New insight concerning transoceanic migratory pathways of Pacific Golden-Plovers (*Pluvialis fulva*): the Japan stopover and other linkages as revealed by geolocators

Oscar W. Johnson[1], Lauren Fielding[2], Joshua P. Fisher[3], Roger S. Gold[2], Roger H. Goodwill[2], Andrea E. Bruner[2], John F. Furey[4], Paul A. Brusseau[5], Nancy H. Brusseau[5], Patricia M. Johnson[1], Joop Jukema[6], Laura L. Prince[2], Mollika J. Tenney[2] & James W. Fox[7]

[1] Dept. of Ecology, Montana State Univ., Bozeman, MT 59717 USA. owjohnson2105@aol.com
[2] Dept. of Biology, BYU-Hawaii, Laie, HI 96762 USA
[3] U.S. Fish and Wildlife Service, 300 Ala Moana Blvd., Honolulu, HI 96850 USA
[4] P.O. Box 502316, Saipan, MP, 96950 USA
[5] P.O. Box 142375, Anchorage, AK 99514 USA
[6] Haerdawei 62, 8854 AC, Oosterbierum, The Netherlands
[7] Migrate Technology Ltd., Box 749, Coton, Cambridge CB1 0QY, UK

Johnson, O.W., Fielding, L., Fisher, J.P., Gold, R.S., Goodwill, R.H., Bruner, A.E., Furey, J.F., Brusseau, P.A., Brusseau, N.H., Johnson, P.M., Jukema, J., Prince, L.L., Tenney, M.J. & Fox, J.W. 2012. New insight concerning transoceanic migratory pathways of Pacific Golden-Plovers (*Pluvialis fulva*): the Japan stopover and other linkages as revealed by geolocators. *Wader Study Group Bull.* 119(1): 1–8.

Keywords: Pacific Golden-Plover, *Pluvialis fulva*, geolocator, data logger, migration, migratory pathways, connectivity, ground speed, flight time, stopovers, rice fields, non-breeding grounds, breeding grounds, mid-Pacific Flyway, East Asian-Australasian Flyway

We used light level archival geolocators (data loggers) to track annual migrations of Pacific Golden-Plovers *Pluvialis fulva* at non-breeding grounds on American Samoa and Saipan, and at nesting grounds near Nome in W Alaska.

Among wintering birds, we deployed loggers in spring 2010 and recovered them during the 2010–2011 non-breeding season when the site-faithful birds had returned; deployment on breeding birds was in summer 2009 and 2010, logger recovery in each group was one year later when the plovers were again nesting.

Logger archives from American Samoa and Nome birds revealed a clockwise, circular transoceanic pattern (previously unknown in this species) consisting of three lengthy movements: 1. southward from Alaska in autumn via the mid-Pacific Flyway (American Samoa birds wintered at the same sites where they had been captured, Nome birds wintered variously at Christmas Island, Marshall Islands, Gilbert Islands, Fiji, and Fraser Is., Queensland); 2. in spring, the plovers traveled north-westward to Japan (the track from Fraser Is. was via Taiwan) where they made stopovers averaging about three weeks; 3. from Japan and Taiwan, the final segment was north-eastward to nesting grounds in Alaska.

Great circle distances along this annual clockwise journey varied with location of wintering grounds ranging from about 16,000 to 26,700 km. Flights on each of the three segments appeared to be mostly nonstop at estimated mean ground speeds of 59–78 kph over periods of about 3–8 days. Three individuals made transoceanic passages at apparent record-setting ground speeds in excess of 100 kph.

In spring, the Saipan birds followed the East Asian-Australasian Flyway with stopovers in Japan and elsewhere in Asia before arriving at nest sites in Chukotka and Kamchatka. Two Saipan birds made long over-water flights from Japan to W Alaska. One of them traveled from the Seward Peninsula to Chukotka and nested there. Where the other bird nested is uncertain because its geolocator failed. In fall, the individual that had reached Chukotka via Alaska backtracked and made a flight from Alaska across the western Pacific to Saipan. The other Saipan birds returned via mainland Asia and Japan.

Our findings indicate that Japan is a key stopover (especially in spring when plovers from widely separated areas of the winter range converge there), and demonstrate that Alaska hosts a breeding population of Pacific Golden-Plovers comprised of birds from most if not all of the Pacific winter range.

INTRODUCTION

The non-breeding range of the Pacific Golden-Plover *Pluvialis fulva* covers a vast area of the world southward from the Hawaiian Islands and S Japan, across the insular Pacific to Australia and New Zealand, westward to India and NE Africa (Hayman *et al.* 1986, Johnson & Connors 2010). With the exception of Hawaii, little was known concerning the migratory strategies and stopover requirements of plovers in this immense geographic region.

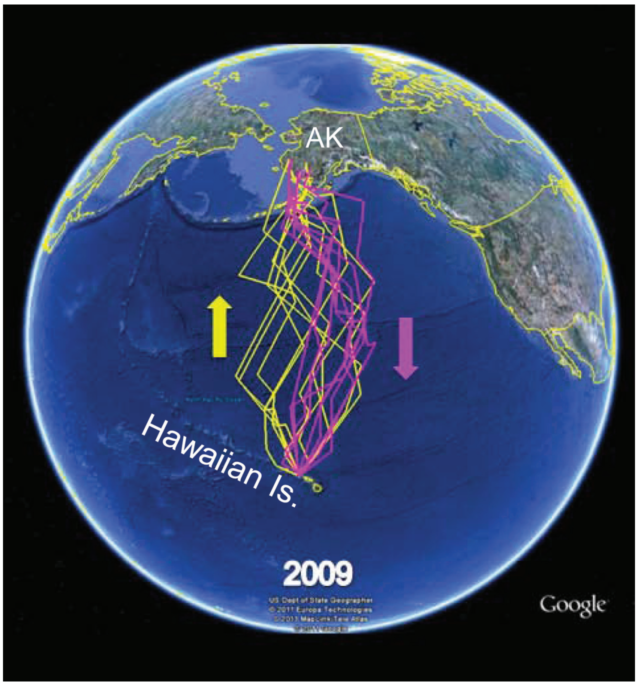

Fig. 1. Geolocator tracks of Pacific Golden-Plovers migrating along the linear pathway between Oahu and Alaska in 2009. Another sample group showed a similar pattern in 2010 (from Johnson *et al.* 2011).

Previous geolocator studies by Johnson *et al.* (2011) had tracked the annual migrations of plovers wintering on Oahu, Hawaiian Islands at the northern end of the species' non-breeding range. From this location, the migratory route was relatively simple being a direct north–south linear pathway with nonstop flights of approximately 4,800 km between Oahu and Alaska (Fig. 1). We surmised that movements in distant regions far beyond Hawaii were likely to be more complicated, and postulated that the migratory pattern of Ruddy Turnstones *Arenaria interpres* as defined many years ago in banding studies by Max Thompson might also apply to Pacific Golden-Plovers. Thompson (1973) showed that the annual migration of turnstones wintering in the central Pacific followed a circular pattern: south in fall via a mid-Pacific path to non-breeding grounds, westward to Japan in spring, thence northward to breeding grounds.

To explore the possibility of similar movements by Pacific Golden-Plovers, we used archival light level geolocators deployed on non-breeding grounds at American Samoa about 4,200 km south of the Hawaiian Islands, and on nesting grounds in W Alaska. These birds revealed that plovers wintering at various sites to the south and south-west of Hawaii follow an annual circular route with spring stopovers in Japan, a pattern that is essentially identical to that of turnstones. Additional evidence of linkage with Japan came from two plovers banded at Saipan that were observed in rice fields on Honshu (one bird in fall, the other in spring; Johnson *et al.* 2006, Johnson *et al.* unpubl. data). These sightings suggested that plovers wintering in the Mariana Islands migrate along the Asian coast via Japan, thus bypassing well-known shorebird stopover sites in the Yellow Sea region (see Johnson *et al.* 2006). To further assess this pathway, we deployed geolocators on wintering plovers at Saipan. Their tracks confirmed the Japan stopover, and revealed two routes from Japan, one northward to nesting grounds in the Siberian Far East, the other north-eastward to Alaska. In addition to the Japan connection, all three groups of logger-carrying plovers demonstrated other linkages between breeding and non-breeding grounds that were heretofore unknown.

The findings detailed in this paper significantly expand previous knowledge of the transpacific pathways followed by this plover, and provide information of fundamental importance from the conservation perspective.

METHODS

This investigation involved three sample groups of plovers: two on the non-breeding range at American Samoa and Saipan, the third on nesting grounds near Nome, Alaska. At American Samoa and Saipan we deployed geolocators in spring (pre-migration), then recaptured the birds for removal of loggers during the subsequent non-breeding period; at Nome deployment was in June, followed by recapture a year later when the birds were again nesting. Locations of the study sites, numbers of geolocators deployed and recovered, and relevant dates are summarized in Table 1.

The selection of individuals on which to deploy loggers differed by season. On non-breeding grounds, both sexes are equally site faithful and returning individuals typically reclaim their previous wintering territories in autumn, whereas on breeding grounds females generally disperse between years while males remain strongly faithful to the same nesting locations (Johnson *et al.* 2001a,b, Johnson & Connors 2010, OWJ unpubl. data). Thus, among wintering birds we attached loggers to both sexes, and at Nome we selectively deployed loggers on males only. Since geolocators must be retrieved in order to recover archived data, the foregoing behavioral characteristics of this plover are particularly well suited for logger-based studies. On wintering grounds, plovers were captured and recaptured with mist nets and/or the "Super Talon" net-gun (see Edwards & Gilchrist 2011, Johnson *et al.* 2011); on breeding grounds birds were caught with a self-triggering nest trap patterned after the "luchock" (hoop) design (Priklonsky 1960).

We used model Mk-10b archival geolocators manufactured by the British Antarctic Survey. This device records light levels every five minutes from which daily sunrise/sunset times can be determined and latitude/longitude calculated. The logger also records potential contact with seawater. We affixed the loggers to leg bands (see Johnson *et al.* 2011 for description and photograph), and the entire composite ranged from 1.8 to 2.0 g, roughly 1% of average mass at migration

Table 1. Sample groups of geolocator-equipped Pacific Golden-Plovers.

Study sites	No. of birds	Deployment	No. recaptured	Recapture period
American Samoa (Tutuila Island) 14.30° S, 170.73° W	19 (10 m, 9 f)	17–19 March 2010	10 (6 m, 4 f)	28 Aug–10 Sept 2010
Saipan, Mariana Islands 15.17° N, 145.75° E	15 (7 m, 8 f)	5–9 April 2010	6 (3 m, 3 f)	6 Dec 10–2 April 2011
Nome, Alaska 64.60° N, 165.50° W	15 males 3 males	15–25 June 2009 22 June 2010	6 2	12–23 June 2010 20 June 2011

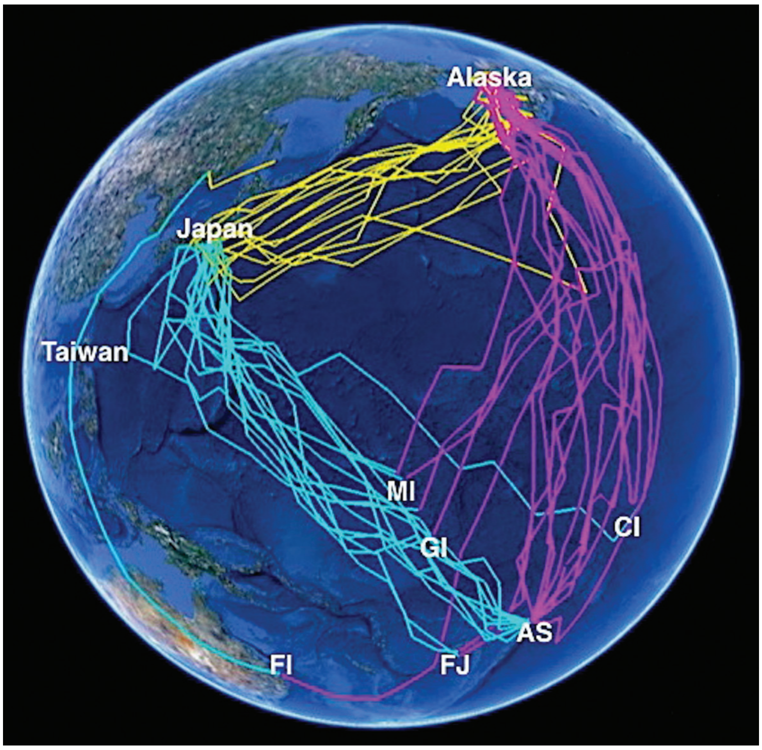

Fig. 2. Migratory tracks of Pacific Golden-Plovers that were captured and logger-equipped on wintering grounds at American Samoa and on nesting grounds near Nome, Alaska. The clockwise pattern of annual migration was the same for all birds: southward (purple) in fall to wintering grounds, westward (blue) in spring to stopovers in Japan, north-eastward (yellow) in spring from Japan to nesting grounds. Variable headings and lengths of 12-hr flight legs, likely caused by shifting winds and other weather factors, produce the angular irregularities evident in the tracks. Predictably, the fall tracks of American Samoa birds (n = 9) converge at Tutuila Is. and clearly demonstrate wintering ground fidelity. The fall migrations of Nome birds (n = 8) led to various wintering destinations: Christmas Is. (CI, 1 bird), Fiji (FJ, 2 birds), Gilbert Is. (GI, 1 bird), Marshall Is. (MI, 3 birds), Fraser Is. (FI, 1 bird). The probable sites within archipelagos where Nome birds actually wintered were: Fiji (Vitu Levu Is. and Kadavu Is.), Gilbert Is. (Tarawa Atoll), Marshall Is. (Mili Atoll, Kwajalein Atoll, and Erikub Atoll). Annual distances traveled by individuals varied according to wintering ground location. The longest journey (about 26,700 km) was made by the Nome bird that wintered at Fraser Is. and migrated to Alaska via Taiwan, distances for the other birds in the figure ranged from approximately 16,000 to 24,000 km.

(Johnson & Connors 2010). Our procedures for deployment of geolocators on plovers, the recovery and removal of the units post-migrations, and the analyses of data archived by the loggers (with BasTrak software provided by British Antarctic Survey) were detailed by Johnson *et al.* (2011).

The site of logger deployment was, of course, known for each individual. For other key sites (stopovers, nesting locations for American Samoa and Saipan birds, wintering locations for Nome birds) BasTrak produced clusters of points, and we consolidated each cluster into a single point representing the average geographic coordinates at that location. Based on positional error estimates that range from ±50 km to ±300 km in other shorebird studies (Conklin *et al.* 2010, Minton *et al.* 2010, 2011, Niles *et al.* 2010), we considered it reasonable to assume margins of error in the present study to be ±100 km for fixed locations (stopovers, nesting locations of American Samoa and Saipan birds, and wintering locations of Nome birds) and ±200 km for birds in flight during migrations. Notably, geolocators record longitude more accurately than latitude, and overall accuracy is best in un-shaded open habitats such as those represented in this study (Fox 2010, Fudickar *et al.* 2011). Using Google Earth, we plotted 12-hour flight legs as integrated from BasTrak output (the program assumes that each leg follows an orthodromic course), and produced individual maps showing fall and spring migratory tracks. On each track, we estimated the plover's ground speed from the distance it traversed during a consecutive series of 12-hr legs (the latter far enough offshore to ensure that the bird was in flight), and then applied that speed over the entire landfall-to-landfall track to estimate total flight hours (see Johnson *et al.* 2011). Depending on the bird and its route, the lengths of tracks measured for estimates of ground speeds varied from 4 legs (48 hours) to 13 legs (156 hours). We emphasize that the only precise geographic locations in this paper are the GPS coordinates where loggers were deployed. Given the positional error inherent to geolocator technology, other locations (nesting sites for American Samoa and Saipan birds, wintering sites of Nome birds, in-flight tracking coordinates and stopover sites for all birds) must be regarded as approximate.

RESULTS

Geolocator recoveries

Of the 24 loggers retrieved (Table 1), one had been carried by a Saipan bird that did not migrate (i.e., the plover over-summered), one had failed completely (on an American Samoa bird), and three contained only partial records (i.e., recording stopped during migrations). Two of the latter (both carried by Nome birds) ceased recording in spring, one at a stopover in Japan, the other while the plover was in flight near Sakhalin Island; the third (carried by a Saipan bird) stopped shortly after arrival on breeding grounds in Alaska. Thus, we secured archival data from 22 birds consisting of 19 round-trip records and 3 partial records. These data defined routes of annual spring and fall migrations, the nesting destinations of American Samoa and Saipan birds, and the wintering sites of Nome birds.

Migratory patterns and seawater contacts

Geolocator tracks of the three sample groups as mapped on Google Earth are shown in Figs. 2 and 3. In spring, all plovers (except for a Nome bird that wintered at Fraser Is., Queensland), initially tracked to Japan where there were lengthy stopovers. From Japan, the American Samoa and Nome birds traveled north-eastward to Alaska and nested there. Two of the five Saipan birds followed the same north-eastward route to Alaska; the other three continued northward to nesting grounds in the Far Eastern Region of Siberia. Ultimately, one of the two Saipan plovers that had crossed over to Alaska flew westward and nested in Chukotka; where the other bird nested is uncertain (see below). The Fraser Is. bird returned to Alaska via the East Asian-Australasian Flyway with stopovers in Taiwan and SE Russia. In fall, the American Samoa birds returned to their previous wintering grounds via the mid-Pacific Flyway. Autumn migration of the Nome birds tracked southward in the mid-Pacific to wintering locations across a wide swath of the non-breeding range from

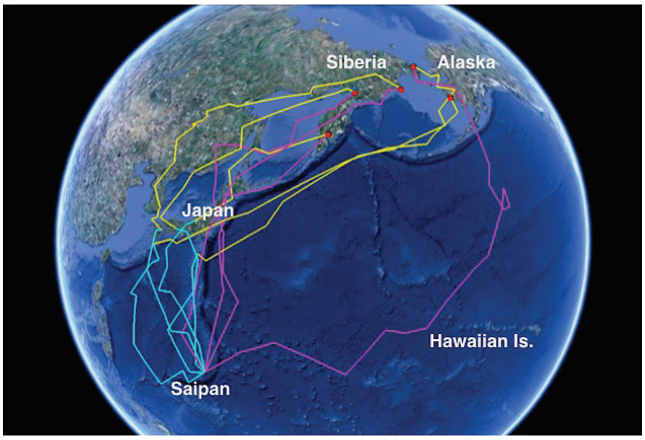

Fig. 3. Migratory tracks of Pacific Golden-Plovers that were captured and logger-equipped on wintering grounds at Saipan, Mariana Is. Color-coding is the same as indicated in Fig. 2. In spring, the birds followed the East Asian-Australasian Flyway to stopovers in Japan. From Japan, some birds continued on the same flyway northward to the Far East Region of Siberia, while others diverged north-eastward on a transoceanic flight to Alaska. Autumn routes were mostly similar to spring pathways. The migrant that reached Chukotka via Alaska (see text) returned to Alaska in fall and followed a lengthy transpacific route back to Saipan. The overall course of this individual's annual migrations resembled the circular pattern shown in Fig. 2. Red dots indicate nesting locations, the dot in Alaska is uncertain (see text).

Christmas Is., Kiribati to Queensland. The return pathways of the Saipan birds in fall were similar to their spring routes.

There were no seawater contacts during any of the transoceanic flights shown in Figs. 2 and 3. Of the entire sample from American Samoa, Saipan and Nome, the only contacts recorded were at spring stopovers (5 of 22 birds in Japan) and fall stopovers (6 of 21 birds in Alaska), overall suggesting that plovers were foraging mostly on inland habitats.

Timing of migrations and stopovers

Spring

Departures of American Samoa and Nome birds ($n = 16$) from Christmas Is., American Samoa, Fiji, Gilbert Islands, and Marshall Islands (Fig. 2) occurred over the period 6–27 Apr, with arrival in Japan from 14–29 Apr. The five Saipan birds departed from 21 Apr to 1 May, and arrived in Japan from 24 Apr to 9 May (Fig. 3). One geolocator failed when the plover (a Nome bird) arrived in Japan. For the remaining birds ($n = 20$), stopover duration in Japan averaged 22 days ±7 (range 2–33 days). Most stopovers were along the south-eastern coast of Honshu; others were in the Izu Islands extending southward from Honshu, and in the Osumi Islands at the southern end of Kyushu (Fig. 4). Because of close proximity between several of these islands and the coastlines of Honshu and Kyushu (50 km or less and within potential geolocator error, see Methods), actual stopover locations for some birds (whether island or mainland) are uncertain. For at least two birds (one each from Saipan and American Samoa) stopovers in the Izu Islands seem definite as their distances from Honshu were beyond probable margin of error at 270 km and 585 km, respectively (Fig. 4).

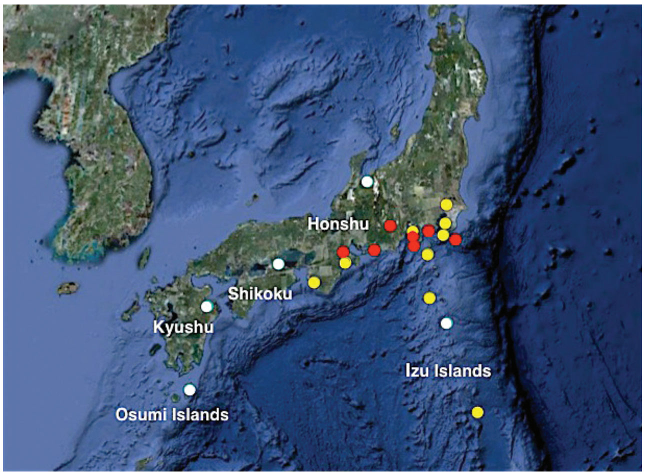

Fig. 4. The distribution of Pacific Golden-Plovers during spring stopovers in Japan. Yellow dots = American Samoa birds, red dots = Nome birds, white dots = Saipan birds.

Plovers bound for Alaska (American Samoa birds, Nome birds, and two Saipan birds; Figs. 2, 3) departed Japan 13–17 May, and arrived at nesting grounds 16–20 May. During the transoceanic flight from Japan to Alaska, tracking records hinted at a brief stop by one of the Saipan birds at Shemya Island (52.72° N, 174.11° E). Otherwise, all flights appeared to be nonstop. Of the two Saipan birds that reached Alaska, one made a 2–3 day northward passage through the Yukon-Kuskokwim Delta and the southern Seward Peninsula, it then crossed the Bering Strait to a nest site in NE Chukotka. The nesting destination of the other Saipan plover is uncertain as its geolocator failed three days after the bird arrived in Alaska (at Nelson Is. 60.64° N, 164.75° W). Three of the Saipan birds that nested in the Siberian Far East traveled northward from Japan (Fig. 3) and at least two of them made additional stopovers. One bird paused four times (in aggregate 13 days) in Ulsan Province, South Korea (35.50° N, 129.28° E), Jilin Province, NE China (42.89° N, 127.23° E), Amur Region, Russia (51.06° N, 128.00° E), and Magadan Region, Russia (59.98° N, 150.88° E); the second individual stopped near Vladivostok (42.85° N, 132.68° E) for 7 days. Saipan birds arrived at their nesting locations (Fig. 3) on 18 and 22 May (Kamchatka), and on 21 and 29 May (Chukotka).

The Nome bird (a male) that wintered at Fraser Island (25.30° S, 153.14° E) began spring migration on 29 Mar and followed the East Asian-Australasian Flyway (Fig. 2). He flew nonstop across interior Australia, thence west of the Philippine Islands, arriving in Taiwan on 3 Apr where he stopped at 23.58° N, 120.97° E and remained for 32 days. The bird's route after leaving Taiwan on 5 May included a 2-day stop in South Korea (37.19° N, 129.11° E), and an 8-day stop north of Vladivostok probably near Lake Khanka (44.50° N, 132.11° E). From there, he began an eastward flight toward Alaska on 19 May whereupon his geolocator failed as indicated by the short yellow track upper left in Fig. 2.

Autumn

After leaving nesting areas, birds typically traveled varying distances southward and stopped over before commencing transoceanic flights. In Alaska, the stopovers of American Samoa and Nome birds ($n = 17$) averaged 23 days ±10 (range 2–36 days) and occurred at the following locations: Yukon-Kuskokwim Delta (in the region extending from 60° N to 61° N and from the coastline inland to 163.5° W; 5 birds), Nunivak Is. (60° N, 166° W; 2 birds), St. Matthew Island

(60.36° N, 172.60° W; 1 bird); Cape Peirce region near Goodnews Bay (59° N, 161° W; 3 birds), eastern Aleutian Islands (between 166° and 171° W; 5 birds), and Alaska Peninsula (55° N, 163° W; 1 bird). The birds departed from Alaska over the period 22 Aug to 24 Sep (median 30 Aug).

The four Saipan birds left their nesting grounds in the Siberian Far East during 3–19 Aug. Like the birds in Alaska, each plover made a prolonged stopover prior to its nonstop passage back to Saipan. By individual, these stops were in NE China (47.79° N, 134.00° E) 16 days; Honshu (35.63° N, 140.38° E) 15 days; S Hokkaido or N Honshu (41.73° N, 141.00° E) 12 days; and Alaska Peninsula (55.47° N, 161.19° W) 22 days. The last bird was the previously mentioned plover that had migrated to Chukotka via W Alaska. As evident in Fig. 3, this bird (and also the plover last recorded in spring at Nelson Island, Alaska), followed migration routes that were much different than the other Saipan birds. Overall records of arrival dates on wintering grounds were as follows: American Samoa 28 Aug – 29 Sep (n = 9); Saipan 24 Aug – 7 Sep (n = 4); Marshall Is. 1–7 Sep (n = 3); Fiji 11–13 Sep (n = 2); Gilbert Is. 29 Sep (n = 1); Christmas Is. 27 Aug (n = 1); Fraser Is. 9 Sep (n = 1).

Breeding ground destinations

The approximate nesting locations in Alaska of the nine American Samoa birds along with the possible nest location of the Saipan bird at Nelson Island are shown in Fig. 5. Their distribution fell within an area that encompasses the northern half of the Alaska breeding range. In Fig. 3, we indicate the approximate sites in the Siberian Far East where the four Saipan birds nested, from north to south the locations were: Chukotka (66.78° N, 173.18° W and 62.60° N, 179.00° E); Kamchatka (61.28° N, 164.09° E and 53.95° N, 158.63° E). Notably, the southernmost nest site in Kamchatka was located well beyond previous records of breeding on the peninsula (the latter at 54.80° N, 155.80° E; P. Tomkovich, pers. comm.) some 200 km to the north-west.

Flight performance

Estimates of ground speeds, lengths of routes flown, and flight-times for American Samoa and Nome birds are summarized in Table 2. Their mean ground speeds of 59–78 kph were similar to comparable estimates for plovers migrating between Hawaii and Alaska (58 kph in autumn, 63 kph in spring; Johnson *et al.* 2011), and there were no statistical differences (by t-tests at the 0.05 level of significance) between the Hawaii findings and the speeds estimated in the present study. Distances traveled during 12-hr flight legs were highly variable; some were lengthy (probably the result of tailwinds), others were short (probably affected by headwinds and other weather-associated factors). There were nine 12-hr legs traversed by American Samoa and Nome birds at impressively high estimated ground speeds ranging from 143 kph to 225 kph. If margin of error is assumed to be ±200 km at the end-points of these legs, speeds might have been as low as 110–192 kph or as high as 176–258 kph. We have not listed the Saipan birds in Table 2 as their tracks (especially in spring) were complicated by probable stopovers of less than 12 hours that we were unable to clearly evaluate. The estimated speeds of Saipan birds on selected oceanic segments (of more than one leg and with no apparent stopover interruptions) were similar to the speeds of American Samoa and Nome birds given in Table 2.

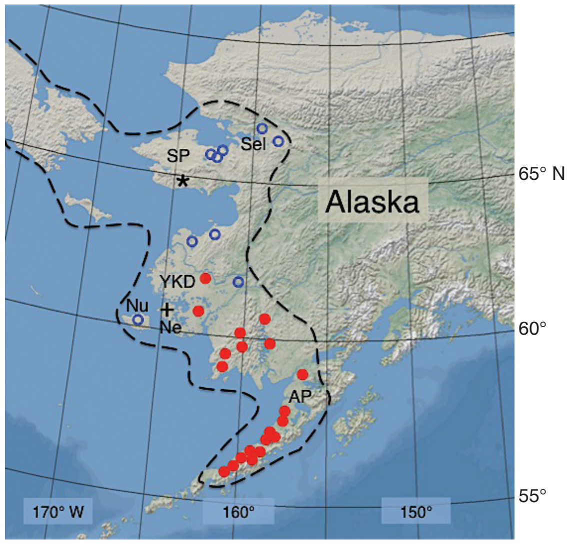

Fig. 5. The nesting locations of geolocator-equipped Pacific Golden-Plovers in Alaska. American Samoa birds are indicated by open blue circles, asterisk shows general location where Nome birds were captured. The cross represents possible nesting by a Saipan bird (see text). Also shown in the figure are the nest locations (solid red dots) of migrants from Oahu as described in a previous study (see Johnson *et al.* 2011). The dashed line defines the approximate portion of Alaska in which the species breeds. The primary nesting range of *P. fulva* extends westward across much of Siberia. Abbreviations: AP (Alaska Peninsula), Ne (Nelson Is.), Nu (Nunivak Is.), Sel (Selawik National Wildlife Refuge), SP (Seward Peninsula), YKD (Yukon-Kuskokwim Delta).

Tracking records for the Fraser Island bird (our longest-distance migrant, Fig. 2) were erratic during autumn migration especially from the equator southward. This was probably caused by pre-equinox conditions. Equinox ± about 10 days constitutes a period that renders latitude difficult to measure with geolocators (see Fox 2010). We estimate that the autumn flight of this bird involved 10 days over a distance of approximately 12,500 km, with possible stopovers in the NW Hawaiian Islands and in the SW Pacific. Measurements of the bird's spring flights can be defined more accurately as follows: 7,253 km nonstop from Fraser Island to Taiwan over a period of 4 days, at a ground speed of 75 kph; thence 1,750 km to eastern South Korea in 2 days, at a ground speed of only 36 kph which implies one or more stopovers en route (possibly on Jeju Island 33.38° N, 126.56° E, and/or the southern coast of South Korea); thence 852 km nonstop to SE Russia in 12 hours, at a ground speed of 70 kph. Further tracking was impossible because of geolocator failure. However, by including the great circle distance from the plover's last known location south-east of Sakhalin Island to its nest site near Nome (no doubt a shorter route than the actual flight), we estimate that the bird's annual migration covered at least 26,700 km.

DISCUSSION

In their consideration of migration routes from American Samoa to Alaska, Johnson *et al.* (2008) regarded a mid-Pacific route through the Hawaiian Islands as the "most likely" path, but went on to say that the primary route might actually be westward via Japan. Present findings demonstrate that the latter possibility was indeed the correct one, and suggest that westward divergence in spring may be the norm for plovers wintering across a huge region south of the Hawaiian Islands. Furthermore, except for plovers wintering in Hawaii where previous studies indicate direct north–south flights to/from Alaska (Johnson *et al.* 2011), the westward shift of spring migrants to Japan infers that the mid-Pacific Flyway is primarily an autumn pathway. With respect to Saipan, Johnson *et al.* (2006) assumed connectivity with Siberia via Japan and raised the possibility that there might also be linkage with Alaska. This study confirms both of these pathways. The annual movements we describe for plovers are much the same as reported in recent studies of two other shorebird species. Battley *et al.* (2012) defined a circular pattern for Bar-tailed Godwits *Limosa lapponica baueri* (this race breeds in Alaska and winters in New Zealand) like that of American Samoa and Nome plovers (Fig. 2), except the spring stopover for godwits is in the Yellow Sea region of E Asia not Japan; and Minton *et al.* (2011) demonstrated pathways for Ruddy Turnstones wintering in Australia that were similar to those of Saipan plovers (Fig. 3) in that the turnstones followed an E Asian route in spring, but returned variously in fall along both Asian and W Pacific paths.

That Japan is a spring stopover for plovers migrating from Central and S Pacific wintering grounds was previously unknown. However, banding studies of Ruddy Turnstones by Max Thompson have long hinted that this might be the case. Based on data from a massive banding project involving 16,152 turnstones, Thompson (1973) described a "circular" pattern of annual migration in the Central Pacific. Like the plovers, turnstones followed a route comprised of three major segments: southward in fall along the mid-Pacific Flyway leading to wintering grounds on islands beyond Hawaii, westward in spring to stopovers in Japan, northward from Japan to breeding grounds. Furthermore, the timing and location of turnstone stopovers in Japan (peak 1–8 May, east of Tokyo) were similar to the plover stopovers described in this paper. Thompson noted that POBSP observers (Pacific Ocean Biological Survey Program, Smithsonian Institution) had found large numbers of turnstones at Laysan and Lisianski Islands in the NW Hawaiian chain during May and June – records that implied an "undefined alternate route". The movements of plovers between Oahu and Alaska (i.e., no connectivity with Japan) shown by Johnson *et al.* (2011), suggests that the turnstones following Thompson's alternate route were migrants from non-breeding grounds in the Hawaiian Islands.

Close agreement between the ground speeds shown in Table 2 and comparable data from the nonstop Hawaii–Alaska route where there is no land and plovers did not contact seawater (Johnson *et al.* 2011) leads us to conclude that the flights of American Samoa and Nome birds were probably all nonstop as well. The only caveat here concerns several instances where relatively short 12-hr flight legs intersected atolls. Whether these shorter legs indicated brief stops or were the result of unfavorable weather is unclear. There were no seawater contacts in these situations, but such would be the case if landing sites were inland (on airstrips, for example). There are a few records attesting to stopovers by Pacific Golden-Plovers during long oceanic passages (Johnson & Connors 2010, Johnson *et al.* 2004); in addition, approximately 1,600 birds were observed on a coralline flat adjacent to the runway at Midway Island in late April 2000 (OWJ and PMJ, unpubl. data), and a plover OWJ banded on American Samoa in spring 2007 was photographed in a stopover flock at Shemya Island, Aleutians in May 2008 (M. Schwitters, pers. comm.). Based on present findings, the latter bird was probably en route between Japan and Alaska.

Our estimates of ground speeds for individuals on lengthy transpacific flights (Table 2) are similar to measurements among other shorebirds that have been tracked with satellite transmitters or geolocators: Eastern Curlew *Numenius madagascariensis* 50 kph (Driscoll & Ueta 2002); Bar-tailed Godwit *Limosa lapponica baueri* 60 kph (Gill *et al.* 2009), 53–76 kph *L. l. baueri* and *menzbieri* (Battley *et al.* 2012); Ruddy Turnstone 30–79 kph (Minton *et al.* 2010, 2011); Red Knot *Calidris canutus* 27–55 kph by our calculations (Niles *et al.* 2010); Great Snipe *Gallinago media* 54–97 kph (Klaassen *et al.* 2011). However, three Pacific Golden-Plovers exceeded the foregoing rates and flew long distances at very high speeds (estimated at 101, 104, and 105 kph, respectively; Table 2). These individuals together with two birds from an earlier study whose ground speeds were estimated at 106 and 112 kph, respectively (Johnson *et al.* 2011) represent the fastest nonstop transoceanic flights that have been recorded among waders. The remarkable ground speeds achieved on certain 12-hr legs (see Results) are comparable to those recorded between Hawaii and Alaska (Johnson *et al.* 2011), and further demonstrate very rapid movements under favorable conditions – presumably when flights coincide with strong tailwinds.

Table 2. Estimated flight performance by Pacific Golden-Plovers during their annual cycle of migration between breeding grounds, the non-breeding range, and stopover sites in Japan (measurements are mean, SD, range).[1]

	Ground speed (kph)	Distance flown (km)	Flight time (hours)	Flight time (days)
American Samoa birds (*n* = 9)				
Autumn, Alaska to AS	64±20 (47–101)	9,794±1,764 (7,972–12,276)	157±25 (121–181)	6.5±1.0 (5.0–7.5)
Spring, AS to Japan	60±4 (54–66)	8,626±745 (7,932–10,395)	145±18 (120–182)	6.0± 0.7 (5.0–7.6)
Spring, Japan to Alaska	73±14 (58–105)	6,133±1,483 (4,814–8,820)	82±11 (67–96)	3.4±0.4 (2.8–4.0)
Nome birds[2]				
Autumn, Alaska to winter range (*n* = 7)[3]	66±10 (47–76)	5,845–9,392	80–138	3.3–5.8
Spring, winter range to Japan (*n* = 7)[3]	59±7 (47–70)	4,808–9,394	83–200	3.5–8.3
Spring, Japan to Nome (*n* = 6)[4]	78±19 (53–104)	5,964±880 (5,118–7,631)	80±18 (60–102)	3.3 (2.5–4.3)

[1] Estimates represent landfall-to-landfall flight performance on tracks consisting of sequential 12-hr legs as plotted by BasTrak software (see Johnson *et al.* 2011). Note that these data are based on positional fixes where the margin of error may be ±200 km (see Methods).
[2] The Nome bird that wintered at Fraser Island is not included in the table as it did not contact Japan.
[3] Ranges only are given for distances flown and hours in flight as wintering locations varied widely across the Pacific (Fig. 2).
[4] One geolocator failed in Japan before departure to Alaska.

The breeding distribution of logger-equipped plovers in Alaska (Fig. 5) hints at a separation in the Yukon-Kuskokwim Delta region with birds wintering south of Hawaii (i.e., the American Samoa sample) nesting primarily northward from the delta and birds wintering in Hawaii nesting primarily southward. The Nome birds add further credence to this in that all of them wintered far beyond the Hawaiian Islands. While this study clearly demonstrated connectivity between the East Asian-Australasian Flyway and Alaska, we were unable (because of geolocator failure) to determine whether the Saipan bird last recorded at Nelson Island actually nested there. That possibility is strengthened by findings from a previous season. In June 2008, OWJ captured a plover at its nest near Nome and banded the bird with a unique combination of color-rings; during the subsequent fall, the marked plover was observed foraging in a rice field near Hiroshima, Japan (T. Hiroi, pers. comm. with photographs). This record was the first definitive evidence for the species of linkage between Alaska and the East Asian-Australasian Flyway (Johnson & Connors 2010).

Other connectivity revealed by the present investigation involves the Siberian Far East and Australia. Prior to this study, the only recovery on the winter range of a bird banded in Siberia was a single individual found dead (killed by a cat) in 1981 on Kwajalein Atoll in the Marshall Islands (Schipper 1985). Contra Johnson & Connors (2010), who reported the banding site of this bird as unknown, this individual was in fact ringed as a chick in Yakutia (Russian East Siberia) at approximately 69.40° N, 158.50° E (P. Tomkovich, pers. comm.). Thus, our tracking of plover migratory routes from Saipan (including a pathway via Alaska) to nesting locations in Kamchatka and Chukotka are the first records of specific linkages with the Siberian Far East. With respect to Australia, the plover that wintered at Fraser Island, Queensland represents the first clearly defined connection between Australia and nesting grounds in Alaska. Previously, the only other record suggesting Alaska linkage was a plover banded in 1966 at the Pribilof Islands and recovered in 1970 in New South Wales (Wyndham 1977).

Seebohm (1890) reported that "great numbers" of Pacific Golden-Plovers pass through Japan in spring and fall. Many years later, Brazil (1991) was of like mind saying "Seebohm's description . . . is as true today as it was a century ago". In contrast to these general impressions, recent studies (based on monitoring counts and modeling) suggest downward trends. According to Fujioka *et al.* (2010) there were fewer birds in both spring and fall of 2000–2003 as compared to 1974–85; and an analysis of counts from 1975 to 2008 by Amano *et al.* (2010b) indicated relatively stable numbers in spring, but declining numbers in fall. Plover counts in Japan are typically much higher in spring as compared to autumn (Fujioka *et al.* 1999, 2010), and this difference is consistent with the circular migration pattern we have described. Fewer plovers in autumn almost certainly reflects separate wintering populations – those plovers tallied during fall in Japan being en route to non-breeding grounds on the East Asian-Australasian Flyway, while the birds "missing" in Japan are at the same time following the mid-Pacific Flyway to other regions of the winter range (Fig. 2). As one would predict from Thompson's (1973) findings, count data from Japan show the same shift in seasonal abundance for Ruddy Turnstones (Fujioka *et al.* 1999).

Our results suggest that plovers stopping over in Japan (also the individual in Taiwan) foraged primarily on inland habitats, most likely rice fields. According to Amano (2010a) plover dependence on rice fields in Japan ranks relatively high (2 on a scale of 0–3), and Fujioka *et al.* (2010) lists the bird as seasonally "common" in rice fields. Stopover periods are in synchrony with rice farming schedules since the fields (often containing an abundance of prey such as earthworms and insects) are accessible as foraging habitat during spring cultivation and planting, and available again in fall when the rice stalks are cut and the grain harvested (Fujioka *et al.* 2010, Maeda 2001, Watanabe 1991, 2001, 2006, 2007). The rice agro-ecosystem of Japan clearly provides feeding grounds for large numbers of migrating Pacific Golden-Plovers, and given its long history (rice culture in Japan dates from about 400 BC, Ishige 2000) this has probably been true for many centuries.

Given the transpacific nature of this plover's annual travels, knowledge of its movements across vast oceanic areas is of fundamental importance from the conservation perspective. Our findings of clockwise migration in the Central and S Pacific, spring convergence in Japan from an immense geographic area, the apparent need for a refueling stop during spring migration from southerly regions beyond Hawaii, wide-ranging connectivity between non-breeding grounds in the Pacific and nesting grounds in Alaska, and various other newly revealed migratory linkages shed substantial light on this aspect of the species' biology. It is likely that successful migration for many of the plovers breeding in Alaska and E Siberia depends on prey organisms foraged from rice fields in Japan. Energy thus acquired is perhaps critical for survival given the vagaries of spring weather when birds arrive on breeding grounds. Various authors have pointed out the importance of rice culture to plovers and other birds, and cautioned against the potential impacts of agricultural intensification (Amano 2009, Amano *et al.* 2008, 2010a, Elphick 2010, Maeda 2001, Parsons *et al.* 2010). The apparent significance of rice field habitats during the annual cycle signals a need for improved understanding of plover behavior and requirements during stopovers in Japan, and for additional studies that focus on relationships between migrating plovers and rice farming practices.

ACKNOWLEDGEMENTS

The project was funded primarily by BYU-Hawaii through two sources: a faculty-mentored student research program, and a faculty professional development program. Additional travel and logistical support was provided by the U.S. Fish and Wildlife Service, Honolulu; the U.S. National Park Service at Nome furnished low-cost housing during periods of fieldwork in Alaska. At American Samoa, the Department of Marine and Wildlife Resources (DMWR) kindly issued the necessary permit for our work there, and we thank the people of Tutuila for allowing us to capture plovers on their lands. Pulemagafa Siaifoi Fa'aumu, Lofi Lalogafu'afu'a, and Cindy Holte (DMWR biologists), and Samuel Goldstein (USDA Wildlife Services, Honolulu) assisted with mist netting on Tutuila. Mr. Fa'aumu also provided invaluable liaison when arranging access to study sites. At Saipan, we are grateful to Paul Radley of the CNMI Division of Land and Natural Resources for assistance in obtaining permits to capture plovers; and to Andre Kozij for his tireless early morning help in the field when recapturing them. We are indebted to Beverly Haid and Sue Hillmann who graciously provided lodging for OWJ and PMJ during periods of writing and other work in Hawaii. Marcel Klaassen and Pavel Tomkovich reviewed the manuscript and offered many helpful comments.

REFERENCES

Amano, T. 2009. Conserving bird species in Japanese farmland: Past achievements and future challenges. *Biological Conservation* 142: 1913–1921.

Amano, T., Y. Kusumoto, Y. Tokuoka, S. Yamada, E-Y. Kim & S. Yamamoto. 2008. Spatial and temporal variations in the use of rice-paddy dominated landscapes by birds in Japan. *Biological Conservation* 141: 1704–1716.

Amano, T., T. Székely, K. Koyama, H. Amano & W.J. Sutherland. 2010a. A framework for monitoring the status of populations: An example from wader populations in the East Asian-Australasian flyway. *Biological Conservation* 143: 2238–2247 *(doi: 10.1016/j.biocon.2010.06.010)*.

Amano, T., T. Székely, K. Koyama, H. Amano & W.J. Sutherland. 2010b. Addendum to "A framework for monitoring the status of populations: An example from wader populations in the East Asian-Australasian flyway". *Biological Conservation* 143: 2238–2247 *(doi:10.1016/j.biocon.2011.06.006)*.

Battley, P.F., N. Warnock, T.L. Tibbits, R.E. Gill, Jr., T. Piersma, C.J. Hassell, D.C. Douglas, D.M. Mulcahy, B.D. Gartrell, R. Schuckard, D.S. Melville & A.C. Riegen. 2012. Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *J. Avian Biol*. 43: 21–32.

Brazil, M.A. 1991. *The Birds of Japan*. Smithsonian Institution Press, Washington, D.C.

Conklin, J.R., P.F. Battley, M.A. Potter & J.W. Fox. 2010. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nature Communications 1: 67 (doi: 10.1038/ncomms1072)*.

Driscoll, P.V. & M. Ueta. 2002. The migration route and behaviour of Eastern Curlews *Numenius madagascariensis*. *Ibis* 144 (online): E119–130.

Edwards, D.B. & H.G. Gilchrist. 2011. A new means of catching shorebirds: the Super Talon Net Gun. *Wader Study Group Bull*. 118: 134–136.

Elphick, C.S. 2010. Why study birds in rice fields? *Waterbirds* 33 (Special Publ. 1): 1–7.

Fox, J.W. 2010. *Geolocator Manual*. vol. 8. British Antarctic Survey, Cambridge, UK. online: *www.antarctica.ac.uk/engineering/geo_downloads*

Fudickar, A.M., M. Wikelski & J. Partecke. 2011. Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. *Methods Ecol. Evol. (doi: 10.1111/j.2041-210X.2011.00136.x)*.

Fujioka, E., J. Fujioka, K. Inada & K. Kuwabara (eds). 1999. *National Counts of Shorebirds in Japan, Autumn 1998*. JAWAN, Nagoya, Japan.

Fujioka, M., S.D. Lee, M. Kurechi & H. Yoshida. 2010. Bird use of rice fields in Korea and Japan. *Waterbirds* 33 (Special Publ. 1): 8–29.

Gill, R.E., Jr., T.L. Tibbitts, D.C. Douglas, C.M. Handel, D.M. Mulcahy, J.C. Gottschalck, N. Warnock, B.J. McCaffery, P.F. Battley & T. Piersma. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. Royal Soc. B* 276: 447–457 (*doi: 10.1098/rspb.2008.1142*).

Hayman, P., J. Marchant & T. Prater. 1986. *Shorebirds: An Identification Guide to the Waders of the World*. Houghton Mifflin, Boston.

Ishige, N. 2000. *The Cambridge World History of Food*. K.F. Kiple & K.C. Ornelas (eds.). Cambridge University Press, Cambridge.

Johnson, O.W. & P.G. Connors. 2010. Pacific Golden-Plover (*Pluvialis fulva*). In: *The Birds of North America* online, No. 202. A. Poole (ed.). Cornell Lab of Ornithology, Ithaca, NY. (*doi:10.2173/bna.202*).

Johnson, O.W., P.L. Bruner, A.E. Bruner, P.M. Johnson, R.J. Kienholz & P.A. Brusseau. 2001a. Features of breeding biology in Pacific and American Golden-Plovers nesting on the Seward Peninsula, Alaska. *Wader Study Group Bull*. 95: 59–65.

Johnson, O. W., P.L. Bruner, J.J. Rotella, P.M. Johnson & A.E. Bruner. 2001b. Long-term study of apparent survival in Pacific Golden-Plovers at a wintering ground on Oahu, Hawaiian Islands. *Auk* 118: 342–351.

Johnson, O.W., P.M. Johnson & D.L. O'Daniel. 2004. Site fidelity and other features of Pacific Golden-Plovers *Pluvialis fulva* wintering on Johnston Atoll. *Wader Study Group Bull.* 104: 60–65.

Johnson, O.W., R. Goodwill & P.M. Johnson. 2006. Wintering ground fidelity and other features of Pacific Golden-Plovers *Pluvialis fulva* on Saipan, Mariana Islands, with comparative observations from Oahu, Hawaiian Islands. *Wader Study Group Bull*. 109: 67–72.

Johnson, O.W., R.H. Goodwill, A.E. Bruner, P.M. Johnson, R.S. Gold, R.B. Utzurrum & J.O. Seamon. 2008. Pacific Golden-Plovers *Pluvialis fulva* in American Samoa: Spring migration, fall return of marked birds, and other observations. *Wader Study Group Bull*. 115: 20–23.

Johnson, O.W., L. Fielding, J.W. Fox, R.S. Gold, R.H. Goodwill & P.M. Johnson. 2011. Tracking the migrations of Pacific Golden-Plovers (*Pluvialis fulva*) between Hawaii and Alaska: New insight on flight performance, breeding ground destinations, and nesting from birds carrying light level geolocators. *Wader Study Group Bull.* 118(1): 26–31.

Klaassen, R.H.G., T. Alerstam, P. Carlsson, J.W. Fox & A. Lindström. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biology Letters* (*doi: 10.1098/rsbl.2011.0343*).

Maeda, T. 2001. Patterns of bird abundance and habitat use in rice fields of the Kanto Plain, central Japan. *Ecol. Res.* 16(3): 569–585.

Minton, C., K. Gosbell, P. Johns, M. Christie, J.W. Fox & V. Afanasyev. 2010. Initial results from light level geolocator trials on Ruddy Turnstones *Arenaria interpres* reveal unexpected migration route. *Wader Study Group Bull*. 117: 9–14.

Minton, C., K. Gosbell, P. Johns, M. Christie, M. Klaassen, C. Hassell, A. Boyle, R. Jessop & J. Fox. 2011. Geolocator studies on Ruddy Turnstones *Arenaria interpres* and Greater Sandplovers *Charadrius leschenaultii* in the East Asian-Australasia Flyway reveal widely different migration strategies. *Wader Study Group Bull*. 118: 87–96.

Niles, L.J., J. Burger, R.R. Porter, A.D. Dey, C.D.T. Minton, P.M. Gonzalez, A.J. Baker, J.W. Fox & C. Gordon. 2010. First results using light level geolocators to track Red Knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways. *Wader Study Group Bull*. 117: 123–130.

Parsons, K.C., P. Mineau & R.B. Renfrew. 2010. Effects of pesticide use in rice fields on birds. *Waterbirds* 33 (Special Publ. 1): 193–218.

Priklonsky, S.G. 1960. Use of automatic "luchock" traps for bird catching. *Zool. Zh*. 39: 623–624. (In Russian).

Schipper, W.L. 1985. Observations of birds on Kwajalein Atoll 1978–1983. *Elepaio* 46: 27–32.

Seebohm, H. 1890. *The Birds of the Japanese Empire*. R.H. Porter, London.

Thompson, M.C. 1973. Migratory patterns of Ruddy Turnstones in the central Pacific region. *Living Bird* 12: 5–23.

Watanabe, T. 1991. Changes in the number of migrating Pacific Golden Plovers *Pluvialis dominica* at Okubo rice field, central Japan. *Strix* 10: 107–114. [In Japanese with English summary].

Watanabe, T. 2001. Habitat selection of Pacific Golden Plovers at a rice field in spring. *Strix* 19: 181–185. [In Japanese with English summary].

Watanabe, T. 2006. Differences in foraging behavior of Pacific Golden Plovers *Pluvialis fulva* between rice field types in spring. *Strix* 24: 23–30. [In Japanese with English summary].

Watanabe, T. 2007. Pacific Golden Plovers *Pluvialis fulva* foraging on leafhoppers *Nephotettix cincticeps* at rice fields after harvest. *J. Yamashina Inst. for Ornithol*. 39: 40–42. [In Japanese with English abstract].

Wyndham, E. 1977. Eastern golden plover banded off Alaska and recovered in New South Wales. *Emu* 77: 39.