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CLARIFYING SUBSPECIES OF PEREGRINE FALCONS ALONG THE LOST COAST OF ALASKA

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ABSTRACT.—The concept of subspecies is an important tool to help categorize and conserve biodiversity; thus, delineating the range of subspecies can have important management and conservation implications. The Peregrine Falcon (*Falco peregrinus*) is a widespread species that occurs throughout North America, where three subspecies are recognized: *F. p. anatum*, *F. p. pealei*, and *F. p. tundrius*. In Alaska, all three subspecies breed and their general distributions during the breeding season are well documented. However, the limits of their distributions were unclear or unconfirmed, especially those of *F. p. anatum* and *F. p. pealei* along the Lost Coast in the northeastern Gulf of Alaska. We describe plumage, morphology, and/or movements of Peregrine Falcons known to have nested (n = 6) or hatched (n = 3) within the Lost Coast and used this information to determine their subspecific group. For all nine birds, we found these characteristics to be consistent with *F. p. anatum*. Our results underscore the importance of delineating geographic range and distribution of subspecies prior to environmental catastrophes and to ensure reliable interpretation of species status and trends. We believe this type of life-history and demographic information will become even more valuable as the effects of a changing climate are realized.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *Alaska*; *morphology*; *plumage*; *subspecies*.

CLARIFICACIÓN DE LAS SUBESPECIES DE *FALCO PEREGRINUS* A LO LARGO DE LA COSTA PERDIDA DE ALASKA

RESUMEN.—El concepto de subespecie es una herramienta importante para ayudar en la categorización y conservación de la biodiversidad; por lo tanto, definir el rango de subespecie puede tener importantes implicaciones en gestión y conservación. *Falco peregrinus* es una especie de amplia distribución en toda América del Norte, donde se reconocen tres subespecies: *F. p. anatum*, *F. p. pealei* y *F. p. tundrius*. En Alaska, las tres subespecies se reproducen y sus distribuciones durante la época reproductiva están bien documentadas a grandes rasgos. Sin embargo, los límites de sus distribuciones estaban poco claros o sin confirmación, especialmente los de *F. p. anatum* y *F. p. pealei*, a lo largo de la Costa Perdida en la parte noreste del Golfo de Alaska. Describimos el plumaje, la morfología y/o los movimientos de individuos de *F. peregrinus* que se sabe que nidificaron (n = 6) o eclosionaron (n = 3) dentro de la Costa Perdida y utilizamos esta información para determinar su grupo subespecífico. Para las nueve aves, encontramos que estas características eran consistentes con la subespecie *F. p. anatum*. Nuestros resultados subrayan la importancia de definir el rango geográfico y la distribución de las subespecies antes de la ocurrencia de catástrofes ambientales y para asegurar una interpretación fiable del estatus y de las tendencias de la especie. Creemos que este tipo de información de la historia de vida y de la demografía va a ser incluso más valiosa a medida que los efectos del cambio climático se materialicen.

[Traducción del equipo editorial]

A subspecies is defined as a breeding segment of a species that occupies a portion of the species' geographic range and that is measurably distinct in phenotype, genotype, or both (Mayr 1982, James 2010). This concept is an important tool used to help categorize, study, and conserve biodiversity (Winker 2010), but there has been much debate

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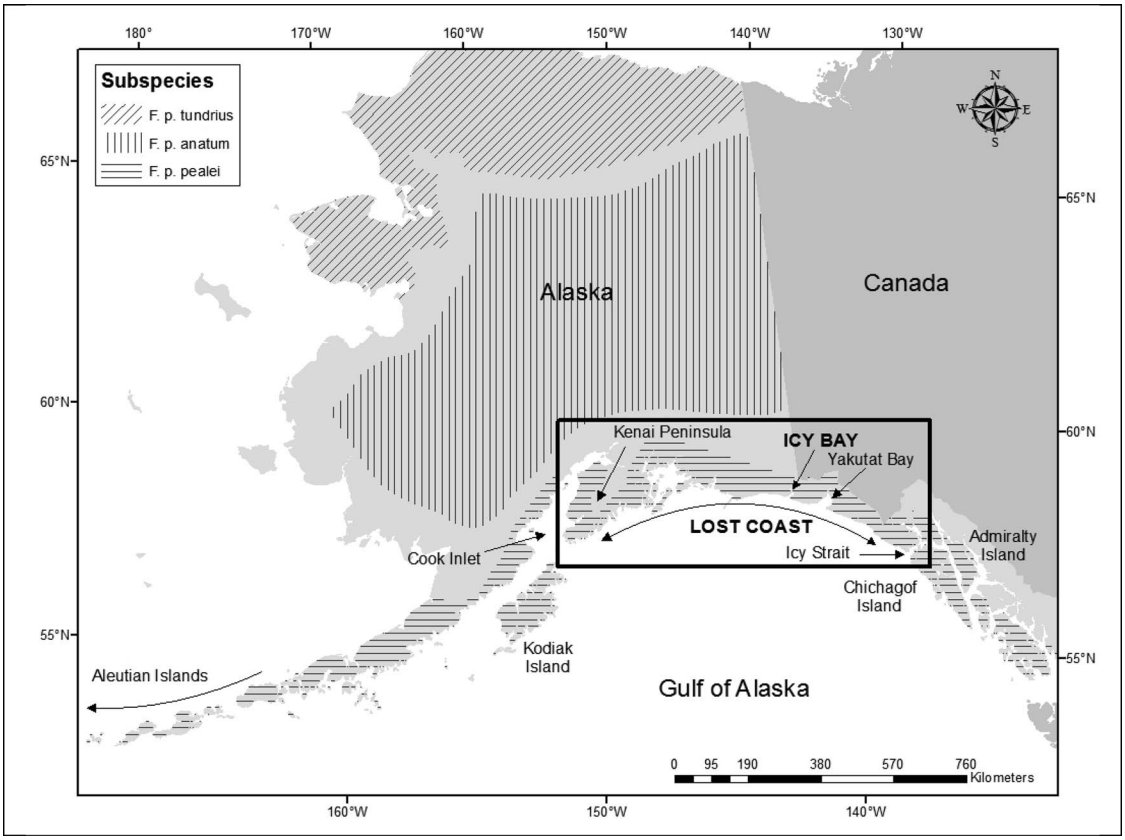

Figure 1. Map of previously assumed approximate distribution of three Peregrine Falcon subspecies in Alaska (see text for detailed description and citations); prominent place names mentioned in text are shown, including Icy Bay study area (in bold capital letters). Inset box shows Lost Coast area where we clarified Peregrine Falcon subspecies occurrence as a result of this study. We conclude that *F. p. anatum*, not *F. p. pealei*, occur along the Lost Coast of Alaska.

about its application (Zink 2004, 2006, James 2010). In a management context, it is useful because a subspecies often is expected to define an evolutionarily independent unit (Wilson and Brown 1953, Mayr 1982, Phillimore and Owens 2006), and thus, subspecies can be protected separately in North America under both the U.S. Endangered Species Act (16 USC 1531–1544) and the Canadian Species at Risk Act (S.C. 2002, c. 29; Haig et al. 2006, Haig and D'Elia 2010, Waples et al. 2013). For these reasons, delineating the range of subspecies, or determining what subspecies occurs in an area can have important management and conservation implications (Lawton 1993), especially when assessing threats to populations.

The Peregrine Falcon (*Falco peregrinus*) is a widespread species that occurs throughout North America, where three subspecies currently are recognized: *F. p. anatum*, *F. p. pealei*, and *F. p. tundrius* (White and Boyce 1988, White et al. 2002). These subspecies were differentiated from one another by breeding range, plumage, and morphological characteristics, and migration behavior originally (White 1968, White and Boyce 1988), and to some degree by genetic differences more recently (Brown et al. 2007, White et al. 2013a). In general, *F. p. tundrius* breeds in tundra habitats of northern Alaska, Canada, and Greenland, *F. p. pealei* breeds along the northern Pacific coast of northern Oregon, Washington, British Columbia, and Alaska, and *F. p. anatum* breeds in the remainder of North America (Fig. 1; White et al. 2002). There is considerable overlap in plumage among Peregrine Falcon subspecies (Clark and Wheeler 2001, Wheeler 2003, Liguori 2005), but general patterns exist that are germane to this comparison. Specifically,

Table 1. Morphological characteristics of Peregrine Falcons measured in Icy Bay, Alaska, 2010–2011, with values from birds of known subspecies for comparison.

SEX	GROUP[1]	WING-CHORD (mm)[2]	TAIL (mm)[2]	CULMEN (mm)[2]
Male	Icy Bay (n = 3)	315.3 ± 4.5 (311–320)	146.0 ± 4.4 (141–149)	19.5 ± 0.0 (19.5–19.5)
	F. p. anatum (n = 36)	306.0 ± 3.9 (291–318)	142.6 ± 6.1 (130–155)	19.8 ± 0.1 (18–22)
	F. p. pealei (n = 32)	318.6 ± 5.2 (305–334)	151.5 ± 5.8 (143–162)	20.1 ± 1.4 (17–22)
	F. p. tundrius (n = 82)	308.3 ± 4.7 (292–330)	140.2 ± 4.9 (130–154)	18.8 ± 0.0 (17–21)
Female	Icy Bay (n = 2)	361.5 ± 2.1 (360–363)	185.5 ± 14.8 (175–196)	22.7 ± 0.2 (22.6–22.8)
	F. p. anatum (n = 45)	349.8 ± 5.8 (333–363)	170.3 ± 6.6 (160–187)	23.9 ± 0.0 (20–25)
	F. p. pealei (n = 27)	363.9 ± 5.8 (347–375)	179.6 ± 4.5 (172–194)	24.4 ± 1.0 (23–27)
	F. p. tundrius (n = 81)	342.4 ± 6.4 (333–368)	168.6 ± 5.6 (153–180)	22.8 ± 0.3 (21–25)

[1] Values from White (1968), cited in White et al. (2002).
[2] Data presented as mean ± SD (range).

F. p. tundrius shows the palest plumage of the three subspecies. *F. p. anatum* is generally darker than *F. p. tundrius*, but lighter colored than *F. p. pealei* with less speckling than *F. p. pealei* on the ventral surface, a clean breast (i.e., little or no markings), and a pink to salmon wash on the belly. *F. p. pealei* is darker overall, with a different shade of blue on the back, dark markings between the breast and crop, and no wash on the belly. *F. p. tundrius* and *F. p. anatum* are similar in size (based on standard morphometric measurements), whereas *F. p. pealei* is larger (Table 1; White et al. 2002). Finally and most definitively, *F. p. tundrius* and northern *F. p. anatum* exhibit long-distance migration, with destinations varying from the southern reaches of the U.S. to Central and South America. *F. p. pealei* is largely nonmigratory or shows only short-distance migration, but has been documented as far south as Baja California Sur, Mexico (based on museum specimens; Ambrose and Riddle 1988, White et al. 2013b).

Alaska is the only region where all three North American Peregrine Falcon subspecies currently breed (White et al. 2002). However, their respective distributions in the state are somewhat unclear or unconfirmed in some areas, especially those that are remote and difficult to access. In an early account of birds in Alaska, Gabrielson and Lincoln (1959) described two distinct geographic races of Peregrine Falcons breeding in Alaska: *F. p. anatum* occurring in interior Alaska, and *F. p. pealei* in the Aleutian Islands and from southeastern Alaska south into British Columbia (Fig. 1). The authors did not find any Peregrine Falcons nesting along the Lost Coast of Alaska during their surveys, nor did Shortt (1939) in Yakutat Bay, but Gabrielson and Lincoln (1959) referred to specimen records of *F. p. anatum*-type falcons taken within the previously described breeding range of *F. p. pealei* from Cook Inlet, Kenai Peninsula, Kodiak Island, and Yakutat Bay (Fig. 1). White (1968) described a new Peregrine Falcon subspecies occurring in tundra areas of northern Alaska. Since then, the general distribution of peregrine subspecies in Alaska was assumed as: *F. p. tundrius* in the northern tundra region, *F. p. anatum* in the forested interior, and *F. p. pealei* in coastal regions of the Aleutian Islands, northern Gulf of Alaska, and southeastern Alaska (Bond 1946, Ambrose et al. 1988, White and Boyce 1988).

There has been some question about which Peregrine Falcon subspecies occurs on the Lost Coast of Alaska (Ritchie 1981; R. Ritchie pers. comm.; C. White pers. comm.), defined here as approximately 1250 km of coastline in the northern Gulf of Alaska extending from the tip of the Kenai Peninsula south to Icy Strait (Fig. 1). Brooks (1926) and Beebe (1960) described the range of *F. p. pealei* as extending from Washington north along the coast and outer islands of British Columbia, Canada, into Alaska and along the coast and around to the Aleutian Islands. Bent (1938) raised doubts about the designation of Peregrine Falcons from the northern part of southeastern Alaska as *F. p. pealei*. White (1968) concurred and thought that birds north of Chichagof Island and the inside islands of southeastern Alaska (e.g., Admiralty Island) were "problematic in terms of subspecies allocation." Several authors, like Gabrielson and Lincoln (1959), assumed Peregrine Falcons breeding along the Lost Coast were *F. p. pealei* (Janik and Schempf 1985, Ambrose et al. 1988, Hughes and Sanger 1999, White et al. 2002). The confusion was exacerbated by apparent low numbers of Peregrine Falcons breeding along the Lost Coast (Isleib and Kessel 1973, Fyfe et al. 1976, Nishimoto and Rice 1987). Peregrine Falcons that

occur on either side of this stretch of coastline appear to be genetically distinct from one another, yet both are classified as *F. p. pealei* (White 1968, Johnson et al. 2010).

As part of a larger study on the raptor community in Icy Bay, Alaska, a small embayment in the center of the Lost Coast, we opportunistically investigated the subspecies of Peregrine Falcons currently occupying the region. Here, we summarize the first data collected on plumage, morphology, and/or movements of nine Peregrine Falcons known to have nested or hatched in this area where the subspecies was in question. We then used these data to determine the subspecific group of each individual.

METHODS

We studied Peregrine Falcons along the Lost Coast of Alaska coast in Icy Bay (59°58.62′N, 141°22.08′W; 110 km northwest of Yakutat, Alaska; Fig. 1). Icy Bay consists of a shallow outer bay adjacent to the northern Gulf of Alaska and a deep inner bay with total surface water covering approximately 240 km^2. The bay was entirely glaciated as recently as 1887, but since then, glacial retreat has caused the glacier fronts to retreat more than 45 km (Barclay et al. 2006). During this period, rocky outcrops and cliffs overlooking open ocean were formed or exposed, creating suitable nesting habitat for peregrines that was previously unavailable. Currently, these recently exposed cliffs provide habitat for at least five pairs of nesting peregrines (S. Lewis unpubl. data). During our study, Icy Bay had a maritime climate with mean temperatures of −5.0°C in January and 9.8°C in July, and mean annual precipitation of 290 cm (National Weather Service 2010).

We captured Peregrine Falcons in June–July 2010 and 2011 near their nesting sites using a dho-gaza net or bal-chatri baited with a rock pigeon (*Columba livia*; Bloom et al. 2007). We banded, measured, and photographed each falcon, and attached a solar-powered, Argos/GPS platform transmitter terminal unit (PTT-100, 22-g Solar Argos/GPS, Microwave Telemetry, Columbia, Maryland, U.S.A.) to each adult. We downloaded GPS locations via the Argos satellite network (CLS America, Lanham, Maryland, U.S.A.) at least every 10 d and plotted points using ArcGIS 10.1 (ESRI, Redlands, California, U.S.A.). We also took high-quality photographs of falcons that we failed to capture, or that nested in areas that were inaccessible or unsafe for us to attempt capture. We followed recommendations for capture and handling of birds (Fair et al. 2010).

We used a combination of photographs, morphometric measurements, and migration behavior to determine subspecies classification. We compared photographs of falcons in Icy Bay (captured and not-captured) to subspecies information provided in several field guides (Wheeler and Clark 1995, Clark and Wheeler 2001, Wheeler 2003, Liguori 2005). Specifically, we noted similarities and differences in the type of the malar stripe by category (Very wide type, Wide type, Moderately wide type, or Narrow type; following Wheeler 2003), presence or absence of spots on the breast and belly, and presence or absence of tawny/rufous color on the belly. We used a small blood sample to determine sex (Zoogen, Inc., Davis, California, U.S.A.). When available, we compared measurements of wing chord, tail, and culmen length of falcons from Icy Bay to published measurements of each peregrine subspecies in Alaska (White et al. 2002).

RESULTS

We captured six Peregrine Falcons (five adults, one fledgling), radio-tagged all five adults, and photographed three additional falcons (one adult, two fledglings) during summers 2010 and 2011. We captured Peregrine Falcons from three nesting territories across the two years. In 2010, we captured an adult male (10.01), an adult female (10.02), and a juvenile female (10.03) at neighboring, but independent, nesting territories. In 2011, we captured a different adult male (11.03) from the same territory as 10.01, and the nesting pair at the nesting territory where we had captured 10.03. We photographed Peregrine Falcons from two additional, but different, nesting territories. Thus, collectively we sampled Peregrine Falcons from five different nesting territories in Icy Bay.

Based on plumage characteristics, we categorized all Peregrine Falcons ($n = 9$) as *F. p. anatum*. All six adults had a Wide type malar stripe, clean breast, and spotted belly with tawny/rufous wash, and all three fledglings had a Moderately wide type malar stripe, narrow tawny forehead, no marking on the auricular area, and tawny/rufous wash on the breast and belly. Morphological measurements of five adults in our study area varied (Table 1). Wing chord and tail measurements were closer to mean values for *F. p. pealei* than to those for *F. p. anatum*; however, *F. p. anatum* from interior Alaska had wing chord measurements similar to those we measured (C. White pers. comm.). Hallux measurements were closer to values for *F. p. anatum* than to those for

F. p. pealei. Therefore, this small sample of measurements alone was not useful in differentiating subspecies.

We affixed transmitters to three male and two female adult Peregrine Falcons, all of which were nesting at the time of capture and successfully fledged young during that year. Four of five birds wore their transmitters until they left the bay on southward post-breeding migration. All four birds performed long-distance migrations from Icy Bay, and we determined the wintering location of three of four peregrines (Fig. 2). Peregrine 10.01 appeared to be still on his southbound migration when his tag stopped reporting in north-central Brazil (4°7.2′N, 62°22.8′W; distance = 9000 km; Fig. 2). Peregrine 11.01 wintered on the Marieta Islands in Banderas Bay, Tepic, Mexico (20°40.2′N, 105°39.0′W; distance = 5201 km; Fig. 2). Peregrine 11.02 wintered in the vicinity of Ojo de Liebre Lagoon (27°54.0′N, 114°9.0′W; distance = 4110 km; Fig. 2), near Guerrero Negro, Baja California Sur, Mexico. Peregrine 11.03 wintered along the Uruguay River near Ubajay, Argentina (31°50.4N, 58°9.6′W; distance = 12 645 km; Fig. 2). In 2010, peregrine 10.02 dropped her transmitter within 2 wk of deployment. However, this falcon was already banded when we captured her, having been previously captured as a hatch-year bird on South Padre Island, Texas, October 2001 (G. Doney pers. comm.).

DISCUSSION

Quantifying a species' distributional limits, and thus its geographic range, is a fundamental part of understanding its biology and is important for its conservation (Lawton 1993, Fortin et al. 2005). The same is true for subspecies (Winker 2010). Although much information about Peregrine Falcon subspecies was known (summarized in White et al. 2002), it remained unclear which subspecies occurred along the Lost Coast of Alaska (C. White pers. comm.; R. Ritchie pers. comm.). This was likely due to the difficult logistics of studying Peregrine Falcons in this area and possibly low numbers of Peregrine Falcons during the mid-20th century. All Peregrine Falcons we examined breeding in or fledged from Icy Bay showed plumage, morphological, and behavioral characteristics consistent with assignment to *F. p. anatum*. Subsequent to our Icy Bay work, Peregrine Falcons (n = 6) observed from close range at eyries during the breeding season in Kenai Fjords National Park (Fig. 1) also showed *F. p. anatum* characteristics (S. Lewis unpubl. data; L. Phillips pers. comm.). Although this was not an exhaustive sample of Peregrine Falcons throughout this portion of the Lost Coast, these observations suggest that Peregrine Falcons currently nesting across this area probably are *F. p. anatum*.

Peregrine Falcons can exhibit great variation in plumage coloration and morphometrics, even at the local scale (White et al. 2002). In fact, some Peregrine Falcon subspecies are known to show hybrid zones where neighboring breeding birds show characteristics of different subspecies (Zuberogoitia et al. 2009, White et al. 2013b). However, the falcons we examined in Icy Bay showed mostly uniform plumage characteristics. *F. p. pealei* are generally larger, perhaps reflecting differences in available prey or flight energetics, but morphological measurements overlap considerably between *F. p. anatum* and *F. p. pealei* (Table 1). Our measurements fell within the range of values for *F. p. anatum* and *F. p. pealei*, perhaps suggesting a potential hybridization zone (White et al. 2013b) or some degree of adaptation to coastal conditions by *F. p. anatum* Peregrine Falcons, and therefore were not helpful in classifying them to subspecies.

We found long-distance migratory behavior of peregrines from Icy Bay to be more compelling in terms of differentiating subspecies designation. All four Peregrine Falcons that maintained their tags migrated south of the southern border of the United States. The fifth bird dropped her tag prior to migration, but she had been banded as a hatch-year bird in 2001 on southbound migration in southern Texas through an area where migrating peregrines are commonly encountered (Seegar et al. 2003). This behavior suggests these birds were of the migratory *F. p. anatum*, not the comparatively nonmigratory *F. p. pealei* subspecies that was thought to occur along the Lost Coast of Alaska (Ambrose and Riddle 1988).

We only can speculate about which subspecies occupied this area historically, especially given natural and anthropogenic events that have occurred within the last few centuries. Prior to glaciation (200–300 yr ago; Barclay et al. 2006, Molnia 2008), *F. p. pealei* may have occurred along the entire Gulf of Alaska coast. Glaciation may have split the *F. p. pealei* population into two populations: one in southeastern Alaska and British Columbia and the other in the Aleutian Islands (Beebe 1960, Johnson et al. 2010). Our evidence suggests that habitat created or exposed by receding glaciers along the Lost

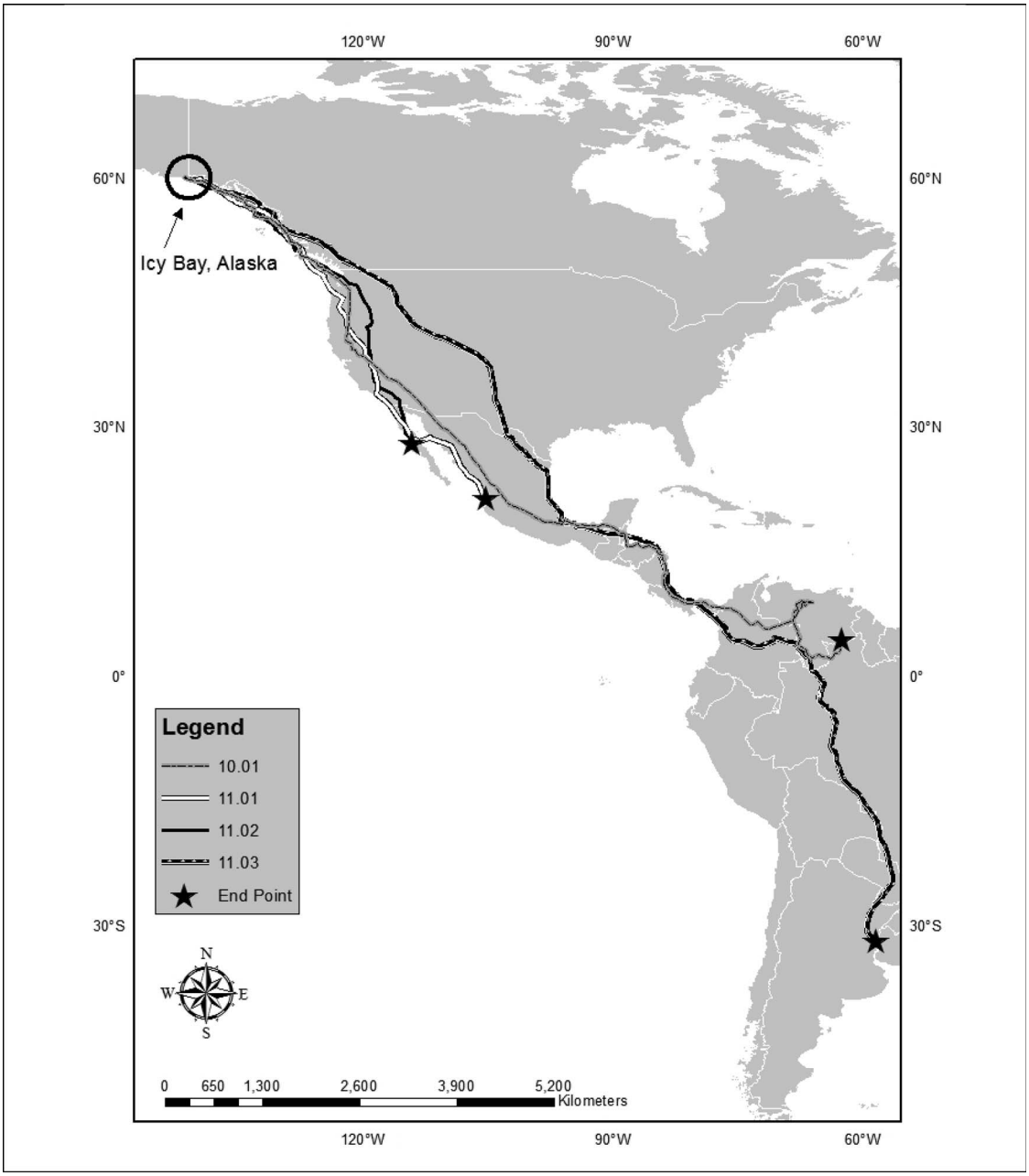

Figure 2. Migration routes of four Peregrine Falcons captured in Icy Bay, Alaska 2010–2011. Circle indicates study area (Icy Bay) and stars indicate final location during migration or wintering area.

Coast has been filled by *F. p. anatum* birds from the interior of Alaska.

During this range expansion by *F. p. anatum*, two anthropogenic factors may have served to slow it by reducing Peregrine Falcon populations in this area. First, during the mid-1900s, Peregrine Falcons experienced a well-documented population crash across much of their North American range due to exposure to dichloro-diphenyl-trichloroethane pesticide, presumably during migration and wintering (Kiff

1988, Enderson et al. 1995). As these effects diminished, the Exxon Valdez Oil Spill occurred in a portion of this population's range. The oil spill did not affect Peregrine Falcons directly, but it caused drastic declines in populations of many of the seabird prey on which coastal peregrines rely (Piatt et al. 1990, S. Lewis unpubl. data, L. Phillips pers. comm.). These anthropogenic factors are now diminished or gone (U.S.F.W.S. 2003, E.V.O.S.T.C. 2010) and most tidewater glaciers in the area continue to recede due to a warming climate (Arendt et al. 2002, Larsen et al. 2007, Molnia 2008). Thus, Peregrine Falcons are likely increasing along the Lost Coast and expanding into previously inhospitable habitats.

Our study underscores the importance of delineating geographic range and distribution of subspecies to ensure reliable interpretation of species status and trends. This allows managers to evaluate factors that may affect such populations throughout their annual cycle. We believe this type of basic life history and demographic information will prove to be more valuable as we realize the effects of a changing climate.

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