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LINKING PEREGRINE FALCONS' (*FALCO PEREGRINUS*) WINTERING AREAS IN PERU WITH THEIR NORTH AMERICAN NATAL AND BREEDING GROUNDS

Oscar Beingolea
International Bird Conservation Partnership, Jiron La Venturosa 114, Los Rosales, Primera Etapa, Lima 33, Peru

Nico Arcilla[1]
International Bird Conservation Partnership, Storövägen 13, 14142 Huddinge, Sweden,
and
University of Nebraska Center for Great Plains Studies, 1155 Q Street, Lincoln, NE 68508 USA

Abstract.—Identifying migratory raptors' wintering areas and migration routes is an essential part of predicting their responses to habitat and climate change throughout their annual cycles, and therefore important for their conservation. Among the world's most widespread migratory species, the Peregrine Falcon (*Falco peregrinus*) has been the subject of intensive study on its breeding grounds and at some migratory stopover sites, but the links between its breeding, stopover, and wintering areas remain poorly known. In particular, few empirical data are available on migratory *F. p. tundrius* and *F. p. anatum* (hereafter, Nearctic peregrines) wintering in South America during the austral spring and summer. Here, we present evidence connecting Nearctic peregrines wintering in Peru with their natal and breeding territories in North America using mark-recapture data collected between 1963 and 2019. We documented eight encounters of banded wintering Nearctic peregrines, whose natal origins or breeding regions included the Northwest Territories, Nunavut, and Yukon Territory in Canada, and Alaska, Minnesota, and Nebraska in the USA. Our findings indicate that both *tundrius* and *anatum* peregrines winter in Peru and originate from a widespread geographic breeding range, corroborating other research suggesting that Nearctic peregrine migration is highly dispersive. Peregrines exhibit sex-related differential migration patterns in which males tend to migrate farther than females, and our data from the capture of 208 Nearctic peregrines suggest that the majority of wintering birds in Peru are males (n =150; 72%). We also report new records of Nearctic peregrine arrivals in Peru that represent advances of approximately 2–3 wk compared to the earliest previously published reports. The variability of peregrines' migratory movements may be related to the behavioral plasticity that facilitated their successful recovery following their catastrophic declines in much of North America. As peregrines remain vulnerable to human impacts including habitat and climate change, continuing to fill gaps in our knowledge of Nearctic peregrines' migratory connectivity will enable continuing conservation measures for these spectacular birds.

Key Words: *Peregrine Falcon*; Falco peregrinus anatum; Falco peregrinus tundrius; Falco peregrinus cassini; *conservation*; *differential migration*; *migratory connectivity*; *Peru*; *South America*; *species recovery*.

CONECTANDO LAS ZONAS DE INVERNADA DE *FALCO PEREGRINUS* EN PERÚ CON SUS ÁREAS DE CRÍA EN NORTEAMÉRICA

RESUMEN.—Identificar las áreas de invernada y las rutas migratorias de las aves rapaces es esencial para predecir sus respuestas ante los cambios de hábitat y el cambio climático a lo largo de sus ciclos anuales siendo, por tanto, importante para su conservación. Una de las especies de aves rapaces con mayor distribución mundial, *Falco peregrinus*, ha sido objeto de intensa investigación en sus áreas de cría y algunas zonas de paso en Norteamérica. Sin embargo, la conectividad entre sus áreas de cría, paso e invernada y rutas migratorias están aún poco estudiadas en las Américas. En concreto, existen pocos datos empíricos disponibles sobre las áreas de invernada en América del Sur, incluyendo Perú, de las poblaciones migratorias de *Falco p. tundrius* y *F. p. anatum* (de aquí en adelante peregrinos neárticos). En este estudio, utilizando datos de captura-recaptura recopilados entre 1963 y 2019, presentamos evidencias de conexión entre las

[1] Email address: nico.arcilla@aya.yale.edu

poblaciones de halcones peregrinos neárticos invernantes en el Perú con sus territorios natales y de reproducción en América del Norte. Documentamos ocho recapturas de peregrinos neárticos en Perú cuyos orígenes natales en América del Norte son conocidos, incluyendo aves anilladas provenientes de los territorios del noroeste, Nunavut y Yukón en Canadá, además de Alaska, Minnesota y Nebraska en Estados Unidos. Nuestros resultados indican que ambas subespecies *tundrius y anatum*, provenientes de una amplia zona de cría, se superponen en sus áreas de invernada, corroborando estudios anteriores que sugieren que la migración de halcones peregrinos neárticos es altamente dispersiva. Los peregrinos neárticos muestran patrones migratorios diferenciales entre sexos, donde los machos tienden a hacer migraciones más largas que las hembras. Nuestros datos de campo de 208 peregrinos neárticos en Perú sugieren que los individuos migratorios en las zonas de invernada están compuestos principalmente de machos (72%; n=150). También informamos sobre nuevos registros de llegada de peregrinos de invernada en Perú, que representan un avance de aproximadamente 2-3 semanas en comparación con los primeros informes publicados anteriormente. La elevada variabilidad de los movimientos migratorios de los peregrinos parece estar relacionada con la plasticidad comportamental de esta especie, que permitió su exitosa recuperación tras su eliminación de la mayor parte del este de Norteamérica. Debido a que los peregrinos neárticos aún son vulnerables a las consecuencias del impacto humano, incluyendo los cambios de hábitat y climáticos, completar los vacíos existentes en el conocimiento sobre la conectividad migratoria permitirá que se mejoren las medidas de conservación de estas espectaculares aves.

[Traducción de los autores editada]

Linking migratory birds' breeding, stopover, and wintering areas is essential for understanding their ecology and evolution and for effective conservation (Faaborg et al. 2010, Trierweiler et al. 2014, Bayly et al. 2017, Marra et al. 2018). Among the world's most widespread terrestrial species, the Peregrine Falcon (*Falco peregrinus*) has been the subject of much study on its breeding grounds and migratory stopover sites, but the wintering areas of migratory individuals and populations remain largely unexplored (Ganusevich et al. 2004). Thus, surprisingly few data are available on peregrines' migratory connectivity, due in part to the significant challenges to tracking birds' movements at different stages of their annual cycles (Schoonmaker et al. 1985, McGrady et al. 2002, Webster et al. 2002, Ganusevich et al. 2004, Faaborg et al. 2010, Marra et al. 2018, White et al. 2020b). Specific research priorities for Peregrine Falcons thus include gathering more extensive data on wintering locations of migratory populations and linking these locations with birds' natal and breeding grounds (White et al. 2020b).

Four of the 19 currently recognized Peregrine Falcon subspecies in the world occur in the Americas (Cade et al. 1988, White et al. 2002, 2013, 2020a, 2020b). North American subspecies known to migrate to Central and South America include *F. p. tundrius* and *F. p. anatum* (hereafter, Nearctic peregrines). *F. p. tundrius* breeds in the North American Arctic tundra from Alaska to Greenland, and is a long-distance migrant with a wintering range that includes the southern USA to southern South America (Burnham and Mattox 1984, Schmutz et al. 1991, White et al. 2002, 2020a, 2020b). *F. p. anatum* breeds in the North American continental taiga, or boreal forested interiors, and locally south into Mexico, and is considered a short- to medium-range migrant (Schmutz et al. 1991), but its wintering range has not been clearly defined (White et al. 2002, 2013, Talbot et al. 2017). Other American subspecies include *F. p. pealei,* which breeds in the coastal Pacific Northwest, Alaskan Peninsula and Aleutian Islands, and *F. p. cassini*, which breeds in western South America from Ecuador to Tierra del Fuego and the Falkland Islands (White et al. 2013, 2020a).

Never abundant in North America, Peregrine Falcons underwent catastrophic declines between the 1940s and 1970s due to reproductive failure caused by the pesticide DDT (White et al. 2002, 2020a, 2020b). As a result, *F. p. tundrius* populations exhibited >50% declines, and *F. p. anatum* populations were extirpated from much of eastern North America (Fyfe et al. 1976, Brown et al. 2007). Subsequently, from 1974 to 1999, the Canadian and American governments made both *F. p. tundrius* and *F. p. anatum* the focus of intense recovery efforts, including reintroduction programs using captive-bred birds (Tordoff and Redig 1997, Ambrose et al. 2016, Talbot et al. 2017, White et al. 2020a, 2020b). Research priorities for Nearctic peregrines include monitoring the distribution of reintroduced and recovering populations and investigating wintering locations of breeding populations (White et al. 2002, 2013, 2020a, 2020b; Faaborg et al. 2010; Bayly et al. 2017). Rigorous monitoring efforts have accompanied conservation efforts on peregrines' breeding grounds, but major gaps persist in our knowledge of Nearctic peregrines' migratory movements and destinations (White et al. 2002, 2013, Lyngs 2003). We also lack information about factors that affect peregrines' conservation status outside their breeding range, such as direct human impacts, climatic variation, and prey population dynamics (Bruggeman et al. 2015).

Tracking birds' movements throughout their annual cycles is particularly important for migratory peregrines as they may spend the majority of their lives (approximately 7 mo/yr) outside of their breeding range (Schmutz et al. 1991, Seegar et al. 1996, Ganusevich et al. 2004, White et al. 2020a, 2020b). Both Nearctic and resident peregrines are known on the Peruvian and Chilean coasts (Schoonmaker et al. 1985, C. Anderson unpubl. data). Nearctic migrant peregrine distributions are poorly known in Peru (Kéry 2002, 2007); some sources have reported predominantly or solely wintering *F. p. tundrius* migrants (Schoonmaker et al. 1985, White et al. 2002, eBird 2020) and others predominantly or solely *F. p. anatum* migrants (Koepcke 1964, Schulenberg et al. 2007). Understanding Nearctic peregrines' occurrences in South America is further complicated by overlap between wintering migrants and resident birds during the austral summer (Schoonmaker et al. 1985, Beingolea and White 2003).

Identifying Nearctic peregrines' wintering sites in Peru is important for their conservation, as well as for understanding their interactions and/or niche partitioning with resident peregrines in Peru. During the austral summer, Nearctic peregrines may vastly outnumber resident birds in coastal areas (O. Beingolea unpubl. data). Shorebirds (e.g., Scolopacidae) are important prey for Nearctic peregrines (Worcester and Ydenberg 2008, Varland et al. 2018), which are known for their affinities for coastal habitats and reliance on wintering shorebirds in the nonbreeding season (Schmutz et al. 1991, Fuller et al. 1998, Ganusevich et al. 2004).

Mark-recapture data and specifically bird band encounters provide insights into life history data, including birds' migratory patterns, timing, and wintering grounds. A cooperative effort between the Canadian and American governments, the North American Bird Banding Program (NABBP) documented 160 encounter reports of banded peregrines in South America between 1960–2008, mainly in Ecuador, Colombia, and Venezuela, but also in central Argentina (Lutmerding et al. 2012) and Brazil (Maestre et al. 2007). Despite these records, there is little mention of Nearctic peregrines in South America in general and Peru in particular in the published literature, especially in terms of their natal origins (White et al. 2020a, 2020b). Kéry (2002) reported observations of 28 peregrines in Peru during the northern winters in 1996 and 2001–2002, but whether these birds were Nearctic migrants or *F. p. cassini* residents was unknown. Banded Canadian-breeding *F. p. anatum* have been reported in Brazil (Maestre 2007) and Colombia (Holroyd et al. 2007), and Alaska-breeding *F. p. anatum* have been recovered in Ecuador, Argentina, and Brazil (Ambrose and Riddle 1988), but no banded *F. p. anatum* have been reported in Peru to date.

METHODS

Study Area and Field Sampling. From 1988 to 1995, we spent approximately 1000 hr trapping and banding peregrines on coastal beaches of Peru, in the Departments of Tumbes (3.56°S, 80.43°W) in northern Peru and Ica (14.06°S, 75.73°W) in central Peru, including sites in the vicinity of Lima (12.05°S, 77.04°W), a city of approximately 10 million people. Using vehicles and on foot, we accessed trapping sites on sandy beaches and mudflats along Peru's northern and central coast that provide important habitat for shorebirds and other waterbirds, particularly boreal migrants (Schulenberg et al. 2007). We also conducted approximately 50 hr of trapping in Peru's interior Andes in the Department of Pasco (10.45°S, 75.15°W), in high-elevation (4100 masl) *puna* grasslands. Nearctic peregrines tend to be larger than Peruvian *F. p. cassini* (White et al. 2020a, O. Beingolea unpubl. data), so we used biometric measurements including wing length to distinguish Nearctic peregrines from *F. p. cassini* and to sex captured birds (White and Boyce 1988, O. Beingolea unpubl. data).

Encounters of Banded Peregrine Falcons. We obtained band encounter data in three ways: (1) we caught banded birds in the course of our mark-recapture studies of peregrines in Peru and reported banded birds to the NABBP; (2) we received reports of injured or trapped falcons in Lima with bands that were reported to the NABBP; and, (3) we obtained all additional band encounter records of Nearctic peregrines in Peru from the NABBP database from 1960 to the present. Following protocols developed

Table 1. Wintering Peregrine Falcons encountered in Peru with known North American natal origins and/or breeding areas.

BIRD NUMBER[a]	BANDING LOCATION	BANDING DATE	AGE AT BANDING[b]	ENCOUNTER LOCATION	ENCOUNTER DATE	AGE AT ENCOUNTER[c]	SEX	DISTANCE[d]
1	Northwest Territories, Canada	1 Aug 1963	HY	Tambopata, Madre de Dios	4 Oct 1969	6 yr	U	9055 km
2	Nunavut, Canada	19 Aug 1982	ASY	Laguna Grande, Ica	24 Mar 1989	9 yr	M	8650 km
3	Yukon Territory, Canada	12 July 1985	HY	Acos Vinchos	27 Feb 1986	<1 yr	U	10,182 km
4	Nebraska, USA	26 Jul 1989	HY	Pisco, Ica	1 Feb 1995	6 yr	M	6430 km
5	Alaska, USA	4 Jul 1998	HY	Lima	2000/2001	2–3 yr	M	9833 km
6	Alaska, USA	27 Jul 1999	HY	Lima	23 Jan 2000	<1 yr	M	10,671 km
7	Minnesota, USA	11 Jun 2015	HY	Callao, Lima	1 Nov 2015	<1 yr	M	6760 km
8	Nunavut, Canada	21 May 2016	ASY	Miraflores, Lima	1 Apr 2019	5 yr	F	8870 km

[a] We assigned bird numbers in chronological order based on encounter dates; the same numbers represent links between birds' banding and wintering locations in Fig 1.
[b] Hatch-Year (HY) birds were those known to have hatched during the calendar year in which they were banded; all six HY birds here were banded as nestlings. After-Second-Year (ASY) birds were those known to have hatched earlier than the calendar year prior to the year of banding.
[c] We calculated age based on birds' minimum age at banding, rounded to the nearest integer.
[d] We calculated straight-line distance between banding and encounter locations; actual distances traveled by birds may have been longer.

by the NABBP, birds had been banded with uniquely numbered aluminum leg bands and their band numbers and associated data deposited at the US Geological Survey Bird Banding Laboratory (BBL). At the discretion of individual banders or banding programs, some birds had additionally been fitted with auxiliary colored leg bands with engraved alphanumeric codes for reasons including improving ease of identification in the field or indicating origins in a particular region (D. Bystrak pers. comm., J. Fallon pers. comm.).

RESULTS

From 1988 to 1995, we captured and banded 213 Peregrine Falcons, of which 208 (98%) were Nearctic migrants; 72% (n = 150) of Nearctic migrants were male. Our captures included two Nearctic peregrines that had been banded on their natal or breeding grounds, and we subsequently received reports of three additional banded Nearctic peregrines in Lima. We reported all five band encounters to the BBL, which also provided details of three additional Nearctic peregrines encountered in Peru (D. Bystrak pers. comm.). These eight individuals represent all records from the BBL to date of marked Nearctic peregrines with known natal or breeding origins found wintering in Peru between 1960 and 2019 (Table 1, Fig. 1), that migrated straight-line distances ranging from 6430 to 10,670 km. Of these eight individuals, five of the six birds (83%) of known sex were male.

Details of Encounters of Banded Birds. In 1989, in coastal Ica, we captured and released a banded *F. p. tundrius* male bearing a blue auxiliary band received in 1982 as an after-second-year (ASY) bird in Rankin Islet, Nunavut (Table 1, number 2). In 1995, in coastal Ica, we captured and released a banded *F. p. anatum* male bearing a black auxiliary band it had received in 1989 (Table 1, Number 4) as a captive-bred nestling in Omaha, Nebraska; this bird subsequently returned to nest in Nebraska (P. Redig pers. comm., Midwest Peregrine Society 2020). In 2006, we received a report of a banded *F. p. anatum* male recovered at Las Leyendas Zoological Park, Lima, in the summer of 2000 or 2001 (C. Párraga pers. comm.; Table 1, number 5); he had a black auxiliary band received in 1998 as a nestling on the Tanana River, Alaska. Unfortunately, this individual was fatally injured when brought to the zoo and died within hours of arrival; the summer timing suggests that either an injury prevented him from returning north, and/or he was kept in captivity for at least several months before arriving at the zoo. In 2015, we received a report of a banded *F. p. anatum* male

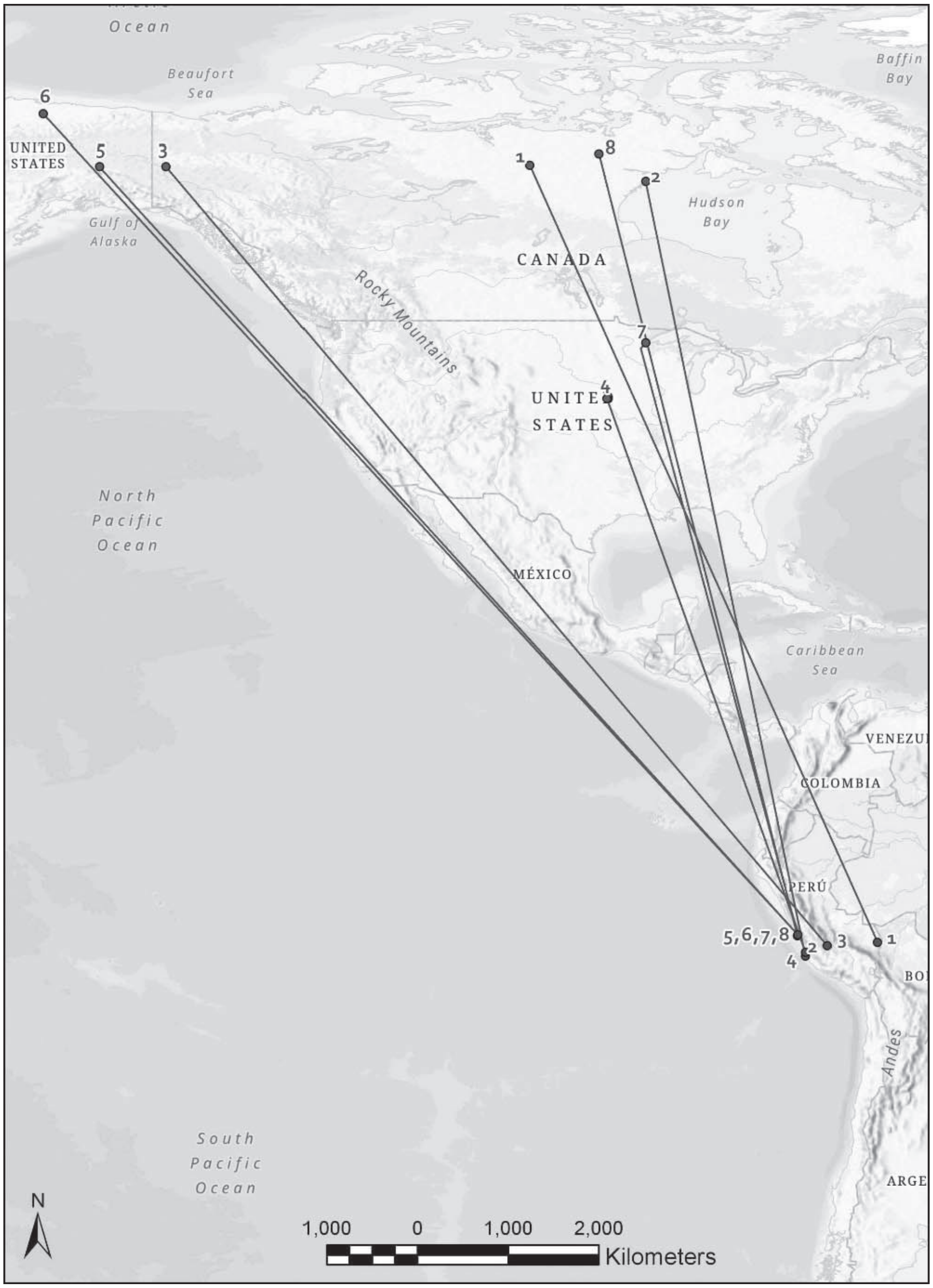

Figure 1. Peregrine Falcons wintering in Peru linked to their known natal and/or breeding locations in North America (see Table 1 and text for details).

Table 2. Peregrine Falcons banded at migration stopovers in the USA and later encountered in Peru[a].

Bird Number[b]	Banding Location	Banding Date	Age at Banding	Encounter Date	Age at Encounter[c]	Sex	Distance[d]
1	Port Isabel, TX	8 Oct 1988	HY	28 Mar 1993	5 yr	F	4710 km
2	Cape May, NJ	9 Oct 1990	HY	2 Dec 1990	$<$1 yr	M	4820 km
3	Port Mansfield, TX	13 Oct 1988	HY	7 Dec 1988	$<$1 yr	M	4910 km
4	Knotts Island, NC	13 Oct 1979	HY	19 Feb 1984	4 yr	M	5610 km
5	Kiptopeke, VA	28 Sep 1996	HY	unknown	unknown	F	5560 km
6	Port Isabel, TX	13 Apr 1982	ASY	28 Dec 1983	$>$3 yr	F	5020 km
7	Chincoteague, VA	2 Oct 1980	HY	10 Dec 1980	$<$1 yr	M	5560 km
8	Port Isabel, TX	3 May 1982	ASY	unknown	unknown	F	3930 km
9	Port Isabel, TX	4 Oct 1982	HY	unknown	unknown	F	4280 km
10	Port Mansfield, TX	11 Oct 1987	HY	2 Dec 1988	1 yr	F	4880 km
11	Port Isabel, TX	24 Apr 2003	ASY	3 Dec 2004	4 yr	F	3850 km
12	Cape May, NJ	19 Oct 1990	HY	4 Dec 1990	$<$1 yr	F	4820 km
13	Cape May, NJ	16 Oct 2012	HY	19 Nov 2014	3 yr	M	5670 km

[a] Data were provided by the BBL; Peru location names were not available in most cases; instead, encounter GPS coordinates are mapped in Fig. 2.
[b] We assigned bird numbers based on the order in which they were listed in BBL records; these numbers correspond to the same birds in Fig 2.
[c] We calculated age based on minimum age at banding, rounded to the nearest integer.
[d] We calculated straight-line distance between banding and encounter locations; actual distances traveled by birds may have been longer.

accidentally trapped in a soccer enclosure in Callao, Lima (J. A. Otero pers. comm.; Table 1, number 7). Subsequently rescued and released, this bird bore two auxiliary bands, one black and one red, received in 2015 as a nestling in Minnesota, the wild descendant of a successful reintroduction program with captive-bred birds (Midwest Peregrine Society 2020). In 2019, we received a report of a banded *F. p. tundrius* female trapped in a building in Lima after crashing through a skylight while capturing a West Peruvian Dove (*Zeneida meloda*; A. García Alcazar pers. comm.; Table 1, number 8). Subsequently rescued and released, she bore a blue auxiliary band received in 2016 as an ASY bird in Nunavut.

In addition to the five band encounters we report above, the BBL provided details of three additional encounters of banded Nearctic peregrines of known natal or breeding origins (Table 1). The BBL also provided records of 13 other band encounters of Nearctic peregrines in Peru between 1960 and 2018 (D. Bystrak pers. comm.), all of which were banded on migration stopovers on the Atlantic and Gulf of Mexico coasts of the USA (Table 2, Fig. 2). Although these individuals' natal origins cannot be determined from these data, they indicate that Peru-bound peregrines have used routes that include coastal areas and offshore islands of Texas ($n = 7$), New Jersey ($n = 3$), Virginia ($n = 2$), and North Carolina ($n = 1$). The majority of these individuals (62%) were female, and many were banded at migration stopovers used primarily by female peregrines (e.g., Ward et al. 1988, Fuller et al. 1998)

Earliest Arrival Records of Wintering Nearctic Migrants in Peru. The earliest known arrival date of a wintering Nearctic peregrine in South America, to our knowledge, was reported as 20 September 2010 in Manizales, Colombia (A. Ospina pers. comm.). Most (57%) Peru band encounter records in the BBL database with known dates occurred in December, but the earliest, on 4 October 1969, represented a 6-yr-old bird of unknown sex that had been banded in 1963 in Canada's Northwest Territories (Table 1). We received a report of a sighting of a Nearctic peregrine in Lima on 23 September 2015, and confirmed the presence of an adult male with features typical of a *F. p. tundrius*. A bird that appeared to be the same individual returned to the same site on 1 October 2016, and 4 October 2017 (M. Mispireta Robles pers. comm.). In addition, an adult male Nearctic peregrine was reported in Chiclayo, Peru, on 1 October 2015 (F. Angulo Pratolongo pers. comm.). These records appear to be the earliest known arrival dates for Nearctic peregrines wintering on or near the Peruvian coast.

Discussion

Nearctic peregrines wintering in Peru include individuals of both *tundrius* and *anatum* subspecies that originate from a widespread geographic breeding range in North America. In addition to the eight

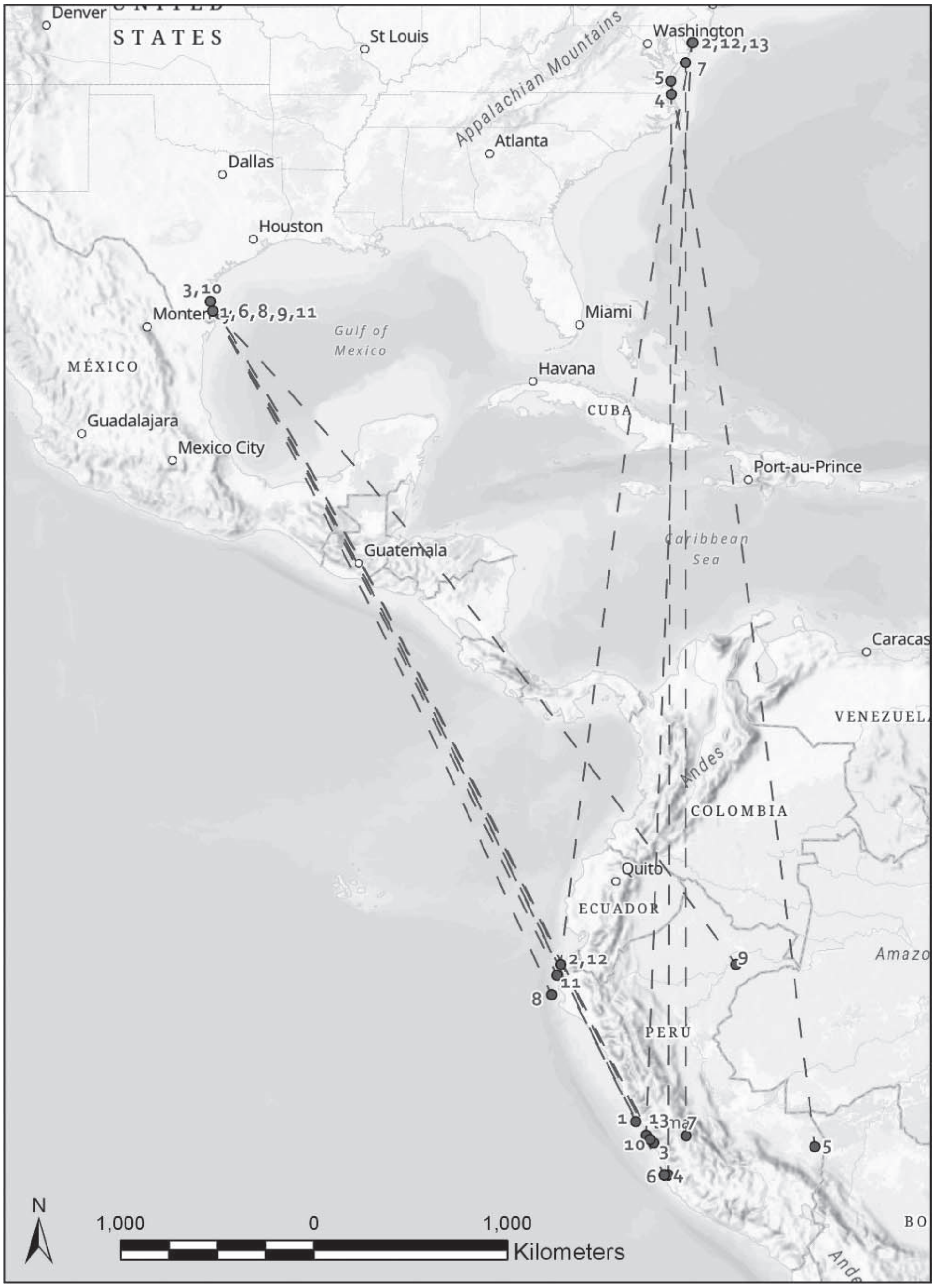

Figure 2. Peregrine Falcons wintering in Peru linked to their migration stopover sites in North America (see Table 2 for details).

Nearctic migrant peregrines originating in Canada and the USA that we report, at least two recoveries of Neartic migrants banded in Greenland have been reported in Peru (both male *tundrius* peregrines; Mattox and Seegar 1996, Lyngs 2003). These findings corroborate other research indicating that Nearctic peregrine migration is highly dispersed, and that both *F. p. tundrius* and *F. p. anatum* peregrines converge during migration and overlap on their wintering grounds (Yates et al. 1988, McGrady et al. 2002, Lyngs 2003, White et al. 2002, 2013, 2020a, 2020b). In addition, recent genetic research has revealed the existence of both recent and historical gene flow between the *F. p. tundrius* and *F. p. anatum* populations, and evidence that these two subspecies are genetically indistinguishable (Brown et al. 2007, White et al. 2013, Talbot et al. 2017). Both *F. p. tundrius* and *F. p. anatum* individuals have been reported wintering in Argentina and Brazil (Ambrose and Riddle 1988), and our data indicate that individuals of both subspecies winter in Peru.

The high variation in Nearctic peregrines' migration movements across their breeding range (Fuller et al. 1998, Lewis and Kissling 2015) may be a manifestation of the behavioral plasticity associated with their demonstrated adaptability in response to recovery efforts following their extirpation from much of eastern North America. Peregrine Falcon siblings and members of breeding pairs from Greenland may follow different migration routes (Mattox and Seegar 1996, Lyngs 2003), so that their natal and breeding grounds do not appear to be reliable predictors of peregrines' wintering destinations. However, individual Nearctic peregrines observed in Peru demonstrate high wintering site fidelity (O. Beingolea unpubl. data), as they also do in Brazil (White et al. 2020a, 2020b), Mexico (McGrady et al. 2002), and Europe (Ganusevich et al. 2004), which contrasts with their weak connectivity on a population level.

Peregrines exhibit sex-related differential migration patterns, with males and females selecting different staging areas, flyways, and wintering areas (Kerlinger 1989, Bildstein 2006). For example, 71% of Nearctic peregrines at an important autumn migration stopover location on the USA's mid-Atlantic coast were female (Ward et al. 1988), and 98% of Nearctic peregrines observed wintering in Mexico were likewise female (McGrady 2002). Telemetry studies indicate that female *F. p. tundrius* from Greenland tend to winter in Central America or the Caribbean, whereas males tend to winter in South America (Restani and Mattox 2000). Male *F. p. tundrius* from Greenland may migrate nearly twice as far as females in winter, and juvenile male *F. p. anatum* from Canada may migrate nearly four times as far as juvenile females (Restani and Mattox 2000, Gahbauer 2008). Our trapping data from 1988–1995, together with the encounter data reported here, likewise suggest that Nearctic peregrines in Peru are predominantly males.

Southward migration of Nearctic peregrines through continental North America peaks in September–October, and is 4–6 wk earlier on the west coast than on the east coast, with timing through the interior believed to be intermediate (Worcester and Ydenberg 2008). The reports of wintering Nearctic peregrines in Peru observed on 24 September and 1 October represent an advance of approximately 2–3 wk from previously published arrival dates of Nearctic peregrines wintering in South America (Venezuela: Meyer de Schauensee and Phelps 1978; Colombia: Hilty and Brown 1986). In Peru, first arrivals of adult Nearctic peregrines have previously been reported for Lima between 8–14 October (O. Beingolea unpubl. data). First-year Nearctic peregrines, which may depart breeding grounds after adults, appear to first arrive in Peru in late October (O. Beingolea unpubl. data). The fact that 98% of our captures along Peru's coastal habitats were Nearctic migrants suggests that Peru's coastal habitats are disproportionately important for Nearctic birds, compared to resident peregrines during the austral summer.

The resounding comeback of Peregrine Falcons from endangered species status in North America exemplifies bird conservation success (Tordoff and Redig 1997, Cade and Burham 2003, Ambrose et al. 2016, Swem and Matz 2018), as well as the resilience and adaptability of this species. Bearing in mind our small sample size, it is notable that birds resulting from reintroduction efforts constitute a quarter of all BBL records to date of Nearctic peregrines with known origins wintering in Peru. The only birds we encountered from the contiguous United States, these two individuals emerged from a coordinated peregrine population restoration program in the Midwest under the supervision of the USFWS Eastern Peregrine Falcon Recovery Team (Tordoff and Redig 1997). The Nebraska male we trapped and released in 1995, named Sky King by the Nebraska Peregrine Falcon Project, nested in Omaha in 1993, 1994, and 1995 (Johnsgard 2014, Midwest Peregrine Society 2020), and in subsequent years was believed to be part of a breeding pair in Lincoln (WoodmenLife Tower Peregrine Falcon Watch 2020). The Minnesota male rescued from a soccer enclosure in Lima, named Lazy by the Midwest Peregrine Society, was released in January 2016 following rehabilitation at a local raptor breeder facility (O. Beingolea unpubl. data, Midwest Peregrine Society 2020). In addition to contributing to scientific research, these and other peregrines from successful reintroduction programs have served as a source of vital public engagement and education.

The data presented here advance our rudimentary understanding of Nearctic peregrine migration patterns and wintering locations and signifies a step toward elucidating peregrine migratory connectivity in South America, a continent that represents a major gap in our knowledge of peregrine distributions. Although their populations have largely recovered, peregrines' relatively low breeding densities and their status as apex predators, ensure that peregrines remain vulnerable to the consequences of human activities. Our encounters and observations of wintering Nearctic peregrines may reflect recent changes in their wintering distributions and arrival times, including advances of approximately 2–3 wk, similar to other long-distance migrants that have advanced their autumn migrations in the face of climate change (Jenni and Kéry 2003).

The ongoing emergence of new technologies to study migration, including new approaches using genetics, tracking devices, and stable isotopes, offers exciting possibilities to identify patterns and test hypotheses about migratory connectivity (Webster et al. 2002, Faaborg et al. 2010, Gow and Wiebe 2014, Marra et al. 2018). Peregrine migration connectivity in the Americas can be further elucidated through studies using telemetry and other tracking technologies (McGrady et al. 2002, Bayly et al. 2017); combining these innovations with field studies will allow us to continue to clarify the migratory connectivity and wintering locations of Nearctic-Neotropical peregrines and other species (Bayly et al. 2017). Continuing to address gaps in our existing knowledge of Nearctic peregrines' migratory connectivity and wintering locations will contribute to enabling full life-cycle conservation plans for this species.

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LITERATURE CITED

Ambrose, S., C. Florian, R. J. Ritchie, D. Payer, and R. M. O'Brien (2016). Recovery of American Peregrine Falcons along the upper Yukon River, Alaska. Journal of Wildlife Management 80:690–620.

Ambrose, R. E., and K. E. Riddle (1988). Population dispersal, turnover, and migration of Alaska peregrines. In Peregrine Falcon Populations: Their Management and Recovery (T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, Editors). The Peregrine Fund, Inc., Boise, ID, USA. pp. 677–684.

Bayly, N. J., K. V. Rosenberg, W. E. Easton, C. Gómez, J. Carlisle, D. N. Ewert, A. Drake, and L. Goodrich (2017). Major stopover regions and migratory bottlenecks for Nearctic-Neotropical landbirds within the Neotropics: a review. Bird Conservation International 28:1–26.

Beingolea O., and C. M. White (2003). First breeding record for *Falco peregrinus* in urban Lima, Peru, with remarks on the Peruvian breeding population. Journal of Raptor Research 37:84–85.

Bildstein, K. L. (2006). Migrating Raptors of the World: Their Ecology and Conservation. Cornell University Press, Ithaca, NY, USA, and London, UK.

Brown, J. W., P. J. van Coeverden de Groot, T. P. Birt, G. Seutin, P. T. Boag, and V. L. Friesen (2007). Appraisal of the consequences of the DDT-induced bottleneck on the level and geographic distribution of neutral genetic variation in Canadian Peregrine Falcons, *Falco peregrinus*. Molecular Ecology 16:327–343.

Bruggeman, J. E., T. Swem, D. E. Andersen, P. L. Kennedy, and D. Nigro (2015). Dynamics of a recovering Arctic bird population: the importance of climate, density dependence, and site quality. Ecological Applications 25:1932–1943.

Burnham W. A., and W. G. Mattox (1984). Biology of the peregrine and Gyrfalcon in Greenland. Bioscience 14:3–25.

Cade, T. J., and W. A. Burham (2003). Return of the Peregrine. The Peregrine Fund, Inc., Boise, ID, USA.

Cade, T. J., J. H. Enderson, C. G. Thelander, and C. M. White (Editors) (1988). Peregrine Falcon Populations: Their Management and Recovery. The Peregrine Fund, Inc., Boise, ID, USA.

eBird (2020). eBird: an online database of bird distribution and abundance. Peregrine Falcon. Cornell Lab of Ornithology, Ithaca, NY, USA. https://ebird.org/map/perfal.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3–48.

Fuller, M. R., W. S. Seegar, and L. Schueck (1998). Routes and travel rates of migrating Peregrine Falcons (*Falco peregrinus*) and Swainson's Hawks (*Buteo swainsonii*) in the western Hemisphere. Journal of Avian Biology 29:433–440.

Fyfe, R. W., S. A. Temple, and T. J. Cade (1976). The 1975 North American Peregrine Falcon survey. Canadian Field Naturalist 90:228–273.

Gabhauer, M. A. (2008). Breeding, dispersal, and migration of urban Peregrine Falcons in eastern North America. Ph.D. Dissertation, McGill University, Montréal, Québec, Canada.

Ganusevich, S. A., T. L. Maechtle, W. S. Seegar, M. A. Yates, M. J. McGrady, M. Fuller, L. Schuek, J. Dayton, and C. J. Henny (2004). Autumn migration and wintering areas of Peregrine Falcons *Falco peregrinus* nesting on the Kola Peninsula, northern Russia. Ibis 146:291–297.

Gow, E. A., and K. L. Wiebe (2014). Males migrate farther than females in a differential migrant: an examination of the fasting endurance hypothesis. Royal Society Open Science 1:140346. doi: 10.1098/rsos.140346.

Hilty, S., and L. Brown (1986). A Guide to the Birds of Colombia. Princeton University Press, Princeton, NJ, USA.

Holroyd, G. L., H. Trefry, and G. Court. (2007). The migration of four Alberta Peregrine Falcons in autumn 2006. Nature Alberta 37:14–17.

Jenni, L., and M. Kéry (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society B 270:1467–1471.

Johnsgard, P. (2014). Seasons of the Tallgrass Prairie: A Nebraska Year. Bison Books, Lincoln, NE, USA.

Kerlinger, P. (1989). Flight Strategies of Migrating Hawks. The University of Chicago Press, Chicago, IL, USA.

Kéry, M. (2002). New observations of the Peregrine Falcon (*Falco peregrinus*) in Peru. Journal of Raptor Research 36:213–217.

Kéry, M. (2007). Wintering Peregrine Falcons (*Falco peregrinus*) in the Peruvian Amazon. Ornitoligía Neotropical 18:613–616.

Koepcke, M. (1964). Las Aves del Departamento de Lima. Grafica Morson S. A., Lima, Peru.

Lewis, S. B., and M. L. Kissling (2015). Clarifying subspecies of Peregrine Falcons along the Lost Coast of Alaska. Journal of Raptor Research 49:367–375.

Lutmerding, J. A., M. Rogosky, B. Peterjohn, J. McNicoll, and D. Bystrak (2012). Summary of raptor encounter records at the Bird Banding Lab. Journal of Raptor Research 46:17–26.

Lyngs, P. (2003). Migration and winter ranges of birds in Greenland: Peregrine Falcon (*Falco peregrinus*). Dansk Ornitologisk Forenings Tidsskrift 97:56–59.

Maestre, L. A. M. (2007). Recuperações no Brasil de Falcões-peregrinos (*Falco peregrinus*) anilhados na América do norte entre 1967 e 2001. Ornitología 2:72–80.

Marra, P. P., E. Cohen, A.-L. Harrison, C. Studds, and M. Webster (2018). Migratory connectivity. Encyclopedia of Animal Behavior, Second Edition. doi:10.1016/B978-0-12-809633-8.20761-9.

Mattox, W. G., and W. S. Seegar (1996). 25 år med de Grønlandske van-drefalke. Tusaat/Forskning i Grønland 4:8–11.

McGrady, M. J., T. L. Maechtle, J. J. Vargas, W. S. Seegar, and M. C. Porras Peña (2002). Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. The Condor 104:39–48.

Meyer de Schauensee, R. M., and W. H. Phelps, Jr. (1978). A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ, USA.

Midwest Peregrine Society (2020). Searchable database on the Peregrine Falcon population in the Midwest and Canadian Great Lakes region from 1981 to the present. St. Paul, MN, USA. http://midwestperegrine.umn.edu/?vw=search.

Restani, L., and W. G. Mattox (2000). Natal dispersal of Peregrine Falcons in Greenland. The Auk 117:500–504.

Schmutz, J. K., R. W. Fyfe, U. Banasch, and H. Armbruster (1991). Routes and timing of migration of falcons banded in Canada. Wilson Journal of Ornithology 103:44–58.

Schoonmaker, P. K., M. P. Wallace, and S. A. Temple (1985). Migrant and breeding Peregrine Falcons in Northwest Peru. The Condor 87:423–424.

Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O'Neill, and T. A. Parker, III (2007). Birds of Peru. Princeton University Press, Princeton, NJ, USA.

Seegar, W. S., P. N. Cutchis, M. R. Fuller, J. J. Suter, V. Bhatnagar, and J. G. Wall (1996). Fifteen years of satellite tracking development and application to wildlife research and conservation. Johns Hopkins APL Technical Digest 17:401–411.

Swem, T., and A. C. Matz (2018). Natural history and recovery of Arctic Peregrine Falcons along the Colville River, Alaska 1981–2011. In Trends and Traditions: Avifaunal Change in Western North America (W. D. Shuford, R. E. Gill, Jr., and C. M. Handel, Editors). Studies of Western Birds 3. Western Field Ornithologists, Camarillo, CA, USA. pp. 132–147.

Talbot, S. L., G. K. Sage, S. A. Sonsthagen, M. G. Gravley, T. Swem, J. C. Williams, J. L. Longmire, S. Ambrose, M. J. Flamme, S. B. Lewis, L. Philipps, et al. (2017). Intraspecific evolutionary relationships among Peregrine Falcons in western North American high latitudes. PLoS ONE 12(11):e0188185. doi.org/10.1371/journal.pone.0188185.

Tordoff, H. B. and P. T. Redig (1997). Midwest Peregrine Falcon demography 1982–1995. Journal of Raptor Research 31:339–346.

Trierweiler, C., R. H. G. Klaassen, R. H. Drent, K.-M. Exo, J. Komdeur, F. Bairlein, and B. J. Koks (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. Proceedings of the Royal Society B 281:20132897. https://doi.org/10.1098/rspb.2013.2897.

Varland, D. E., J. B. Buchanan, T. L. Fleming, M. K. Kenney, and C. Vanier (2018). Scavenging as a food-acquisition strategy by Peregrine Falcons. Journal of Raptor Research 52:291–308.

Ward, F. P., K. Titus, W. S. Seegar., M. A. Yates, and M. R. Fuller (1988). Autumn migrations of Peregrine Falcons at Assateague Island, Maryland/Virginia 1970–1984. In Peregrine Falcon Populations: Their Management and Recovery (T. J. Cade, J. H. Enderson, C. G. Thelander and C. M. White, Editors). The Peregrine Fund, Boise, ID, USA. pp. 485–495.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

White, C. M., and D. C. Boyce (1988). An overview of Peregrine Falcon subspecies. In Peregrine Falcon Populations: Their Management and Recovery. (T. J. Cade, J. H. Enderson, C. G. Thelander and C. M. White, Editors). The Peregrine Fund, Boise, ID, USA. pp. 789–810.

White, C. M., T. J. Cade, and J. H. Enderson (2013). Peregrine Falcons of the World. Lynx Edicions, Barcelona, Spain.

White, C. M., D. A. Christie, E. de Juana, and J. S. Marks (2020a). Peregrine Falcon (*Falco peregrinus*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. https://www.hbw.com/node/53247.

White, C. M., N. J. Clum, T. J. Cade, and W. G. Hunt (2002). Peregrine Falcon (*Falco peregrinus*). In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna.org/Species-Account/bna/species/perfal.

White, C. M., N. J. Clum, T. J. Cade, and W. G. Hunt (2020b). Peregrine Falcon (*Falco peregrinus*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.perfal.01.

WoodmenLife Tower Peregrine Falcon Watch (2020). History of the WoodmenLife Falcons. https://www.woodmenlife.org/falcons/woodmenlife-falcon-history.cfm.

Worcester, R., and R. Ydenberg (2008). Cross-continental patterns in the timing of southward Peregrine Falcon migration in North America. Journal of Raptor Research 42:13–19.

Yates, M. A., K. E. Riddle, and F. P. Ward (1988). Recoveries of Peregrine Falcons migrating through the eastern and central United States, 1955–1985. In Peregrine Falcon Populations: Their Management and Recovery (T. J. Cade, J. H. Enderson, C. G. Thelander and C. M. White, Editors). The Peregrine Fund, Boise, ID, USA. pp. 471–484.

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