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SCAVENGING AS A FOOD-ACQUISITION STRATEGY BY PEREGRINE FALCONS

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ABSTRACT.—Although best known for capturing live prey, five of the six members of the genus *Falco* in the United States or Canada are documented facultative scavengers. During 1109 surveys of three coastal beaches in Washington between 1983 and 2015, we observed hunting and feeding by Peregrine Falcons (*Falco peregrinus*), a species that migrates through and overwinters at those coastal beaches. Excluding records of Peregrine Falcons with food items of unknown origin ($n = 44$), our 172 observations of feeding included 77 prey items that we concluded the falcons had captured, 46 direct observations of prey captures, and 49 cases of scavenging. Scavenging records represented 29% of our observations of Peregrine Falcons with food items, and included food items representing 19 taxa. Seabirds and waterbirds were the most common food items consumed as carrion (44 of 49 items; 90%), whereas other captured or targeted prey were most often shorebirds or other small birds (206 of 277 items; 74%). We observed 21 color-banded falcons, ranging in age from <1 to 4 yr, scavenging up to three times each. We observed more scavenging by immature (<1 yr old) falcons than by adults, even though hunting success was similar between immature and adult falcons. We detected no difference in the occurrence of scavenging by season. Given the frequency of scavenging, the biomass of carrion potentially consumed, and the apparently predictable presence of carrion in the study area, we concluded that scavenging by peregrines in coastal Washington is relatively common. Additionally, carrion may represent a commonly used and important source of food in other regions of the world, particularly where carrion is common and persistent in the environment.

KEY WORDS: *Peregrine Falcon*; *Falco peregrinus*; *behavior*; *carrion*; *feeding*; *foraging*; *prey*; *scavenging*.

ALIMENTACIÓN CON CARROÑA COMO ESTRATEGIA DE ADQUISICIÓN DE ALIMENTO EN *FALCO PEREGRINUS*

RESUMEN.—Aunque son mejor conocidos por capturar presas vivas, cinco de los seis miembros del género *Falco* en los Estados Unidos o Canadá son carroñeros facultativos. Durante 1109 censos en tres playas costeras en Washington entre 1983 y 2015, observamos los hábitos de caza y alimentación de individuos de *Falco peregrinus*, una especie que migra hacia estas playas e inverna en ellas. Excluyendo los registros de individuos de *F. peregrinus* con presas de origen desconocido ($n = 44$), sobre 172 observaciones de alimentación incluyeron 77 ítems de presas capturadas por los halcones, 46 observaciones directas de captura de presas y 49 casos de alimentación con carroña. Los registros de alimentación con carroña representaron el 29% de nuestras observaciones de individuos de *F. peregrinus* portando alimento e incluyeron presas que

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representaron 19 taxa. Las aves playeras y acuáticas fueron los ítems de presas más frecuentemente consumidos como carroña (44 de 49 ítems; 90%), mientras que otras presas capturadas o perseguidas fueron por lo general aves playeras u otras aves pequeñas (206 de 277 ítems; 74%). Observamos 21 halcones con anillos de colores, con un rango de edad de entre <1 y 4 años, alimentándose de carroña de 1 a 3 veces cada uno. Observamos una mayor tendencia a la alimentación con carroña en halcones inmaduros (<1 año de edad) que en adultos, aunque el éxito de caza fue similar entre halcones inmaduros y maduros. No detectamos diferencias en la ocurrencia de alimentación con carroña entre temporadas. Dada la frecuencia de alimentación con carroña, la biomasa de carroña potencialmente consumida y la presencia aparentemente predecible de carroña en el área de estudio, concluimos que la alimentación con carroña por parte de *F. peregrinus* en la costa de Washington es relativamente común. Adicionalmente, la carroña puede representar una fuente de alimento importante y de uso habitual en otras regiones del mundo, particularmente donde la carroña es común y perdura en el ambiente.

[Traducción del equipo editorial]

Scavenging is a well-documented strategy for securing food in numerous and diverse taxa and communities distributed globally across terrestrial and aquatic ecosystems (DeVault et al. 2003, Beasley et al. 2012). Among terrestrial vertebrates, vultures (i.e., some Old and New World species; Houston 1994) are the only true obligate scavengers—species dependent on finding and securing carrion as their exclusive food resource (Wilson and Wolkovich 2011). Most vertebrate predators are, to some extent, considered to be opportunistic or facultative scavengers (DeVault et al. 2003, Wilson and Wolkovich 2011). In North America, the Golden Eagle (*Aquila chrysaetos*; Kochert et al. 2002, Watson 2010) and Bald Eagle (*Haliaeetus leucocephalus*; Stalmaster 1987, Buehler 2000) are notable examples of facultative scavengers within the guild of raptorial species, and for both species scavenging is recognized as an important component of their varied approach to food acquisition. Nonetheless, the occurrence of scavenging, including the role of facultative scavengers, has been underappreciated across many taxa, in part due to the lack of long-term or intensive studies (Selva and Fortuna 2007). This dearth of information may be important, as it likely influences our understanding of behavioral ecology and population dynamics (Houston 1979), disease and pollutant exposure (Straub et al. 2015, van den Brand et al. 2015, Beasley et al. 2016, Golden et al. 2016), the structure of animal communities and energy flow in food webs (Selva and Fortuna 2007, Wilson and Wolkovich 2011, Beasley et al. 2012, 2016), and the importance of scavenging to facultative avian scavengers (DeVault et al. 2003, Beasley et al. 2012, 2016, Margalida et al. 2017).

As a group, falcons are well known for capturing avian and other prey during hunting attacks that typically involve rapid and direct flight (Newton

1979, Cade 1982). The ranges of prey species and biomass, as well as the general and specific tactics used to secure prey, differ substantially among falcon species in North America (e.g., Smallwood and Bird 2002, White et al. 2002, Warkentin et al. 2005, Booms et al. 2008, Steenhof 2013) and globally (Cade 1982). Although there are few published records of scavenging by North American falcons, five of six species in the genus *Falco* that occur in the United States or Canada are documented facultative scavengers: American Kestrel (*F. spawerius*; Ganis 1976), Merlin (*F. columbarius*; Thomas 1992, McIntyre et al. 2009), Prairie Falcon (*F. mexicanus*; Holroyd 1999), Peregrine Falcon (*F. peregrinus*; Beebe 1960, Holland 1989, Buchanan 1991, Dekker 1999), and Gyrfalcon (*F. rusticolus*; Tømmerass 1989).

On the Pacific Coast of North America, hunting Peregrine Falcons typically target shorebirds, waterfowl, waterbirds, seabirds, and a variety of other avian taxa at estuaries and beaches (Dobler and Spencer 1989, Dekker 1995, Buchanan 1996, 2012). The abundance and availability of prey at these sites may influence prey selection by peregrines. Shorebirds are often the most commonly taken prey species at marine estuaries and coastal beaches (Dekker 1995, Buchanan 1996, 2012), where large aggregations of Dunlins (*Calidris alpina*) overwinter (Buchanan 1992, Buchanan and Evenson 1997). Perhaps due to the abundance of suitable prey in these coastal environments (e.g., Buchanan et al. 2001) and the scarcity of observations of scavenging by Peregrine Falcons reported in the literature, scavenging by peregrines has heretofore been considered rare (Beebe 1960, Buchanan 1991). In this paper, we report on the occurrence of scavenging by Peregrine Falcons in coastal Washington.

STUDY AREA

We conducted our study on three ocean beaches on the southern coast of Washington, USA: Ocean Shores, Grayland, and Long Beach (Fig. 1). The 23.5-km-long Ocean Shores study area extended from the jetty at the mouth of Grays Harbor north to the mouth of the Copalis River. The 11.8-km-long Grayland Beach study area extended from the Warrenton-Cannery Road beach access north to the Bonge Road beach access. The 39.9-km-long Long Beach study area extended for the length of the Long Beach Peninsula (currently 0.3 km longer than reported in Varland et al. (2012), due to sand accretion at the north end of the peninsula), starting at North Head. We frequently excluded the southernmost part of Ocean Shores Beach and both ends of Grayland Beach in our driving surveys (see below), because soft sand precluded safe driving.

The beaches are backed by low dunes stabilized by introduced European beach grass (*Ammophila arenaria*; Buchanan et al. 2001). All of the beaches incline slightly toward the ocean and vary in width depending on season, tide height, and surf conditions. Lower portions of the beaches were generally free of debris transported by waves, whereas upper portions were often strewn with drift logs, kelp, and other fine and coarse debris (Gonor et al. 1988). Incoming tides generally deposited carcasses in or below this wrack zone. Buchanan et al. (2001) provide additional information on the characteristics of beach-dune habitat on the Washington and Oregon coasts.

Food Resources. Food resources for Peregrine Falcons appeared to be plentiful at our study sites. The three study beaches were near Grays Harbor or Willapa Bay (Fig. 1), two extensive estuaries that support large bird populations, particularly shorebirds (Buchanan et al. 2001). Waterfowl and waterbirds were not abundant at the beaches, although we sometimes observed small groups flying overhead, larger numbers passing by or foraging offshore, and some occasionally resting on the beach. Conversely, shorebirds were abundant at times on the outer beaches, with typical fall and winter estimates ranging from 1000 to >5000 Sanderlings (*Calidris alba*) and 6000 to >50,000 Dunlins (Buchanan 1992, J. Buchanan unpubl. data). Other shorebird species (Black-bellied Plover [*Pluvialis squatarola*], Western Sandpiper [*Calidris mauri*]) were seasonally present in numbers (hundreds or low thousands) that varied seasonally and among beaches (Buchanan 1992).

Carrion in the form of dead birds, fish, and mammals is commonly observed on outer coastal beaches in Washington (Hamel et al. 2009) and these potential food items likely arrive by different pathways. Most carrion appears to either wash ashore after the animals die at sea (Hamel et al. 2009) or come ashore alive and subsequently die. We also observed birds that had been hit by vehicles on the beach; such events appeared rare (several observations during our combined studies) and included gulls (Laridae; J. Buchanan unpubl. data) and flocks of shorebirds (Buchanan 2011). Marine mammals frequently wash ashore on the coast of Washington (Huggins et al. 2015), sometimes alive upon stranding, and we observed dead land mammals (i.e., elk [*Cervus canadensis*], black-tailed deer [*Odocoileus hemionus*], horse [*Equus caballus*], and beaver [*Castor canadensis*]) on several occasions. We assumed the land mammals floated down a river or out from a bay, and then were cast ashore on the beaches, perhaps in the same manner as downed wood transported from upland sites (Gonor et al. 1988).

METHODS

Field Procedures. We observed scavenging by Peregrine Falcons during the course of ongoing studies of shorebird abundance (Buchanan 1992), falcon hunting behavior (Buchanan 1996), and long-term raptor banding focused on Peregrine Falcons (Varland et al. 2008a, 2008b, 2012). Our observations of scavenging were made while conducting vehicle-based surveys along the three study beaches between January 1983 and May 2015. JBB conducted 89 surveys mostly alone (several times with one additional observer) between 1983 and 2015; TLF and one additional observer (usually JBB) conducted 37 surveys between 2000 and 2014; and DEV conducted 973 surveys between 1995 and 2015 with 1–3 additional observers. DEV and TLF banded Peregrine Falcons in the study area between 1995 and 2015. We conducted surveys in all seasons, which we classified according to the meteorological definition for the northern hemisphere (Trenberth 1983): fall (September–November), winter (December–February), spring (March–May), and summer (June–August). We made most of our observations during winter and migration periods; observations during the breeding season did not involve breeding peregrines on territories.

We observed Peregrine Falcons during field efforts that we classified as either complete or incomplete

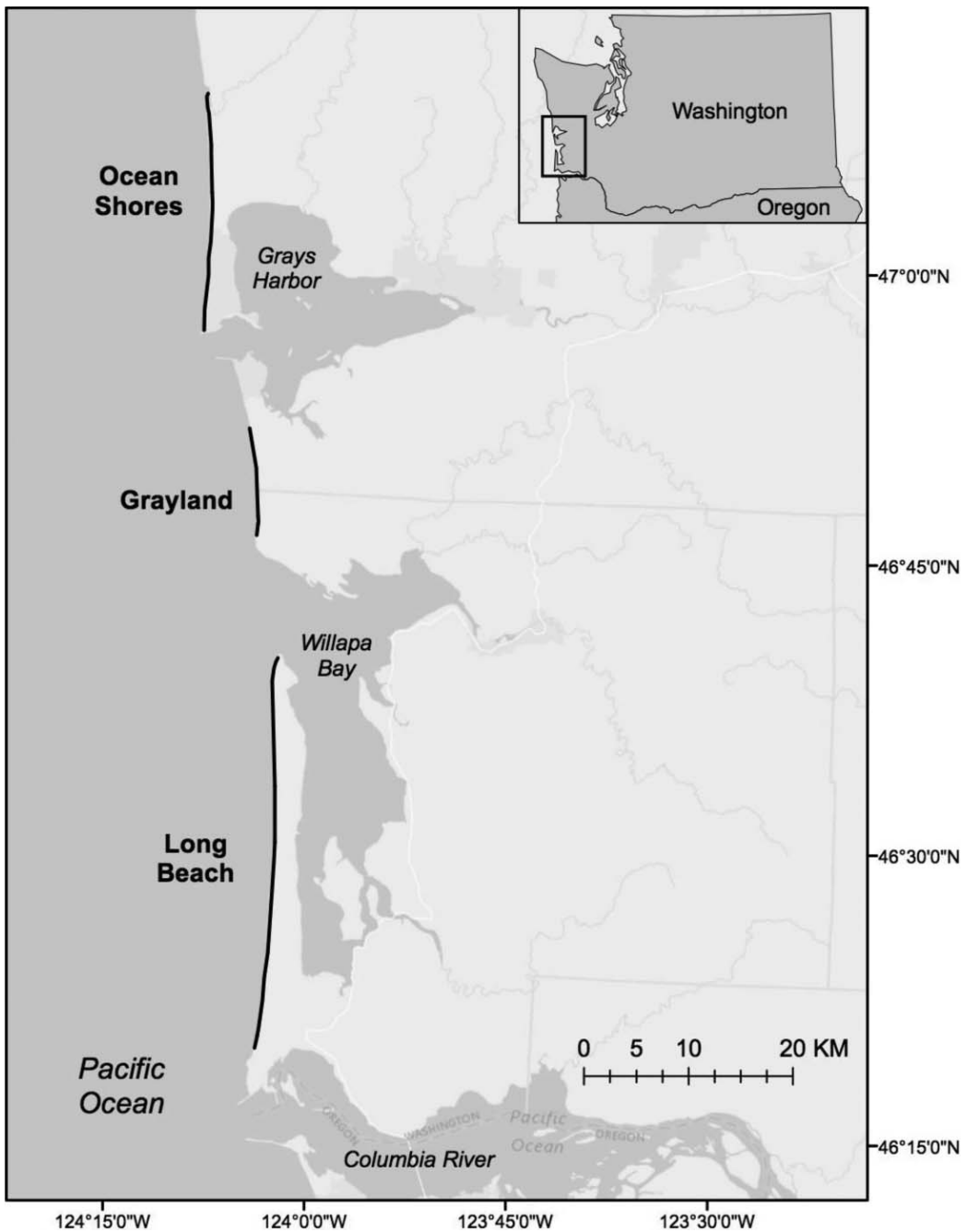


Figure 1. Map of three study area beaches where Peregrine Falcon surveys were conducted on the southern coast of Washington, USA. Black lines indicate segments of beaches covered in search efforts.

Table 1. Survey effort (number of surveys and mean survey length in km) at Ocean Shores, Grayland, and Long Beach study area beaches on the southern Washington coast, January 1983–May 2015.

SURVEY TYPE	OCEAN SHORES	GRAYLAND	LONG BEACH	ALL SURVEYS
Complete Raptor Surveys: % (<i>n</i>)	83 (599)	94 (108)	69 (181)	81 (888)
Mean (SD) survey length	20.4 (1.7)	11.1 (0.4)	38.9 (1.2)	
Incomplete Raptor Surveys: % (<i>n</i>)	17 (121)	6 (7)	31 (83)	19 (211)
Mean (SD) survey length	13.5 (5.6)	4.2 (4.1)	30.3 (9.9)	
Total number of surveys	720	115	264	1099

raptor surveys. We classified surveys as *Complete Raptor Surveys* when: (1) all Peregrine Falcon observations were fully documented; (2) $\geq 70\%$ of a study area beach was surveyed; and (3) weather conditions were favorable (i.e., visibility was ≥ 200 m and mean wind speed was ≤ 32 km/hr). Conversely, we classified surveys as *Incomplete Raptor Surveys* when one or more of the conditions identified above were not met. In total, 80% ($n = 888$) of our surveys were Complete Raptor Surveys and 20% ($n = 211$) were Incomplete Raptor Surveys (Table 1). During some surveys we were unable to drive the full length of the beaches because of severe weather, unsafe driving conditions (from high tides, high creek waters, storm surge, soft sand), or time constraints. In a few other cases, documenting peregrine behavior was secondary to other research objectives (Varland 2015).

We used similar field methods during all phases of the overall field effort. We used four-wheel drive vehicles to conduct surveys on the beaches, driving at speeds of 16–32 km/hr. This allowed us to use the vehicles as mobile blinds, minimizing disturbance to falcons and other birds, while enabling the greatest possible survey coverage on any given site visit. Surveys were usually completed in 2–4 hr, including stops as needed to observe or capture Peregrine Falcons. We recorded the time and location of each falcon observation, as well as the falcon's age and details of hunting behavior or prey use. Although we also recorded the sex and subspecies of each falcon, herein we report sex and subspecies only for those falcons we were able to capture. For these individuals, 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 by outside experts as described in Varland et al. (2012) to classify individuals by subspecies. We captured and banded 192 peregrines from 1995 through May 2015 using capture and color-banding techniques described in

Varland et al. (2012). Observers used spotting scopes, cameras with telephoto or zoom lenses, and sometimes binoculars to identify color-banded falcons resighted during the study.

We classified our observations of prey-acquisition behavior and food types of Peregrine Falcons into five categories based on the conditions under which the prey or food item was secured. Using these categories allowed us to describe the occurrence of scavenging in the context of other methods used to obtain food. A hunting flight (*Hunt*) was any flight where ≥ 1 capture attempt was made (Buchanan 1996) at targeted prey, but no prey capture occurred or the outcome was unknown. This category was the only one that did not involve actual possession of a food item, but we included it and made the distinction between unsuccessful (*Hunt*) and successful hunting flights (*PreyCap*; see below) because it was a common behavior associated with food acquisition and provided an indication of intent to capture various taxa. The remaining categories included: (2) prey capture (*PreyCap*), which involved observation of an actual prey capture; (3) observation of a falcon feeding on captured prey (*ObsPrey*); (4) observation of a falcon feeding on carrion (*ObsCarrion*); and (5) observation of a falcon feeding on a food item of uncertain origin (*UncOrigin*). We classified an observation as *UncOrigin* when (a) we were unable or chose not to approach a falcon during feeding to identify the food item, (b) we could not identify the food item because the falcon was too distant or departed the study area before we could identify the item, or (c) our priority was to capture and band and we did not examine the item closely.

We classified food items as carrion using one or more of the following criteria: (a) the carcass was cold to the touch; (b) a falcon was observed landing on a carcass; (c) the carcass was already partially consumed when first visited by a falcon; (d) another predator or scavenger had previously been observed

feeding on the carcass; (e) the carcass was partly covered by beach debris or sand; or (f) the carcass did not exhibit signs of physical trauma (pointing to death by disease or starvation rather than predation). We did not classify as carrion any small birds (e.g., sandpipers and other taxa with body mass of approximately <100 g) that were consumed by falcons. Small birds, including Dunlins (J. Buchanan unpubl. data) and various landbirds (Buchanan and Fleming 2008), are rarely observed dead on beaches, and most dead or injured small birds are likely taken and consumed quickly by other scavengers that are much more abundant than falcons (e.g., gulls, American Crows [*Corvus brachyrhynchos*], and Common Ravens [*Corvus corax*]; e.g., Buchanan 1991).

To classify falcons by age, we assumed the coastal peregrines we encountered during surveys hatched in May and we assigned age classes based on molt condition and the capture or observation date. Because we were able to carefully examine the molt condition of peregrines we captured for banding, we were able to assign those peregrines to one of two age classes: immature (<1 yr) and adult (≥ 1 yr). We assigned peregrines observed during surveys, but not captured, to the same two age classes (Hunt et al. 1975): immature (<15 mo old with brown or mostly brown backs and brown vertical streaking on the breast) or adult (>15 mo old with blue-gray backs and horizontal barring on the breast). We classified banded peregrines observed on subsequent surveys according to this two-age-class system for the purpose of analyses with peregrines not captured. We used only the data from the complete raptor surveys to report on the proportion of Peregrine Falcons observed by age class during surveys.

Data Analyses. We assessed differences between captured food items and scavenged food items, both in the identity of species consumed and relative to the body mass of the taxa involved. We consulted Dunning (1984) for body mass data for birds, most of which were from banding studies of live birds. When Dunning (1984) reported differences between sexes and we were unable to identify the sex of food items, we used the value reported for females. For food items we could not identify to species, we assigned them masses of surrogate taxa based on the prevalence of those taxa in our overall sample or their relative abundance in the local environment: i.e., scaup species = Lesser Scaup (*Aythya affinis*), scoter species = Surf Scoter (*Melanitta perspicillata*), unidentified duck = Green-winged Teal (*Anas crecca*), grebe species = Western Grebe

(*Aechmophorus occidentalis*), shearwater species = Sooty Shearwater (*Ardenna grisea*), shorebird species = Dunlin, alcid species = Cassin's Auklet (*Ptychorampus aleuticus*), gull species = Western Gull (*Larus occidentalis*), thrush species = American Robin (*Turdus migratorius*), and unidentified small bird (<100 g) = Dunlin. For unidentified birds >100 g and unknown prey, we used the body mass of the intermediate-sized Cassin's Auklet. Finally, we used Verts and Carraway (1998) for body mass of mammals, using the reported mass for females or values in the center of reported ranges, and Groot and Margolis (1991) for the body mass for Pacific salmon (*Oncorhynchus* spp.).

We used a Kruskal-Wallis nonparametric ANOVA to assess differences in body mass among the four categories of known-origin food items: observed feeding on carrion (*ObsCarrion*); observed with captured prey (*ObsPrey*); observed capturing prey (*PreyCap*); and observed pursuing prey, outcome unsuccessful or uncertain (*Hunt*). To further evaluate possible differences in food types, we calculated the Sorenson Index (Magurran 1988) to assess similarity of carrion food items and all other actual food items combined. An index value of 0.0 indicates no similarity and a value of 1.0 indicates no difference between the two categories.

Under the assumption that scavenging by Peregrine Falcons is a successful foraging strategy in our study area, we hypothesized that we would see falcons that scavenged more often during surveys than falcons that did not scavenge. To test this hypothesis, we used the nonparametric Wilcoxon rank sum test to compare the numbers of banded falcons we resighted scavenging versus those with food items they had not scavenged.

During the fall, a large number of comparatively less-experienced juveniles either migrate through or begin to overwinter at our study area (Varland et al. 2012). Moreover, late fall and winter days are shorter and rainfall and winds are more frequent and intense during winter compared with all other seasons in Washington (Mass 2008), thereby possibly reducing opportunities for effective hunting flights. Similarly, winter diurnal high tides are much higher than in other seasons and shorebirds consequently roost for much longer periods each day on the beaches (Buchanan 1992), where falcon hunting success is significantly lower than at the adjacent estuaries (Buchanan 1996). Consequently, we tested potential associations between food-acquisition strategy and several variables, including falcon age, sex,

and subspecies, as well as the season and time of day when the observation was made.

We used a chi-square test to evaluate the hypothesis that younger falcons would be observed scavenging more frequently than older falcons, given the relative lack of hunting experience in immature individuals. We had no ecological reason to hypothesize differences in food-acquisition strategy by sex or among subspecies, but we suspected our results might further illuminate, or at least facilitate development of, testable hypotheses about factors that may influence scavenging by Peregrine Falcons.

We used a chi-square test to evaluate the hypothesis that most scavenging would occur during fall and winter, and less in spring. We excluded summer from the analysis because we conducted relatively few surveys in that season. We hypothesized that falcons scavenge more frequently in the early morning hours, given that carcasses washing ashore overnight would not yet have been consumed by other diurnal scavengers. To evaluate possible time-of-day influences on scavenging rates, we divided the day into three periods (before 1000 H, 1000–1400 H, and after 1400 H) and compared the frequencies of scavenging observations (observed values) and the frequencies of initial observations of individual Peregrine Falcons (expected values) in the three periods. Because 80% ($n = 418$) of the initial observations occurred in the morning period, when most of the surveys occurred, the sample sizes in subsequent periods were much lower. For this reason, we combined the mid-day and afternoon periods and used a chi-square test for this analysis.

As in many observational data sets, some categories of subjects or behavior were observed far less often than others. For example, in this study, the number of immature males was small ($n = 7$), whereas there were 34 immature females. Because more complex models were not stable in the face of such unbalanced data, we used Fisher's exact tests to determine independence between variables such as sex and food-acquisition strategy. To follow up on the hypothesis predicting more scavenging in young birds, we used a Fisher's exact test to evaluate whether adult birds had a higher success rate when attempting to capture prey compared to immature birds. We used the definition of hunting flights from Buchanan (1996) for this analysis. We used an analysis of deviance based on a generalized linear model with binomial error to test for main effects and interactions between season and age on scavenging behavior (Nelder and Wedderburn 1972).

Chi-square and Fisher's exact tests can establish that groups are behaving differently, but they do not provide descriptive information about the direction and magnitude of effects. To accurately describe the observations, we report proportions and 95% confidence intervals (CIs) to describe patterns in the data. We computed 95% CIs using the Wilson method with no continuity correction if the smallest category count was >5 , and the Clopper-Pearson interval if the smallest category count was ≤ 5 (Newcombe 1998: methods 3 and 5, respectively). The confidence intervals are intended to describe the uncertainty associated with the reported estimates, rather than being interpreted as an inferential tool. We conducted all analyses using R v. 3.4.1 (R Core Team 2017) or Statistix 10.0 (Statistix 2013).

RESULTS

We commonly observed Peregrine Falcons with a wide range of food items that they obtained by capture or scavenging at our study area. We observed falcons with food items of known origin 172 times and unknown origin 44 times. We concluded that 71% of the known-origin food items were captured by falcons (*ObsPrey*, $n = 77$; *PreyCap*, $n = 46$) and 29% were scavenged (*ObsCarriion*, $n = 49$). The scavenged food items represented 19 taxa (Appendix 1; Fig. 2). Thirty-four of the 49 carrion items (69%) belonged to four taxa (gulls, $n = 12$; Common Murre [*Uria aalge*], $n = 10$; Western Grebe, $n = 6$; and Northern Fulmar [*Fulmarus glacialis*], $n = 6$), whereas 12 taxa were recorded only once as scavenged carrion (representing 24% of all carrion items). The most unusual carrion were salmon, beaver, harbor seal (*Phoca vitulina*), Brown Pelican (*Pelecanus occidentalis*), and Great Blue Heron (*Ardea herodias*). Twelve (63%) of the 19 taxa scavenged by falcons were unique to the carrion category of food acquisition, which was a greater percentage of unique taxa than for other categories of acquired or targeted food items (Appendix 1).

The number of taxa in other food-acquisition categories ranged from 21 in the *ObsPrey* category to 10 in the *Hunt* category (Appendix 1). We identified relatively few passerines taken as prey ($n = 9$, Appendix 1). Most unidentified small birds ($n = 30$) were likely shorebirds, based on the large number of occasions when we saw peregrines capturing or feeding on shorebirds ($n = 61$). If we combine the number of unidentified small birds and shorebirds we saw falcons pursue (*Hunt*), capture (*PreyCap*), or feed upon (*ObsPrey*), the total repre-

sents the most commonly observed food of falcons in the study (206 of 277 [74%] total food items). In contrast, seabirds and waterbirds were the most common food items consumed as carrion (44 of 49 [90%] items). The Sorenson index ($C_N = 0.128$) indicated little similarity in the species composition of *ObsCarrion* food items and the combined group of captured food items (*PreyCap* and *ObsPrey*). Consistent with the difference in species composition between carrion and other known-origin food items, we found that the median mass of carrion taxa (1010 g) was substantially greater than the median mass of taxa in the other three food categories: *ObsPrey*, *PreyCap*, and *Hunt* (all 59.6 g; Kruskal-Wallis test, $H = 166.6$, $df = 3$, $P < 0.0001$).

Immature falcons were more likely to be observed scavenging ($n = 32$) than adults ($n = 16$); 67% of all scavenging observations involved immature falcons, whereas only 46% of all peregrines observed during surveys were immatures ($n = 443$ immature and 529 adult falcons) ($\chi^2 = 8.2$, $df = 1$, $P = 0.005$). Immature females were more likely to scavenge than adult females (Fisher exact test: $P = 0.029$). We detected no corresponding difference in scavenging by age among males (Fisher exact test: $P = 1.0$); however, our estimate for males should be considered preliminary because of small sample sizes. Although immature peregrines scavenged more often than adults, hunting success did not differ by age class: 38% (19 of 50 hunting flights; 95% CI: 26–52%) for adults and 33% (19 of 58 hunting flights; 95% CI: 22–46%) for immatures (two proportion test: $P = 0.687$; excludes hunting flights where success was unknown).

We examined two aspects of the relationship between season and scavenging by Peregrine Falcons. First, seasonal variation in the percentage of carrion-feeding observations did not differ significantly from expectations given the numbers of surveys conducted in each season ($\chi^2 = 3.36$, $df = 2$, $P = 0.19$; Fig. 3). Second, although we observed immature birds scavenging more often than adults (deviance = 4.34, $df = 1$, $P = 0.037$), the proportional representation of age groups among the scavengers did not differ across seasons (deviance = 1.59, $df = 2$, $P = 0.45$), and the frequency of scavenging relative to live prey capture did not vary seasonally (deviance = 0.50, $df = 2$, $P = 0.78$; Fig. 4).

We observed Peregrine Falcons scavenging throughout the day. We first observed most individual Peregrine Falcons in the morning (80%, $n = 418$), but observed only 55.3% of the records of

scavenging (26 of 47 records where time was recorded) in that time period. We observed 44.7% of the scavenging in the combined two subsequent periods of the day (21 of 47 observations). The daily temporal occurrence of scavenging differed from the pattern of first observations of Peregrine Falcons ($\chi^2 = 7.05$, $df = 1$, $P = 0.01$).

Scavenging by Color-banded Falcons. Peregrine Falcons with VID bands (hereafter, bands) accounted for 70% (34 of 49) of our observations of scavenging; in three cases, we were unable to read the code on the band. We observed 21 falcons, ranging in age from <1–4 yr, scavenging 1–3 times each; 13 individuals on one occasion, 6 on two occasions, and 2 on three occasions. Nineteen falcons were <1 yr old when first observed scavenging; of these, three individuals were observed scavenging again at 1, 2, and 3 yr old. We observed one first-year peregrine scavenging twice on the same day. The median span between first and last observations of individual falcons scavenging was 266 d ($n = 8$); the maximum span was 1038 d (female observed at <1 yr and again at 3 yr).

We observed seven Peregrine Falcons scavenging on the day we captured and banded them. We captured four of these falcons after we had observed them scavenging. We observed the other three falcons scavenging 0.75–8.5 hr after we banded and released them. Six of these falcons were female *F. p. pealei*. The mean mass of four of these females was 1069 g (range: 1016–1146 g), which was comparable to the mean mass (1082 ± 105.3 [SD]) of all female *F. p. pealei* ≤ 1 yr old ($n = 76$) that we captured and banded during the study period.

We resighted 17 of the 21 falcons that we observed scavenging at least once after banding. Four of these falcons, including one banded elsewhere by other researchers, were never seen again after we saw them scavenging. Fifteen peregrines we saw scavenging showed fidelity to the beach where they were banded (observed ≥ 1 d after capture on the same beach where banded; Varland et al. 2008b, 2012) and two other falcons showed fidelity to a beach other than where they were banded (D. Varland unpubl. data). The median number of resightings of banded peregrines we saw scavenging did not differ from the median number of resightings of banded peregrines we saw with a food item they acquired without scavenging (median = 4.0, $n = 17$ for *ObsCarrion*; median = 4.5, $n = 18$ for *ObsPrey* or *PreyCap*; Wilcoxon Rank Sum Test, $z = 0.7$, $P = 0.48$).

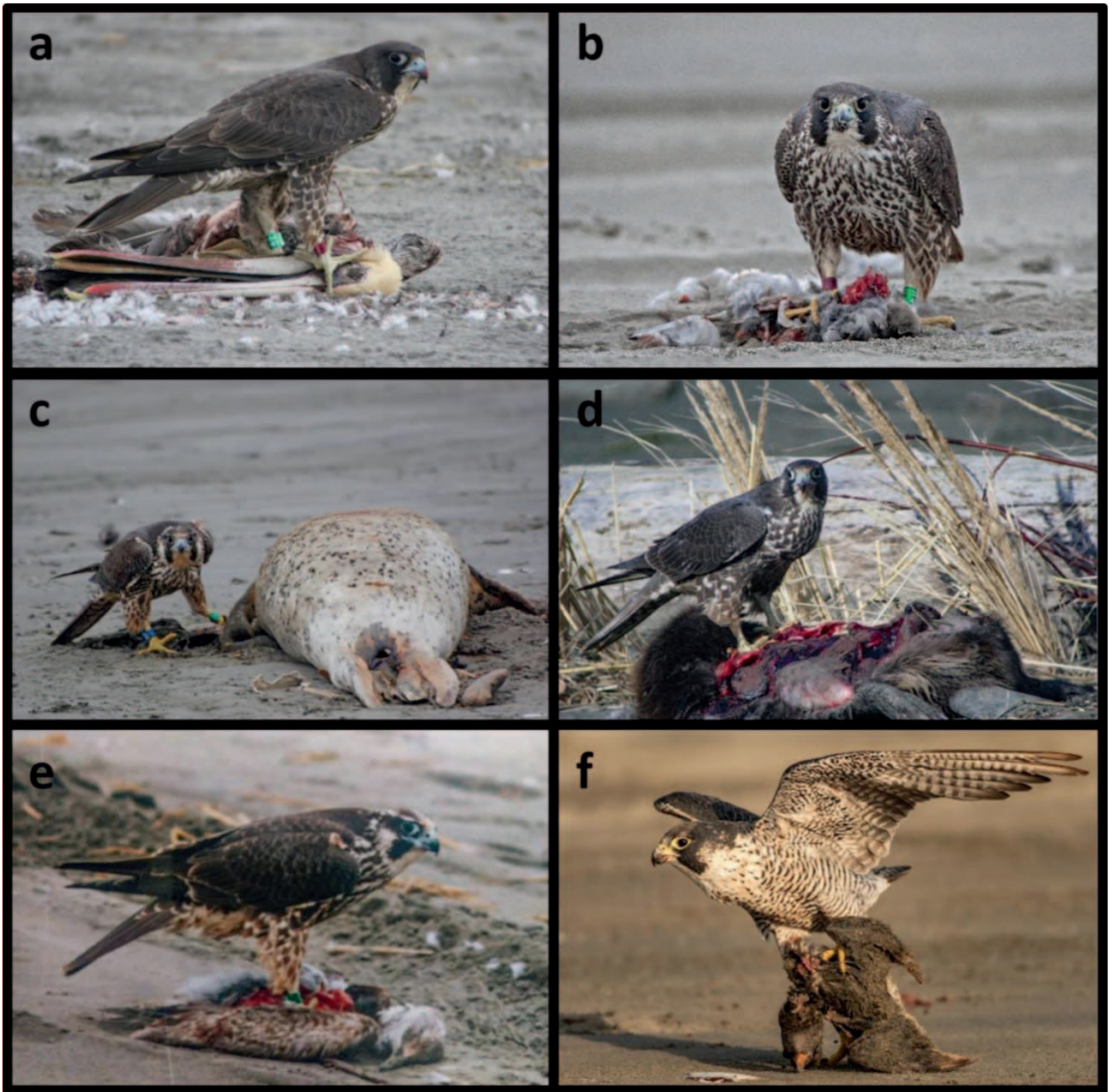


Figure 2. Female Peregrine Falcons feeding on carrion on the Washington coast: (a)–(e) <1 yr old; (f) 1 yr old. Food items include: (a) Brown Pelican on 27 Jan 2010, Dan Varland photo; (b) Northern Fulmar on 27 Feb 2009, Rob Palmer photo; (c) harbor seal on 31 Dec 2012, Joe Buchanan photo; (d) beaver on 2 Feb 2012, Dan Varland photo; (e) Glaucous-winged Gull (*Larus glaucescens*) on 11 Mar 2001, R. Wayne Nelson photo; and (f) Rhinoceros Auklet (*Cerorhinca monocerata*) on 3 Aug 2016, Tim Boyer photo.

Compared to the proportions of banded females (66%, $n=126$) and males (34%, $n=66$), we observed proportionately more scavenging females (84%, $n=26$) than scavenging males (16%, $n=5$; $\chi^2=4.58$, $df=1$, $P=0.03$). Relative to subspecies, we did not observe differences in scavenging frequency among the three subspecies found at our study sites (Fisher

exact test; $P=0.66$). *F. p. pealei* composed 90% ($n=19$) of the banded Peregrine Falcons we saw scavenging and 81% ($n=156$) of the peregrines we banded during the study. We saw one *F. p. anatum* scavenging, and we banded five individuals of this subspecies during the study. We were unable to classify the subspecies of one peregrine we saw

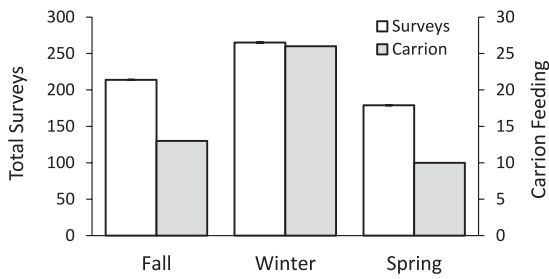


Figure 3. Number of carrion-feeding observations and total surveys conducted by season for Peregrine Falcons on the Washington coast from January 1983 to May 1985.

scavenging, because it showed intermediate plumage characteristics, which was the case for 12% ($n = 22$) of the peregrines we banded.

DISCUSSION

Our results indicate that in coastal Washington the Peregrine Falcon is not only a facultative scavenger, but one that commonly employs this feeding strategy. We observed this behavior in fall, winter, and spring, on all three of our study area beaches, and with such observations spanning more than 30 yr. Nearly 30% of our observations of feeding Peregrine Falcons involved scavenging. We acknowledge, however, that falcons frequently targeted shorebirds and could easily fly from the beach with such small prey items, thus escaping detection, which may have biased our estimate high. Nonetheless, we suspect this potential bias was insubstantial, given that we frequently saw falcons feeding on shorebirds on the beaches and that falcons could potentially have visited some large carrion items multiple times (e.g., a color-banded falcon visited a Great Blue Heron carcass three times; T. Boyer pers. comm.). Because the scavenged items were far larger than the median size of targeted or captured live prey, falcons feeding on the beach may have acquired more than 30% of their food biomass from carcasses. Although we are not the first to report scavenging behavior (e.g., Beebe 1960, Holland 1989, Buchanan 1991), this is the first long-term and comprehensive assessment of scavenging by Peregrine Falcons, and the first to indicate that use of carrion may be a common feeding strategy, particularly during migration and overwintering periods.

Because facultative scavengers are adapted to also obtain food by other means, a variety of environmental and species-specific ecological, morphologi-

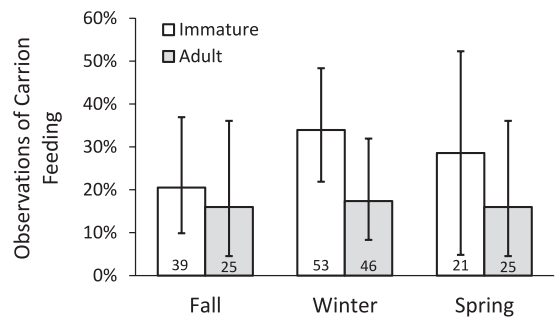


Figure 4. Percent of observations in which birds were feeding on carrion (as opposed to capturing live prey) by age and season for Peregrine Falcons on the Washington coast from January 1983 to May 2015. Total number of all feeding observations are shown inside bars (sum of: carrion feeding + capturing prey + feeding on captured prey). Error bars are 95% CIs.

cal, and behavioral factors likely influence the occurrence of scavenging in such species (Selva and Fortuna 2007, Moreno-Opo et al. 2016). In many raptors, the survival rates of immature birds are substantially less than for adults of the same species, because of the young birds' inexperience and lower social status (Newton et al. 2016). Margalida et al. (2017) found that hunting success increased with age in a raptor population where immatures scavenged regularly, that scavenging was independent of habitat quality, and that its occurrence among immature individuals was not associated with low prey density. This suggested that immatures used scavenging as a means to compensate for hunting skills that were less effective than those of adults. Although we found no difference in success for adult and immature peregrines hunting on the study beaches, the prominence of scavenging by immature peregrines on the beaches might have reflected poorer hunting success than adults in habitats away from the beaches. This is consistent with our observation of a greater amount of scavenging than expected after the morning period. Other factors, such as weather and competitive interactions with adults or other species, also may have influenced use of carrion.

A potential energetic value of scavenging is the comparably inconspicuous nature of the acquisition and consumption of carrion. When falcons hunt shorebirds at our study area, they attack flocks of as many as 12,000 birds over the ocean surf zone (Buchanan 1996). These hunting flights are visible to a human at distances up to 5 km and may be a

conspicuous signal of hunting activity to potential kleptoparasites present at estuaries and beaches (Buchanan 1988). In contrast, use of carrion offers no signal to potential kleptoparasites, except for the flurry of feathers that often ensues when the falcon begins to pluck an avian food item. We observed interactions between raptor species during hunting flights and that involved attempted kleptoparasitism, but such observations were infrequent enough to preclude drawing definitive conclusions about kleptoparasitism. In general, we observed little interaction between Peregrine Falcons and potential competitors associated with possession and consumption of carrion.

A number of environmental factors result in at-sea mortality and subsequent delivery of carcasses to shorelines where they are available to Peregrine Falcons. Nearshore and pelagic waters of the northeastern Pacific Ocean support large aggregations of migratory and overwintering seabirds and waterbirds. Large aggregations of seabirds are associated with the California current (Menza et al. 2016), the Columbia River plume off the Long Beach peninsula (Zamon et al. 2014), and substantial regional aggregations occur along the northern coast of Washington, just north of our study area (Nur et al. 2011). At-sea mortality resulting from severe storms, inadequate food resources, and other factors (Schreiber and Burger 2001, Parrish et al. 2007, Phillips et al. 2011) occurs regularly and some segment of this population of dead birds washes ashore (Wiese 2003) to potentially be scavenged. For example, other observers reported Peregrine Falcons feeding on carcasses of Rhinoceros Auklets (*Cerorhinca monocerata*; T. Boyer pers. comm., 3 August 2016), Cassin's Auklets (D. Moore, pers. comm., 29 Oct 2014, 4 Nov 2014), and Red-throated Loons (*Gavia stellata*; G. Shugart, pers. comm., 24 Oct 2009) following "wrecks" where up to thousands of birds washed ashore dead in our study area over short periods (e.g., Phillips et al. 2011). The resource of dead birds is augmented by dead marine mammals (Huggins et al. 2015) and by other birds and land mammals that likely originate in or pass through adjacent estuaries before they wash into the ocean and are subsequently deposited on beaches. Populations of species that become carrion on our study area are present nearly year-round, but especially during the northern hemisphere fall, winter, and spring (Wahl et al. 2005). Although we did not collect data on carcass availability, we observed multiple bird carcasses on the beaches

during most site visits. A comprehensive monitoring program (Coastal Observation and Seabird Survey Team [COASST]; Hamel et al. 2009) documented the abundance of dead birds on coastal beaches in Washington during part of our study period, and future analyses could examine carcass availability in our study area.

The persistence and nutritional value of carcasses present in the marine environment influences their subsequent availability to, and use by, scavenging Peregrine Falcons on coastal beaches. When a bird (or mammal) dies at sea or in a nearby estuary, it will become available as carrion for terrestrial scavengers only if it is not consumed by marine scavengers or otherwise lost in the marine environment before being washed ashore (Bodkin and Jameson 1991, Wiese 2003, Beasley et al. 2012). Simulations using drift-blocks suggest that carcasses typically travel short distances (<10 km) before washing ashore, although some may move substantial distances (>400 km; Hlady and Burger 1993). Currents, winds, and storms may influence the pattern of movement and deposition of carcasses (Bodkin and Jameson 1991). In addition, although decomposition rates of animal flesh are positively associated with increasing temperatures in terrestrial environments, in marine environments cold water temperatures moderate bacterial growth that would otherwise compromise the value of carrion through the introduction of toxins (Beasley et al. 2012). This factor likely extends the amount of time, compared to terrestrial environments, that carrion is available and of nutritional value to scavenging Peregrine Falcons on coastal beaches.

Although Peregrine Falcons do not possess some of the physical (Si et al. 2015) and behavioral (Houston 1979) attributes that characterize obligate scavengers, they commonly scavenged carrion on our study beaches. Several behavioral traits of the Peregrine Falcon may facilitate the frequent scavenging we observed. Peregrine Falcons tend to have large home ranges during the nonbreeding season (Dobler et al. 1989, Enderson et al. 1995, McGrady et al. 2002) and, although we did not document their use of space in our study area, we saw falcons moving back and forth between the adjacent estuaries and beaches (J. Buchanan unpubl. data) and hunting along the beaches (Buchanan 1996). Some of these movements covered substantial distances, and we assume that during these flights the falcons had opportunities to evaluate resource availability, including live prey and carrion. Indeed, twice we

observed falcons approach carrion directly and alight to begin feeding, suggesting prior knowledge about the presence of the carrion (D. Varland unpubl. data).

Other behaviors also may have facilitated adoption of scavenging as a viable strategy for food acquisition. Twice we saw Peregrine Falcons capture birds that had obviously washed ashore alive and were too weak to fly. Such experience with compromised and easily available avian prey may have contributed to an enhanced search image for carrion. Food caching is a common behavior of adult Peregrine Falcons at nest sites on the northern Pacific Coast of North America (Nelson 1970), and has been recorded in all seasons for at least 21 falcon species (White et al. 1994). Caching was a rare behavior on our study area, however; we never observed caching and only once did we see a falcon retrieve cached prey (a Dunlin).

Peregrine Falcons are exposed to contaminants and infectious pathogens in the environment (Ratcliffe 1993), and this exposure likely occurs through the consumption of both live prey and carrion. Although transmission risk may be the same as through live-captured prey, individuals with underlying health issues are more likely to perish, increasing the likelihood of encounter by scavengers and leading to potentially greater exposure for Peregrine Falcons. We did not directly link consumption of a contaminated food item with peregrine mortality, but in December 2014 one of our banded peregrines died from the highly pathogenic avian influenza (HAPI) virus H5N8 (USGS 2015), 2 km from where it was banded nearly 7 yr earlier. Also in December 2014, three Gyrfalcons at a falconer's facility in western Washington died from the same virus, after having been fed an infected American Wigeon (*Mareca americana*; Ip et al. 2015). In 2006, van den Brand et al. (2015) examined 624 raptors of nine species found dead after an outbreak of HPAI H5N1 in waterbirds in Germany. They found the virus only in Peregrine Falcons and Common Buzzards (*Buteo buteo*), species they concluded were more vulnerable because they hunt or scavenge medium-sized birds. Consequently, the degree to which individual Peregrine Falcons scavenge may influence their exposure to certain contaminants or pathogens.

The Peregrine Falcon is part of an avian community of obligate and facultative scavengers present at our study site. Based on our observations, other members of this community, which is seasonally

variable, include several other raptors, various gull species, shorebirds, corvids, and other taxa such as coyotes (*Canis latrans*) and numerous invertebrates (see Ford and Zafonte 2009). Of the members of this community, we think the Bald Eagle, Gyrfalcon, Turkey Vulture (*Cathartes aura*), Red-tailed Hawk (*Buteo jamaicensis*), and Rough-legged Hawk (*Buteo lagopus*) are likely to be consistently dominant over the Peregrine Falcon for control of food items on the beach. Unlike in Boundary Bay, Canada, where Bald Eagles and Gyrfalcons routinely kleptoparasitized peregrines (Dekker et al. 2012), we saw a Bald Eagle challenge a Peregrine Falcon for food only twice. The Turkey Vulture commonly scavenges carrion during the summer at our study site, but is mostly absent in other seasons (Wahl et al. 2005, D. Varland unpubl. data). We observed no interactions between Turkey Vultures and Peregrine Falcons during our study, but we are aware of one case where several vultures approached on foot a peregrine shielding a food item, which then departed with the item (D. Bailey pers comm.). We rarely encountered Gyrfalcons, Red-tailed Hawks, or Rough-legged Hawks in our study area and we never observed one approach a Peregrine Falcon at carrion. The high rate of carrion use by Peregrine Falcons suggests that the influence—direct or indirect—of these other species was minimal. Behavior that minimizes the temporal and spatial occurrence of these species near carrion (e.g., Sergio et al. 2007, Buchanan 2012) may reduce the level of competitive interactions for resources. Consequently, although it is not clear whether Peregrine Falcons function as apex or mesopredator scavengers in our study area, our results indicate that they (a) are present on the beaches year-round (Varland et al. 2008b, 2012), (b) commonly scavenge, (c) rarely relinquish food items to other species, and (d) are capable of opening up fresh carcasses that then become more readily available to other scavengers in the community (D. Varland, J. Buchanan, and T. Fleming unpubl. data).

It is likely that scavenging by Peregrine Falcons occurs regularly in other parts of the world, and is a more common behavior than appreciated, which may be true for facultative scavengers as a group (Wilson and Wolkovich 2011). If conditions at our study area are an indicator of key factors associated with scavenging during the nonbreeding season, we suggest that the behavior should be expected to occur where many of the following conditions are found: an abundance of birds that can become commonly available as carrion and detectable by

falcons; ocean currents and prevailing winds that influence the rate at which bird carcasses wash ashore; water temperatures cold enough to limit the rate of decomposition of carcasses; and an abundance of live prey. These conditions describe temperate coastal areas, but we recognize that scavenging may occur in noncoastal areas as well. In some regions of the world, such as our study area, substantial marine nutrients are carried ashore and supplement terrestrial ecosystems in numerous ways, including augmentation of food supplies to raptors in the form of carrion (Schlacher et al. 2013). Research is needed to understand the global distribution of this dynamic and its influence on community composition and ecological relationships and their functions at the marine-terrestrial interface.

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Appendix 1. Number of individual vertebrates by taxon observed as food items or as targets of attempted captures by Peregrine Falcons at three beaches in coastal Washington from January 1983 to May 2015.

FOOD ITEMS	FOOD-ACQUISITION TYPE				
	FEEDING: CARRION (OBSCARRION)	FEEDING: UNCERTAIN (UNCORIGIN)	FEEDING CAPTURED PREY (OBSPREY)	PURSUING PREY: CAPTURED (PREYCAP)	PURSUING PREY OUTCOME UNCERTAIN (HUNT)
Fish					
Salmon (<i>Oncorhynchus</i> spp.)	1				
Mammals					
Beaver (<i>Castor canadensis</i>)	1				
Harbor Seal (<i>Phoca vitulina</i>)	1				
Birds					
Seabirds and waterbirds					
Cackling Goose (<i>Branta hutchinsii</i>)	2				
American Wigeon (<i>Mareca americana</i>)		1			
Green-winged Teal (<i>Anas crecca</i>)		4	1		
Lesser Scaup (<i>Aythya affinis</i>)			1		
Scaup species (<i>Aythya</i> spp.)		1			
Surf Scoter (<i>Melanitta perspicillata</i>)			2		
White-winged Scoter (<i>M. fusca</i>)	1		1	1	
Scoter species (<i>Melanitta</i> spp.)			1		
Bufflehead (<i>Bucephala albeola</i>)		1	2	1	
Unidentified duck		1			
Common Loon (<i>Gavia immer</i>)	2				
Horned Grebe (<i>Podiceps auritus</i>)		1		2	
Eared Grebe (<i>P. nigricollis</i>)	1		1		
Western Grebe (<i>Aechmophorus occidentalis</i>)	6	1		2	
Grebe species (Podicipedidae)		1			2
Northern Fulmar (<i>Fulmarus glacialis</i>)	6				
Shearwater species (<i>Ardenna</i> spp.)	1				
Brown Pelican (<i>Pelecanus occidentalis</i>)	1				
Great Blue Heron (<i>Ardea herodias</i>)	1				
Common Murre (<i>Uria aalge</i>)	10	2	1	2	
Alcid species (Alcidae)		1			
Bonaparte's Gull (<i>Chroicocephalus philadelphia</i>)	1				
Western Gull (<i>Larus occidentalis</i>)		1	1	1	
California Gull (<i>L. californicus</i>)			1		
Glaucous-winged Gull (<i>L. glaucescens</i>)	1				
Western x Glaucous-winged Gull (hybrid)	2				
Gull species (Laridae)	9	4	2		2
Shorebirds					
Black-bellied Plover (<i>Pluvialis squatarola</i>)			2		
Sanderling (<i>Calidris alba</i>)			5		
Dunlin (<i>C. alpina</i>)			12	15	53
Least Sandpiper (<i>C. minutilla</i>)					1
Western Sandpiper (<i>C. mauri</i>)			1	2	3
Red Phalarope (<i>Phalaropus fulicarius</i>)			1		
Shorebird species (Charadriiformes)			16	7	58
Passerines					
American Crow (<i>Corvus brachyrhynchos</i>)	1	1	1	1	
Pacific Wren (<i>Troglodytes pacificus</i>)				1	
Varied Thrush (<i>Ixoreus naevius</i>)				1	
Thrush species (Turdidae)				1	
Spotted Towhee (<i>Pipilo maculatus</i>)				1	

Appendix 1. Continued.

FOOD ITEMS	FOOD-ACQUISITION TYPE				
	FEEDING: CARRION (<i>ObsCARRION</i>)	FEEDING: UNCERTAIN (<i>UncORIGIN</i>)	FEEDING CAPTURED PREY (<i>ObsPREY</i>)	PURSUING PREY: CAPTURED (<i>PREYCAP</i>)	PURSUING PREY OUTCOME UNCERTAIN (<i>HUNT</i>)
Fox Sparrow (<i>Passerella iliaca</i>)			1		
Golden-crowned Sparrow (<i>Zonotrichia atricapilla</i>)				2	
Dark-eyed Junco (<i>Junco hyemalis</i>)					1
Other					
Northern Flicker (<i>Colaptes auratus</i>)					1
Unidentified large birds (>100 g)	1	19	6	2	25
Unidentified small birds (≤100 g)			18	4	8
Unknown prey		5			
Total number of food items	49	44	77	46	154
Total number of taxa	19	14	21	17	10
Percent (number) of taxa unique to category	63 (12)	29 (4)	38 (8)	29 (5)	30 (3)