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SUMMER DIET OF THE PEREGRINE FALCON IN FAUNISTICALLY RICH AND POOR ZONES OF ARIZONA ANALYZED WITH CAPTURE-RECAPTURE MODELING

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Abstract. We collected prey remains from 25 Peregrine Falcon *(Falco peregrinus)* territories across Arizona from 1977 to 1988 yielding 58 eyrie-years of data. Along with 793 individual birds (107 species and six additional genera). we found seven mammals and nine insects. In addition, two nestling peregrines were consumed. We found a larger dependence upon White-throated Swifts *(Aeronautes saxatalis)* and birds on migration in northern Arizona, while in southeastern and central Arizona average prey mass was greater and columbiforms formed the largest dietary component. In northern, central, and southeastern Arizona, 74, 66, and 56 avian prey taxa, respectively, were recorded. We used capture-recapture modeling to estimate totals of 111 ± 9.5, 113 ± 10.5, and 86 ± 7.9 (SE) avian taxa taken in these same three areas. These values are counterintuitive inasmuch as the southeast has the richest avifauna. For the entire study area, 156 ± 9.3 avian taxa were estimated to be taken by peregrines.

Key words: Arizona, diet, Falco peregrinus, *Peregrine Falcon, prey.*

Dieta Estival de *Falco peregrinus* en Arizona Cornparando Zonas Ricas y Pobres en Avifauna Mediante un Modelo de Captura-Recaptura

Resumen. Desde 1977 a 1988 colectamos restos de presas en 58 nidos de *Falco peregrinus* a través de Arizona. Conjuntamente con 793 aves individuales (107 especies y seis géneros adicionales), encontramos siete mamiferos y nueve insectos. Además, fueron consumidos dos pichones de *Falco peregrinus.* En la zona norte encontramos una mayor dependencia sobre *Aeronautes saxatalis* y aves en migración, mientras que en las zonas sureste y central la masa promedio de presa fue mas grande y los columbiformes constituyeron el componente principal de la dieta de *Falco peregrinus.* En las zonas norte, central y sureste se registraron 74, 66 y 56 taxa de aves presa, respectivamente. Para estimar el ndmero total de taxa capturados por *Falco peregrinus* usamos un modelo de captura-recaptura. Los valores calculados fueron 111 ± 9.5, 113 ± 10.5 y 86 ± 7.9 (EE) taxa para las zonas norte, central y sureste, respectivamente. Estos valores no reflejan los que esperabamos, ya que la zona sureste tuvo una avifauna más rica. Se estimó que 156 ± 9.3 taxa fueron capturados por *Falco peregrinus* en la totalidad del área de estudio.

INTRODUCTION

With the exception of the Barn Owl (*Tyto alba*; Clark et al. 1978, Marti 1988), perhaps more data have been collected on diet for the Peregrine Falcon (*Falco peregrinus*) than for any other raptor (Ratcliffe 1980, Porter et al. 1987, White et al. 2002). Unlike the Barn Owl, which concentrates on one or a few species of locally abundant small mammals, the peregrine usually takes a wide variety of prey, except when nesting on islands and feeding on seabirds (e.g., An-

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STATISTICAL ANALYSIS

Proportion of prey by numbers. To test if avian prey taxa were taken in similar proportions across the three regions, we used a log-linear model (McCullagh and Nelder 1989) implemented in the statistical package GenStat (Payne et al. 1993). A log-linear model is an example of a generalized linear model where the log of the expectation of a count (μ) is related to a sum of covariate effects, just as in ordinary regression analysis (including ANOVA): $\log(\mu_{ijk}) = a + b\,(taxon_i) + c\,(region_j) + d\,(taxon \times region_{ij}) + e_k$. A significant interaction $taxon \times region_{ij}$ would indicate that the distribution of taxa taken as prey is not the same across the three regions. As in ordinary ANOVA, this interaction can be partitioned into contrasts to further study differences among regions.

To avoid having low frequencies of occurrence invalidate the analysis (i.e., for species detected as prey only once or a few times), we pooled taxa into the following groups: Anatidae (ducks only); Odontophoridae (quail only); Threskiornithidae (White-faced Ibis [Plegadis *chihi*] only); Falconiformes (Sharp-shinned Hawk and American Kestrel only); Rallidae; small shorebirds (20–100 g); large shorebirds (>100 g); Laridae; Columbidae; Strigidae; Caprimulgidae; Apodidae; Trochilidae; Picidae; Corvidae; Alaudidae (Homed Lark [Eremophila alpestris] only); Hirundinidae; bluebirds (Sialia spp.); Orioles (*Icterus* spp.); Icteridae (excluding orioles); other small Passeriformes (5–30 g); and other mid-sized Passeriformes (31–100 g).

Estimating the variety of prey taken. Because our collections constitute only a sample of the prey taken by peregrines in Arizona and because of imperfect detectability, not every taxon actually taken appears in our samples. This condition results in an underestimate of prey richness, and this underestimate is inversely proportional to the size of the prey list.

To compensate for this undersampling bias, we used capture-recapture modeling. This approach assumes that not all species actually taken will show up in prey lists, but that the empirical species-abundance distribution contains information about the probability with which a species will be detected. Because there were no repeated sampling occasions in our study (i.e., only one sample was taken from an eyrie in any year), we used the limiting form of the jacknife estimator (Burnham and Overton 1979) of the widely used heterogeneity model M_h (Otis et al. 1978) implemented in program SPECRICH (Hines et al. 1999) to estimate the total number of avian taxa taken in each zone as well as across Arizona. Although this is a new application of capture-recapture modeling, similar modeling has been used many times to estimate the size of animal populations (Otis et al. 1978, Burnham and Overton 1979, Boulinier et al. 1998). Our estimates for prey taken in each region are provided as estimates ± SE with significance level set at 0.05.

Proportion of prey by mass. We assigned published values (Dunning 1993) of average adult mass for species recorded as prey. This practice ignores the fact that juveniles, often taken as prey, typically weigh less than adults. Therefore, this practice overestimates biomass (Rosenfield et al. 1995) but would not affect prey variety and should have a minimal effect on our comparisons between zones.

RESULTS

TOTAL NUMBER OF TAXA TAKEN

Our list of prey taken for all of Arizona (Appendix) included 113 avian taxa (i.e., 107 species, plus six additional genera that could not be identified to species), three species of mammals, and three insect taxa. For the entire study area, capture-recapture modeling estimated that 156 ± 9.3 avian taxa were taken by peregrines during the study period. In our lists, we recorded 113 species, 72% of this value. Comparing the estimated total prey taxa taken in Arizona with our list of potential prey taxa, we estimated that peregrines preyed on 71% (156 of 221) of the total available avian prey taxa.

In the northern, central, and southeastern zones, we recorded 73, 66, and 55 avian prey taxa, respectively. Using capture-recapture modeling, we estimated that 111 ? 9.5, 113 + 10.5, and 86 ± 7.9 avian taxa were taken in these same three zones. This suggests that among the available avian taxa (Table 1), peregrines in northern, central, and southeastern Arizona preyed on 67%, 56%, and 42% of the available avian taxa, respectively.

PREY USE BY NUMBER AND MASS

In Arizona, the three most common groups of birds taken were swifts, columbids, and shorebirds (Table 2). Although White-throated Swifts were consistently important in the diet by numcient Murrelets [Synthliboramphus antiquus], Nelson 1990; Heermann's Gulls [Larus heermanni], Velarde 1993).

In Arizona, incidental records of peregrines were recorded by various ornithologists from 1884–1975 (Ellis and Monson 1989). Organized studies of the Peregrine Falcon began in Arizona in 1975 (Ellis 1988). An intensive survey of old sites (begun in 1975) and a search for new eyries (begun in 1977) documented a general trend toward reoccupancy and high productivity (Ellis and Glinski 1988, Brown et al. 1992). This finding is consistent with moderate pesticide levels for prey and minimal eggshell thinning (Ellis et al. 1989).

In this long-term study, we compared dietary differences for three regions of Arizona, including southeastern, where the diversity of avian prey is 20% greater than for northern Arizona (Table 1). We also make a new application of capture-recapture models to adjust for differential undersampling bias resulting from prey lists that vary greatly in size.

TABLE 1. Number of bird species that are potential Peregrine Falcon prey in three zones of Arizona.

Zone	Breeders	Migrants	Total species
North	112	54	166
Central	150	52	202
Southeast	140	67	207

METHODS

For this study, we included Arizona and a narrow swath of habitat in New Mexico and Utah where peregrines nesting within those states must, at least sometimes, hunt in Arizona. Because no Peregrine Falcons were known to breed along the lower Colorado River or elsewhere in southwestern Arizona during the study, we gathered diet only for northern, central, and southeastern Arizona, three broad geographic zones (see map in Ellis 1988) based on topography and vegetation (Brown and Lowe 1980). The northern zone consisted of the canyons and mesas of the Colorado Plateau including the drainages of the Virgin, Colorado, Little Colorado, San Juan, and Paria Rivers with their myriad associated canyons. The central zone consisted of a broad swath of forests and mountains in the topographically complex region dropping away south and west from the Mogollon Rim and lying north of the Gila River. The southeastern zone consisted of basin-and-range habitats with conifer- and live oak-covered mountain ranges surrounded in the east by Chihuahuan Desert grasslands and in the west by Sonoran Desert plant communities.

POTENTIAL PREY

To measure food preference, we must compare what is actually taken with what is available. For this purpose, we assembled lists of likely prey species in each zone. Because the largest prey item we collected in Arizona was a Northern Pintail (*Anas* acuta, 1011 g, Dunning 1993) and because Paine et al. (1990) found that the largest prey for peregrines at Tatoosh Island, Washington, was the Common Murre (Uria aalge; 1010 g), we used 1100 g as the upper limit for prey. The smallest birds found as prey in the eyrie middens were two species of hummingbirds (Black-chinned Hummingbird [Archilochus alexandri] 4 g, and Broad-tailed Hummingbird [*Selasphorus* platycercus] 3 g). Hummingbirds are so small and were so seldom taken (n = 3) that they were judged unimportant in the diet, by either number or mass, and excluded from our lists of potential prey in each zone. Our lists included all species (except as stated below) lying between 5 g and 1100 g. To avoid inflating our list, we excluded rare or accidental birds, even if they appeared once or twice as prey. We also excluded owls (except the diurnal Burrowing Owl [Athene cunicularia]) and all but the smallest Falconiformes (i.e., we included only the American Kestrel [Falco *sparverius*] and the Sharp-shinned Hawk [Accipiter *striatus*]). Larger raptors were excluded because attacks on them were considered territorial defense, not predation. Nestling peregrines (recorded as prey twice; Ellis, Oliphant, and Fackler 2002) were likewise excluded from our analyses as not having been captured elsewhere and brought to the eyrie. Cannibalization of young peregrines has occasionally been reported (White and Cade 1971, Court et al. 1988, Bradley and Oliphant 1991).

In compiling potential prey lists, we included only prey which were likely to have been taken during the breeding season (1 March to 1 August). The birds present within this time frame were divided into two categories: breeding birds (including both resident breeders and migratory breeders) and migrants. Table 1 provides totals of potential prey species for the Peregrine Falcon in the three zones. As expected, the list for northern Arizona was much smaller (i.e., the avifauna was less diverse) than the list for the southeast. However, contrary to our expectations, the central Arizona list was nearly as large as for the southeast (Table 1). It might appear that these latter two zones could be combined, but the actual species in these zones were different enough that we decided to treat the two zones separately.

PREY SAMPLING

We collected Peregrine Falcon prey remains for 58 eyrie-years representing 25 territories from 1977 through 1988. Of these, 21, 20, and 17 eyrie-years were from the northern, central, and southeastern zones, respectively. Because some sites had no young in some years (Ellis 1988), and because some eyries were under overhung ledges and others were on inaccessible spires (Ellis 1982), only a few sites were sampled in any one year (mean 5.3 sites per year, range = 1–10), and the number of times a site was sampled during the study varied from 1–6 (mean 2.3 ± 1.0 [SD] samples). Of 18 sites sampled more than once, the interval between samples at the same site ranged from 1–4 years (mean 1.8 ± 1.2 years). We visited eyries only after the young had fledged to avoid adversely affecting reproduction of this endangered subspecies (F. p. *anatum*; now listed as threatened).

Feather remains were analyzed using reference collections at the University of Arizona, the U.S. National Museum (Smithsonian Institution), and the Western Foundation for Vertebrate Zoology. Nearly all bones were identified using the collection at the San Diego Natural History Museum and the A. M. Rea collection (now at the University of New Mexico, Albuquerque). Insects were identified only to family as suggested by Rosenberg and Cooper (1990).

For prey identification purposes, we prepared a series of flat skins (i.e., skins with minimal body stuffing and with the tail and one wing spread). Comparisons of feather patterns, especially in the wing, were thereby facilitated and damage to the reference specimen minimized. Our methods of identifying prey were described by Ellis, Sabo et al. (2002). To prevent loss of sample feathers and for ease in handling, we recommend use of a hemostat to grasp a feather when comparing it with a series of museum specimens.

In documenting food habits, we collected most items from eyries, but some prey items were gathered from plucking perches in the immediate vicinity of an eyrie. However, only those items were counted for which enough material was present, or for which feathers showed bill marks, to indicate that the material was indeed falcon prey. For example, although molted raven (*Corvus* corax or *C.* cryptoleucus) feathers were frequently found beneath cliffs used by peregrines, the only raven tabulated as prey was represented by a sizable tuft of feathers connected by flesh and found directly in one eyrie. Also, White-throated Swift (Aeronautes *saxatalis*) feathers were regularly found (sometimes copiously) at the base of some eyrie cliffs: all of these we ignored.

One peregrine eyrie was evidently used previously by Spotted Owls (Strix occidentalis): others had been used by ravens or Prairie Falcons (Falco mexicanus). To avoid the risk of tabulating as prey an item which was collected in an earlier year by another species, the bony remains found in falcon eyries were counted only if they showed clinging tendons or flesh, evidence of their having been depredated during that breeding season. Bony remains from a particular species were subtracted from the feather remains of that species (or vice versa) to avoid counting an individual twice.

When a large number of feathers in one eyrie sample were attributed to one species, we used diagnostic feathers, bills, or feet to determine the minimum number of individuals present. For doves and swifts, the outermost left or right primary most often provided our minimum count.

Regurgitated pellets found in the eyries were not analyzed in this study. Our primary reason for not using pellets was that five pellets may represent one prey item fed to five young. Also, it is easier to identify a prey species from clean feathers than from a regurgitated pellet. Further logic for not using pellet analysis is that vegetable and insect remains often found in pellets may actually come from the stomach contents of avian prey, not from insects captured by the falcons. In fact, the only insects tallied in our lists were those for which large wings or large legs were found intact in the eyries.

TABLE 2. Proportions of avian groups commonly found in the diet of Peregrine Falcons. Of the total, 793 items statewide, 390 were from northern, 194 from central, and 209 from southeastern Arizona. Numbers are minimum counts of individuals recovered from eyries and plucking perches. Values for mass are from Dunning (1993).

Taxonomic Group	North			Central			Southeast		
	n	% by number	% by mass	n	% by number	% by mass	*n*	% by number	% by mass
Anatidae	1	<1	1	3	2	10	1	<1	2
Odontophoridae	0	0	0	2	1	2	2	1	2
Threskiornithidae	2	<1	3	0	0	0	0	0	0
Falconiformes[a]	5	1	2	4	2	2	2	1	1
Rallidae	4	1	5	2	1	3	0	0	0
Shorebirds, 20–100g	11	3	1	1	<1	<1	3	1	1
Shorebirds, > 100g	30	8	26	4	2	5	5	2	5
Laridae	6	2	6	3	2	3	0	0	0
Columbidae	53	14	22	52	27	45	77	37	56
Strigidae	0	0	0	1	<1	<1	1	<1	<1
Caprimulgidae	7	2	1	1	<1	<1	4	2	1
Apodidae	102	26	9	37	19	5	33	16	5
Trochilidae	1	<1	<1	1	<1	<1	1	<1	<1
Picidae	11	3	3	15	8	7	10	5	5
Corvidae	26	7	7	12	6	6	10	5	9
Alaudidae	14	4	1	3	2	<1	4	2	<1
Hirundinidae	9	2	<1	5	3	<1	6	3	1
Turdidae									
Bluebirds (*Sialia* spp.)	11	3	<1	4	2	<1	1	<1	<1
Icteridae									
Orioles (*Icterus* spp.)	0	0	0	3	2	<1	3	1	<1
Other Icteridae	0	0	0	2	1	1	1	<1	<1
Other Passeriformes, 5–30 g	43	11	2	11	6	<1	17	8	2
Other Passeriformes, 30–100 g	45	12	8	21	11	6	22	11	8
Unidentified birds	9	2	<1	7	4	2	6	3	<1

[a] Excludes 2 cannibalized nestling peregrines.

ber (26%, 19%, and 16% in the north, central, and southeast, respectively), they made up only 5–10% of the diet by biomass. By far the most important family by mass for the three zones combined was Columbidae. Columbids were most important by numbers in the central and southeastern zones. In the north, large shorebirds were most significant in the diet by mass, a fact reflecting a greater dependence on migrants.

Prey importance by number. There were 390, 194, and 209 items recorded in the northern, central, and southeastern zones, respectively. Prey taxa were not taken in even proportions in the northern, central, and southeastern zones (log-linear analysis: *taxon* × region interaction, $\chi^2_{42} = 114.2$, $P < 0.001$). When we further partitioned this interaction by combining zones, we found that the north + central versus southeast contrast contributed $\chi^2_{21} = 52.9$, while the north versus central + southeast contrast contributed $\chi^2_{21} = 94.1$ to the total chi-square. This indicates that central and southeastern zones were more similar in terms of the distribution of peregrine prey among taxa than were northern and central Arizona.

A comparison of observed and expected number of captures per taxon group and zone (Table 3) shows that in northern Arizona, Rallidae, small and large shorebirds, Laridae, Apodidae, Alaudidae, and Turdidae among others, were more frequently taken than the average for all of Arizona. In central Arizona, the following taxa were most prominent: Anatidae, Falconiformes, Columbidae, and Picidae. In southeastern Arizona, Columbidae, among others, was prominent.

Prey importance by mass. Ignoring taxonomic group and focusing only on mass, significantly heavier prey were caught in the central and southeastern zones than in northern Arizona (ANOVA, $F_{1,792} = 6.1$, $P = 0.002$). Mean mass of prey caught was 56.6 g (95% CI: 50.6–63.5) in the north, 72.4 g (95% CI: 61.5–85.1) in the central zone, and 70.6 g (95% CI: 60.4–82.4) in the southeast. Here, once again, central and southeastern Arizona were more similar than were the northern and central zones.

By mass, Columbidae was the most important taxon in the central and southeastern zones and was second in importance in northern Arizona, where shorebirds made the greatest contribution to total prey mass. Other prey taxa important in the north were Laridae, Rallidae, and Threskiornithidae (Table 2). In central Arizona, Columbidae contributed 46% of the biomass, with Anatidae and Picidae also important. In the southeast, Corvidae was second, but far behind Columbidae. Across Arizona, the most important taxa by mass, in order of increasing importance, were Laridae, Rallidae, Anatidae, Picidae, Apodidae, Corvidae, large shorebirds, and Columbidae, with columbids representing over 40% of prey mass.

DISCUSSION

METHODS OF COMPILING PREY LISTS

Each method of gathering dietary information has advantages and disadvantages (Rosenberg and Cooper 1990, Redpath et al. 2001, Booms and Fuller 2003). Where direct observations of hunting are not available, pellet analysis may be necessary to estimate the importance of insects and small mammals (Bradley and Oliphant 1991, Morimando et al. 1997). Another potential bias in dietary studies using prey remains is that rare items can be overemphasized. For example, 1000 swift feathers from 100 individuals may tally only 10 birds, but one bluebird feather will tally one bluebird. Remnants of rare birds, rather than being discarded, are emphasized. For example, the first Arizona specimen record for the Common Grackle (Quiscalus quiscula) was recovered from a peregrine eyrie (LaRue and Ellis 1992), just as the first specimen record for the Wood Lark (*Lullula* arborea) on the Isle of Man was a presumed peregrine kill (Oxenham 1979).

Surely the most accurate method for assessing the diet of breeding raptors would be to follow the adults and observe the species and size of prey taken. But following a predator long term is nigh impossible logistically. We know of only one such study; White and Nelson (1991) used a helicopter to follow two peregrines and two Gyrfalcons (Falco *rusticolus*) on hunting forays. Another way to lessen sampling biases is long-term observations from very near the eyries (including the use of videocameras). This method should more accurately show the importance of nestling birds in the diet (as found for peregrines, Rosenfield et al. 1995; and Gyrfalcons, Booms and Fuller 2003). As an alternative, data can be taken from lengthy watches at prey concentration sites (Dekker 1980, 1999). However, some bias is also associated with these labor-intensive methods. Most of the literature on rap-

TABLE 3. Proportions of avian taxa in prey remains of Peregrine Falcons in three zones of Arizona. Excepted number of occurrences are based on a log-linear model that assumes prey are caught in equal proportions in the three regions of Arizona. Discrepancy is the percent difference between observed and expected captures and shows percent over or underrepresentation of a taxon in a region relative to the expectation when lumping all three zones.

Taxonomic group	North			Central			Southeast		
	Observed[a]	Expected[a]	Discrepancy (%)	Observed[a]	Expected[a]	Discrepancy (%)	Observed[a]	Expected[a]	Discrepancy (%)
Anatidae	1	2.5	–60	3	1.2	147	1	1.3	–24
Odontophoridae	0	2.0	–100	2	1.0	106	2	1.1	90
Threskiornithidae	2	1.0	102	0	0.5	–100	0	0.5	–100
Falconiformes[a]	5	5.4	–8	4	2.7	50	2	2.9	–31
Rallidae	4	3.0	35	2	1.5	37	0	1.6	–100
Shorebirds, 20–100g	11	7.4	48	1	3.6	–73	3	4.0	–24
Shorebirds, >100g	30	19.3	56	4	9.5	–58	5	10.3	–51
Laridae	6	4.5	35	3	2.2	37	0	2.4	–100
Columbidae	53	89.9	–41	52	44.1	18	77	47.9	61
Strigidae	0	1.0	–100	1	0.5	106	1	0.5	90
Caprimulgidae	7	5.9	18	1	2.9	–66	4	3.2	27
Apodidae	102	85.0	20	37	41.7	–11	33	45.3	–27
Trochilidae	1	1.5	–33	1	0.7	37	1	0.8	27
Picidae	11	17.8	–38	15	8.7	72	10	9.5	6
Corvidae	26	23.7	10	12	11.6	3	10	12.6	–21
Alaudidae	14	10.4	35	3	5.1	–41	4	5.5	–28
Hirundinidae	9	9.9	–9	5	4.9	3	6	5.3	14
Turdidae									
Bluebirds (*Sialia* spp.)	11	7.9	39	4	3.9	3	1	4.2	–76
Icteridae									
Orioles (*Icterus* spp.)	0	3.0	–100	3	1.5	106	3	1.6	90
Other Icteridae	19	17.8	7	8	8.8	–8	9	9.5	–5
Other Passeriformes									
5–30 g	43	33.6	28	11	16.5	–33	14	18.0	–22
31–100 g	26	28.7	–9	15	14.1	7	17	15.3	11

[a] Units are number of individuals.

tor food habits derives from methods known to be biased (namely, pellet analyses and prey remains from eyries; Sherrod 1978). Some studies have even relied only on materials collected at the base of breeding cliffs (Oro and Tella 1995).

Prey remains sometimes adequately document the proportion of each prey species in the diet of certain raptors (e.g., Collopy 1983, Golden Eagle [*Aquila chrysaetos*]). Other studies suggest that prey remains alone are inadequate; see Simmons et al. (1991) for the African Marsh-Harrier (Circus ranivorus), Bielefeldt et al. (1992) for the Cooper's Hawk (Accipiter cooperii), Redpath et al. (2001) for the Hen Harrier (*C.* cyaneus), Booms and Fuller (2003) for the Gyrfalcon, and Marti (1987) for a general discussion. For the Peregrine Falcon in Greenland, Rosenfield et al. (1995) found similar frequencies and rankings for six major prey species when prey remains were compared to direct observations of prey deliveries. However, they noted that prey remains frequently did not adequately show the age of the prey (with the result of skewing biomass estimates too high through the use of adult weights). Although this bias is present in our study, we believe that we achieved good zonal comparisons in both the biomass and the variety of avian prey in the diet of the Peregrine Falcon in Arizona from prey remains. We are confident, however, from direct observations of hunting behavior (Ellis and LaRue, unpubl. data), that insects and bats are grossly underrepresented in our samples. As a result, our regional comparisons must be viewed as predation rates for avian prey only.

Our analysis was strengthened by the fact that feather and osteological remains were almost always (98% of the time) identified to species. Greene and Jaksić (1983) found that a precise level of prey identification (to the generic or specific level) versus ordinal identification (to family level only) was necessary to accurately represent food-niche parameters. They also suggested that taxonomic identification of prey items is more relevant than size class in documenting competitive interactions among predators.

ESTIMATION OF THE TRUE LENGTH OF PREY LISTS

As far as we are aware, this is the first application of capture-recapture modeling to estimate the total number of taxa taken by a raptor and to properly deal with unequal probability of taxa being included in prey lists of different lengths. In our study the concept of trapping occasions was not important; we used instead the frequency with which each taxon was captured. From this, an estimator of a widely used, closed-population, capture-recapture M_h model was computed (Burnham and Overton 1979). In other studies, a sampling occasion might be defined as an individual eyrie visit, or a sample may be all prey gathered in a year. More sophisticated models may allow for the inclusion probability to vary by occasion, or may directly estimate the number of species that are common to prey lists for two regions (using the methods of Boulinier et al. 1998, Nichols et al. 1998).

PREY CLASSES

The preponderance of birds in the diet of the Peregrine Falcon worldwide is well known (Ratcliffe 1980, Mearns 1983); some studies report avian prey exclusively (e.g., Rosenfield et al. 1995 for Greenland). In our study of prey remains from Arizona, 98% were birds.

Few mammals (chipmunk [*Eutamius* spp.], cottontail [*Silvilagus* auduboni], and unidentified) were reported from prey remains in each of the three zones in Arizona. Predation on bats was probably significant based on hunting observations (Glinski 1998), but the lack of bats in our prey remains in eyries may stem from the fact that pellets were not analyzed (Bradley and Oliphant 1991).

Ratcliffe (1980) speculated that insect remains found in pellets could derive from insects captured on the eyrie ledge, meaning that the insects were not being brought as prey by the adults. Insects are seldom reported as food items in peregrine prey studies, but Snyder and Wiley (1976) estimated that insects represented 20% of the diet (by number) in a sample of 116 stomachs. Also, Oro and Tella (1995) found arthropod remains important in pellets, but not in prey remains, under eyries in Spain, and Ritchie (1982) reported insects in the diet of Alaskan peregrines. Dekker (1999) concluded that insects are commonly taken by recently fledged peregrines. Visual observations of peregrines hunting in Arizona (Ellis and LaRue, unpubl. data) showed that insects were important in the diet, at least numerically.

REGIONAL COMPARISONS

Major differences between the prey taken in northern, central, and southeastern Arizona were found in both numbers and biomass. We expected that Peregrine Falcons in the species-rich southeast would take a larger variety of prey than peregrines in the relatively depauperate north. However, the opposite was true. One explanation is that peregrines in the north have limited prey available and are therefore forced to take whatever birds are available, both breeding birds and birds on migration. That White-throated Swifts comprised a larger percentage of the diet in the north than in either of the other two zones is perhaps related to a smaller prey base in the north, or at least limited vulnerability of other species. Peregrines in the central and southeast may focus on fewer species of breeding birds near their eyries; they do take heavier prey. These results are consistent with the tenets of optimal foraging theory (Orians and Pearson 1979).

Finally, a larger percentage of the species available was being used by Peregrine Falcons in the north than in either the central or southeastern zones. This may not be due to the lower diversity of prey in the north, but it may be a response to a smaller number of birds of each species (except swifts) being available and vulnerable (i.e., aloft, far from cover). The greater dependence of falcons in the north on migrating birds was perhaps related to the assumption that migrating birds are more vulnerable to predation because they are forced to travel far from cover.

An abundance of a few favorite prey species (as in southeastern Arizona) may characterize an ideal peregrine foraging area, whereas the use of a wide variety of prey at one eyrie or in one zone, as in northern Arizona, may signify that the area lacks a consistently available prey base of one or a very few species. However, it is noteworthy that, over the period from 1976 through 1985 (when the bulk of our prey data were gathered), peregrines in the north produced more young per attempt than did pairs in either central or southeastern Arizona (Ellis 1988). In the diet of peregrines for areas where breeding density is (or has been) very high, such as in the Queen Charlotte Islands, one species, the Ancient Murrelet, constitutes >90% of prey by number (Nelson 1977). In evaluating these and related concepts for the diet of 11 genera of raptors, Jaksić and Braker (1983) concluded that local diet was influenced more by prey availability than by species-specific preferences. This explanation is consistent with observations that even this supposedly obligate ornithophage is able to shift to a diet high in mammals during microtine eruptions in the Arctic (Court et al. 1988, Bradley and Oliphant 1991) or feast on insect swarms (Ellis and LaRue, unpubl. data). Arizona peregrines seem to focus on a few species but, through time, take a wide variety as opportunity allows.

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APPENDIX. Frequency of occurrence and mass (g) for prey species from Peregrine Falcon eyries in three areas of Arizona.[abc]

	North	Central	Southeast	Total	Mass
Anatidae					
Northern Pintail (*Anas* acuta)		1		1	1011
Green-winged Teal (*Anas* crecca)		1		1	341
Teal spp. (*Anas* spp.)	1		1	2	371
Ring-necked Duck (Aythya collaris)		1		1	705
Odontophoridae					
Quail spp. (Callipepla spp.)		2		2	184
Northern Bobwhite (Callipepla spp.)			1	1	178
Montezuma Quail (Cyrtonyx montezumae)			1	1	186
Threskiornithidae					
White-faced Ibis (Plegadis *chihi*)	2			2	622
Accipitridae					
Sharp-shinned Hawk (Accipiter striatus)	1	1		2	139
Falconidae					
American Kestrel (*Falco sparverius*)	4	3	2	9	116
Peregrine Falcon (Falco peregrinus)	1		1	2	782
Rallidae					
Virginia Rail (Rallus limicola)		1		1	82
Sora (Porzana Carolina)	1			1	75
American Coot (Fulica Americana)	3	1		4	642
Charadriidae					
Killdeer (Charadrius vociferous)	2		2	4	97
Recurvirostridae					
American Avocet (Recurvirostra Americana)	2			2	316
Scolopacidae					
Lesser Yellowlegs (Tringa *flavipes*)	1	1		2	81
Solitary Sandpiper (*Tringa* solitaria)	1			1	48

APPENDIX. Continued.

	North	Central	Southeast	Total	Mass
Tringa spp.			1	1	44
Willet (*Catoptrophorus semipalmatus*)	11	1	3	15	215
Spotted Sandpiper (*Actitis macularia*)	1			1	40
Long-billed Curlew (*Numenius americanus*)	4			4	587
Marbled Godwit (*Limosa fedoa*)	10	2	1	13	371
Least Sandpiper (*Calidris minutilla*)	1			1	23
Calidris spp.	2			2	36
Dowitcher spp. (*Limnodromus* spp.)	2	1	1	4	107
Common Snipe (*Gallinago gallinago*)	1			1	122
Red-necked Phalarope (*Phalaropus lobatus*)	3			3	34
Laridae					
Franklin's Gull (*Larus pipixcan*)	2	1		3	280
Bonaparte's Gull (*Larus Philadelphia*)	1	1		2	212
California Gull (*Larus californicus*)	2			2	691
Black Tern (*Chlidonias niger*)	1	1		2	65
Columbidae					
Rock Pigeon (*Columbia livia*)	5	3	3	11	355
Band-tailed Pigeon (*Patagioenas fasciata*)	2	13	7	22	343
White-winged Dove (*Zenaida asiatica*)			2	2	153
Mourning Dove (*Zenaida macroura*)	46	35	64	145	119
Zenaida spp.		1	1	2	136
Strigidae					
Flammulated Owl (*Otus flammeolus*)		1		1	54
Burrowing Owl (*Athene cunicularia*)			1	1	155
Caprimulgidae					
Lesser Nighthawk (*Chordeiles acutipennis*)		1	2	3	50
Common Nighthawk (*Chordeiles minor*)	7			7	62
Common Poorwill (*Phalaenoptilus nuttallii*)			2	2	52
Apodidae					
White-throated Swift (*Aeronautes saxatalis*)	102	37	33	172	32
Trochilidae					
Black-chinned Hummingbird (*Archilochus alexandri*)	1		1	2	4
Broad-tailed Hummingbird (*Selasphorus platycercus*)		1		1	3
Picidae					
Acorn Woodpecker (*Melanerpes formicivorus*)		2	3	5	81
Williamson's Sapsucker (*Sphyrapicus thyroideus*)		1		1	48
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	2			2	50
Ladder-backed Woodpecker (*Picoides scalaris*)			1	1	30
Hairy Woodpecker (*Picoides villosus*)		2		2	67
Northern Flicker (*Colaptes auratus*)	9	10	6	25	111
Tyrannidae					
Cassin's Kingbird (*Tyrannus vociferans*)	3			3	46
Laniidae					
Loggerhead Shrike (*Lanius ludovicianus*)	1			1	47
Vireonidae					
Plumbeous Vireo (*Vireo plumbeus*)		1		1	17
Corvidae					
Steller's Jay (*Cyanocitta stelleri*)		5	1	6	128
Western Scrub-Jay (*Aphelocoma californica*)	2	2	2	6	80
Mexican Jay (*Aphelocoma ultramarina*)		2	6	8	124
Pinyon Jay (*Gymnorhinus cyanocephalus*)	21	2		23	103
Clark's Nutcracker (*Nucifraga columbiana*)	3	1		4	135
Raven spp. (*Corvus* spp.)			1	1	867

APPENDIX. Continued.

	North	Central	Southeast	Total	Mass
Alaudidae					
Horned Lark (*Eremophila alpestris)*	14	3	4	21	32
Hirundinidae					
Purple Martin *(Progne subis)*		2	3	5	49
Tree Swallow *(Tachycineta bicolor)*	1			1	20
Violet-green Swallow *(Tachycineta thalassina)*	7	1	2	10	14
Northern Rough-winged Swallow *(Stelgidopteryx serripennis)*	1	2		3	16
Cliff Swallow *(Petrochelidon pyrrhonota)*			1	1	22
Paridae					
Poecile or *Baeolophus* spp.			1	1	11
Aegithalidae					
Bushtit *(Psaltriparus minimus)*	1		1	2	5
Sittidae					
Red-breasted Nuthatch *(Sitta Canadensis)*	1			1	10
White-breasted Nuthatch *(Sitta carolinensis)*	4			4	21
Pygmy Nuthatch *(Sitta pygmaea)*	3	1		4	11
Troglodytidae					
Rock Wren *(Salpinctes obsoletus)*	2			2	17
Canyon Wren *(Catherpes mexicanus)*	1	1		2	13
Bewick's Wren *(Thryomanes bewickii)*		1		1	10
Turdidae					
Western Bluebird *(Sialia mexicana)*	4	2		6	28
Mountain Bluebird *(Sialia currucoides)*	5		1	6	30
Bluebird spp. *(Sialia* spp.)	2	2		4	29
Townsend's Solitaire *(Myadestes townsendi)*			1	1	34
Hermit Thrush *(Catharus guttatus)*	1	1		2	31
American Robin *(Turdus migratorius)*	4	2	2	8	77
Mimidae					
Northern Mockingbird *(Mimus polyglottos)*	1	1	2	4	49
Sage Thrasher *(Oreoscoptes montanus)*		1		1	44
Crissal Thrasher *(Toxostoma crissale)*		2	1	3	63
Sturnidae					
European Starling *(Sturnus vulgaris)*	8	2	4	14	83
Parulidae					
Orange-crowned Warbler *(Vermivora celata)*	1			1	9
Yellow-rumped Warbler *(Dendroica coronata)*	1			1	12
Dendroica spp.		1		1	9
American Redstart *(Setophaga ruticilla)*	1			1	8
Yellow-breasted Chat *(Icteria virens)*	1	1		2	26
Thraupidae					
Hepatic Tanager *(Piranga flava)*		2	2	4	38
Western Tanager *(Piranga ludoviciana)*	1		2	3	28
Emberizidae					
Spotted Towhee *(Pipilo maculates)*	2	2	3	7	41
Chipping Sparrow *(Spizella passerina)*	1			1	12
Brewer's Sparrow *(Spizella breweri)*			1	1	11
Spizella spp.	1		2	3	12
Vesper Sparrow *(Pooecetes gramineus)*	1			1	26
Lark Sparrow *(Chondestes grammacus)*	6			6	29
Black-throated Sparrow *(Amphispizu bilineata)*	1		1	2	14
Lark Bunting *(Calamospiza melanocorys)*			1	1	38

APPENDIX. Continued.

	North	Central	Southeast	Total	Mass
Melospiza spp.			1	1	19
Dark-eyed Junco (Junco *hyemalis*)	2	1	1	4	20
Cardinalidae					
Black-headed Grosbeak (Pheucticus *melanocephalus*)	1	2	1	4	42
Indigo Bunting (Passerina cyanea)	1			1	15
Icteridae					
Meadowlark spp. (Sturnella spp.)	7	3	5	15	95
Yellow-headed Blackbird (Xanthocephalus *xanthocephalus*)	1	1	1	3	65
Brewer's Blackbird (Euphagus cyanocephalus)	3	1	1	5	63
Common Grackle (Quiscalus quiscula)		1		1	114
Great-tailed Grackle (Quiscalus mexicanus)		1	1	2	149
Bronzed Cowbird (Molothrus aeneus)			1	1	62
Brown-headed Cowbird (Molothrus *ater*)	8	1		9	44
Hooded Oriole (Icterus *cucullatus*)		1		1	24
Bullock's Oriole (Icterus bullockii)		1	1	2	34
Scott's oriole (Icterus *parisorum*)		1	2	3	37
Fringillidae					
Purple Finch (Carpodacus *purpureus*)		1	2	3	25
Cassin's Finch (Carpodacus cassinii)	3			3	27
House Finch (Carpodacus mexicanus)	8	1	2	11	21
Red Crossbill (Loxia *curvirostra*)	4			4	41
Pine Siskin (Carduelis *pinus*)	2			2	15
Lesser Goldfinch (Carduelis psaltria)		1		1	10
Evening Grosbeak (Coccothraustes vespertinus)	1			1	59
Passeridae					
House Sparrow (Passer domesticus)		1		1	28
Unidentified bird	1		2	3	1–10
Unidentified bird	5	1	1	7	11–20
Unidentified bird	1	1	1	3	21–30
Unidentified bird	1	1	1	3	31–40
Unidentified bird	1		1	2	41–50
Unidentified bird		2		2	51–60
Unidentified bird		2		2	81–90
Total birds	391	194	210	795	
Number of taxa	74	66	56	114	

[a] Biomass data are from Dunning (1993).
[b] The following mammals were detected as prey: Colorado chipmunk (Eutamias umbrinus) once and unidentified chipmunk (Eutamias spp.) twice; desert cottontail (Silvilagus auduboni) once; and three other unidentified small mammals.
[c] The following insects were detected among prey remains: cicada (Cicadidae) twice; flying ant (Dolichoderinae) once; grasshopper (Acrididae) six times.
[d] Nestling Peregrine Falcons (n = 2), included here, were not included in computations in Tables 1–3.