The breeding range extends from the Yamal Peninsula to western Alaska across the Arctic into the Subarctic, thus covering much of the Siberian tundra. This continuous breeding range (Figure 2) is interrupted only by the Bering Strait between Alaska and Chukotka (~82 km wide), the De Long Strait separating Wrangel Island from the

FIGURE 1. A male Pacific Golden-Plover in its breeding area (Taymyr), displaying the wings-high posture in concluding the territorial song flight. Photo credit: Bas van den Boogaard

Siberian mainland (∼140 km), and the Gulf of Ob between the Gydan and Yamal peninsulas (∼50 km) (Byrkjedal and Thompson 1998, Johnson and Connors 2010a, 2010b, Lappo et al. 2012). The wintering range includes almost all Pacific islands, along with coastal areas in Southeast Asia, Indonesia, Australia, and New Zealand (e.g., Byrkjedal and Thompson 1998, Johnson and Connors 2010a, 2010b). This "winter" range no longer includes northwestern Europe, where evidence for regular winter occurrences until the 1940s was assembled on the basis of oral history (Jukema and Piersma 2002).

The Pacific Golden-Plovers nesting in Alaska are known to differ from their western conspecifics in several ways: (1) They make very long, nonstop oceanic flights to the Pacific isles (Figure 2), whereas flights of Siberian birds are apparently transcontinental (thus allowing stops) and without extensive barriers (Dement'ev and Gladkov 1951, Byrkjedal and Thompson 1998, Johnson et al. 2001, 2011, 2012, Johnson and Connors 2010a, 2010b, Lappo et al. 2012); (2) they molt flight feathers in their winter quarters (Kinsky and Yaldwyn 1981, Connors 1983, Johnson and Johnson 1983, Barter 1988), whereas Siberian birds start wing molt in the breeding area (Tulp et al. 1997, 2000, Tulp and Schekkerman 2001, Jukema et al. 2013, P. Tomkovich personal communication); and (3) their first molt of secondaries in the second year of life is partial and all subsequent secondary molts are complete, whereas Taymyr birds molt half of their secondaries in all years (Jukema et al. 2013). Here, on the basis of newly collected

data from both the breeding and nonbreeding ranges, we present a new review of the morphometrics of the Pacific Golden-Plover and interpret the patterns with reference to known differences in their annual cycle. We propose that there is evidence for incipient subspeciation and define 2 distinct flyway populations.

METHODS

Skins

Specimens ($n = 557$) from many museums were examined: Amsterdam (11), Auckland (9), Chicago (50), Christchurch (17), Honolulu (60), Leiden (124), Melbourne (12), Moscow (195), New York (6), Sydney (40), Tring (1), and Wellington (34) (see Acknowledgments). In many cases, the skins were shipped to the Netherlands and studied in the Natuurmuseum Fryslân, Leeuwarden. To avoid variability, all measurements were made by J.J. These were length of bill (to 0.1 mm), tarsus length (straight to 0.1 mm), wing length (mm; primaries maximally flattened and straightened), and distances (mm) between primary tips P10–P9, P10–P8, P10–P7, and P10–P6. The latter measurements were made to determine wing pointedness (e.g., Mönkkönen 1995, Byrkjedal and Thompson 1998, Kaboli et al. 2007, Baldwin et al. 2010). Molt stage for each of the 10 primaries was scored on a 5-point scale (0 = unmolted old feather, 5 = fully developed new feather; Ginn and Melville 1983). From May (to include all arriving birds in the breeding area) until the following molt period, all primaries were considered old (score 0). We classified each bird as follows: "primary molt not yet started" (all primaries old); "beginning primary molt" (1 or a few primaries at score 1); "proceeding primary molt" (1 or more primaries at score 2); "suspended primary molt" (temporary interruption: 1 or more primaries scored at 5 and all others at 0, or a single primary scored at 4 between the rows of scores 5 and 0; Prater et al. 1977); "resumed primary molt" (1 or a few primaries at score 1 between a series scored 5 and a series scored 0; and "completed primary molt" (all primaries at 5, or the final feather in a row of score 5 was scored 4).

Classification of Geographic Regions

We divided the sample skins into 15 groups (each comprising ≥10 adults [>1 yr old]) representative of the following geographic regions (Figure 2): (1) Taymyr (including Yamal and Gydan), (2) Yakutia, (3) Chukotka (including Wrangel Island), (4) Kamchatka, (5) Alaska, (6) southern Siberia (Baikal region and farther westward), (7) southeastern Siberia (Sahkalin Island and the southeastern Siberian coastal area), (8) western Indonesia (Sumatra and farther northwestward), (9) central Indonesia (including Christmas Island and all skins from "Indonesia" without any further detail), (10) New Guinea (including the
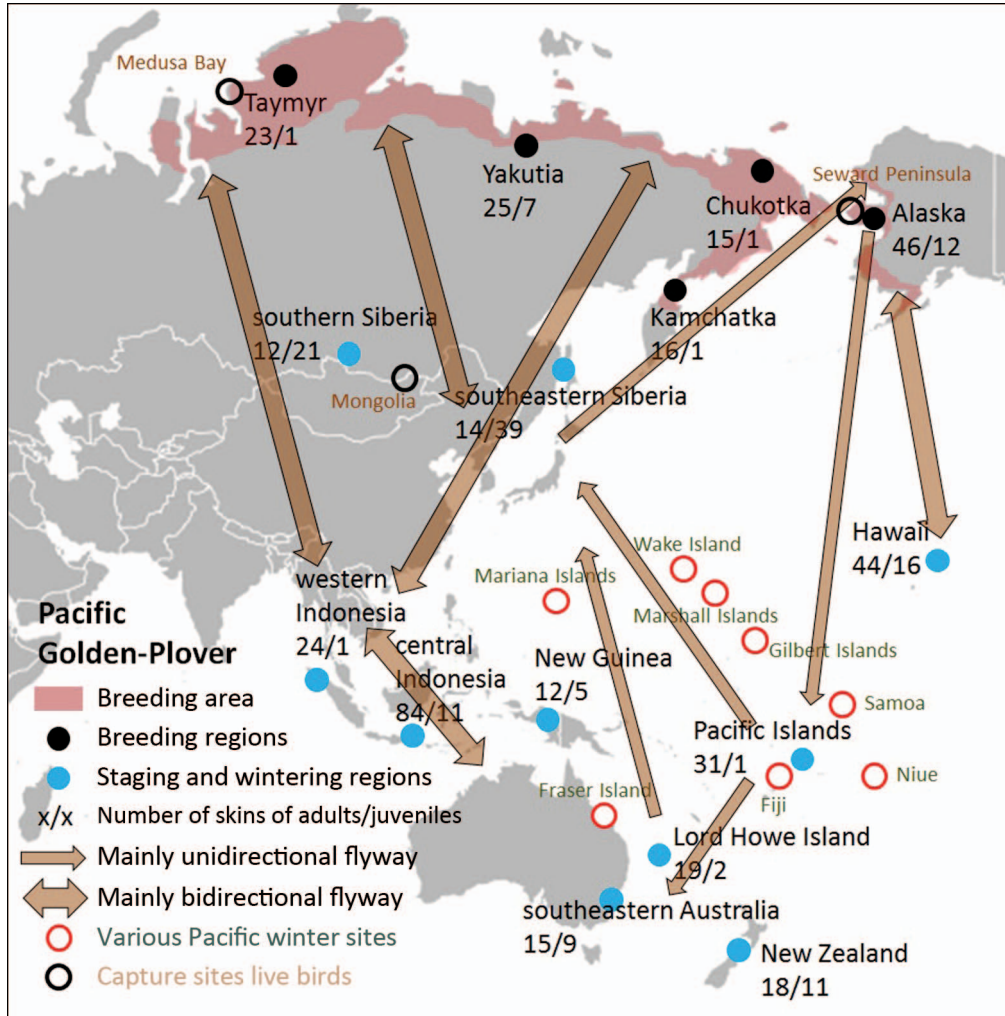
FIGURE 2. Pacific Golden-Plover breeding area (based on Byrkjedal and Thompson 1998, Johnson and Connors 2010a, 2010b, Lappo et al. 2012), centers of the breeding and staging or wintering regions for grouping the skins, approximate major flyways (based on Byrkjedal and Thompson 1998, Johnson and Connors 2010a, 2010b, Johnson et al. 2011, 2012), Pacific wintering sites mentioned in the text, and capture sites of live birds. For each region, total numbers of adult and juvenile skins are given.

Moluccas Islands and northeastern Australia), (11) Hawaii, (12) Pacific Islands (Fiji and Niue), (13) Lord Howe Island, (14) southeastern Australia, and (15) New Zealand. Groups 1–5 comprise breeding regions; groups 6–15 comprise staging and wintering regions.

Live Pacific Golden-Plovers

In addition to museum specimens, J.J. measured wing length (mm; primaries maximally flattened and straightened) and recorded sex and age ($\leq$1 yr old or $>$1 yr old) in live Pacific Golden-Plovers captured in the field (Figure 2): 21 nesting birds, captured in 1996 at Medusa Bay, Taymyr (73°N, 81°E); 294 captured in 2005 at a staging ground in northeastern Mongolia (49°N, 116°E; see Wijmenga et al. 2011); and 34 nesting birds trapped in 2008 and 2010 on the Seward Peninsula, western Alaska (near Nome: 65°N, 166°W).

Comparisons and Corrections

We compared adults ($>$1 yr old) only with adults, juveniles ($\leq$1 yr old) only with juveniles, skins only with skins, and live birds only with live birds. Because previous studies did not find sexual size dimorphism among Eurasian Golden-Plovers (*P. apricaria*; Jukema and Piersma 1992) and Pacific Golden-Plovers (Byrkjedal and Thompson 1998, Johnson and Johnson 2004, Johnson and Connors 2010a, 2010b), we did not treat the sexes separately in our analyses.

To compare the skins from the 15 geographic regions, averages and indices were calculated separately for adults and juveniles (see Figure 3; all raw data and the frequencies, averages, and standard deviations per region are listed in the Supplemental Material Appendix). The measurements are bill length (B), tarsus length (T), wing
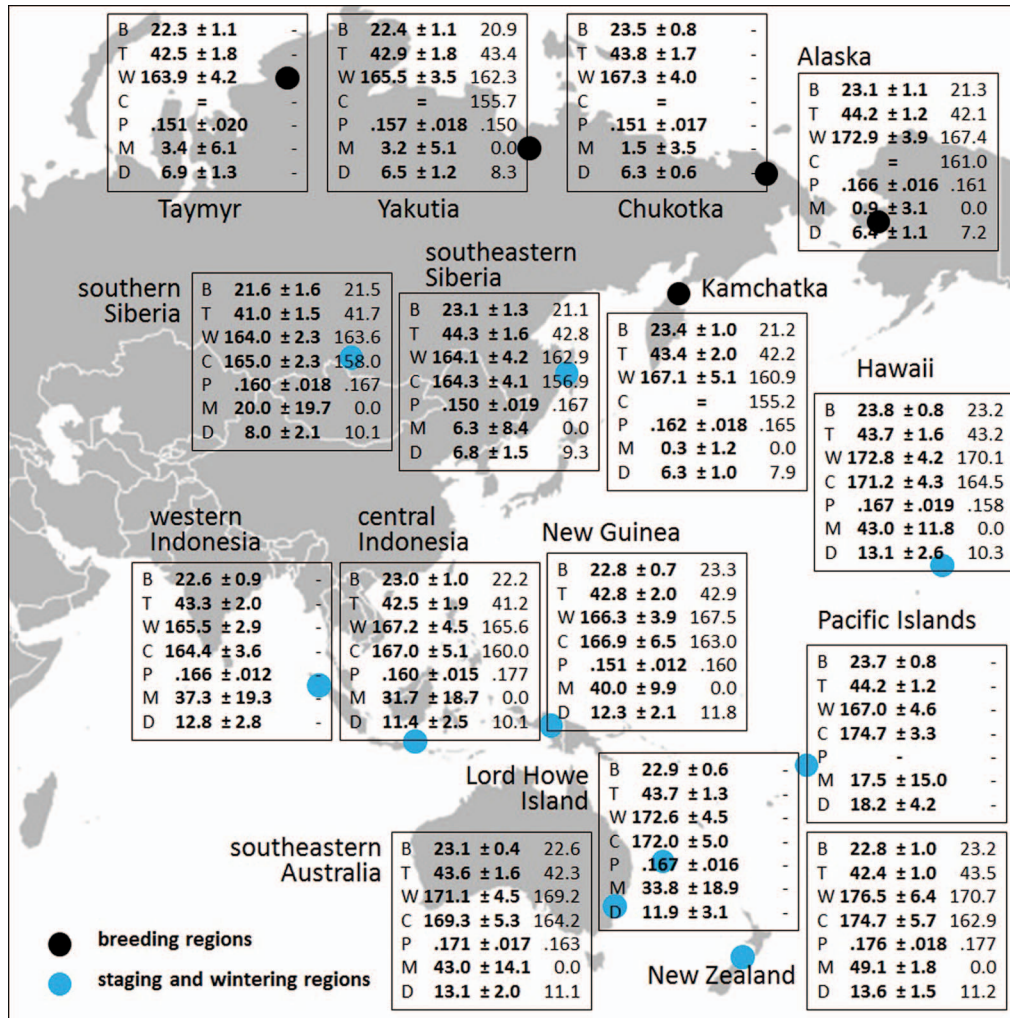
Taymyr
B	22.3 ±1.1	-
T	42.5 ±1.8	-
W	163.9 ±4.2	-
C	=	-
P	.151 ±.020	-
M	3.4 ±6.1	-
D	6.9 ±1.3	-

Yakutia
B	22.4 ±1.1	20.9
T	42.9 ±1.8	43.4
W	165.5 ±3.5	162.3
C	=	155.7
P	.157 ±.018	.150
M	3.2 ±5.1	0.0
D	6.5 ±1.2	8.3

Chukotka
B	23.5 ±0.8	-
T	43.8 ±1.7	-
W	167.3 ±4.0	-
C	=	-
P	.151 ±.017	-
M	1.5 ±3.5	-
D	6.3 ±0.6	-

Alaska
B	23.1 ±1.1	21.3
T	44.2 ±1.2	42.1
W	172.9 ±3.9	167.4
C	=	161.0
P	.166 ±.016	.161
M	0.9 ±3.1	0.0
D	6.4 ±1.1	7.2

southern Siberia
B	21.6 ±1.6	21.5
T	41.0 ±1.5	41.7
W	164.0 ±2.3	163.6
C	165.0 ±2.3	158.0
P	.160 ±.018	.167
M	20.0 ±19.7	0.0
D	8.0 ±2.1	10.1

southeastern Siberia
B	23.1 ±1.3	21.1
T	44.3 ±1.6	42.8
W	164.1 ±4.2	162.9
C	164.3 ±4.1	156.9
P	.150 ±.019	.167
M	6.3 ±8.4	0.0
D	6.8 ±1.5	9.3

Kamchatka
B	23.4 ±1.0	21.2
T	43.4 ±2.0	42.2
W	167.1 ±5.1	160.9
C	=	155.2
P	.162 ±.018	.165
M	0.3 ±1.2	0.0
D	6.3 ±1.0	7.9

Hawaii
B	23.8 ±0.8	23.2
T	43.7 ±1.6	43.2
W	172.8 ±4.2	170.1
C	171.2 ±4.3	164.5
P	.167 ±.019	.158
M	43.0 ±11.8	0.0
D	13.1 ±2.6	10.3

western Indonesia
B	22.6 ±0.9	-
T	43.3 ±2.0	-
W	165.5 ±2.9	-
C	164.4 ±3.6	-
P	.166 ±.012	-
M	37.3 ±19.3	-
D	12.8 ±2.8	-

central Indonesia
B	23.0 ±1.0	22.2
T	42.5 ±1.9	41.2
W	167.2 ±4.5	165.6
C	167.0 ±5.1	160.0
P	.160 ±.015	.177
M	31.7 ±18.7	0.0
D	11.4 ±2.5	10.1

New Guinea
B	22.8 ±0.7	23.3
T	42.8 ±2.0	42.9
W	166.3 ±3.9	167.5
C	166.9 ±6.5	163.0
P	.151 ±.012	.160
M	40.0 ±9.9	0.0
D	12.3 ±2.1	11.8

Pacific Islands
B	23.7 ±0.8	-
T	44.2 ±1.2	-
W	167.0 ±4.6	-
C	174.7 ±3.3	-
P	-	-
M	17.5 ±15.0	-
D	18.2 ±4.2	-

Lord Howe Island
B	22.9 ±0.6	-
T	43.7 ±1.3	-
W	172.6 ±4.5	-
C	172.0 ±5.0	-
P	.167 ±.016	-
M	33.8 ±18.9	-
D	11.9 ±3.1	-

southeastern Australia
B	23.1 ±0.4	22.6
T	43.6 ±1.6	42.3
W	171.1 ±4.5	169.2
C	169.3 ±5.3	164.2
P	.171 ±.017	.163
M	43.0 ±14.1	0.0
D	13.1 ±2.0	11.1

New Zealand
B	22.8 ±1.0	23.2
T	42.4 ±1.0	43.5
W	176.5 ±6.4	170.7
C	174.7 ±5.7	162.9
P	.176 ±.018	.177
M	49.1 ±1.8	0.0
D	13.6 ±1.5	11.2

● breeding regions
● staging and wintering regions

FIGURE 3. Averages and SD per region of bill length (B: mm), tarsus length (T: mm), wing length (W: mm), corrected wing length (C: mm = breeding area), wing pointedness (P), primary molt completion (M), and dates (D: May = 5, January = 13, etc.) for skins of adult Pacific Golden-Plovers (>1 yr old, in bold) and averages for skins of juveniles (≤1 yr old, not in bold). For definitions, see text. Averages were calculated only when data from ≥5 skins were available.

length (W), an index **P** for wing pointedness (see below), an index **M** for primary molt completion (see below), and time–date (D; see below).

We developed our own index **P** of wing pointedness on the basis of 4 measures that had been taken (the distances between primary tips P10–P9, P10–P8, P10–P7, and P10–P6). Pointed wings should have large values, especially between the outermost primary tips P10–P9, and less pronounced between following primary tips. For that reason we added measure P10–P9 to the average distances between adjacent tips calculated from P10–P8, P10–P7, and P10–P6. To account for structural size (large wings should have large distances between primary tips), the summation was divided by wing length. Thus:

$$P = [(P10 - P9) + (P10 - P8)/2 + (P10 - P7)/3 + (P10 - P6)/4]/W$$

Index **M** on primary molt completion was obtained by adding the molt scores of the 10 primaries (minimum = 0, maximum = 50). Time–date (D) when the skins were collected had to reflect calendar month and whether the bird stayed an extra season in the wintering area. It was scored by the month's number for birds collected in the breeding areas (May = 5, June = 6, etc.), for those collected in the staging and wintering areas (August = 8 to December = 12, January = 13, etc.), and for those that stayed there during the summer (May = 17 to September = 21).

As the tips of the primaries wear away, wing length shortens during the intermolt period. The degree of shortening varies widely, with a report of 0.09% mo^{-1} in the Dutch Wadden Sea (Engelmoer 2008) and a report of 0.4% mo^{-1} in the Wash in eastern England (Pienkowski and Minton 1973). The latter estimate appeared to best fit our data when wing lengths of wintering versus breeding birds (likely the same populations, based on migration routes) were compared. Therefore, we applied a correction of 0.4% mo^{-1} (Pienskowski and Minton 1973) to convert all measurements from the staging and wintering areas to wing length in the breeding area on July 1, before primary molt started (**C**). For skins of adults with new outer primaries, corrected wing length was calculated as

$$W_b = W_m \times [1 - (f \times 0.004)]$$

in which W_b is expected wing length in the breeding area, W_m is measured wing length, and f is the number of months up to the *forthcoming* July 1. This formula was also used for wintering juveniles (≤ 1 yr old), because their first large flight-feather molt starts in their second summer (e.g., Jukema et al. 2013).

For skins of adults with old outer primaries, corrected wing length was calculated as

$$W_b = W_m \times [1 + (p \times 0.004)]$$

in which W_b is expected wing length in the breeding area, W_m is measured wing length, and p is the number of months since the *previous* July 1.

Statistics

For all comparisons of skins between the 5 breeding areas, and between all 15 areas that were distinguished, we first applied single-factor analysis of variance (ANOVA), followed by Games-Howell tests between separate groups, because sample sizes differed considerably (Zaiontz 2014). We used t-tests to compare wing lengths of live birds from Taymyr, Mongolia, and Alaska.

RESULTS

Breeding Areas

The geographic distribution (Figure 3) of bill lengths in museum specimens of adults was nonrandom (single-factor ANOVA, $F_{4,118} = 5.48$, $P < 0.001$). Bills from Taymyr and Yakutia birds were significantly shorter than bills from Chukotka and Kamchatka birds (Games-Howell tests, $P < 0.05$). Bills of Alaskan breeding birds did not differ significantly from those of any other area. Also, tarsus-length distribution in skins of adults was nonrandom

(single-factor ANOVA, $F_{4,115} = 4.73$, $P = 0.001$), tarsus lengths from Taymyr and Yakutia being significantly smaller than those from Alaska (Games-Howell tests, $P < 0.05$). Tarsus lengths from Chukotka and Kamchatka did not differ significantly from the tarsi in other areas. Wing-length distribution in skins of adults was highly nonrandom (single-factor ANOVA, $F_{4,117} = 23.32$, $P < 0.001$), wings from Taymyr, Yakutia, Chukotka, and Kamchatka being significantly shorter than those from Alaska (Games-Howell tests, $P < 0.05$). Overall, 81% of the wings from Siberia (skins) were <170 mm, whereas 87% of those from Alaska were ≥ 170 mm.

Table 1 gives the averages of the 5 wing-pointedness measures. The distributions of almost all were nonrandom (single-factor ANOVAs). Only differences in index **P** were compared by subsequent Games-Howell tests ($P < 0.05$). Wings from Alaska were significantly more pointed than those from Taymyr. None of the other pairwise comparisons appeared to be significant. Distribution of primary molt scores in skins of adults was nonrandom (single-factor ANOVA, $F_{4,119} = 2.56$, $P = 0.042$), but none of the pairwise comparisons showed significant differences (Games-Howell tests, all $P > 0.05$). However, Siberian birds (all 4 areas combined) showed more advanced primary molt than the birds from Alaska (t-test, $t = 2.01$, df = 122, $P = 0.046$).

The data on wing length of birds captured alive on western and eastern breeding grounds were in agreement with the skin measurements. Average wing length in live adults from Taymyr was 168.8 mm (SD = 4.7, $n = 21$); from Alaska, 175.4 mm (SD = 4.4, $n = 34$); and from Mongolia, 169.7 mm (SD = 4.1, $n = 272$). The difference between Taymyr and Alaska was highly significant (t-test, $t = 4.96$, df = 53, $P < 0.001$). The difference between Mongolia and Alaska was also highly significant (t-test, $t = 5.82$, df = 304, $P < 0.001$), but that between Mongolia and Taymyr was not (t-test, $t = 0.89$, df = 291, $P = 0.38$). Wings from Mongolia were expected to become ~0.5% shorter by wear upon arrival in the breeding area; with this correction, their wing lengths are identical to those from Taymyr but diverge even more from those of Alaska birds. Overall, 76% of the wings from Taymyr (live birds) were <173 mm, whereas 76% of those from Alaska were ≥ 173 mm; 83% of the wings from Mongolia were <173 mm (after correction).

Wintering and Staging Areas

Distribution of bill length in museum specimens of adults was nonrandom (single-factor ANOVA, $F_{9,247} = 7.33$, $P < 0.001$); the longest bills were from Hawaii (Games-Howell tests, $P < 0.05$). Tarsus-length distribution in skins of adults was nonrandom (single-factor ANOVA, $F_{9,209} = 5.67$, $P < 0.001$). Tarsus lengths were largest from the Pacific Islands and shortest from southern Siberia (Table 2;

TABLE 1. Wing-pointedness measures (and index **P**; see text) taken from skins of adult Pacific Golden-Plovers from the different breeding regions.

Averages in mm ($\pm$ SD)	n	P10–P9	P10–P8	P10–P7	P10–P6	Index **P**
Taymyr (+ Jamal and Gydan)	22	2.8 (1.1)	11.6 (2.8)	22.3 (3.6)	34.7 (2.4)	0.151
Yakutia	22	3.5 (1.6)	12.0 (1.7)	23.2 (1.9)	35.0 (2.4)	0.157
Chukotka (+ Wrangel Island)	15	3.1 (1.4)	11.8 (1.9)	23.1 (1.9)	34.7 (2.2)	0.151
Kamchatka	14	3.6 (1.7)	12.8 (2.2)	24.3 (2.4)	36.6 (2.5)	0.162
Alaska	40	3.9 (1.2)	13.5 (1.3)	25.7 (3.5)	38.0 (1.9)	0.166
Single-factor ANOVA		$F_{4,108} = 2.46$	$F_{4,108} = 4.55$	$F_{4,108} = 5.54$	$F_{4,108} = 11.70$	$F_{4,108} = 3.34$
P		0.07	0.002	<0.001	<0.001	0.013

Games-Howell tests, $P < 0.05$). Corrected wing-length distribution in skins of adults was highly nonrandom (single-factor ANOVA, $F_{9,235} = 15.71$, $P < 0.001$). Wing lengths from Hawaii, Pacific Islands, Lord Howe Island, and New Zealand were significantly larger than those from other areas; wing lengths from southern and southeastern Siberia and western and central Indonesia were significantly smaller than those from other areas (Games-Howell tests, $P < 0.05$; Table 3).

Distributions of wing-pointedness measures in skins of adults were, in most cases, nonrandom (single-factor ANOVAs, P10–P9: $F_{8,155} = 1.63$, $P = 0.12$; P10–P8: $F_{8,155} = 3.36$, $P = 0.001$; P10–P7: $F_{8,154} = 5.73$, $P < 0.001$; P10–P6: $F_{8,151} = 10.24$, $P < 0.001$; index **P**: $F_{8,151} = 2.99$, $P = 0.004$). Index **P** was largest in birds from New Zealand and southeastern Australia, and smallest in birds from southeastern Siberia and New Guinea, but the differences between the wintering areas were not significant in pairwise comparisons (Games-Howell tests, $P < 0.05$). Distributions of primary molt scores in adults were highly dissimilar (single-factor ANOVA, $F_{9,256} = 13.03$, $P < 0.001$). Birds from southeastern Siberia had significantly lower scores than those from several other areas, whereas birds from New Zealand, southeastern Australia, Lord Howe Island, and Hawaii had significantly higher scores (Games-Howell tests, $P < 0.05$). The same trends were found in the proportions of adult birds that had not yet started, had begun, were proceeding with, had suspended, had resumed, or had completed primary molt.

DISCUSSION

We found strong heterogeneity across the breeding and wintering ranges of Pacific Golden-Plovers, as have other studies on their geographic morphological variation (Byrkjedal and Thompson 1998, Johnson and Johnson 2004). The question we would like to pose here is whether the trends from west to east are continuous or discontinuous and, if the latter, where any such discontinuity is geographically situated. Because all our measurements were made by only one experienced observer, the present study is better suited to solve these questions than earlier studies that were based on measurements by many observers and whose results thus included an extra source of variation.

Differential Migration and Wintering Ranges

Uncorrected wing length in skins from the Pacific Islands (Fiji and Niue) was in the same range as that in skins from Siberia and Indonesia—and not, as expected on the basis of known migration patterns (Johnson et al. 2012), the same as in skins from Alaska. This anomaly is attributable to the

TABLE 2. Results of Games-Howell tests ($P < 0.05$) between wintering and staging areas on tarsus-length distribution in adult Pacific Golden-Plovers (single-factor ANOVA, $F_{9,209} = 5.67$, $P < 0.001$). Abbreviations: SS = southern Siberia, SES = southeastern Siberia, WI = western Indonesia, CI = central Indonesia, NG = New Guinea, HA = Hawaii, PI = Pacific Islands, LH = Lord Howe Island, SA = southeastern Australia, and NZ = New Zealand. Symbols: * same area; + value for column region significantly larger than for row region; − value for column region significantly smaller than for row region.

	SS	SES	WI	CI	NG	HA	PI	LH	SA	NZ
SS	*					+	+	+	+	
SES		*								
WI			*							
CI				*			+			
NG					*					
HA	−					*				
PI	−			−			*			−
LH	−							*		
SA	−								*	
NZ							+			*

TABLE 3. Results of Games-Howell tests ($P < 0.05$) between wintering and staging areas on corrected wing-length distribution in adult Pacific Golden-Plovers (single-factor ANOVA, $F_{9,235} = 15.71$, $P < 0.001$). For abbreviations and symbols, see Table 2.

	SS	SES	WI	CI	NG	HA	PI	LH	SA	NZ
SS	*					+	+	+		+
SES		*				+	+	+		+
WI			*			+	+	+		+
CI				*		+	+	+		+
NG					*					
HA	−	−	−	−		*				
PI	−	−	−	−			*			
LH	−	−	−	−				*		
SA									*	
NZ	−	−	−	−						*

fact that all the skins from Fiji and Niue were collected during a small number of expeditions between June and September in 1971–1974 (Kinsky and Yaldwyn 1981); no skins from the winter months were available. The sample included mostly young "over-summering" individuals (1–2 yr old, $n = 26$) with short wings ($\bar{x} = 165.7$ mm; corrected: 174.6 mm) and a few, probably older, individuals ($n = 5$) with longer wings ($\bar{x} = 173.6$ mm; corrected: 175.3 mm) that had just returned from their breeding area. Apparently, as noted by Johnson and Johnson (1983), Pacific Golden-Plovers that stay on the equatorial Pacific Islands during the summer show excessive primary wear, probably due to heavy sun radiation.

Pacific Golden-Plovers that were measured by Johnston and McFarlane (1967) at Wake Island (see Figure 2) also had shorter wings (wing chord = 163 mm) than those from Alaska. Wing chord measurements are shorter ($\sim$5 mm) than those on flattened wings such as we used. However, this difference is too small for them even to approach our Alaskan data ($\bar{x} = 175.4$ mm in live birds). In addition, the birds from Wake Island were all captured in autumn, winter, or early spring. Thus, over-summering could not be the reason in this case. Most probably, Wake Island is a wintering area for Siberian populations. A closer inspection of the data from New Guinea also confirms conformity with the Siberian populations. Australia seems to be visited by Pacific Golden-Plovers both from Siberia (in northwestern Australia) and from Alaska (in southeastern Australia). Nebel et al. (2013) reported that wing lengths in the former group ($\bar{x} = 168.7$ mm, $n = 12$) were smaller than those in the latter ($\bar{x} = 173.5$ mm, $n = 36$). C. Minton, H. Sitters, and M. Remisiewicz (personal communication), using a larger sample, confirmed that wing lengths of Pacific Golden-Plovers captured in northwestern Australia ($\bar{x} = 165.3$ mm, $n = 21$) were consistent with the Siberian populations, whereas those from southeastern Australia ($\bar{x} = 172.0$ mm, $P = 0.024$, $n = 151$) were consistent with the populations from Alaska. The differences in both cases were significant (t-test, $t = 2.42$, df = 23, $P = 0.024$).

In addition, primary molt schedules (C. Minton et al. personal communication) in individuals captured in northwestern Australia ($n = 16$) appeared to run ahead of those captured in southeastern Australia ($n = 153$), in line with the differences between other wintering Pacific Golden-Plovers from Siberia and Alaska.

The long wings that were distinctive for the breeding populations from Alaska were found in various wintering areas, including Hawaii, Pacific Islands (after correction), southeastern Australia (including Lord Howe Island), and New Zealand. This is consistent with recent findings that show these birds to belong to the same populations. By fitting Pacific Golden-Plovers with VHF transmitters and geolocators (Johnson et al. 1997, 2001, 2011, 2012), it has been established that breeding birds from Alaska winter on Hawaii and other Pacific islands. Birds wintering on Hawaii could be traced as early-breeding birds in southern Alaska, whereas those wintering on most other Pacific islands were later-breeding birds in northwestern Alaska (O. W. Johnson personal communication). On the basis of wing-length measurements in live Pacific Golden-Plovers captured in Australia (Barter 1988), the connection between Alaska and southeastern Australia could be made. Geolocator studies (Johnson et al. 2012) confirmed that at least some birds from northwestern Alaska winter in Australia (Fraser Island; see Figure 2). Similar connectivity with New Zealand seems likely but has not been demonstrated. Geolocator studies (Johnson et al. 2012) have clearly shown that breeding Pacific Golden-Plovers from northern Alaska winter on American Samoa, Fiji, Gilbert Islands, and Marshall Islands (see Figure 2). These studies also showed that wintering Pacific Golden-Plovers on American Samoa breed in northern Alaska. By contrast, wintering Pacific Golden-Plovers from Saipan (Mariana Islands; see Figure 2) probably breed mainly in eastern Siberia (Johnson et al. 2012), as do those on Wake Island (see above). Three individuals from Kwajalein (Marshall Islands) have even been detected flying to eastern Chukotka, and 6 others went to northern Alaska (O. W. Johnson personal communication).

Thus, our data on wing length, combined with data from other studies, strongly suggest that Pacific Golden-Plovers from Alaska have their wintering areas in Hawaii, most of the Pacific Islands, eastern Australia, and New Zealand. Some islands in the western Pacific (New Guinea, Mariana Islands, and Wake Island), however, are visited by birds from Siberia during the winter. As had been assumed, western and central Indonesia and central and eastern Asia accommodate Siberian birds too.

Geographic Variation on the Breeding Grounds

On the basis of the molt patterns of the secondary flight feathers, Jukema et al. (2013) concluded that Pacific Golden-Plovers from Alaska differ fundamentally from those that were studied on Taymyr. From the age of 2 yr, birds from Alaska molt all their secondaries every year, whereas birds from Taymyr molt only half of them. In addition, almost all birds from Alaska start their large flight-feather molt in the wintering area (Kinsky and Yaldwyn 1981, Connors 1983, Johnson and Johnson 1983, Barter 1988, Johnson et al. 2011, 2012), whereas many individuals from Siberia (best documented for Taymyr) start the large flight-feather molt in the breeding area (Tulp et al. 1997, 2000, Byrkjedal and Thompson 1998, Tulp and Schekkerman 2001, P. Tomkovich personal communication). It has been proposed that this is functionally associated with their migration patterns: Birds from Alaska make very long, nonstop flights to their wintering areas on Hawaii and the Pacific Islands (Johnson et al. 2001, 2011, 2012, Johnson and Connors 2010a, 2010b, Jukema et al. 2013), whereas birds from Siberia are supposed to migrate more slowly to the wintering areas in southeastern Asia. The present study confirms that many Siberian Pacific Golden-Plovers start primary molt in their breeding areas, whereas those from Alaska rarely do so, although the latter tend to breed earlier (see below).

Our data on skins (and supported by the comparisons with live birds) show that the birds from Alaska and from Siberia are even more distinct. Despite their geographically widespread origin, the group of Siberian birds is relatively homogeneous. Birds from Alaska have longer and (to a lesser extent) more pointed wings, and longer legs. In various species of birds, differences in length and pointedness of wings have also been associated with migration pattern (Pérez-Tris and Tellería 2001, Fernández and Lank 2007, Kaboli et al. 2007, Jukema et al. 2013), long and pointed wings being most common among species or populations making the longest flights.

We thus propose that there are good reasons to distinguish the Alaskan breeding population from the Siberian population, and we suggest that the differences between these 2 types are maintained by reproductive isolation. The Bering Strait itself ($\geq$82 km open water) cannot act as an effective barrier between 2 types that are capable of making long flights. However, climatic differences between the 2 sides of the Bering Strait enable Pacific Golden-Plovers from Alaska to start their breeding cycle 3–4 wk earlier than those from northeastern Siberia (Byrkjedal and Thompson 1998). Because of this, synchronization of breeding might be difficult between members of the 2 types.

Conclusion: Two Flyway Populations

As in an earlier comparison between the different tundra plover species (Jukema et al. 2013), wing length, molt patterns, and probably wing pointedness may be considered adaptations to long, nonstop flights during migration. Pacific Golden-Plovers from the Alaskan populations (probably including birds from eastern Chukotka) have to make such flights, possess long and pointed wings, and have a complete molt of the flight feathers, whereas most of those from Siberia do not have to make such exhausting flights, possess shorter wings, and have a less complete flight feather molt.

The differences between Alaskan and Siberian Pacific Golden-Plovers reflect a clear discontinuity, probably maintained by reproductive isolation. We therefore propose that the international conservation community, in conservation assessments (e.g., Delany and Scott 2006), treat the Alaskan and Siberian breeding birds as distinct flyway populations. We also propose distinguishing them as subspecies that differ in wing measurements. The type specimen for *Pluvialis fulva* (collected on Tahiti in 1773 by J. R. Forster during Captain Cook's second voyage, described by J. F. Gmelin) has been lost (Johnson 1993), so we cannot compare its wing measurements with those of the skins we studied. However, Tahiti should be regarded as a wintering site for Alaskan Pacific Golden-Plovers only. Therefore, the Alaskan populations are compatible with the holotype (the subspecies name should be *Pluvialis fulva fulva*), and the Siberian populations represent a new subspecies. We suggest the name *Pluvialis fulva johnsoni* in honor of two long-term students of the species, Oscar W. and Patricia Johnson.

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Supplemental Material Appendix. All raw data and the frequencies, averages, and standard deviations per region from our comparisons of Pacific Golden-Plover skins from the 15 geographic regions in the study. Averages and indices were calculated separately for adults (Ad) and juveniles (Juv). Available at doi:10.1642/AUK-14-303.1.s1