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PREY USE AND SELECTION IN RELATION TO REPRODUCTION BY PEREGRINE FALCONS BREEDING ALONG THE YUKON RIVER, CANADA

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Abstract.—Some raptors are considered to be generalist predators and switch among different species of prey according to their availability in the environment. In contrast, other raptor species are specialists with narrow dietary niche widths, selecting only one or a few types of prey; reproductive success in these species is often closely related to variability in abundance of preferred prey species. Determining whether raptors are generalist or specialist predators is important for understanding the degree to which fluctuations in their population sizes are influenced by individual responses to changes in prey availability. We assessed diet components based on prey remains collected at nest ledges to determine whether Peregrine Falcons breeding along the Yukon River in northern Canada were specialist feeders or, conversely, whether they took prey according to its relative abundance. We also examined whether the use of certain types of prey had consequences for reproductive success. Compositional analyses showed that peregrines exhibited nonrandom prey selection, with shorebirds, jays and thrushes, and waterbirds being used more than expected based on their abundance, whereas sparrows and other small passerines were used significantly less than expected. Similarly, medium-sized prey was selected by peregrines, but small (<50 g) and large (>1000 g) prey were used significantly less than expected. Pairs occupying territories in which the diet included large numbers of waterbirds, and few sparrows and small passerines, fledged more young. Although prey >1000 g were among the least selected by pairs in our study population, pairs that used these larger prey species fledged more offspring. These patterns may relate directly to the contribution of female parents to provisioning. Females that are able to capture large prey items may deliver larger amounts of biomass to their nests and, as a consequence, may have high reproductive output. We conclude that Peregrine Falcons in the Yukon are selective predators and that some of the variation in reproductive rates in this population may be attributed to variation in the types of prey available to and utilized by individual pairs.

Key Words: *Peregrine Falcon*; Falco peregrinus anatum; *compositional analysis*; *diet*; *foraging ecology*; *prey selection*; *reproductive rate.*

USO Y SELECCIÓN DE PRESAS EN RELACIÓN CON LA REPRODUCCIÓN EN *FALCO PEREGRINUS* EN ÁREAS DE CRÍA A LO LARGO DEL RÍO YUKON, CANADÁ

Resumen.—Se considera que algunas aves rapaces son depredadoras generalistas que cambian las especies que depredan de acuerdo a su disponibilidad en el ambiente. En contraste, otras especies de rapaces son especialistas con nichos alimenticios estrechos, que seleccionan sólo un tipo o pocos tipos de presas; el éxito reproductivo en estas especies frecuentemente se relaciona con la variabilidad en la abundancia de las

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especies de presas preferidas. Determinar si las rapaces son depredadoras generalistas o especialistas es importante para entender el grado al cual sus fluctuaciones en tamaño poblacional están influenciadas por las respuestas individuales a los cambios en la disponibilidad de presas. Evaluamos los componentes de la dieta con base en restos de presas recolectados en salientes de rocas donde había nidos para determinar si los *Falco peregrinus* que crían a lo largo del río Yukon en el norte de Canadá son especialistas dietarios, o si por el contrario consumen presas de acuerdo a su abundancia relativa. También evaluamos si el uso de ciertos tipos de presas tenía consecuencias para el éxito reproductivo. Los análisis de composición mostraron que los individuos exhibieron una selección de presas no aleatoria: las aves playeras, los córvidos, los túrdidos y las aves acuáticas fueron consumidas en mayor grado al esperado de acuerdo a su abundancia, mientras que los gorriones y otros paserinos pequeños fueron consumidos con menor frecuencia que la esperada. De modo similar, las presas de tamaño medio fueron seleccionadas, mientras que las pequeñas (<50 g) y grandes (>1000 g) se consumieron menos de lo esperado. Las parejas que ocupaban territorios en los que la dieta incluía números grandes de aves acuáticas, y pocos gorriones y paserinos pequeños, produjeron más volantones. Aunque las presas de más de 1000 g estuvieron entre las menos seleccionadas por las parejas en nuestra población de estudio, las parejas que usaron esas especies de presas más grandes produjeron más volantones. Estos patrones podrían relacionarse directamente con la contribución de las madres al aprovisionamiento. Las hembras que fueron capaces de capturar presas grandes podrían llevar mayores cantidades de biomasa a sus nidos, por lo cual podrían tener un alto rendimiento reproductivo. Concluimos que en el Yukon, *F. peregrinus* se comporta como un depredador selectivo y que parte de la variación de las tasas reproductivas en esta población podría ser atribuible a variación en los tipos de presas disponibles para, y utilizados por, las parejas individuales.

[Traducción del equipo editorial]

Food supply can have a wide range of effects on biological processes, including social behavior, home-range sizes, and patterns of foraging and dispersal (Whittingham and Robertson 1994, Burke and Nol 1998, Johnson and Sherry 2001, Andersson 2005, Wiebe 2005, Legagneux et al. 2009). Natural variation in food supply is also an important determinant of reproductive success in birds, affecting life-history traits such as the number and quality of young that parents are able to raise (reviews in Martin 1987, Boutin 1990). In addition, food availability can influence costs incurred by parents while provisioning offspring, which may have implications for the future survival and reproduction of parents (Martin 1995, Daan et al. 1996). Variation in the amount of food in the environment therefore can not only limit reproductive rate but ultimately has the potential to determine the demographics of avian populations (Newton 1998).

Among raptors, some species take prey in proportion to their relative abundance within the environment and so are considered to be opportunistic or generalist predators (Jaksić 1989). Such generalists typically have wide dietary-niche widths and respond functionally to changing prey availability by switching prey species and consumption rates. In contrast, some raptors selectively target certain types of prey, often those that are most energetically profitable, and are considered to be specialist predators (Jaksić 1989). Specialist predators are characterized by narrow dietary-niche widths and, as a result, production of young is often closely related to availability of preferred prey species (Newton 1979). Determining whether raptors are generalist or specialist predators is important for understanding the degree to which fluctuations in their population sizes are determined by how individuals respond to changes in prey availability (Newton 1979).

Peregrine Falcons (*Falco peregrinus*) are medium-sized birds of prey, and have one of the widest distributions of all avian species. Peregrines breed on every continent except Antarctica and on most major island chains with the exception of New Zealand and Iceland (Ratcliffe 1993). The global distribution of Peregrine Falcons is due, in part, to their correspondingly broad diet of predominantly avian species (Ratcliffe 1993). While sometimes described as generalist and opportunistic feeders (Newton 1979), Peregrine Falcons are also recognized as morphologically and behaviorally specialized predators in open environments (Cade 1982), and some populations and individuals are known to specialize on one or a few types of prey (reviewed in White et al. 2002).

We examined the relationships between productivity and the use, abundance, and selection of prey by individual pairs of Peregrine Falcons (*F. p. anatum*) breeding along the Yukon River, Yukon Territory, Canada. The heterogeneity of the landscape can result in spatial variation of food resources available to breeding individuals, which in turn can affect the production of young (Newton 1998, Krebs et al. 2001). Therefore, the variation in reproductive rate exhibited among individuals in a population may be the result of different prey availabilities on different territories (e.g., Dawson and Bortolotti 2000). Few avian studies have examined the relationship between reproductive rate and the food supply available on the territory in explaining reproductive variation among individuals in a population.

As in other areas (e.g., Ratcliffe 1993, Kirk and Hyslop 1998), densities of peregrines in the Yukon have surpassed those that occurred prior to the pesticide-induced population crash of the 1970s, but since the early 1990s reproductive output in this population has been highly variable (Mossop 2003, 2004). We were therefore interested in elucidating the potential roles of prey abundance and selection in determining reproductive variation of peregrines in the Yukon. Our study had three objectives: (1) to describe the diet of breeding Peregrine Falcons in our study area, (2) to determine whether peregrines were selective predators, or, conversely, whether they took prey according to its relative abundance, and (3) to examine whether observed patterns of prey selection were associated with variable reproductive success.

METHODS

Study Area and Nest Locations. We studied Peregrine Falcons breeding along a 200-km stretch of the Yukon River valley in the western Yukon Territory, Canada, in 2003 and 2004. The study area extended from the mouth of the Stewart River (63°N, 138°W) on the upstream side of Dawson City, YK, to Sheep Rock near the Alaska border (64°N, 140°W). This area is within the subarctic boreal forest, with major communities of black spruce (*Picea mariana*) forest, mixed spruce-deciduous forest, and riparian deciduous woodland (Rowe 1972). Past forest fires (1993, 1998) have left extensive burned areas, consisting of snags and little shrub cover, throughout the river valley. A large forest fire also burned extensive portions of the river valley in the study area in 2004.

Peregrine Falcons nested on cliff ledges along the river, with elevations of nests ranging from 30 to 300 ft above the river (Cade 1960), and there were approximately 50 nesting cliffs known to exist in the area prior to our study (Mossop 2003). After it became possible to navigate the river by boat in early May each year, we conducted surveys to determine whether nesting territories were occupied by Peregrine Falcons. The approach of an observer within the proximity of the nest usually elicited a nest-defense response from the resident pair (Fyfe and Olendorf 1976), and we used this criteria to define a territory as occupied. Once a territory was identified as occupied, we monitored pairs every week throughout the breeding season using a spotting scope from a distance of approximately 200–300 m from the nesting cliff to minimize disturbance (Nelson 1977). Territories were monitored to determine the exact location of a nest on the cliff ledge. After nests were located, we visited them in late May or early June to determine clutch size, and then again when young were approximately 30–40 d old to band offspring and collect prey remains. Clutch-initiation date was determined by estimating the hatching date of nestlings (using photographs of known-age nestlings; Clum et al. 1996) and backdating to account for the egg laying and incubation periods. We considered any young that survived to 40 d of age to have fledged (Cade 1960, Court et al. 1988).

Prey Abundance. To quantify the relative abundance of prey on individual nesting territories, during early June of each year we conducted avian prey counts at 15 different randomly selected territories: six in 2003 and nine in 2004. At each territory, we counted birds along two terrestrial transects and one river transect. The terrestrial transects were 1250 m long, oriented perpendicular to the river, with each transect located 1 km upstream or downstream from the nest site on the opposite shore. Counts were conducted every 250 m along the terrestrial transects using the variable circular-plot method (Reynolds et al. 1980). The initial point count began 100 m from the river shore and 6 points were sampled on each terrestrial transect. Each point count was a total of 6 min in duration and began 1 min after the observer arrived at the point. All birds encountered between points were recorded and their distances and angles from transects were estimated to eliminate duplicate counting of individuals. Terrestrial sampling began at 04:00 H and finished by 08:00 H. The river transect was censused from a drifting boat in each nesting territory to determine the relative abundance of birds in riverine/riparian areas (Hunter et al. 1988). River counts were conducted immediately following terrestrial counts at each territory, beginning at 08:00 H and finishing by 09:00 H. River transects began 1 km upriver of the nest site and ended 1 km past the nest, and all birds seen or heard on one side of the river were counted. Although peregrines in some populations have large hunting areas (e.g., Enderson and Craig 1997), the area sampled at each territory during our surveys was well within a radius of 3 km from the nest site, which is where the majority of foraging flights by Peregrine Falcons occur in our area (Hunter et al. 1988); thus, our data should provide a reasonable index of prey abundance on individual territories. In 2004 only, we performed a second count at the same territories approximately 2 wk after the first count to determine whether there was a significant temporal variability in prey abundance; the two prey counts did not differ from each other in terms of abundance for each species observed (Wilcoxon signed-ranks test, $P > 0.15$), so we averaged numbers of prey observed on each count, so that data would be directly comparable between years.

Prey Use. Prey use was determined from prey remains (Errington 1932, Oro and Tella 1995) collected from 13 nests sites in 2003 and from 12 different sites in 2004. We collected prey remains from nesting ledges in mid-July of each year, when the young were approximately 30–40 d of age. At each site, all prey remains in the vicinity of the nest were gathered, including those directly below the ledge and on all accessible perches. Prey remains were identified by comparing feathers, wings, feet, skulls, and other anatomical features with specimens from the University of Northern British Columbia and University of Alberta museum collections. All remains were identified to species, except for *Catharus* thrushes and *Empidonax* flycatchers which were identified to genus, and scaup species (*Aythya affinis* and *A. marila*), which were pooled. We identified the minimum number of individuals present in prey remains based on the most commonly found bone or body part representing one individual (Poole and Boag 1988). We also identified mammalian prey remains (*Tamiascuirus hudsonicus*, *Microtus* spp., *Peromyscus maniculatus*); however, these constituted a small percentage of the total prey (1.3%) and were thus excluded from further analysis. Although some authors have expressed concern about the utility of using prey remains or pellets to estimate diet in birds of prey (e.g., Oro and Tella 1995), there is often good agreement between direct observation of prey items and those found in prey remains (e.g., Collopy 1983, Mañosa 1994, Rosenfield et al. 1995). Furthermore, pellet analysis for falcons is problematic because bones are more completely digested in falcons than in some other pellet-producing species (Duke et al. 1975), and in our study pellets were not present at all ledges.

For each territory, we divided prey remains into eight prey-type classes on the basis of both taxonomic (family) and habitat associations (for example waterbirds included ducks, geese, and grebes). These prey classes were: shorebirds, waterbirds, woodpeckers, thrushes and jays, finches, sparrows, small passerines, and other birds. Warblers, flycatchers, and other small songbirds were combined into small passerines based on relatively similar size and habitat associations. The other birds group, which included raptors (Falconiformes and Strigidae), gulls (Laridae), ravens (Corvidae), and grouse (Phasianidae), accounted for species that were present in small numbers and not included in other classes. Using data found in Dunning (1993) for each species, we estimated mass for prey items to provide a coarse measure of the composition of prey biomass utilized by breeding Peregrine Falcons. For species that showed sexual size dimorphism, we used the average mass of the sexes. To examine the use of different-sized prey items in each territory, we separated prey remains into four biomass classes: <50 g, 51–250 g, 251–1000 g and >1000 g. Finally, we classified each potential prey item detected in surveys (above) into these same eight prey type classes and four biomass classes. Although our prey counts were conducted over a 2-wk period, and prey remains we collected at or near nests may have accumulated since the beginning of the breeding season each year, we assume that our prey counts were representative of the prey available to breeding pairs over the majority of the breeding season.

Selection Analysis. We used compositional analysis (Aitchison 1986, Aebischer et al. 1993) to test whether Peregrine Falcons in the Yukon showed patterns of prey selection for both biomass and prey classes. Compositional analysis compares matrices of log-ratio transformed use and availability proportions to detect nonrandom use of a resource and ranks resource classes from least selected to most selected. The overall test for selection relies on the likelihood ratio statistic Λ, where $-n * \ln(\Lambda)$ shows a chi-square distribution with $k - 1$ degrees of freedom (n is the sample size of animals and k is the number of resource classes), and t-tests are used to determine where nonrandom use occurs (Aebischer et al. 1993). As these tests used to evaluate significance can have elevated Type I error rates (see Thomas and Taylor 2006), significance in our analyses was determined using randomization tests as advocated by Pendleton et al. (1998). For instances where a particular prey or biomass class was not detected in prey remains, a value of 0.01 was used (Aitchison 1986, Aebischer et al. 1993). To ensure adequate sample size for the compositional analysis (Aebischer et al. 1993), we pooled data from both years of the study ($n = 15$ individual territories where both prey abundance and prey use were determined).

Prey Use and Reproductive Rate. To investigate whether patterns of prey use had consequences for reproductive output of peregrines in our study population, we first used correlation analysis to test for relationships between number of offspring fledged and diet diversity. We calculated Levins' diet diversity measure for prey classes used by breeding Peregrine Falcons, using the formula: $B = 1/\sum p_i^2$, where p_i is the proportion of prey class i in the diet (Levins 1968). The diversity measure was then standardized to a scale of 0 to 1, using Hurlbert's (1971) equation: $B_s = (B - 1)/(n - 1)$, where B is Levins' diversity measure and n is the number of categories ($n = 8$ prey classes). Indices of diet diversity were calculated using the prey classes for each territory with collected prey remains ($n = 25$). As expected, diversity increased with increasing numbers of prey that were collected at nests. To control for this in subsequent analyses, we used the residuals from a linear regression of diversity on number of prey items collected ($F_{1,23} = 4.47$, $P = 0.04$). Next, we used analysis of covariance (ANCOVA) to test whether number of offspring fledged could be predicted either by number of prey in each prey type or biomass class. We ran separate analyses using either prey type or biomass class as explanatory variables. We included year as a categorical explanatory variable and Julian date of clutch initiation as an additional covariate in our models.

Statistical analyses were performed using SPSS 13.0 (Norušis 2005) and SAS 9.1 (SAS Institute Inc. 2002). All tests are two-tailed and results were considered significant at the $P < 0.05$ level. Means are presented ±1 SE.

RESULTS

During 2003 and 2004, we monitored 42 and 51 territories, respectively, that were occupied by Peregrine Falcons along the Yukon River. We estimated clutch-initiation dates at a subsample of nests by backdating based on chick size (2003, $n = 30$; 2004, $n = 33$), and found no differences between years in timing of breeding ($F_{1,61} = 0.35$, $P = 0.55$). Clutch size ranged from 2 to 4 eggs, with the majority of birds having 3 or 4 eggs (94%, $n = 44$), and showed no annual differences (Mann-Whitney $U = 89.5$, $P = 0.13$). Also, clutch size did not decline with later dates of clutch initiation ($r_s = -0.08$, $n = 28$, $P = 0.68$). In 2003, 32/42 (67.7%) territories that were occupied produced at least one fledgling, whereas in 2004, 31/51 (60.8%) territories successfully produced a fledgling ($G_1 = 2.54$, $P = 0.11$). When we included data only from territories where we had evidence that birds laid eggs, we found that more offspring fledged in 2003 (2.35 ± 0.11, $n = 30$) than in 2004 (1.20 ± 0.11, $n = 33$; $F_{1,60} = 54.22$, $P < 0.001$), and the number of young fledged declined with the date that pairs initiated breeding during the season ($F_{1,60} = 7.68$, $P < 0.01$).

Prey Availability and Selection. During counts of prey abundance within territories of peregrines, we identified 1456 individuals belonging to 65 species in 2003 during the single survey, and an average 2262 individuals from 63 species during two surveys in 2004. Avian species weighing <50 g were the most commonly encountered prey in each territory. With the data from all years and all territories pooled, sparrows (Emberizidae) were the most abundant prey group, accounting for 25.2% of the total detections, followed by thrushes and jays (21.4%).

We identified 218 individuals representing 41 species and 223 individuals representing 48 species in 2003 and 2004, respectively, from the prey remains collected from perches and nesting ledges. There were no annual differences in number of prey items collected per territory (2003: 16.8 ± 0.96 items, $n = 13$ territories; 2004: 18.6 ± 1.00 items, $n = 12$ territories; $F_{1,23} = 1.70$, $P = 0.21$). American Robins (*Turdus migratorius*) were the most frequently used prey item (8.8%), followed by Gray Jays (*Perisoreus canadensis*, 6.8%), Varied Thrushes (*Ixoreus naevius*, 6.3%), Dark-eyed Juncos (*Junco hyemalis*, 5.2%) and Lesser Yellowlegs (*Tringa flavipes*, 5.0%). The prey classes most frequently collected as prey remains were the thrushes and jays (28.8%) followed by waterbirds (16.6%), and most prey were in the <50 g (30.8%) or 51–250 g (44.9%) biomass categories.

Compositional analysis indicated nonrandom selection of prey type classes by Peregrine Falcons ($\Lambda = 0.125$, $\chi^2 = 31.14$, df = 7, $P < 0.01$). Shorebirds, thrushes and jays, and waterbirds were identified as being most important in the diet of breeding Peregrine Falcons (Table 1), and pair-wise t-tests indicated differences in selection of these groups compared to both small passerines and sparrows (all $P < 0.02$),

Table 1. Simplified ranking matrix for Peregrine Falcons breeding along the Yukon River, Canada, based on a compositional analysis comparing prey classes utilized in each territory ($n = 15$) with the proportion of each class available within the territory. Each mean log-ratio difference in the matrix was replaced by its sign, with a triple sign indicating significant deviation from random selection ($P < 0.05$). For example, the ''+++'' in the cell for the Small Passerines column and Shorebirds row indicates that Shorebirds are selected significantly more often than are Small Passerines. Ranks range from least important (0) to most important (7) prey classes.

	PREY CLASS								
PREY CLASS	FINCHES	OTHER	SHOREBIRDS	SMALL PASSERINES	SPARROWS	THRUSHES AND JAYS	WATERBIRDS	WOODPECKERS	RANK
Finches		−	−	+	+	−	−	−	2
Other	+		−	+	+	−	−	+	4
Shorebirds	+	+		+++	+++	+	+	+	7
Small Passerines	−	−	− − −		+	− − −	− − −	−	1
Sparrows	−	−	− − −	−		− − −	− − −	−	0
Thrushes and Jays	+	+	−	+++	+++		−	+	5
Waterbirds	+	+	−	+++	+++	+		+	6
Woodpeckers	+	−	−	+	+	−	−		3

which were least important. Compositional analysis also indicated nonrandom selection of prey among the biomass classes ($\Lambda = 0.059$, $\chi^2 = 42.55$, df = 3, $P < 0.001$). The relative rankings of biomass classes from most to least important were 251–1000 g, 51–250 g, <50 g and >1000 g (Table 2). Pair-wise *t*-tests suggested no differences in selection between the 51–250 g and 251–1000 g classes ($P = 0.91$) but that both of these classes were selected more than either the <50 g or >1000 g classes (all $P < 0.01$).

Prey Use and Reproductive Output. We found no relationship between the total number of potential prey items detected on surveys and number of offspring fledged ($r = 0.01$, $n = 15$, $P = 0.97$). Similarly, there was no relationship between the number of prey items collected at nests and number of offspring fledged ($r = -0.06$, $n = 25$, $P = 0.78$); however, we did find that the average mass of prey items increased with larger brood sizes ($r = 0.81$, $n = 25$, $P < 0.001$). Diet diversity was also related to reproductive output of Peregrine Falcons, with pairs that fledged more offspring using a less diverse array of prey species ($r = -0.40$, $n = 25$, $P < 0.05$). When we used ANCOVA to examine how the number of prey in various prey-type classes was related to reproductive success, we found that pairs with more sparrows ($F_{1,17} = 9.27$, $P < 0.01$; Fig. 2) and other small passerines ($F_{1,17} = 3.99$, $P = 0.06$) in their diet fledged fewer young, and those with large numbers of waterbirds in their diet fledged higher numbers of offspring ($F_{1,17} = 9.63$, $P < 0.01$; Fig. 3). This analysis also indicated that more offspring fledged in 2003 than in 2004 ($F_{1,17} = 7.08$, $P = 0.02$), and that number fledged increased with earlier clutch-initia-

Table 2. Simplified ranking matrix for Peregrine Falcons breeding along the Yukon River, Canada, based on a compositional analysis comparing biomass class of prey utilized in each territory ($n = 15$) with the proportion of each class available within the territory. Each mean log-ratio difference in the matrix was replaced by its sign, with a triple sign indicating significant deviation from random selection ($P < 0.05$). For example, the ''+++'' in the cell for the <50 g column and the 51–250 g row indicates that prey in the 51–250 g class are selected significantly more often than are those in the <50 g class. Ranks range from least (0) to most important (3) biomass classes.

	BIOMASS CLASS				
BIOMASS CLASS	<50 g	51–250 g	251–1000 g	>1000 g	RANK
<50 g		− − −	− − −	+++	1
51–250 g	+++		−	+++	2
251–1000 g	+++	+		+++	3
>1000 g	− − −	− − −	− − −		0

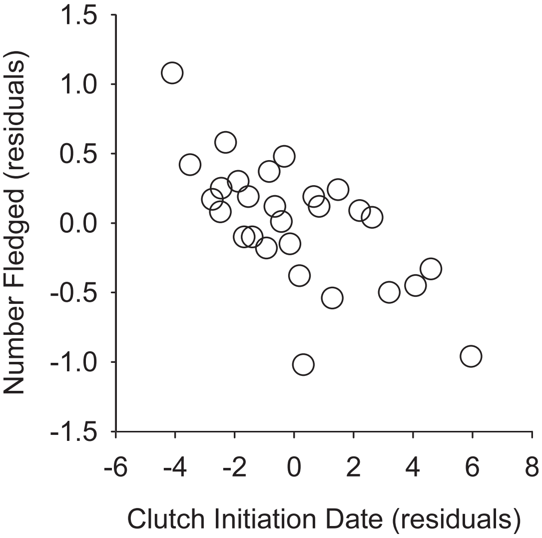

Figure 1. Number of offspring fledged by Peregrine Falcons breeding along the Yukon River decreases with later clutch-initiation dates. Plots are residuals of the independent variable and the residuals of the dependent variable when both variables are regressed separately on the other independent variables in the model (see Results).

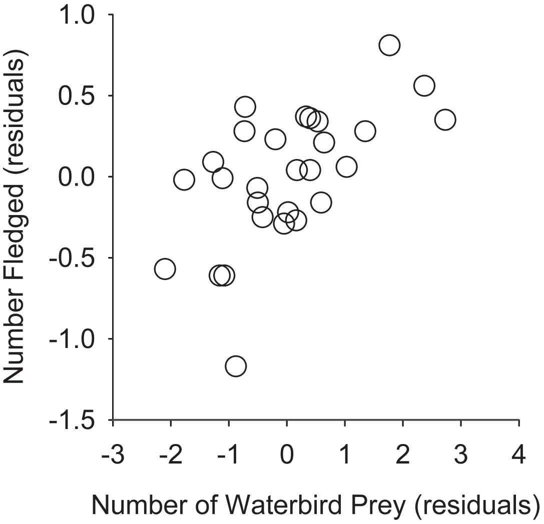

Figure 3. Relationship between number of offspring fledged and number of waterbirds in the diet of Peregrine Falcons along the Yukon River. Plots are residuals of the independent variable and the residuals of the dependent variable when both variables are regressed separately on the other independent variables in the model (see Results).

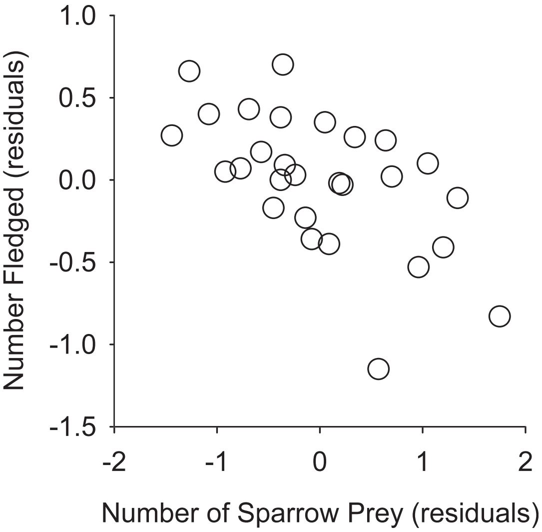

Figure 2. Peregrine Falcons breeding along the Yukon River fledge fewer offspring as the number of sparrows in their diet increases. Plots are residuals of the independent variable and the residuals of the dependent variable when both variables are regressed separately on the other independent variables in the model (see Results).

tion dates ($F_{1,17} = 13.95$, $P < 0.01$; Fig. 1). Number of young fledged was not influenced by the number of prey in any other prey type class (all $P > 0.55$). A second ANCOVA examining prey biomass showed similar results for year ($F_{1,21} = 4.55$, $P = 0.04$) and clutch-initiation date effects ($F_{1,21} = 3.10$, $P = 0.09$). The only biomass class to have an effect on reproductive output was the $>$1000 g class ($F_{1,21} = 8.29$, $P < 0.01$), which suggested that even though this type of prey was not selected by peregrines (Table 2), those that were able to utilize it had higher reproductive success (Fig. 4).

Discussion

Prey Use and Selection. It has been suggested that Peregrine Falcons in temperate environments are usually specialized predators, but as their environments become more extreme (e.g., tundra), peregrines become more generalized (Jenkins and Avery 1999). We showed that Peregrine Falcons breeding in the boreal environment of the Yukon did not use prey in accordance with its abundance but instead showed significant selection of several prey types (see also Olsen et al. 2008). Peregrines in our study area did not use small prey such as sparrows, finches, and other small passerines as fre-

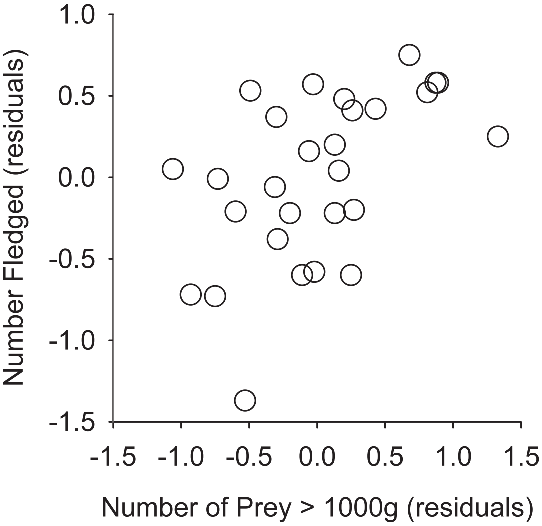

Figure 4. Relationship between number of offspring fledged by Peregrine Falcons breeding along the Yukon River and the number of prey items over 1000 g in their diet as determined from prey remains. Plots are residuals of the independent variable and the residuals of the dependent variable when both variables are regressed separately on the other independent variables in the model (see Results).

quently as expected, and showed significant selection of prey in the shorebird, waterbird, and thrushes and jays prey classes (Table 1).

White et al. (2002) suggested that one of the most important factors influencing whether certain prey types were selected by peregrines was the vulnerability of the prey. Although relative abundance of prey may influence its vulnerability (e.g., thrushes and jays in our study), habitat associations and behavior of the prey are likely also important. For example, prey that are habitat generalists (Gray Jays and American Robins), use open or riverine habitats (shorebirds, waterbirds), and perch near tree tops (Lesser Yellowlegs, American Robins) may be more vulnerable to predation by Peregrine Falcons in our study area. Prey such as sparrows and other small passerines may be more difficult to capture in or near cover (see also Hunter et al. 1988) and are less energetically valuable than larger species, so are less frequently taken.

Although it is possible that small prey are consumed whole and not detected in prey remains (Grønnesby and Nygård 2000), our results indicated that prey weighing <50 g were used significantly less than expected based on their abundance (Table 2). Similarly, large prey (over 1000 g) and medium-sized prey (>50 g but under 1000 g) were the least and most selected prey, respectively (Table 2). Male peregrines capture the majority of prey items brought to the nest during the breeding season (Cade 1982) and the body mass of male peregrines (652 g in the Yukon; White et al. 2002) relative to prey items may explain these results. Cade (1982) hypothesized that the range in mass of prey most commonly taken is related to the aerodynamic characteristics of peregrines and their ability to strike and hold potential prey items. Studies have shown that male peregrines hunt medium- and small-sized birds more successfully than do the larger females (977 g; White et al. 2002), presumably due to the male's smaller size and greater aerial maneuverability (Andersson and Norberg 1981, Thiollay 1988, Jenkins 2000). Larger prey items, such as waterfowl, generally do not appear in the diet of nestlings until the female begins to forage (Rosenfield et al. 1995) after the young have reached thermoregulatory independence (about 21 d; Enderson et al. 1972). Although the ability of individual females to capture large prey can have dramatic implications for the amount of biomass brought to nests, the fact that all prey and biomass groups were utilized to some extent in our study suggests that Peregrine Falcons can be quite flexible in meeting the nutritional requirements of nestlings.

Reproductive Output and Prey Use. We found no decline in clutch size but we did find declines in reproductive output as the breeding season progressed. These findings suggest that there are few energetic constraints on the ability of female peregrines to form eggs, but that some pairs have difficulty raising offspring as the season progresses. Declines in reproductive output with later breeding is often attributed to poorer quality or younger individuals breeding later in the season, or because of seasonally deteriorating environmental conditions such as food availability (review in Verhulst and Nilsson 2008). As we did not trap adult peregrines, we were unable to assess the importance of individual quality in influencing the patterns that we detected. Moreover, our study was not specifically designed to investigate seasonally decreasing reproductive success, and so the underlying mechanisms that were responsible remain unknown.

We found no relationship between the number of prey items detected on surveys and the number of young fledged by Peregrine Falcons. Nonetheless, those pairs that had fewer sparrows (Fig. 2) and more waterbirds (Fig. 3) in their diet were able to raise larger numbers of offspring to fledging. These two results may suggest that the overall abundance of prey on a territory is relatively unimportant, but rather that species composition may be critical for reproductive success. Olsen et al. (2008) found that when the main prey (European Starlings [*Sturnus vulgaris*] and Silver Gulls [*Larus novaehollandiae*]) of Australian peregrines (*Falco peregrinus macropus*) decreased in abundance, they compensated by switching to a larger variety of other prey species. In our population, peregrines might similarly be compensating when few of their most preferred prey, shorebirds, are available on their territory by relying on a larger diversity of smaller prey, such as sparrows, with the consequence that fewer offspring are fledged (Fig. 2). Indeed, we found that diet diversity increased among pairs that had smaller brood sizes.

The average biomass of prey collected at or near nests of Peregrine Falcons along the Yukon River increased with brood size. Many previous investigations have shown that while larger birds such as waterfowl can be relatively rare in the diet of peregrines, such prey made up a large amount of biomass brought to nests (e.g., Cade et al. 1968). Palmer et al. (2004) also found that larger prey were brought to larger broods of peregrines. Our selection analysis showed that within our study population of peregrines, prey items >1000 g were the least selected biomass class (Table 2), but our subsequent analyses revealed that pairs with larger numbers of these heavy prey items in their diet had greater reproductive success (Fig. 4). Although males may be able to kill large prey, they may not be able to physically carry it to their nests. Instead, these large prey items are probably captured and brought to the nest by females. For example, Court et al. (1988) showed that although passerines were an important prey group for peregrines at Rankin Inlet, NT, Canada, waterfowl were also used but only once the female began to hunt. The relationship between the use of large prey items and brood size in our study might suggest that rather than overall numbers of prey, the amount of biomass that parents bring to the nest is a determinant of reproductive success. If so, then in addition to the ability of individual females to capture these large prey items, the availability of these prey within a territory would be important. Female falcons tend to remain close to the nest site (Nelson 1977), and an abundance of large prey types (e.g., waterbirds) proximal to the nest site would be beneficial in meeting the nutritional requirements of larger broods. Different regions along the river valley may be more favorable as staging and nesting areas for waterbirds than other areas, so surveys of such prey along the river may be an indicator of the quality of individual territories.

Conclusions. We showed that Peregrine Falcons in the Yukon were selective feeders, preferring shorebirds, waterbirds, and thrushes and jays. Pairs showed selection for medium-sized prey, and used both small (<50 g) and large prey (>1000 g) less than expected based on the abundance of these prey types. The use of various prey types also was related to reproductive output, with those pairs having few sparrows and more waterbirds in the diet having greater reproductive success. Interestingly, although prey >1000 g were the least selected prey by pairs in our population, those pairs that used such prey fledged more offspring. We suggest that these patterns related directly to the contribution of individual females to provisioning; females that are able to capture these large prey items may be able to deliver larger amounts of biomass to their nests, and, as a consequence, may have high reproductive output. In contrast, when individual females lack the ability to subdue large prey, or when such prey is unavailable, pairs must instead rely upon smaller prey such as sparrows that yield comparatively little energy for growing young and so such females have smaller brood sizes.

Our study supports the idea that food supply is an important determinant of reproductive output in the Yukon's Peregrine Falcons and may potentially be responsible for some of the recent fluctuations in productivity in this population. The abundance of shorebirds in the Yukon declined precipitously over the same decade when variable reproductive output of peregrines was observed (D. Mossop unpubl. data), further implicating food resources as being important. Nonetheless, other factors such as weather, nest-site quality, and individual quality also are probably important influences, and their effects may not act independently from food. Further research is needed to fully understand the factors influencing variable reproductive success in this population of Peregrine Falcons.

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