J. Raptor Res. 42(3):161–171

PEREGRINE FALCON SURVIVAL AND RESIGHTING FREQUENCIES ON THE WASHINGTON COAST, 1995–2003

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Abstract.—We estimated survival for Peregrine Falcons (*Falco peregrinus*) in beach-dune habitat along the Washington coast. We captured and color-banded 76 Peregrine Falcons during 438 surveys by vehicle on three coastal beaches in Washington from January 1995 to May 2003. We captured 45 females and 31 males; 68% (52) were <1 yr old and 32% (24) were ≥1 yr old. Based primarily on photographs ($N = 72$) showing plumage coloration, 76% ($N = 55$) of the individuals captured were *F. p. pealei*, 7% ($N = 5$) were *F. p. anatum*, 3% ($N = 2$) were *F. p. tundrius*, and 14% ($N = 10$) showed intermediate characteristics and could not be identified to subspecies. Thirty-nine (51%) of the color-banded individuals were observed alive at least once after banding. Using program MARK, we estimated that the apparent survival rate (Φ) for all age and sex classes over a 3-mo interval was 87.9 ± 2.0% (±SE) and the annual survival rate was 59.7 ± 5.4%. We found relatively high use of the study areas by peregrines in fall, winter, and spring, and low use in summer. Resighting probabilities (P) were lower in summer compared with other seasons. During fall, winter, and spring, the 3-mo resighting probability (P) was 45.4 ± 7.9% for juveniles, 35.9 ± 5.0% for adult females, and 16.7 ± 4.5% for adult males.

Key Words: *Peregrine Falcon*; Falco peregrinus; *apparent survival*; *banding*; *mark-recapture model*; *resighting probability*; *survival.*

SUPERVIVENCIA DE *FALCO PEREGRINUS* Y FRECUENCIA DE REAVISTAMIENTOS EN LA COSTA DE WASHINGTON, 1995–2003

Resumen.—Estimamos la supervivencia del halcón *Falco peregrinus* en el hábitat de playa-duna a lo largo de la costa de Washington. Capturamos y marcamos con anillos de color a 76 halcones durante 438 censos realizados con vehículo en tres playas costeras en Washington desde enero de 1995 a mayo de 2003. Capturamos 45 hembras y 31 machos; 68% (52) tuvieron <1 año de edad y 32% (24) tuvieron ≥1 año de edad. Principalmente con base en fotografías ($N = 72$) de la coloración del plumaje, 76% ($N = 55$) de los individuos capturados fueron *F. p. pealei*, 7% ($N = 5$) fueron *F. p. anatum*, 3% ($N = 2$) fueron *F. p. tundrius* y 14% ($N = 10$) mostraron características intermedias y no pudieron ser identificados a nivel de

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subespecie. Treinta y nueve (51%) de los individuos anillados fueron observados vivos por lo menos una vez luego de ser anillados. Usando el programa MARK, estimamos que la tasa de supervivencia aparente (Φ) para todas las clases de edad y sexo, para un intervalo de tres meses, fue de 87.9 ± 2.0% (±EE) y que la tasa de supervivencia anual fue de 59.7 ± 5.4%. Encontramos que los halcones hacen un uso relativamente alto del área de estudio en otoño, invierno y primavera, y un uso bajo en verano. Las probabilidades de reavistamiento (*P*) fueron bajas en verano comparadas con las de otras estaciones. Durante otoño, invierno y primavera, la probabilidad de reavistamiento (*P*) en un lapso de tres meses fue de 45.4 ± 7.9% para los juveniles, 35.9 ± 5.0% para las hembras adultas y 16.7 ± 4.5% para los machos adultos.

[Traducción del equipo editorial]

Peregrine Falcons (*Falco peregrinus*) frequent the coastal beaches of North America and Mexico during migration and in winter (e.g., Washington: Anderson et al. 1988; Mexico: McGrady et al. 2002; Texas: Hunt et al. 1975; Maryland/Virginia: Ward et al. 1988). Coastal beaches have a combination of unobstructed airspace preferred for hunting by peregrines (Beebe 1974) and abundant shorebirds and other avian species to serve as prey (Hunt et al. 1975, Enderson et al. 1995, Buchanan 1996). In this habitat, research on peregrines has been conducted on migration (Hunt et al. 1975, Titus et al. 1988, Ward et al. 1988), hunting behavior (Hunt et al. 1975, Buchanan 1996, Enderson et al. 1995), habitat selection (Hunt and Ward 1988), and activity in wintering areas (Enderson et al. 1995, McGrady et al. 2002, Juergens 2003). Fidelity of beach use in winter and spring has been observed in peregrines monitored by radiotelemetry (Hunt and Ward 1988, Enderson et al. 1995, McGrady et al. 2002, Juergens 2003); however, these studies were of short duration (1–2 seasons) with sample sizes of 7–15 individuals. Additionally, none of these studies reported on peregrine survival, a fundamental demographic parameter important to species conservation and management. Only in the last decade was the Peregrine Falcon removed from the U.S. Endangered Species List (Swem 1994, Mesta 1999). In the state of Washington, peregrines were removed from the state endangered species list in 2002, but are still classified as a ''sensitive'' species (Washington Department of Fish and Wildlife 2008).

In 1995, we began banding Peregrine Falcons on coastal beaches in Washington. Our objectives were to: (1) document occurrence by subspecies type of Peregrine Falcon in coastal beach habitat, (2) document fidelity of beach use by marked individuals across seasons and years, and (3) estimate survival and resighting rates.

STUDY AREA AND METHODS

We conducted this study at three beaches in western Washington: Ocean Shores, Grayland, and Long Beach (Fig. 1). These beaches contain unvegetated, fine-grained sand with scattered driftwood and other debris deposited by tidal action (Buchanan 1996, Buchanan et al. 2001). The beaches are bordered on the east by sand dunes vegetated with European beach grass (*Ammophila arenaria*), other grasses, herbaceous plants, and shrubs (Buchanan et al. 2001). This habitat makes up about 40% of the outer coastlines of Washington and Oregon (Buchanan et al. 2001).

Borders of the three study areas extended from the inter-tidal beaches west to 100 m over the Pacific Ocean and east to the eastern edge of the sand dunes (Fig. 1). The 14-km^2 Ocean Shores study area extended 23.5 km northward from Grays Harbor (46°55.67′N, 124°10.44′W) to the Copalis River (47°8.23′N, 124°11.18′W), and the 5-km^2 Grayland study area extended northward 11.3 km from the Warrenton-Cannery Road beach access (46°44.79′N, 124°5.73′W) to ca. 200 m south of the Bonge Avenue beach access (46°50.82′N, 124°6.68′W). The 26-km^2 Long Beach study area extended 39.0 km north from North Head (46°18.37′N, 124°4.37′W) to the end of the Long Beach Peninsula (46°39.24′, 124°3.46′W).

One to four experienced observers surveyed each study area for Peregrine Falcons from January 1995 to May 2003. Observers conducted surveys by 4-wheel-drive vehicle driven approximately 30 km/hr along the beach. Mean survey start time was 0733 H (N = 441; SE = 6 min; range = 0530–1930 H), mean end time was 0948 H (N = 400; SE = 8 min; range = 0650–2030 H) and mean survey duration was 2 hr 15 min (N = 400; SE = 4 min; range = 28 min–9 hr 2 min). Surveys were conducted in all seasons, here defined according to the meteorological definition of seasons for the northern hemisphere: fall: Sep–Nov; winter: Dec–Feb; spring: Mar–May; and summer: Jun–Aug. Surveys generally were not conducted when visibility was poor (<100 m), during high winds (sustained ≥32 km/hr) or when beach travel was unsafe due to high surf or tide or soft sand. Whenever we saw peregrines, we attempted to trap

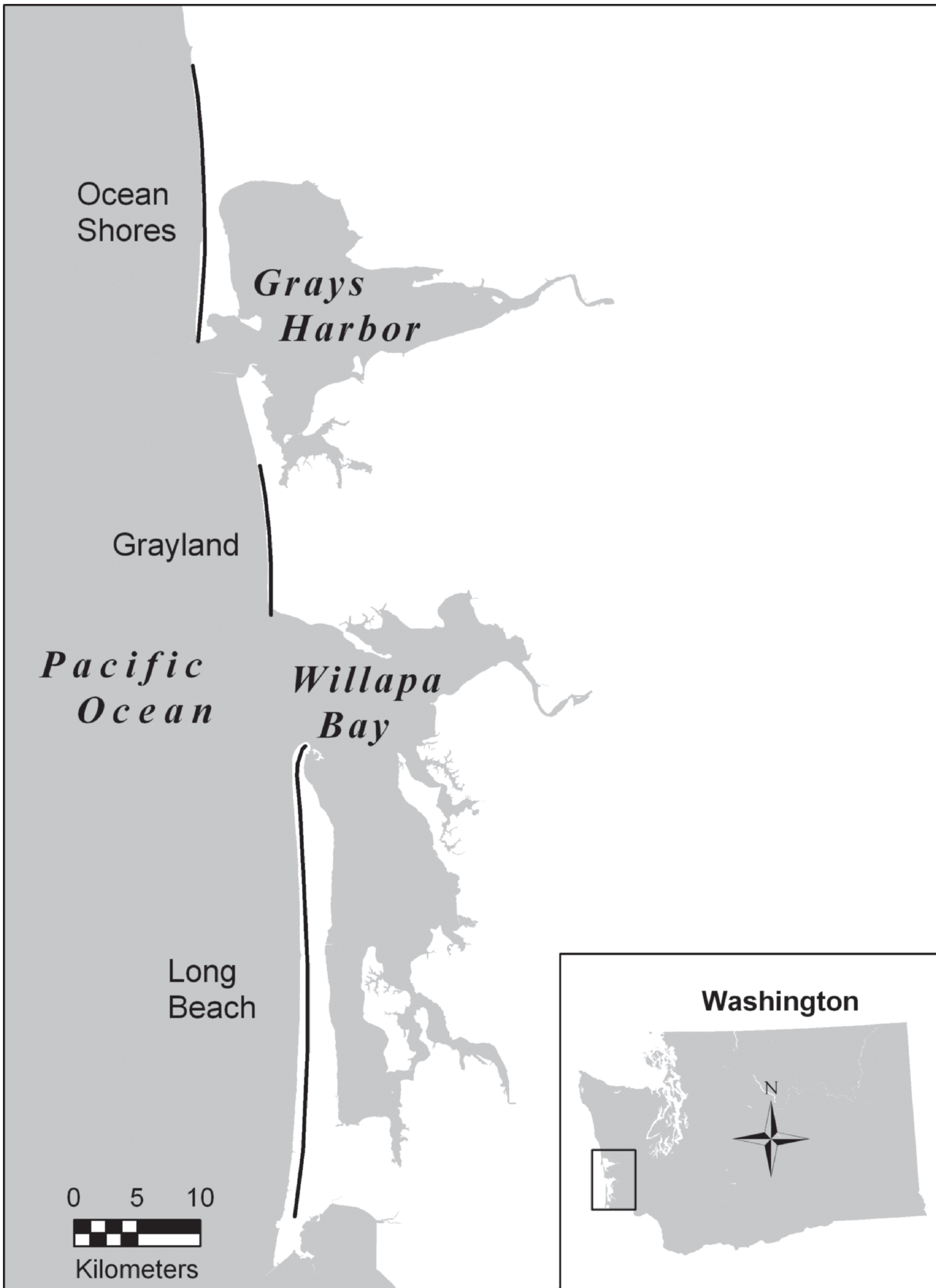

Figure 1. Survey transects (indicated by black lines) for Peregrine Falcons on three coastal beaches, Ocean Shores, Grayland, and Long Beach, in western Washington, U.S.A.

and band them or to resight individuals that were previously color-banded. We attempted to retrap color-banded individuals once each year to obtain blood and feather samples for research objectives other than those reported here.

Capturing and Banding. We captured Peregrine Falcons with a harnessed Rock Pigeon (*Columba livia*; $N = 75$) or phai trap ($N = 1$; Bloom 1987). Each peregrine was fitted with a U.S. Geological Survey (USGS) band on one leg and an Acraft® color-coded alphanumeric band (Edmonton, Alberta, Canada) on the other. Beginning in 1999, we used anodized USGS bands (blue or red) and right/left leg combinations to assist in identifying the bander (DEV and MKK placed anodized bands on the right leg; TLF placed them on the left) and the beach where banding occurred. We could read the alphanumeric codes on the color bands with a spotting scope up to 150 m away; nearly all resightings were made at much closer distances. We defined a resighting as the identification of an individual peregrine by reading the alphanumeric code on its color band with a spotting scope or with the bird in hand at recapture.

From 1995–98, we fitted all peregrines with black-above-blue (black/blue) color bands. Starting in 1999, we adopted the international protocol for peregrine banding in North America (USGS 2008), using black/blue color bands (for migrating and wintering individuals) on peregrines that appeared to be of the *anatum* or *tundrius* subspecies and green color bands on the *pealei* subspecies. We used black/blue bands when subspecies was uncertain. We photographed 72 of the 76 individuals captured; final determinations on subspecies were made by examinations of these photographs in comparison to subspecies information in Clark and Wheeler (1987, 2001), and in two cases, in combination with measurements (wing chord, culmen, cranium). Because of the difficulty in clearly identifying subspecies, we refer to the occurrence of subspecies-type (i.e., *F. p. pealei*-type, *F. p. anatum*-type, and *F. p. tundrius*-type) as suggested by plumage and measurements.

We assumed that captured peregrines hatched in May. Thus, we assigned peregrines to one of four nonexclusive 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.

We used a chi-square test to determine if the proportion of peregrines banded by age and sex varied by season. We collapsed the data into two age classes (<1 yr and ≥ 1 yr), and excluded the summer season due to the limited sample size. We also determined whether the proportion of resighted peregrines, from our banded sample, varied by season. We examined the Ocean Shores and Long Beach study areas separately. We were unable to do so for Grayland because of the small number of birds resighted there. For both analyses, chi-square test results were the same whether data from study areas were analyzed separately or pooled; consequently, we present results only from the pooled tests. One peregrine (bird 4/D) made up 29% ($N = 61$) of the resightings. At Ocean Shores where bird 4/D was observed, we ran chi-square tests with and without resightings of this individual. Because chi-square results remained the same (among beaches, with vs. without bird 4/D), we pooled the data for the three study areas and included bird 4/D in the analysis.

Fidelity of Beach Use. We defined fidelity of beach use as a resighting of a marked individual on the beach where it was banded ≥ 1 d after it was captured.

Apparent Survival. We used mark-recapture methods to estimate apparent survival, the likelihood that an animal survived and did not emigrate (Dinsmore and Johnson 2005). We used a Cormack-Jolly-Seber (C-J-S) mark-recapture model for our survival analysis (Pollock et al. 1990, Williams et al. 2002) following standard procedures in program MARK (White and Burnham 1999); thus, our C-J-S analysis could not distinguish mortality from permanent emigration (Pollock et al. 1990). We estimated apparent survival rates (Φ, the probability that animal remained alive on the study site during the time interval) and resighting probabilities (P, the probability that an animal would be detected during the time interval, if it remained alive on the study site) for each of the 35, 3-mo observation periods from January 1995 to May 2003. We constructed capture histories for individuals we banded ($N = 76$) that were within and outside our study areas and individuals banded by other researchers ($N = 4$) that we observed on our study areas. Based on MARK program terminology, our analysis actually estimates ''recapture'' probability. However, most of our ''recaptures'' were actually resightings of marked peregrines. Therefore, we used the ''recapture'' probability value as an estimate of the probability of resighting a marked bird during a 3-mo time interval.

We assessed the goodness-of-fit of our data to the model structure using program MARK's bootstrap goodness-of-fit simulation procedure. We compared

Table 1. Alternate models and model selection statistics considered for estimating survival and recapture rates of Peregrine Falcons captured and banded in western Washington, January 1995–May 2003. Each model resulted in estimates of 3-mo apparent survival (Φ) and recapture (p) rates during Fall, Winter, Spring (FWSp) and Summer (S). Age and sex classes were adult (A), juvenile (J), male (M), female (F), or pooled (.). Only models with AIC weights >0.01 are shown; 15 other models with combinations of time-, age-, and sex-specific parameters were considered.

MODEL	MODEL STRUCTURE	AIC_c	ΔAIC_c	w_i	k[a]
1	$\Phi(.)\,p_{FWSp}(J,AM,AF)\,p_S(.)$	502.9	0.0	0.350	5
2	$\Phi(J,A)\,p_{FWSp}(J,AM,AF)\,p_S(.)$	503.8	0.9	0.227	6
3	$\Phi(J,A)\,p_{FWSp}(J,AM,AF)\,p_S(J, A)$	504.1	1.2	0.190	7
4	$\Phi(M,F)\,p_{FWSp}(J,AM,AF)\,p_S(.)$	505.0	2.1	0.125	6
5	$\Phi(.)\,p_{FWSp}(.)\,p_S(.)$	506.8	3.9	0.051	3
6	$\Phi_{FWSp}(.)\,\varphi_S(.)\,p_{FWSp}(.)\,p_S(.)$	508.9	5.9	0.018	4
7	$\Phi(.)\,p(J,AM,AF)$	509.4	6.5	0.014	4
8	$\Phi(J,A)\,p(J,AM,AF)$	509.8	6.8	0.012	5

[a] k = the number of parameters estimated by each model.

the deviance of our best model to the range of deviances from 100 simulations; the goodness-of-fit P-value was calculated by determining the percentage of simulated deviances that exceed the deviance from our data (Cooch and White 2006).

We used Akaike's Information Criterion (AIC) to distinguish among alternate models in program MARK (Burnham and Anderson 2002; Table 1). We considered 23 models that included sex-specific, age-specific, time-specific (e.g., allowing estimates of survival and resighting probability to vary over each of the 3-mo observation periods) and season-specific survival and recapture probabilities (White and Burnham 1999). We used an AIC corrected for smaller samples sizes (Burnham and Anderson 2002); the model with the smallest AIC_c value was selected as the best model. However, when alternate models had small differences in AIC_c scores (ΔAIC_c of <2.0) we used the principle of parsimony to select the models with fewer parameters (Burnham and Anderson 2002). Because models with ΔAIC_c of <2.0 could be considered reasonable (Burnham and Anderson 2002), we used confidence intervals to test for differences between parameters (e.g., sex-specific survival rates) with ΔAIC_c of <2.0. We tested for differences in survival rate among the 3-mo observation periods and among years. We calculated a 12-mo survival estimate by raising the 3-mo survival rate estimate (Φ; Table 1, model 1) to the 4th power after analyses revealed no differences in survival rates among seasons (summer [S] 95% C.I., Φ_S: 0.66–0.95; fall-winter-spring [FWSp] C.I., Φ_{FWSp}: 0.78–0.94; Table 1, model 6).

To determine the effect of the bird banded with band 4/D on our estimates of survival and resighting estimates, we compared survival and resighting estimates with bird 4/D and without bird 4/D in the sample. With bird 4/D, the overall (all age- and sex-classes, pooled across all seasons) 3-mo survival was 0.879 (95% C.I. = 0.834–0.914); with bird 4/D removed, this estimate was 0.863 (95% C.I. = 0.812–0.903). With bird 4/D, the overall 3-mo resighting probability was 0.279 (95% C.I. = 0.22–0.34). With bird 4/D removed from the analyses, the resighting probability rate dropped slightly to 0.255 (95% C.I. = 0.19–0.33). Because these differences were not significant, we included bird 4/D in all subsequent analyses.

We tested whether there were sex- or age-specific differences in survival and resighting estimates, based on two age classes at capture: juvenile (<1 yr old; N = 52) and adult (≥1 yr old; N = 24). The sample of older-aged peregrines included 9 individuals that were 1 yr old at capture, 10 that were ≥1 yr old and five that were ≥2 yr old. Twenty-two (42.3%) juveniles entered the study cohort during the fall, 21 (40.4%) juveniles entered in the winter, and nine (17.3%) entered in the spring. Our age-structured model dictated that juveniles were classified as adults when they entered their second summer season. All means are expressed as $\bar{x} \pm 1$ SE.

RESULTS

We conducted 438 surveys from January 1995 to May 2003; 71% (N = 310) were on the Ocean Shores study area, 22% (N = 98) were on the Long Beach study area and 7% (N = 30) were on the Grayland study area. The mean number of surveys annually was 34.4 ± 0.7 (range = 16–52) at Ocean Shores, 10.9 ± 0.8 (range = 4–25) at Long Beach,

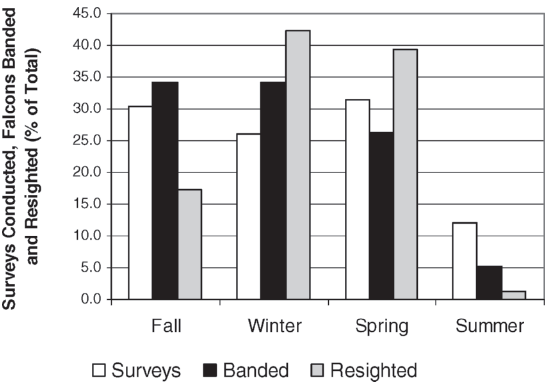

Figure 2. Percentage of Peregrine Falcons banded (N = 76) by season and percentage resighted (N = 33) by season in relation to the frequency of beach surveys by season, January 1995–May 2003. Data from Ocean Shores, Long Beach, and Grayland beaches were pooled.

and 4.3 ± 0.4 (range = 1–8) at Grayland. However, few surveys were conducted at Long Beach and Grayland in comparison with Ocean Shores in the earlier years of the study (1995–98: Grayland, N = 5; Long Beach, N = 20; Ocean Shores, N = 140). We conducted 30% (N = 133) of our surveys in fall, 26% (N = 114) in winter, 32% (N = 138) in spring and 12% (N = 53) in summer. Most of the surveys conducted in summer were done between 1997 and 2000 (45 of 52, 87%) and 71% (N = 37) of all summer surveys were at Ocean Shores, where we did 3–4 surveys each mo during that time period.

We color-banded (hereafter, banded) 76 individuals, 48.7% (N = 37) at Ocean Shores, 46.0% (N = 35) at Long Beach, and 5.3% (N = 4) at Grayland. We banded 34.2% (N = 26) of all individuals in the fall, 34.2% (N = 26) in winter, 26.3% (N = 20) in spring, and 5.3% (N = 4) in summer. The proportion of peregrines banded by season was similar to the percentage of surveys by season (χ^2 = 5.2, P = 0.158, df = 3; Fig. 2).

Most of the peregrines we banded were *F. p. pealei*-type; 76% (N = 55) of individuals were this subspecies type, 7% (N = 5) were *F. p. anatum*-type, 3% (N = 2) were *F. p. tundrius*-type, and 14% (N = 10) showed intermediate characteristics and were undetermined as to subspecies type. We captured 45 females and 31 males and the proportion of each sex banded did not vary by season (χ^2 = 0.84, P = 0.66, df = 2; Table 2). Of the 76 peregrines caught, 68% were <1 yr of age and 32% were ≥1 yr, but the sex ratio differed between age classes; 63% (N = 33) of trapped peregrines <1 yr of age were females, compared to 50% (N = 12) of the birds ≥1 yr old. The percentage of peregrines banded by age class varied by season, with young birds making up a greater percentage of the birds captured in fall and winter (>80%) than in spring (45%, χ^2 = 10.32, P < 0.01, df = 2; Table 2).

Resightings and Recoveries. We observed 51% (N = 76) of the Peregrine Falcons we banded alive at least once after banding, including 60% (N = 52) of those banded at <1 yr old and 33% (N = 24) of those at ≥1 yr old. Of 211 resightings, 130 were at Ocean Shores (N = 21 falcons), 46 were at Long Beach (N = 17 falcons), 19 were at Grayland (N = 3 falcons), and 16 were off the study areas (N = 8 falcons). We made 175 observations of banded peregrines (N = 37) on the study areas during project surveys. An additional 20 observations (N = 7 falcons) were made on the beaches by biologists and banders not participating in the research effort. Individuals were resighted a mean of 5.0 ± 0.6 (range = 1–61; N = 42) times. One peregrine (bird 4/D)

Table 2. Percent, by sex, age and season of Peregrine Falcons captured and banded (N = 76) at Ocean Shores, Grayland, and Long Beach study area beaches on coastal Washington, Jan 1995–May 2003.

	FALL SEP–NOV % (N)	WINTER DEC–FEB % (N)	SPRING MAR–MAY % (N)	SUMMER JUN–AUG % (N)	TOTAL % (N)
Sex					
Female	53.8 (14)	65.4 (17)	55.0 (11)	75 (3)	59.2 (45)
Male	46.2 (12)	34.6 (9)	45.0 (9)	25 (1)	40.8 (31)
Age[a]					
<1 yr	84.6 (22)	80.8 (21)	45.0 (9)	0.0 (0)	68.4 (52)
≥1 yr	15.4 (4)	19.2 (5)	55.0 (11)	100.0 (4)	31.6 (24)

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

Study Area	1995				1996				1997				1998				1999				2000				2001				2002				2003	
CB[a]; Sex; Age[b]	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S	Su	F	W	S
Ocean Shores																																		
3/W; F; ≥1	B								R	r			r				r	r							r									
8/3; M; <1				B		r																												
4/D; F; <1									B	R		R	R	R		r	R	R		R	R	r		R	R			R	R			r	R	
9/8; M; <1									BR	R	R	R		r																				
8/7; M; <1										B								R			R					r			r					
4/H; F; ≥1														B			R																	
9/4; M; <1														BR		r																		
7/R; F; ≥1																		B			r	R												
7/Z; F; 1																		B		r														
P/D; F; <1																					B	r							r				R	
M/V; M; <1																												Br	R	R				
M/W; M; <1																												B	R					
P/K; F; <1																													Br					
V/C; F; ≥1																													B					r
W/R; M; <1																																	Br	
X/X; M; <1																																		BR
Grayland																																		
4/K; F; <1																B	r	r	R	R	R	r												
V/M; F; <1																																	Br	
Long Beach																																		
9/2; M; <1													B							r									r					
4/N; F; <1																	Br	R		r														
M/M; M; <1																	B	R						r										
8/E; M; 1																			B						r								r	
7/S; F; ≥2																				Br														
P/M; F; <1																					B	r												
7/Y; F; <1																								BR	r	R			R	R				r
M/B; M; <1																								B	r				r					
P/Z; F; <1																										BR								
P/V; F; <1																												B	R	R				
P/2; F; <1																													B	R		r		r
V/H; M; <1																													Br	r				
V/V; F; <1																																	B	R

[a] CB = alphanumeric code on color band.
[b] Age = age at banding.

Figure 3. Peregrine Falcons banded and resighted on Ocean Shores, Grayland, and Long Beach study areas in western Washington, Jan 1995–May 2003. Individuals are identified by the alphanumeric code on their color bands, where, in the same season, B = banded and no resightings; Br = banded and one resighting; BR = banded and ≥1 resighting; r = one resighting; and R = ≥2 resightings. Data are summarized across years by season: W = Winter: Dec–Feb; S = Spring: Mar–May; Su = Summer: Jun–Aug; and F = Fall: Sep–Nov.

was resighted more than any other individual (29% of 211 resightings). Resighting frequency varied by season. Proportionally fewer resightings of birds we banded occurred on surveys in summer and fall than on surveys in winter and spring ($\chi^2 = 37.2$, $P < 0.001$, df = 3; Fig. 2).

Of the banded peregrines that were observed off the study areas, two birds banded at Ocean Shores were found nesting, one on a cliff in western Washington east of Ocean Shores and another on a cliff 1000 km north on Langara Island in British Columbia (W. Nelson pers. comm.).

Three of the peregrines we banded were found dead, all of unknown causes. One was found on the Ocean Shores study area (banded at Grayland), one at Cannon Beach, Oregon (banded at Ocean Shores), and one at Newport, Oregon (banded at Ocean Shores).

We observed four peregrines on our study area beaches that had been banded as nestlings by other researchers. Three were banded in the San Juan Islands, Washington (112, 379, and 529 d from banding to observation; B. Anderson pers. comm.), and one was banded along the lower Columbia River in Oregon (124 d from banding to observation; J. Pagel pers. comm.).

Beach Use Fidelity. Within seasons and across seasons and years, peregrines of both sexes and four age classes showed fidelity of beach use (Fig. 3). Of 31 individuals resighted on ≥1 occasions on the same beach where they were banded, 54.8% (N = 17) were observed again during the fall-winter-spring period that they were banded or during one other, 29.0% (N = 9) were resighted in two fall-winter-spring periods, 12.9% (N = 4) were resighted in 3–4 of these periods, and one, bird 4/D, was resighted in seven periods (Fig. 3). Peregrines 9/8 and 4/K were observed on >1 occasion in summer and also during fall-winter-spring periods (Fig. 3).

Among the 31 peregrines showing beach fidelity, three were resighted on one of the other two study area beaches on >1 occasion. Three peregrines did not exhibit fidelity of beach use; they were never observed on the beach where they were banded, but were observed on one of the other study area beaches.

Resighting Frequencies. Estimates of resighting probability (P) were highest for juveniles (p_{FWSp} = 45.4 ± 7.9%) and lowest for adult males (p_{FWSp} = 16.7 ± 4.5%; Table 1, model 1). Estimates did not vary over time, but instead were a function of the study season. In fact, the top six models in our model comparison incorporated variation in resighting frequencies by season (models 1–6, Table 1). The model that best fit the data (model 1, Table 1) in resighting probability (P) suggested that birds of all age and sex classes had similar resighting rates during the summer; resighting frequency was lower in the summer (P = 9.9%, ±3.9%) than during all other seasons combined. During other seasons, juveniles (45.4 ± 7.9%) and adult females (35.9 ± 5.0%) had higher resighting frequencies than adult males (16.7 ± 4.5%). Models, such as model 1, with age and sex-specific resighting frequencies fit the data better than models with constant resighting frequency (comparison with no-age model: $\Delta AIC_c = 6.9$; comparison with no-sex model: $\Delta AIC_c = 7.0$). The simplest model we tested, $\Phi(.)p(.)$, was ranked 23 of 23 models ($\Delta AIC_c = 17.9$, $w_i < 0.001$; the top models with $\Delta AIC_c < 2.0$ each incorporated variation in resighting rates among season and age/sex groups (Table 1). The pooled, 3-mo resighting frequency for all age and sex classes during fall, winter, and spring was 32.4 ± 3.5% (model 5, Table 1).

Apparent Survival. Apparent survival estimates did not vary by season, time, age- or sex-class, or study area. Model selection, based on AIC_c (Table 1), indicated that the best model (model 1) incorporated pooled survival estimates (Φ_{3mo} = 87.9% ± 2.0%). The best model varied significantly from the simplest model we tested, $\Phi(.)p(.)$. However, all differences were due to variation in resighting frequencies among groups; the survival parameter in the $\Phi(.)p(.)$ model was the same as our top model, with pooled survival (Table 1). The annual apparent survival estimate for all age and sex classes, as extrapolated from the 3-mo estimate was 59.7% (±5.4%). Goodness-of-fit simulations showed that our mark-recapture data met the assumptions of mark-recapture analysis (P = 0.50).

Although survival did not vary significantly by age- or sex-class, models with considerable weight incorporated age- or sex-specific survival rates (models 2–4, Table 1). The best model with age-specific survival rates (model 2, Table 1) estimated that the 3-mo survival for adults was about 7% higher (89.4%, 95% C.I. = 84.0%–93.1%) than that for juveniles (82.6%, 95% C.I. = 69.6%–90.7%). The 95% C.I.'s for adult and juvenile survival rate estimates overlap, supporting our selection of model 1 (Table 1) as the best model, without age-specific survival rates. Similarly, survival estimates for male and female peregrine were almost identical; the best model with sex-specific survival (model 4, Table 1) estimated survival for males as 88.9% (95% C.I. = 79.3%–94.4%) and 87.6% for females (95% C.I. = 82.1%–91.5).

DISCUSSION

Our surveys represent snapshots of Peregrine Falcon use of the study areas through time, so we do not know the full extent to which individuals used these areas for wintering or as short-term stopover places in winter or on migration. Still, our observations demonstrate fidelity of beach use by peregrines of both sexes and a range of ages across seasons and years. The relatively low frequency of peregrine bandings and resightings in summer compared to fall, winter, and spring (Fig. 3) is not surprising, given that the coastal beach-dune habitat in our study areas lack adjacent cliffs or other potential nest sites for breeding.

We documented use of the Washington beaches by all three of the currently recognized North American subspecies. Our method of subspecies determination, using plumage coloration and measurements, may have resulted in some incorrect subspecies designations. However, we banded a similar percentage of *F. p. pealei*-type (76%; $N = 55$) as did Anderson and colleagues working on Washington's outer coast from 1984–1986 and using the same approach to identify subspecies (73% *F. p. pealei*, 27% unknown subspecies, $N = 22$ total; Anderson et al. 1988). Brown et al. (2007) found strong genetic differentiation of *F. p. pealei* from *F. p. tundrius* and *F. p. anatum*, but no differentiation between *tundrius* and *anatum*; they recommended that *F. p. tundrius* be subsumed into *F. p. anatum*. We suggest our findings be interpreted broadly as indicating that approximately three of four peregrines we captured were *F. p. pealei*, originating on the Pacific Northwest coast. The others originated on the coast or east and north to the Arctic tundra (Varland et al. 2008).

Sex and Age. We caught fewer males (41%) than females (59%), perhaps because of behavioral differences between the sexes. Other studies involving capture of peregrines on coastal beaches using pigeons as lures also have reported more females captured (Ward and Berry 1972, Hunt et al. 1975, Juergens 2003), suggesting a trap response favoring females (Hunt et al. 1975). However, Anderson et al. (1988) caught more males (64%, $N = 14$) than females on the Washington coast during fall and spring banding on the Long Beach Peninsula and at Cape Flattery using pigeons as lures; however, their sample size was small ($N = 22$).

Our higher estimate of resighting probability (P) for banded adult females (36%) compared to adult males (17%) also suggests that males, even when present, were not as likely to be seen. Adult males may have been more wary or more active (i.e., less time perching) on the study areas than females, making them harder to detect and/or identify.

Apparent Survival. We estimated that the annual apparent survival rate was 59.7%, but given that our study areas were apparently not used by peregrines year-round, some proportion of birds assumed to have died likely emigrated permanently instead. Some of the peregrines we marked during winter, for example, may have elected to remain on their breeding territories in subsequent winters. Adult Peregrine Falcons have been documented overwintering near their eyries in British Columbia (Langara Island, W. Nelson pers. comm.; Vancouver Island, E. McClaren pers. comm.).

Our estimate of apparent annual survival (59.7%), which includes both juvenile (<1 yr old) and adult (≥1 yr old) peregrines, was intermediate between estimates of annual survival for these two age classes from other studies. The overall survival for first-year birds in mid- and south-coast regions of California was 33% (Kauffman et al. 2003), which included a survival estimate of 65% for peregrines fledging from urban areas, and 28% for peregrines fledging from rural areas. Second-year and adult survival rate of peregrines in California was 86%, which is similar to adult survival estimates from other portions of their range (White et al. 2002, Kauffman et al. 2003). Annual return rates (survivorship rates) for breeders on Langara Island, coastal British Columbia, was 63% for females and 74% for males (Nelson 1990).

There were many cases in which peregrines went undetected for long periods in our study areas before they were eventually resighted alive, suggesting that their home ranges far exceeded the sizes of our study areas or that they were undetected even when present. Indeed, winter home ranges of peregrines have been documented to have a mean size of 169 km^2 (McGrady et al. 2002), more than six times the size of Long Beach, our largest study area (26 km^2).

Our survival estimate is the first reported for Peregrine Falcons in a coastal beach environment. This estimate may be compared to peregrine survival estimates from other areas or to estimates from our study area in the future. Although the apparent survival rate we report underestimates true survival because of emigration, it provides baseline information useful in monitoring the status of this species of conservation concern on the Washington coast, and yields information unattainable through survey count data alone (van Horne 1983).

ACKNOWLEDGMENTS

Thanks to C. Anderson who taught D. Varland how to capture peregrines, and to the Washington State Parks and Recreation Commission for allowing research access to the beaches. M. Gustafson, at the time of this study with the USGS Bird Banding Lab, provided valuable insight and assistance with color-banding and also facilitated permits. We also greatly appreciate the field assistance of S. Tomlinson, D. Moore, T. McBride, B. Davies, J. Bauder, and M. Zaremba. We thank B. Wheeler and C. White for their assistance in identifying peregrines to subspecies by plumage. Thanks to V. Molenaar for working with us to develop and maintain the project database. J. Enderson, D. Dekker, S. Horton, J. Buchanan, B. Linkhart and two anonymous reviewers provided valuable comments on earlier drafts of this manuscript and J. Buchanan also contributed to fieldwork. Thanks to Rayonier for providing financial support. This paper is a contribution of the University of Nebraska Agricultural Research Division, Lincoln, NE, Journal Series No. 14574. This research was supported in part by funds provided through the Hatch Act.

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Received 12 August 2004; accepted 15 April 2008
Associate Editor: James C. Bednarz