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

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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 lifecycles, and therefore 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 North American breeding grounds and migratory stopover sites, but the links between their breeding, stopover, and wintering areas remain poorly understood in the Americas. In particular, few empirical data are available on migratory Arctic (*F. p. tundrius*) and American (*F. p. anatum*) Peregrine Falcons (hereafter, Nearctic peregrines) wintering in South America during the austral

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spring and summer. Here, we present evidence connecting wintering Nearctic peregrines wintering in Peru with their natal and breeding territories in North America using multiple sources of mark-recapture data collected between 1963 and 2019. We document eight band encounters with wintering Nearctic peregrines in Peru of known natal or breeding origins, including banded birds from the Northwest Territories, Nunavut, and Yukon Territory in Canada as well as 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 where males tend to migrate farther than females, and our field sampling data of 208 Nearctic peregrines in Peru suggest that wintering migrants may comprise a majority of male birds (72%; *n*=150). We also report new records of Nearctic peregrine arrivals in Peru that represent advances of ~2-3 weeks compared to the earliest previously published reports. The high variability of peregrines' migratory movements may be a manifestation of the behavioral plasticity associated with their resilience in response to recovery efforts following their extirpation from much of eastern North America. As peregrines remain vulnerable to human impacts including habitat and climate change, continuing to address 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; *migratory connectivity; differential migration*; *Peru*; *South America*; *conservation*.

CONECTANDO LAS ZONAS DE INVERNADA DE HALCÓN PEREGRINO (*FALCO PEREGRINUS*) EN PERÚ CON SUS ÁREAS DE CRÍA EN NORTEAMÉRICA

RESUMEN.— Identificar las áreas de invernada y las rutas de migración 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 y, por tanto, para su conservación. Una de las especies de aves rapaces con mayor distribución mundial, el halcón peregrino (*Falco peregrinus*), ha sido objeto de intensa investigación en sus áreas de cría y zonas de paso en Norteamérica, sin embargo, la conectividad entre sus áreas de cría, paso e invernada están aún poco estudiadas en las Américas. Existen pocos datos empíricos disponibles sobre las áreas de invernada en América del Sur, incluyendo Perú, de las poblaciones migratorias de halcones peregrinos árticos y americanos ((*Falco peregrinus tundrius, F. p. anatum;* posteriormente peregrinos neárticos). En este estudio, utilizando múltiples fuentes de datos de captura-recaptura recopilados entre 1982 y 2019, presentamos evidencias de conexión entre las poblaciones de peregrinos Neárticos invernantes en el Perú con sus territorios natales y de reproducción en América del Norte. Documentamos 8 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 Yukon en Canada, además de Alaska, Minnesota y Nebraska en Estados Unidos. A pesar de que individuos particulares pueden mostrar una fuerte fidelidad en sus áreas de invernada, los datos sugieren que los peregrinos neárticos que invernan en Perú presentan una conectividad migratoria débil, ya que los individuos son originarios de una zona de cría geográficamente amplia, y que ambas subespecies *tundrius* y *anatum* se superponen en sus áreas de invernada. Los halcones peregrinos muestran patrones migratorios diferenciales entre sexos, y 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 llegadas de peregrinos de invernada en Perú, que representan un avance de ~ 2-3 semanas en comparación con los primeros informes publicados anteriormente. Estos hallazgos subrayan cómo, a pesar de su resiliencia, los peregrinos son vulnerables a las consecuencias del impacto humano incluyendo los cambios de hábitat y climático, aún después de los exitosos esfuerzos de conservación y recuperación de la especie tras su eliminación de la mayor parte del este de Norteamérica. Continuar enfocándose en responder los vacíos existentes en el conocimiento sobre la conectividad migratoria de los peregrinos neárticos permitirá que se mejoren las medidas de conservación de estas espectaculares aves.

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 North American breeding sites and migratory stopover sites, but the links between breeding, stopover, and wintering areas of migratory individuals and populations have remained largely unexplored. Due to the significant challenges to tracking birds' movements at different stages of their annual cycles (Webster et al. 2002, Faaborg et al. 2010, Marra et al. 2018), few data are available on peregrines' migratory connectivity, particularly in South America (Schoonmaker et al. 1985, McGrady et al. 2002, Kéry 2007).

Four of the 19 currently recognized Peregrine Falcon subspecies in the world occur in the Americas, of which two are migratory and two generally year-round residents (Cade et al. 1988, White et al. 2002, White et al. 2018). Migratory North American subspecies include Arctic (*F. p. tundrius*) and American (*F. p. anatum)* Peregrine Falcons (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. White et al. 2018). *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 never been well-defined (White et al. 2002, White et al. 2013, Talbot et al. 2017). Resident subspecies in the Americas include *F. p. pealei*, which inhabits the North American northwest Pacific coast, Alaskan Peninsula and Aleutian Islands year-round, and *F. p. cassini*, which resides in South America, including Peru, and offshore islands year-round (White et al. 2018).

Never abundant in North America, Peregrine Falcons underwent catastrophic declines between the 1940's and 1970's due to reproductive failure caused by the pesticide DDT (White et al. 2002, 2018). As a result, *tundrius* Peregrine Falcon populations exhibited >50% declines, and *anatum* Peregrine Falcons 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 *tundrius* and *anatum* Peregrine Falcons the focus of intense recovery and conservation efforts, including reintroduction programs using captive-bred birds (Ambrose et al. 2016, Talbot et al. 2017, White et al. 2018). However, major knowledge gaps persist in our knowledge of Nearctic peregrines' migratory movements (White et al. 2002, Lyngs 2003, White et al. 2013), and their responses to climatic variation and prey population dynamics and movements (Bruggeman et al. 2015). Research priorities for Nearctic peregrines include monitoring the distribution of reintroduced and recovering populations and investigating wintering locations of breeding populations (i.e., migratory connectivity) (White et al. 2002, Faaborg et al. 2010, White et al. 2013, Bayly et al. 2017, White et al. 2018).

Tracking birds' movements throughout their annual cycles is particularly important for Nearctic peregrines as they may spend the majority of their lives (~7 months/year) outside of their breeding range (Schmutz et al. 1991, Seegar et al. 1996, White et al. 2002). Southward migration of Nearctic peregrines through continental North America peaks in September-October, and is 4–6 weeks earlier on the west coast than the east coast, with timing through the interior believed to be intermediate between the coasts (Worcester and Ydenberg 2008). Migrant peregrine distributions are not well defined in Peru (Kéry 2002, 2007), as some sources have reported wintering *tundrius* migrants (Schoonmaker et al. 1985, White et al. 2002, ebird 2019) and others predominantly or solely *anatum* migrants (Koepke 1964, Schulenberg et al. 2007). Nearctic peregrine surveys in South America are 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, particularly in coastal areas (OB, pers. obs.).

Mark-recapture data and specifically bird band encounters provide insights into important 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 over 54,000 encounter reports of banded raptors during the period 1960–2008, including 160 peregrines mainly in the northern South American countries of Ecuador, Columbia, and Venezuela as well as 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 regarding their natal origins (White et al. 2018). Nearctic peregrines are well-known along the Chilean coast (C. Anderson, *in litt.*), and Kéry (2002) reported observations of 28 peregrines in Peru during the northern winters in 1996 and 2001-2002, but whether or what proportion of these birds were residents or Nearctic migrants could not be determined. Banded Canadian-breeding *anatum* have been reported in Brazil (Maestre 2007) and Columbia (Holroyd et al. 2007), and Alaska-breeding *anatum* have been recovered in Ecuador, Argentina, and Brazil (Ambrose and Riddle 1988), but no banded *anatum* birds have been reported for Peru until now.

METHODS

Study Area and Field Sampling. From 1988 to 1995, we spent approximately 1000 hours 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 ~10 million people. Sandy beaches and mudflats along Peru's north and central coast provide important habitat for shorebirds (e.g. Scolopacidae) and other waterbirds, particularly boreal migrants (Schulenberg et al. 2007). Shorebirds are important prey for Nearctic peregrines (Worcester and Ydenberg 2008, Varland et al. 2012), who are known for their affinities for coastal habitats in the non-breeding season (Schmutz et al. 1991, Fuller et al. 1998). We also conducted ~50 hours of sampling in Peru's interior Andes in the department of Pasco (10.45 ° S, 75.15 ° W), in high elevation (4100 m asl) puna grasslands.

Band Encounter Data. We obtained band encounter data in three ways: (1) we caught previously banded birds in the course of our field sampling of peregrines in Peru and reported banded birds to the NABBP; (2) OB received reports of injured or trapped falcons in Lima with bands that we reported to the NABBP; and (3) we requested all additional band encounter records of Nearctic peregrines in Peru from the NABBP database, which were provided to us by the the U. S. Geological Survey (USGS) Bird Banding Laboratory (BBL) (D. Bystrak, pers. comm.). Following protocols developed by the NABBP, peregrines were banded with uniquely numbered aluminum leg bands and some were fitted with auxiliary markers in the form of colored leg bands with engraved alphanumeric codes, including blue for *tundrius* birds, black for wild *anatum* birds, and red for captive-bred *anatum* birds. Nearctic peregrines tend to be larger than Peruvian resident *cassini* birds (White et al. 2002, 2018), and during our field sampling, we used biometric measurements including wing length to distinguish Nearctic (>300 mm; White and Boyce 1988) from resident *cassini* birds, as well as to sex birds.

RESULTS

From 1988 to 1995, we captured and banded a total 213 birds, of which 208 (98%) were Nearctic migrants; 72% (*n*=150) of Nearctic migrants were male. Two of the Nearctic peregrines we captured had been banded on their natal or breeding grounds and we subsequently received reports of three additional banded Nearctic peregrines in Lima. All five bands encountered were reported to the BBL and are described below; the BBL also provided details of three additional Nearctic peregrines encountered in Peru (D.

Bystrak, pers. comm.). To our knowledge, these eight individuals represent all records from the NABBP of marked Nearctic peregrines with known natal or breeding origins found wintering in Peru (Table 1). Of these eight individuals, two were of unknown sex and five of the six birds (83%) of known sex were male. The map (Fig. 1) indicates the links between these eight falcons' natal and wintering grounds, representing straight-line migration distances ranging from 6,430-10,670 km.

Band Encounters. Below we present details of each of our five encounters with banded Nearctic peregrines in Peru (Table 1, Fig. 1). In addition, we report the two earliest known records for Peregrine Falcons wintering in Lima, Peru (-12°S, 77°W), from 24 September and 1 October, representing an advance of ~2-3 weeks from the earliest previously published reports of birds wintering in South America.

1. In 1989, in coastal Ica, we captured and released a banded *tundrius* male bearing a blue auxiliary band received in 1982 as an after-second-year (ASY) bird in Nunavut.

2. In 1995, in coastal Ica, we captured and released a banded *anatum* male bearing a black auxiliary band received in 1989. This bird was bred in captivity and released to the wild in Nebraska, where he returned to reproduce successfully in 1994 and 1995 (P. Redig, pers. comm.).

3. In 2006, we received a report of a banded *anatum* male recovered at Las Leyendas Zoological Park, Lima, in the summer of 2000 or 2001. This bird had a black auxiliary band received in 1998 as a nestling in 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 this bird from returning north, and/or he was kept in captivity for at least several months before arriving at the zoo.

4. In 2015, we received a report of a banded *anatum* male accidentally trapped in a soccer enclosure in Callao, Lima. Subsequently rescued and released, this bird bore black and red auxiliary bands received months earlier in 2015 as a nestling in Minnesota, the descendant of a successful reintroduction program.

5. In 2019, we received a report of a banded *tundrius* female trapped in a building in Lima after successfully depredating a Pacific Dove (*Zeneida meloda*). Subsequently rescued and released, she bore a blue auxiliary band received in 2016 as an ASY bird in Nunavut.

We provide details of three additional band encounters with Nearctic peregrines of known natal or breeding origins from the NAABP database in Table 1. In addition, the NABBP received reports 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). While 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 13 individuals (62%) were female, perhaps in part because they were banded at stopovers primarily used by migrating female peregrines (e.g., Ward et al. 1988, Fuller et al. 1998)

Earliest Arrival Records of Wintering Nearctic Migrants in Peru. The earliest arrival of a wintering Nearctic peregrine in South America, to our knowledge, was 20 September at Manizales, Columbia (A. Ospina, pers. comm.). Most (57%) Peru band encounter records in the NABBP database with known dates occurred in December, but the earliest, on 4 October 1969, represented a six-year-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 *tundrius* peregrine. A bird with the same appearance, who was likely 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.).

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 NABBP band encounters we report in Peru of Nearctic migrants of known origin in Canada and the US (Fig. 1), at least two band recoveries in Peru of *tundrius* Nearctic migrants from Greenland have been reported (Mattox and Seegar 1996, Lyngs 2003). These findings corroborate other research indicating that Nearctic peregrine migration is highly dispersive, and that both *tundrius* and *anatum* peregrines converge during migration and may overlap considerably on their wintering grounds (Yates et al. 1988, McGrady et al. 2002, Lyngs 2003, White et al. 2002, 2013, 2018). Both *tundrius* and *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 and distances across their breeding range (Fuller et al. 1998, Lewis and Kissling 2015) may be a manifestation of the behavioral plasticity associated with their demonstrated resilience in response to conservation and recovery efforts following their extirpation from much of eastern North America. Recent genetic research has revealed the existence of both current and historical gene flow between the *tundrius* and *anatum* populations, and evidence that these two subspecies were genetically indistinguishable historically (Brown et al. 2007, White et al. 2013, Talbot et al. 2017). Individual genetic variation may influence connectivity between the natal, breeding, and wintering sites of individual birds, such as those we describe here. Findings from Nearctic peregrines breeding in Greenland, for example, show that siblings and members of breeding pairs may follow different migration routes (Mattox and Seegar 1996, Lyngs 2003). Individual Nearctic peregrines observed at wintering sites in Peru demonstrate high wintering site fidelity (OB, pers. obs.), as they have been observed to do in Brazil (White et al. 2018), in contrast to 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, over 99% of Nearctic peregrines sampled at a migratory stopover location on the USA's mid-Atlantic coast were female (Ward et al. 1988), and 94% of Nearctic peregrines sampled wintering in Mexico were likewise female (McGrady 2002). Telemetry studies have revealed that female *tundrius* peregrines from Greenland tend to winter in Central America or the Caribbean, whereas males tend to winter in South America (Restani and Mattox 2000). Correspondingly, male *tundrius* peregrines from Greenland may migrate nearly twice as far as females in winter, and juvenile male *anatum* peregrines from Canada may migrate nearly four times as far as juvenile females (Restani and Mattox 2000, Gahbauer 2008). Our Nearctic peregrine sampling data from 1988-1995, together with the full list of Nearctic peregrines of known sex and natal and/or breeding origins in Peru, likewise suggest that Nearctic peregrines in Peru comprise predominantly male birds.

The reports of wintering Nearctic peregrines in Peru observed on 24 September and 1 October, represent an advance of ~2-3 weeks from previously published references of arrival dates of Nearctic peregrines wintering in South America (Meyer de Schauensee 1978, Hilty and Brown 1986). In Peru, first arrivals of adult Nearctic peregrines have previously been observed in Lima between 8-14 October (OB, pers. obs.). First-year Nearctic peregrines, which may depart breeding grounds later than adults, appear to first arrive in Peru in late October (OB, pers. obs.). 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 data presented here contribute to our rudimentary understanding of Nearctic peregrine migration patterns and wintering locations and represents a step towards elucidating peregrine migratory connectivity in South America, a continent that represents a major gap in our knowledge of peregrine distributions. While their populations are now considered to have fully recovered, peregrines' relatively low breeding densities and reproductive rates and their status as apex predators mean that peregrines remain vulnerable to the consequences of human activities. Our encounters and observations of wintering Nearctic peregrines may also reflect recent changes in their wintering distributions and arrival times, including advances of ~2-3 weeks compared to previous reports, similar to other long-distance migrants who have advanced their autumn migrations under climate change (Jenni and Kery 2003).

The resounding comeback of Peregrine Falcons from their status as endangered species in North America exemplifies the possibilities of coordinated, targeted bird conservation efforts (Cade and Burham 2003, Ambrose et al. 2016, Monroe 2017, Swem and Matz 2018). The ongoing emergence of new technologies to study migration, including new approaches using genetics, tracking devices, and stable isotopes, offer 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 should be further elucidated through the publication of studies using telemetry and other tracking technologies as well as targeted field studies (McGrady et al. 2002, Bayly et al. 2017). Combining these innovations with field studies should 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 these spectacular birds.

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[Table 1: See Attachment 1]

[Table 2: See Attachment 1]

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

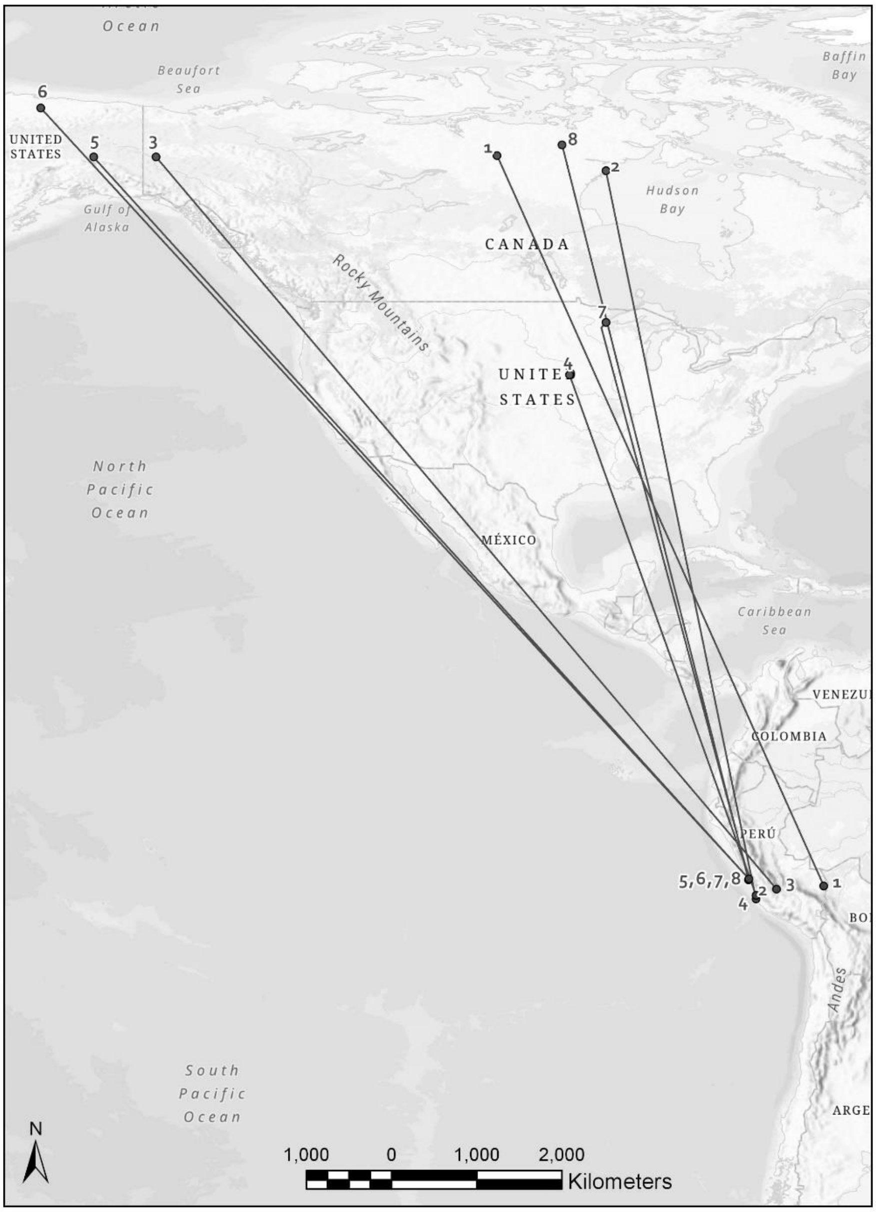

Figure 2. Peregrine Falcons wintering in Peru linked to their migration stopover sites in North America (see Table 2 for details).