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Estimated Annual Abundance of Migratory Peale's Peregrine Falcons in Coastal Washington, USA

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ABSTRACT.—Following the recovery of Peregrine Falcons (*Falco peregrinus*), the US Fish and Wildlife Service began a process to allow "take" (capture) of wild peregrines for falconry in the United States. Recently, that effort involved generating updated estimates of the collective abundance of the three North American peregrine subspecies: *F. p. anatum*, *F. p. tundrius*, and *F. p. pealei* (Peale's Peregrine Falcon). Because of the more limited distribution of *F. p. pealei*, we conducted an analysis specific to its geographic range. We analyzed data from a long-term banding and resighting program on three beaches on the southern coast of Washington, USA, to estimate the annual abundance of migrating and overwintering *F. p. pealei*, using the capture histories of 250 Peregrine Falcons, nearly all of which were captured during 1277 vehicle surveys between 1995 and 2024. Because we studied an open population of migratory individuals, we used a zero-inflated Poisson log-normal mark-resight model to estimate annual abundance. For the analyses, we partitioned our survey data into sighting periods, each of which extended from 1 September of one year to 31 May of the next. We anticipated that first-year *F. p. pealei* would be identified for falconry take, and our annual abundance estimates for first-year birds of this subspecies ranged from a high of 24.8 ± 6.1 (SE) individuals in the 2014–2015 sighting period to a low of 1.9 ± 1.4 individuals in the 2023–2024 sighting period. Peregrine Falcon abundance varied annually and appeared to decline during the last two sighting periods. Our sighting rate of marked peregrines was negatively associated with Bald Eagle (*Haliaeetus leucocephalus*) encounter rate. There was a lesser relationship to human activity, and we suspect the change in sighting rate was a behavioral response by Peregrine Falcons to the threat of kleptoparasitism by Bald Eagles. We currently lack comprehensive information about the natal origin of the individual peregrines in our study area, which prevented us from assessing the degree to which falconry take from the pool of falcons migrating to or through Washington might potentially impact local or regional abundances. Although a better understanding of natal origins is needed, our data add clarity to the migration and overwinter abundance of *F. p. pealei* on the Washington coast and may inform decisions about the take of this subspecies for falconry.

KEY WORDS: *abundance*; *falconry*; *migration*; *population modeling*.

ABUNDANCIA ANUAL ESTIMADA DE INDIVIDUOS MIGRATORIOS DE *FALCO PEREGRINUS PEALEI* EN LA COSTA DE WASHINGTON, EEUU

RESUMEN.—Tras la recuperación de *Falco peregrinus*, el Servicio de Pesca y Vida Silvestre de Estados Unidos inició un proceso para permitir la "extracción" (captura) de ejemplares silvestres para cetrería en

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EEUU Recientemente, ese esfuerzo incluyó generar estimaciones actualizadas de la abundancia colectiva de las tres subespecies norteamericanas de *F. peregrinus*: *F. p. anatum*, *F. p. tundrius* y *F. p. pealei*. Debido a la distribución más limitada de *F. p. pealei*, realizamos un análisis específico de su área geográfica. Analizamos datos de un programa a largo plazo de anillamiento y reavistamiento en tres playas de la costa sur de Washington para estimar la abundancia anual de individuos migratorios e invernantes de *F. p. pealei*, utilizando los historiales de captura de 250 halcones peregrinos, casi todos capturados durante 1277 censos vehiculares entre 1995 y 2024. Debido a que estudiamos una población abierta de individuos migratorios, utilizamos un modelo de distribución log-normal de Poisson de marcado-reavistamiento con exceso de ceros para estimar la abundancia anual. Para los análisis, dividimos los datos de los censos en períodos de observación, cada uno extendiéndose desde el 1 de septiembre de un año hasta el 31 de mayo del siguiente. Anticipamos que los ejemplares del primer año de vida de *F. p. pealei* serían identificados para la extracción y uso en cetrería. Nuestras estimaciones anuales de abundancia para estas aves oscilaron entre un máximo de 24.8 ± 6.1 (EE) individuos en el período 2014–2015 y un mínimo de 1.9 ± 1.4 individuos en el período 2023–2024. La abundancia de *F. peregrinus* varió anualmente y pareció disminuir durante los dos últimos períodos de observación. Nuestra tasa de observación de halcones marcados se asoció negativamente con la frecuencia de encuentros con *Haliaeetus leucocephalus*. La relación con la actividad humana fue menor, y sospechamos que el cambio en la tasa de avistamientos fue una respuesta conductual de *F. peregrinus* ante la amenaza de cleptoparasitismo por parte de *H. leucocephalus*. Actualmente carecemos de información completa sobre el origen natal individual de los halcones en nuestra área de estudio, lo que nos impidió evaluar en qué medida la extracción de halcones para cetrería del pool de individuos migrando hacia o a través de Washington podría afectar las abundancias locales o regionales. Aunque se necesita una mejor comprensión del origen natal, nuestros datos aportan claridad sobre la migración y la abundancia invernal de *F. p. pealei* en la costa de Washington y pueden servir de base para decisiones sobre su captura con fines de cetrería.

[Traducción del equipo editorial]

INTRODUCTION

The Peregrine Falcon (*Falco peregrinus*) has a nearly global distribution consisting of 18–20 subspecies (White et al. 2013), most of which were substantially impacted by the effects of environmental contaminants in the twentieth century (Cade et al. 1988). Widespread conservation actions led to species recovery (Cade and Burnham 2003) and delisting of two North American subspecies—*F. p. tundrius* and *F. p. anatum*—identified and protected under the Endangered Species Act (ESA; US Fish and Wildlife Service [USFWS] 1994,1998). The Peale's Peregrine Falcon (*F. p. pealei*) was not ESA-listed but was protected under the similarity of appearances clause (USFWS 1998). However, this subspecies was listed at the state-level; for example, all subspecies of the Peregrine Falcon were state-listed as endangered in Washington in 1980 and state-delisted in 2016 (Vekasy and Hayes 2016). These substantial recoveries renewed interest in take of wild Peregrine Falcons for falconry within the United States, prompting the need for abundance estimates within and across subspecies.

Three subspecies of the Peregrine Falcon are available for falconry take in the United States (USFWS 2023). *F. p. tundrius* breeds in the Arctic and subarctic from Alaska to Greenland and *F. p. anatum* breeds across continental Canada, the United States, and Mexico (White et al. 2013). *F. p. tundrius* and *F. p. anatum*, which may be the same subspecies (Talbot et al. 2017; but see Johnson et al. 2023), and intergrades of these and other subspecies used in reintroduction efforts (White et al. 2013) migrate south across significant portions of the continent, with aggregations of falcons from the far north occurring along parts of the Atlantic and Gulf coasts. In contrast, *F. p. pealei* breeds coastally from northern Oregon through Washington, British Columbia, Canada, and much of southern Alaska through the Aleutian Islands to the Commander Islands, in Russia (White et al. 2013, Lewis and Kissling 2015). Although some *F. p. pealei* individuals may migrate as far south as northwestern Mexico during winter (Enderson et al. 1991), it is considered the least migratory of the three subspecies and in parts of its range individuals remain on breeding territories year-round (White et al. 2013).

Following recovery and delisting, the USFWS endeavored to assess the potential for take of wild Peregrine Falcons for the purpose of falconry (Millsap and Allen 2006, USFWS 2007, 2008). An initial assessment of Peregrine Falcon abundance across the United States and Canada that included all three subspecies resulted in an estimated population of between 4543 and 10,368 pairs and an annual production of young ranging between 6862 and 16,960 (USFWS 2007, 2008). These estimates were later updated, which produced a larger estimated abundance of 94,366 in the northern management population and 9583 in the southern management population (USFWS 2023). These analyses of abundance (USFWS 2023) are likely representative for *F. p. tundrius* and *F. p. anatum* because of their broad distribution and substantial abundance. In contrast, the coastal distribution and relatively small migratory range of *F. p. pealei* suggests that this subspecies could be underrepresented in the national analysis. We therefore analyzed data from a long-term banding and resighting program in coastal Washington (Varland et al. 2020) to estimate the abundance of *F. p. pealei* that overwinter on the Washington coast or migrate through Washington. This information can be used to add clarity to the seasonal occurrence of *F. p. pealei* on the Washington coast and to inform decisions about the take of this Peregrine Falcon subspecies for falconry.

METHODS

Study Area. Our study area consisted of three beaches on the outer coast of southwest Washington (Fig. 1): Ocean Shores (23.5 km long), Grayland (11.8 km long), and Long Beach (39.9 km long). These beaches are bordered by the Pacific Ocean to the west and to the east by sand dunes vegetated primarily with European beach grass (*Ammophila arenaria*). For additional information on the characteristics of this beach habitat, see Varland et al. (2018) and Buchanan et al. (2001).

Field Methods. We conducted beach surveys by vehicle from January 1995 to May 2024. Peregrine Falcons were captured, banded, and resighted during several survey types, including surveys done under favorable weather and driving conditions where all raptors were counted (hereafter complete raptor surveys) and surveys under unfavorable conditions or where field work was focused on other avian species (hereafter incomplete raptor surveys). During complete raptor surveys, beginning in 1998, we documented the occurrence of all raptors encountered and counted the number of people, vehicles, dogs on leash, and dogs off leash on the survey route and calculated the numbers observed per 100 km driven.

To meet model assumptions (see data analysis), we limited data used in this paper to resightings we made during the surveys. This approach contrasts with our earlier research in which resightings from observers outside our survey group were included to estimate apparent survival rates (Varland et al. 2008, 2020).

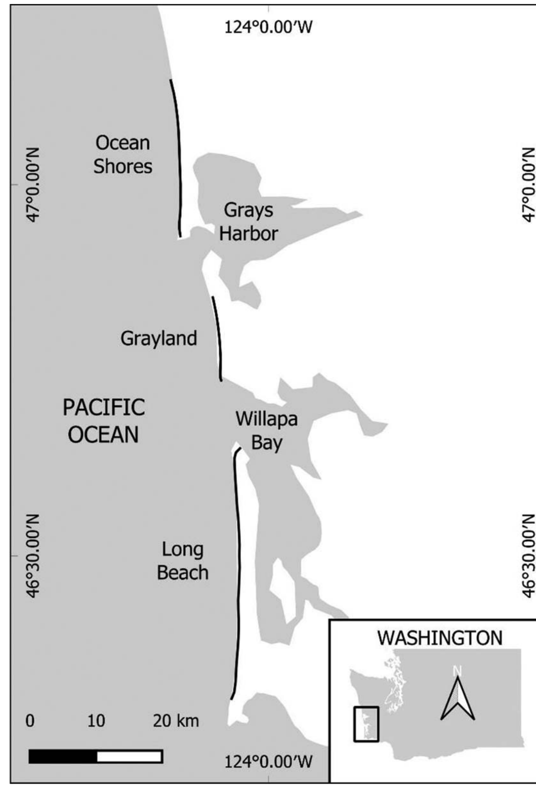

Figure 1. Location of our study area in southwestern Washington: Ocean Shores beach, Grayland beach, and Long Beach, USA. Survey transects, indicated by black lines, represent the areas where we captured and banded Peregrine Falcons between 1995 and 2024.

Details on capturing techniques and banding are provided in Varland et al. (2008, 2012) and summarized here. The vast majority of Peregrine Falcons were captured with a harnessed Rock Pigeon (*Columba livia*; Bloom et al. 2007). After capture we secured a US Geological Survey band to one leg and a color-coded alphanumeric band to the other. We resighted color marked individuals by reading the alphanumeric codes on their bands by using a spotting scope, camera with telephoto lens, binoculars, or on occasion with the falcon in hand during recapture. We used measurements (e.g., wing chord, culmen, and tail length) to classify individuals by sex and plumage features, photograph review, and morphometric data to classify individuals to subspecies (see also Varland et al. 2012).

Data Analysis. We used mark-resight methods allowing for an unknown number of marked birds (Arnason et al. 1991, McClintock and White 2011, McClintock et al. 2019) to estimate the abundance of *F. p. pealei* that migrate through or overwinter along the coast of Washington. The sample population of interest (i.e., those falcons that use the study area; not to be confused with the biological population [see Morrison et al. 2020]) was migratory and open (i.e., individuals observed in one year may winter off the study area in the next year or die between years). Encounters with marked birds during surveys were infrequent. Further, we could not be certain to have counted all marked individuals during surveys or to have confirmed the identity of each falcon encountered. Given these limitations, we used the zero-inflated Poisson log-normal (ziPNE) mark-resight model developed by McClintock et al. (2019). Further, we used the "within" individual heterogeneity version of the model (McClintock et al. 2019), which allows for individual heterogeneity to vary among primary sampling periods, because the temporally constant heterogeneity version did not converge in preliminary runs of the model. We assessed model convergence based on individual parameter standard errors (SE) and the total number of estimable parameters after fitting each model. If the number of parameters was less than specified when setting up the model because the SE of a parameter was extremely large, we assumed that the model did not fully converge. This model estimates several parameters, including the size of the unmarked sample population (U), log-scale mean sighting rate (α; we use sighting rate, following McClintock et al. [2019], which we consider to be synonymous with resighting), log-scale standard deviation for sighting rate across individuals (σ), probability that a marked bird is identified to individual (r), probability that a newly marked individual was alive and did not permanently emigrate at time $t(w)$, probability that a newly marked individual was within the study area at time $t(g)$, apparent survival (φ), transition probability from an observable state to an unobservable state (γ''), and transition probability of staying in an unobservable state given that the individual was already in an unobservable state (γ'). Consideration of unobservable states is necessary because some individuals that we banded may not return to the beaches we sampled because they temporarily or permanently emigrated from the study area. Not considering these emigration events would bias detection or survival rate estimates (Kendall et al. 1997, Kendall 2004). Total abundance of unmarked and marked falcons that compose the superpopulation that migrates through or overwinters along the Washington coast (N_W) is estimated as a derived parameter.

This mark-resight model conditions on first capture rather than first sighting, which allowed more efficient use of the data since we did not have sightings of many falcons after capture. For each sampling period, this model required the total number of: (1) sightings of each individually identified peregrine per sighting period; (2) unmarked peregrines observed, pooled over all subspecies; (3) marked birds that were not identified to individual; and (4) known marked individuals pooled over all subspecies. We established sampling periods (hereafter sighting periods) that began on 1 September and ended on 31 May of the following year. We assumed that a peregrine captured and banded during sighting period t could not be counted as sighted until time $t + 1$. For example, a bird captured and banded during November of 2000 could not be considered to have been sighted until the subsequent 1 Sept 2001–31 May 2002 sighting period; any sightings between November 2000 and 31 May 2001 of the marked bird in this example, would be included as an observation of an unmarked bird (Appendix A). Peregrines cannot be classified as marked immediately before the subsequent sighting periods begin because of the extended time span between marking and the first possible sighting period for each individual. Consequently, we assumed that we did not know the number of newly marked birds on study area beaches at the beginning of each sighting period; this uncertainty is accommodated by the ziPNE model.

We observed some falcons during surveys and were unable to determine whether they were marked. In a preliminary analysis, we randomly allocated each of those observations to either marked but not individually identified, or unmarked. Next, we ran an analysis where those birds were excluded. The abundance estimates were similar between the two approaches; consequently, we excluded from our final analysis birds whose status as marked was uncertain. Our first sighting period extended from 1 September 1996 to 31 May 1997 and our last sighting period ended on 31 May 2024, which resulted in 28 sampling occasions.

Estimating abundance of Peregrine Falcons. In our first set of analyses, we fit our ziPNE models using data from the 1996/1997 sighting period to the 2023/2024 sighting period with the objective of estimating annual abundance of Peregrine Falcons. We did not include data from the 1995/1996 sighting period in the analysis because of very few bandings ($n = 4$) and sightings ($n = 1$) as the study was beginning. We assumed that the size of the unmarked population segment varied annually (i.e., U_t) and considered five alternative models on mean sighting rate. One model assumed that the mean sighting rate varied categorically through time (α_t), another assumed α was constant among years ($\alpha_.$), and the three others were modeled as a function of annual covariates (survey effort [α_{Effort}], Bald Eagle (*Haliaeetus leucocephalus*) encounter rate [$\alpha_{Bald\ Eagle}$], and an additive effect of effort and Bald Eagle encounter rate [$\alpha_{Effort+Bald\ Eagle}$]). We assumed the Peregrine Falcon sighting rate would positively correlate with survey effort, which we defined as the number of complete raptor surveys where all peregrine observations, including bandings, sightings, and non-banded birds, were tallied during surveying. Based on findings that aggregations of Bald Eagles can influence the behavior of overwintering Peregrine Falcons (Dekker and Drever 2015), we assumed that increased numbers of eagles could similarly reduce the activity of peregrines or detection rates on the survey beaches. We calculated Bald Eagle encounter rates as the number of eagles observed per 100 km driven. Although we did not have actual abundance estimates for Bald Eagles on our study area, the index of eagles observed per 100 km driven was used to explore the potential correlation between relative abundances of eagles with Peregrine Falcons. We compared models assuming Markovian temporary emigration (i.e., $\gamma' \neq \gamma''$) to models assuming random temporary emigration (i.e., $\gamma' = \gamma''$; Kendall et al. 1997) for each of these five alternative models (i.e., we fit a total of 10 models). We standardized the effort and Bald Eagle abundance indices by subtracting the mean from each annual covariate and dividing the difference by the standard deviation. Due largely to small sample sizes and our focus on estimating trends in abundance, we constrained σ, r, w, g, φ, γ', and γ'' to be constant through time and used second-order Akaike information criteria (AIC$_c$; Burnham and Anderson 2002) to compare the five alternative models on mean sighting rate (α). We conducted all ziPNE analyses in program MARK (version 10.1, McClintock and White 2011). We provide model-averaged estimates (Burnham and Anderson 2002) for σ, r, w, g, φ, γ', γ'', and N_W using only the group of models where all parameters converged. We provide estimates of parameters from the top model.

An objective of this analysis was to estimate the abundance of first-year *F. p. pealei* ($N_{P,W}$) that migrate through or overwinter in Washington. Due to small sample sizes and inability to identify subspecies without capture (i.e., the unmarked birds used in the analysis), we did not separate age and subspecies in the mark-resight analysis. Instead, we portioned juvenile Peale's abundance from N_W post analysis. Banding efforts from this study indicated that 77% (n = 164) of peregrines that could be identified to subspecies (n = 214) were first-year *F. p. pealei* (Table 1). To this end, we multiplied the overall estimate of abundance N_W by 0.77 and used the delta method (Powell 2007) to estimate standard errors:

$$SE_{N_{P,W}} = \sqrt{0.77^2 \times \sigma^2_{N_W}}.$$

Table 1. Number (n = 241) of Peregrine Falcons banded by subspecies and age along beaches in southwestern Washington, 1995–2024. Three additional falcons are not included in the table total because information on subspecies was insufficient to make subspecies determinations.

	<1 yr	≥1 yr	Total (%)
Subspecies	n (%)	n (%)	n (%)
pealei	164 (82.8)	27 (62.8)	191 (79.2)
uncertain	18 (9.1)	9 (20.9)	27 (11.2)
anatum	2 (1.0)	5 (11.6)	7 (2.9)
tundrius	14 (7.1)	2 (4.5)	16 (6.6)
Total	**198 (100.0)**	**43 (99.8)**	**241 (100.0)**

Peregrine Falcon encounter rate comparison. In earlier research on Peregrine Falcon encounter rates during 1995 to 2017 (number sighted/100 km), we found no difference in encounter rates, 1995–2007 vs. 2008–2017 (Varland et al 2020). Since that comparison we noticed a decline in the number of peregrines encountered in the later years of the study. We therefore compared Peregrine Falcon encounter rates between periods 1995–2017 and 2018–2024 using an analysis of variance (ANOVA).

Influence of human activity on sighting rates. The goal of a second set of analyses was to use our ziPNE models to evaluate potential influence of human activity on sighting rate of Peregrine Falcons. We recorded the number of people, dogs on leash, dogs off leash, and vehicles encountered on surveys and then calculated the number observed under each parameter per 100 km driven during surveys along the beach transects. We standardized the covariates in the same manner as for survey effort and Bald Eagle encounter rate. Because the covariates were highly correlated ($r \geq 0.53$; Appendix B), we ran models separately for each covariate. Because we were interested in how sighting rate varied as a function of human activities more

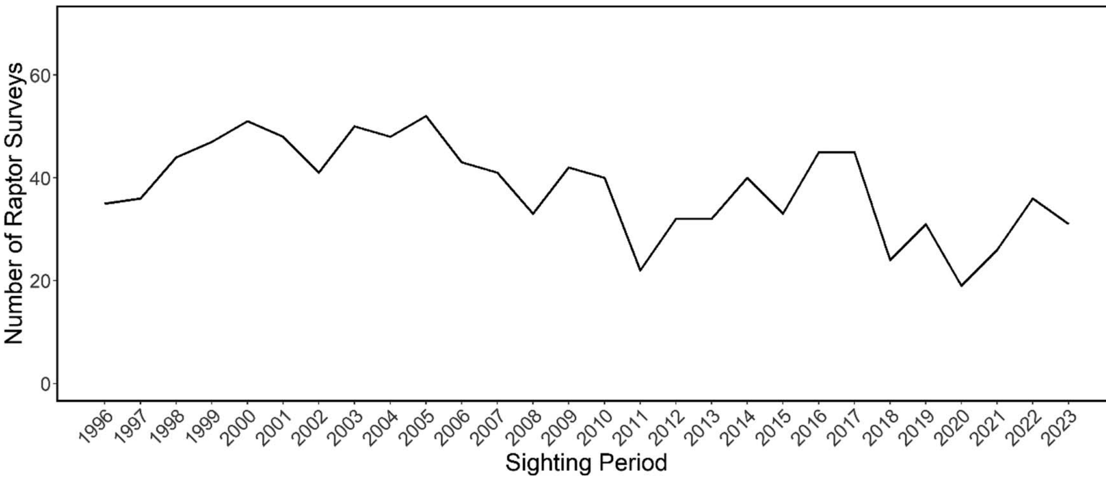

Figure 2. Annual number of raptor surveys completed along the southwest Washington coast for sighting periods between 1996/1997 and 2023/2024.

broadly, we used the first principal component from a principal components analysis (PCA) of the four covariates as an overall metric of human activity. We ran the PCA using the *vegan* package (version 2.6-4, Oksanen et al. 2022) in program R (version 4.3.2, R Core Team 2023). We also included a model with Bald Eagle encounter rate to compare with the influence of human activity. For each of the single covariate models, we ran a model with and without the survey effort variable used in the first analysis (i.e., 12 models total) to control for its effect on sighting rate. At least one of the parameters in all models exploring correlations of Bald Eagle encounter rate and human activity with Peregrine Falcon detection failed to converge. Therefore, we do not report on these analyses further.

RESULTS

Survey effort varied considerably among years and tended to be greater during the first half of the study (Fig. 2). From January 1995–May 2024, we conducted 1086 surveys where complete tallies of all Peregrine Falcons observed were made, and of these 711 (65%) were done at Ocean Shores Beach, 247 (23%) at Long Beach, and 128 (12%) at Grayland Beach. Over the survey period we conducted another 191 surveys on the study area where we banded or sighted peregrines but where other data were not collected to a standard that would facilitate peregrine abundance and encounter rate (observations/100 km driven) estimates (e.g., distance traveled, number of unmarked peregrines observed). The total number of raptor surveys annually ranged from 18 to 52 (Fig. 2). We captured and uniquely marked 244 individual Peregrine Falcons in our study (Table 1) and detected an additional eight falcons that were banded by other researchers away from our study area. Although we had a total of 252 Peregrines that were uniquely identified in our study, two were banded during the final sighting period and were not included in the capture histories (although they were included as “unmarked” during the final resighting period). We therefore used 250 capture histories in the mark-resight analysis (Appendix A).

Most banded individuals were not sighted during a subsequent sighting period after banding ($n = 189$) or only during one sighting period after banding ($n = 35$). When individuals were sighted during a sighting period ($n = 128$), the number of sightings ranged from 1 to 13; with most sightings limited to one ($n = 66$) or two ($n = 22$) during a sighting period (i.e., some individuals were sighted in >1 sighting period). When we encountered a marked falcon, we were able to confirm the individual’s band 78% of the time (Table 2, *r* value). During a sighting period, we observed 0–9 known individuals, with most sighting periods (~64%) having 4–7 known individuals sighted. We had 87 cases where a banded bird was observed but could not be identified (range = 0–9 per sighting period).

Our largest sample of observed falcons was unmarked ($n = 651$ over the full study), with counts of unmarked birds in sighting periods ranging from 3 to 51. Sixty-one percent ($n = 400$) of those counted

Table 2. Model-averaged parameter estimates, on the real scale, from the zero-inflated Poisson log-normal mark resight model used to estimate abundance ($N_{P,W}$), standard error (SE), and 95% confidence intervals of Peregrine Falcons along the coast of southwest Washington, for sighting period between 1996/1997 and 2023/2024. Each sighting period lasted from 1 September of one year to 31 May of the next year. A full description of the parameters is provided in the methods section of this paper; these are consistent with the definitions in McClintock et al. (2019).

			95% CI	
Parameter	Estimate	SE	Lower	Upper
σ	0.86	0.11	0.53	0.97
r	0.78	0.02	0.73	0.82
w	0.40	0.15	0.16	0.69
g	0.69	0.25	0.19	0.95
φ	0.68	0.05	0.57	0.78
γ'	0.09	0.12	0.01	0.65
γ'	0.73	0.33	0.10	0.99

as unmarked for analysis purposes were marked falcons (see Methods). The total included 234 individuals captured and banded on our study area during a sighting period (Appendix A). We encountered Peregrine Falcons that had not been marked 251 times, and although none of these were marked to facilitate certain identification it seems likely that some number of them were observed on multiple occasions.

Annual abundance estimates of Peregrine Falcons on the study area beaches ranged from a high of approximately 32 ± 7.8 [SE], 95% confidence interval [CI]: 17, 48) during the 2014–2015 sighting period, to a low of approximately 3 ± 2.0, 95% CI: 0, 6) during the 2023–2024 sighting period (Fig 3a). Annual abundance increased from the 1996–1997 sighting period to the 3-yr period between about 2012–2014, and then began a decline toward the end of the study. In fact, we found a significant difference in mean number of falcons sighted/100 km driven comparing two time periods (1995–2017: mean = 4.01 ± 1.37 [standard deviation (SD)]; 2018–2023: mean = 2.59 ± 1.59; ANOVA; $F_{1,26} = 4.19$ $P = 0.05$). The estimates of Peregrine Falcon abundance were imprecise, with coefficients of variation ranging from 19% to 78% ($\bar{x} = 30\%$; Fig. 3a).

Most of the Peregrine Falcons we captured and banded on study area beaches were of the *pealei* subspecies. Estimates of abundance of first-year *F. p. pealei* were 77% of the total number of falcons, ranging from approximately 2 ± 1.5 (SE; 95% CI: 0, 5) during the 2023–2024 sighting period to approximately 25 ± 6.1 (95% CI: 13, 37) during the 2014–2015 season (Table 3).

Four of the 10 models considered in the first analysis resulted in convergence for all parameters and we only used these four models in subsequent calculations (Table 4). Model-averaged estimates of sighting rate declined throughout the study (Fig. 3b). The covariate for Peregrine Falcon sighting rates with the greatest empirical support was Bald Eagle encounter rate ($\alpha_{Bald\ Eagle}$ AIC$_c$ weight = 0.68) which negatively correlated with Peregrine Falcon sighting rates ($\beta_{Bald\ Eagle} = -0.33 \pm 0.11$ [SE], 95% CI: −0.56, −0.11). We expected a strong positive correlation between survey effort (i.e., number of surveys) and sighting rate, but the only model with effort that converged had a lower AIC$_c$ weight (0.14) with confidence intervals for the parameter estimate that overlapped zero ($\beta_{Effort} = 0.17 \pm 0.12$, 95% CI: −0.07, 0.41). The model-averaged estimate of annual apparent survival was 0.68 ± 0.05 (95% CI: 0.57, 0.78). We provide estimates of model averaged temporally constant parameters (σ, r, w, g, φ, γ', and γ'') in Table 2.

DISCUSSION

The history of Peregrine Falcon conservation and management is known for the species' dramatic decline—caused by environmental contaminants—in many parts of the world, and its subsequent recovery, which was a widely recognized conservation success story (Cade and Burnham 2003). Despite general recovery of falcon populations across North America, little information has been compiled assessing the *pealei* subspecies. Using data from a long-term banding study, we estimated the abundance of *F. p. pealei* that migrate through or overwinter on three beaches on the southern coast of Washington, USA, in part to help inform decisions about the take of these falcons for falconry. We found that the estimated abundance of first year *F. p. pealei* was variable and low, ranging from 9.34 to 24.84 individuals between the 1996–1997 and 2019–2020 sighting periods (Table 3). Excluding the two sighting periods during the COVID-19 pandemic, our lowest levels of abundance were in the 2022–2023 (4.44 individuals) and 2023–2024 sighting periods (1.94 individuals).

In our multi-decade study, there were potential indicators of change that warranted explanation. These included the model-derived sighting rate of marked falcons, which declined steadily after 2003 (Fig. 3b); model-derived estimated abundance, which declined in the last 5 yr, and included the lowest levels in the study (Fig. 3a); and encounter rates (i.e., number observed per 100 km driven),

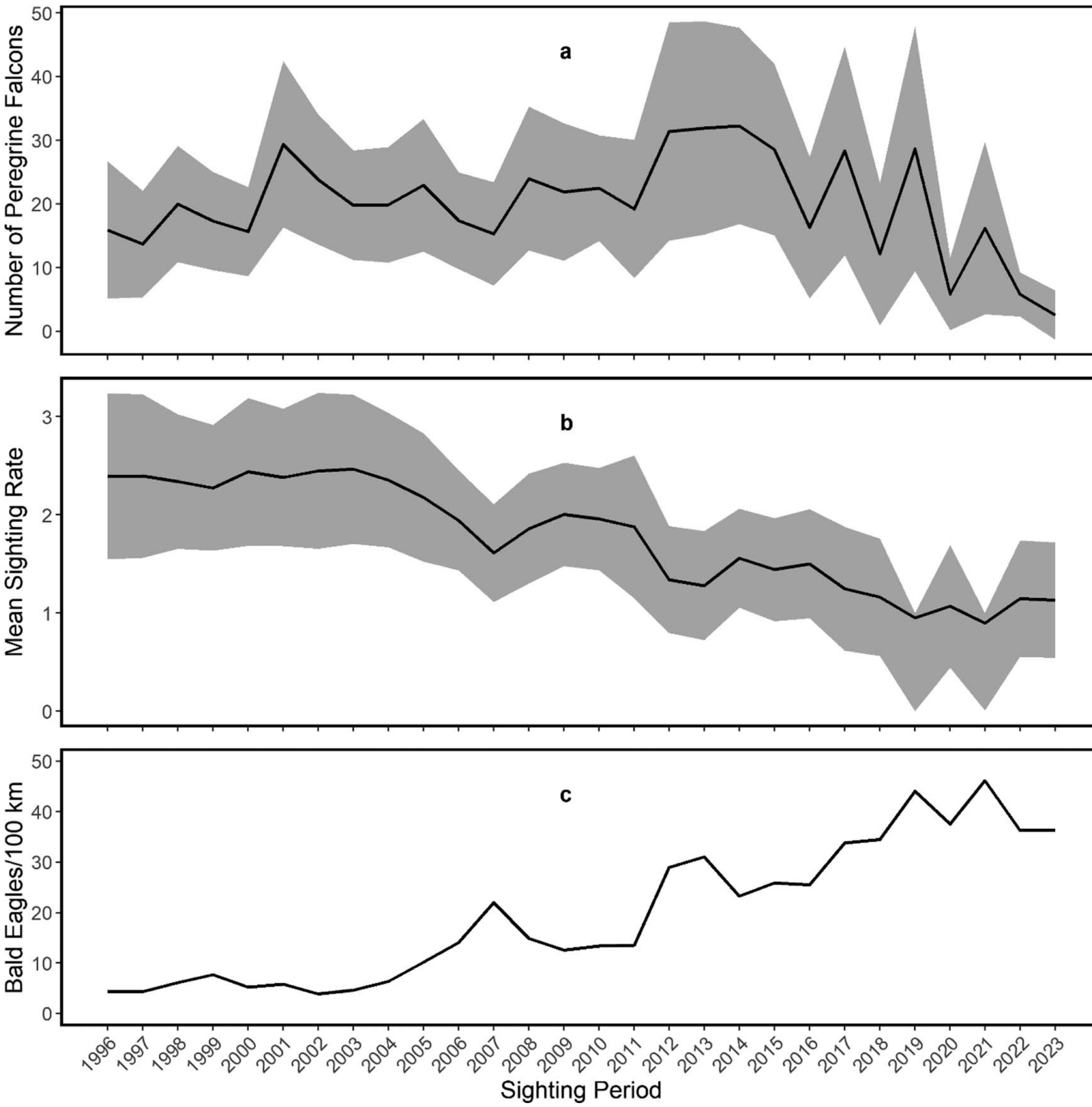

Figure 3. (a) Model-averaged estimated number (N_w) of all Peregrine Falcons, (b) model-averaged mean individual sighting rate of Peregrine Falcons, and (c) annual number of Bald Eagles observed/100 km driven during raptor surveys along coastal beaches in southwest Washington for sighting periods between 1996/1997 and 2023/2024. Shaded areas represent 95% confidence intervals.

which were significantly lower in the last 5 yr compared to earlier in the study (Varland et al. 2020). Recall that low levels of field effort for two sighting periods during the pandemic likely influenced our results and occurred during the 5-yr period mentioned above.

The most obvious factor with the potential to influence these trends was the increasing abundance of Bald Eagles (Fig. 3c). Bald Eagles, especially when they aggregate in areas where Peregrine Falcons hunt, can substantially disrupt hunting behavior, primarily due to the threat of kleptoparasitism (Dekker and Drever 2015; Supplemental Material Fig. S1) and the direct or indirect effects of intraguild predation (Cresswell 2008, Sergio and Hiraldo 2008). Falcons can reduce their exposure to this threat by

Table 3. Estimated abundance ($N_{P,W}$), standard error (SE), and 95% confidence intervals (CIs) for first-year *F. p. pealei* encountered along beaches in southwest Washington, 1996–2024.

			95% CI	
Sighting Period[a]	$N_{P,W}$	SE	Lower	Upper
1996/1997	12.25	4.23	3.96	20.54
1997/1998	10.54	3.28	4.12	16.97
1998/1999	15.38	3.59	8.34	22.42
1999/2000	13.32	3.04	7.36	19.27
2000/2001	12.05	2.76	6.64	17.45
2001/2002	22.62	5.15	12.53	32.71
2002/2003	18.38	4.02	10.50	26.26
2003/2004	15.26	3.38	8.64	21.88
2004/2005	15.30	3.56	8.32	22.27
2005/2006	17.66	4.09	9.65	25.68
2006/2007	13.36	2.98	7.52	19.21
2007/2008	11.78	3.20	5.51	18.05
2008/2009	18.47	4.45	9.75	27.19
2009/2010	16.85	4.25	8.51	25.19
2010/2011	17.32	3.27	10.92	23.73
2011/2012	14.80	4.26	6.45	23.15
2012/2013	24.16	6.75	10.93	37.39
2013/2014	24.57	6.59	11.66	37.49
2014/2015	24.84	6.07	12.94	36.74
2015/2016	21.97	5.28	11.61	32.33
2016/2017	12.53	4.37	3.96	21.10
2017/2018	21.81	6.46	9.15	34.46
2018/2019	9.34	4.40	0.72	17.95
2019/2020	22.06	7.56	7.24	36.88
2020/2021	4.49	2.23	0.11	8.87
2021/2022	12.46	5.33	2.02	22.91
2022/2023	4.44	1.36	1.77	7.11
2023/2024	1.94	1.52	−1.03	4.92

[a] Each sighting period lasted from 1 September of the first year to 31 May of the second.

moving exclusively to other areas where Bald Eagles do not pose a threat or by altering their behavior to facilitate coexistence in areas with plentiful food resources. Employing the first strategy would likely have resulted in a reduced estimate of peregrine abundance beginning earlier in the study, for example, when the sighting rate began to decline. We also suspect that the complete abandonment of our study area would be reflected in lower estimates of apparent survival rate over time. However, apparent survival rate from the entire 1995–2024 study period, not accounting for age class, was 0.68, which was higher than the rate calculated for the 1995–2003 period (0.597, Varland et al. 2008), and approximates apparent survival rate estimates for two of three age classes for the study area between 1995 and 2018 (hatching year = 0.42; second year = 0.66; and after second year = 0.74; Varland et al. 2020).

Peregrine Falcons may also have responded to increased numbers of Bald Eagles by reducing their time spent on the beach for hunting, plucking prey, and/or feeding. Peregrine Falcons regularly hunted on the study area beaches (Buchanan 1996, Varland et al. 2018), and this activity was typically visible at great distances (DV, JB, TF, unpubl. data) due to the predator evasion behavior of their shorebird quarry, likely also making the activity conspicuous to Bald Eagles. On numerous occasions, we observed peregrines plucking or consuming captured or scavenged food items at the beach (Varland et al. 2018). As Bald Eagle abundance increased, the threat of kleptoparasitism to feeding peregrines might have been greater, in which case it would be logical that falcons with prey would leave the beach to use more secure locations rather than remaining where their plucking and feeding activity might be noted by Bald Eagles. This scenario seems more consistent with the declining sighting rates, etc., we noted, coupled with an apparently stable survival rate. We acknowledge that some of the factors identified in our study were correlated and due to issues with convergence, we were unable to reach definitive conclusions with respect to factors such as human activity, which was positively correlated with Bald Eagle abundance.

Although identifying other causal factors for the downward trend in Peregrine Falcon abundance at the end of our study period was beyond the scope of our project, potentially relevant factors include increased human activity, exposure to highly pathogenic avian influenza (HPAI), and natural population fluctuations (e.g., fluctuations in prey abundance influenced by oceanic conditions). The level of human activity (e.g., recreation) in the study area increased strongly over a period of three decades (J. Buchanan unpubl. data), but we have no data conclusively indicating that such changes influenced falcon occurrence. Changes in the abundance of prey species (e.g., alcids) have been documented in the eastern Pacific Ocean (e.g., Cushing et al. 2018) and such changes could conceivably influence Peregrine Falcon reproductive success. In 2014, HPAI H5N8 was the cause of death of one of our banded falcons (Varland et al. 2018), the timing of which coincided with the highest abundance of Peregrine Falcons during our study (Fig. 3a). In 2021, a strain of the virus far more virulent to wild birds, HPAI H5N1, was detected in eastern North America, and subsequently spread continent-wide to the Pacific coast (Conservation of Migratory Species [CMS] and Food and

Table 4. Model selection results comparing correlations between indices of various factors on detection rates of Peregrine Falcons during beach surveys for raptors in southwest Washington, 1996–2023. Models U_t, $\alpha_{Bald\ Eagle}$, U_t, $\alpha_{.}$, U_t, $\alpha_{Effort+Bald\ Eagle.,\gamma' = \gamma''}$, and U_t, $\alpha_{.\ .,\gamma' = \gamma''}$ were used in model averaging because they were the only models where all parameters converged.

Model[a]	$-2\log(L)$	Number of Parameters[b]	AIC$_c$	ΔAIC$_c$	AIC$_c$ Weights
U_t, $\alpha_{Bald\ Eagle}$	1378.43	37 (37)	1453.17	0	0.50
U_t, α_t	1326.69	63 (61)	1454.82	1.65	0.22
U_t, $\alpha_{Effort+Bald\ Eagle.,\gamma' = \gamma''}$	1381.97	37 (37)	1456.71	3.54	0.09
U_t, $\alpha_{Bald\ Eagle.,\gamma' = \gamma''}$	1384.58	36 (30)	1457.28	4.12	0.06
U_t, $\alpha_{t.,\gamma' = \gamma''}$	1332.31	62 (60)	1458.38	5.21	0.04
U_t, $\alpha_{Effort.,\gamma' = \gamma''}$	1385.97	36 (30)	1458.67	5.51	0.03
U_t, $\alpha_{Effort+\ Bald\ Eagle}$	1382.36	38 (37)	1459.14	5.97	0.03
U_t, $\alpha_{.}$	1387.55	36 (36)	1460.24	7.08	0.01
U_t, α_{Effort}	1385.97	37 (34)	1460.71	7.55	0.01
U_t, $\alpha_{.\ .,\gamma' = \gamma''}$	1392.50	35 (35)	1463.16	10.00	0.00

[a] The symbol + indicates an additive relationship between the two variables.

[b] Number of parameters that converged are in parentheses.

Agricultural Organization [FAO] 2023; Youk et al. 2023). While we have no data to suggest that the presence of H5N1 affected falcon abundance on our study area, annual abundance of peregrines was lowest during the 2022–2023 and 2023–2024 sighting periods (Fig. 3a) when wildlife mortality from HPAI was increasing significantly across North America (CMS and FAO 2023, Youk et al. 2023). To our knowledge, a Netherlands-based study by Caliendo et al. (2025) is the only published report linking H5N1 to peregrine mortalities.

The USFWS recently completed an analysis to inform decisions about potential revisions to the allocation of Peregrine Falcons for falconry take in the United States (USFWS 2023). This national-level analysis determined that the special restrictions on take of Peregrine Falcons for falconry implemented in 2008 (USFWS 2008) were not biologically necessary to ensure take is sustainable based on data from a northern analysis zone (north of 54° latitude) and a southern zone (from the southern edge of the northern zone to the southern extent of the United States (USFWS 2023). The northern zone is characterized by highly migratory Peregrine Falcons while the southern zone includes resident and migratory individuals.

The two management zones established by the USFWS (2023) covered the entirety of the breeding range of Peregrine Falcons in Arctic and subarctic portions of the western hemisphere, and the areas south of there in Canada and the United States through which falcons migrate. The spatial extent of the analysis was appropriate for *F. p. anatum* and *F. p. tundrius*, both of which have large breeding distributions. Indeed, their abundance and distribution were well documented through analyses of data from band recoveries, occupied nesting territories, Breeding Bird Survey efforts, and fall migration counts (USFWS 2023). In contrast, the known breeding distribution of *F. p. pealei* is limited to the Pacific coast. This range extends from the northern coast of Oregon through coastal areas of Washington and British Columbia to Alaska where it occurs coastally with some breaks in distribution (Lewis and Kissling 2015) to and through the length of the Aleutian Islands, including Russia's Commander Islands (White et al. 2013). This linear distribution of islands and headlands broken by unsuitable upland nesting conditions and open ocean extends in an arc approximately 1800 km in length across the north Pacific Ocean.

Our estimates of abundance in southern coastal Washington beaches, which is a segment of the primary migration route and overwintering area used by this subspecies, indicate that only a small percentage of the entire population of *F. p. pealei* moves south into the conterminous United States. The *F. p. pealei* population is coastal, and our study area beaches are near the southern edge of the breeding range, thus, virtually all southbound migrant *F. p. pealei* that overwinter south of Washington likely pass through Washington, and similarly must pass through the state to return to northerly breeding areas. Consequently, although individuals of this subspecies have been documented overwintering as far south as northwestern Mexico (Enderson et al. 1991; and see Fig. 4), our data suggest they are far less abundant than other Peregrine Falcon subspecies south of Canada, the

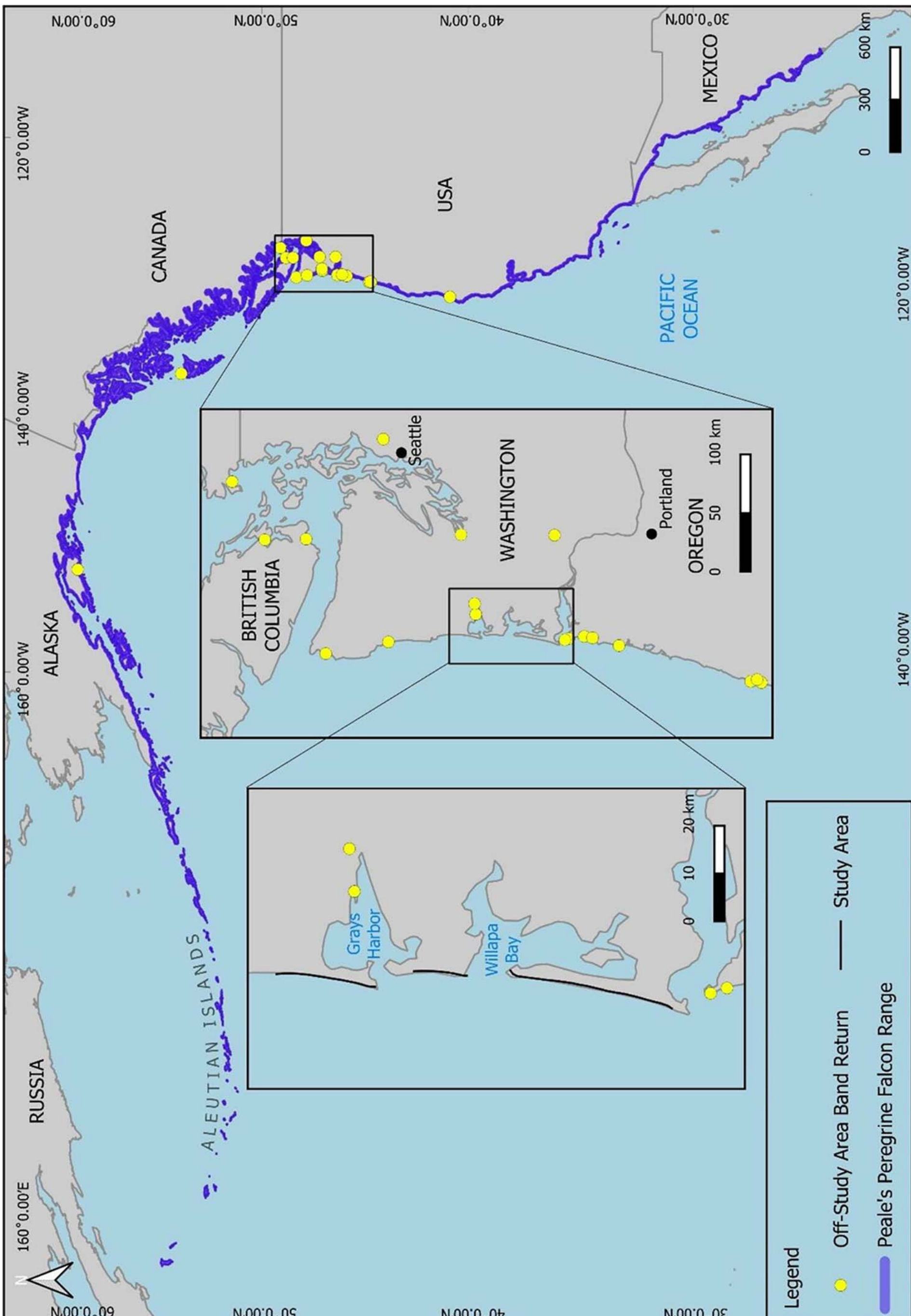

Figure 4. Annual distribution of *F. p. pealei* that captures the breeding, migration and over-wintering areas of the subspecies. The area depicted represents a 10-km buffer adjacent to the marine coast extending from the Commander Islands, Russia to the southernmost documented record in Sinaloa, Mexico. Yellow points represent sightings or recoveries of *F. p. pealei* we banded and were found or sighted >10 km from the study area (Supplemental Material Table S1). The depicted range is based on White et al. (2013) and Enderson et al. (1991). *F. p. pealei* are absent from some areas shown, likely in many cases because of a lack of seabird prey (K. Titus pers. comm.). (Sources of information used to generate this map: Natural Earth 2024a, 2024b; map created using QGIS.org 2024.)

Table 5. Estimated abundance of *F. p. pealei* from across its range, summarized from White et al. (2013). Some of these estimates were based on tallies of known breeding sites (e.g., Washington outer coast), whereas others were based on extrapolations. Localized areas that support *F. p. pealei* and *F. p. anatum* (e.g., the Puget Sound region of Washington; Hayes and Buchanan 2002) were not included in the estimates of White et al. (2013). See Gibson and Byrd (2007) for additional information for specific localities.

Region	Estimated Number of Pairs
Commander Islands[a], Russia	18
Aleutian Islands, Alaska[b]	262–580
Shumagan Islands to Alaska Peninsula	12
Kodiak Island and Barren Islands	12
Cook Inlet to Kayak Island	30–57
Southeast Alaska (Dixon Entrance to Cape Spencer)	100
British Columbia	100
Washington	17–20
Oregon	5–7
Total	**556–906**

[a] Western extent of the Aleutian Islands.

[b] Two estimates were reported: one of 262 pairs, and another that ranged from 375 to 580 pairs.

area where they would be available for falconry take in the conterminous United States, during the nonbreeding period. White et al. (2013) estimated the size of the *F. p. pealei* population as 556–906 pairs (Table 5, White et al. 2013), with approximately one-half of those found in the Aleutian Islands (see Gibson and Byrd 2007). In contrast, population size estimates for *F. p. anatum* and *F. p. tundrius* are much larger. The mean population size estimate for *F. p. anatum* and *F. p. tundrius* in the northern zone was 94,366 individuals and 9583, respectively, for the southern zone (USFWS 2023).

The origin of the *F. p. pealei* peregrines that migrated to or through the southern coast of Washington is poorly known. Although most of the falcons encountered through our capture work had plumage considered typical of the Haida Gwaii subgroup of *F. p. pealei* (White et al. 2013), both banded and unbanded individuals with plumage characteristic of the Aleutian subgroup of *pealei* (Wheeler 2003: Plate 559; White et al. 2013: Fig. 73) were also documented, although far less often. Sighting and recovery data reveal movement of *F. p. pealei* between our study site and known or likely natal areas in Alaska and coastal British Columbia (Fig. 4, Table S1; Varland et al. 2012) over the 29-yr span of our study thereby indicating at least a low level of connectivity across an unknown portion of the breeding distribution. We documented sighting of only one banded falcon (Y/6) from north of British Columbia (Fig. 4, Table S1). Peregrine Falcons, including first year birds, from the Langara Island (Kiis Gwaii) area and the Aleutian Islands are recognized as being largely year-round residents (White et al. 2013). Currently, we lack the information necessary to estimate the proportion of *F. p. pealei* on our study area that originated locally in Washington, more distantly in British Columbia, or as far north as Alaska.

Mark-resight is an attractive method for estimating population size and other demographic parameters because the approach requires that individuals only need to be captured and marked once, and information from individuals that are never captured (i.e., unmarked samples) are included in the estimator. Therefore, the technique is relatively inexpensive, is often more efficient for animals that are difficult to capture and is less stressful to individual animals compared to methods that require at least one capture of each individual in the analysis (McClintock et al. 2009). The original derivation of mark-resight methods required specific assumptions to be met that are often untenable in field situations, including equal sighting rates of marked and unmarked individuals, that marking doesn't influence detection, knowledge of the exact number of marked individuals, demographic and geographic closure, and sampling without replacement (McClintock et al. 2006). Over the past few decades, researchers have extended mark-resight models so that some of these assumptions could be relaxed and the methods applied to a broader range of field studies (e.g., McClintock et al. 2006, Chandler and Royle 2013, Rutledge et al. 2015, Lyons et al. 2016, Efford and Hunter 2018).

Our constraint of keeping several parameters constant could influence some of our inferences from this study. We allowed α, the log-scale mean sighting rate, and U, the size of the unmarked sample population, to vary among years. If the parameters we constrained to be constant were in fact variable, temporal variability in α and U would have been confounded by unmodeled variation in the other parameters. Therefore, if we had sufficient data to allow for temporal variation in other parameters, we could have made more precise estimates of population size and stronger inferences about temporal variability in abundance. Further, if the constrained parameters varied among years, some of the annual estimates of abundance could be biased, which would indicate that our analysis provides more of an estimate of average abundance over the study period rather than unbiased or precise annual estimates.

Peregrines in our study are migratory, highly mobile, and often can be difficult to capture. Further, marking occurred during the sighting period, so for analysis purposes we could not use sightings of marked birds until the subsequent sighting period which led to an extended time interval between marking (e.g., 2014/2015) and usable sightings (e.g., 2015/2016). Therefore, we were particularly concerned about violating assumptions of closure, known number of marked birds, and sampling without replacement. The ziPNE model (McClintock et al. 2019) and the consistent tracking of marked and unmarked birds during this study allowed us to derive reasonable estimates of abundance for a demographically and geographically open sample population with a relatively extended time frame between marking and sighting. The parameters within the ziPNE allowed us to estimate the probability that individuals permanently (w) or temporarily (g) emigrated from the study area between marking and first sighting. The ziPNE also allowed us to use data over an extended period (i.e., Sept through May) when sampling with replacement is highly likely because we would count the same individual more than once. Lastly, because our sighting rate was confounded by availability and detectability, our inferences are to the "super population" (i.e., all individuals that are present on the study area at any time during fall, winter, or spring; Kendall 1999). We had a relatively small sample of individuals and high heterogeneity in sighting among individuals, which could result in small biases in estimates of abundance (McClintock et al. 2019). Therefore, with adequate sampling effort this approach is an appropriate means to assess the abundance of Peregrine Falcons and likely other species.

Management Implications. In the recent assessment of Peregrine Falcon abundance in Canada and the United States, the USFWS discussed the prospects for liberalization of falconry take (USFWS 2023). In Pacific Flyway states, the current allocation of take was based on reproductive output and the abundance of breeding falcons in each state, with an overall limit on take established for the western states (USFWS 2008). Based on the USFWS (2023) analysis, some states in the Pacific Flyway may subsequently elect to adopt a liberalized approach to take of Peregrine Falcons for falconry. We posit that uncertainty about the geographic origin of *F. p. pealei* that migrate south of Canada and become available for take in the United States requires additional consideration when setting take guidelines. If all areas of the *F. p. pealei* range were equally represented in the cohort of falcons that passed through coastal areas south of Canada, the impact of take would be well distributed. Conversely, if most of the *F. p. pealei* captured on our study area originated, for example, in Washington (with an estimate of 17 breeding pairs along the outer coast as per Wilson et al. 2000; see also Hayes and Buchanan 2002), harvest for falconry would potentially have a disproportionate impact on that segment of the population. Consequently, a cautious approach to management of take is warranted. Additional research on annual movements and population genetics could enhance our understanding of natal origins of the *F. p. pealei* that migrate to and through Washington and better inform the allocation of Peregrine Falcon take for falconry.

SUPPLEMENTAL MATERIAL (available online). Figure S1: Bald Eagle chasing Peregrine Falcon with shorebird prey. Nick Dunlop photo. Table S1. Peale's Peregrine Falcons banded on study area beaches and sighted or recovered dead ≥ 10 km from the study area. "Large map" and "map inset" designations refer to Fig. 4.

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APPENDICES

Appendix A. Number of marked Peregrine Falcons counted as “unmarked” (BU, UM) and number assigned capture histories (CH) for use in the zero-inflated Poisson log-normal mark-resight model analyses.

Capture Category	BU, UM, CH[a]	Falcon Count	Description
Summary of all categories involving captures or sightings of marked and unmarked birds	BU	234	Marked on the study area during a sighting period, counted as “unmarked” for the sighting period when marked
	BU	159	Sighted during the same sighting period as when marked, counted as “unmarked”
	BU	7	Marked off study area by other researchers, first observed on study area during a sighting period, consequently counted as “unmarked”
	Total	400	Total number of marked falcons counted as “unmarked” for the analysis: 234 + 159 + 7
	UM	251	Observations of peregrines confirmed as unmarked
	Total	651	Total count of “unmarked” falcons: 400 + 251
Summary of individuals that were marked and tracked with an individual capture history	CH	234	See description in row 1 above
	CH	7	See description in row 3 above
	CH	7	Marked on study area in summer
	CH	4	Marked on study area before first sighting period
		−2	Removed from CH because banded in the last sighting period and therefore unavailable to enter the “marked” population until after the study (after 2023–2024 sighting period)
	Total	250	Total number of individuals with capture histories: 234 +7 + 7 + 4 + (−2)

[a] BU: Banded falcons counted as unmarked; UM: Observations of peregrines that were confirmed as unmarked; CH: Banded falcons assigned a capture history and therefore included in the analyses. Capture histories consist of a vector of numbers that track the number of times an individual was sighted during each sighting period following the period of original capture.

Appendix B. Pearson correlation coefficients among Bald Eagle and human activity indices. Based on data collected during Peregrine Falcon surveys along beaches in southwestern Washington, 1998–2024.

	Bald Eagles	People	Vehicles	Dogs on Leash	Dogs off Leash
Bald Eagles	1.00	0.53	0.65	0.77	0.55
People		1.00	0.85	0.73	0.79
Vehicles			1.00	0.71	0.92
Dogs on leash				1.00	0.62
Dogs off leash					1.00