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PEREGRINE FALCONS ON COASTAL BEACHES OF WASHINGTON: FIFTEEN YEARS OF BANDING AND SURVEYS

DANIEL E. VARLAND¹ Coastal Raptors, 90 Westview Drive, Hoquiam, WA 98550 U.S.A.

JOSEPH B. BUCHANAN Cascadia Research Collective, Waterstreet Building, 218½ West Fourth Avenue, Suite 201, Olympia, WA 98501 U.S.A.

> TRACY L. FLEMING 2516 NE 148th Street, Vancouver, WA 98686 U.S.A.

MARY KAY KENNEY 872 Waterman Road South, Jacksonville, FL 32207 U.S.A.

THOMAS M. LOUGHIN Simon Fraser University, 250 – 13450 102 Avenue, Surrey, British Columbia V3T 0A3 Canada

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THOMAS M. LOUGHIN

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ABSTRACT.—Aspects of Peregrine Falcon (Falco peregrinus) migration along the northern Pacific coast are less well understood than are those along other flyways in North America. As part of a continuing long-term project, we captured and color-banded 140 Peregrine Falcons (90 females and 50 males, 105 of which were <1 yr old) during 841 surveys on three coastal beaches in Washington in all seasons between 1995 and 2010. Eighty-three percent of the falcons identified to subspecies (n = 137) were F. p. pealei, the northeastern Pacific coastal subspecies. Others had plumage characteristics consistent with F. p. anatum (n = 4), F. p. tundrius (n = 4) or showed intermediate characteristics (n = 15). Forty-seven percent (n = 75) of marked individuals were resignted alive, and 6.4% (n = 9) were recovered dead. Fifty-one peregrines exhibited beach-use fidelity, defined as reobservation on the same beach ≥ 1 d after banding, and >50%of these exhibited within-beach use fidelity, defined as reobservation in the same general area on the same beach ≥ 1 d after banding. Marked individuals were reobserved as far as 1019 km north on Langara Island, British Columbia, 1679 km south to the Salton Sea, California, and locally 83 km east to the Kennedy Creek estuary near Shelton, Washington. Future banding studies in coastal Washington designed to investigate migration strategies or space use by falcons would be informative and address information gaps in our understanding of peregrines on the North American Pacific coast. Additionally, data from banding programs may provide valuable input to models that in turn inform decisions on the sustainable take of F. p. pealei for falconry purposes.

KEY WORDS: Peregrine Falcon; Falco peregrinus; banding survey, trapping.

FALCO PEREGRINUS EN LAS PLAYAS COSTERAS DE WASHINGTON: QUINCE AÑOS DE ANILLAMIENTO Y DE MUESTREOS

RESUMEN.—Los aspectos de la migración del halcón *Falco peregrinus* a lo largo de la costa norte del Pacífico son menos conocidos que los de las otras rutas a lo largo de América del Norte. Como parte de un continuo proyecto de largo plazo, hemos capturado y marcado con anillas de color a 140 halcones (90 hembras y 50 machos, 105 de los cuales fueron de <1 año de edad) en 841 muestreos en tres playas de la costa de Washington en todas las temporadas entre 1995 y 2010. Ochenta y tres por ciento de los halcones identificados hasta el nivel de subespecies (n = 137) fueron *F. p. pealei*, la subespecie de la costa noreste del Pacífico. Otros tenían características del plumaje consistentes con *F. p. anatum* (n = 4), *F. p. tundrius* (n = 4) o

¹ Email address: danvarland@coastalraptors.org

mostraban características intermedias (n = 15). Cuarenta y siete por ciento (n = 75) de los individuos marcados fueron reavistados vivos, y el 6.4% (n = 9) fueron recuperados muertos. Cincuenta y un individuos mostraron fidelidad al uso de playas, definida como reobservación en la misma playa por >1 día después del anillado, y > 50% de estos exhibieron fidelidad de uso dentro de la playa, definida como reobservación en la misma área general en la misma playa por >1 día después del anillado. Individuos marcados fueron reobservados hasta 1019 km al norte de Langara Island, British Columbia, 1679 km al sur del Mar de Salton, California, y localmente 83 km al este del estuario Kennedy Creek, cerca de Shelton, Washington. Estudios futuros que consideren anillado en la costa de Washington que estén diseñados para investigar las estrategias de migración o el uso del espacio por parte de los halcones serían informativos y considerarían lagunas de información en nuestra comprensión sobre *F. sparverius* en la costa pacífica norteamericana. Además, los datos de programas de anillado pueden hacer un valioso aporte a los modelos, que a su vez, informan las decisiones sobre el uso sustentable de *F. p. pealei* para fines de cetrería.

[Traducción del equipo editorial]

Raptor banding in North America has been ongoing since the first part of the twentieth century. Federal banding offices opened in the United States in 1920 and in Canada in 1922 (Bildstein 2006). By 1935 more than 4000 raptors of 17 species had been banded in North America (Bildstein 2006). The first recovery of a banded Peregrine Falcon (Falco peregrinus) occurred on 28 September 1924, in New Jersey; this individual had been banded on 1 June 1924, in Massachusetts (D. Bystrak pers. comm.). Today the U.S. and Canadian banding offices hold more than 47000 electronic records on banded peregrines, including about 25000 records for peregrines with auxiliary markers (D. Bystrak pers. comm.). In 1973, F. Prescott Ward began a color-banding scheme for Peregrine Falcons captured on Assateague Island on the Atlantic coast in Maryland, thereby greatly increasing information gained from banded birds compared to aluminum bands used alone (Ward 1975). Patterned after a program developed for swans using visual identification (VID) bands, this color-marking scheme was one of the earliest established for raptors.

Sites along the Atlantic and Gulf coasts of North America have long been recognized as important areas for Peregrine Falcon migration. For example, the magnitude of the migration of tundra Peregrine Falcons (*F. p. tundrius*) was documented at Assateague Island in 1938 (Seegar et al. 2003) and numerous studies involving banding and telemetry have been conducted there (e.g., Ward and Berry 1972, Ward et al. 1988). Similarly, Padre Island on the southern coast of Texas was identified as an important area for migrating peregrines in 1890 (Griscom and Crosby 1925) and has been a study area for many investigations of the ecology and behavior of Peregrine Falcons (Hunt et al. 1975, Enderson et al. 1995, Juergens 2003; for review, see Seegar et al. 2003).

Few banding studies have been conducted of migrating or overwintering Peregrine Falcons on the northern Pacific coast of North America. Anderson et al. (1988) published the first comprehensive account of peregrine migration along the Pacific coast of North America, using information from band returns and field observations. Among the records reported were those of seven falcons previously banded or recovered in Washington, 71 sightings of fall migrant peregrines at Long Beach, on the southern Washington coast, and 22 captures of migrant falcons from the Washington coast. Movement patterns of overwintering Peregrine Falcons were later documented by VHF-radiotelemetry at Grays Harbor, Washington (Dobler and Spencer 1989), the northern Olympic Peninsula near Sequim, Washington (Dobler 1993), and at Vancouver Island, British Columbia (E. McClaren pers. comm.).

In 1995, we began a long-term banding study of raptors on the outer coast of Washington (Fig. 1), including color-marking and surveys of Peregrine Falcons and other species. We previously reported on survival rates, resighting rates, beach use fidelity, and subspecies occurrence for the period 1995 to 2003 (Varland et al. 2008a) and summarized the occurrence of F. p. tundrius through May 2007 (Varland et al. 2008b). Here we extend the analysis period to 15 yr (1995 to 2010) and document or update analyses for Peregrine Falcons relating to: (1) occurrence by subspecies, (2) site fidelity of marked individuals, and (3) observation rates by season and subarea. We also identify information gaps and topics relevant for future investigations involving banding of Peregrine Falcons in coastal Washington or elsewhere along the Pacific coast of North America.

STUDY AREA AND METHODS

Study Area. We conducted this study at three beaches on the southern Pacific coast of Washington



Figure 1. Map of the three study area beaches where we captured and banded Peregrine Falcons on the southern coast of Washington, U.S.A. Segments of the beaches that we covered in our search efforts are indicated by black lines.

(Fig. 1): Ocean Shores (23.5 km long), Grayland (11.3 km long), and Long Beach (39.6 km long). The beaches are generally broad and gently sloping expanses of sand backed by low dunes dominated by European beachgrass (*Ammophila arenaria*). For details of the study area, see Varland et al. (2008a).

Survey Methods. We conducted surveys on the beaches from January 1995 to May 2010. One to four experienced observers surveyed each beach in a four-wheel drive vehicle in all seasons, here defined as: fall (September-November), winter (December-February), spring (March-May), and summer (June-August). Due to unsafe driving conditions, time constraints, and other factors, we were occasionally unable to drive the full length of a beach during a survey. Therefore, for our assessment of within-beach use fidelity, we defined "complete beach coverage" as those surveys covering \geq 18.7 km at Ocean Shores (80% of full length), \geq 10.8 km at Grayland (96% of full length), and \geq 39.3 km (99% of full length) at Long Beach. For peregrine counts, we did not include results obtained during surveys with high winds (sustained >32 km/hr) or heavy fog. We counted only those peregrines associated with one or more of three adjacent habitats: beach, dunes, and ocean areas within 100 m of the beach. We did not count peregrines in surveys if we observed them after the vehicle was stopped >1 min (e.g., during capture attempts). We counted only peregrines observed while "on transect" during surveys, which is here defined as the length of beach surveyed by first passage of the survey vehicle (>1 pass was frequently made).

We determined peregrine counts from surveys with three patterns of beach travel. For one pattern (523 surveys), we drove the length of the beach in two passes with the "on transect" portion consisting of the first pass over the area. At Ocean Shores and Grayland we accessed the beach at a point approximately midway along the beach. In each case we drove north "on transect" from the access point to the north end of the beach, returned to the road access point and from there drove south "on transect" to the south end of the beach, before returning north "off transect" to the access point where we exited the beach. We alternated the starting direction at the access point for these surveys. The second pattern (103 surveys) occurred only at Long Beach where we accessed the beach at the southmost access road, drove "off-transect" to the south end of the beach, and then drove the entire length of the beach "on-transect." We then drove south "off-transect" to the start point at the south end of the beach, departing "off-transect" at the closest access road. The third pattern (71 surveys) occurred at all three beaches. For these surveys we accessed the beach at the access point nearest the south end, drove to the south end and initiated the survey at that point, driving the full length of the beach and exiting near the opposite end. We generally alternated the sequence of initial directions, except in situations when the tide was very high and this then influenced the width of some beach segments and the potential for unsafe traveling conditions.

Capture and Banding. We captured most peregrines with a harnessed Rock Pigeon (Columba livia) or European Starling (Sturnus vulgaris; Bloom et al. 2007). On occasion we captured peregrines using a dho gaza net, phai trap, or a noose carpet (Bloom et al. 2007). Each peregrine was banded with two bands: a U.S. Geological Survey lock-on band on one leg and an Acraft[®] color-coded alphanumeric rivet-on band, also known as a Visual Identification Band (VID), on the other leg. We began using anodized lock-on bands in 1999. We applied blueanodized bands to peregrines banded at Ocean Shores or Grayland and red-anodized bands to peregrines banded at Long Beach. TLF placed anodized bands on the left leg; DEV and MKK placed them on the right. We used black-blue VID bands from 1995-98 and in 1999 we adopted the international protocol for peregrine banding in North America (USGS 2010a).

On most occasions, we attempted to determine whether the peregrines we saw were already banded before we tried to capture them. We used a windowmounted spotting scope, or sometimes binoculars, to read alphanumeric codes on peregrines with color bands. We defined a reobservation as the identification of an individual peregrine by reading the alphanumeric code on its VID band with a spotting scope or with the bird in hand at recapture.

To determine the proportions of peregrines encountered during surveys that were banded, unbanded, or undetermined, we used data from surveys with peregrine counts (n = 697). We were unable to use all surveys (n = 841) for this determination because, on some surveys, we did not record whether peregrines were banded.

To determine subspecies, we compared photographs of individuals we captured to subspecies information in Clark and Wheeler (1987, 2001) and Wheeler (2003). In addition, B. Wheeler, C. White, and W. Clark reviewed photographs and provided input on subspecies identification for many of the birds we captured. In some cases, we used subspecies measurements (culmen, wing chord, tail; White et al. 2002, Pyle 2008) to assist with subspecies identifications. A small number of falcons had plumage or other features that were intermediate. These individuals were not identified to subspecies.

Analysis. To evaluate whether the percentage of peregrines banded by age and sex varied by season, and whether the proportion of resighted peregrines varied by season, we used the Pearson chi-square test, following the approach used previously (Varland et al. 2008a). We assumed captured peregrines hatched in May. Accordingly, we assigned them to one of four age classes based on their molt condition (Hunt et al. 1975, White et al. 2002) and time of year captured: <1 yr, 1 yr, ≥ 1 yr, or ≥ 2 yr. To this end, we collapsed the data into two age classes $(<1 \text{ yr and } \ge 1 \text{ yr})$ and excluded the summer season due to the small sample size. For both analyses, we examined the Ocean Shores and Long Beach data separately and did not analyze data from Grayland because of the small number of birds resighted there. For both analyses (percentage banded by age and sex, by season; percentage resighted by season), Pearson chi-square test results were the same whether data from study areas were analyzed separately or pooled. As a result, we present results only from the pooled tests, which included all three beaches.

We analyzed Peregrine Falcon observation rates as the number of Peregrine Falcons observed per 100 km driven (Peregrine Falcons/100 km). To this end, we recognized that differences in Peregrine Falcons/100 km across beaches could become confounded with differences across season if sampling intensity was not proportionally consistent across beaches in all seasons. Therefore, before evaluating the observation-rate data, we first examined whether sampling intensity was proportionally similar across beaches in all seasons. We then investigated whether patterns of Peregrine Falcon observation rates across seasons were similar for all beaches, or if they varied among beaches. If they were similar, it would allow us to summarize seasonal patterns with a single set of comparisons for all beaches, rather than make separate comparisons for each beach. This is important, because comparisons using all beaches together would be more powerful and more sensitive to changes than separate comparisons by beach.

To evaluate differences in sampling intensity, we tabulated the number of surveys by beach and season. We then conducted a Pearson chi-square test comparing the distributions of surveys by beaches across the four seasons (Agresti 2007). For comparing consistency of seasonal resighting patterns across beaches, we used a Poisson regression of the number of Peregrine Falcons/100 km for n =697 surveys against season, beach, and the seasonby-beach interaction (Agresti 2007). The deviance/ df was used as a measure of overdispersion of the data relative to a Poisson distribution, and a negative binomial distribution was used as an alternative if overdispersion was indicated (values should be close to 1 if data are from a Poisson distribution; Agresti 2007). Likelihood ratio tests were used to test for effects of season, beach, and the interaction. The latter of these three effects indicates whether seasonal resighting patterns are consistent across beaches. Differences in mean number of Peregrine Falcons/100 km by season were examined using pairwise comparisons of season effects (Wald chisquare tests). We used Bonferroni adjustment for multiple comparisons, so that, with alpha = 0.05, we considered differences significant if P < 0.05/6= 0.00833. Confidence intervals for mean Peregrine Falcons/100 km were obtained as 95% Wald intervals on the linear predictor, then exponentiated (Agresti 2007).

Site fidelity. We defined site fidelity at three spatial scales, with the understanding that falcons may evaluate, use, or select areas at scales other than those we were able to assess. Our use of three scales was analogous to the assertion that both habitat use and selection occur and can be evaluated at several hierarchical scales (Johnson 1980). The spatial scales we used were necessarily constrained by the geographic limits of our study area. Consequently, study-area use fidelity was indicated when we reobserved a Peregrine Falcon on any of the three study area beaches ≥ 1 d after it was banded. The mouths of major estuaries (Grays Harbor and Willapa Bay) provided distinct boundaries between the three beaches (Fig. 1). We therefore defined beach use fidelity as reobservation of a Peregrine Falcon on the same beach ≥ 1 d after it was banded. The third spatial scale was within-beach use fidelity, which we defined as reobservation of a Peregrine Falcon in the same general area on the same beach >1 d after it was banded. It was possible for individual falcons to exhibit fidelity at any of the three spatial scales we considered.

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Because we trapped and marked Peregrine Falcons up to the end date for the analysis period, some of the most recently marked birds had a lower likelihood of being reobserved. This presented potential for bias in comparisons between falcons banded and reobserved and those banded and never reobserved (e.g., age and sex comparisons). To address this lower likelihood, we calculated from the reobservation data the amount of time required for 90% of the birds to be reobserved; this value was 25 mo. Consequently, for analysis of data comparing falcons reobserved with falcons never reobserved, we subtracted 25 mo from the end of our study period, and thus included only those falcons trapped and marked before 31 March 2008.

We tested the null hypothesis that Peregrine Falcons do not exhibit within-beach use fidelity. That is, peregrines use space and resources on a given beach at random and exhibit no fidelity to particular areas. Under the null hypothesis, we would expect no difference between the variance in peregrine locations and the variance associated with random point locations on the same beach. We tested this hypothesis with data on the capture and resighting locations of 35 peregrines on the three beaches. A capture location was the location where a peregrine was first captured and banded. Resighting locations for this analysis were the locations where banded birds were resighted on the same beach where banded. We included only those peregrines in this analysis with >1 resighting on a survey where we had complete beach coverage. Number of captures and resightings per peregrine included in this analysis ranged from 2-54; 19 peregrines were included in the analysis from Ocean Shores, 14 from Long Beach, and two from Grayland. We assessed a capture or resighting location as the distance between the sighted/resighted bird and the south end of the beach where it was observed.

Under the null hypothesis that peregrines used a beach at random, the sighting locations should be distributed uniformly across the length of the beach. Under the alternative hypothesis that peregrines exhibit within-beach fidelity, we expect that resighting locations of individual peregrines should be less variable than a random selection of points. We therefore assessed within-beach fidelity by testing whether the variance of peregrine resighting locations was less than what would be expected under random use.

The variance of the uniform distribution is $Var_U = L^2/12$, where *L* is the length of the beach on which a

peregrine is sighted (Navidi 2008). We tested whether the mean resighting variance among peregrines was less than Var_U as follows: for peregrine *i* on beach *j*, we calculated the sample variance of its sighting locations; call this s_{ij}^2 , i = 1,...,35. For beach j =1,2,3, we pooled these variances across all peregrines in the usual manner for pooling variances:

$$Var_{pooled,j} = \sum \left(n_{ij} - 1 \right) s_{ij}^2 / \left(N_j - b_j \right),$$

where n_{ij} is the number of times peregrine *i* from beach *j* was sighted, N_j is the total number of sightings and b_j the total number of peregrines sighted on beach *j*, and the sum is taken over all b_j peregrines on a beach *j*. Because each beach is a different length, we calculated its uniform variance separately as

$$Var_{u,j} = \frac{L_j^2}{12},$$

where L_j is the length of beach *j*. To compare the observed variances to the uniform variances, we calculated the ratio of pooled variance to uniform-use variance for each beach:

$$r_j = \frac{Var_{pooled,j}}{Var_{u,j}}$$

We then computed a mean of the ratios from the three beaches, weighted according to the number of peregrines seen on the beach,

$$\overline{r} = \sum_{j=1}^{3} b_j r_j / \sum_{j=1}^{3} b_j.$$

The test statistic is \overline{r} .

We wished to know whether this mean ratio of observed variance to uniform-use variance was significantly smaller than 1. This required knowing the sampling distribution of \overline{r} under the null hypothesis; that is, assuming that the peregrines used locations on the beach at random. Because this test statistic does not have a sampling distribution that is easily calculated using statistical theory, we used a parametric bootstrap simulation to estimate this sampling distribution. Specifically, we simulated a large number of data sets $(10\,000)$ under the assumption that the null hypothesis is true, using the same number of beaches, peregrines per beach, and sightings per peregrine as we had in the original data. We calculated the same test statistic from each simulated data set, and then computed the fraction of these simulated test statistics that were less than or equal to the

EFFORT VARIABLE	Ocean Shores (23.5 km long)	Grayland (11.3 km long)	Long Beach (39.6 km long)	Total
Surveys % (n ^a)	66.1 (529)	8.9 (71)	25.0 (200)	100% (800)
Mean number surveys/yr (SE; range) ^a	33.4 (0.4; 17–52)	5.1 (0.4; 1–11)	12.9 (0.4; 4–21)	
Mean survey start time (range) ^a	07:05 (05:20-19:30)	07:24 (06:35-16:15)	09:26 (05:15-18:23)	
Mean survey duration	2 hr, 4 min	1 hr, 25 min	3 hr, 37 min	
(range) ^a	(28 min-5 hr)	(30 min-3 hr, 45 min)	(40 min-9 hr, 02 min)	
Banding % (n)	42.8 (60)	6.4 (9)	50.7 (71)	100% (140)
Resightings on beach $\%$ $(n)^{b,c}$	65.2 (272)	5.7 (24)	18.9 (79)	100% (375)
Number of individuals resighted ^{b,c}	31	8	29	
Mean no. resighted/ individual (SE; range) ^{b,c}	8.8 (±0.8; 1–70)	3.0 (±1.1; 1–17)	2.7 (±0.3; 1–11)	

Table 1. Survey, banding and resighting effort at Ocean Shores, Grayland, and Long Beach study area beaches on the southern coast of Washington, January 1995–May 2010.

^a Totals exclude 23 surveys at Ocean Shores and 19 at Grayland that did not include efforts to capture and band falcons during surveys.

^b Includes 55 resightings of 19 falcons made by individuals not participating in the survey effort.

^c Some individuals resighted on >1 beach.

observed value from the original data. This fraction is the bootstrap estimate of the *P*-value for the test.

RESULTS

We conducted 841 surveys from January 1995 through May 2010 at Ocean Shores, Grayland, and Long Beach. We had "complete beach coverage" for 75% (n = 629) of the surveys. Two-thirds of all surveys took place at Ocean Shores (Table 1). At all three beaches, surveys were usually initiated in the morning; survey duration was longest at Long Beach (Table 1) due to its size. We conducted 31.7% (n =267) of our surveys in fall, 28.4% (n = 239) in winter, 29.5% (n = 248) in spring and 10.3% (n = 87) in summer. There was no evidence that differences in sampling intensity across beaches varied by season ($\chi^2_6 = 3.7$, P = 0.72).

The initial fit of the Poisson log-linear model to the mean number of Peregrine Falcons/100 km results indicated drastically over-dispersed data relative to a Poisson distribution (deviance/df > 5; Agresti 2007), so the negative binomial distribution was used instead. The fit of this model was much more reasonable (deviance/df = 1.03). The test for beach-by-season interaction was not significant (χ^2_6 = 7.2, *P* = 0.30). From this we concluded that the pattern of Peregrine Falcons/100 km across seasons did not vary substantially across beaches. The lack of interaction suggests that differential seasonal patterns by beach would not be hidden by combining data from all beaches, and we therefore proceeded to assess mean Peregrine Falcons/100 km using data combined across beaches.

Observation rates of Peregrine Falcons (mean number of Peregrine Falcons/100 km) varied by season (Fig. 2). The mean number of Peregrine Falcon observations/100 km was 3.8 (95% CI = 2.9-5.0) in autumn, 5.1 (3.9–6.6) in winter, 2.3 (1.7–3.2) in spring, and 0.7 (0.4-1.3) in summer. Pairwise comparisons of peregrine observation rates by season showed fall/winter and fall/spring rates were not significantly different ($Z^2 = 2.18$, P = 0.14and $Z^2 = 4.93$, P = 0.03, respectively (Bonferroni $\alpha = 0.05/6 = 0.0083$; spring observation rates were smaller than those in winter ($Z^2 = 13.0, P < 0.001$), and summer observation rates were smaller than those in any of the other three seasons $(Z^2 =$ 12.0, P < 0.001 vs. spring, $Z^2 = 35.3$, P < 0.001 vs. fall and winter).

Observation rates of banded peregrines and adult peregrines were significantly higher in winter than in any other season (Table 2). Observation rates in summer were low for banding and age categories, but the number of falcons observed was small and precluded meaningful analysis. From 1995 through May 2010, we banded 140 individuals on the three



Figure 2. Number of Peregrine Falcons/100 km of beach by 10-d segments per month for the period 1995 to 2010. The points show number of Peregrine Falcons/100 km for every survey (n = 697) for which observation rate calculations were made and the smoothed line represents the smoothing spline (Hastie et al. 2009).

beaches (Table 1). We banded 39% (n = 55) of captured individuals in the fall, 36% (n = 50) in winter, 21% (n = 30) in spring, and 4% (n = 5) in summer. We banded all three of the North American peregrine subspecies. Most peregrines (83%; n = 114) were *F. p. pealei*, but 3% (n = 4) were *F. p. anatum* and 3% (n = 4) were *F. p. tundrius*. An additional 15 falcons (11%) showed characteristics that were intermediate and were not identified to subspecies type.

We noted differences in the age and sex composition of the birds we captured. The proportion of females (n = 90, 64%) in our captured sample was higher than that of males (n = 50, 36%); however, the proportion of each sex banded did not vary by season ($\chi^2 = 2.39$, df = 2, P = 0.30; Table 3). Of the 140 peregrines caught, 75% (n = 105) were <1 yr of age and 25% (n = 35) were ≥ 1 yr. The percentage of peregrines banded by age class varied by season, with young birds making up a greater percentage of the birds captured in autumn and winter (>89%) than in spring (14.4%; $\chi^2 = 14.59$, df = 2; P < 0.01; Table 3).

Many of the Peregrine Falcons we banded were observed again. Of 140 banded peregrines, 47% (n = 66) were resighted alive at least once after banding; 19% (n = 26) of those resighted were recaptured at least once. Of the Peregrine Falcons we banded, 95% were reobserved for the first time ≥ 6 d after banding (mean = 206.8 d; SE = ± 43.5 d; range = 1–1531 d). Fifty-one of the 105 peregrines banded at <1 yr old were resighted at <1 yr, 24 banded at <1 yr were re-sighted at ≥ 2 yr, and 11 of 35 banded at ≥ 1 yr were resighted again. Of 417

Table 2. Mean number (\pm SE) of Peregrine Falcons observed/100 km driven per season by falcon age and banding status, for all three of our study area beaches in southern coastal Washington, U.S.A., between 1995 and 2010. Results of the Kruskal-Wallis multiple sample comparison do not include birds of undetermined age or band status. Seasonal values with different letters in the same row were significantly different in post-analysis pairwise comparisons. Sample sizes were the number of surveys conducted in each season: 222 in fall, 209 in winter, 205 in spring and 73 in summer.

BANDING STATUS AND AGE	FALL	WINTER	Spring	SUMMER	k	Р
Banding status						
Banded	0.97 (0.13) B	2.46 (0.24) A	1.42 (0.19) B	0.32 (0.14) B	43.1	< 0.001
Not banded	1.33 (0.20) A	1.23 (0.17) A	0.81 (0.15) A	0.34 (0.17) A	16.6	< 0.001
Undetermined	1.06 (0.14)	1.02 (0.16)	0.74 (0.14)	0.23 (0.11)		
Age						
Adult ^a	1.69 (0.19) B	3.27 (0.27) A	1.39 (0.20) BC	0.35 (0.14) C	62.9	< 0.001
Juvenile	1.76 (0.22) A	1.78 (0.21) A	1.44 (0.18) AB	0.43 (0.18) B	15.8	0.001
Undetermined	0.37 (0.08)	0.47 (0.11)	0.21 (0.07)	0.10 (0.07)		

^a Adult-plumaged individuals: ≥15 mo old.

Sex and Age	Fall September– November % (n)	WINTER DECEMBER-FEBRUARY $\%$ (n)	Spring March–May % (n)	Summer June–August % (n)	TOTAL $\%$ (<i>n</i>)
Sex					
Female	58.2 (32)	72.0 (36)	60.0 (18)	80.0 (4)	64.3 (90)
Male	41.8 (23)	28.0 (14)	40.0 (12)	20.0 (1)	35.7 (50)
Agea					
<1 yr	89.1 (49)	80.0 (40)	53.3 (16)	0.0 (0)	75.0 (105)
≥1 yr	10.9 (6)	20.0 (10)	46.7 (14)	100.0 (5)	25.0 (35)

Table 3. Percent, by sex, age, and season of Peregrine Falcons captured and banded (n = 140) at Ocean Shores, Grayland, and Long Beach study area beaches on coastal Washington, January 1995–May 2010.

^a Age determination was based on stage of molt at capture. Individuals were assumed to have hatched in May of hatch year.

resightings in total, 320 were of 57 peregrines during project surveys and an additional 55 observations of 19 falcons were made on study area beaches by individuals not participating in our research. Mean number of resightings was highest for Ocean Shores, where the majority of surveys took place (Table 1). Fifty-percent (n = 210) of all resightings involved 5% (n = 7) of the peregrines we banded. The Peregrine Falcon with alphanumeric code 4/D was the most frequently resighted individual with 70 resightings throughout a 7-yr period after being banded in 1997 (Fig. 3). Peregrine W/M ranked second with 38 resightings spanning 6 yr. Five percent (n = 23) of the peregrines we banded were resighted once. The mean number of resightings per peregrine (n = 67) after banding was 6.2 $(SE \pm 0.5)$

Resightings off the study area that were made by us and others made up 10% (n = 40; 11 peregrines) of all resightings. Peregrines we captured and banded were resighted as far north as Langara Island, British Columbia (1019 km), south to the Salton Sea, California (1679 km), and locally east to the Kennedy Creek estuary near Shelton, Washinton (85 km). There were 76 resightings of 24 peregrines made by individuals not connected to our research effort; 47% (n = 36) were made by field biologists, 22% (n = 17) were made by professional or amateur photographers, and 30% (n = 23) were made by people out watching birds and other wildlife.

We resighted six peregrines banded by others, which provided information on the geographic range of peregrines using the coastal beaches. All six were banded as nestlings: four on the San Juan Islands, Washington, banded by C.M. Anderson, one on Langara Island, British Columbia, banded by R.W. Nelson, and one from the lower Columbia River banded by J.E. Pagel.

Longevity and Mortality. Our resighting data provide estimates of the longevity of peregrines on our study area. Among those peregrines banded and resighted alive ≥ 1 d after banding (n = 66), the median interval from banding to first resighting was 52 d (range = 1 d-4.2 yr) and the median interval from banding to last resighting was 365 d (range = 1 d-8.9 yr). Whereas most peregrines were resighted for the last time <1 yr after banding, a substantial number was seen >1 yr after banding (Fig. 4). Six peregrines were last resighted >6 yr after banding; five of these were <1 yr old when banded and one was ≥ 1 yr old when banded.

We captured four peregrines that were injured. All four falcons were <1 yr old; three were *F. p. pealei* and one was a *F. p. tundrius*. Two of the injuries were substantial: a falcon captured on 11 November 2000 had suffered the loss of the distal one-third of the lower mandible. The falcon was emaciated and the injury probably affected its ability to eat. A falcon captured on 21 January 2006 suffered from a bacterial infection (*Staphylococcus*) in one foot. Both of these birds subsequently died in captivity. On 16 November 2005, we captured a falcon that had a 2.5-cm-deep puncture wound in the breast muscle, and on 17 November 2005, we captured a *F. p. tundrius* on the same beach that had a laceration on its tarsus.

Nine of the peregrines we banded during our study were later recovered dead. Five of these were resighted alive at least once before they died. The median interval from banding date to last resighting alive for birds found dead was 57 d and this contrasted with the interval of 1.1 yr for birds resighted

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^b Age = age at banding.

^e Banded and re-sighted on this beach before summer 2003 (see Varland et al. 2008)

Figure 3. Summary of inter- and intra-annual resightings of Peregrine Falcons captured on our study area between 2003 and 2010. As indicated in the second column, some falcons were captured and banded before the period covered by this figure; see Fig. 3 in Varland et al. (2008) for details about those individuals. Individuals are identified by the alphanumeric code on their color bands, where, in the same season, \mathbb{B} = banded and no resighting; $\mathbb{B}\mathbb{R}$ = banded and ≥ 1 resighting; \mathbb{T} = one resighting; and \mathbb{R} = ≥ 2 resightings. Data are summarized across years by season: W = Winter: December–February; S = Spring: March–May; Su = Summer: June–August; and F = Fall: September–November.

alive and never found dead. Seven of the banded peregrines found dead were banded at <1 yr of age and two were ≥ 2 yr old when banded. Four of the younger birds were found dead at <1 yr of age, one was found as a one-year-old, and one as a two-yearold. Seven of nine peregrines found dead were found on or within 300 m of Pacific coast beaches in Oregon or Washington. Two died on our study area,



Figure 4. Frequency distribution of the maximum period between initial capture and reobservation of Peregrine Falcons at our study area on the southern coast of Washington, U.S.A.

both at Ocean Shores. One peregrine was killed and eaten by a Bald Eagle (*Haliaeetus leucocephalus*) at Newport, Oregon, and one was found shot at Ocean Shores. Cause of death was unknown for the other five birds found in coastal areas. One peregrine died after flying into a wire fence 4.5 km east of the Pacific coast at Mad River Slough Wildlife Hunting Area, in Humboldt County, California. Away from the coast, one was shot in a hunting area at the Salton Sea in southern interior California.

Site Fidelity. Seventy-four (52.8%) Peregrine Falcons were detected on our study area only when they were captured and banded, suggesting little site fidelity. Six Peregrine Falcons observed on our beaches were banded as nestlings by researchers at other study areas and were observed only once at ours: four from the San Juan Islands, Washington, one from the lower Columbia River, Oregon, and one from Langara Island, British Columbia. Similarly, five peregrines we banded were never observed again in our study area but were resighted elsewhere (Appendix). Female peregrine 3/Z in this group was found in 2002 nesting on Grays Harbor, 12.7 km from where she was banded; despite the close proximity of the eyrie to our study area, she

Table 4. Percentages of all Peregrine Falcons (n = 111) and Peale's Peregrine Falcons (n = 91) that were either reobserved or not reobserved after their capture in the season indicated at our study area beaches in coastal Washington, U.S.A., between January 1995 and March 2008. Data are limited to peregrines captured and banded between 1995 and March 2008 (see Methods). Chi-square analyses (2×3 contingency table, df = 2) were based on samples and proportions from fall, winter, and spring.

Birds	Fall September– November	Winter December-February	Spring March-May	Summer June–August	CHI-SQUARE; P-VALUE
All peregrines					
Not reobserved	47.2 (25) ^a	26.4 (14)	20.8 (11)	5.7 (3)	
Reobserved	27.6 (16)	44.8 (26)	24.1 (14)	3.4 (2)	5.6; 0.06
Peale's falcons					
Not reobserved	50.0 (19)	29.0 (11)	15.8 (6)	5.3(2)	
Reobserved	26.4 (14)	45.3 (24)	24.5 (13)	3.8 (2)	5.8; 0.06

^a Number in parentheses = n.

was never observed on the beach after banding in 1999.

To establish context for our assessment of site fidelity, we first compared proportions of falcons that were never resighted with those that were resighted. Fifty-three of 111 (47%) peregrines we banded between 1995 and March 2008 were never resighted alive or found dead during the study period (1995-31 May 2010). Of the 58 Peregrine Falcons that were resighted on the study area, 47 (81%) were <1 yr at banding; this was a greater proportion than of the peregrines that were never observed again (35 of 53, 66%; chi-square test of proportions, z = -1.8, P = 0.07). Of peregrines never seen again, the percentage captured in the autumn was higher and that in the spring was lower compared to falcons that were captured in those seasons and reobserved ($\chi^2 = 5.6$, df = 2; P = 0.06; Table 4). The percentages of falcons that were females were nearly identical in the two groups: 36 of 53 (68%) of falcons never seen again were females and 38 of 58 (65%) that were reobserved were females. Not surprisingly, 53 of 58 (91%) resighted falcons were of the *pealei* subspecies, whereas only 38 of 53 (71.7%) falcons that were never resignted were this subspecies (z = 2.45, P = 0.014). Ratios of females: males were 2.1:1 for falcons never seen again and 1.9:1 for falcons reobserved.

Because *F. p. pealei* was the most abundant peregrine subspecies on our study area, we further evaluated our data on whether falcons of this subspecies were reobserved. In the sample of *F. p. pealei*, there were no differences in the proportions of falcons by age class in the two groups (never resighted: 31 of 38 [82%] were ≤ 1 yr old; resigned: 42 of 53 [79\%] were ≤ 1 yr old; chi-square test, z = 0.28, P = 0.78). Additionally, the proportions of females were similar (never resighted: 27 of 37 [73%] were females; resighted: 36 of 53 [68%] were females; chi-square test, z = 0.51, P = 0.61). A higher proportion of falcons that we captured in fall were never seen again compared to falcons that were reobserved (Table 4). Finally, we found that hatch-year F. p. pealei that were observed again were captured comparatively later in the autumn (mean of falcons never seen again: 15 October, SE = 5.8, n = 16; mean of falcons observed again: 4 November, SE = 5.6, n = 11; comparison of Julian dates, t = 2.26, P =0.03); individuals banded throughout the fall period were known to overwinter on the study area. The timing difference we observed was not explained by sex of the falcons involved, as there were no differences in the proportion of females in either of the groups (never observed again = 75%, observed again = 64%; Fisher exact test = 0.68).

Study-area use fidelity. Sixteen Peregrine Falcons exhibited study-area use fidelity and little or no beach use fidelity. Eleven peregrines we banded were never observed on the beach where they were banded but were observed at least once on one of the other study area beaches. Five peregrines were resighted at least once on the beach where they were banded, indicating beach use fidelity (Fig. 3), and then resighted on ≥ 1 occasion on one of the other two study area beaches. One of these individuals, P/U, was banded at Long Beach and resighted at Ocean Shores on 21 occasions from 2002–05. Seven peregrines showed *beach use fidelity* but were also resighted off the study area (Appendix).

Several of the falcons for which we documented beach use fidelity were observed outside our study area. Peregrine Falcons P/D, V/C and W/M, which were banded at Ocean Shores, were all observed off our study area, but within 1.3 km of the beach on other occasions (Appendix). Peregrine V/M was resighted once on the same beach during the same winter she was banded, and then was resighted twice the next winter on Vancouver Island, British Columbia (Appendix). Peregrine W/R was resighted six times on two study area beaches between 2003 and 2005, and then was resighted in three winters (2007-09) at Boundary Bay, British Columbia. Female 4/H was banded at ≥ 1 yr of age at Ocean Shores in spring 1998, and then found nesting on Langara Island, British Columbia, that same spring (R. Nelson pers. comm.). We resighted this peregrine twice at Ocean Shores the following winter, and that summer she was observed nesting again at Langara Island.

Beach use fidelity. The pattern of beach use fidelity varied. Some peregrines were present in one or two seasons in multiple years (e.g., M/K observed only in winter) whereas others were observed consistently across seasons and years (e.g., W/M; Fig. 3). Of 51 individuals resignted on ≥ 1 occasions on the same beach where they were banded, 53% (n = 27) were observed again in the combined fall-winter-spring period that they were banded or during one other of these periods, 23.5% (n = 12) were resighted in two combined fall-winter-spring periods, 18% (n = 9) were resigned in 3-5 of these periods, and three birds were resighted in 6-9 of these periods. Six peregrines resignted during ≥ 2 combined fall-winter-spring periods were also observed on ≥ 1 occasion in summer. Two of the three birds observed in summer, W/X and A/4, were 1 yr old at the time and the third, W/M, was a 2-yr-old.

Within-beach use fidelity. Some Peregrine Falcons were faithful to local areas on beaches. Our analysis of 35 peregrines on 3 beaches where we had complete beach coverage resulted in rejection of the null hypothesis that peregrines we captured, banded, and subsequently reobserved were randomly distributed on the beaches. Included in this group were 4/H, V/C, W/R, V/M and W/M that were resigned off our study area on >1 occasion (Appendix). The test statistic was $\bar{r} = 0.43$, based on observed vs. uniform variance ratios of 0.52 for

Ocean Shores, 0.36 for Long Beach, and 0.06 for Grayland. The smallest of the 10 000 randomly-generated values of \bar{r}_s was 0.74, so the *P*-value for the test was <1/10000 = 0.0001. We concluded that individual peregrines exhibited much less variability in their sighting locations than would be expected if they were using the beaches at random. Moreover, these locations tended to be clumped on the three beaches (Fig. 5).

DISCUSSION

Few beach surveys of Peregrine Falcons reported encounters per linear distance traveled. Enderson (1965) surveyed South Padre Island, Texas, in autumn and reported an overall mean that translates to 3.1 peregrines observed/100 km driven, with a mean of 0.8 Peregrine Falcons/100 km for South Beach and 7.8 Peregrine Falcons/100 km for North Beach. Enderson et al. (1991) conducted a fall survey on a beach in coastal Sinaloa, Mexico, and presented results that we extrapolated to 3.9 Peregrine Falcons/100 km. The mean observation rate for Peregrine Falcons in our study in fall was 3.8 Peregrine Falcons/100 km driven, which was similar to the fall rates reported for Padre Island and the Mexican coast at Sinaloa. Peregrine Falcon encounter rates during beach surveys have also been reported as birds observed per unit time (Padre Island, Texas [Juergens 2003, Seegar et al. 2003]; Assateague Island, Maryland/Virginia [Ward et al. 1988, Seegar et al. 2003]; coastal Sinoloa, Mexico [Enderson et al. 1991]). Estimated encounter rates from time spent or distance traveled afield only provide an index to abundance. Juergens (2003) obtained population estimates of peregrines overwintering on South Padre Island using the Jolly-Seber method for open populations (e.g., his mid-January estimate in 2001 was 8.0 peregrines (95% CI = 4.9-19.2). Our data should allow us to make annual and seasonal population estimates for peregrines on our study area (L. Powell pers. comm.).

The vast majority of falcons we banded were of the subspecies *F. p. pealei*. Only 17 occurrences of *F. p. tundrius* were documented in Washington between 1913 and 2007 (Varland et al. 2008b), based on evaluations of three falcons we had in-hand for banding, our field observations of five falcons during surveys, band returns (Anderson et al. 1988), and museum specimens in Washington. We also documented the rare occurrence of a wintering tundra Peregrine Falcon on our study area, far north of the reported winter range for the subspecies (Palm-



er 1988, Wheeler 2003). More recently, in winter 2010, we captured and banded a tundra Peregrine Falcon at Ocean Shores (K/2, Fig. 3), providing another example of an apparently unusual winter occurrence of *F. p. tundrius* at our study site.

Longevity and Mortality. The longest span from banding to resighting for a marked peregrine in our study was 8.9 yr (8/7, a first-year male banded 29 March 1997). Because our study period spanned 15 yr, it was conceivable that we could have resightings of banded peregrines approaching or within the maximum 15-20-yr lifespan known for the species through banding records (White et al. 2002, USGS 2010b). That no peregrine we banded was reobserved over >9 yr of the study period was not surprising, given the potential for banded individuals to go unnoticed, the vagile nature of the species, and mortality. We estimated annual apparent survival on our study area was 60% and found that resighting probabilities varied by season (summer vs. fallwinter-spring) and by age and sex (juveniles and adult females had higher resighting probabilities than did adult males; Varland et al. 2008a). During our surveys with peregrine counts (n = 697), we were able to read the alphanumeric code on bands for 33.3% (n = 698) of our observations. For 33.3%(n = 699) of these, we were unable to read the code, and for 33.4% (n = 698) we could not determine whether the individuals we saw were banded.

Migration. Anderson et al. (1988) provided the most comprehensive documentation of peregrine migration along the northern Pacific Coast of North America by reporting their banding and survey work, and band recovery information. Based on these sources, they concluded that autumn migration of peregrines along the Pacific Coast of North America was well underway by mid-September and suggested that the peak dates for the peregrine migration on the Washington coast were 1–10 October. The mean number of Peregrine Falcons/100 km in our study increased during September and through the fall (Fig. 2). Though our data show some high counts for surveys in early October, they do not show a clear

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Figure 5. Location of capture sites associated with Peregrine Falcons (n = 35)exhibiting within-beach use fidelity on three study areas. Five of the capture locations are not visible because they are identical to other capture locations included on the map.

peak in abundance (Fig. 2). However, our data do not distinguish between strictly migrant and winterresident falcons, nor do they account for length-ofstay.

Fidelity. Other than the falcons we captured and never saw again, we observed site fidelity by falcons at our study area. Many of the falcons we captured were hatch-year birds that were migrating to or selecting their first overwintering areas, and many birds we saw or captured likely continued on to more distant destinations, as has been documented previously for peregrines migrating along the Pacific coast (Anderson et al. 1988, Earnheart-Gold and Pyle 2001, Hayes and Buchanan 2002). In autumn, the percentage of falcons we banded that were not reobserved was higher than the percentage we banded and reobserved, suggesting that segments of the population of fall-captured falcons exhibited differing stopover or migration strategies. Because our study area is at the southern limit of the breeding range of F. p. pealei (White et al. 2002), a substantial number of migrants from this population may migrate through our study area each autumn. Consequently, some falcons that were never resighted may overwinter farther south. That we never saw a substantial number of these birds in subsequent seasons may reflect random chance in some cases, and an unknown amount of mortality. Additionally, we suspect the likelihood that a falcon will be reobserved may be substantially influenced by subtle differences in migration pathways. For example, large numbers of migrant Peregrine Falcons visit Grays Harbor and Willapa Bay (Herman and Bulger 1981, Buchanan et al. 2011), two large estuaries immediately adjacent to our study area beaches. Shorebird prey is abundant in these estuaries (Herman and Bulger 1981, Buchanan and Evenson 1997), and some peregrines may make exclusive use of those areas and not visit the outer beaches. Indeed, three of the peregrines we banded, 4/C, 4/G, and 3/Z, were resighted in Grays Harbor after banding but never seen again on our study area. There were no differences in sex ratios or age of Peale's Peregrine Falcons that were never seen again compared to those reobserved, which led us to conclude that these factors did not influence the likelihood of reobservation.

Peregrine Falcons exhibited site fidelity at three spatial scales: the study area, the individual beach, and specific areas along beaches. Some falcons exhibited only fidelity at one of these scales and some exhibited fidelity at two or all three scales. Peregrine Falcons have very large home ranges during the winter (Dobler and Spencer 1989, Dobler 1993, McGrady et al. 2002) and we suspect that the variation we noted in fidelity reflects to some extent the varying use of beaches by falcons that also used the adjacent estuaries. Moreover, we think the patterns of within-beach use fidelity were influenced in at least some cases by the distribution of prey populations on the beaches. For example, the northern end of the Long Beach study site, where falcons tended to exhibit within-beach use fidelity (see Fig. 5), typically supported large numbers of overwintering shorebirds, generally Dunlins (Calidris alpina; J. Buchanan unpubl. data). Large flocks of Dunlins and other shorebirds move from the adjacent estuaries to the outer beaches where they roost on wide sand beaches during high tides (Buchanan 1992). Peregrine Falcons regularly hunted Dunlins at these sites (Buchanan 1996) during high tide periods that may extend for several hours each day depending on tide height.

Future Directions. The Peregrine Falcon is one of the most extensively studied raptors in the world (Ratcliffe 1993, White et al. 2002). Although this likely reflects, in part, its status as a charismatic apex predator that captivates the interests of ornithologists and falconers alike, its global population decline resulting from chemical contaminants was the impetus for much of the research in the last several decades. With the recovery of Peregrine Falcon populations, limited conservation and management funds are now being directed to other species and issues. Nonetheless, topics of management significance remain that require attention. In addition, basic information gaps of interest to the scientific community exist, particularly relative to the ecology of Peale's Peregrine Falcons during the nonbreeding season in coastal Washington and elsewhere along the Pacific Flyway.

Four years after the Peregrine Falcon was delisted, the U.S. Fish and Wildlife Service developed and implemented a range-wide monitoring plan (Green et al. 2003). Although considered important —indeed, peregrines are clearly susceptible to environmental contaminants (Cade et al. 1988) and some localized populations with poor reproductive output still accumulate and carry high contaminant loads (Mora et al. 2002, 2007)—an active contaminant monitoring plan, with requisite funding support, was not implemented. There is a need to generate information on contaminant loads in peregrines that can be used to track the presence of potentially harmful environmental pollutants, e.g., emerging compounds of concern, such as polybrominated diphenyl ethers (PBDEs; Henny and Elliott 2007). Some of this information can be collected during standard banding operations (Henny et al. 2009).

The Peregrine Falcon has long been a desired and prized bird in falconry (Beebe 1974, Weaver 1988). Following the recent recovery of Peregrine Falcon populations, the U.S. Fish and Wildlife Service (USFWS) authorized a limited take of nestlings (U.S. Fish and Wildlife Service 2006, 2007; see Millsap and Allen 2006) and eventually extended this to include the capture of hatch-year birds away from the eyrie until 31 August (U.S. Fish and Wildlife Service 2008). In support of the latter decision, the USFWS relied on an analysis of banding and other data from across North America (U.S. Fish and Wildlife Service 2008). The analysis divided the North American continent into three broad zones for the purpose of evaluating risks to generalized populations resulting from take of falcons, including migrants, for falconry. The broad geographic scope of the analysis units did not allow for an assessment specific to Peregrine Falcons, particularly F. p. pealei, that migrate along the Pacific coast, that is more independent from other western populations in North America. Moreover, the extremely limited distribution of F. p. pealei at largely inaccessible sites in the conterminous U.S.A., coupled with the outcome of the analyses and subsequent regulations (take is limited to the period prior to migration), result in almost no opportunity to take Peale's Falcons for falconry south of Alaska. Additional and more specific analyses of Peregrine Falcon migration along the Pacific coast of North America will help inform future decisions regarding falconry take of migrating Peale's falcons.

Information on natal origin of Peregrine Falcons that migrate to or through Washington was summarized by Anderson et al. (1988) and subsequently updated (Hayes and Buchanan 2002) and augmented (this study). From this information we know that migrant Peregrine Falcons originate from areas as distant as northern and northwestern Alaska. Similarly, peregrines captured and banded in Washington have been observed or recovered in southern California and in coastal British Columbia. Some northern peregrines migrate through western Washington on their way to wintering areas far to the south, as these falcons have been observed and/or banded in coastal Washington and at locations farther south (Anderson et al. 1988, Earnheart-Gold and Pyle 2001, Hayes and Buchanan 2002, Varland et al. 2008a). Although Anderson et al. (1988) indicated that no Peale's Peregrine Falcons banded in Alaska had been recovered south of Alaska, it is highly likely that Alaskan Peale's Peregrine Falcons migrate to and through Washington. Peale's Peregrine Falcons are thought to be less migratory than *F. p. anatum* and *F. p. tundrius*, with some birds remaining on territory year-round.

Our finding that juveniles captured in later autumn were more likely to be reobserved than those captured earlier in autumn suggests the possibility of either leapfrog or chain-migration strategies (Salomonsen 1955, Boulet and Norris 2006, Newton 2008). Under the leapfrog strategy, falcons from more northerly breeding areas would migrate to our study area, whereas more local birds remained on their territories before dispersing southward. The northern birds would then continue southward as the local falcons arrived at our study area. If chain migration were occurring, local falcons would arrive first at our study area and subsequently be replaced by falcons from farther north (see Fig. 23.6 in Newton 2008). These strategies potentially result in substantially different cohorts of falcons settling in an area for winter. The technology involved in satellite transmitters (McIntyre et al. 2009), geolocators (Stutchbury et al. 2009), and use of intrinsic markers including stable isotopes (Boulet and Norris 2006, Inger and Bearhop 2008) is rapidly changing, and it appears that these or other means to identify natal origins or track migratory movements can provide a more complete understanding of both natal origin and winter destination of migrant Peale's Peregrine Falcons that occur in coastal Washington.

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LITERATURE CITED

AGRESTI, A. 2007. An introduction to categorical data analysis, Second Ed. Wiley-Interscience, New York, NY U.S.A.

- ANDERSON, C.M., D.G. ROSENEAU, B.J. WALTON, AND P.J. BENTE. 1988. New evidence of a peregrine migration on the west coast of North America. Pages 507–516 in T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.
- BEEBE, F.L. 1974. Field studies of the falconiformes of British Columbia: vultures, hawks, falcons, eagles. British Columbia Prov. Mus. Occas. Pap. No. 17, British Columbia Prov. Mus., Victoria, BC Canada.
- BILDSTEIN, K.L. 2006. Migrating raptors of the world: their ecology and conservation. Comstock Publishing Associates, Ithaca, NY U.S.A.
- BLOOM, P.H., W.S. CLARK, AND J.W. KIDD. 2007. Capture techniques. Pages 193–219 in D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House Publishers, Surrey, BC Canada.
- BOULET, M. AND D.R. NORRIS. 2006. The past and present of migratory connectivity. Ornithological Monographs 61:1–13.
- BUCHANAN, J.B. 1992. Winter abundance of shorebirds at coastal beaches of Washington. Washington Birds 2:12–19.
- . 1996. A comparison of behavior and success rates of Merlins and Peregrine Falcons when hunting Dunlins in two coastal habitats. *Journal of Raptor Research* 30:93–98.
 - —— AND J.R. EVENSON. 1997. Abundance of shorebirds at Willapa Bay, Washington. Western Birds 28:158–168.
- —, L.J. SALZER, G.J. WILES, K. BRADY, S.M. DESIMONE, AND W. MICHAELIS. 2011. An investigation of Red Knot *Calidris canutus* spring migration at Grays Harbor and Willapa Bay, Washington. *Wader Study Group Bulletin* 118:97–104.
- CADE, T.J., J.H. ENDERSON, C.G. THELANDER, AND C.M. WHITE [EDS.]. 1988. Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.
- CLARK, W.S. AND B.K. WHEELER. 1987. Hawks of North America. Houghton Mifflin Company, New York, NY U.S.A.
- AND ———. 2001. Hawks of North America, Second Ed. Houghton Mifflin Company, New York, NY U.S.A.
- DOBLER, F.C. 1993. Wintering Peregrine Falcon (*Falco per-egrinus*) habitat utilization near Sequim, Washington. Northwest Science 67:231–237.
 - AND R.D. SPENCER. 1989. Wintering Peregrine Falcon *Falco peregrinus* habitat utilization in Grays Harbor, Washington. Pages 71–78 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world: Proceedings of the III World Conference on Birds of Prey and Owls. World Working Group on Birds of Prey, Berlin, Germany.
- EARNHEART-GOLD, S. AND P. PYLE. 2001. Occurrence patterns of Peregrine Falcons on Southeast Farallon Island, California, by subspecies, age, and sex. Western Birds 32:119–126.

- ENDERSON, J.H. 1965. A breeding and migration survey of the Peregrine Falcon. Wilson Bulletin 77:327–339.
- —, C. FLATTEN, AND J.P. JENNY. 1991. Peregrine Falcons and Merlins wintering in Sinaloa, Mexico, in winter. *Journal of Raptor Research* 25:123–126.
- —, J. LARRABEE, Z. JONES, C. PEPER, AND C. LEPISTO. 1995. Behavior of peregrines in winter in south Texas. *Journal of Raptor Research* 29:93–98.
- GREEN, M., R. MESTA, M. MORIN, M. AMARAL, R. CURRIE, P. DELPHEY, R. HAZELWOOD, K. HOLLAR, M. KLEE, A. MATZ, M. MILLER, AND T. SWEM. 2003. Monitoring plan for the American Peregrine Falcon, a species recovered under the Endangered Species Act. U.S. Fish and Wildlife Service, Portland, OR U.S.A.
- GRISCOM, L. AND M.S. CROSBY. 1925. Birds of the Brownsville region-southern Texas. Auk 42:519–537.
- HASTIE, T., R. TIBSHIRANI, AND J. FRIEDMAN. 2009. The elements of statistical learning. Springer, New York, NY U.S.A.
- HAYES, G.E. AND J.B. BUCHANAN. 2002. Washington State status report for the Peregrine Falcon. Washington Department of Fish and Wildlife, Olympia, WA U.S.A.
- HENNY, C.J. AND J.E. ELLIOTT. 2007. Toxicology. Pages 329–350 in D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House Publishers, Surrey, BC Canada.
- —, M.A. YATES, AND W.S. SEEGAR. 2009. Dramatic declines of DDE and other organochlorines in spring migrant Peregrine Falcons from Padre Island, Texas, 1978–2004. *Journal of Raptor Research* 43:37–42.
- HERMAN, S.G. AND J.B. BULGER. 1981. The distribution and abundance of shorebirds during the 1981 spring migration at Grays Harbor, Washington. Contract report DACW67-81-M-0936 to Army Corps of Engineers, Seattle, WA U.S.A.
- HUNT, W.G., R.R. ROGERS, AND D.J. SLOWE. 1975. Migratory and foraging behavior of Peregrine Falcons on the Texas coast. *Canadian Field-Naturalist* 89:111–123.
- INGER, R. AND S. BEARHOP. 2008. Applications of stable isotope analyses to avian ecology. *Ibis* 150:447–461.
- JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- JUERGENS, P.W. 2003. Wintering Peregrine Falcons (Falco peregrinus) on South Padre Island, Texas. M.S. thesis, Texas State Univ.-San Marcos, San Marcos, TX U.S.A.
- McGRADY, M.J., T.L. MAECHTLE, J.J. VARGAS, W.S. SEEGAR, AND M.C. PORRAS PENA. 2002. Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor* 104:39–48.
- MCINTYRE, C.L., D.C. DOUGLAS, AND L.G. ADAMS. 2009. Movements of juvenile Gyrfalcons from western and interior Alaska following departure from their natal areas. *Journal of Raptor Research* 43:99–109.
- MILLSAP, B.A. AND G.T. ALLEN. 2006. Effects of falconry harvest on wild raptor populations in the United States: theoretical considerations and management recommendations. *Wildlife Society Bulletin* 34:1392–1400.

MORA, M.A., R. SKILES, B. MCKINNEY, M. PAREDES, D. BUCKLER, D. PAPOULIAS, AND D. KLEIN. 2002. Environmental contaminants in prey and tissues of the Peregrine Falcon in the Big Bend region, Texas, U.S.A. *Environmental Pollution* 116:169–176.

—, —, AND M. PAREDES. 2007. Further assessment of environmental contaminants in avian prey of the Peregrine Falcon in Big Bend National Park, Texas. *Southwestern Naturalist* 52:54–59.

- NAVIDI, W. 2008. Statistics for engineers and scientists, Second Ed. McGraw Hill, New York, NY U.S.A.
- NEWTON, I. 2008. The migration ecology of birds. Academic Press, London, U.K.
- PALMER, R.S. 1988. Handbook of North American birds, Vol. 5. Yale Univ. Press, New Haven, CT U.S.A.
- PYLE, P. 2008. Identification guide to North American birds, Part II. Slate Creek Press, Point Reyes Station, CA U.S.A.
- RATCLIFFE, D.A. 1993. The Peregrine Falcon, Second Ed. T. and A.D. Poyser, London, U.K.
- SALOMONSEN, F. 1955. The evolutionary significance of bird migration. *Biologiske Meddelelser* 22:1–62.
- SEEGAR, W.S., M. YATES, AND T. MAECHTLE. 2003. Research on migratory peregrines. Pages 212–227 in T.J. Cade and W. Burnham [EDS.], Return of the peregrine: a North American saga of tenacity and teamwork. The Peregrine Fund, Boise, ID U.S.A.
- STUTCHBURY, J.M., S.A. TAROF, T. DONE, M. GOW, P.M. KRAMER, J. TAUTIN, J.W. FOX, AND V. AFANASYEV. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896.
- U.S. FISH AND WILDLIFE SERVICE. 2006. Migratory bird permits; allowed take of nestling American Peregrine Falcons. *Federal Register* 71:9143–9144.
 - 2007. Final environmental assessment: Take of raptors from the wild under the falconry and the raptor propagation regulations. U.S. Fish and Wildlife Service, Arlington, VA U.S.A.
 - —. 2008. Final environmental assessment and management plan. Take of migrant Peregrine Falcons from the wild for use in falconry, and reallocation of nestling/ fledgling take. U.S. Fish and Wildlife Service, Arlington, VA U.S.A.
- U.S. GEOLOGICAL SURVEY. 2010a. The Peregrine Falcon color banding protocol in North America. Bird banding laboratory: the North American bird banding program.

USGS Patuxent Wildlife Research Center, Laurel, MD U.S.A, http://www.pwrc.usgs.gov/bbl/homepage/pefaprot.cfm (last accessed 10 November 2011).

- 2010b. Longevity records of North American birds. Bird banding laboratory: the North American bird banding program. USGS Patuxent Wildlife Research Center, Laurel, MD U.S.A, http://www.pwrc.usgs.gov/ BBl/homepage/longvrec.htm (last accessed 29 October 2010).
- VARLAND, D.E., T.L. FLEMING, AND J.B. BUCHANAN. 2008b. Tundra Peregrine Falcon (*Falco peregrinus tundrius*) occurrence in Washington. Washington Birds 10:48–57.
- —, L.A. POWELL, M.K. KENNEY, AND T.L. FLEMING. 2008a. Peregrine Falcon survival and resighting frequencies on the Washington coast, 1995–2003. *Journal* of Raptor Research 42:161–171.
- WARD, F.P. 1975. Colored and numbered tarsal bands as an aid to raptor demographic studies. Pages 98–102 in M. Harwood [ED.], Proceedings of the North American Hawk Migration Conference. Hawk Migration Association of North America, Syracuse, NY U.S.A.
- AND R.B. BERRY. 1972. Autumn migrations of Peregrine Falcons on Assateague Island, 1970–71. *Journal of Wildlife Management* 36:484–492.
- ——, K. TITUS, W.S. SEEGAR, M.A. YATES, AND M.R. FULLER. 1988. Autumn migrations of Peregrine Falcons at Assateague Island, Maryland/Virginia, 1970–84. Pages 485–495 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.
- WEAVER, J. 1988. The Peregrine Falcon in relation to contemporary falconry. Pages 821–824 in T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.
- WHEELER, B.K. 2003. Raptors of western North America. Princeton Univ. Press, Princeton, NJ U.S.A.
- WHITE, C.M., N.J. CLUM, T.J. CADE, AND W.G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 600. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.

Received 6 December 2010; accepted 6 August 2011 Associate Editor: Bruce Peterjohn Appendix. Peregrine Falcons banded on study area beaches and resighted alive at other locations. Resightings of these peregrines on study area beaches are also summarized.

CB ^a , Banding Date	Beach Where Banded	BEACH WHERE RESIGHTED (NUMBER AND YEAR OF RESIGHTINGS)	OFF-STUDY AREA RESIGHTINGS (n)
4/C, 14 November 1996	Ocean Shores	None	Hoquiam airport, on Grays Harbor, WA ^b : (2 winter 1996–97)
4/G, 29 December 1997	Ocean Shores	None	Hoquiam airport, on Grays Harbor, WA: (1 spring 2002)
4/H, 12 March 1998	Ocean Shores	Ocean Shores (2; both in 1999)	Langara Island, Queen Charlotte Islands, BC ^c : nesting; (1 spring 1998, 1 summer 1999)
3/Z, 9 January 1998	Ocean Shores	None	Grays Harbor, WA: nesting; (6 spring through summer 2002, 1 summer 2003, 5 spring through summer 2004, 1 spring and 1 summer 2005)
P/D, 16 December 1999	Ocean Shores	Ocean Shores (1 in 2000, 2 in 2002, 1 in 2003, 2 in 2004); Grayland (1 in 2000)	Residential area, Ocean Shores, WA: (1 spring 2003)
P/E, 29 October 2000	Long Beach	None	Residential area, Aberdeen, WA: (1 spring 2001)
V/C, 30 January 2002	Ocean Shores	Ocean Shores (3 in 2003)	Oyhut Wildlife Recreation Area, Ocean Shores, WA: (1 summer 2002 and 1 fall 2002, 1 summer 2003)
W/R, 21 December 2002	Ocean Shores	Ocean Shores (1 in 2003, 3 in 2004, 1 in 2005); Grayland (1 in 2004)	Boundary Bay, BC: (2 winter 2006–07, 1 fall 2007, 4 winter 2007–08, 3 fall 2008, 1 winter 2008–09)
V/M, 22 January 2003	Grayland	Grayland (1 in 2003)	Esquimalt Lagoon, Vancouver Island, BC: (2 winter 2004)
W/M, 6 December 2004	Ocean Shores	Ocean Shores (37 total, each year 2004–2009)	2.3 km north of Ocean Shores, WA along Hwy 115: (1 winter 2006–07)
D/5, 25 February 2010	Long Beach	Ocean Shores (1 in 2010)	Yaquina Head Outstanding Natural Area, Newport, OR: (1 spring 2010)
A/3, 2 March 2008	Long Beach	None	Kennedy Creek estuary, WA: (2 spring 2008)

^a CB = alphanumeric code on color band.

^b WA = Washington, U.S.A.

^c BC = British Columbia, Canada.