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PEREGRINE FALCON SURVIVAL RATES DERIVED FROM A LONG-TERM STUDY AT A MIGRATORY AND OVERWINTERING AREA IN COASTAL WASHINGTON, USA

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ABSTRACT.—After a well-documented recovery following substantial population declines throughout most of North America, the Peregrine Falcon (*Falco peregrinus*) was delisted under provisions of the Endangered Species Act in 1999. Post-delisting monitoring for the Peregrine Falcon stipulated surveys of breeding locations and did not specifically emphasize other metrics of population dynamics such as survival. We used banding data from Peregrine Falcons captured on the Washington coast during 1212 vehicle surveys between 1995 and 2018 to assess apparent survival and resighting frequencies. Our mark-recapture data set included 226 Peregrine Falcons: 148 females and 78 males. Fourteen Peregrine Falcons were recovered dead and another eight were found injured or uninjured and unable to fly due to illness or substantially soiled feathers. We had 744 resightings, 67.1% ($n = 499$) by our research group during surveys (Group A) and 32.9% ($n = 245$) by others (Group B). We found a dramatic increase in Group B contributions beginning in 2008 due to the emergence of digital camera use in wildlife photography and increased public awareness of our project. Data from 1995 to 2018 supported the estimation of apparent survival for three age classes of Peregrine Falcons: 0.424 (SE = 0.057) for hatch-year (<1 yr old); 0.663 (SE = 0.066) for second-year (1–2 yr old), and 0.738 (SE = 0.030) for after-second-year (>2 yr old). Our long-term mark-resighting analyses of overwintering and migratory Peregrine Falcons along the Washington coast provide evidence of a reasonably high level of apparent survival that suggests good population performance.

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

TASAS DE SUPERVIVENCIA DE *FALCO PEREGRINUS* DERIVADAS DE UN ESTUDIO A LARGO PLAZO EN UN ÁREA MIGRATORIA Y DE INVERNADA DE LA COSTA DEL ESTADO DE WASHINGTON, EEUU

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RESUMEN.—Tras una bien documentada recuperación, posterior a declives poblacionales sustanciales en la mayor parte de Norteamérica, *Falco peregrinus* fue excluido en 1999 de la Ley de Especies en Peligro de Extinción. El seguimiento posterior a la exclusión de *F. peregrinus* estipuló muestreos de sus sitios de reproducción pero sin enfatizar otras métricas de dinámica poblacional, tales como la supervivencia. Usamos datos de anillamiento para individuos de *F. peregrinus* capturados en la costa del estado de Washington durante 1212 muestreos en vehículo entre 1995 y 2018 con el fin de evaluar las frecuencias de supervivencia aparente y de reavistamientos. Nuestro conjunto de datos de marcaje y recaptura incluyó 226 individuos: 148 hembras y 78 machos. Catorce individuos fueron recuperados muertos y otros ocho fueron encontrados heridos o incapaces de volar como resultado de enfermedad o por tener el plumaje muy sucio. Obtuvimos 744 reavistamientos, 67.1% (n=499) por nuestro grupo de investigación durante los muestreos (Grupo A) y 32.9% (n=245) por otros (Grupo B). Encontramos un aumento dramático en las contribuciones del Grupo B comenzando en 2008 debido a la aparición del uso de cámaras digitales en la fotografía de vida silvestre y al aumento del conocimiento público de nuestro proyecto. Los datos de 1995 a 2018 apoyaron la estimación de supervivencia aparente para tres clases de edad de *F. peregrinus*: 0.424 (EE = 0.057) para los individuos eclosionados ese año (<1 año de edad); 0.663 (EE=0.066) para los individuos del segundo año (1–2 años de edad) y 0.738 (EE = 0.030) para los individuos posteriores al segundo año (>2 años de edad). Nuestros análisis a largo plazo de marcaje y reavistamiento de individuos invernantes y migrantes de *Falco peregrinus* a lo largo de la costa del estado de Washington muestran evidencia de un nivel razonablemente alto de supervivencia aparente, lo que sugiere un buen estado de la población de esta especie.

[Traducción del equipo editorial]

Long-term capture and monitoring programs have potential value in the assessment of population trends for management and conservation. In addition to simply covering relevant temporal periods, use of long-term mark-resighting studies may decrease bias in survival estimation of longer-lived animals. Mark-resighting studies estimate apparent survival as the product of true survival and permanent emigration (Williams et al. 2002), in contrast to estimates of true survival from known-fate or other analyses that can account for emigration. By extending the length of a mark-resighting study, apparent survival estimates may come closer to true survival estimates if "wandering" individuals eventually return to a study site. Of course, longer-term studies also have the potential to experience changes in observer effort (Butcher et al. 1990), which can be accounted for through variation in estimates of resighting probabilities (Powell and Gale 2015). Therefore, assessments of survival from long-term data sets can be useful for conservation and management planning to aid in assessments of population dynamics (Wootton and Bell 1992, Bildstein 1998). Investigations of raptor population dynamics have concluded that survival can be an important indicator of population trends (Newton et al. 2016).

Populations of Peregrine Falcons (*Falco peregrinus*) throughout most of North America experienced widespread and substantial declines caused by environmental contaminants (Kiff 1988). The recovery of Peregrine Falcon populations in the latter part of the twentieth century was a well-documented success story of modern conservation (Cade et al. 1988, Cade and Burnham 2003) and resulted in Endangered Species Act (ESA) delisting in 1999 (US Fish and Wildlife Service [USFWS] 1999). Shortly after delisting, a monitoring strategy was developed and implemented to confirm that the species continued on a healthy trajectory (USFWS 2003). The primary emphasis of the post-delisting monitoring strategy was collection of data from breeding territories (i.e., territory occupancy, nest success, reproductive output). Investigation of data on contaminants and eggshell thickness was also encouraged (USFWS 2003), but a framework for collecting such information was not developed.

Peregrine Falcons may be at risk from factors that negatively influence survival and population trends. At the forefront is dietary exposure to contaminants, including mercury (Ackerman et al. 2016) and infectious pathogens (Lee et al. 2015). As has been amply demonstrated, Peregrine Falcons and other raptor species are vulnerable to certain contaminants (Ratcliffe 1993, Beyer and Meador 2011, Finkelstein et al. 2012). Of note, mercury levels in feathers of Peregrine Falcons from our study area in western Washington are among the highest levels recorded for this species (Barnes et al. 2018). Similarly, the effects of wildlife diseases have the potential to impact populations of birds, including raptors (Friend et al. 2001). We previously reported the death of a Peregrine Falcon on our study area due to infection from highly pathogenic avian influenza (HPAI) virus H5N8 (Varland et al. 2018). Although currently there are few concerns about the effects of mercury and HPAI on subspecies or regional populations, such concerns may develop if levels of exposure increase (Peterson and Williams 2008, Herring et al. 2018).

A number of factors, including some that may be unrelated to actual survival, have the potential to influence estimates of survival rates. A growing body of literature indicates that the presence of apex predators may influence the distribution or behavior of subordinate predators (Sergio et al. 2003, 2007, Cresswell 2008, Mueller et al. 2016). In southern coastal British Columbia, 225 km northeast of our study area, the hunting behavior of overwintering Peregrine Falcons at a large estuary was strongly influenced by the presence of large numbers of Bald Eagles (*Haliaeetus leucocephalus*), primarily due to kleptoparasitic interactions (Dekker et al. 2012, Dekker and Drever 2015). Although we observed little evidence that Bald Eagles stole food items from Peregrine Falcons (Varland et al. 2018), we realize that a passive interaction of the two species (e.g., Lima 1998, Sergio and Hiraldo 2008) could potentially influence survival estimates and resighting rates of Peregrine Falcons by reducing their occurrence on our study area and at other sites where the two species co-occur.

In this report, we used data from a 22-yr banding study on the Washington coast that began in 1995 (Varland et al. 2008a) to: (1) evaluate trends in the occurrence of Peregrine Falcons and Bald Eagles, (2) evaluate the occurrence of Peregrine Falcon subspecies, and (3) estimate apparent survival probability and resighting probability for age and sex classes of Peregrine Falcons for designated time periods. In addition, we evaluated the effects of changing levels of observer effort on apparent survival and on the probability of resighting Peregrine Falcons.

METHODS

Study Area. Our study area consisted of three intertidal sand beaches on the outer coast of southwestern Washington. North to south, these beaches were Ocean Shores (23.5 km long; 46°56′N, 124°10′W; Fig. 1), Grayland (11.3 km long; 46°45′N, 124°06′W), and Long Beach (39.9 km long; 46°18′N, 124°04′W). All three beaches are linear, bordered by the Pacific Ocean to the west, and to the east are backed by sand dunes stabilized primarily by European beach grass (*Ammophila arenaria*; Buchanan et al. 2001, Varland et al. 2018). The three beaches are not contiguous, each being separated from an adjacent beach by the mouth (entrance) of Grays Harbor or Willapa Bay.

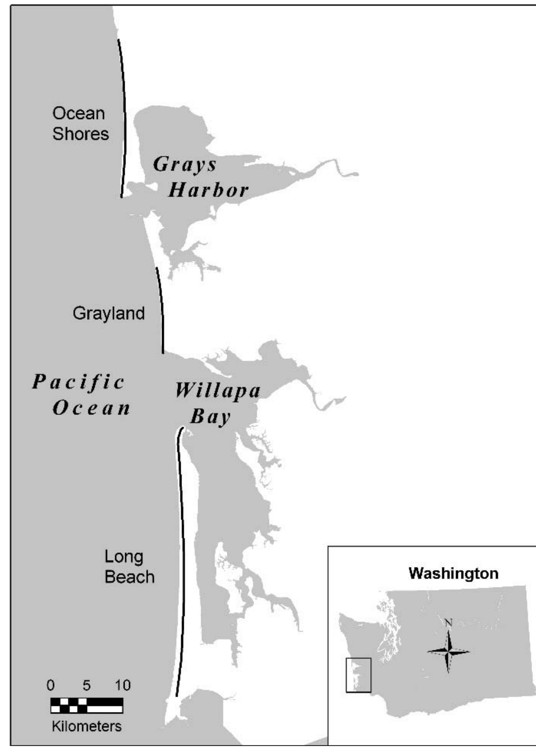

Figure 1. Location of three study area beaches in southwestern Washington (Ocean Shores, Grayland, and Long Beach) where we captured and banded Peregrine Falcons between 1995 and Feb 2018. Survey transects are indicated by black lines.

Field Procedures. We surveyed the beaches, for the purpose of capturing, banding, and resighting Peregrine Falcons, between January 1995 and February 2018. We used four-wheel-drive vehicles for all surveys, which we classified as either complete or incomplete: *Complete Raptor Surveys* were conducted under favorable driving and weather conditions, and when ≥70% of a study area beach could be surveyed. We recorded the occurrence of all raptors encountered in three adjacent habitats: beach, sand dunes, and ocean (to 100 m offshore). For the counts of Peregrine Falcons and Bald Eagles used to determine number observed per 100 km, we used data only from Complete Raptor Surveys. For a complete description of these survey methods, see Varland et al. (2012). *Incomplete Raptor Surveys* included visits involving lesser survey area coverage, adverse weather, or poor visibility, and situations where raptor counts were not a research objective (i.e., trapping Bald Eagles from a fixed location; Varland 2015). The methods used to count individual peregrines were also used to count Bald Eagles; Complete Raptor Surveys were counts of all raptors (e.g., peregrines, eagles, and other species).

Details on capturing techniques and banding are provided in Varland et al. (2008a, 2012), but are briefly summarized here. We captured most Peregrine Falcons with a harnessed Rock Pigeon (*Columba livia*). For all birds captured, we secured one band on each leg: a US Geological Survey band anodized red or blue on one and a color-coded alphanumeric band, also described as a Visual Identification Band (VID), on the other. We fitted Peregrine Falcons with black-above-blue (black/blue) color bands from 1995–1998. Beginning in 1999 and thereafter, we adopted the international protocol for banding Peregrine Falcons in North America (black/blue for *F. p. tundrius*, *F. p. anatum*, and subspecies uncertain; green for *F. p. pealei*). We used measurements (e.g., wing chord, culmen, and tail length) to classify individuals by sex and a combination of plumage characteristics, measurements, and photo review to classify individuals by subspecies (Varland et al. 2012).

After release, we resighted color-banded (hereafter, banded) individuals by reading the alphanumeric codes on their VID bands using a spotting scope, binoculars, or camera with telephoto lens, or sometimes with the bird in hand at recapture. We made numerous resightings of marked Peregrine Falcons, but we also received resighting reports from people outside our survey group, including field biologists, wildlife photographers, and others (Varland et al. 2012). Reports were obtained when individuals contacted us directly by telephone or email, or indirectly after they first had contacted the US Geological Survey Bird Banding Laboratory, Patuxent, Maryland, which then notified us. We used resighting information we collected and resighting information provided by other observers in our analyses. Herein, Group A includes the core survey group and involves the sightings we made; Group B includes all other observers and involves the resightings they provided.

Site Fidelity. We previously documented that Peregrine Falcons on our study area represented individuals from across the spectrum of migratory patterns along the Pacific coast. To summarize, a very small number of Peregrine Falcons originated from or moved to 1–2 breeding territories within 15 km of our study area. However, the vast majority of Peregrine Falcons we encountered were migrants, and based on resighting and band recovery data (Varland et al. 2008a, 2012), Peregrine Falcons passing through coastal Washington may migrate to or from relatively nearby areas (e.g., 50–200 km) or regions quite distant (e.g., >1000 km). A number of Peregrine Falcons overwintered on our study area each year, whereas only a few were detected in summer. This varied pattern of movement therefore likely influences estimates of site fidelity, which is a measure of repeated use, or faithfulness, to a particular area. We defined site fidelity at two spatial scales: *study-area use fidelity* was indicated by the resighting of a color-banded Peregrine Falcon on any of the three study area beaches $\geq$1 d after banding, and *beach use fidelity* was indicated by the resighting of a banded Peregrine Falcon on the same beach $\geq$1 d after banding (Varland et al. 2012).

Statistical Analyses. Over the years of study, we noted an increase in Peregrine Falcon resighting reports from Group B. A preliminary assessment of our data showed a dramatic increase in Group B contributions beginning in 2008 and continuing to the close of the study period, in February 2018. Given the increase in reporting by Group B, we tested for differences in apparent survival, resighting frequencies, survey effort by Group A (total number of surveys per year; total distance surveyed per year), and annual observations of Peregrine Falcons and Bald Eagles between two time periods: 1995–2007 and 2008–2017. Because surveys in 2018 were limited to January and February, we omitted 2018 from analyses of annual survey efforts and annual observations of Peregrine Falcons and Bald Eagles. Further, we limited our analysis of survey effort and observation rates for Peregrine Falcons and Bald Eagles to data collected from Complete Raptor Surveys, due to inconsistencies in data collection during Incomplete Raptor Surveys.

We were particularly interested in evaluating whether there were differences in annual observations between the two time periods (1995–2007 and 2008–2017) for three dependent variables: number of Peregrine Falcons per 100 km, number of Bald Eagles per 100 km, and number of kilometers surveyed. We tested for differences across beaches by time period using a generalized linear model (GLM; Poisson error) with square-root transformed dependent variables. For each model, when there was no interaction between beach and time period, we summed the data from the three beaches by year, and the final models included time period as the only factor. We also estimated the contributions made by the additional observers (Group B) toward the total number of banded Peregrine Falcon resightings (total resightings, total individuals resighted) in a GLM with Poisson error which included group and time period as main effects, as well as the group by time period interaction. Back-transformed means and 95% confidence intervals are reported from all of the models. For years and sites that had survey results for Bald Eagles and Peregrine Falcons, we used a Spearman correlation to estimate the relationship between the number of Bald Eagles and the number of Peregrine Falcons per 100 km.

Apparent survival. We used Cormack-Jolly-Seber (C-J-S) mark-recapture methods (Pollock et al. 1990, Williams et al. 2002) to estimate the probability of apparent annual survival (ϕ) which was the likelihood that an animal survived 12 mo and did not emigrate (Dinsmore and Johnson 2005) and capture probability (p) during 3-mo time periods. We conducted our analysis using the RMark package in program R (White and Burnham 1999, Laake 2013). Although we recaptured some Peregrine Falcons for other research objectives (e.g., Barnes et al. 2018), most of our encounters with marked Peregrine Falcons were resightings only. Consequently, hereafter we use the term *resighting probability* to include both resightings and recaptures.

We constructed capture histories for Peregrine Falcons banded on our study area and individuals banded by other researchers elsewhere that we resighted on our study area. Because our estimates were for survival rates of Peregrine Falcons encountered on our study area, we considered the date when we first saw individuals banded by others as the banding date for the analysis in MARK. We grouped our captures for banding and resightings into 3-mo observation periods by season, adopting the meteorological definition of seasons for the northern hemisphere (Trenberth 1983). Under this scenario, the season breakdown as used by Varland et al. (2008a) was fall: September–November; winter: December–February; spring: March–May; and summer: June–August.

We constructed models to account for variation in apparent annual survival and 3-mo resighting probability based on (1) age at encounter: hatch-year (HY; first summer, fall and winter: age <1 yr), second-year (SY; first spring, second summer, fall and winter; age 1–2 yr) or after-second-year (ASY; second spring and past; age >2 yr); (2) sex: male or female; (3) season, as previously described; and (4) time periods (1995–2007 and 2008–2018) to account for potential effects of an increase in resightings from Group B after 2007.

We allowed for a seasonal effect in resighting probability because of lower survey effort in the summer 3-mo period (two season groups: fall/winter/spring and summer) based on our earlier results (Varland et al. 2008a). We conducted an *a priori* comparison of the null model (constant survival, constant resighting probability) with a model that included constant survival and the effect of season to describe variation in resighting probability. We used Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) for the comparison, and based on that analysis we selected the model with seasonal variation in resighting probability as our base, or null, model. We constructed 64 models by creating all possible combinations of structures for ϕ and p (Table 1). We structured models with interactions between sex and age when both factors were present; season and time period were additive, as we expected the effects (e.g., fewer summer surveys and increased resightings from Group B) to apply equally to all age and sex groups.

Once banded, individuals in a C-J-S-type analysis are considered "at-risk" although their actual live/dead status is not typically known. However, we received confirmation that some Peregrine Falcons in our banded sample were found dead ("recoveries"; Barker 1997), at which time we removed them from at-risk status (Varland et al. 2008a). Similarly, when individuals were found injured or otherwise incapacitated we removed them from at-risk status in the analysis since these Peregrine Falcons would have died had they not been retrieved from the field for rehabilitation.

We used a model selection assessment with Akaike's Information Criterion corrected for small sample sizes (AICc) to distinguish among alternate models that described the variation in apparent survival and resighting probability. We were prepared to model average coefficients if model uncertainty existed, and we inspected coefficients estimated by all models within ΔAICc = 2 (Arnold 2010).

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. Structures of models considered to evaluate variation in apparent survival (ϕ) and capture/resighting probability (p) for Peregrine Falcons captured and banded in southwestern Washington, January 1995–February 2018. Age at encounter was hatch-year (HY), second-year (SY), or after-second-year (ASY); sex was male or female; time periods for effects of additional observers was 1995–2007 and 2008–2018; seasonal effect for resighting probability was structured as two season groups: fall/winter/spring and summer. With the exception of the null model, all models of capture/resighting probability (p) included season, based on *a priori* results and Varland et al. (2008a). Models were constructed by creating all possible combinations of structures for ϕ and p.

APPARENT SURVIVAL (ϕ)		CAPTURE/RESIGHTING PROBABILITY (p)	
MODEL NAME	STRUCTURE	MODEL NAME	STRUCTURE
Null	Constant ϕ	Null	Constant p
Age	Age	Season	Season
Sex	Sex	Age	Season + age
Time period	Time period	Sex	Season + sex
Sex/age	Sex * age	Time period	Season + time period
Sex/time period	Sex + time period	Sex/age	Season + sex * age
Age/time period	Age + time period	Sex/time period	Season + sex + time period
Sex/age/time period	Sex * age + time period	Age/time period	Season + age + time period
		Sex/age/time period	Season + sex * age + time period

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 exceeded the deviance from our data (Cooch and White 2006). When estimates of resighting probability were extended from 3-mo periods to annual estimates, we used $p_{\text{annual}} = 1 - (1 - p_{3\text{mo}})^4$ and the delta method (Powell 2007) to provide approximations of variance for the new temporal period of interest.

RESULTS

We conducted 1212 surveys from January 1995 to February 2018. The greatest number of surveys, both Complete Raptor Surveys and Incomplete Raptor Surveys, were conducted at Ocean Shores (Table 2). The mean annual number of Complete Raptor Surveys was 22% lower during the 2008–2017 time period compared with 1995–2007 (likelihood ratio $\chi^2 = 11.9$, df = 1, $P < 0.001$; Fig. 2). Surveys also covered less distance during 2008–2017 compared to 1995–2007, but the distance surveyed each year was highly variable year to year (ANOVA; $F_{1,21} = 2.3$, $P = 0.146$; Fig. 3). Although we found little difference in mean number of Peregrine Falcons sighted per 100 km surveyed between the two time periods (1995–2007: mean = 3.5, SE = 0.3; 2008–2017: mean = 4.0, SE = 0.4; ANOVA; $F_{1,21} = 0.94$, $P = 0.342$), we found substantially more Bald Eagles in the second time period (1995–2007: mean = 5.2, SE = 1.0; 2008–2017: mean = 20.1, SE = 2.2; ANOVA; $F_{1,21} = 46.6$, $P < 0.001$); all three beaches showed the same pattern (Fig. 4). However, there was no relationship between the number of Bald Eagles observed per 100 km surveyed and the number of Peregrine Falcons observed per 100 km surveyed ($r_s = -0.15$, $P = 0.507$).

Our mark-recapture data set included 226 Peregrine Falcons (148 females, 78 males). Ages at time of banding were 109 HY, 85 SY, and 32 ASY. We banded 99 individuals in our fall season, 73 in winter, 48 in spring, and six in summer.

The number of Peregrine Falcons banded varied by study area beach and we encountered individuals of all three North American subspecies, including Peregrine Falcons banded elsewhere. Although we conducted more surveys at Ocean Shores (Table 2),

Table 2. Survey effort at Ocean Shores, Grayland, and Long Beach study beaches on the southwestern Washington coast, January 1995–February 2018.

	OCEAN SHORES % (n)	GRAYLAND % (n)	LONG BEACH % (n)	TOTAL % (n)
Complete raptor surveys	67.5 (652)	12.2 (118)	20.3 (196)	100.0 (966)
Incomplete raptor surveys	56.1 (138)	4.9 (12)	39.0 (96)	100.0 (246)
Total surveys (n)	790	130	292	1212

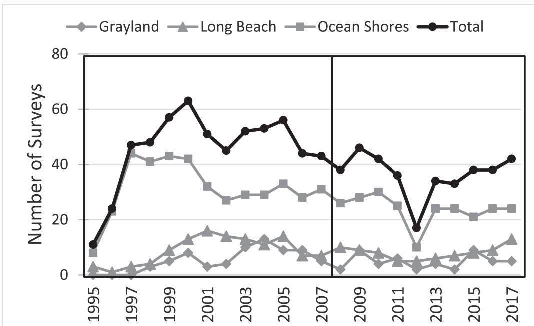

Figure 2. Number of Complete Raptor Surveys conducted annually on three coastal beaches in southwestern Washington (Ocean Shores, Grayland, and Long Beach) for two time periods of sampling 1995–2007 and 2008–2017. The overall mean for 1995–2007 was 46 surveys/yr (95% CI = 42–49) and for 2008–2017 was 36 surveys/yr (95% CI = 33–40).

we banded more Peregrine Falcons at Long Beach than Ocean Shores or Grayland (Table 3). In addition to the 219 Peregrine Falcons we captured and banded on the beaches, we captured seven others on our study area that were banded elsewhere by other researchers. We were able to classify 98.2% ($n = 222$) of the captured individuals to subspecies: 79.7% ($n = 177$) were *F. p. pealei*, 5.4% ($n = 12$) were *F. p. tundrius*, 3.6% ($n = 8$) were *F. p. anatum*, and 11.3% ($n = 25$) had intermediate characteristics. We were unable to assign subspecies to four Peregrine Falcons captured in the early years of the study because we did not take photos and measurements.

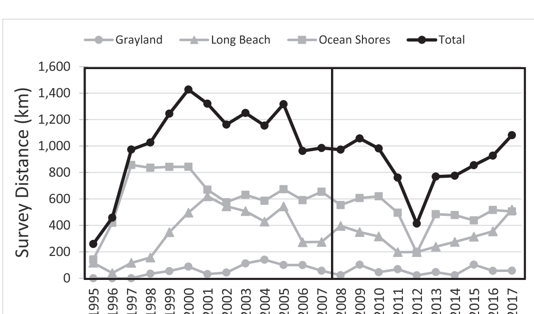

Figure 3. Length (km) of Complete Raptor Surveys conducted annually on three coastal beaches in southwestern Washington (Ocean Shores, Grayland, and Long Beach) for two time periods of sampling, 1995–2007 and 2008–2017. The overall mean survey length for 1995–2007 was 1041 km (95% CI = 876–1207) and for 2008–2017 was 859 km (95% CI = 671–1048).

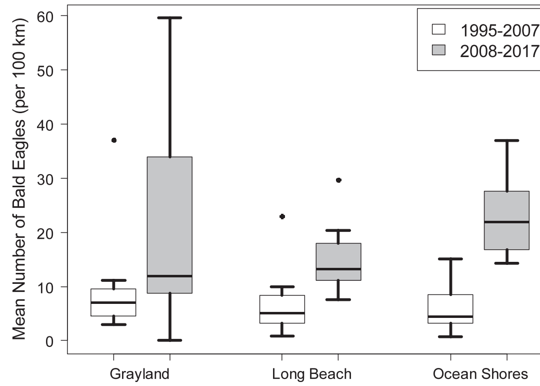

Figure 4. Number of Bald Eagles observed per 100 km surveyed on three coastal beaches in southwestern Washington (Ocean Shores, Grayland, and Long Beach) for two time periods of sampling, 1995–2007 and 2008–2017. The horizontal line inside the box represents the median, the top and bottom edges of the box represent the 25th and 75th percentiles, respectively, and the upper and lower whiskers (open lines) represent 1.5 times the interquartile range above or below the box. Circles represent values that were outside the range shown by the whiskers.

Resightings and Recoveries. One-hundred-six (46.9%) of the banded Peregrine Falcons in our study were resighted alive at least once after release. We had 744 resightings in total; 90.5% ($n = 673$) of these were made at our study area beaches, with the highest percentage at Ocean Shores (Table 3). The balance of the resightings (9.5%; $n = 71$) occurred elsewhere in Washington ($n = 47$), or in British Columbia ($n = 17$), Oregon ($n = 5$), Alaska ($n = 1$), and California ($n = 1$).

A greater percentage of *F. p. pealei* that we banded were resighted at least once compared with *F. p. tundrius* or *F. p. anatum* or those with intermediate plumage characteristics. We resighted, at least once, 50.5% ($n = 88$) of the *F. p. pealei* that we banded, whereas only 25% ($n = 3$) of *F. p. tundrius* were resighted at least once. We had no resightings of *F. p. anatum*. Among the group of Peregrine Falcons we banded that had intermediate characteristics, 34.8% ($n = 8$) were resighted. Many more *F. p. pealei* were resighted on $\geq$1 occasion than *F. p. tundrius* or those with intermediate characteristics: 33 *F. p. pealei* were resighted once, 26 were resighted 2–5 times, and 29 were resighted on >5 occasions. One *F. p. tundrius* was resighted once, another was resighted eight times across 14 mo, and one was resighted nine times between 2000 and 2003 (Varland et al. 2008b). Among those Peregrine Falcons with intermediate

Table 3. Percent of Peregrine Falcons banded and percent resightings by Group A (our survey team) and Group B (all others) at Ocean Shores, Grayland, and Long Beach study area beaches on the southwestern Washington coast, January 1995–February 2018.

	OCEAN SHORES % (*n*)	GRAYLAND % (*n*)	LONG BEACH % (*n*)	TOTAL % (*n*)
Peregrine Falcons banded	42.9 (94)	7.8 (17)	49.3 (108)	100.0 (219)
Resightings, group A	76.7 (368)	2.5 (12)	20.8 (100)	100.0 (480)
Resightings, group B	73.1 (141)	15.5 (30)	11.4 (22)	100.0 (193)

characteristics, four were resighted once, one was resighted four times and three were resighted >5 times.

A total of 46.0% ($n=104$) of the Peregrine Falcons were resighted on at least one of the study area beaches, a measure of *study area use fidelity*. Over 22 yr of surveys, 38.5% ($n=87$) of the resightings were at the beach where the individual was banded, but not on the other two; 7.5% ($n=17$) were resighted on a study area beach, but not on the beach where they were banded. We documented *beach use fidelity* within seasons, across seasons and across years (Supplemental Material, Fig. S1). Of the 87 individuals showing *beach use fidelity*, 55.2% ($n = 48$) were observed again in the combined fall/winter/spring period they were banded or another one, 23.0% ($n=20$) were observed in two combined fall/winter/spring periods, 16.1% ($n=14$) were resighted in 3–5 periods, and 5.7% ($n=5$) in >5 periods.

We noted a substantial change in the contribution of information provided by observers not associated with our project (Group B). Over the 22-yr study, we obtained 96.5% ($n = 718$) of the resighting reports from the observers (Group A and Group B) and 3.5% ($n = 26$) from the USGS Bird Banding Lab (Group B reporting first to the Lab). Group B made 32.9% ($n=245$) of all resightings, with 193 of these on study-area beaches (Table 3). Group B was responsible for most off-study-area resightings, at 73.2% of the total ($n=71$). Group B resighted nine

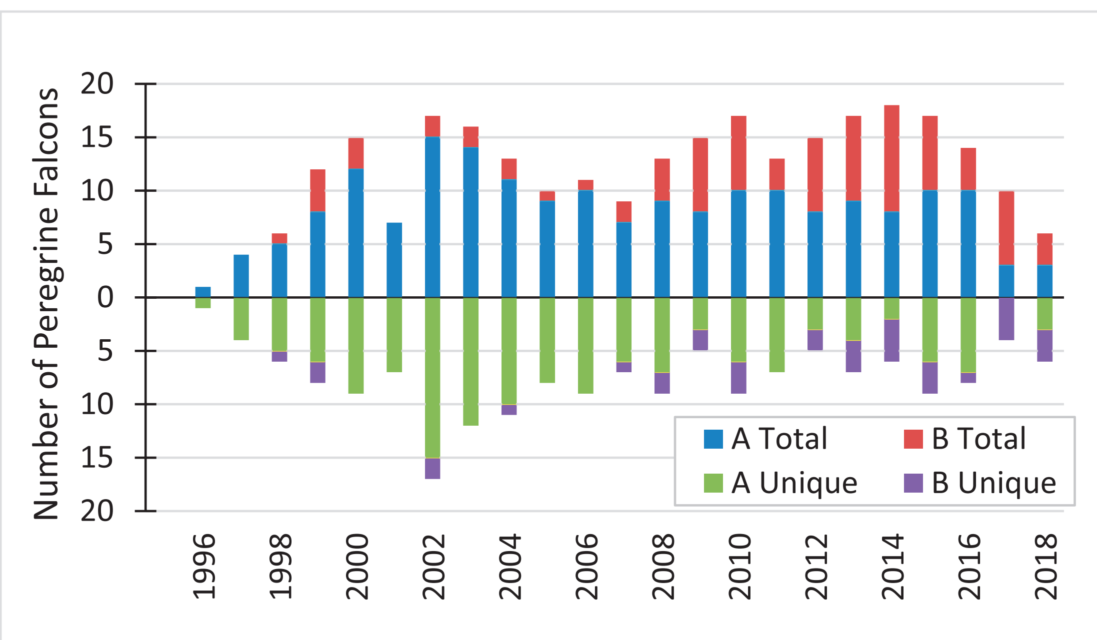

Figure 5. Number of Peregrine Falcons resighted after banding by Group A (our survey group) and Group B (all other individuals) in southwestern Washington at three coastal beaches, Ocean Shores, Grayland, and Long Beach, January 1995 to February 2018. Unique resightings were those made by one group only.

Table 4. Comparison of top-ranked competing models to describe variability in apparent annual survival (ϕ) and 3-mo resighting probability (p) for Peregrine Falcons captured and banded in southwestern Washington, January 1995–February 2018. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc); ΔAICc is the difference in AICc score relative to the highest-ranked model, ωAICc is the Akaike weight indicating the relative support of the model, and k is the number of parameters. Age at encounter was hatch-year (HY), second-year (SY), or after-second-year (ASY); sex was male or female; time periods for effects of additional observers was 1995–2007 and 2008–2018; seasonal effect for resighting probability was structured as two season groups: fall/winter/spring and summer. Sixty-four models were compared, and only the models with cumulative ωAICc = 0.90 are shown. Effects for each structure are shown; see Table 1 for exact structures for each model.

Model	Model Effects	k	AICc	ΔAICc	ωAICc	Deviance
1	ϕ(age) p(season/sex/age/time period)	11	1900.1	0.0	0.46	1751.0
2	ϕ(age/time period) p(season/sex/age/time period)	12	1901.4	1.3	0.24	1750.3
3	ϕ(sex/age) p(season/sex/age/time period)	14	1902.8	2.8	0.12	1747.5
4	ϕ(sex/age/time period) p(season/sex/age/time period)	15	1903.8	3.7	0.07	1746.3
5	ϕ(age) p(season/sex/age)	10	1904.3	4.3	0.05	1757.4
6	ϕ(age/time period) p(season/sex/age)	11	1906.4	6.3	0.02	1757.3
7	ϕ(sex/age) p(season/sex/age)	13	1907.1	7.1	0.01	1753.9
8	ϕ(age) p(season/sex/time period)	7	1903.0	7.9	0.01	1767.3
9	ϕ(sex/age/time period) p(season/sex/age)	14	1909.1	9.0	0.01	1753.7

Peregrine Falcons that were never resighted by Group A, and Group A resighted 54 Peregrine Falcons that group B never observed. Group B resighted 17 Peregrine Falcons following the last date they were resighted by Group A; the longest span between last resighting of an individual by Group A with a subsequent resighting by Group B was 14 yr 2 mo, the longest gap in resightings, representing the oldest individual in this study (age 15 yr).

Although the number of resightings was the same in both time periods for Group A (1995–2007: mean = 22.5, SE = 2.2; 2008–2017: mean = 22.4, SE = 2.2); $\chi^2 = 1.12$, df = 1, $P = 0.653$), resightings for Group B were significantly higher during 2008–2017 (mean = 20.4, SE = 2.6) compared to 1995–2007 (mean = 2.7, SE = 2.6; $\chi^2 = 180.68$, df = 1, $P < 0.001$). Likewise, the number of banded Peregrine Falcons observed did not differ significantly between time periods for Group A (1995–2007: mean = 7.9, SE = 0.8; 2008–

Table 5. Logit-scale estimates (β), standard error and 95% confidence intervals (CI) for the top-ranked model to describe variation in 12-mo apparent survival, ϕ, and capture probability during a 3-mo period, p, for Peregrine Falcons captured and banded in southwestern Washington, January 1995–February 2018. Age at encounter was hatch-year (HY), second-year (SY), or after-second-year (ASY); sex was male or female; time periods for effects of additional observers was 1995–2007 and 2008–2018; seasonal effect for resighting probability was structured as two season groups: fall/winter/spring and summer. Age of ASY, sex of female, fall/winter/spring season, and the 1995–2007 time period are baseline conditions, and estimates are derived from the intercepts.

Effect	β	SE	95% CI	
ϕ intercept	1.0367	0.1527	0.7373	1.336[a]
ϕ age: HY	−1.3438	0.2787	−1.8900	−0.7975[a]
ϕ age: SY	−0.3580	0.3566	−1.0569	0.3409
p intercept	−0.8352	0.1483	−1.1259	−0.5445[a]
p season: summer	−1.5043	0.2110	−1.9178	−1.0908[a]
p sex: male	−0.9117	0.2109	−1.3249	−0.4984[a]
p age: HY	0.8585	0.2424	0.3834	1.3336[a]
p age: SY	0.3663	0.2098	−0.0448	0.7774
p time period: 2008–2018	−0.3841	0.1523	−0.6827	−0.0856[a]
p sex: male * Age: HY	−0.2177	0.4247	−1.0501	0.6147
p sex: male * Age: SY	−0.1294	0.3993	−0.9119	0.6531

[a] Estimates in these rows have CIs that do not overlap 0.

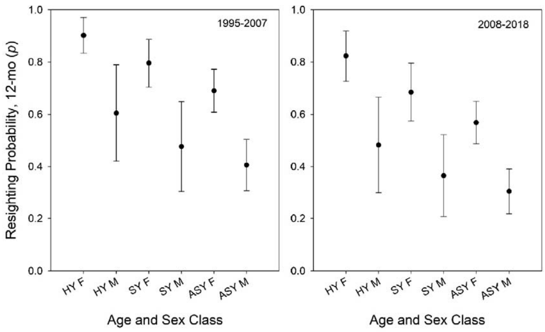

Figure 6. Probability of resighting, *p*, during 12 mo and 95% confidence intervals for age (hatch-year, HY; second-year, SY; after-second-year, ASY) and sex classes (female, F; male, M) of Peregrine Falcons captured and banded in southwestern Washington during two time periods of sampling, 1995–2007 and 2008–2018.

2017: mean = 8.5, SE = 0.8; $\chi^2 = 0.23$, df = 1, $P = 0.718$), but Group B made many more resightings during 2008–2017 (mean = 6.4, SE = 0.6) compared to 1995–2007 (mean = 1.4, SE ± 0.6; $\chi^2 = 40.84$, df = 1, $P < 0.001$). Not surprisingly, the number of people included in Group B was significantly larger in 2008–2017 (mean = 8.7, SE = 0.9) compared to 1995–2007 (mean = 1.2, SE = 0.9; $\chi^2 = 74.22$, df = 1, $P < 0.001$). In evaluating the overall contribution of Group B, we noted that even though they resighted many Peregrine Falcons—in some recent years, numbers comparable to Group A—they largely observed individuals also resighted by Group A (Fig. 5).

Fourteen Peregrine Falcons were recovered dead and another eight were found injured or uninjured but unable to fly due to illness or substantially soiled feathers (Appendix). Ten were recovered at <1 yr old, five at 1–2 yr old, and seven at >2 yr old with the oldest 11 yr old (Appendix). The mean number of months from the last sighting alive until recovery was 8.6 (range = 0.4–65.3 mo). Of these 22 Peregrine Falcons, 13 were found in Washington, seven in Oregon, and two in California. Sixteen were found on or adjacent to coastal beaches: nine in Washington, six in Oregon, and one in California. Five additional Peregrine Falcons were recovered 11–91 km inland; in one additional case, the distance to the coast was unclear in the information provided by the Bird Banding Lab. The most important known cause of mortality was collision with a stationary object (Appendix). One Peregrine Falcon died from exposure to highly pathogenic avian influenza (USGS 2015) during an outbreak of that disease in the Pacific Northwest (Ip et al. 2015) and another was likely killed and eaten by a Bald Eagle on the beach at Newport, Oregon (Appendix; T. Conroy pers. comm.).

Apparent Survival. Survival varied only by age class, according to the top-ranked model (ωAICc = 0.46; Table 4, Model 1; Table 5). The second-ranked model (ωAICc = 0.24) was the only other model with ΔAICc < 2, and this model was identical to the top model except for the addition of an effect of time period on apparent survival (Table 4). However, the time period effect in the second-ranked model was not significant ($\beta_{2008\text{-}2018} = 0.195$, SE = 0.225, 95% CI = –0.246–0.635). Therefore, we used the more parsimonious, top-ranked model to draw inferences about variability of apparent survival and resighting probability.

Hatch-year birds had the lowest 12-mo probability of apparent survival of the three age classes: 0.424 (SE = 0.057, 95% CI: 0.318–0.537). Survival probability of second-year birds was 0.663 (SE = 0.066, 95% CI: 0.524–0.779). For after-second-year birds, the 12-mo probability of apparent survival was 0.738 (SE = 0.030, 95% CI: 0.676–0.792).

Resighting Probabilities. Resighting probability varied by season, age, sex, and time period (Tables 4, 5). On average, summer resighting probabilities ($\beta_{summer} = -1.504$, SE = 0.211) were 28% of resighting probabilities for the same age and sex classes during fall, winter, and spring. Male resighting probabilities ($\beta_{male} = -0.912$, SE = 0.211), on average, were 43% of female resighting probabilities, and resighting probabilities during 2008–2018 ($\beta_{2008\text{-}2018} = -0.384$, SE = 0.152) were 73% of the level of resighting probabilities for the same age and sex classes during 1995–2007 (Fig. 6). Our calculations for the probability of being resighted during 12 mo ranged from 0.90 (SE = 0.03) for HY females to 0.41 (SE = 0.05) for ASY males during 1995–2007, and from 0.82 (SE = 0.05) for HY females to 0.30 (SE = 0.04) for ASY males during 2008–2018 (Fig. 6).

DISCUSSION

Apparent Survival. Our long-term mark-resighting analyses of wintering and migratory Peregrine Falcons along the Washington coast provide evidence of a reasonably high level of survival that suggests good population performance. This is corroborated by our finding that the observation rate of Peregrine Falcons was stable across the 22-yr study (1995–2007, mean = 3.5 Peregrine Falcons per 100 km driven; 2008–2017, mean = 4.0 Peregrine Falcons per 100 km driven). Although total mercury levels in the feathers from Peregrine Falcons captured on our study area are among the highest reported for the species (Barnes et al. 2018), we believe these contaminant levels did not affect survival, although we did not address this directly. Nonetheless, we suggest ongoing assessment of mercury levels is warranted, and could be coupled with future assessments of survival, given the potential significance of this contaminant.

Our long-term data supported the estimation of survival for three age classes, in contrast to the earlier analysis presented by Varland et al. (2008a), which reported an annual apparent survival rate of 0.597 (SE = 0.054) with no age class differences. We found that survival increased from 0.424 for HY birds (<1 yr old) to 0.738 for AHY birds (>2 yr old). Lower survival rates for younger age classes are well documented for raptors (Newton et al. 2016). Our annual apparent survival estimates for adult Peregrine Falcons are comparable to estimates reported for Peregrine Falcons in other parts of their range and for other raptor species (Newton et al. 2016; e.g., Dykstra et al. 2019). Age-specific estimates of apparent survival are useful for population modeling and in conservation plans (Wootton and Bell 1992). In research spanning 7.5 yr, Varland et al. (2008a) reported a pooled, apparent survival estimate for all age classes of 0.597. Our current analyses benefited from additional birds banded during the 22-yr study, as well as additional resightings and recoveries (falcons found dead). One-third of the Peregrine Falcons recovered dead or incapacitated in our study were ≥2 yr old when recovered; the oldest was 11 yr old. Each resighting or recovery provides evidence of survival for a period of time since banding or the last resighting, which reduces the uncertainty in C-J-S type models related to emigration vs. mortality of marked individuals, and improves our ability to estimate survival.

Bald Eagles have made a strong recovery in the region (Kalasz and Buchanan 2016) and sometimes congregate in substantial numbers in certain seasons or favored habitats (Elliott et al. 2011). Based on this and the documented interactions between Bald Eagles and Peregrine Falcons that influence the behavior of the latter species (Dekker et al. 2012, Dekker and Drever 2015), we anticipated that the observed increase in abundance of eagles could alter the behavior of Peregrine Falcons. One of the Peregrine Falcons we banded was likely killed by a Bald Eagle on the Oregon coast in 2009, and in 2006 a Bald Eagle killed a Peregrine Falcon on the Grayland study area beach; the Peregrine Falcon was captured in flight but the observers were unable to ascertain whether it was banded (R./P. Sullivan unpubl. data; http://wos.org/tweeters-archive/).

Examples of analogous dynamics between other raptors in different communities have been documented (Sergio et al. 2003, 2007, Cresswell 2008, Mueller et al. 2016). If eagle presence caused some marked Peregrine Falcons to hunt elsewhere, their probability of detection would be reduced, and if widespread and persistent across the local population, estimates of survival would underestimate actual survival. Our data indicated a clear increase in the abundance of Bald Eagles since 2008. Nonetheless, that increase did not negatively influence resighting or survival estimates of Peregrine Falcons. We saw only two interactions between Bald Eagles and Peregrine Falcons involving possession of food items (Varland et al. 2018). This low level of direct interaction was likely due to the unique abundance of avian, fish, and mammal carrion on our study area available to and used by both species (Varland et al. 2018, D. Varland unpubl. data, see Watson et al. 1991). Given this abundance of food resources, we think that kleptoparasitism may not be energetically necessary or particularly profitable for Bald Eagles, which allows these two species to coexist at current densities without causing significant avoidance of the beaches by Peregrine Falcons.

Resighting Contributions by Others. Resightings by individuals not associated with our project (i.e., Group B) increased during the 2008–2018 period. However, estimates of resighting probability declined during that period. Group B individuals resighted nine Peregrine Falcons that our team (Group A) never resighted, which had the potential to increase resighting probability to some degree. The number of surveys during the latter period of our project was 22% lower than in the first period, which was most likely responsible for the declines in our estimates of resighting probability.

We attribute the increased contribution of Group B to our resighting data in the second period to the emergence of digital camera use in wildlife photography and increased public awareness of our project over those years. Coincidently, Dykstra and colleagues (2019) reported similar findings in a long-term (1996–2018) study of color-banded Red-shouldered Hawks (*Buteo lineatus*) in Ohio covering the same years as our research. They also incorporated resightings by others into their study and, as we found, showed a marked increase in these resightings beginning in 2007. Dykstra and colleagues (2019) also attributed the increase to the onset of digital camera use. In contrast to our results and more in line with expectations, Red-shouldered Hawk encounter probability was greater in 2007–2018 compared with 1996–2006.

We had hypothesized that the abundance of reports from others (Group B) during the second period had the potential to result in more resighting data that might confirm survival of marked Peregrine Falcons beyond what we (Group A) established. Such trends could have positively influenced estimates of apparent survival probability in the same manner that our longer-term data set allowed for more opportunities to confirm living members of the marked sample of Peregrine Falcons. However, the lack of difference in apparent survival between periods suggests that the Group B observers' efforts during 2008–2018 did not influence our estimates of apparent survival. Group B observers did provide 17 reports of birds at later dates than those reported by Group A observers for the same individuals, but the difference in timing was not substantial enough to influence apparent survival estimates relative to the size of our overall sample of marked birds. Dykstra and colleagues (2019) also found no difference in apparent survival rate for 1996–2006 vs. 2007–2018 despite an increase in encounter rates during the second half of their study.

Reports from Group B did not appear to have a significant impact on our demographic estimates, but it is possible that supplementary observation could modify such analyses. Where the appropriate data collection structure has been created and target species are relatively easily resighted, the accumulated observations of other parties may substantially augment resighting rates and estimates of survival. Consequently, monitoring programs that can develop methods to incorporate information from "outsiders" into their data could assess the value to meeting project objectives from additional observations made by the public. The advent of digital photography and a dedicated group of individuals with interest in Peregrine Falcons led to the abundance of sightings from these individuals and their contributions were often matched by our Group A observations during 3-mo time periods in our analysis. Multiple sightings of the same individuals during the time periods were not useful for the current analysis, given the manner in which we summarized our data. However, Group B observations might have been very useful had we intended to track movements of individual birds on the beach study sites or had we summarized our data by shorter time periods (i.e., monthly rather than quarterly by season).

The differences we found in apparent survival by age class are due in part to differences in emigration patterns. To gain a deeper understanding of the effect of emigration on survival estimates, we recommend that future research on our study area—and in other study areas with similar migration patterns and use by Peregrine Falcons—focus on monitoring the year-round movements of Peregrine Falcons using telemetry tracking. This would provide a more complete understanding of actual survival and the degree to which survival estimates are influenced by permanent emigration. Such results would be potentially valuable to state and federal agencies, especially given the lack of monitoring programs.

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Appendix. Number of months from last observation alive until recovery and causes of mortality or incapacitation for Peregrine Falcons banded at Ocean Shores, Grayland, and Long Beach study area beaches on the southwestern Washington coast, January 1995–February 2018.

Bird Identification (CB)[a]	Date Last Observed Alive	Date Recovered	Number Months Since Live Encounter	Status at Recovery[b]	Age (yr) at Recovery	Cause of Mortality or Incapacitation
8/M[c]	14 Sep 2002	26 Jan 2008	65.3	1	5	Shot
B/3	3 Mar 2013	29 Dec 2014	22.2	1	7	Disease (highly pathogenic avian influenza)
9/7[c]	27 May 1999	17 Feb 2001	21.1	1	≥2	Unknown
R/2	14 Mar 2010	21 Nov 2011	20.6	2	2	Collision with bridge
U/3	19 Dec 2010	15 Dec 2011	12.0	2	1	Collision with unknown object
W/Z	2 Mar 2015	29 Nov 2015	9.1	1	8	Collision with powerline
69/A[c]	23 Sep 2000	12 May 2001	7.7	2	1	Feathers soiled from coal slurry
P/E[c]	20 Oct 2000	19 Mar 2001	4.7	2	<1	Feathers soiled from mud
C/5	28 Feb 2014	14 Jul 2014	4.5	1	5	Unknown
X/P[c]	28 Oct 2007	10 Feb 2008	3.5	1	<1	Collision with fence
V/X	24 Nov 2002	3 Mar 2003	3.3	1	<1	Unknown
R/3[c]	6 Dec 2008	28 Feb 2009	2.8	1	<1	Unknown
V/P[c]	6 Jan 2007	17 Mar 2007	2.3	2	<1	Unknown
U/6[c]	10 Dec 2012	10 Feb 2013	2.1	1	<1	Unknown
V/V	25 Jan 2014	11 Mar 2014	1.5	2	11	Collision with unknown object
H/4	1 Mar 2009	10 Apr 2009	1.3	1	<1	Predation by Bald Eagle[d]
U/2	25 Feb 2007	1 Apr 2007	1.2	1	≥2	Unknown
X/D	27 Feb 2009	26 Mar 2009	0.9	1	<1	Shot
P/S[c]	6 Jan 2018	27 Jan 2018	0.7	2	<1	Puncture wound[e]
4/K	3 Apr 2000	19 Apr 2000	0.5	1	1	Unknown
K/2	20 Feb 2011	8 Mar 2011	0.5	2	1	Unknown
Z/P	6 Jan 2018	18 Jan 2018	0.4	1	<1	Collision with powerline

[a] CB = alphanumeric code on color band.
[b] 1 = dead; 2 = incapacitated from injury or soiled feathers.
[c] Only two encounters: one at banding and one when recovered.
[d] Although the observer (T. Conroy) did not see the predation event, he found Bald Eagle tracks around the Peregrine Falcon carcass remains (both wings, the sternum and one leg). Prior to finding the remains, Conroy reported observing two Bald Eagles kill gulls on several occasions at the same location where the Peregrine Falcon carcass was found; these eagles launched attacks from a tree <20 m away.
[e] Recovered inside duck pen.