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COVER: Cuban Black-Hawk (*Buteogallus anthracinus gundlachii*). Painting by Nils Navarro.

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TAXONOMIC STATUS AND BIOLOGY OF THE CUBAN BLACK-HAWK, *BUTEOGALLUS ANTHRACINUS GUNDLACHII* (AVES: ACCIPITRIDAE)

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ABSTRACT.—We reevaluate the taxonomic status of the Cuban population of the Common Black-Hawk (*Buteogallus anthracinus*) based on our examination of additional specimens, nests, eggs, and voice data. *Buteogallus a. gundlachii* is smaller than mainland populations of *anthracinus* and differs from mainland birds in plumage coloration and pattern. The common (alarm) call of *gundlachii* is a series of three or four notes, differing from that of mainland *anthracinus*, whose call consists of 9–24 notes. In the Isla de Pinos, Cuba, we observed *gundlachii* eating two species of land crabs (71.4%), centipedes (7.1%), lizards (10.7%), mammals (7.1%), and a bird (3.6%). We consider *Buteogallus gundlachii* Cabanis 1854 (1855), the Cuban Black-Hawk, to be a full species, endemic to Cuba, Isla de Pinos, and many of the cays of the Cuban Archipelago.

KEY WORDS: *Common Black-Hawk*; Buteogallus anthracinus; *Cuban Black-Hawk*; Buteogallus gundlachii; Buteogallus subtilis; *ecology*; *taxonomy*.

ESTADO TAXONÓMICO Y BIOLOGÍA DE *BUTEOGALLUS ANTHRACINUS GUNDLACHII* (AVES: ACCIPITRIDAE)

RESUMEN.—En este estudio re-evaluamos el estatus taxonómico de la población cubana de *Buteogallus anthracinus* (subespecie *gundlachii*) con base en exámenes de especimenes adicionales, nidos, huevos y datos de la voz. Los individuos de *B. a. gundlachii* son más pequeños que los individuos de las poblaciones continentales de *B. anthracinus,* y difieren de las aves del continente en la coloración y patrón del plumaje. El llamado común de alarma de *gundlachii* es una serie de tres o cuatro notas, mientras que el llamado de *anthracinus* en el continente consiste de entre 9 y 24 notas. En la Isla de Pinos, Cuba, observamos a *gundlachii* alimentándose de dos especies de cangrejos terrestres (71.4%), ciempiés (7.1%), lagartijas (10.7%), mamíferos (7.1%) y un ave (3.6%). Consideramos *Buteogallus gundlachii* Cabanis, 1854 (1855) debe ser tratado como una especie distinta, endémica de Cuba, la Isla de Pinos y muchos de los cayos del archipiélago cubano.

[Traducción del autores]

The New World genus *Buteogallus* Lesson, 1830 includes five species, mostly restricted to tropical areas, including Great Black-Hawk (*Buteogallus urubitinga*) of the lowlands of Mexico to northern Argentina, Savanna Hawk (*B. meriodionalis*) inhabiting savannas and marshes of western Panama to northern Argentina, Rufous Crab-Hawk (*B. aequinoctialis*) occurring in mangroves of northeastern

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Venezuela to eastern Brazil (Paraná), and Mangrove Black-Hawk (*B. subtilis*), which is restricted to the Pacific coasts and rivers of El Salvador south to northwestern Peru. The Common Black-Hawk (*Buteogallus anthracinus,* Deppe 1830) ranges from southwestern United States, south to extreme northern South America (coastal Venezuela to northeastern Guiana), Colombia, to northern Peru, including Trinidad, and some of the West Indies (Bond 1950, American Ornithologists' Union 1998). One of the West Indian populations (*B. a. cancrivorus* Clark 1905b) is restricted to St. Vincent, St. Lucia, Union Island (Grenadines), and Grenada (accidental and doubtful in last two islands; no specimens taken; Clark 1905a, 1905b, 1905c, Bond 1950, Evans 1990) in the Lesser Antilles, whereas the only other Antillean population (*B. a. gundlachii* Cabanis 1854 [1855]) occurs in Cuba and its satellites. The taxonomic status of the Cuban population has been controversial, with some considering the form as a full species, *Buteogallus gundlachii* (as originally described by Cabanis [1854, actually 1855]) instead of *Buteogallus anthracinus gundlachii* (American Ornithologists' Union 1998). Among those authorities who have considered the Cuban form *gundlachii* conspecific with the continental species (*anthracinus*) are Sharpe (1874, 1899), Cory (1887, 1892), Bangs and Zappey (1905), Bond (1956a, 1956b), Amadon (1961), Brown and Amadon (1968), Mayr and Short (1970), Stresemann and Amadon *in* Mayr and Cottrell (1979), Palmer (1988), Sibley and Monroe (1990), Ferguson-Lees and Christie (2001), Dickinson (2003), and others. Conversely, other authors have considered *gundlachii* different from *Buteogallus anthracinus* at the species level: Cabanis (1855), Gundlach (1854, 1865–1866a, 1865–1866b, 1871, 1876), Ridgway (1876), Gurney (1876, 1934), Bangs (1905), Swann (1921–1922, 1930), Peters (1931), Bond (1936), Hellmayr and Conover (1949), Friedmann (1950), Monroe (1963, 1968), Wetmore (1965), and others. Some of these authors subsequently changed their opinions on the Cuban form's status, later considering *gundlachii* conspecific with *anthracinus* (e.g., Gundlach 1893, Bond 1950, 1956a, 1956b). With rare exception, however, previous evaluations did not consider the important characteristics of breeding biology and voice, mainly because of the limited knowledge of the Cuban form resulting from the difficulty in reaching its breeding habitats. The lack of natural history information is not unique to *gundlachii,* but is also true for other forms of the genus *Buteogallus,* e.g., *anthracinus* and *subtilis,* which are currently recognized as different species (Aldrich and Bole 1937, Amadon 1982, Mayr and Cottrell 1979, Stiles and Skutch 1989, Sibley and Monroe 1990, American Ornithologists' Union 1998, Ridgely and Greenfield 2001), but with reservation by some authors (Stiles and Skutch 1989, American Ornithologists' Union 1998, Ridgely and Greenfield 2001).

Here, we reevaluate the taxonomic status of the Cuban population of *Buteogallus anthracinus gundlachii,* based on our examination of more specimens, nests, eggs, and behavioral data, especially vocalizations, than were considered by previous workers. All published work on the Cuban form has been based on information from the few specimens collected before 1960, all of which are deposited in foreign institutions. In this study, we include specimens in North American and Cuban collections, including those collected after 1960, and not evaluated previously.

Our main comparison in this assessment is with *anthracinus,* the taxon most often linked to *gundlachii.* In these comparisons, we refer to Cuban populations as *gundlachii* and other forms as *anthracinus.* It is not the purpose of this contribution to speculate on the taxonomic status of *Buteogallus subtilis* (including the three subspecies), although we make some comparisons between *subtilis* and *gundlachii.*

STUDY AREA

Many of the observations reported here were made during our 30 yr of field experience throughout Cuba. We made more intensive observations of nesting black-hawks from 1996 to 1998 at the Los Indios Ecological Reserve, Isla de Pinos (now Isla de la Juventud). Major vegetational communities at Los Indios include: (1) mangrove forest formation, characterized by black mangrove (*Avicennia germinans*) and red mangrove (*Rhizophora mangle*); (2) semi-deciduous gallery forests, with prominent Cuban royal palm (*Roystonea regia*), beach hibiscus (*Hibiscus tiliaceus*), and pond apple (*Annona glabra*); (3) the open forest (savanna) formation of an open pine (*Pinus caribaea* and *P. tropicalis*) and Cuban bottle palm (*Colpothrinax wrightii*), with silver saw palm (*Acoelorraphe wrightii*) and a sparse undergrowth; and (4) the pine-barren formation, with pines and palms, and an undergrowth predominantly of *Pachyanthus cubensis, P. poiretii, Kalmiella aggregata, Miconia delicatula, Polygala uncinata, Lyonia myrtilloides,* and *Pinguicula filifolia* (Jennings 1917, Alaín 1946). Black-hawk observations were made mainly in the mangrove and gallery forests. Additional intensive observations in red and black mangrove habitats were made in Ciénaga de Zapata in December 1999. An elevated road bed, lined with *Casuarina equisetifolia* and scrub veg-

etation, bisects the mangrove forest where we made our observations near Playa Larga.

METHODS

We examined specimens of *Buteogallus a. anthracinus* ($N = 37$), *B. a. gundlachii* (12), *B. a. cancrivorus* (4), *B. subtilis* (25), *B. aequinoctialis* (3), and *B. urubitinga* (24) deposited in the Field Museum of Natural History (Chicago), Museum of Comparative Zoology (Harvard University), American Museum of Natural History, United States National Museum of Natural History, Academy of Natural Sciences of Philadelphia, Louisiana State University Museum of Natural History, Museo Nacional de Historia Natural de Cuba (La Habana), and Instituto de Ecología y Sistemática (Cuba) (Table 1). Conventional measurements of wing chord (flattened against the ruler), tail, tarsus, and exposed culmen were taken to the nearest 0.1 mm with calipers. Egg masses were measured to the nearest gram using spring scales. We present summary descriptive statistics (mean, SD, and range) for the specimens. We plotted body measurements to assess the pattern of spatial segregation among populations and forms. The hypothesis of separation derived from the plots of body measurements was tested using discriminate function analysis (DFA; Kleinbaum and Kupper 1978). SPSS (1999) for Windows was used to run DFA.

RESULTS

Morphometrics and Plumage. *Adult morphology.* Our examinations of the two taxa of *B. anthracinus* (*anthracinus* and *gundlachii*) revealed differences in size and coloration. We found sexual size dimorphism in three of the measurements taken of specimens of mainland *anthracinus* (Table 1). Therefore, size comparisons between *anthracinus* and *gundlachii* were made within sex; i.e., male *anthracinus* with male *gundlachii* and female *anthracinus* with female *gundlachii.* Tarsal length was not different in either population, so for comparing *anthracinus* with *gundlachii* tarsi we combined male and female measurements for that morphometric parameter. Only measurements of wing and exposed culmen for *gundlachii* revealed sexual size dimorphism ($P < 0.01$; Table 1), although the small sample size of females ($N = 5$) precluded a reliable analysis. Measurements of *gundlachii* yielded a mean Dimorphic Index (Storer 1966) of 6.9, compared with a mean index of 5.6 for *anthracinus* (Table 1).

Birds from Cuba (*gundlachii*) are substantially smaller than mainland (*anthracinus*) birds in some conventional measurements, including wing chord in both sexes and tail length in males (Table 2). Also, tarsal lengths (combined male and female measurements) were significantly different between the two forms ($P = 0.001$). A stepwise selection procedure within DFA revealed wing chord, tail length, and exposed culmen were the most important of the size variables measured. Plots contrasting these variables within sex showed *anthracinus* and *gundlachii* tended to occupy generally distinct regions of the morphological space (Fig. 1).

To further examine size differences between the two populations, we used linear discriminant analysis to classify specimens into two groups ("race"), mainland *anthracinus* and Cuban *gundlachii,* using lengths of wing chord, tail, culmen, and tarsus as predictors. For male *anthracinus,* the analysis produced a true group classification proportion of 0.938 (15 of 16 correctly classified) and 0.857 (6 of 7 correctly classified) for *gundlachii* males, for an overall proportion correct of 0.913 (21 of 23) (Wilks's lambda = 0.375; $\chi^2 = 17.646$; df = 4, $P < 0.001$). For females, the analysis produced a true group classification proportion of 0.857 (18 of 21) for *anthracinus* and 0.800 (4 of 5) for *gundlachii* individuals, for an overall proportion correct of 0.846 (22 of 26) (Wilks's lambda = 0.4.95; $\chi^2 = 14.781.1$; df = 4, $P < 0.005$).

The four adult female St. Vincent (*B. a. cancrivorus*) specimens we examined were somewhat larger in wing chord ($\bar{x} = 389 \pm 7.63$, range = 385–401; $t = -4.99$, $P = 0.002$, df = 6) than *gundlachii* females, whereas we found no difference between the two island forms in tail (213.3 ± 12.4; range = 200–230; $t = -1.83$, $P > 0.05$, df = 6), culmen (27.3 ± 0.8; range = 26.8–28.4; $t = 0.60$, $P > 0.05$, df = 5), or tarsus (85.5 ± 6.4; range = 81.0–94.9; $t = -1.63$, $P > 0.05$, df = 4) length. We found no differences ($P > 0.05$) in measurements between *anthracinus* and *cancrivorus.*

In general coloration, *gundlachii* differs from *B. anthracinus* and *B. subtilis* in being chocolate-brown, not slate blackish or even black as in the latter two forms. However, some specimens of *anthracinus,* especially of the race *cancrivorus,* have a tendency to be less blackish, almost dark brown.

The underparts feathers of *gundlachii* have a light (brownish-gray) edge, more conspicuous toward the abdominal region and more broadly edged on the alula coverts than in *anthracinus,* with the edging on the terminal alula coverts becoming white bands. The margins of the flank and thigh feathers are heavily marked, forming a series of bands, although these bands tend to disappear in older birds. The shoulder feathers are boldly barred in white, contrasting with the chocolate-

Table 1. Sexual size dimorphism in four body measurements from specimens of *Buteogallus anthracinus* (mainland *Buteogallus a. anthracinus* and Cuban *B. a. gundlachii*), *B. subtilis*, *B. aequinoctialis*, and *B. urubitinga*, expressed as mean, standard deviation, range, and sample size (in parentheses). Statistical analyses are between-sex comparisons (two-sample *t*-test; equal variances not assumed).

Species Structure	Sex: Male	Sex: Female	*t*	df	*P*	Significance[a]	D.I.[b]
Buteogallus anthracinus							
Wing	371.69 ± 11.95 (16) 341–393	385.19 ± 11.21 (21) 360–421	−3.50	31	0.001	*	3.6
Tail	195.50 ± 7.40 (16) 183–210	213.81 ± 10.61 (21) 190–230	−6.18	34	0.0001	*	8.9
Exposed culmen	26.27 ± 0.82 (16) 25.1–28.1	27.40 ± 1.25 (20) 23.6–30.3	3.24	32	0.003	*	4.2
Tarsus	85.94 ± 2.65 (16) 80–90.0	85.42 ± 4.00 (21) 80.3–92.7	0.48	34	0.636	ns	−0.6
Mean D.I.							4.0
Buteogallus gundlachii							
Wing	342.71 ± 12.16 (7) 323–370	363.00 ± 8.43 (5) 350–372	−3.41	9	0.008	*	5.8
Tail	179.29 ± 9.12 (7) 167–197	191.60 ± 22.16 (5) 182–233	−1.15	4	0.313	ns	6.6
Exposed culmen	25.32 ± 0.69 (7) 24.5–28.5	27.54 ± 0.61 (5) 26.7–28.1	−5.84	9	0.0001	*	8.3
Tarsus	81.33 ± 3.57 (6) 75.4–87	79.67 ± 3.56 (5) 79.0–87.7	0.77	8	0.464	ns	−2.1
Mean D.I.							4.7
Buteogallus subtilis							
Wing	348.0 ± 13.68 (12) 330–370	352.31 ± 13.43 (13) 328–373	−0.79	22	0.436	ns	1.2
Tail	189.92 ± 14.58 (12) 168–220	191.69 ± 8.65 (13) 180–205	−0.37	17	0.719	ns	0.9
Exposed culmen	25.46 ± 2.06 (12) 19.7–27.8	26.56 ± 1.56 (12) 23.1–28.8	−1.47	20	0.157	ns	4.2
Tarsus	79.78 ± 3.09 (11) 73.3–84.1	79.55 ± 2.76 (13) 75.0–84.0	0.19	19	0.848	ns	−0.3
Mean D.I.							1.5
Buteogallus aequinoctialis							
Wing	315.5 ± 0.71 (2) 315–316	322 (1)					
Tail	155.0 ± 2.83 (2) 153–157	155 (1)					
Exposed culmen	23.55 ± 0.92 (2) 22.9–24.2	16.8 (1)					
Tarsus	74.5 ± 3.54 (2) 72–77	72.8 (1)					
Buteogallus urubitinga							
Wing	384.94 ± 16.68 (16) 362–412	389.63 ± 18.36 (8) 365–415	−0.61	12	0.555	ns	0.1
Tail	225.13 ± 13.50 (16) 190–250	234.63 ± 17.54 (8) 210–260	−1.35	11	0.206	ns	4.1
Exposed culmen	29.72 ± 1.05 (16) 26.7–30.9	30.78 ± 2.20 (8) 27.2–34.2	−1.84	8	0.103	ns	3.5
Tarsus	112 ± 8.25 (16) 85.9–118.9	113.16 ± 7.76 (8) 98.8–123.0	−0.11	14	0.910	ns	1.0
Mean D.I.							2.2

[a] Significance, * = $P < 0.05$, ns = not significant.
[b] D.I. = Dimorphic Index (Storer 1966).

Table 2. Mean, standard deviation, and sample size (parentheses) for wing chord, tail, culmen, and tarsus length for mainland (*Buteogallus a. anthracinus*) and Cuban (*Buteogallus a. gundlachii*) populations of the Common Black-Hawk. Statistical analyses are within-sex comparisons (two-sample *t*-test; equal variances not assumed) between mainland and Cuban specimens, except for tarsus, for which we found no sexual size dimorphism.

		TAXON					
STRUCTURE	SEX	*B. A. ANTHRACINUS*	*B. A. GUNDLACHII*	*t*	df	*P*	SIGNIFICANCE[a]
Wing	M	371.69 ± 11.95 (16)	342.71 ± 12.16 (7)	5.28	11	<0.001	*
	F	385.19 ± 11.21 (21)	363.00 ± 8.43 (5)	4.94	7	0.002	*
Tail	M	195.50 ± 7.40 (16)	179.29 ± 9.12 (7)	4.14	9	0.003	*
	F	213.81 ± 10.61 (21)	191.60 ± 22.16 (5)	2.14	4	0.099	ns
Exposed	M	26.27 ± 0.82 (16)	25.32 ± 0.69 (7)	2.86	13	0.013	*
culmen	F	27.40 ± 1.25 (20)	27.54 ± 0.61 (5)	−0.36	13	0.728	ns
Tarsus	M and F[b]	85.64 ± 3.45 (37)	80.57 ± 3.49 (11)	4.24	16	0.001	*

[a] Significance, * = $P < 0.05$, ns = not significant.
[b] Male and female tarsus data combined because specimens did not display sexual size dimorphism.

brown ground color. Remiges are dark brown, with wing coverts edged in grayish-cinnamon, especially the secondaries. The undersides of primaries and some secondaries have an extensive white patch, which constitutes the most distinctive character of the Cuban form. In *subtilis,* and especially *anthracinus,* this patch is mottled with grayish-brown. The tertiaries of *gundlachii* are heavily mottled grayish. This mottling is similar to the coloration of the primaries and secondaries of *anthracinus,* which has only an inconspicuous whitish patch on the undersides of these feathers. On the other hand, some specimens of *subtilis* display more white in this region than does *anthracinus,* but do not approach the amount shown in *gundlachii.*

The upperparts in *gundlachii* are also brown, with brownish-gray or with a trace of cinnamon on the feather margins. The head and pileum are uniformly chocolate brown. The rectrices are darker brown, almost blackish, with a broad white band of variable width (averaging 40 mm) in the middle of the tail. The tip of the tail is edged in white (as wide as 13 mm), which is a purer white than in *anthracinus* and *subtilis.* The feet and cere are yellow, the claws are black, and the iris is dark brown. The bill is blackish at the tip, becoming more yellowish toward the base on maxilla and mandible.

Immature morphology. Immature *gundlachii* individuals are not chocolate brown ventrally, but rather whitish, and heavily mottled with brown, having some feathers with considerable beige suffusion. Many feathers are mottled with medallion-like marks, whereas others are marked with elongated blotches, and some with streak-like dashes; these marks are seldom present in fully-feathered immature birds. The sides of the face and throat are whitish, speckled with brown. The pileum, nape, and neck are heavily mottled or spotted with brown on a light (white or beige) background. Flanks and thighs also display considerable variation, with younger birds showing a lighter (whitish to brownish-beige) background, whereas older birds display more mottling or barring. The thighs are distinctly barred with light and dark bands in *subtilis* and *anthracinus,* whereas *gundlachii* has mottled or very lightly barred thighs.

The white patch of the underside of primaries is even more expanded and conspicuous in subadult than in adult *gundlachii.* Also, the subadult's tail is distinct from that of the adult's tail. When still not in full adult plumage, the subadult's tail shows remnants of several (as many as nine) thin, brownish bands, instead of displaying a single broad white band in the middle of the tail as in the adult. Some bands are complete, whereas others are somewhat broken. In Cuban birds, these bands are straight and parallel, whereas in the other forms they are oblique (chevron-like), as well as being much wider than in *gundlachii.* The bands become less delimited toward the tip; compared with the adult, the white tip of the subadult's tail is less demarcated, more grayish than white, and becomes browner from the tip toward the base.

Natural History. *Habitat.* Although we occasionally observed black-hawks within the white sand palm savanna of Los Indios, Isla de Pinos, nearly all observations were made in the coastal zone, primarily in mangrove forests or at the edges of that

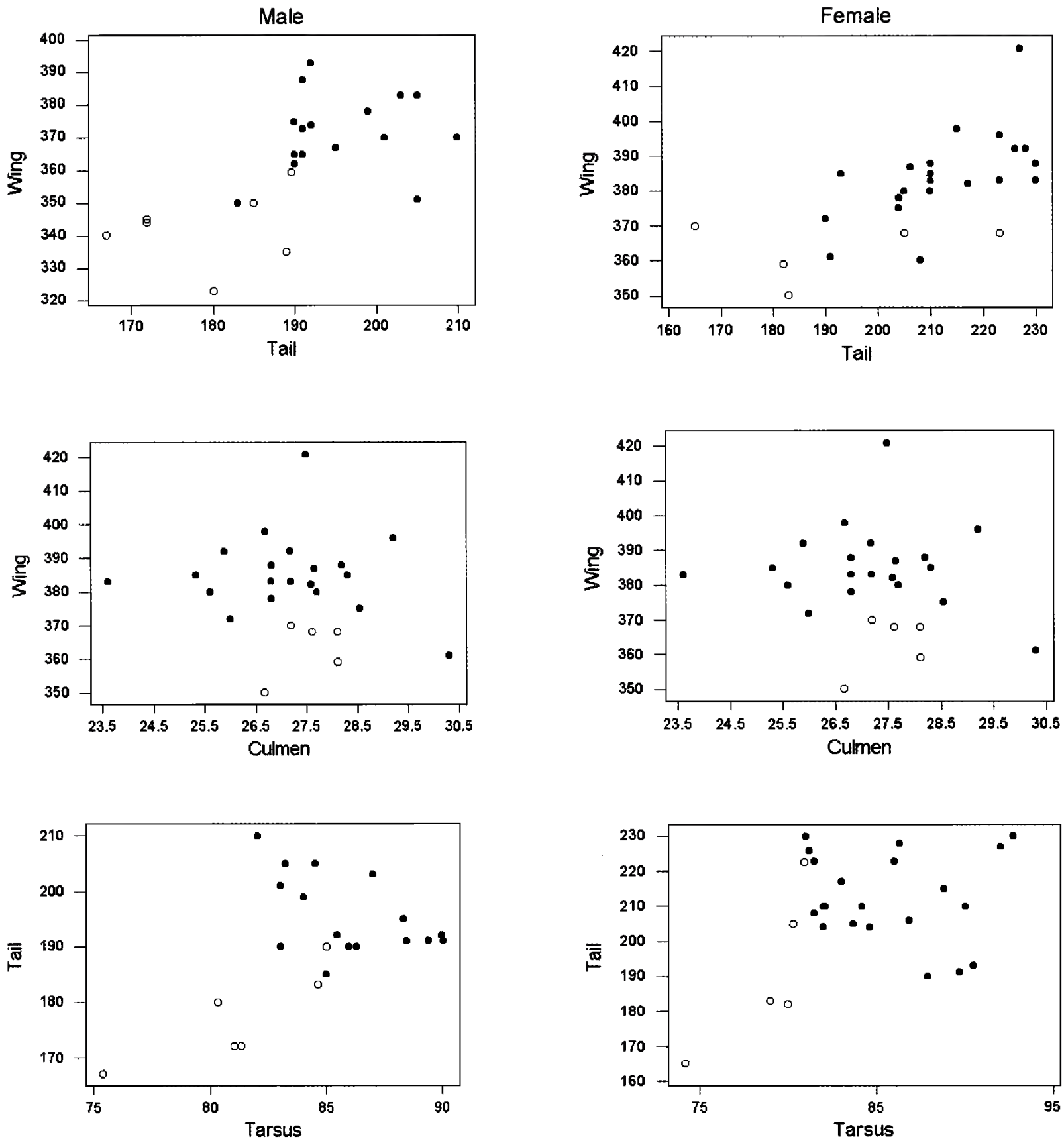

Figure 1. Plots contrasting body measurements of specimens of mainland *Buteogallus anthracinus anthracinus* (solid dots; N = 16 males, 21 females) and Cuban *B. a. gundlachii* (open circles; N = 7 males, 5 females).

habitat. Hawks hunted in the sparsely-vegetated mangrove pannes and flooded openings, where they foraged by perching in young or dead mangroves. We also saw black-hawks foraging or roosting in beach and coastal habitats, frequently perching in windbreaks of *Casuarina equisetifolia* at the edge of mangroves and dirt roads.

Nidification. We examined eight nests at Los Indios within the period of 14–27 May 1996–98. All contained eggs, except the nest examined on 27 May 1996, which had one chick. During our observations at Isla de Pinos, which were well into the breeding season, we observed no aerial courtship, although individual *gundlachii* regularly soared silently for short periods above their nesting areas.

Of the eight *gundlachii* nests we examined at Los Indios, half were placed in black-mangroves and half in red-mangroves (Table 3). Each of the nests

Table 3. Nest and contents data for eight *Buteogallus anthracinus gundlachii* nests at Los Indios, Pinos, Cuba, 1996–98.

	Year								
	1996			1997			1998		
	Nest Number								
Component	1	2	3	1	2	3	1	2	3
Nest tree species[a]	*Avicennia*	*Rhizophora*	*Rhizophora*	*Avicennia*	*Avicennia*	*Avicennia*	*Avicennia*	*Rhizophora*	*Rhizophora*
Nest height (m)	4	3.5	4	4	4.5	5	4	6	8
Nest diameter (cm)	70	98	93	105	80	99	105	107	85
Nest depth (cm)	45	88	89	95	75	91	95	94	72
Nest bowl depth (cm)	10	15	14	10	12	15	10	14	10
Contents[b]	1 E	2 E	1 C	2 E	1 E	2 E	2 E	2 E	1 E
Egg size (mm) No. 1	56.3 × 42.4	55.6 × 42.1		56.9 × 43.2	55.8 × 43.1	56.1 × 43.6	55.1 × 42.3	55.1 × 42.3	55.7 × 42.3
No. 2		55.3 × 41.9		56.3 × 42.2	56.4 × 42.9	54.7 × 42.9			
Egg mass (g) No. 1	61	59		62	59	63		60	61
No. 2		60		63				64	

[a] *Avicennia* = *Avicennia germinans*, *Rhizophora* = *Rhizophora mangle*.
[b] E = egg, C = chick.

was in the subcanopy, shaded by foliage and was constructed completely of *Avicennia* and *Rhizophora* twigs. The nests showed a large range of sizes, probably the result of additions made in successive years. Two of the nests we monitored from 1996 through 1998 were reused by black-hawks, and increased in size with the addition of more nest materials in subsequent years. All nests examined at Los Indios contained fresh or older lining materials, consisting of green leaves and sprigs of *Avicennia* and *Rhizophora,* and some debris. Both adults were observed bringing green lining material to nests.

Nests had notably deep bowls (Table 3) and when adults were on nests incubating or brooding, they remained low in the bowl and were difficult to detect. During our inspections of nests at Los Indios, adults at three nests regularly perched placidly within 2 m of us while we measured eggs and chicks. Adults at a fourth nest were somewhat more aggressive, but the pair only flew low above our heads, occasionally calling, and vocalized from a nearby perch while we measured eggs.

We measured 11 eggs at Los Indios (Table 3). Three eggs collected by O. H. Garrido in Cayo Cantiles (Archipiélago de los Canarreos; deposited at Instituto de Ecología y Sistemática) measured 55.16 × 44.1 mm, 55.8 × 42.6 mm, and 57.08 × 42.34 mm. The 14 *gundlachii* eggs we measured averaged 55.87 ± 0.69 (range = 54.7–57.08) × 42.71 ± 0.62 (range = 41.9–44.1) mm. Eggs of *gundlachii* are typically short sub-elliptical to elliptical, with a finely granulated texture. Eggs have a dull grayish-white ground color, sometimes with a greenish or bluish cast early in incubation, and are marked with spots and blotches of dark or reddish-brown, particularly at the larger end. Clutch sizes at Los Indios averaged 1.57 ± 0.53 (N = 8; range = 1–2) eggs (Table 3). The egg of *gundlachii* is usually more colored (bluish to greenish suffusion) than those of *anthracinus* or *subtilis,* which are typically grayish or whitish (Bent 1937, Wetmore 1965, O. Garrido pers. obs.).

Diet and foraging behavior. Cuban birds were found to feed on a variety of prey (Table 4). Notable was the lack of fish prey, although fishes were available in tidal channels in the study area. However, twice, hawks were observed wading in shallow tidal channels and making foot thrusts at probable fish prey. During our observation periods (May–June) at Los Indios, land crab populations were particularly high, and crabs were active and con-

Table 4. Prey of *Buteogallus anthracinus gundlachii* at Los Indios, Isla de Pinos, Cuba, 1996–1998, and Ciénaga de Zapata, Cuba, 1999–2000.

	Number (%)			
Prey	Observed Brought to Nest	Prey Remains	Observed Captures	Total (%) All Observations
Invertebrates				
Crab				
Cardisoma guanhumi	4	12	2	18 (64.3)
Ucides cordatus	1	1		2 (7.1)
Centipede sp.	1	1		2 (7.1)
Totals (invertebrates)	6 (21.4)	14 (50.0)	2 (7.1)	22 (78.6)
Vertebrates				
Reptiles				
Lizards				
Anolis spp.	1	1		2 (7.1)
Ameiva auberi	1			1 (3.6)
Totals (reptiles)	2 (7.1)	1 (3.6)		3 (10.7)
Birds				
Sora *Porzana carolina*		1		1 (3.6)
Totals (birds)		1 (3.6)		1 (3.6)
Mammals				
Rattus rattus		2		2 (7.1)
Totals (mammals)		2 (11)		2 (7.1)
Total (vertebrates)	2 (7.1)	4 (14.3)		6 (21.4)
Total (all observations)	8 (28.6)	18 (64.3)	2 (7.1)	28

spicuous in the early mornings and evenings, when most of our observations of prey delivery and captures were made. In December 1999, we also observed *gundlachii* capturing several crabs (*Cardisoma guanhumi*) along the coast of Ciénaga de Zapata, where the hawks hunted from a mixed mangrove-*Casuarina equisetifolia*-coastal scrub zone.

During our observations in the Los Indios mangrove habitat, *gundlachii* displayed passive still hunting from low ($\bar{x}$ = 1.3 ± 0.94; range = 0.2–3 m; N = 54) mangrove tree perches or from the ground. Prey captures were made in a low-angle flight, snatching the item (all observations of crabs) and continuing to a nearby perch, or the hawk landed near the crab and stalked it on foot. Once the hawk grasped the crab, it controlled the claws and legs on either side of the prey with its feet, then removed the carapace with a quick tug at the head region using its bill.

We found apparent caches of uneaten, though dismembered, land crabs near (range = 5–20 m) used *gundlachii* nests. However, we did not observe hawks returning to the caches to feed on the stockpiled crabs.

Although *B. a. anthracinus* has been observed (O. Garrido pers. obs.) in Mexico hunting at the edge of a meadow in a fashion similar to that of the coursing behavior of the Northern Harrier (*Circus cyaneus*), *gundlachii* was not observed foraging aerially in an active manner.

Vocal behavior. The common call of *gundlachii* is a series of three or, uncommonly, four notes, with emphasis on the first two elements, suggesting its Cuban common name, *BA-TIS-ta* (Gundlach 1893, Garrido and Schwartz 1969, Garrido and Kirkconnell 2000; Fig. 2A). The call has a much shorter duration and fewer elements than in other populations of *Buteogallus anthracinus* (Table 5). The common call of mainland *anthracinus* consists of 9–24 notes, with the middle to the final third of the notes accentuated (Fig. 2C–F, Table 5). Stiles and Skutch (1989) characterized the call of mainland *anthracinus* as "*klee klee klee KLEE KLEE klee kle kle ke ki ki.*" The comparable call of *cancrivorus* consists

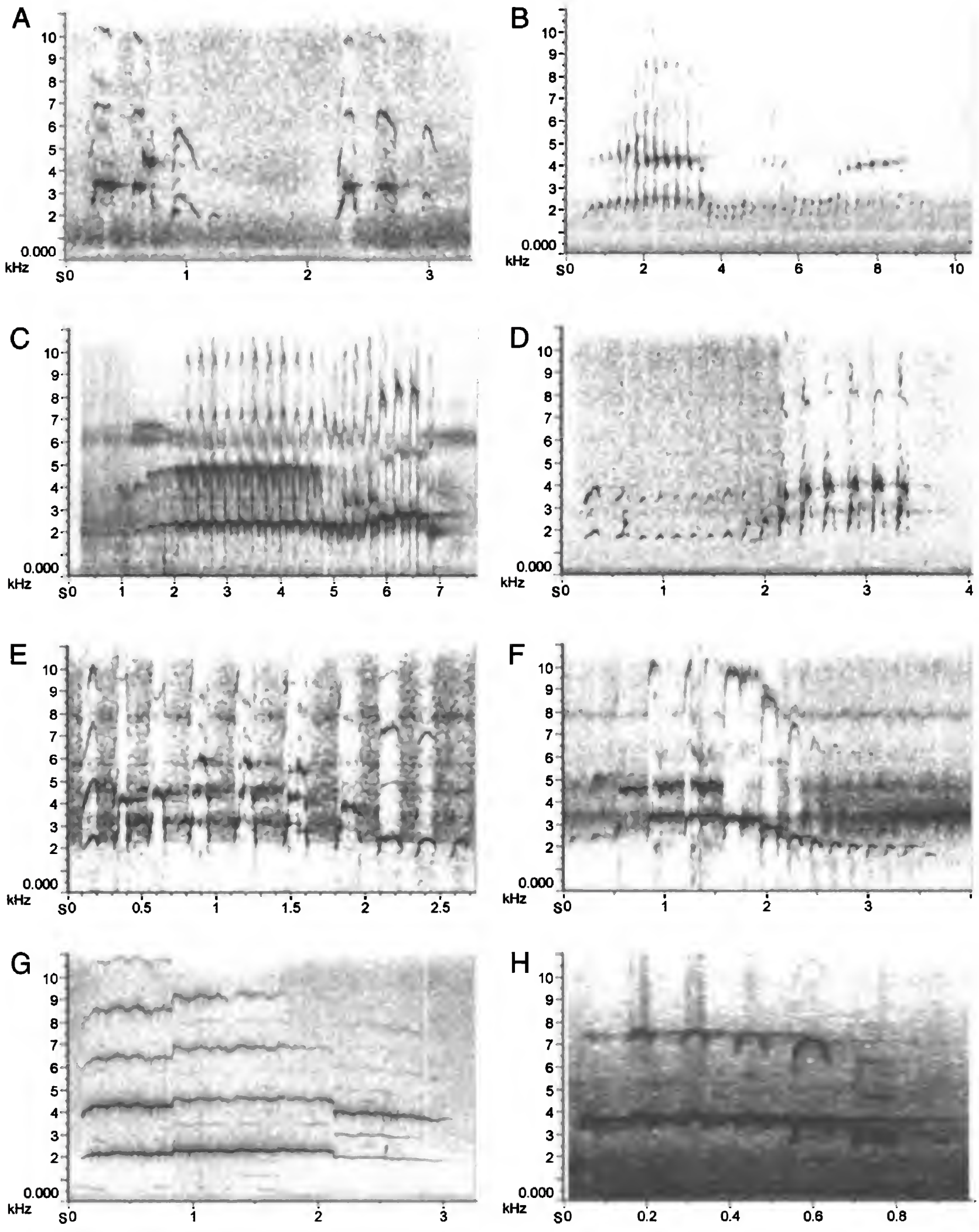

Figure 2. Sonographs of common (alarm) calls of *Buteogallus* species. A. *Buteogallus anthracinus gundlachii,* showing typical three element "ba-tis-ta" phrase, Cuba (G.B. Reynard). B. *Buteogallus a. cancrivorus,* St. Vincent (J. Roche, courtesy British Library Sound Archive). C. *Buteogallus a. anthracinus,* Costa Rica (Cornell Library of Natural Sounds 27216). D. *Buteogallus a. anthracinus,* Venezuela (P. Schwartz). E. *Buteogallus a. anthracinus,* male, Arizona (courtesy J. Schnell). F. *Buteogallus a. anthracinus,* female, Arizona (courtesy J. Schnell). G. *Buteogallus urubitinga,* Venezuela (P. Schwartz). H. *Buteogallus aequinoctialis,* Surinam (Paul Donahue, courtesy British Library Sound Archive).

Table 5. Characteristics ($\bar{x} \pm$ SD, range in parentheses) of the common (advertisement) call of *Buteogallus anthracinus anthracinus, B. a. cancrivorus, B. a. gundlachii, B. urubitinga,* and *B. aequinoctialis.*

Form	N	Duration (s)	Frequency (Hz)[a] Low	Frequency (Hz)[a] High	No. Elements	Emphasized Elements
B. a. gundlachii	7	0.9 ± 0.1 (0.8–1.1)	1769 ± 96.6 (1632–1896)	3751 ± 463.6 (3487–4786)	3.1 ± 0.4 (3–4)	1–2
B. a. anthracinus (Arizona)	4	3.3 ± 0.7 (2.4–3.9)	1317 ± 200.9 (1058–1524)	3862 ± 333.1 (3647–4359)	12.5 ± 3.0 (9–15)	5–7
B. a. anthracinus (Costa Rica)	5	4.5 ± 1.3 (2.7–6.3)	1626 ± 198.9 (1359–1919)	3054 ± 517.3 (2279–3725)	16.2 ± 5.4 (11–24)	8–20
B. a. anthracinus (Venezuela)	2	2.6 ± 1.0 (1.9–3.3)	1597 ± 20.0 (1583–1611)	3632 ± 899.5 (2997–4269)	12.5 ± 5.0 (9–16)	4–16
B. a. cancrivorus	8	7.3 ± 1.7 (5.0–9.5)	1504 ± 99.3 (1340–1701)	4555 ± 305.9 (4304–5087)	29.5 ± 5.9 (22–37)	9–25
B. urubitinga	6	2.3 ± 1.6 (1.25–4.67)	1734 ± 66.8 (1673–1862)	3146 ± 270.2 (2794–3408)	1.0 ± 0 (1)	—
B. aequinoctialis	5	1.0 ± 0.1 (0.9–1.0)	2352 ± 126 (2199–2521)	4140 ± 134.3 (4041–4348)	7.6 ± 0.6 (7–8)	2–4

[a] Fundamental tone.

of a large number of elements (22–37), with emphasis on several middle elements (Fig. 2B, Table 5). Similarly, the common call of *B. subtilis* is substantially different from that of *gundlachii,* consisting of several, rapidly repeated elements, described by Ferguson-Lees and Christie (2001) as a series of shrill whistles, indistinguishable from *anthracinus.* The call of *Buteogallus urubitinga* consists of a single note, drawn out in a high shrill "*keeeeeeeeh*" (Ferguson-Lees and Christie 2001; Fig. 2G), whereas that of *Buteo aequinoctialis* is a distinct series of whistle-like notes (Ferguson-Lees and Christie 2001; Fig. 2H, Table 5).

DISCUSSION

As is normal among most birds of prey, female *gundlachii* are somewhat larger than males, with culmen and wing length significantly different between genders. Sexual size dimorphism was less evident in *anthracinus* ($\bar{x}$ Dimorphic Index = 4.0) than *gundlachii,* where we found a mean Dimorphic Index of 4.7 with males significantly larger than females in wing and culmen length (Table 1). Snyder and Wiley (1976) reported a lower index (2.7) of sexual size dimorphism for *B. anthracinus.*

Whereas measurements of selected body parts did not show complete distinction between *anthracinus* and *gundlachii* (Table 2, Fig. 1), Cuban birds were consistently smaller or at the small end of the range for *anthracinus* measurements. In contrast to our measurements, Bangs (1905) partly based his determination of separating *gundlachii* from *anthracinus* on the former being slightly larger than the latter, and in having a decidedly heavier, broader bill. As a general pattern, Schnell (1994) noted that Common Black-Hawks of continental (inland) North and Central America are largest. Mainland *anthracinus* populations inhabiting mangrove habitat tend to be smaller and browner than others. The race *B. subtilis rhizophorae,* which inhabits mangrove habitat (Monroe 1963, 1968, Blake 1977), shows a dark-brown plumage. Our observations revealed that Cuban birds, also mangrove inhabitants, are consistently browner with substantial differences in plumage pattern compared with mainland birds. Thus, such color differences may be a result of ecological parallelism, rather than of phylogenetic relationships.

The species of *Buteogallus* are partial to wetlands, swampy woods, and seacoasts (Amadon 1982). In its mainland range, *anthracinus* has been characterized as inhabiting woodlands around coastal

swamps, ponds, and streams, and especially mangroves in the swampy woodlands adjacent to the poorly-drained inlands that are affected by tidewaters (Phillips et al. 1964, Wetmore 1965, Davis 1972, Schnell 1994). Wetmore (1965) noted that along large rivers they extend their range farther inland. Thomas (1908) reported *anthracinus* in stretches of sand dunes and savannas with clumps of palmettos and pines. The Cuban population shows a similar preference for lowland coastal areas. Gundlach (1893) and Bangs (1905) noted *gundlachii* was found only in mangrove swamps and on the banks of large rivers. In broad contrast, the other West Indian population, *Buteogallus anthracinus cancrivorus* of St. Vincent, mainly keeps to the high wooded valleys, although it seldom occurs far from water (Lister 1880, Clark 1905b, Bond 1956a).

Cuban populations of the black-hawk breed from January through June (Garrido and Kirkconnell 2000), with egg-laying occurring in late March or April. Bangs (1905) collected a female containing a soft-shelled egg and found another tending a nest on 15 April. Bond (1950) reported a nest with a newly-hatched chick on 4 April. Garrido and Schwartz (1969) and Valdés Miró (1984) commented *gundlachii* builds its nest at a considerable distance above the ground. Gundlach (1876) reported a nest at 8 "varas" (6.8 m), whereas Bond (1936) noted one at 6.2 m.

Nests of the Cuban form are typically rough structures of twigs, lined with green leaves and, sometimes, debris (Gundlach 1893, Bond 1936, Garrido and Schwartz 1969, Valdés Miró 1984). Bond (1936), describing nests found in St. Vincent (*B. a. cancrivorus*) and Cuba (*gundlachii*), noted, "The nest, a rough mat of sticks, is placed at various elevations in trees." All nests located by us at Los Indios in 1996–98 were in mangroves (*Avicennia, Rhizophora*). In contrast, Bond (1936) described black-hawk nests in St. Vincent as "placed on top of clumps of mistletoe and were rather small." As Bond (1936) suggested, nests of the Cuban species are somewhat larger than those of birds in St. Vincent. Schnell (1994) gave the dimensions of mainland *anthracinus* nests as ranging from 38 cm diameter × 20 cm deep to 1.2 m diameter × 0.67–1.2 m deep. Bangs (1905) and Bond (1936) also noted *gundlachii* re-used nests in more than one season, which we believe accounts, in part, for the larger nest size of Cuban birds.

Black-hawks at Los Indios were remarkably non-aggressive toward humans at their nests and allowed us to approach much closer than other local raptor species tolerated, perhaps relying on their cryptic behavior to avoid detection at the nest. Others have also noted this tolerance in Cuban black-hawks (Todd 1916, Barbour 1923, Garrido and Schwartz 1969).

Schnell (1994) reviewed available egg specimens for *Buteogallus anthracinus,* summarizing mean measurements from Bent (1937) as 57.3 × 44.9 mm (N = 60 eggs) and examples in the Western Foundation of Vertebrate Zoology as 57.30 × 45.50 mm (N = 12 clutches, 19 eggs; range = 52.61–62.02 mm length, 42.69–47.35 mm breadth). Eggs of *anthracinus* we measured at the Delaware Museum of Natural History averaged 57.46 (53.1–63.2) × 45.25 (41.7–49.1) mm (N = 13 clutches, 21 eggs). Interestingly, an egg reported from St. Vincent is at the high end for the species: 61 × 47 mm (Bond 1936) and exceeds the range for *gundlachii.* Eggs of *gundlachii* we measured at Los Indios averaged only slightly smaller than those of mainland *B. anthracinus* analyzed by Schnell (1994). Gundlach (1876) reported that Cuban eggs measured 58 × 45 mm, whereas Bangs (1905) reported 56 × 45.5 mm. Measurements presented by Valdés Miró (1984) are obviously in error; i.e., $\bar{x}$ = 56.0 (range = 55.0–57.0) × 24.6 (23.0–26.5) mm. The mean mass (61.0 ± 1.8 g) of eggs we measured at Los Indios was somewhat lighter compared with Schnell's estimated mean mass of 63.8 g for *anthracinus.*

Although we observed differences in egg coloration and pattern among *anthracinus, subtilis,* and *gundlachii,* these characters show considerable variation and do not appear to be a good character for determining relationships (L. Kiff pers. comm.).

Schnell (1994) noted that, in general, clutch size of *Buteogallus anthracinus* decreased from two eggs in the northern range to one in the southern range; several reported three-egg clutches were questionable. Clutch sizes at Los Indios fell within that range, averaging 1.57 eggs per clutch.

Buteogallus anthracinus feeds mainly on invertebrates and lower vertebrates, with occasional small birds or mammals in the diet (Schnell 1994). For mainland populations, Thomas (1908) reported *anthracinus* preying on burrowing land crabs, which form almost the sole diet of the hawks in British Honduras (Belize). The St. Vincent population (*B. a. cancrivorus*) reportedly feeds on cray-

fish and freshwater crabs (Lister 1880). In Cuba, Gundlach (1893) reported remains of crustaceans, as well as frogs, snakes, and fishes in the stomachs of black-hawks. Barbour (1943) reported land crabs as its prey in Cuba. Garrido and Kirkconnell (2000) reported its prey as mainly crabs and birds, whereas Ramsden (C. Ramsden, Museo de Historia Natural, Universidad de Oriente, Santiago de Cuba unpubl. data) noted the hawk fed on crabs and fishes.

The hunting behavior of *Buteogallus,* in general, has been characterized as sluggish. Schnell (*in* Palmer 1988, 1994) noted *B. anthracinus* normally hunts from a stationary perch, often near the ground, from branches up to 15 m high, on boulders, other low perches, and gravel beds along streams. For Cuban hawks, Barbour (1923) described crab predation similar to our observations: "The hawk pounces on the crab, gathers the legs and claws of each side in one of its feet, and reaching down removes the carapace by hooking the bill under its front edge." Kirkconnell and Garrido (1991) reported *gundlachii* drowning its avian prey (Common Moorhen [*Gallinula chloropus*]), which they suggested was unusual and perhaps related to the abundant rain that caused the raising of the water level in the swamp, rendering crabs difficult to find.

We observed Cuban Black-Hawks caching crab prey near their nest, a habit that has also been reported for *B. anthracinus* in mainland sites (Thomas 1908, Schnell 1991, 1994).

As noted by Schnell (1994), descriptions of the vocal behavior of *Buteogallus anthracinus* have been confusing and conflicting. Schnell (1994) characterized the common call (= alarm call) as of a complex, un-raptor-like quality. The common call of mainland *Buteogallus anthracinus* is distinct from the three-note call of *gundlachii,* consisting of 9–24 notes (Reynard and Garrido 1988, Schnell 1994) (Figs. 2A, 2C–F, Table 5). Similarly, the common call of *B. subtilis* is distinct from that of *gundlachii,* consisting of several, rapidly-repeated elements, described by Ferguson-Lees and Christie (2001) as a series of shrill whistles, indistinguishable from that of *anthracinus.* The call of *Buteogallus aequinoctialis* is a series of six or seven whistle-like notes, the first three rapid, followed by slower and descending elements (Fig. 2H; Ferguson-Lees and Christie 2001). Finally, *B. meriodionalis* has a call consisting of a prolonged whistle, described as "*eeeeee-eh*" or "*kree-ee-ee-er*" (Ferguson-Lees and Christie 2001).

CONCLUSIONS

We consider *Buteogallus anthracinus* (with its geographical races, *cancrivorus* and *anthracinus*), *B. urubitinga, B. aequinoctialis,* and *B. gundlachii* as separate species. This treatment of the Cuban population agrees with Wetmore (1965:234), who stated the other forms stand apart: ". . . from the bird of the island of Cuba which it appears appropriate to treat as a separate species, *Buteogallus gundlachii.*" Thus, the Cuban Black-Hawk *Buteogallus gundlachii* Cabanis, 1854 (1855), becomes a species endemic to Cuba, distributed in the main island, where it is relatively uncommon and quite localized, Isla de Pinos, and many of the keys of the Cuban Archipelago.

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HOME RANGE AND HABITAT USE OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON

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ABSTRACT.—We studied movements and habitat selection of 20 adult northern Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula, Washington in 1987–89. Median annual home range size of individual owls was 1147 ha based on the 75% isopleth of the Fixed Kernel (FK), 2406 ha based on the 95% FK, and 2290 ha based on the 100% Minimum Convex Polygon (MCP). Annual ranges of individual owls tracked >1 yr overlapped by a mean of 70–73%, depending on which estimator was used. Size of annual and cumulative ranges was negatively correlated with the amount of old forest within the cumulative MCP home range and within a 4.3 km radius of the center of activity. Overlap of annual ranges of owls that were paired averaged 64 ± 5% based on the MCP and 69 ± 5% based on the 95% FK. On average, ranges used during the nonbreeding season overlapped breeding season ranges by 65.0 ± 4.5%, and breeding season ranges overlapped nonbreeding season ranges by 62.6 ± 4.9%. Compositional analysis of habitat selection indicated that old forests were the most preferred cover type for foraging and roosting and that clear-cuts and non-forest cover types were rarely used. There was little evidence that owls selected riparian areas or forest edges for foraging or roosting. Our observations are consistent with the hypotheses that northern Spotted Owls use larger foraging areas in regions where northern flying squirrels (*Glaucomys sabrinus*)are their primary source of food, that they prefer old forests for foraging and roosting, and that their home ranges become larger as the amount of old forest declines. The large size of annual ranges on the Olympic Peninsula may be a response to low prey biomass.

KEY WORDS: *Northern Spotted Owl;* Strix occidentalis caurina; *home range; habitat use; radiotelemetry; Olympic Peninsula; Washington.*

RANGO DE HOGAR Y USO DE HÁBITAT DE *STRIX OCCIDENTALIS CAURINA* EN OLYMPIC PENINSULA, WASHINGTON

RESUMEN.—Estudiamos los movimientos y la selección de hábitat de 20 individuos adultos de *Strix occidentalis caurina* en Olympic Peninsula, Washington, entre 1987 y 1989. La mediana del tamaño del área de hogar de un individuo fue de 1147 ha basada en la isolínea de 75% del kernel fijo (KF), 2406 ha basada en el 95% KF y 2290 ha basada en el 100% del polígono convexo mínimo (PCM). Los rangos anuales de los individuos seguidos por menos de un año se superpusieron en promedio entre un 70% y un 73%, dependiendo del estimador que usamos. Los tamaños de los rangos anuales y acumulativos se correlacionaron negativamente con la cantidad de bosque maduro presente dentro del PCM acumulativo del rango de hogar y a menos de 4.3 km del centro de actividad. La superposición promedio de los rangos de hogar anuales de individuos que conformaban parejas fue de 64 ± 5% basado en el PCM y 69 ± 5% basado en el 95% del KF. En promedio, los rangos usados durante el período no reproductivo se superpusieron con los rangos del período reproductivo en 65.0 ± 4.5%, y los rangos del período reproductivo se superpusieron con los rangos del período no reproductivo en 62.6 ± 4.9%.

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Los análisis de composición de los ambientes seleccionados indicaron que los bosques maduros fueron el tipo de cobertura preferida para alimentarse y reposar, mientras que las áreas completamente taladas y no boscosas fueron usadas en muy pocas ocasiones. Encontramos muy poca evidencia de que las lechuzas seleccionan las áreas riparias o los bordes de bosque para alimentarse o reposar. Nuestras observaciones son consistentes con la hipótesis de que *S. o. caurina* usa grandes áreas de forrajeo en las regiones donde las ardillas voladoras (*Glaucomys sabrinus*) son su fuente principal de alimento, que prefieren bosques maduros para alimentarse y reposar y que sus áreas de hogar aumentan a medida que disminuye la cantidad de bosque maduro. El gran tamaño de los rangos anuales en Olympic Peninsula podría responder a una baja biomasa de presas.

[Traducción del equipo editorial]

Spotted Owls (*Strix occidentalis*) exhibit considerable variation in home range size and patterns of seasonal movements, both within and among regions. For example, in some parts of their range, Spotted Owls may migrate during winter, moving 16–58 km from their breeding season ranges into lowland forests (Laymon 1989, Zabel et al. 1992). In other regions, they are largely resident in the same areas throughout the year (Forsman et al. 1984, Carey et al. 1990, 1992).

Home ranges and habitat selection of Spotted Owls have been studied extensively in Oregon and California, but with the exception of a study by Hamer (1988), little information is available from Washington. We examined home ranges and habitat selection of northern Spotted Owls on the Olympic Peninsula, Washington to determine if patterns of habitat use differed near the northern edge of the range of the owl compared to earlier studies conducted in Oregon (e.g., Forsman et al. 1984, Carey et al. 1990, 1992, Carey and Peeler 1995) and northern California (Solis and Gutiérrez 1990, Zabel et al. 1992, 1995).

STUDY AREA

We conducted our study on two areas on the west side of the Olympic Peninsula, one located 3 km SE of the town of Forks, Clallam County, and the other located 10 km SE of the town of Quinault, Jefferson County (Fig. 1). Both areas were located on the Olympic National Forest, had similar climate, topography and vegetation, and will hereafter be referred to collectively as the "study area."

The study area was characterized by mountainous terrain covered by forests of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Sitka spruce (*Picea sitchensis*) was common on mesic, low elevation areas, and Douglas-fir (*Pseudotsuga menziesii*) and Pacific silver fir (*Abies amabilis*) were often intermixed with western hemlock on upland sites (Henderson et al. 1986). Elevations ranged from 150–1500 m. Precipitation ranged from 280–460 cm/yr, mostly falling as rain during October–May.

The area included a mosaic of seral stages, ranging from clearings in which all trees had been recently harvested (clear-cuts) to old-growth forests in which overstory trees were over 500 yr old (Henderson et al. 1986). Approximately half of the area had been clear-cut within the previous 30 yr, but harvested areas were not uniformly distributed within the study area. Some areas were heavily fragmented by recent clear-cuts, whereas other areas had extensive blocks of mature and old-growth forest. Much of the study area was hit by hurricane-force winds in 1921 which severely damaged many stands (Pierce 1921). As a result, many stands included a mixture of 60–80-yr-old trees that regenerated after the wind event, interspersed with old trees (80–500+ yr) that survived the windstorm. All types of natural (unlogged) forest typically had high canopy closure (65–80%), high variation in tree size and age, and high volumes of logs and snags (Henderson et al. 1986). Regenerating stands of young trees in clear-cut areas were usually even-aged, with high canopy closure.

METHODS

Capture and Radio-marking. We captured owls with noose poles (Forsman 1983) and marked them with back-pack transmitters (Model P2, AVM Instrument Company, Livermore, CA U.S.A.), as described by Forsman et al. (1984). Total mass of transmitter and harness was 18–20 g, and transmitter life was 9–15 mo. We tried to obtain a minimum of 12 mo of data from each owl. We replaced transmitters on six individuals after 9–12 mo, and tracked them for nearly 2 yr.

Sampling Schedule. We attempted to obtain one nocturnal foraging location per night on each owl at least 3 nights per wk, and one diurnal roost location per owl at least 3 d per wk. Our sampling schedule was intended to reduce autocorrelation between sequential locations (Swihart and Slade 1985a, 1985b). However, Aebischer et al. (1993) and Otis and White (1999) have suggested that autocorrelation is generally irrelevant when individual animals are used as the sample unit in home-range studies, so we used all of our data, including a few cases (129 of 7346 locations) when we obtained 2–3 locations on the same owl in one night. We classified all locations as foraging locations if they occurred from 0.5 hr after sunset to 0.5 hr before sunrise. We excluded locations of incubating or brooding females from analyses of habitat selection, until females began to forage when the young were about 2 wk old.

Radio Triangulation. We estimated owl locations by triangulating with a Telonics hand-held H-antenna and TR2 receiver (Telonics, Mesa, AZ U.S.A.). We used a hand-held compass to estimate azimuths from ≥3 locations

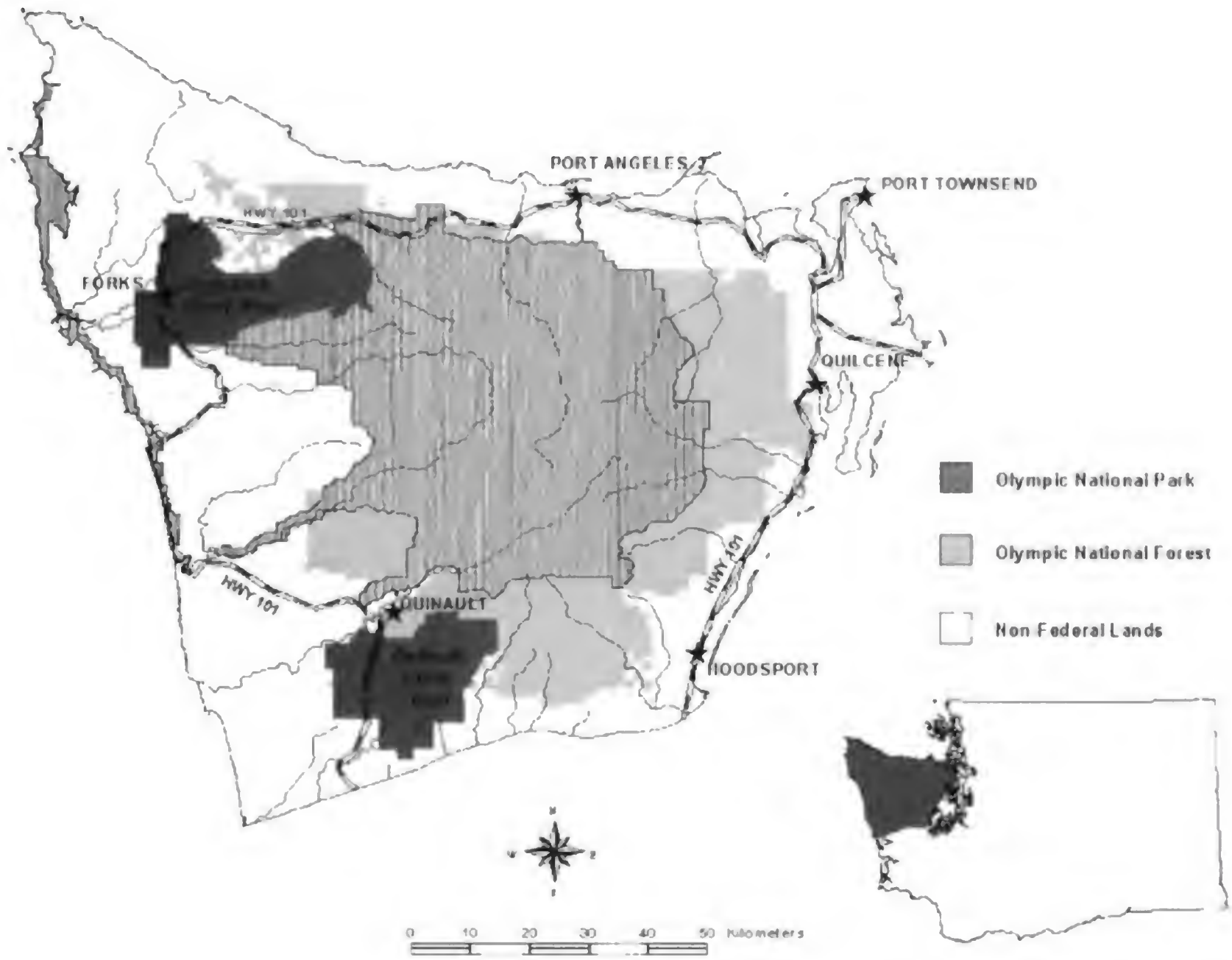

Figure 1. Location of radiotelemetry study areas on the Olympic Peninsula, Washington, 1987–89.

along roads (Guetterman et al. 1991). Azimuths were plotted on 1:12 000 or 1:24 000 scale U.S. Geological Survey orthophotos or topographic maps. We considered the position of the owl to be the geometric center of the polygon formed by the intersection of ≥3 bearings (Nams and Boutin 1991). If weak signals or inconsistencies in the direction of bearings caused us to suspect signal deflection or movement of an owl during triangulation, we discarded the location. We used all locations to estimate home ranges, but only locations with error polygons ≤8 ha were used for analyses of habitat use.

Telemetry Error. We estimated telemetry error with 63 blind trials in which one observer placed transmitters in trees in owl home ranges and another observer then triangulated on the transmitters at night. The median distance between estimated and actual transmitter locations was 100 m ($\bar{x}$ = 140 ± 17 m). This estimate was similar to or less than error estimates in previous telemetry studies of Spotted Owls (Carey et al. 1990, Glenn et al. 2004). Errors of this magnitude undoubtedly resulted in some locations falling in the wrong cover types, but we made the assumption that classification errors due to telemetry error were similar in all cover types, and that our overall assessment should reflect actual habitat use.

Home-range Estimation. We estimated cumulative and annual ranges with the Minimum Convex Polygon (MCP) and Fixed-Kernel (FK) methods (Hayne 1949, Seaman and Powell 1996). For estimates of MCP ranges, we used 100% MCP polygons. For FK estimates, we used 95% and 75% isopleths, which we interpreted as the "home range," and "area of concentrated use," respectively. We used Program CALHOME (Kie et al. 1996) to estimate MCP ranges and Version 4.28 of Program KERNELHR (Seaman et al. 1998) to estimate FK ranges. Contrary to the recommendation of Seaman and Powell (1996), we used the FK method without least-squares-cross-validation (LSCV). We did so because we believe that kernel estimates based on locations where owls stop long enough for the observer to obtain a location tend to underestimate home range areas of owls (because movements across intervening non-forest areas usually happen so quickly that they cannot be documented with a point on the map). Thus, we feel that the LSCV option, which tends to fit the home range isopleth more tightly to the observed points, is likely to cause an even greater underestimate of home ranges. We used all locations for MCP estimates, but we only used foraging locations for FK estimates (because FK estimates that include large

Table 1. Vegetation cover types used to map landscapes for analyses of habitat use by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89.

Old Forest	Multilayered stands of western hemlock and western redcedar in which the dominant overstory trees were typically ≥100 cm DBH. Pacific silver fir was often subdominant or codominant with hemlock or redcedar. Douglas-fir was codominant on a few areas. Also included mixed-age stands of mature and old forest in which both age classes were common. Many of the latter stands were the result of a hurricane force windstorm in January 1921 (Pierce 1921).
Mature Forest	Conifer-dominated stands in which the overstory trees were typically 50–99 cm DBH.
Young Forest	Relatively even-aged stands in which most trees were 31–60 cm DBH. Regenerated on burned areas and old clear-cuts.
Mixed-young Forest	Same as Young Forest except with inclusions of mature trees, usually remnants left during previous fires or harvest.
Pole-sapling	Single-layered conifer stands in which most trees were 10–30 cm DBH. Mostly young stands regenerating on old clear-cuts.
Hardwood/Riparian	Riparian areas dominated by red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and variable amounts of western redcedar.
Clear-cut/Non-forest	Recent clear-cuts dominated by bare soil, grasses, shrubs or small seedling conifers. Also included small areas of meadows, gravel pits, and agricultural, or residential areas.

numbers of roosting locations clustered at the nest site or central place will underestimate foraging areas during the breeding season).

Estimation of Annual, Cumulative, and Seasonal Ranges. Although we marked some owls in June or July of 1987, we did not begin regular sampling of most individuals until late July or August 1987. For these owls, we estimated the first annual range through the end of July 1988. If they were monitored after July 1988, we computed a second annual range for the second year. A few individuals were not marked until fall 1987 or summer 1988, in which case the annual range was estimated for one year only. There was only a weak positive correlation between the number of days in the tracking period and estimates of annual home-range size, regardless of which home range estimator was used (95% FK $r_{32} = 0.221$, $P = 0.223$; MCP $r_{32} = 0.208$, $P = 0.253$). Therefore, we used all annual ranges for comparisons among owls, regardless of the monitoring period.

For six owls tracked in both years, we estimated the cumulative range from the union of the annual ranges (range A + range B minus the area of overlap). Estimates of home range overlap between years, seasons, pair members, or owls on adjacent territories were based on the percent of range A overlaid by range B or the percent of range B overlaid by range A. In most cases, we computed overlap of ranges based on three different frames of reference (75% FK, 95% FK, and 100% MCP). For estimates of overlap of seasonal ranges, we only used the 95% FK.

For seasonal analysis of home ranges, we divided each year into two phenological periods, the "breeding season" (March–August), when Spotted Owls nest and feed young, and the "nonbreeding season" (September–February), when Spotted Owls are largely solitary. Estimates of seasonal ranges were limited to owls tracked ≥120 d during the season of interest.

Habitat Mapping and Assessment of Habitat Use. We examined second-order habitat selection (i.e., use of different forest cover types within the home range of each owl). We developed a cover-type map of the study area that included seven cover types based on structural differences in vegetation as determined from on-the-ground examination of stands and aerial photo interpretation (Table 1). We visited virtually all stands within the study area on one or more occasions to determine the size and species composition of trees. We did not use canopy closure to differentiate among cover types because nearly all forests on the study area had relatively high (≥70%) canopy closure, regardless of stand age or tree size. Cover types were mapped on 1:12 000 scale orthophotos and digitized into an ARC/INFO (ESRI Inc., Redlands, CA U.S.A.) GIS layer. For convenience, we use the term cover type, even though we recognize that our designation of cover type was based on only one component of habitat (i.e., vegetation structure). Site visits to 403 randomly selected grid coordinates indicated that map accuracy was 83%.

We used compositional analysis (Aebischer et al. 1993) to evaluate relative preference of cover types for foraging and roosting. This method treats the individual as the sample unit, accounts for lack of independence among proportions, is not sensitive to serial correlation between locations, and is based on a unique set of observed and expected values for each cover type in the home range of each individual. Expected use was equal to the proportion of the cumulative MCP home range covered by each cover type, and the observed use was the proportion of locations in each cover type. We used Program RSW (Leban 1999) to conduct the analysis. Results of this analysis included a numeric ranking of the different cover types according to their relative "preference," as well as a table of pair-wise comparisons (*t*-tests) indicating the degree to which preference differed between types.

We used paired *t*-tests to determine if the distribution of foraging or roosting locations differed from random locations relative to elevation, distance to the nearest stream, or distance to the nearest open area (clear-cuts/non-forest in Table 1). For these analyses, we computed

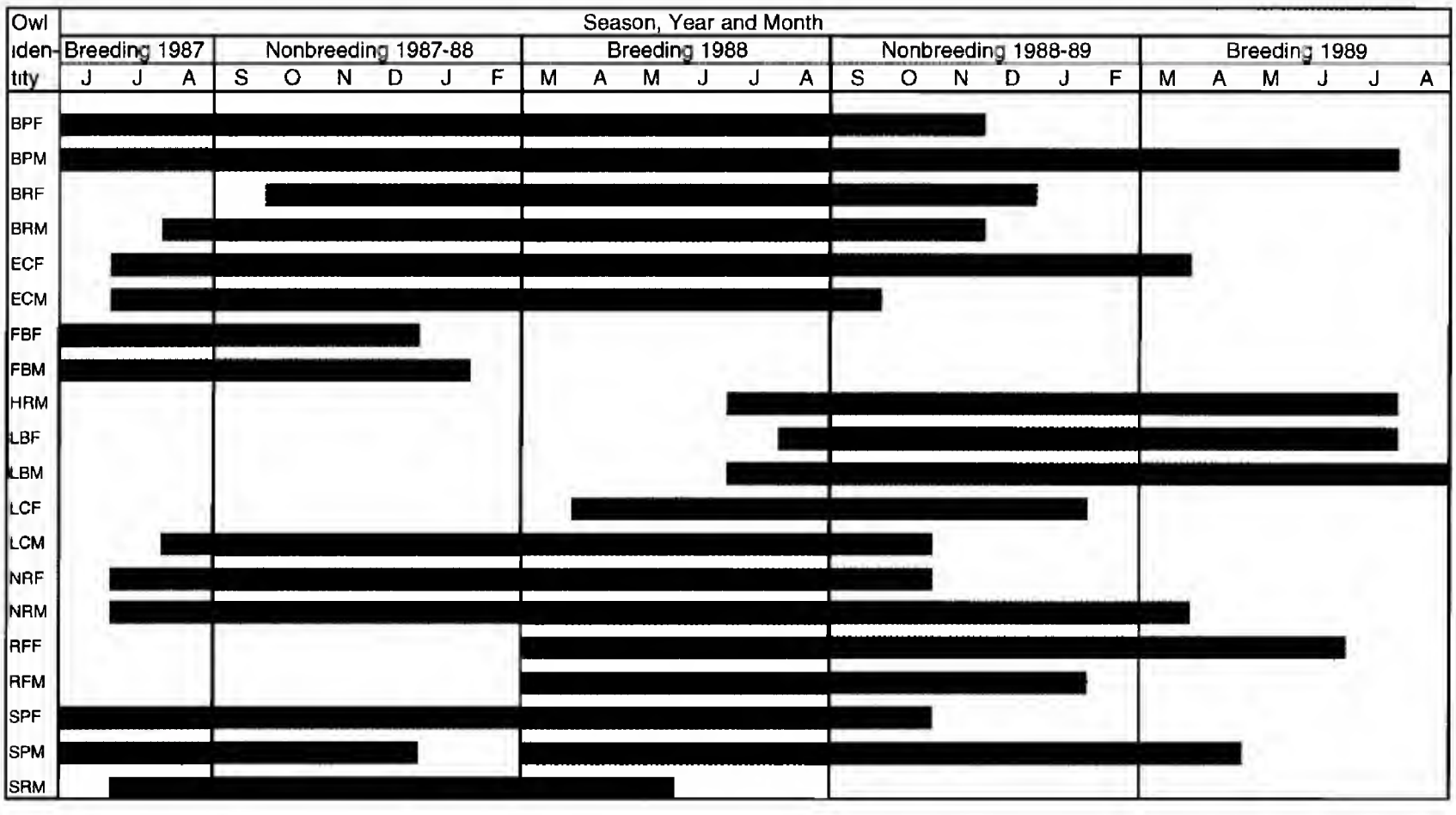

Figure 2. Observation periods of 20 radio-marked northern Spotted Owls observed on the Olympic Peninsula, Washington, 1987–89. Vertical lines indicate intervals used for calculation of seasonal ranges.

mean expected values from a random sample of 200 locations in forest areas in the 100% MCP home range of each owl. We used digital stream layers and elevation layers in GIS to compute elevation and distance to the nearest stream for each owl location and each random location.

Based on a preliminary analysis of our data, the Washington State Forest Practices Board (1996) adopted land management guidelines in which they stipulated that land managers should maintain a minimum of 5863 acres (2372 ha) of "suitable habitat" within a 4.3-km radius around Spotted Owl site centers (known or suspected nest areas) on the Olympic Peninsula. To evaluate the amount of protection afforded by these guidelines, we examined the proportion of each cumulative owl home range that fell within a 4.3-km radius of the nest area or main roost area of each owl, and we compared median and mean areas of "suitable habitat" in cumulative owl ranges with the target in the Forest Practices Rules. All means are expressed as $\bar{x} \pm 1$ SE.

RESULTS

Sample Size and Tracking Periods. We monitored 22 owls in 12 territories, including 10 resident pairs, one territory where we marked one member of a resident pair, and one territory where we marked an adult female that did not appear to have a mate. We did not use the data from the unpaired adult female because she did not exhibit site fidelity. We also did not use data from one female that died shortly after she was radio-marked. Of the 11 pairs in which one or both members were radio-marked, three nested during the study, including one pair in 1987 and two pairs in 1988.

On average, we tracked individual owls for 438 ± 34 d (range = 166–711 d; Fig. 2). Total relocations per owl, not counting incubation locations, averaged 366 ± 35 (range = 126–685). Of 3262 roost locations, we estimated 2360 (72%) by triangulation and located 902 (28%) by homing in on transmitters to locate owls visually in their roost trees.

Annual Ranges. Median estimates of annual ranges of individual owls were 1147 ha (75% FK), 2406 ha (95% FK), and 2290 ha (100% MCP; Table 2). Most mean estimates of ranges were larger than medians because means were skewed by a few individuals with large ranges (Table 2). All owls with annual MCP or FK ranges >5000 ha were individuals that expanded their ranges substantially during fall and winter. Annual ranges were smaller for females than for males, with the exception of the 75% FK estimate (Table 2). In six cases in which we monitored owls for two yr, the sequential annual ranges overlapped by 70 ± 6% based on the 75% FK (range = 18–100%), 73 ± 5% based on the 95% FK (range = 27–100%), and 73 ± 4% based on the MCP (range = 38–100%).

Table 2. Estimates of annual home-range areas of individual northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Estimates include the 100% minimum convex polygon (MCP) and the 75% and 95% isopleths of the Fixed Kernel (FK).

Owl, Sex, and Year[a]	Number of Days and Number of Locations in Sample Period[b]			Home Range Estimates (ha)		
	Days	Roost Locations	Forage Locations	75% FK	95% FK	100% MCP
BPF87	410	160	191	771	1696	1779
BPF88	116	66	70	2209	4196	3295
BPM87	386	147	180	1935	4865	6122
BPM88	325	144	145	3106	8469	8351
BRF87	302	51	136	415	1189	1402
BRF88	142	39	58	804	1720	1151
BRM87	373	52	172	532	1172	1367
BRM88	123	26	37	530	1045	683
ECF87	354	72	129	7927	15 212	10 704
ECF88	276	100	128	1404	4207	6668
ECM87	370	68	159	1108	2104	1917
ECM88	65	55	62	982	1876	1294
FBF87	166	73	79	1586	3483	3086
FBM87	206	99	106	1202	2411	2230
HRM88	366	201	186	2465	6924	7954
LBF88	345	137	143	2195	4931	4950
LBM88	391	168	184	1513	3232	3288
LCF88	246	65	109	967	2235	1915
LCM87	354	45	140	678	1504	2000
LCM88	94	23	42	509	1074	894
NRF87	387	133	174	734	1786	2350
NRF88	95	58	58	2597	5795	4537
NRF88	95	58	58	2597	5795	4537
NRM87	387	165	210	1186	3084	4284
NRM88	274	153	157	5003	11 558	11 252
RFF88	348	208	190	980	2092	2235
RFF89	114	50	44	554	1294	975
RFM88	309	152	144	2516	7059	6704
SPF87	396	154	169	468	1115	1323
SPF88	86	48	55	1228	2402	1406
SPM87	396	154	167	568	1583	1861
SPM88	247	151	142	1072	2533	3593
SRM87	314	34	92	2817	5693	3879
Mean				1642	3736	3608
Median				1147	2406	2290
Mean ♀[c]				1656	3557	3185
Mean ♂[d]				1631	3893	3981
Median ♀[c]				967	2235	1915
Median ♂[d]				1186	2533	3288

[a] First two letters indicate owl name, third letter indicates sex of owl, and numbers indicate year of estimate.
[b] Total locations for NRF87 and SPF87 also included 63 and 76 incubation locations, respectively.
[c] $N = 16$ owl years.
[d] $N = 17$ owl years.

Table 3. Estimates of the cumulative home-range areas of northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Estimates include the 100% minimum convex polygon (MCP) and the 75% and 95% isopleths of the Fixed Kernal (FK) estimator.

Owl Code Name, Sex	Number of Days and Number of Locations in Sample Period			Home Range Estimates (ha)		
	Days	Roost Locations	Forage Locations	75% FK	95% FK	100% MCP
BPF	526	226	261	2216	4303	3527
BPM	711	291	325	3235	8521	8715
BRF	444	90	194	804	1746	1562
BRM	496	78	209	645	1281	1372
ECF	630	172	257	7927	15 212	10 916
ECM	435	134	221	1215	2166	1932
LCM	449	68	182	845	1636	2026
NRF[a]	482	191	232	2580	5995	4852
NRM	661	318	367	5003	11 561	11 252
RFF	462	258	234	985	2164	2298
SPF[a]	482	202	224	1230	2436	1831
SPM	643	305	309	1090	2643	3716
Mean[b]				2315	4972	4500
Median[b]				1222	2539	2912
Mean ♀[c]				2624	5309	4164
Mean ♂[c]				2006	4635	4836
Median ♀[c]				1173	3384	2912
Median ♂[c]				1152	2404	2870

[a] Total locations for NRF and SPF also included 62 and 76 incubation locations, respectively.
[b] $N = 12$.
[c] $N = 6$.

Overlap of annual ranges of nine owls of the same sex that occupied adjacent territories averaged 5 ± 2% for the 75% FK (range = 0–25%), 21 ± 3% for the 95% FK (range = 3–58%), and 26 ± 4% for the MCP (range = 0–58%). These estimates probably did not reflect total overlap with adjacent residents because there were adjacent pairs that we did not have radio-marked and because tracking periods for individual owls were not always exactly the same. However, even with incomplete data on some individuals and no data on the pairs that were not radio-marked, it was clear that home ranges of neighbors overlapped considerably, particularly during winter. In one case, a male from one territory (BPM) was found on several occasions during winter, roosting in the traditional nest area of an adjacent male (HRM).

Cumulative Ranges. Median estimates of cumulative ranges of individual owls monitored in two sequential years were 1222 ha (75% FK), 2539 ha (95% FK), and 2912 ha (MCP; Table 3). Cumulative ranges of females averaged larger than cumulative ranges of males for all comparisons except the mean MCP (Table 3).

Seasonal Ranges. Ranges of individual owls based on the 95% FK averaged 3360 ± 572 ha during the breeding season (range = 883–10 205 ha, median = 2052 ha, $N = 21$) and 3175 ± 572 ha during the nonbreeding season (range = 611–12 352 ha, median = 2168 ha, $N = 29$). There was no consistent pattern of larger ranges in one season or the other. Median estimates of seasonal ranges were smaller than means because means were positively skewed by a few individuals with large ranges. Overlap of nonbreeding season ranges on breeding season ranges averaged 65 ± 4.5% (range = 8–98%, $N = 36$), and overlap of breeding season ranges on nonbreeding ranges averaged 63 ± 4.9% (range = 1–100%, $N = 36$). Overlap of breeding season ranges of two owls tracked in two different breeding seasons averaged 74 ± 8.9% (range = 58–91%). Overlap of nonbreeding ranges of nine owls tracked in two different nonbreed-

Table 4. Results of compositional analysis of habitat use for foraging by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Rank scores indicate relative preference of cover types from highest (6) to lowest (0). Results of pairwise *t*-tests indicate the relative preference of cover types. A positive *t*-value indicates that the row cover type ranked higher than the column cover type and a negative *t*-value indicates that the row cover type ranked lower than the column cover type. A significant *P*-value suggests that confidence in the direction of the relationship was high.

Cover Type[a]		Old Forest	Mature Forest	Mixed-Young Forest	Young Forest	Pole-sapling	Hardwood/Riparian	Clear-cut/Non-forest	Rank
Old Forest	*t*		3.127	4.459	4.637	8.427	4.443	8.103	6
	P		0.006	<0.001	<0.001	<0.001	<0.001	<0.001	
Mature Forest	*t*	−3.127		−1.454	0.774	2.429	0.391	4.183	4
	P	0.006		0.162	0.448	0.025	0.700	0.001	
Mixed-young Forest	*t*	−4.459	1.454		2.756	6.676	2.743	6.528	5
	P	<0.001	0.162		0.013	<0.001	0.013	<0.001	
Young Forest	*t*	−4.637	−0.774	−2.756		1.561	−0.471	2.631	2
	P	<0.001	0.448	0.013		0.135	0.643	0.017	
Pole-sapling	*t*	−8.427	−2.429	−6.676	−1.561		−2.826	2.370	1
	P	<0.001	0.025	<0.001	0.135		0.011	0.029	
Hardwood/Riparian	*t*	−4.443	−0.391	−2.743	0.471	2.826		3.860	3
	P	<0.001	0.700	0.013	0.643	0.011		0.001	
Clear-cut/Non-forest	*t*	−8.102	−4.183	−6.528	−2.631	−2.370	−3.860		0
	P	<0.001	0.001	<0.001	0.017	0.029	0.001		

ing seasons averaged 59 ± 6.3% (range = 10–100%).

During the breeding season, movements of owls were typically centered on the nest tree or, in the case of nonnesting pairs, a regularly-used roost area. Winter ranges typically included part of the breeding-season range plus areas peripheral to the breeding-season range. However, a few individuals spent little time in their breeding-season ranges during the winter season. The most dramatic example was the Elk Creek Female (ECF). After nesting and producing a juvenile in 1987, she left the nest area in August and spent most of the fall and winter in an area 5–15 km away from the nest area before eventually returning to the nest area in June of 1988. The Neilton Ridge Male (NRM) also had a very large nonbreeding range in 1988–89, but in his case, the nonbreeding range overlapped most of the breeding season range.

Ranges of Pairs. There were 14 cases where we monitored annual ranges of paired owls in the same year. The annual ranges of these pairs (union of annual ranges of male and female) averaged 2397 ± 558 ha for the 75% FK (median = 1570 ha), 5449 ± 1111 ha for the 95% FK (median = 4081 ha), and 5414 ± 895 ha for the MCP (median = 5032 ha). Overlap of annual ranges of paired owls averaged 70 ± 5% based on the 75% FK (range = 14–100%), 69 ± 5% based on the 95%FK (range = 14–100%), and 64 ± 5% based on the MCP (range = 14–100%). Estimates of mean overlap of annual ranges were similar, regardless of which sex was used as the frame of reference, so we based the above averages on all possible combinations of overlap.

Cumulative ranges of five pairs that were monitored in both years averaged 3945 ± 1282 ha for the 75% FK (median = 4053 ha), 8278 ± 2550 ha for the 95% FK (median = 9329 ha), and 7488 ± 1951 ha for the MCP (median = 9195 ha). Overlap of cumulative 95% FK ranges of paired individuals averaged 68 ± 14% for males on females and 72 ± 12% for females on males.

Habitat Selection. Use of cover types for foraging and roosting was nonrandom. Old Forest was the most preferred type for foraging, followed by Mixed-young Forest, Mature Forest, Hardwood/Riparian Forest, Young Forest, Pole-sapling, and Clear-cut/Non-forest (Table 4). Pairwise comparisons of rank indicated that Old Forests were consistently preferred over all other cover types (Table 4). Although Mixed-young Forest ranked higher than Mature Forest, pairwise comparisons of rank indicated little difference between the two types

Table 5. Results of compositional analysis of habitat use for roosting by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Rank scores indicate relative preference of cover types from highest (6) to lowest (0). Results of pairwise *t*-tests comparisons indicate the relative preference of cover types. A positive *t*-value indicates that the row cover type ranked higher than the column cover type and a negative *t*-value indicates that the row cover type ranked lower than the column cover type. A significant *P*-value suggests that confidence in the direction of the relationship was high.

Cover Type[a]		Old Forest	Mature Forest	Mixed-Young Forest	Young Forest	Pole-sapling	Hardwood/Riparian	Clear-cut/Non-forest	Rank
Old Forest	*t*		2.605	3.326	4.823	8.079	4.752	16.554	6
	P		0.017	0.004	<0.001	<0.001	<0.001	<0.001	
Mature Forest	*t*	−2.605		0.121	1.141	5.124	1.361	10.527	5
	P	0.017		0.905	0.268	<0.001	0.189	<0.001	
Mixed-young Forest	*t*	−3.326	−0.121		1.163	5.195	1.711	9.010	4
	P	0.004	0.905		0.259	<0.001	0.103	<0.001	
Young Forest	*t*	−4.823	−1.141	−1.163		3.541	0.447	7.540	3
	P	<0.001	0.268	0.259		0.002	0.660	<0.001	
Pole-sapling	*t*	−8.079	−5.124	−5.195	−3.541		−3.271	2.543	1
	P	<0.001	<0.001	<0.001	0.002		0.004	0.020	
Hardwood/Riparian	*t*	−4.752	−1.361	−1.711	−0.447	3.271		6.477	2
	P	<0.001	0.189	0.103	0.660	0.004		<0.001	
Clear-cut/Non-forest	*t*	−16.554	−10.527	−9.010	−7.540	−2.543	−6.477		0
	P	<0.001	<0.001	<0.001	<0.001	0.020	<0.001		

(Table 4). Similarly, Young Forest ranked lower than Mature and Hardwood Forest, but pairwise comparisons indicated that these differences were weak (Table 4). Pole-sapling stands ranked lower than all other types except Clear-cuts, but the pairwise comparisons with other types indicated that preference for Pole-sapling was not greatly different from Young Forest (Table 4). Large *P*-values for all pairwise comparisons of Clear-cuts relative to other cover types indicated that Clear-cuts were the least preferred cover type for foraging. In fact, out of 3822 foraging locations where cover type could be determined, only 57 (1.5%) occurred in Clear-cuts or Non-forest areas, and we suspected that some of these cases were due to telemetry or mapping error.

Use of cover types for roosting indicated that Old Forests were preferred over all other cover types (Table 5). Mature Forest ranked higher than Mixed-young, Young Forest, and Hardwood/Riparian Forest, but pairwise comparisons of these types indicated that differences among them were weak (Table 5). Pole-sapling, Clear-cuts, and Non-forest areas were rarely used for roosting. Of 902 roosts located visually, none were located in Clear-cuts or Non-forest. Of 2275 roosts located by triangulation alone, and for which cover type was determined, eight were in Clear-cuts or Non-forest types; we suspected these were due to triangulation or mapping error.

Habitat Use Relative to Forest Edges, Streams, and Elevation. On average, foraging locations and roost locations were closer to openings (233 ± 24 m, and 271.9 ± 33.0 m, respectively) than were random locations (304 ± 34 m; $t_{forage} = -4.10$, $P = 0.001$, $t_{roost} = -2.04$, $P = 0.055$; $N = 20$ owls). However, the number of locations within 100 m of an edge was similar between random locations and foraging locations (28.4% vs. 33.5%) and random locations and roost locations (28.4% vs. 29.9%), so we concluded that there was little evidence that owls either preferred or avoided forest edges for roosting or foraging.

Mean elevations at foraging locations (315 ± 29 m) and roosting locations (322 ± 31 m) were slightly lower than elevations at random locations (354 ± 36 m; $t_{forage} = -3.63$, $P = 0.002$, $t_{roost} = -3.09$, $P = 0.006$, $N = 20$ owls). Mean distance to the nearest stream was similar for foraging (98 ± 14 m), roosting (112 ± 19 m), and random locations (94 ± 10 m; $t_{forage} = 0.73$, $P = 0.475$, $t_{roost} = 1.75$, $P = 0.097$, $N = 20$ owls).

Landscape Composition and Home Range Size. Size of annual ranges was negatively correlated

with the percent cover of older forest (cover types: Old and Mature forest) in the cumulative MCP range, regardless of whether the estimator was the 75% FK ($r_{31} = -0.53$, $P = 0.002$), 95% FK ($r_{31} = -0.59$, $P < 0.001$), or MCP ($r_{31} = -0.67$, $P < 0.001$). Size of annual ranges was also negatively correlated with the amount of older forest in a 4.3 km circle centered on the central place (75% FK $r_{31} = -0.34$, $P = 0.058$; 95% FK $r_{31} = -0.40$, $P = 0.028$; MCP $r_{31} = -0.46$, $P = 0.009$).

Overlap of Management Circles with Home Ranges. On average, a 4.3-km radius circle centered on the nest site or center of activity included 94 ± 2% of the annual 75% FK home range, 86 ± 4% of the annual 95% FK home range, and 83 ± 4% of the annual MCP range. For 12 owls tracked in both years, average overlap of the 4.3-km radius circle on the cumulative range was 99 ± 13% for the 75% FK range, 79 ± 7% for the 95% FK range, and 76 ± 7% for the MCP range. The counter-intuitive result in which overlap of the 4.3-km circle was lower on the 75% FK annual range than on the 75% FK cumulative range occurred because the estimates were based on different individuals. If we defined "suitable habitat" as the cover types that had the top three preference rankings based on compositional analysis (cover types = Old, Mature, and Mixed-young Forest), then the mean amount of suitable habitat within a 4.3-km radius circle was 3105 ± 236 ha.

DISCUSSION

Home Range Attributes. The large ranges observed in our study suggest that biomass of suitable prey for Spotted Owls is lower on the Olympic Peninsula than in western Oregon and northwestern California, where home ranges tend to be smaller (Forsman et al. 1984, Carey et al. 1990, 1992, Zabel et al. 1995, Bingham and Noon 1997, Glenn et al. 2004). We did not have data on total prey biomass in our study area, but Carey et al. (1992) found that flying squirrels, which are the primary prey of Spotted Owls on the Olympic Peninsula, were relatively uncommon on the peninsula compared to western Oregon.

As in our study, Carey et al. (1990) and Glenn et al. (2004) found that home range size of northern Spotted Owls was inversely related to the amount of old forest in the home range. This suggests that Spotted Owls respond to decreasing amounts of their preferred habitat by increasing the size of their ranges to encompass more old forest. However, Zabel et al. (1995) found no correlation between home-range size of Spotted Owls and the proportion of the range covered by large trees. Instead, they found that home-range size was positively correlated with the proportion of flying squirrels in the diet and negatively correlated with the proportion of woodrats (*Neotoma* spp.) in the diet. In our study area, the diet was dominated by flying squirrels (Forsman et al. 2001), which tend to be most abundant in old forests (Carey et al. 1992, Waters and Zabel 1995). This could explain why home ranges in our study area became larger as the amount of old forest declined. However, for a central-place forager like the Spotted Owl, the ability to increase the size of the home range and still function as a part of the resident breeding population is probably limited by energetic and social constraints (Carey et al. 1992).

In our study, annual home ranges of paired owls typically overlapped by 50–80%. Similar estimates were obtained in a number of other studies (Forsman et al. 1984, Carey et al. 1990, Glenn et al. 2004). Our estimates of mean overlap of annual ranges of owls on adjacent territories were higher than values reported by Forsman et al. (1984:23; MCP overlap = 12%) and Glenn et al. (2004:41; 95% FK overlap = 14.9 ± 4.3% and 6.7 ± 2.2% on two different study areas).

Habitat Selection. Our study, and most other studies in which telemetry methods have been used to examine habitat selection by northern Spotted Owls, indicated that, given a choice, most individuals selectively used older forests for foraging and roosting and that younger stands generally provided lower quality habitat (e.g., Forsman et al. 1984, Call 1989, Carey et al. 1990, 1992, Solis and Gutiérrez 1990, Gutiérrez et al. 1995). However, there have been two radiotelemetry studies of northern Spotted Owls in landscapes dominated by young forest, where patterns of habitat selection were less clear. Glenn et al. (2004) examined habitat selection by Spotted Owls in young forests in northwest Oregon and did not find strong selection for any cover type. In a landscape where old forest comprised less than 10% of the available cover, Irwin et al. (2000) found that northern Spotted Owls infrequently used stands <25 yr of age and foraged primarily in mid-age stands (25–79 yr old) or in remnant patches of old forest. However, Irwin et al. (2000) did not conduct a landscape-level analysis of use-versus-availability with their data, so

we could not determine if use of different cover types differed from availability.

California Spotted Owls (*S. o. occidentalis*) in the Sierra Nevada Mountains tended to forage in forests with ≥40% canopy cover, but did not show a strong preference relative to tree age or tree size (Zabel et al. 1992). However, at two of the three study areas described by Zabel et al. (1992), the majority of foraging and roosting locations were in stands dominated by large (>53 cm DBH) trees.

Of the 5–6 species of small mammals that comprise the primary diet of Spotted Owls, several appear to be most abundant in older forests. For example, there are a number of studies that suggest that red tree voles (*Arborimus longicaudus*) and red-backed voles (*Clethrionomys californicus*) are most abundant in older forests (Corn and Bury 1986, Aubry et al. 1991, Rosenberg et al. 1994). While not all studies of northern flying squirrels have found significantly higher numbers in old forests, the trend in most studies was toward higher numbers in old forests (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995, Lehmkuhl et al. (in press). Therefore, an obvious hypothesis is that differences in abundance of preferred prey cause northern Spotted Owls to select for older forests (Forsman et al. 1984, Carey et al. 1992). Ward et al. (1998) posed a similar hypothesis to explain high use of forest edges by Spotted Owls in northwestern California, where the diet was dominated by dusky-footed woodrats (*N. fuscipes*), which were most abundant in brushy openings adjacent to forests. In contrast, in areas where they feed mainly on flying squirrels, Spotted Owls either avoid non-forest edges or use them in proportion to availability (Zabel et al. 1995, Glenn et al. 2004, this study).

Streams and Elevation. Although Glenn et al. (2004) found evidence that Spotted Owls foraged selectively in riparian vegetation, we found no evidence that foraging or roosting locations were closer to streams than were random locations. We concluded that there was no evidence from our data that owls were either selecting or avoiding riparian areas. Although Spotted Owls in our study foraged at lower elevations than expected, the mean difference between observed and expected foraging locations was only 39 m. We were not convinced that this relatively small difference was biologically meaningful.

Management Implications. Based on the results of our study, we agree with Forsman et al. (1984), Thomas et al. (1990), and Carey et al. (1992) that management for northern Spotted Owls in western Washington and Oregon should focus on the retention of old forests. Although Franklin et al. (2000) and Olson et al. (2004) found that northern Spotted Owls may have higher reproductive output in landscapes that include a mixture of old forest and edges with other forest types, those studies were conducted in areas where woodrats were a primary prey, and the results may not apply to areas like the Olympic Peninsula, where flying squirrels are the primary prey.

Bingham and Noon (1997, 1998) suggested that the U.S. Fish and Wildlife Service should focus on the most heavily-used portion of the home range, or "core area," as the frame of reference for assessment of "take" of Spotted Owls. If this approach is used on the Olympic Peninsula, then we believe it would be reasonable to use our estimates of the 75% isopleth of the FK annual range as the criteria for estimates of core areas, although other methods have been proposed (Bingham and Noon 1997). We agree with Bingham and Noon (1997) that it makes sense to use repeatable measures of home range areas as the frame of reference for assessments of "take," but this should not be misconstrued as a recommendation to manage Spotted Owls based only on core areas. If the objective is to provide Spotted Owls with enough habitat to survive and reproduce on a site, then we agree with Buchanan et al. (1998) that management should be based on amounts of habitat within the entire home-range areas of radio-marked owls, not just core areas.

Our estimates of the median and mean amounts of "suitable habitat" within cumulative MCP ranges of Spotted Owls (1824 ha and 2253 ± 286 ha) are similar to or slightly lower than the management target adopted by the Washington State Forest Practices Board (1996) for management around Spotted Owl nest sites (2373 ha of suitable habitat within a 4.3-km radius). We found that a 4.3-km radius circle centered on the nest site encompassed about 83–87% of the mean cumulative home range used by individual Spotted Owls on the peninsula. Based on these results, we see no reason to suggest changes to the 1996 Forest Practices Rules (Washington State Forest Practices Board 1996). However, it remains to be seen if Spotted Owls will persist in areas where old and mature forests are gradually replaced with less-preferred types that are also classified as "suitable."

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FIRST-CYCLE MOLTS IN NORTH AMERICAN FALCONIFORMES

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ABSTRACT.—I examined 1849 specimens of 20 North American Falconiform species to elucidate the occurrence and nomenclature of partial first-cycle molts. As reported in the literature, American Kestrel (*Falco sparverius*) and White-tailed Kite (*Elanus leucurus*) have relatively complete body-feather molts that occur during the first fall; in the kite, this molt can also include up to all rectrices and 2–6 secondaries, but no primaries—an unusual pattern for such partial molts in first-year birds. Evidence of partial first-cycle molts was found in 16 of 18 other species (among *Pandion, Haliaeetus, Circus, Accipiter, Asturina, Buteo, Aquila,* and *Falco*) for which such molts have not been previously elucidated. Maximum extent of body-feather replacement among individuals of these 16 species varied from 5–50%. On the other hand, most species showed evidence that this molt could be absent (11–100% of birds remaining in juvenile plumage until commencement of the complete or near-complete prebasic molt that occurs during the first summer). I argue that these partial molts are best considered *preformative molts* (following Howell et al. 2003) rather than "first prebasic" molts, as defined by Humphrey and Parkes (1959). Variation in the extent and timing of preformative molts may reflect various constraints according to species-specific breeding, migrating, and foraging strategies. The apparent lack of function for this molt suggests that ancestral Falconiformes exhibited a more extensive preformative molt, as found in related orders of birds, but that this molt has since become vestigial, at least in the larger species.

KEY WORDS: *American Kestrel;* Falco sparverius; *White-tailed Kite;* Elanus leucurus; *preformative molt; hawks; falcons.*

MUDAS DEL PRIMER CICLO EN FALCONIFORMES NORTEAMERICANOS

RESUMEN.—Examiné 1849 especímenes de 20 especies norteamericanas de Falconiformes para establecer la ocurrencia y la nomenclatura de mudas parciales del primer ciclo. Como había sido informado en la literatura, *Falco sparverius* y *Elanus leucurus* presentan mudas relativamente completas de las plumas corporales que tienen lugar durante el primer otoño, aunque en *E. leucurus* esta muda puede también incluir algunas o todas las rectrices y 2–6 secundarias pero ninguna primaria. Esto constituye un patrón poco usual de mudas parciales durante el primer año de vida. Encontré evidencia de mudas parciales en el primer ciclo en 16 de las 18 especies adicionales (en los géneros *Pandion, Haliaeetus, Circus, Accipiter, Asturina, Buteo, Aquila* y *Falco*) para las cuales no se había determinado previamente la ocurrencia de mudas de este tipo. El máximo grado de reemplazo de las plumas del cuerpo en los individuos de esas 16 especies varió entre el 5% y el 50%. Por otra parte, la mayoría de las especies mostraron evidencia de que esta muda podría estar ausente, pues entre el 11% y el 100% de los individuos mantuvieron el plumaje juvenil hasta comenzar la muda prebásica completa, o casi completa, que tiene lugar durante el primer verano. Sugiero que estas mudas prebásicas deben considerase mudas preformativas (siguiendo la terminología de Howell et al. 2003) en lugar de "primeras mudas prebásicas", como fueron definidas por Humphrey y Parkes (1959). La variación en la extensión y en el momento de ocurrencia de las mudas preformativas podría reflejar distintos limitantes de acuerdo a las estrategias reproductivas, de migración y de forrajeo específicas de cada especie. La falta aparente de funcionalidad de esta muda sugiere que los Falconiformes ancestrales exhibían una muda preformativa más extensiva, como se ha documentado en órdenes de aves relacionados, pero que esta muda se ha vuelto vestigial, al menos en las especies de mayor tamaño.

[Traducción del equipo editorial]

North American Falconiformes exhibit various molt strategies during their first year of life. In most species, juvenal plumage is reportedly retained until the first spring or summer (when a year old), at which point a complete or near-complete prebasic molt commences, usually with the shedding of the innermost primaries in Accipitri-

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dae or the medial primaries in Falconidae (e.g., Miller 1941, Palmer 1988, Forsman 1999, Wheeler 2003). In American Kestrel (*Falco sparverius*) and certain kites, by contrast, most to all juvenal body feathers are replaced during the first fall, well before molt of the primaries commences during the following summer (Bent 1937, 1938, Parkes 1955, Palmer 1988, Miller and Smallwood 1997).

For some species of Falconiformes, a limited number of body feathers are reported to be replaced during the first fall, winter, or spring, prior to the shedding of primaries during the first spring or summer. For example, Wheeler (2003) reported that in the Red-shouldered Hawk (see Table 1 for scientific names), "the first prebasic molt begins on the breast, then is noticeable on the back and scapulars" before molt of primaries begins, and Forsman (1999) reported that in the Northern Harrier, "single body-feathers and tail-feathers may be replaced from late winter" prior to the complete molt the following May to October. Similar limited molts in fall, winter, or spring have been reported for Osprey (Bent 1937), Northern Goshawk (Bent 1937, Dement'ev and Gladkov 1951, Forsman 1999), Gray Hawk (Dickey and van Rossem 1938, Wheeler 2003), and several species of Falconidae (Cramp and Simmons 1980, Forsman 1999, Wheeler 2003).

Most authors consider this limited body-feather replacement to be the initiation of the prebasic molt at a year of age (hereafter, "first complete molt") rather than a separate molt; indeed, Wheeler (2003) even interprets the fall molts in first-year American Kestrel and kites as part of the first complete molt, terminating with the flight feathers the following summer. This interpretation appears to disregard the additional body molt that occurs in one-year-old birds concurrent with flight-feather molt in these species (Parkes 1955, Palmer 1988). Herremans and Louette (2000), on the other hand, document that such molts in certain Old-World species of *Accipiter* are distinct from the first complete molt.

Thus, there remains confusion about both the occurrence of partial first-cycle molts in Falconiformes and whether or not body-feather replacement in the first fall, winter, or spring should be considered part of a separate partial molt or as the initiation of the first complete molt. To investigate the occurrence and extent of partial first-cycle molts in Falconiformes, I examined 1227 specimens of 20 North American species collected during their first year (age = 0–12 mo), prior to initiation of primary molt, and 622 specimens collected in their second year (12–24 mo old) or later.

METHODS

Specimens of Falconiformes were examined at the California Academy of Sciences (CAS), San Francisco, the Museum of Vertebrate Zoology (MVZ), Berkeley, and the National Museum of Natural History (USNM), Washington, DC. Specimens were collected throughout North, Central, and South America, but all specimens represented species or subspecies exhibiting boreal breeding cycles. Data are presented for 20 species with $N \geq 16$ first-year individuals examined (Table 1).

Specimens examined included birds collected during their first year of life, prior to the shedding of primaries during the first complete molt, and birds determined to be in their second year of life. Age of first-year birds was determined by plumage features (Palmer 1988, Wheeler 2003), the presence of indicative fault bars (Hammerstrom 1967), tapered and relatively worn outer primaries and rectrices, and absence of wear and color patterns among flight feathers indicating previous molts. Birds in their second year were aged by the presence of predefinitive plumage in some species or the retention of juvenal feathers during the first "complete" molt, particularly among the lesser coverts, on the rump, or within the secondaries (Wheeler 2003).

Each first-year specimen was examined carefully for replaced body feathers in patterns indicating molt. Body molt in Falconiformes typically begins on the head and throat and proceeds caudally (Palmer 1988, Wheeler 2003). Thus, feathers showing wear patterns suggesting replacement in a caudal direction were assumed to have resulted from molt rather than adventitious replacement (e.g., after accidental loss). Replaced feathers were often intermediate in color or patterning between those of first-year and second-year birds (Fig. 1), facilitating their identification. The proportion of newly-replaced body feathers, to the nearest 5%, was estimated for each specimen. Those showing <2.5% replacement were scored as 0%, further ensuring that birds with adventitiously replaced feathers were not included in the sample evincing molt. All primaries, secondaries, and rectrices were also examined for evidence of symmetrical replacement indicating molt. Secondaries were numbered proximally from the outermost (s1) to the innermost (s13 in most species) feather.

Second-year birds were examined for uniformity of feather generations, particularly in tracts for which partial molts were detected in first-year birds. The goal of this examination was to assess whether or not feathers replaced during the first year, prior to initiation of primary molt, had been replaced for a second time during the first complete molt.

RESULTS

Partial First-year Molts in White-tailed Kite and American Kestrel. I examined 22 specimens of

Table 1. Proportion of individuals showing evidence of molt and maximum percent of body feathers replaced, among specimens of 18 species of North American Falconiformes, during three time periods within the first year Values represent sample size of specimens examined, proportion of individuals showing evidence of molt, and maximum proportion of body feathers replaced among individuals sampled.

	SEPTEMBER–NOVEMBER			DECEMBER–FEBRUARY			MARCH–MAY		
SPECIES	*N*	PROPORTION MOLTING	MAXIMUM PERCENT FEATHERS REPLACED	*N*	PROPORTION MOLTING	MAXIMUM PERCENT FEATHERS REPLACED	*N*	PROPORTION MOLTING	MAXIMUM PERCENT FEATHERS REPLACED
Osprey (*Pandion haliaetus*)	10	0.40	10%	3	1.00	20%	2	1.00	35%
Bald Eagle (*Haliaeetus leucocephalus*)	8	0.12	5%	5	0.60	30%	3	1.00	40%
Northern Harrier (*Circus cyaneus*)	35	0.00	0%	18	0.33	15%	16	0.44	50%
Sharp-shinned Hawk (*Accipiter striatus*)	80	0.00	0%	43	0.12	10%	48	0.31	45%
Cooper's Hawk (*Accipiter cooperii*)	59	0.08	10%	26	0.31	10%	14	0.64	10%
Northern Goshawk (*Accipiter gentilis*)	30	0.00	0%	6	0.00	0%	10	0.00	0%
Gray Hawk (*Asturina nitida*)	12	0.00	0%	7	0.14	5%	6	0.33	10%
Red-shouldered Hawk (*Buteo lineatus*)	11	0.45	10%	11	0.45	10%	2	0.00	0%
Broad-winged Hawk (*Buteo platypterus*)	10	0.00	0%	9	0.00	0%	7	0.00	0%
Swainson's Hawk (*Buteo swainsoni*)	7	0.57	10%	5	1.00	25%	15	0.86	40%
Red-tailed Hawk (*Buteo jamaicensis*)	48	0.21	5%	54	0.26	10%	27	0.37	20%
Ferruginous Hawk (*Buteo regalis*)	23	0.13	5%	10	0.50	5%	5	0.60	10%
Rough-legged Hawk (*Buteo lagopus*)	16	0.31	5%	10	0.50	15%	4	1.00	10%
Golden Eagle (*Aquila chrysaetos*)	6	0.17	5%	9	0.22	5%	3	1.00	5%
Merlin (*Falco columbarius*)	51	0.04	5%	33	0.33	15%	18	0.50	50%
Gyrfalcon (*Falco rusticolus*)	15	0.07	10%	12	0.42	30%	5	0.20	25%
Peregrine Falcon (*Falco peregrinus*)	27	0.19	10%	13	0.46	25%	13	0.85	20%
Prairie Falcon (*Falco mexicanus*)	24	0.29	15%	12	0.50	15%	9	0.89	20%

White-tailed Kite and 183 specimens of American Kestrel collected between September and May of their first year. A partial to complete body-feather molt during the first fall was confirmed for all individuals of both of these species. Proportions of replaced feathers indicated that, in both species, this molt had completed or nearly completed by December, with little or no additional molt taking place during January–May, until initiation of the first complete molt. Examination of six White-tailed Kites and 15 American Kestrels undergoing their first complete molt and 73 kites and 274 kestrels in definitive plumage (showing uniform body plumage) confirmed that another complete body

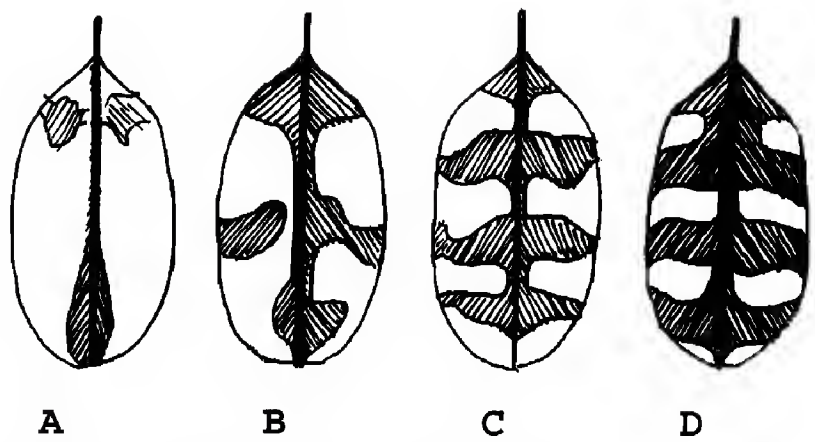

Figure 1. Pigment patterns on underpart feathers of Cooper's Hawks. A—Typical juvenal feather; B—Formative feather replaced in September (CAS62145); C—Formative feather replaced in January (CAS33560); D—Typical definitive feather.

molt occurs in these species concurrent with the flight-feather molt at a year of age.

In White-tailed Kite, 13 first-year individuals collected between January and the initiation of the first complete molt (with shedding of the innermost primaries) had replaced a mean 97.7% of body feathers. All 13 kites had replaced at least some lesser coverts (but no median coverts) and the central two to all 12 rectrices ($\bar{x}$ = 6.9 feathers). In addition, five individuals were found that had replaced 2–6 secondaries during the partial molt, symmetrically on both wings and apparently in the same sequence as observed in complete molts, as determined from clines in wear. The two specimens with the most extensive partial first-year molts were collected in California: MVZ24493 (10 January) and CAS73280 (22 February), each with 100% of the body feathers, all 12 rectrices, and s1–s2, s5, and s11–s13 replaced. No primaries had been replaced during this molt in any individual.

In American Kestrel, 92 individuals collected between their first January and the initiation of the first complete molt had replaced a mean of 90.8% of body feathers. The amount of feathers replaced ranged from 40% of the body and no wing coverts (CAS 73504 collected 26 April) to 100% of the body feathers, all lesser coverts, and up to three proximal median coverts, but no flight feathers (several specimens).

First-year Molts in other North American Falconiformes. Evidence of body-feather replacement prior to initiation of primary molt was recorded in 16 North American Falconiformes (all but Northern Goshawk and Broad-winged Hawk; Table 1). Replaced feathers were observed primarily on the back and breast (Fig. 2). Specimens collected in fall and early winter had replaced some feathers on the crown, throat, and upper back; whereas many spring specimens had replaced larger scapulars and some breast feathers, but had retained most to all feathers of the crown, upper back, and throat. Newly-replaced feathers on the underparts tended to show patterns resembling juvenal feathers when molted in fall and definitive feathers when molted in spring, with a clinal rate of pattern change with time (Fig. 1). The seasonal timing at which definitive characteristics in these feathers were acquired appeared to vary, occurring during the late fall and winter in some species (e.g., Sharp-shinned Hawk, Red-shouldered Hawk, and Peregrine Falcon) and during the spring or later in others (e.g., Swainson's and Rough-legged hawks).

Extent of this molt showed substantial intraspecific and interspecific variation (Table 1). Among the 16 species showing these molts, the mean maximum recorded extent for all species combined was 25.6%, varying from 5% in Golden Eagle to 50% in Northern Harrier and Merlin (Table 1). Examples of specimens showing extensive body-feather replacement included Northern Harrier MVZ144731 (collected in March with 35% replacement), Sharp-shinned Hawk MVZ99723 (May, 45%), Swainson's Hawk CAS13889 (April, 40%), Red-tailed Hawk CAS27181 (April, 20%), Rough-legged Hawk MVZ173433 (December, 20%), and Peregrine Falcon CAS73587 (December, 25%; Fig. 2). On the other hand, at least some individuals (11–80%) of 12 species (or 11–100% of 14 species when Northern Goshawk and Broad-winged Hawk are included) collected in March–May showed no feather replacement (Table 1), and six specimens were recorded that had begun shedding primaries during the first complete molt, but remained in complete juvenal body plumage. No first-year birds of these 22 species showed symmetrical replacement of any flight feathers prior to initiation of the first complete molt.

Two replacement patterns according to season were observed among these 16 species (Table 1, Fig. 3). In Northern Harrier, Sharp-shinned, Cooper's, Gray, and Ferruginous hawks, Merlin, and Peregrine and Prairie falcons, molt had commenced in few birds in fall, some birds in winter, and most birds in spring. In Osprey and Red-shouldered, Red-tailed, and Rough-legged hawks, molt had occurred in some birds in fall, appeared to be suspended in many birds over winter, and was re-

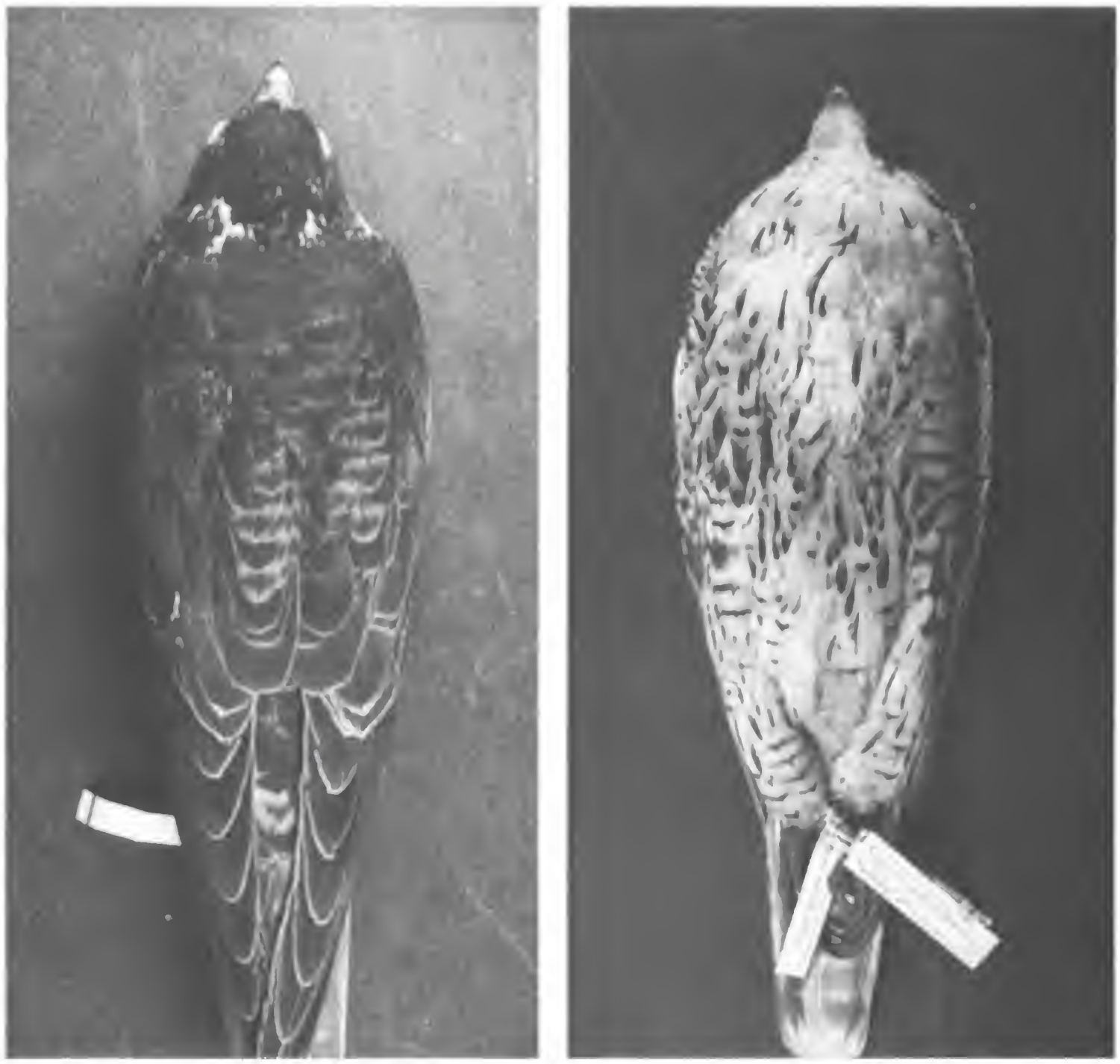

Figure 2. Dorsal and ventral aspects of a first-year Peregrine Falcon (*F. p. anatum*) collected 15 December in California (CAS73587) showing evidence of 25% body-feather replacement during a preformative molt (see Discussion). Formative feathers on the dorsum are bluish and barred, and formative feathers on the underparts are unstreaked (breast) and barred (belly and flanks), resembling definitive feathers in these regions.

sumed or initiated in some birds in spring. The patterns for Bald and Golden eagles, Swainson's Hawk, and Gyrfalcon appeared to be intermediate, with molt occurring throughout the first year (Table 1).

Feather-replacement Patterns in Second-year Birds. Totals of 27 birds collected while undergoing the first complete molt and 146 second-year (12–24 mo-old) birds following completion of this molt were examined, including at least six individuals of all species in Table 1, except for Gray Hawk, Red-shouldered Hawk, and Merlin, for which second-year and older individuals could not be distinguished. For the smaller species (including all falcons), there was no evidence that feathers replaced during the first fall, winter, or spring had been retained during the first complete molt. All 27 birds undergoing this complete molt appeared to be replacing all body feathers (or most feathers in the case of the larger species; see below). On second-year birds that had completed body molt, all scapulars as well as crown, back, and underpart feathers were uniform in wear, reflecting a complete molt within a relatively short time period. For the three species mentioned above, examination of 75 birds in definitive plumage (likely including second-year birds) also showed no variation in feather wear. For five of the larger species, Osprey, Bald and Golden

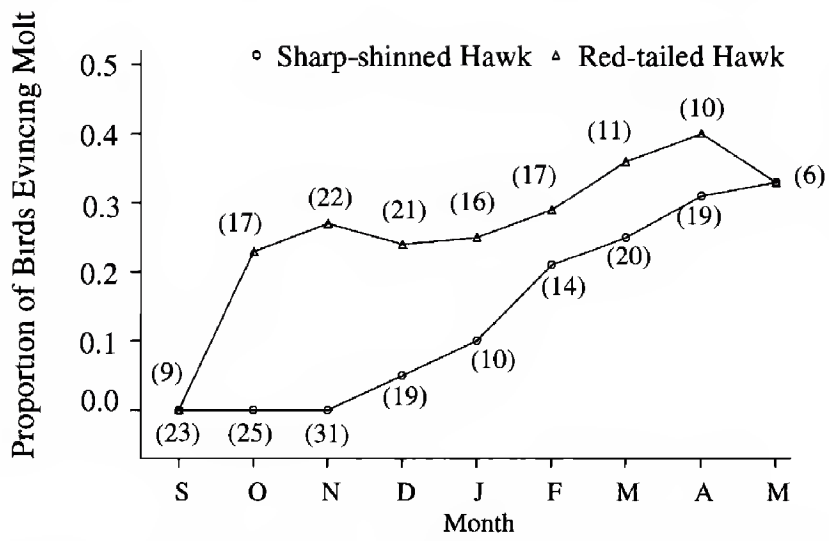

Figure 3. Proportion of individuals evincing body molt, by month, in two species of North American Falconiformes showing differing seasonal-replacement strategies.

eagles, and Red-tailed and Ferruginous hawks, variation in wear among the body feathers precluded confirmation that feathers replaced during the first year were replaced again during the first complete molt. In the two species of eagle, up to many juvenal body feathers could be retained during the first "complete" molt, so it is possible that feathers replaced during the first year may also have been retained during this molt.

DISCUSSION

Traditionally, both the partial first-fall molts of North American Kestrels and kites and the complete molts of other 1-yr-old Falconiformes have been considered the "first prebasic molts," according to the molt terminology of Humphrey and Parkes (1959). However, Howell and Corben (2000) suggested that the complete first prebasic molts of most Falconiformes may be homologous with the second prebasic molts of kestrels, kites, and most other birds. Accordingly, Howell et al. (2003) proposed a revised molt terminology for the first cycle, redefining the *prejuvenal molt* as synonymous with the *first prebasic molt,* the complete molt at the end of the first molt cycle as the *second prebasic molt,* and any inserted molts during the first cycle as *preformative molts.*

Evidence of body-feather replacement during the first year was found in 18 of 20 species examined and, for at least 15 species, the "first complete molt" appeared to include those feathers replaced during the first cycle. By definition (Humphrey and Parkes 1959, Howell et al. 2003), the additional body-feather replacement during the first year should be considered separate, inserted molts; using the terminology of Howell et al. (2003), they should be considered preformative molts followed by the complete or near-complete second prebasic molt at a year of age. Under the terminology of Humphrey and Parkes (1959), the "first prebasic molt" referred to the limited body-feather molt during the first fall, winter, or spring of some individuals or species and to the complete molt at a year of age in other individuals, even within species (*cf. Elanus caeruleus* in Marchant and Higgins 1993), and presumed homology between individuals and species was lost.

In the remaining two species, Northern Goshawk and Broad-winged Hawk, evidence of preformative molts may have been missed in this study due to low sample sizes, especially in spring. Indeed, body-feather replacement during the first year has been reported for Northern Goshawk (Bent 1937, Dement'ev and Gladkov 1951, Forsman 1999). A first-year Broad-winged Hawk (Slater Museum of Natural History No. 2367) collected 1 June reportedly had replaced some breast feathers (Clark and Anderson 1984), although this individual had initiated the second prebasic molt (D. Paulson pers. comm.). It is possible that the constraints of migration may preclude the occurrence of a preformative molt in Broad-winged Hawk; however, substantial evidence of this molt was found in the migratory Swainson's Hawk. In general, birds that migrate to the tropics or Southern Hemisphere often display more extensive first-winter molts, possibly due to more abundant and stable food resources and greater day-lengths with which to forage (Myers et al. 1985, Pyle 1998). Thus, preformative molts should be expected in some Broad-winged Hawks. The evidence, therefore, suggests that preformative molts likely occur in at least some individuals of all North American Falconiformes.

Including the pattern of White-tailed Kite and American Kestrel, three seasonal strategies of preformative molt were identified. Consideration of the ecology and life history of the species comprising each group revealed no evident explanations for conditions or constraints leading to each molt pattern. There appeared to be a slight phylogenetic component, with a majority of species among *Accipiter* and *Falco* delaying preformative molts until winter or spring (see Herremans and Louette 2000), whereas more species among *Buteo* initiated preformative molts in fall. Northerly breeding and wintering species also tended to

show a greater amount of preformative molt in fall; perhaps first-year birds of these species can take advantage of abundant food resources in the fall, but suspend molting during winter when food becomes scarce. Such variation might also be expected within species that show a wide latitudinal breeding range. Within genera, smaller species (including White-tailed Kite and American Kestrel) generally showed higher proportions of birds molting a greater amount of feathers. This correlation is expected based on the added energy required to replace larger feathers (Lindström et al. 1993), and may also be part of a signaling mechanism for species more likely to undergo breeding in their first year (Kemp 1999, Herremans and Louette 2000). Finally, species inhabiting open areas exposed to higher amounts of UV radiation appeared to undergo more extensive preformative molts. However, there were exceptions to all of these patterns, and it is likely that the extent and timing of preformative molts in Falconiformes reflect various constraints according to a complex combination of species-specific, breeding, migrating, and foraging strategies.

Replacement patterns by season indicate that breast feathers and scapulars can be molted later in winter or spring during preformative molts, while juvenal crown, throat, and upper back feathers had been retained, an unusual sequence of feather replacement for Falconiformes (Palmer 1988, Wheeler 2003). This suggests a triggering mechanism for the preformative molt, by which body molt of some feathers is bypassed, resulting in spring birds initiating molt at a later point in the sequence. Thus, sequence as well as extent may vary individually, depending on initiation date. Similarly, hormonal processes controlling feather pattern appear to develop clinally throughout the first year (and sometimes beyond), resulting in delayed acquisition of definitive plumage that varies in timing by species. In Swainson's Hawk and Crested Caracara (*Caracara cheriway*), acquisition of definitive plumage is delayed until the following summer or later, resulting in identifiable second-basic plumages, intermediate in pattern between juvenal and definitive plumages (Wheeler 2003). For the two eagle species, acquisition of definitive plumage requires up to 4 or 5 yr to complete.

Within many species, the preformative molt appears to occur in only a proportion of individuals, with some birds retaining full juvenal plumage until the second prebasic molt. Similar variation in the preformative molt was found among Eurasian *Accipiters* (Herremans and Louette 2000). Thus, some individuals exhibit a "Simple Basic Strategy" (lacking a preformative molt) whereas others exhibit a "Complex Basic Strategy" (including a preformative molt, but lacking prealternate molts) according to Howell et al. (2003). However, at the species level, Falconiformes are best described as exhibiting the Complex Basic Strategy, with the preformative molt ranging in extent from absent to partial.

Evolutionarily, the existence of these variable and at times ephemeral preformative molts may suggest that ancestral Falconiformes exhibited more extensive preformative molts that have become vestigial in most (larger) species that do not breed at age one and can commence the second prebasic molt at an earlier age (Wheeler 2003). Phylogenetic evidence suggests that ancestral Falconiformes branched from a common ancestor that also included Podicipediformes, Pelecaniformes, and Ciconiformes (Sibley and Ahlquist 1990), orders which currently display extensive preformative molts (Palmer 1962, Howell et al. 2003). Alternatively, it is possible that these preformative molts in Falconiformes have become inserted over time, from an ancestral species that lacked such molts; however, the apparent lack of functionality for these molts may argue against this alternative hypothesis. A better understanding of molt and plumage homologies in Falconiformes awaits further study of both molts and phylogenetic relationships.

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MORPHOMETRIC ANALYSIS OF LARGE *FALCO* SPECIES AND THEIR HYBRIDS WITH IMPLICATIONS FOR CONSERVATION

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ABSTRACT.—Morphometric examination of several large falcon species and their hybrids was conducted to ascertain whether phenotype was an accurate indicator of hybrid parentage. Six external body measurements were recorded from 167 Gyrfalcons (*Falco rusticolus*), Saker (*F. cherrug*), Peregrine (*F. peregrinus*), and New Zealand Falcons (*F. novaezeelandiae*) and from 100 F1, F2, and backcross hybrids of these species. Principal Component Analysis separated pure species and also indicated clusters for F1 peregrine × saker, gyr × peregrine, and gyr × saker hybrids. Gyr × peregrine hybrids were distinguishable from their parent species, but it was impossible to discriminate accurately between a complex (F1, F2, and backcross) of gyr × saker hybrids and between these and the parent species. Escaped or released falconry hybrids are perceived as a significant threat to the conservation of wild falcon populations. Under current legislation, gyrs and their hybrids are CITES Appendix I species, and sakers are Appendix II species. We suggest that phenotypic characteristics are not reliable for identification of such hybrids for legal purposes. Furthermore, analysis of measurements also identified a "paternal effect," whereby F_1 hybrids, irrespective of gender, were phenotypically more similar to their paternal than their maternal progenitors.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *Gyrfalcon*; Falco rusticolus; *Saker Falcon*; Falco cherrug; *New Zealand Falcon*; Falco novaezeelandiae; *Falcon hybrids*; *morphometric*; *principal component analysis*; *PCA*; *CITES*.

ANÁLISIS MORFOMÉTRICO DE LAS ESPECIES DE *FALCO* DE TAMAÑO GRANDE Y DE SUS HIBRIDOS, E IMPLICACIONES PARA LA CONSERVACIÓN

RESUMEN.—Se analizó la morfología de varias especies de halcones y de sus híbridos para averiguar si el fenotipo es un indicador preciso de la paternidad de los híbridos. Se registraron seis medidas corporales para un total de 167 individuos pertenecientes a las especies *Falco rusticolus, F. cherrug, F. peregrinus* y *F. novaezeelandiae,* y para un total de 100 híbridos F1, F2 y retrocruces de estas especies. Un análisis de componentes principales separó a las especies puras e identificó grupos formados por híbridos F1 *F. peregrinus* × *F. cherrug, F. rusticolus* × *F. peregrinus* y *F. rusticolus* × *F. cherrug.* Los híbridos *F. rusticolus* × *F. peregrinus* se diferenciaron de las especies parentales, pero fue imposible distinguir claramente entre un complejo (F1, F2, retrocruces) de híbridos *F. rusticolus* × *F. cherrug,* y entre este complejo y las especies parentales. Los halcones híbridos de cetrería que escapan o son liberados se consideran una amenaza para la conservación de las poblaciones silvestres. Bajo la actual legislación, *F. rusticolus* y sus híbridos están registradas en el Apéndice I de CITES y *F. cherrug* en el Apéndice II. Consideramos que las características fenotípicas no son confiables para la identificación de estos híbridos con propósitos legales. Además, el análisis morfométrico identificó "efectos paternos," en donde los híbridos F1, independientemente de su sexo, fueron fenotípicamente más similares a sus progenitores paternos que a los maternos.

[Traducción del equipo editorial]

One of the first domestic hybrid falcons was produced in 1971 from a female Saker Falcon (*Falco cherrug*) and male Peregrine Falcon (*F. peregrinus*; Morris and Stevens 1971, Morris 1972). Since then, falconers and raptor breeders have produced many different hybrids from members of the Falconifor-

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Table 1. Identity of hybrid falcons used in the analysis.

HYBRID IDENTITY[a]	SAMPLES SIZES	MALE PARENT	FEMALE PARENT
F1s			
Gyr × Peregrine	6 ♂, 7 ♀	Gyr	Peregrine
Gyr × Saker	7 ♂, 5 ♀	Gyr	Saker
Peregrine × Saker	3 ♂, 13 ♀	Peregrine	Saker
Peregrine × Gyr	1 ♂	Peregrine	Gyr
Peregrine × New Zealand	1 ♂	Peregrine	New Zealand
Gyr/Saker × Peregrine	1 ♂, 1 ♀	Gyr × Saker F2 hybrid	Peregrine
F2s			
Gyr × Saker	4 ♂, 5 ♀	Gyr × Saker F1 hybrid	Gyr × Saker F1 hybrid
Backcrosses—1st generation			
Gyr × Gyr/Saker	3 ♂, 1 ♀	Gyr	Gyr × Saker F1 hybrid
Saker × Gyr/Saker	3 ♂, 3 ♀	Saker	Gyr × Saker F1 hybrid
Gyr/Saker × Saker	14 ♂, 17 ♀	Gyr × Saker F1 hybrid	Saker
Gyr/Peregrine × Peregrine	2 ♂	Gyr × Peregrine F1 hybrid	Peregrine
Backcrosses—2nd generation			
Gyr (3/8)[b]/Saker	1 ♂	Gyr × Saker F1 hybrid	Gyr/Saker × Saker (backcross hybrid)
Gyr (5/8)[b]/Saker	1 ♂, 1 ♀	Gyr	Gyr/Saker × Saker (backcross hybrid)

[a] When naming hybrids, the paternal species is cited first. For example, a cross between a male gyr and female saker is a gyr × saker (or gyr/saker) hybrid, whereas a male saker crossed with a female gyr is a saker × gyr (saker/gyr) hybrid.

[b] These numbers represent a simple way to show the proportion of genes from the parent species, assuming that a F1 hybrid inherits ½ of the genes from both the male and female parent species. For example, a gyr (3/8)/saker, produced by backcrossing a gyr × saker F1 hybrid with a gyr/saker backcross hybrid, has 3/8 gyrfalcon and 5/8 saker genes.

mes (Boyd and Boyd 1975, Cade and Weaver 1976, Bunnell 1986, Weaver and Cade 1991), including intergeneric hybrids (e.g., Harris's Hawks [*Parabuteo unicinctus*] × Cooper's Hawk [*Accipiter cooperi*] and Harris's Hawk × Ferruginous Hawk [*Buteo regalis*]; Fox and Sherrod 1999a) for falconry purposes.

Many F_1 hybrids are fully viable (Heidenreich 1997), in their turn producing F_2 hybrids or backcrosses (B_1 and B_2 representing 1st and 2nd generation backcrosses) to one or other parent species. Indeed, hybrids from within the subgenus *Hierofalco,* the "desert falcon" group (Heidenreich 1997), exhibit full fertility, presumably over indefinite generations. Less closely-related pairs of species, such as gyr (*F. rusticolus*) and peregrine, produce hybrids with reduced fertility, manifest as deformed spermatozoa, completely sterile females (Heidenreich and Kuspert 1992), or unviable embryos (Rosenkranz 1995).

This extended viability of some falcon hybrids coupled with increasing demand over the last 10 yr for domestic falcons from North American, European, and Arabian falconry markets (Fox and Sherrod 1999b) has prompted conservation concerns. Escaped domestic hybrids may be merely a curiosity (Forseman 1999), a nuisance for bird watchers (Gantlett and Millington 1992), or a threat to the integrity of wild populations. Indeed, falcon pairs made up of an escaped hybrid and a wild, pure individual have been documented several times (e.g., Kleinstäuber and Seeber 2000, Lindberg 2000). A further conservation issue presumably concerns illegal-trade in falcons, whereby protected falcon species may be "laundered" as domestic hybrids. In this study, we examine the relationship between falcon species and their hybrids, particularly the accuracy of using morphometric characters for identification, and discuss the conservation issues concerning falcon hybrids.

METHODS

We investigated four large falcon species, namely Peregrine, Gyr, Saker, and New Zealand falcons (*F. novaezeelandiae*) and several of their hybrid types used for falconry. Hybrid falcons were all bred in captivity and, therefore, their parentage was known. Six external body

Table 2. Principal Component Analysis (PCA) of six anatomical measurements from juvenile male Gyrfalcon, Saker, Peregrine, and New Zealand falcon species and hybrids of those species. Eigenvalues and eigenvectors (based on the correlation matrix).

	Principal Component			
	1	2	3	4
Eigenvalue	3.0328	1.3691	0.7459	0.6833
Percent of variability	0.5055	0.2282	0.1243	0.1139
Cumulated Percent	0.5055	0.7336	0.8580	0.9718
Characters	Eigenvectors			
Wing chord	0.4990	−0.2324	0.1490	−0.3852
Wing width	0.5552	−0.0321	−0.0688	−0.1697
Tail length	0.5195	0.2308	−0.2347	−0.1471
Tail step	0.0247	0.6402	0.7536	−0.1395
Tarsus length	0.3536	0.3591	−0.1598	0.7769
Digit three length	0.2170	−0.5940	0.5697	0.4221

measurements were collected from live juvenile Gyrfalcons (N = 7 males and 6 females), Saker (N = 34 males and 40 females), Peregrine (N = 17 males and 24 females), and New Zealand falcons (N = 25 males and 14 females), and their various hybrids (Table 1). Apart from European Peregrine Falcon subspecies, the majority of which were *F. peregrinus peregrinus,* no other differentiation was made between subspecies or geographic morphs. All birds were kept at the National Avian Research Center's Falcon Facility in Carmarthen, Wales, U.K. The majority of F_2 and backcross 1 and 2 hybrids were between gyrs and sakers. This is because hybrids between members of the subgenus *Hierofalco* remain fertile for an indefinite number of generations, whereas hybrids between more out-crossed falcon species, such as peregrines and sakers, have a reduced fertility. Some of the hybrids included are produced in very low numbers (e.g., Peregrine Falcon × New Zealand Falcon), and published data on these are rare. Therefore, we included them in the analysis.

One of us (C. Eastham) took six measurements, namely wing chord length and width, tail length, tail step (the difference between the outermost tail feather [rectrix 6] and the tip of the center tail feather [rectrix 1] on the same side), tarsus length, and third digit length from each bird. Measurement protocols followed standard methods described by Baldwin et al. (1931), Fox (1977), Biggs et al. (1978), Kemp (1987), and Fox et al. (1997). Feather characters were measured to the nearest 1 mm and non-feather characters to the nearest 0.1 mm using a pair of digital calipers, a steel ruler, and tape measure. Inclusion of single individuals, for example, a male Peregrine Falcon × New Zealand Falcon, allowed us to employ Principal Component Analysis (PCA) on XLSTAT-Pro (Fahmy 1998) statistical software as a suitable method for data analysis. Male and female data were analyzed separately to eliminate background variation due to reversed sexual size dimorphism (Brown and Amadon 1968, Cade 1982), or other sex-linked or sex-limited characters. We used wing chord length to distinguish males and females, as this measurement was reported by Wyllie and Newton (1994) and Eastham (2000) to be the most reliable indicator of overall body size.

RESULTS

Males. Principal Component (PC) 1 (Table 2, Fig. 1) accounted for the majority (50.5%) of variation. Because all eigenvectors for PC1 showed positive and nearly equal values, we concluded this component represents overall body size (Wiley 1981). Male gyrs and F1 and F2 gyr/saker hybrids had the largest body size, whilst male peregrines and New Zealand Falcons were the smallest.

PC 2 (Table 2, Fig. 1) accounted for 22.8% of the variation, as indicated by a contrast in eigenvectors between the positively weighted tail step, tail and tarsus length, the negatively weighted digit three length, and wing chord length and width (Table 2). This component summarizes variation related to body shape. Tail step and digit three length showed the strongest positive and negative weightings, respectively. With a low negative weighting, wing width was of limited use in further analysis of PC 2. New Zealand Falcons had the relatively longest tail step (indicating a more rounded tail), tail and tarsus length, and shortest digit three and wing chord, whilst peregrines, the single peregrine × New Zealand hybrid and gyr/saker × peregrine hybrid had the relatively longest digit three and wing chord length and shortest tail step and tail and tarsus length. F1 gyr × peregrines and sakers showed a wide variation in PC 2 values, with an individual saker having the highest PC 2 value.

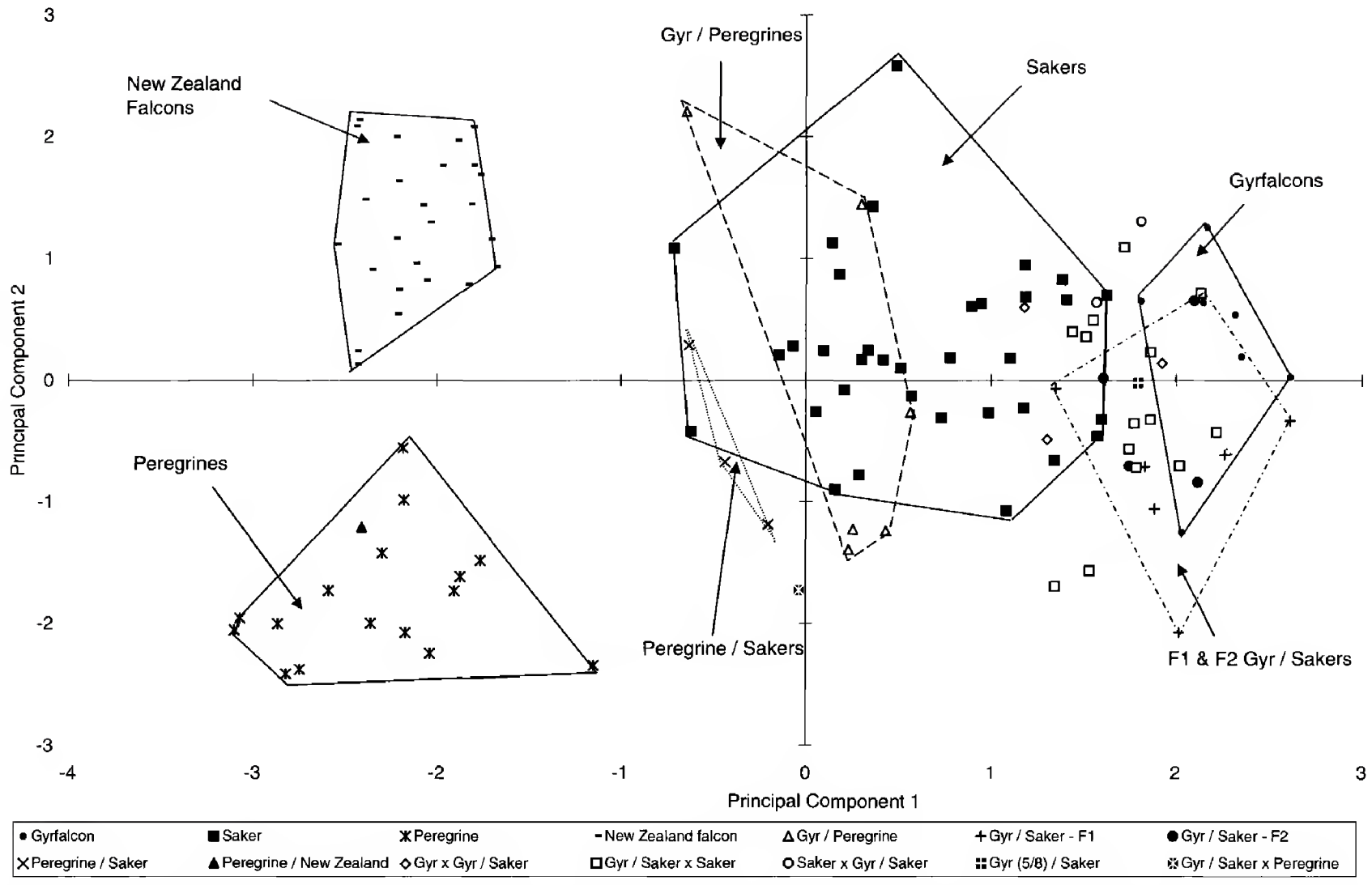

Figure 1. Principal component scores from morphometric comparison of various male falcon species and their hybrids.

PC 3 and 4 (Table 2) accounted for only 12.4% and 11.3% of the residual variation, respectively. Tail step and digit three length had a high positive weighting in PC 3, and in PC 4, there was a contrast between positively weighted tarsus and digit three length and negatively weighted wing chord length. As PC 1 and 2 together accounted for the majority (73%) of variation, we did not consider PC 3 and 4 further.

Females. The PCA for juvenile female falcons showed a similar pattern of variation as that seen in juvenile males. Again PC 1 (Table 3, Fig. 2) accounted for the largest proportion (44.7%) of variation and as indicated by mostly positive and nearly equal values represents, as with males, overall size (Wiley 1981). Gyrs and the various gyr/saker F1, F2 and backcrosses had the largest size, whilst Peregrine and New Zealand falcons were the smallest.

PC 2 (Table 3, Fig. 2) accounted for a further 21.8% of the variation, and we concluded that this, again like males, was related to shape. This was indicated by a contrast in eigenvectors between the positively weighted tail step, tail and tarsus length, the negatively weighted digit three length, and wing chord length and width (Table 3). Positively weighted tail step and negatively weighted digit three and wing chord length had the highest eigenvectors for this PC. New Zealand Falcons had the longest tail step and the shortest digit three and wing chord length, whilst F1 gyr × peregrines and peregrines had the shortest tail length and the longest digit three and wing chord length. PC 3 and PC 4 (Table 3) accounted for 18.4% and 11.4% of the variation, respectively. As for males, we did not consider these principal components further.

DISCUSSION

Using PCA we found that the four falcon species, irrespective of sex, were clearly separated into groups: New Zealand Falcons with a small size, long rounded tails and tarsi, and short wings; peregrines, also with a small size, long digit three lengths, and long narrow wings; sakers with a large

Table 3. Principal Component Analysis (PCA) of six anatomical measurements from juvenile female Gyrfalcon, Saker, Peregrine, and New Zealand falcon species and hybrids of those species. Eigenvalues and eigenvectors (based on the correlation matrix).

	PRINCIPAL COMPONENT			
	1	2	3	4
Eigenvalue	2.6826	1.3071	1.1023	0.6864
Percent of variability	0.4471	0.2179	0.1837	0.1144
Cumulated percent	0.4471	0.6649	0.8487	0.9631
CHARACTERS	EIGENVECTORS			
Wing chord	0.4717	−0.3853	−0.1963	0.4118
Wing width	0.5765	−0.1767	−0.0356	−0.0129
Tail length	0.5737	0.1670	−0.0642	−0.1107
Tail step	0.0866	0.6865	0.1871	0.6869
Tarsus length	0.3077	0.2169	0.6899	−0.4484
Digit three length	−0.1177	−0.5236	0.6672	0.3809

size, long rounded tails, and short digits; and gyrs with the largest size.

Using these external body measurements, we also found it possible to identify three main hybrid groups: a complex of F1, F2 and backcross gyr/sakers; F1 gyr × peregrines and F1 peregrine × sakers. Further, it was possible to separate gyr × peregrines from their parent species, but impossible to separate completely the F1, F2, and backcross gyr/sakers hybrid-complex from pure sakers or particularly, from pure gyrs.

Overall, we found that the hybrids were generally of intermediate phenotype between their parents. However, beyond this it appears that the paternal progenitor influences the phenotype to a greater extent than maternal. For example, for both males and females, the clusters representing F1 gyr × peregrine hybrids, hybrids whose male parents were gyrs, were spatially closer to the gyr clusters than to the peregrine clusters (Fig. 1, 2). Thus, both male and female gyr × peregrine hybrids have a morphology closer to that of gyrs than to peregrines. Further, that the single female peregrine × gyr, whose sire was a peregrine, was spatially closer to the peregrine cluster than the gyr cluster, adds further weight to this proposed generality. Similarly, the male and female F1 gyr × sakers, both with gyrs as male parent, appear more gyr-like than saker-like in morphology. Except for male F1 peregrine × sakers this "paternal effect" seems true for all species combinations. We explain this by considering that two thirds of the sex linked genes in a population are carried by the homogametic sex (male in birds; Mittwoch 1977) and only one third by the heterogametic sex (Falconer 1967). Therefore, falcon sires (the homogametic sex) will contribute more sex-linked alleles to their hybrid offspring than will (heterogametic) dams.

International trade in endangered species, such as some falcons, can be a profitable enterprise and, if unregulated, can threaten their conservation. Regulation of the trade in such endangered species is by international agreements, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). According to their degree of endangerment in the wild, all species are classed in one of three CITES appendices. Special conditions apply to the most endangered, known as Appendix I species (i.e., those threatened with extinction and whose survival could be impaired by trade), which allows restricted trade in captive and domestic bred individuals. Appendix II includes species considered less threatened. The saker is an Appendix II species, and although trade is regulated, this is less exacting than for Appendix I species. Despite relatively healthy world populations and for reasons which are largely political (White and Kiff 1998), gyrs and peregrines and their hybrids are included in Appendix I.

The results we present here show that it can be difficult to discriminate falcon species accurately from their hybrids, especially hybrids of Appendix I gyrs and Appendix II sakers. Similarly, plumage variation, especially in juvenile falcons, is difficult

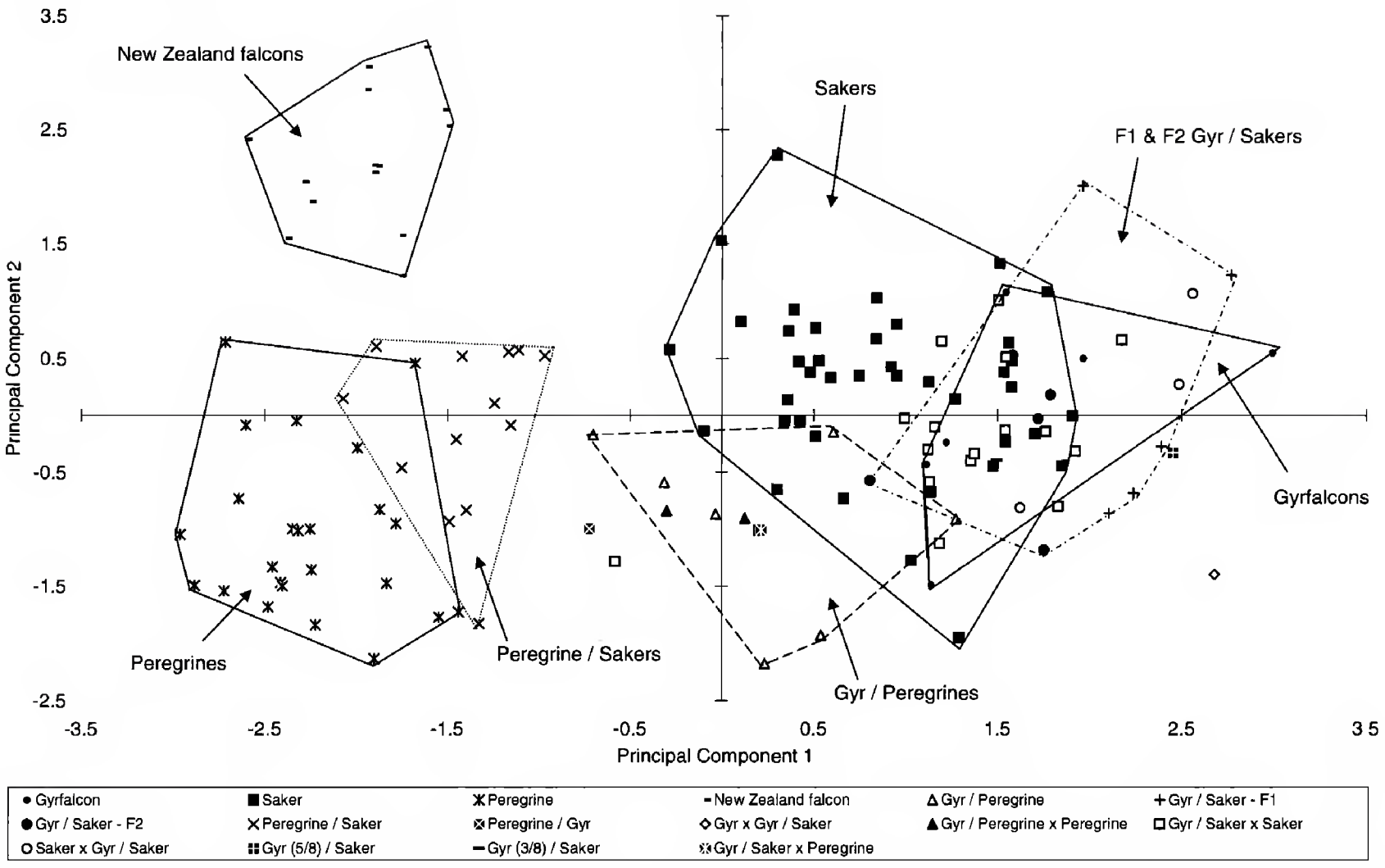

Figure 2. Principal component scores from morphometric comparison of various female falcon species and their hybrids.

to assess objectively and make comparisons between species and their hybrids. These observations may provide fuel for two separate arguments.

Ornithologists are increasingly aware of the widespread genomic compatibility and potential for hybridization amongst what appear to be very dissimilar species (Grant and Grant 1992), such that hybridization between avian species is considered more common than originally thought (Gill 1998). Mayr and Short (1970) estimated that up to 10% of North American bird species regularly hybridize; it's so common that hybrids are even included in birdwatchers' field guides (Sibley 2000). The presence of natural hybrids is not believed to be a threat to the integrity of a species, even though they may challenge the biological species concept of taxonomists (Brookes 1999). Amongst free-living, wild birds of prey such hybridization is increasingly documented at the subspecific (Fefelov 2001), specific (Hamer et al. 1994), and even to the intergeneric levels (Corso and Gildi 1998, Yosef et al. 2001).

Introgressive hybridization may therefore be a process by which species evolve, rather than something that will corrupt them. Thus, if the species concept for birds is much looser than conservation law dictates, then perhaps it is the legislation and not the species concept that must be challenged. For example, the so-called "Altai falcon" (*Falco altaicus* Menzbier), whose phenotype seems to share characters with both gyrs and sakers, is believed by some to be the result of introgressive hybridization between gyrs and sakers, rendering all these as allospecies within a single superspecies (Pfander 1987, Ellis 1995a, 1995b). This being so, then to discriminate between Appendix I gyrs and Appendix II sakers may be irrelevant, and artificially produced crosses between these two may be of no evolutionary threat should they escape to the wild. If, however, the Altai Falcon is merely a large, dark race of the saker (Eastham and Nicholls 2002), and any resemblance to gyrs is merely superficial, then escaped hybrids between these species could potentially compromise wild populations, and the integrity of gyrs and sakers must be recognized and CITES regulations enforced.

A different view of the role of natural hybridization accepts that avian species are dynamic entities,

which in certain circumstances, freely exchange genes with other such entities. Despite these interactions, the integrity of the whole is a fragile one, and to short circuit gene flow *via* artificial hybrids is a danger to this integrity. CITES protocols are the response to perceived conservation status, and therefore, it should be mandatory to discriminate between species as we know them. Accurate identification to assist in controlling the trade in falcons is paramount, and we have shown that criteria other than phenotypic characteristics (e.g., DNA markers) must be employed to identify individuals and species. This is imperative if CITES is to remain an effective means of regulating legitimate trade and protecting species in the wild.

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A CHANGE IN FORAGING SUCCESS AND COOPERATIVE HUNTING BY A BREEDING PAIR OF PEREGRINE FALCONS AND THEIR FLEDGLINGS

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ABSTRACT.—The foraging habits of one pair of Peregrine Falcons (*Falco peregrinus*) nesting on a power plant in central Alberta were studied over seven consecutive breeding seasons (1998–2004). We observed 386 attacks that resulted in 117 captures of prey. The success rate increased from 21.9% in the first year to 39.1% in the seventh year and averaged 30.3%. The majority of hunts (76.7%) were initiated from soaring, and the peregrines commonly used the hot air above the plant's smoke stacks to gain height. The success rates of hunts launched from soaring versus perches were not significantly different (28.7% versus 35.6%). Tandem hunts by the pair ($N = 100$) were more successful than solo hunts (39.0% versus 27.3%), but the difference was not significant. The main prey species were Franklin's Gull (*Larus pipixcan*) and small passerines, which made up 53.0% and 27.4% of kills, respectively. There was a significant difference in the respective capture rates of these prey types (42.5% versus 24.1%). The success rates of the male and the female peregrines were not significantly different, but there was a notable difference in the prey taxa taken by each gender. The male captured 84.4% of the passerines, but only 22.9% of the gulls. After the first year, there was a significant switch from passerines to gulls, which paralleled a significant change in gender participation in foraging. All gulls captured by the male were surrendered to the female or to the fledged juveniles. In 23.3% of hunts, one or both parents were accompanied by one or more fledglings. The male participated in 76.7% of all parent-fledgling hunts ($N = 90$), the female in 10.0%, and the remainder by both parents. Aerial prey transfers from adults to flying young were feet-to-feet or through aerial drops. The hypothesis that parent peregrines make live-drops of prey to their fledged young to teach them how to hunt is confounded by observations that live-drops of just-caught prey are also made by the adult male to his mate. However, the hypothesis that peregrines assist their young in capturing prey is supported by anecdotal evidence.

KEY WORDS: *Peregrine Falcon;* Falco peregrinus; *tandem hunting; fledgling hunting; adult hunting; cooperative hunting.*

CAMBIOS EN EL ÉXITO DE FORRAJEO Y CAZA COOPERATIVA EN UNA PAREJA DE *FALCO PEREGRINUS* Y SUS VOLANTONES

RESUMEN.—Se estudiaron los hábitos de forrajeo de una pareja de *Falco peregrinus* que anidó en una planta de energía en el centro de Alberta a lo largo de siete épocas reproductivas consecutivas (1998 a 2004). Observamos 386 ataques, los cuales resultaron en 117 capturas de presas. La tasa de éxito se incrementó del 21.9% en el primer año al 39.1% en el séptimo año, y en promedio fue del 30.3%. La mayoría de los eventos de caza (76.7%) fueron iniciados a partir de vuelos elevados; los halcones emplearon frecuentemente el aire caliente que se encontraba encima de las columnas de humo de la planta para alcanzar mayores alturas. La tasa de éxito de los ataques iniciados en vuelo no fue significativamente diferente de la de los ataques iniciados desde perchas (28.7% versus 35.6%). Los eventos de caza en los que ambos miembros de la pareja participaron en tándem ($N = 100$) fueron más exitosos que aquellos en los que participó un solo individuo (39.0% versus 27.3%), pero la diferencia no fue significativa. Las presas predominantes fueron la gaviota *Larus pipixcan* y varias aves paserinas pequeñas, representando el 53.0% y el 27.4% de las capturas, respectivamente. Existió una diferencia significativa en las tasas de captura de los distintos tipos de presa (42.5% para *L. pipixcan* y 24.1% para las aves

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paserinas). Las tasas de éxito no fueron diferentes entre el macho y la hembra, pero existió una notable diferencia en los taxa capturados por cada individuo. El macho capturó el 84.4% de las aves paserinas, pero sólo el 22.9% de las gaviotas. Después del primer año, existió un cambio significativo de paserinas a gaviotas de forma paralela con un cambio significativo en la participación de los miembros de la pareja en el forrajeo. Todas las gaviotas capturadas por el macho fueron entregadas a la hembra o a los volantones. En el 23.3% de los eventos de caza, uno o los dos padres estuvieron acompañados por uno o más volantones. El macho participó en el 76.7% de todas las cacerías en las que participaron volantones ($N = 90$), la hembra en el 10.0% de éstas, y ambos individuos en el porcentaje restante. Los adultos entregaron las presas a los juveniles en vuelo directamente de garras a garras, o dejándolas caer en el aire. La hipótesis de que los parentales dejan caer presas vivas para enseñarles cómo cazar a sus volantones es difícil de apoyar ya que el macho adulto también dejó caer presas recién capturadas en vuelo para que su pareja las tomara. Sin embargo, la hipótesis de que los peregrinos le ayudan a sus volantones a capturar presas es apoyada por información anecdótica.

[Traducción del equipo editorial]

Cooperative or tandem hunting by mated pairs of Peregrine Falcons (*Falco peregrinus*), in which both partners attack the same prey simultaneously, has been reported from many locations across the species' worldwide range (e.g., Cade 1960, Bird and Aubry 1982, Thiollay 1988, Frank 1994, Treleaven 1998, Jenkins 2000). The success rate of tandem hunts has been reported to be higher than hunts by single peregrines (Thiollay 1988), but whether or not tandem hunting by mated pairs actually involves a degree of coordination between the two individuals is unclear. On their breeding range, Peregrine Falcons are also known to hunt together with their fledglings, although data are limited (Brown and Amadon 1968, Palmer 1988, White et al. 2002). The notion that juvenile peregrines need to be taught hunting skills by their parents is contradicted by the fact that captive-reared peregrines, deprived of parental instruction, begin pursuing and capturing prey at about the same age as young falcons at natural nest sites (Cade and Burnham 2003). Apparently, the peregrine does not need to be taught how to chase and kill prey (Cade 1982, Sherrod 1983). However, Newton (1979) and Ratcliffe (1993) state that more critical observation is needed during the period in which fledglings achieve independence.

This paper presents empirical data on the foraging behavior of one mated pair of peregrines hunting solo or in tandem over seven consecutive breeding seasons. Additionally, we present anecdotal observations on parent-fledgling interactions.

STUDY AREA AND METHODS

The study area is in central Alberta, Canada, at 53°N. In this largely agricultural region, peregrines nested commonly on cliffs and cutbanks along rivers and creeks until they became extirpated (Dekker 1967, Fyfe 1976). A government program of releasing captive-reared peregrines in central Alberta began in 1975 and led to the establishment of breeding pairs on city buildings by 1981 (Holroyd and Banasch 1990). By the mid 1990s, peregrines began using nest boxes on high industrial structures in rural regions. The breeding site selected for this study is a power plant on the north shore of Wabamun Lake, which is roughly 8 × 20 km in size. The nest box was built by the Alberta Falconry Association in 1993 and put in place by TransAlta Utilities (Wabamun, Alberta) on a catwalk just below the top of a 91 m smoke stack. Lower down, the flat roof of the main building functions as a landing pad for newly-fledged young. Power line pylons in the vicinity provide high perches and plucking posts. Settling ponds and bare ground adjacent to the plant are used as loafing areas by the fledglings and by the adults that bring down large prey such as gulls and ducks. The landscape around the Wabamun plant is mainly wooded with small marshes and an extensive area (5–10 km^2) of excavated and reclaimed terrain to the north. The lake receives light recreational use, and some shoreline sections are developed with cottages and small marinas.

The nest box is in plain view from a public road that runs between the lake and the plant. Depending on weather conditions, we watched from different vantage points 0.1–2 km away, and we used 8× wide-angle binoculars and 20–60× telescopes. Observation periods, lasting 3–6 hr each, usually between mid-afternoon and sundown, were spaced arbitrarily and increased during the period when the fledglings were on the wing. Over 7 yr, 1998–2004, the number of observation days was 196: 15 in June, 58 in July, 101 in August, 21 in September, and 1 in October. The only two days of observation in 1997 were added to the 1998 total. The median date when the first juvenile (always a male) fledged was 16 July (13–25 July). The number of young fledged was three or four per season with a mean of 3.6 (N = 11 males and 14 females). As indicated by their leg bands and plumage characteristics, the breeding pair consisted of the same individuals for the duration of the study, and we classified the female as a 2-yr old falcon in 1998 based on her brown dorsal color in 1997. The subspecific origin of these falcons is *F. p. anatum* and both originated from captive-reared stock nesting in the cities of Edmonton

and Calgary (Gordon Court, Alberta Environment, pers. comm.).

Prey species upon which peregrines are known to feed, such as waterbirds and small passerines, are common in the study area. With a mass of 220–335 g (Dunning 1984), the Franklin's Gull (*Larus pipixcan*) is close to the mass limit that male peregrines can or are willing to carry over long distances. Although Franklin's Gulls are locally scarce in early summer, large migrating flocks begin arriving in mid-July. Rock Pigeons (*Columba livia*), which are the dominant prey for peregrines in human altered environments (Ratcliffe 1993), were resident at the plant site but only in small numbers (<20).

The terms hunt and attack are used interchangeably and represent one attempt at capturing prey including one or more stoops or passes at the same target of which the outcome was known. Tandem hunts were simultaneous attacks by both adults on a flock of prey or an individual prey. Group hunts by a combination of parents and juveniles were tallied as adult hunts, and their kills were considered to have been made by the adults, although in a few cases it was the juvenile which actually seized (or was allowed to seize) the prey. Hunts by juveniles alone were not tallied.

Details of hunts and kills were entered into field diaries and annotated tabulations. Observer bias in comparing results between years, we believe, was not a factor as D. Dekker recorded observations over the 7-yr study period. R Taylor was associate observer the last 3 yr of the project. Data sets were compared for significance by chi-square Test of Independence with a Williams' correction as described in Sokal and Rohlf (1981).

RESULTS

Hunting Methods and Prey Species. We observed 386 hunts by the adult peregrines. Nearly all (99.5%) were directed at airborne prey and consisted of two primary methods: attacks launched from soaring flight (76.7%) or from a perch (23.3%; Table 1). The falcons typically began a soaring sequence by circling up over the plant and using the hot air of the three stacks to gain height rapidly. Drifting downwind, the soaring falcons reached altitudes estimated to exceed 1000 m. By flapping their wings or gliding, they cruised upwind. Attacks on prey flying lower than the falcon were made by deep stoops with wings partly or fully flexed. Some of these attacks began with a burst of wing flaps and ended in a stoop, which could either be near-vertical or oblique. If the prey evaded the initial stoop, the falcon might follow up with one or more additional stoops or passes.

Still-hunting attacks were launched from high perches such as the catwalk railing near the top of the 91 m stacks. With rapid wing flaps, these falcons headed for targets some distance away (>100 m). After unsuccessful or aborted attacks, the peregrines commonly returned to the plant, either to perch or to regain altitude by soaring. Some hunting sequences lasted 3–4 hr before a prey was captured. On other days, we observed falcons catch three prey in less than 1 hr.

The success rate of all hunts (N = 386) by the adult peregrines, either attacking prey solo or in tandem, was 30.3% (Table 1). Perch hunts were not significantly (G = 0.77, P = 0.379) more successful than soar hunts (35.5% and 28.7%, respectively). The success rate of the female was 37.1%, not significantly (G = 2.37, P = 0.124) different from that of the male (24.1%), but there was a notable difference in the taxa of the prey taken by the two sexes (Table 2). The male caught 84.4% of 32 small passerines, but only 22.9% of 62 gulls. Nearly all gulls seized by the male were released to his mate or a fledgling <1 sec after capture. If neither the female nor any of the fledglings were nearby, the male, upon seizing a gull, brought it down steeply and left it on open ground or on the roof of the plant (N = 5). The female carried gulls with apparent ease over distances exceeding 1 km.

The majority (84.9%) of gull kills observed at close range or found as prey remains (N = 73) were juveniles. Juvenile Franklin's Gulls were often seized in mid air during the falcon's first stoop. By contrast, adult gulls typically evaded a peregrine by rising steeply. Some evaded two or more additional passes and were eventually left alone. Others descended and plunged into water. In seven instances, the female peregrine repeatedly swooped at the swimming gull. Three were retrieved from the water and carried off. Some white birds, assumed to be gulls, that evaded 20 or more diving attacks far out over the lake may have been Common Terns (*Sterna hirundo*). Two terns were carried to the plant, but their capture had not been observed. Ring-billed Gulls (*Larus delawarensis*) were sometimes forced down, but we found no evidence that any were killed.

Rock Pigeons were seldom attacked. On two occasions, the female stooped unsuccessfully at free-flying flocks of pigeons. Both adults made opportunistic passes at pigeons that flushed from plant ledges below them, but the only successful pigeon hunts (N = 2) were initiated by fledglings. In at least one of these hunts, the capture was made by the adult female, who joined the attack.

During the sixth year of study, we gained the impression that the falcons had become more successful—in particular, at capturing gulls—than during the preceding years. This impression was

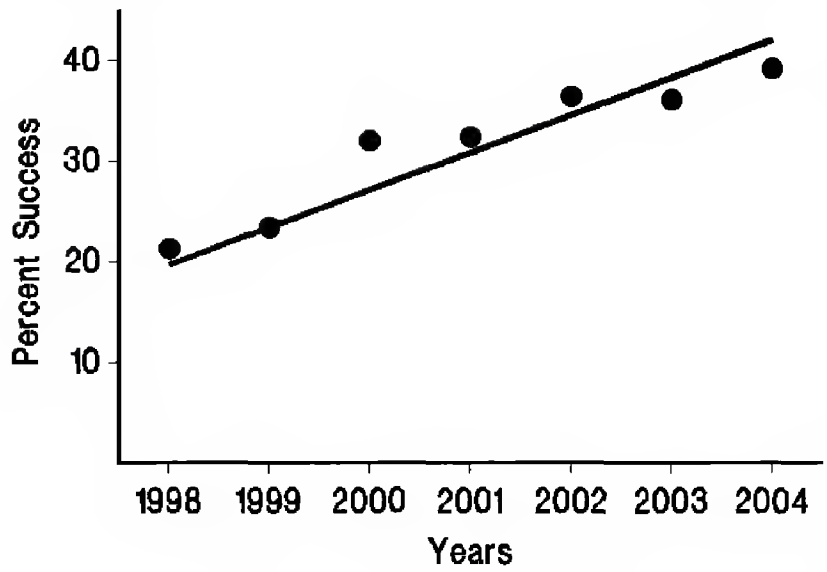

Figure 1. Hunting success per year of the same pair of Peregrine Falcons breeding in central Alberta, 1998–2004. The respective number of hunts/kills for the 7 yr of study were as follows: 108/23, 47/11, 25/8, 37/12, 44/16, 61/22, 64/25.

strengthened in year 7 and confirmed by subsequent data analysis. The overall success rate of the adults increased from 21.3% in the first year of study to 39.1% in the seventh year of study (Fig. 1).

Tandem Hunts. Each year from mid June onwards, both parents often began soaring together. The male gained height quicker and always circled higher than the female. Stooping alternately, they attacked 68 prey from soaring flights (Table 1). If no prey had been sighted for some time, the pair separated or headed off into the distance, one following the other, either in soaring or flapping flight. Tandem attacks were also launched from high perches on the plant. In tandem attacks, both falcons could take the lead, and the male flew higher than the female. While the female approached the prey directly, the male typically attacked from above in a near vertical stoop. A high percentage (60–75%) of tandem hunts were lost from view before we could either see the target or the result. Tandem hunts of which the outcome was known (N = 100) represented 25.9% of all hunts, and their success rate was higher than in 286 solo hunts (39.0% versus 27.3%), but the difference was not significant (G = 2.39, P = 0.121). The success rate of 32 tandem attacks launched from a perch was 50.0%, compared to 33.8% for tandem attacks from soaring position.

Tandem hunts resulted in 39 kills (Table 1). Of these, 26 captures of prey were observed in detail: seven were seized by the female, 19 by the male. Prey caught by the male in tandem attacks were surrendered at once to the female, either by feet-to-feet transfer (N = 5) or released in the air (N = 14). Thirteen of these aerial drops were gulls, which resumed flight upon release. Nine were subsequently seized by the female; four evaded her passes and were let go or escaped by splashing down into water.

Hunts by Groups of Adults and Fledglings. In 23.3% of hunts (N = 386), one or both parents were accompanied, and often harassed, by one or more juveniles (Table 3). Some fledglings closely followed the adults prior to the start of a hunt, others approached hurriedly from a distance to join a hunt in progress. A significant majority of group hunts (G = 37.96, P = 0.001) were led by the adult male, which made 71.0% of the 31 kills (Table 3). Prey caught by the parents were transferred, usually at once, to the approaching juveniles, either by feet-to-feet transfers (N = 15) or through aerial drops (N = 7). At least three small passerines that were dropped were still alive and resumed flight. They were recaptured by a juvenile or by the adult and released again. Three live-drops were gulls. In addition, four of 11 gulls caught in adult-juvenile hunts were seized in flight by the juveniles "chaperoned" by adults.

After successful group hunts, one or more juveniles fed on the kill. If the feeding site was in an open area away from the plant, the adult female typically perched on a pole nearby (N = 14). At

Table 1. Hunts and kills made by a pair of Peregrine Falcons nesting on a power plant in central Alberta, 1998–2004. The hunting success rates are presented in parentheses.

	HUNTS/KILLS FROM SOARING	HUNTS/KILLS FROM PERCH	TOTAL HUNTS
Adult male (24.1%)	176/44 (25.0%)	40/8 (20.0%)	216/52
Adult female (37.1%)	52/18 (34.6%)	18/8 (44.4%)	70/26
In tandem hunts (39.0%)	68/23 (33.8%)	32/16 (50.0%)	100/39
Totals (30.3%)	296/85 (28.7%)	90/32 (35.5%)	386/117

the approach of people, she vocalized and "swooped" overhead. She also stooped at crows or *Buteo* hawks, apparently to drive them away. After the fledglings were satiated and left, the adult female sometimes fed on the remains of the kill ($N = 5$).

DISCUSSION

Hunting Success. The hunting success of adult peregrines on breeding territory is generally higher than that of migrating or wintering peregrines (Dekker 1980, Roalkvam 1985). Jenkins (2000) compared data presented in eight publications on breeding peregrines and found an extreme variation (9.3–84.1%) in hunting success, but much less variation in hunting methods. The majority (58–75%) of attacks summarized in his review were launched from a perch. By contrast, the percentage of perch hunts was only 23% at Wabamun. The "still-hunting strategy" of perch hunts reduces the energy cost of foraging. However, high-soaring flight is also relatively energy-efficient and widens the radius of the attack zone (Enderson and Craig 1997). Soaring flight has been reported as a common hunting method in many regions, but not to such a high degree as documented in this study. The second highest use was recorded in Africa, where breeding pairs launched 30–42% of hunts from flight (Thiollay 1988, Jenkins 2000). The use of factory exhaust to facilitate soaring flight by the Wabamun peregrines was described in an earlier publication (Dekker 1999), but this phenomenon has to our knowledge not been reported elsewhere.

It is noteworthy that the falcons in this study attacked nearly all of their prey in flight, often at great altitudes. This is in sharp contrast to migrating or wintering peregrines, which commonly use surprise methods to attack prey on the ground or in shallow water (Dekker 1980, 2003, Cresswell 1996). However, there is also an element of surprise involved if a soaring peregrine stoops from a great height at prey flying far below. In solo hunts, the male frequently made long stoops that levelled out low over woods and were aimed at flocks of small passerines flying just beyond the trees. Surprise is probably also a factor in tandem hunts in which the male stoops from high above while the female pursues the prey at a lower altitude.

A key factor in the hunting success of peregrines is the vulnerability of individual prey, which is difficult to assess for the human observer. It is well-known that predation risk for land birds increases over water (Herbert and Herbert 1965). Conversely, water birds become vulnerable over land (Hunt et al. 1975, Dekker 1980). Mature prey on home territory should be harder to catch for a raptor than juvenile prey passing over unfamiliar terrain. In central Alberta, the migrations of juvenile prey species approximately coincide with the period when fledgling peregrines are on the wing and when the parental task of provisioning them is most demanding. In this study, the peregrines were very successful at capturing juvenile Franklin's Gulls. For instance, on 7 d between 17 July and 9 August 2003, when thousands of gulls were passing through the area, the adult female, hunting solo, captured each of seven juvenile gulls in her first attack of the afternoon and each requiring only one stoop. While it does not seem surprising that bird-hunting falcons should become better at what they do as they become older and gain in experience, data in support of that notion have, to our knowledge, not been published before. An explanation for the year-to-year increase in the success rate of the Wabamun pair is that these falcons became specialists on juvenile Franklin's Gulls, which differ from adults by their dusky color and absence of black on the head. Juvenile targets were probably pre-selected before the falcons began their attack. A similar pre-selection hypothesis was advanced for the high success rate (73–93%) of "Red Baron," an adult male peregrine hunting over coastal marshes in New Jersey (Cade and Burnham 2003:333).

In this study, the prey component changed significantly after the first year (Tables 4 and 5). In the first year of study, gulls made up only 8.7% of kills compared to 63.8% in years 2–7 ($G = 10.85$, $P = 0.001$). The proportion of small passerines changed significantly from 60.9% in the first year to 19.1% in years 2–7 ($G = 7.01$, $P = 0.008$). Overall, the capture success on gulls (of both age groups) was significantly higher ($G = 5.35$, $P = 0.021$) than on small passerines (42.5% versus 24.1%). Successful taking of juvenile gulls may be even higher than for adults, but an adequate sample was not available for adults. As reported in results, the sample of gull kills ($N = 73$) included 84.9% juveniles.

Coincident with the observed prey switch, we recorded a major change in foraging participation between the sexes after the first year (Table 6). The male's solo hunts in the first year were 78.7%

Table 2. Prey taxa captured by the Peregrine Falcon pair hunting solo or in tandem.

	FRANKLIN'S GULLS	SMALL PASSERINES	SMALL SHOREBIRDS	DUCKS	OTHER OR UNIDENTIFIED
Adult male	14	27	1	1	9
Adult female	21	2	1	2	0
Pair in tandem	27	3	5	0	4
Totals	62	32	7	3	13

of total hunts (N = 108), significantly greater (G = 8.08, P = 0.004) than the 47.1% of hunts in years 2–7 (N = 278). By contrast, the female's share during the first year was 2.7%, and this rose significantly to 24.1% in years 2–7 (G = 23.51, P = 0.001). A possible explanation is that the female lacked skill and experience in her first year on territory. As she became older and gained expertise, she began to play a more active role in foraging. There was no significant change (G = 2.70, P = 0.1) in the proportion of tandem hunts between the first year and years 2–7 (Table 6).

Our findings that the primary prey of the male was passerines, whereas the female's main prey was gulls (Table 2), lends support to the hypothesis that the reversed sexual size dimorphism in raptors such as seen in the peregrine allows them to exploit a wider prey base and reduces competition between the sexes (Selander 1966).

Cooperative Hunting. Are peregrines that attack the same prey simultaneously with their mates or fledglings actually cooperating? Or, are the individuals simply reacting at the same time to the stimulus of sighting prey? True cooperative hunting differs fundamentally from other forms of group predation, such as pseudo-cooperative hunting (Ellis et al. 1993). In true cooperative hunting, the group consists of at least two members that are a stable social unit, and their cooperation should benefit the group rather than just the individual. An example of true cooperative foraging is described by Bednarz (1988) for the Harris's Hawk (*Parabuteo unicinctus*). Ellis et al. (1993) conclude that cooperative hunting is the most efficient strategy for capturing prey in many situations and that each form of social foraging should have evolved as an adaptive advantage enhancing the fitness of all individuals in the group. In the Aplomado Falcon (*Falco femoralis*), pair hunting is more than twice as productive as solo hunting when the prey are birds (Hector 1986). Similarly, the success rate of pair hunting in peregrines may depend on the species of prey hunted (Jenkins 2000).

In this study, tandem hunts by the mated pair of peregrines were more successful than solo hunts (39.0 versus 27.3%), although the difference was not statistically significant. Moreover, the individual success rate of the two partners in tandem hunts is actually halved. So what, if any, is the fitness value of tandem hunting for this pair of breeding peregrines? It may lie in the fact that any action by the male that benefits his mate or their progeny should be of adaptive advantage.

At Wabamun, the adult male was not seen to eat the gulls he killed, although on two occasions he fed on gull remains abandoned by fledglings. The fact that he mainly hunted such prey in the company of his mate or fledglings suggests that his role was a cooperative one. This view is supported by anecdotes such as the following. By mid September 1999, after the fledglings had dispersed, the adults were still hunting together. One evening, shortly after both had soared up over the plant, the male caught a small passerine and landed on a pylon to

Table 3. Hunts/kills made by one or both Peregrine Falcon parents accompanied by one or more fledgling juveniles.

	1 JUVENILE	2 JUVENILES	3 JUVENILES	TOTALS
Adult Male	29/10	34/10	6/2	69/22
Adult female	3/2	6/4	0/0	9/6
Both adults	6/3	5/0	1/0	12/3
Totals	38/15	45/14	7/2	90/31

Table 4. Prey captured by a pair of Peregrine Falcons as a percentage of total prey per year.

YEAR	PERCENT GULLS	PERCENT PASSERINES	PERCENT OTHER	NO. TOTAL PREY	NO. HUNTS
1	8.7	60.9	30.4	23	108
2	63.6	27.3	9.1	11	47
3	62.5	12.5	25.0	8	25
4	58.3	16.7	25.0	12	37
5	43.7	31.3	25.0	16	44
6	63.6	27.3	9.1	22	61
7	80.0	4.0	16.0	25	64
Totals	53.0	27.4	19.6	117	386

consume his prey. Instead of interfering, the female perched on the next pylon and waited for her mate to finish his meal. Presently, both soared up again and eventually flew out high over the lake, stooping in tandem at gulls. Like many similar observations, this incident suggests that the male's role was truly a cooperative one—to assist his mate in her foraging.

The question of whether attacks on the same prey by a combination of adults and fledglings can be considered cooperative seems even less clear, for it is apparent that the juvenile is primarily intent on kleptoparasitizing the adult. If there is cooperation, it is one-sided and benefits only the juveniles (i.e., this may be considered as parental investment). Nevertheless, the evolutionary value of adult/fledgling combinations is undeniable, as a well-fed progeny enhances the future of the family genes. In support of the hypothesis that the participation of adults in joined hunts with their fledglings indeed represents parental care, we present a number of anecdotal observations in the appendix.

Live-drops of Prey. Cade (1982) and Sherrod (1983) characterize the behavior of paired male peregrines in social interactions with their bigger mate as submissive and even fearful. Females take food from males in an aggressive manner, not only during the breeding season but also on migration or at the wintering grounds. Unmated females routinely force males to drop just-caught prey (Dekker 1980, 2003). Tandem hunting by unmated peregrines is relatively common and driven by competition rather than cooperation. Two or more (up to six) migrating or wintering peregrines were seen in joint pursuit of the same prey in Alberta and British Columbia. Male peregrines were forced to make live-drops of prey not only to female conspecifics, but also to other kleptoparasitic raptors, such as Prairie Falcons (*Falco mexicanus*) and Bald Eagles (*Haliaeetus leucocephalus*; Dekker 1995, 1998).

I concur with Sherrod (1983) that the release of just-caught prey by the male peregrine at the approach of an aggressive female may be triggered by the impulse to avoid close contact. The importance of a timely release was demonstrated on 21 August 2003, when the Wabamun male, carrying a just-caught prey and flying 20–25 m high, was met by a screaming juvenile female in typical begging flight. Apparently, the male was just too late in releasing his prey, for he was seized by the juvenile. Locked by their feet, both birds tumbled about 15

Table 5. Comparison of main prey taxa captured by a pair of Peregrine Falcons in study years 1 and 2–7.

	PREY TAXA	NO. KILLS	PERCENT OF TOTALS KILLS	*N*
Year 1	Gulls	2	8.7	23
Years 2–7		60	63.8	94
Year 1	Passerines	14	60.9	23
Years 2–7		18	19.1	94

Table 6. Number of hunts by the adult male and female, either hunting solo or in tandem, in year 1 and years 2–7.

		NO. HUNTS	PERCENT OF TOTAL
Year 1	Adult male	85	78.7
N = 108 hunts	Adult female	3	2.7
	Tandem	20	18.5
Years 2–7	Adult male	131	47.1
N = 278 hunts	Adult female	67	24.1
	Tandem	80	28.8

m before separating again, while the prey item fell into the bushes below and was lost.

Based on a thorough review of the literature and on his own studies, Sherrod (1983) observed that the behaviors of parents and fledglings complement each other. While the youngster only wants food, the adult appears to be very willing to supply that food. Some live-drops are no doubt the result of the aggressive approach of the begging falcon. However, as argued by Newton (1979), other live-drops are clearly intentional as parent peregrines will recapture the live-dropped prey and release it again if the fledgling fails to catch it the first time. Such repeat drops were seen in this and other studies (Frank 1994, Treleaven 1998).

CONCLUSION

Some of the aerial drops of just-caught and still live prey from adult to fledgling (described in the appendix) lend support to the hypothesis that the parents were teaching their young by example. Although young falcons do not need to be taught to hunt, such extended parental care might well give them a certain survival advantage after leaving the nest site. The observation that live-drops were also made from adult to adult, both at Wabamun and at a natural nest site in northern Alberta (Dekker 1999), may seem to refute the above hypothesis. Because there can be no doubt that adult females are accomplished hunters, the male's reason for making live-drops to his mate can have nothing to do with teaching. However, here a secondary and complementary factor comes into play. Whether hunting with his mate or a fledgling, the male plays a dual role, either in support of his mate or progeny.

It is difficult, if not impossible, to translate all of the anecdotes detailed in the appendix into hard data in support of the teaching hypothesis. As to the alternative, but not exclusive, hypothesis that parent peregrines assist their fledglings in capturing their first prey, on the evidence presented here, we are convinced that the answer is affirmative.

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APPENDIX. Observations of parental care by a pair of peregrines toward their fledglings and nearly-fledged juveniles.

(1) On 16 August 1999, having stooped at a gull and missed his target, the adult male maneuvered under it in a peculiarly slow flying style. He appeared to drive the gull upward and prevent it from dropping into the water below. Seconds later, a juvenile female stooped from above, just missing the gull. The adult male then stooped again, just short of the target. Chased by both peregrines, the gull eventually escaped. In this case, as in others, it seemed clear that the male did not want to catch the gull himself. Instead, he attempted to set it up for the approaching juvenile.

(2) On two occasions, when a gull was chased by a group of one adult and one fledgling, the adult hit or touched the prey, causing it to cartwheel in the air. In the next instant, the gull was seized by the closely-following juvenile. Our impression was that the adults were not intent on taking the gull themselves.

(3) On 12 August 2000, the adult male, while soaring in tandem with his mate, suddenly sprinted away (400–500 m) to hit a shorebird that was being chased by two juveniles at an altitude estimated at 75 m. Dead or stunned, the prey fell into reeds and was lost before the juveniles could recover it. This was one of only four instances when these peregrines hit their prey in the air, as opposed to the common method of binding to the prey and carrying it down. The remarkable point is that the adult male did not stoop and recover the plunging shorebird himself, which would have been a normal procedure if he had been hunting alone.

(4) A Rock Pigeon pursued by a fledgling was taken by the adult female, who transferred it at once to the juvenile. On their own, the adults seldom pursued pigeons.

(5) Fledglings that have been on the wing for only a few days have difficulty carrying a gull. After making an aerial transfer to an unskilled juvenile, the adults will accompany it in flight and retrieve the gull if dropped. By the same token, seemingly aware of the lack of ability in a badgering female youngster, the adult female refused to transfer a just-caught gull and instead carried it ca. 500 m to the roof of the plant, where she at once surrendered it to the fledgling.

(6) The adult male demonstrated an awareness of the different needs of the genders. In group hunts with male offspring, he selected mostly passerines or small shorebirds (41 of 45). By contrast, he usually attacked gulls in the company of females. After capturing one or more gulls for his mate or the fledglings, he hunted smaller prey for himself.

The above interactions between parents and fledglings parallel numerous anecdotes described by long-term peregrine observers in New York and Great Britain (Frank 1994, Treleaven 1998).

It is our impression that adult peregrines appear to know how to assist their progeny in gaining independence. For a start, there is a change in food exchanges when the first of the juveniles are close to fledging. Both at Wabamun and a natural nest site in central Alberta, the adult male appeared to coax a fully-feathered male youngster to fly. Instead of transferring the prey item in the usual direct manner, he cruised back and forth just

out of reach, holding the prey in his lowered feet. His behavior cannot be explained as having been prompted by fear of a bigger bird for this incident involved a male juvenile. After the young male failed to fledge, the adult gave the food item to another juvenile, a fully-feathered female sitting on the catwalk. Similarly, on two other occasions when he arrived with a small prey, he flew right up to a screaming juvenile male that was perched on the edge of a catwalk, but instead of exchanging the prey feet-to-feet, he dropped it and recovered the falling item in a quick stoop. He repeated this teasing show three or four times. After the fully-feathered juvenile male failed to fly, the adult gave the food item directly to a less-developed female still in the nest box.

Another noteworthy exchange involved the female One day, after she had delivered a prey to two juvenile males, which shared the food, the male arrived, also with prey. He gave it directly to one of the same two youngsters. Instantly, the adult female interfered. She took the food item away from the young male and offered it instead to a juvenile female which had not been fed for several hours. Similar incidents were seen at Wabamun and at a natural nest site in central Alberta (D. Dekker unpubl. data).

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NESTING ECOLOGY AND BEHAVIOR OF BROAD-WINGED HAWKS IN MOIST KARST FORESTS OF PUERTO RICO

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ABSTRACT.—The Puerto Rican Broad-winged Hawk (*Buteo platypterus brunnescens*) is an endemic and endangered subspecies inhabiting upland montane forests of Puerto Rico. The reproductive ecology, behavior, and nesting habitat of the Broad-winged Hawk were studied in Río Abajo Forest, Puerto Rico, from 2001–02. We observed 158 courtship displays by Broad-winged Hawks. Also, we recorded 25 territorial interactions between resident Broad-winged Hawks and intruding Red-tailed Hawks (*Buteo jamaicensis jamaicensis*). Broad-winged Hawks displaced intruding Red-tailed Hawks from occupied territories ($P = 0.009$). Mayfield nest survival was 0.67 across breeding seasons (0.81 in 2001, $N = 6$; 0.51 in 2002, $N = 4$), and pairs averaged 1.1 young per nest (years combined). The birds nested in mixed species timber plantations and mature secondary forest. Nests were placed in the upper reaches of large trees emerging from the canopy. Nest tree DBH, understory stem density, and distance to karst cliff wall correctly classified (77.8%) nest sites.

KEY WORDS: *Broad-wing Hawk*; Buteo platypterus brunnescens; *endangered*; *nest success*; *prey delivery*; *habitat model*; *karst forest*; *Puerto Rico.*

ECOLOGÍA REPRODUCTIVA DE *BUTEO PLATYPTERUS BRUNNESCENS* EN BOSQUES DE CALIZA HÚMEDOS DE PUERTO RICO

RESUMEN.—*Buteo platypterus brunnescens* es una subespecie de rapaz endémica a los bosques montanos de Puerto Rico. Investigamos la ecología reproductiva y el comportamiento de *B. p. brunnescens* en el Bosque de Río Abajo, Puerto Rico, durante 2001 y 2002. Observamos 158 despliegues de cortejo en Río Abajo. Observamos 25 encuentros territoriales entre *B. p. brunnescens* y *B. jamaicensis jamaicensis. B. p. brunnescens* desplazó a *B. j. jamaicensis* de sus territorios el 84% de las veces ($P = 0.009$). La supervivencia de los nidos en ambas temporadas fue de 0.67 (0.81 en 2001, $N = 6$; 0.51 en 2002, $N = 4$). Los nidos produjeron un promedio de 1.1 volantones por nido (años combinados). Encontramos nidos en áreas de bosque secundario maduro y plantaciones forestales. La altura del dosel, diámetro del árbol, densidad del sotobosque y distancia a farallón de mogote clasificaron correctamente (77.8%) los nidos en Río Abajo.

[Traducción de los autores]

The Broad-winged Hawk (*Buteo platypterus brunnescens*) is an endemic woodland raptor of upland montane forests of Puerto Rico. This subspecies is listed as endangered (Federal Register 1994) by the Puerto Rico Department of Natural and Environmental Resources (DNER) and the U.S. Fish and Wildlife Service (USFWS). The Broad-winged Hawk in Puerto Rico is nonmigratory and exhibits a limited geographic range with known populations restricted to montane forests (Delannoy 1997). Breeding in Puerto Rico begins in late December, with nests placed in the upper reaches, but below the high canopy (Delannoy and Tossas 2002). This insular subspecies is smaller and darker than its North American nominate counterpart *Buteo platypterus platypterus,* but larger than the Lesser Antillean subspecies (Raffaele 1989, Goodrich et al. 1996). The most recent population estimate for the Broad-winged Hawk in forest reserves of Puerto Rico is approximately 125 individuals (Delannoy 1997).

The nesting biology of the Broad-winged Hawk in North America has been described by a number of authors (e.g., Fitch 1974, Matray 1974, Rosenfield 1984, Titus and Mosher 1987, Crocoll and Parker 1989). However, knowledge on the reproductive biology of the insular endemic subspecies

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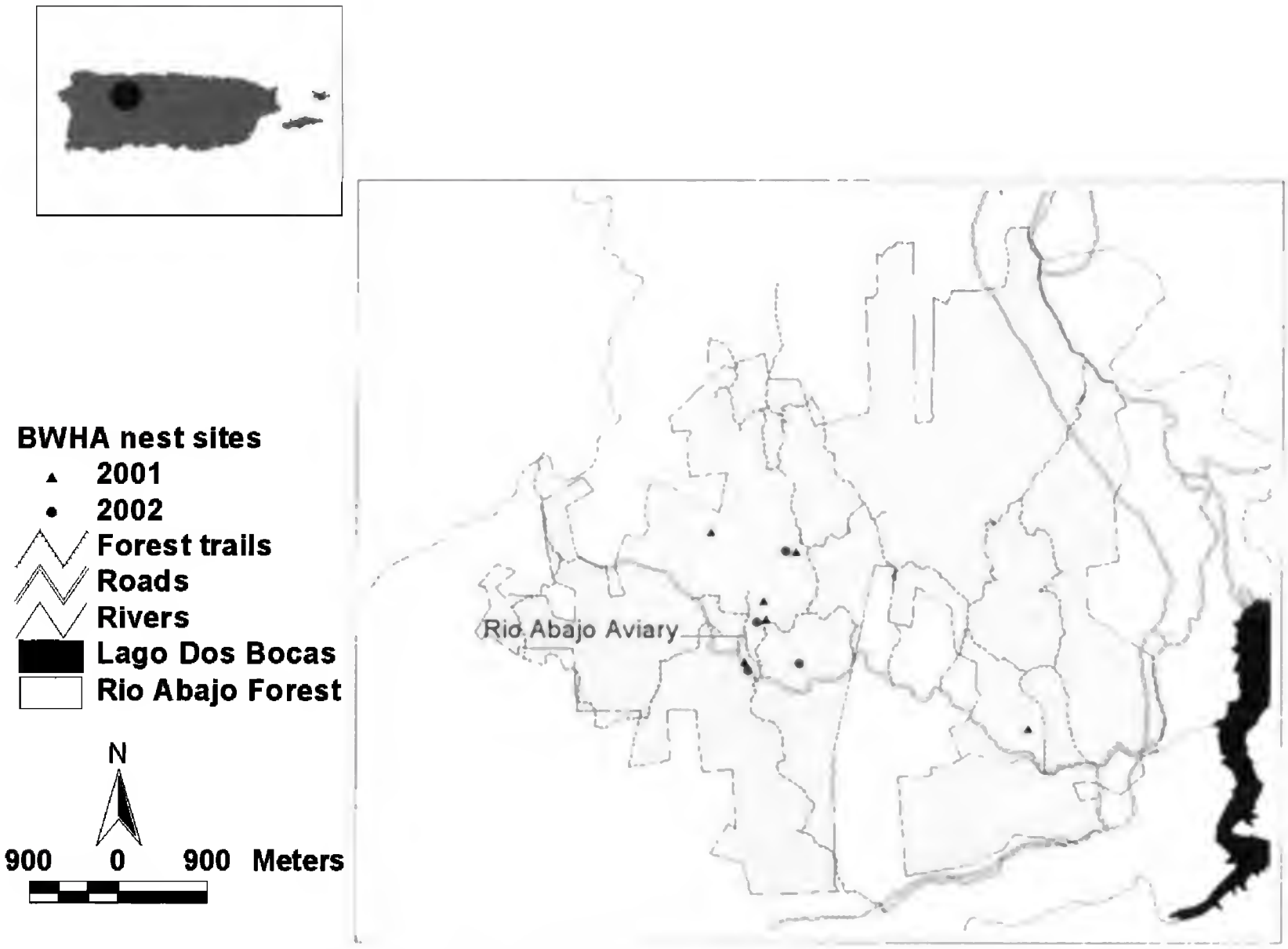

Figure 1. Locations of Broad-winged Hawk nest sites during the breeding season of 2001 and 2002 in Rio Abajo Forest, Puerto Rico.

of Puerto Rico, and forest raptors of the West Indies in general, are limited (Goodrich et al. 1996). Similarly, the available information on nesting behavior and diet of Broad-winged Hawks in Puerto Rico is based on a few observations by Snyder and Kepler (1987).

Additional information on the Puerto Rican Broad-winged Hawk's reproductive ecology and nest habitat use is required to better understand current limiting factors, and provide recommendations for future research on habitat conservation in public and private lands. Herein, we report on the nesting ecology and behavior of the Broad-winged Hawk in a forest reserve in the moist limestone forest region of Puerto Rico. Specifically, we provide baseline information on courtship behavior and territorial defense, nest success and productivity, prey delivery rates by nesting pairs, and their habitat use. Moreover, we discuss the implications our results on interactions between the Broad-winged Hawk and Red-tailed Hawk (*Buteo jamaicensis jamaicensis*) may have on future plans to establish a second wild population (by releasing captive-reared individuals) of the critically endangered Puerto Rican Parrot (*Amazona vittata*) in the Río Abajo Forest (White et al. 2005).

STUDY AREA AND METHODS

Study Area. We studied Broad-winged Hawks in the Río Abajo Forest and surrounding private lands in Puerto Rico from 2000–02 (Fig. 1). The Río Abajo Forest (18°20′N, 66°42′W) is managed by the Forestry Division of DNER and is in west-central Puerto Rico within the moist limestone region of the island (Ewel and Whitmore 1973). This forest reserve comprises an area of 2300 ha with elevations ranging from 200–420 m. We obtained climate data for the study period from the site closest to our study area, the Dos Bocas NOAA weather station (NOAA 2002).

Annual precipitation during our study averaged 18.3 cm (range = 6.9–34.9 cm) in 2001 and 14.7 cm (range = 5.2–45.1 cm) in 2002. Mean annual temperature was 25.3°C (range = 19.9–30.6°C) in 2001 and 25.5°C (range = 20.1–30.9°C) in 2002.

The rugged limestone region (i.e., karst) of Puerto

Rico encompasses 27.5% of the island's surface (Lugo et al. 2001). Topography in this region is extreme and characterized by karst formations of subterranean drainages, caves, dome shaped hills or "mogotes," and deep sinkholes. Karst forest contains the largest tree species richness of Puerto Rico (Lugo et al. 2001). Río Abajo Forest is fragmented on the eastern end by a double lane highway and in the south-central part by a small community (Fig. 1). About 75% of the forest is within the subtropical wet zone, the remaining quarter lies within the subtropical moist zone (Ewel and Whitmore 1973).

Previous studies indicated Broad-winged Hawks in Puerto Rico have a limited geographic range, and their abundance is higher in the Karst region compared to other life zones on the island (Delannoy 1997). As our primary objectives were to expand current knowledge on breeding ecology, habitat use, and movement patterns of Broad-winged Hawks (Hengstenberg and Vilella 2004), we selected the Río Abajo Forest. Moreover, we were interested in comparing our results with findings of recently completed studies in Río Abajo Forest (Delannoy and Tossas 2002).

Vegetation of Río Abajo is comprised of a mix of secondary growth forests and timber plantations (Cardona et al. 1987). The midstory of some areas of secondary forest was characterized by abandoned shade-grown coffee and citrus plantations. Forest overstories were dominated by moca (*Andira inermis*), capá prieto (*Cordia alliodora*), and guaraguao (*Guarea guidonia*). Approximately 6.9% of the forest (171.7 ha) are managed timber plantations. Some stands are actively maintained (open understory), while others had a developing understory. Timber plantations, approximately 30–50 yr old, of Honduras mahogany (*Swietenia macrophylla*), maría (*Calophyllum brasiliense*), teca (*Tectona grandis*), and mahoe (*Hibiscus elatus*) occur in valley bottoms and along mid-slopes (Cardona et al. 1987).

As part of additional research efforts, we trapped Broad-winged Hawks in Río Abajo Forest (Hengstenberg and Vilella 2004). Between January 2001 and July 2002, we trapped eight Broad-winged Hawks in the Rio Abajo Forest. We used octagonal and quonset style bal-chatri traps (Berger and Mueller 1959, Erickson and Hoppe 1979), a modified dho-gaza trap (Hamerstrom 1963, Clark 1981) with a live Red-tailed Hawk, and a Rock Pigeon (*Columba livia*) with noose harness.

Each captured individual was banded with a unique color-coded leg band on the left leg and a standard U.S. Geological Survey (USGS) Bird Banding Laboratory band on the right leg. We also recorded morphometric measurements and determined gender. We collected a small amount (±5 mL) of blood from the brachia vein of the left wing of every captured individual and determined gender through DNA typing. Each bird was fitted with a backpack mounted radio transmitter attached via a break-away backpack harness and a leather keel patch (Vekasy et al. 1996). Furthermore, we used visible size differences and markings to separate individual members of a broad-wing pair.

Territorial Defense. We documented territorial encounters between resident Broad-winged Hawks at Río Abajo Forest and surrounding lands. Moreover, to examine the behavioral interactions of the two sympatric *Buteos,* we observed territorial interactions between Broad-winged Hawks and intruding Red-tailed Hawks from limestone hilltops. We recorded the behavior of both birds (aggressive or passive) and the end result (deterred or not deterred). We used a binomial sign test for a single sample (Daniel 1990, Sheskin 2000) to test the hypothesis that both species of raptors displaced the other randomly during aerial displays.

Nest Searches and Monitoring. Broad-winged Hawk use areas were delineated through direct observations from limestone hills and hawk locations were plotted on USGS topographic quadrangles. We then extensively searched areas with radio-marked adults and documented aerial displays or other territorial behavior. Spot maps and historical nesting information were used to extend our searches into other potential nesting territories. All potential nests were monitored for reproductive activity beginning in February of each year.

When a nest site was located, we built observation blinds 50–100 m from the nest tree at a location on a nearby cliff wall looking down on the nest with clear line-of-sight visibility. In one instance, it was not possible to build a blind with a direct view because of nest location, dense vegetation, or steep rock walls. In this instance, the nest was monitored from the ground at a similar distance. Nest activities were recorded throughout the breeding season using spotting scopes, video cameras, and binoculars from the observation blind. The distance (m) between all occupied nests (nest-site spacing) for the 2001 and 2002 breeding seasons was measured on the ground with surveying tape and verified on a study area map with Geographical Information System (GIS) measurements. A two-sample *t*-test was used to determine if the spatial distribution of nest sites varied between years (Sheskin 2000).

Continuous nest observations were conducted daily throughout the breeding season. Nest checks were randomly conducted throughout the day to include all hours when Broad-winged Hawks were active. Based on nest observations and nest checks, we estimated dates of incubation, hatching, and fledging. We calculated nest survival (Mayfield 1975) from start of incubation to fledging (total nest survival) and determined nest attentiveness patterns. A nest was considered successful if the pair produced young. We estimated Mayfield nest survival during the incubation and nestling periods using a combined total of 198 incubation exposure-days and 274 nestling exposure-days.

Prey Delivery. Food provisioning by adult Broad-winged Hawks to the nest during the breeding season was determined from direct observation. To assess if the birds regularly delivered prey throughout the day, occupied nests were monitored weekly in equal proportion during four time periods: early morning (0800–1100 H), early morning to mid afternoon (1101–1400 H), mid afternoon (1401–1700 H), and late afternoon to early evening (1701–2000 H). Nests were monitored from hatching until the young fledged or the nest failed. We calculated the mean number of prey items delivered and the proportion of prey deliveries per time period. We divided the prey items into two general categories, large (e.g., birds and rats) and small (e.g., macroinvertebrates and lizards), to determine prey provisioning patterns.

An analysis of variance in a randomized complete block design (PROC GLM; SAS Institute 1999) was used to test if Broad-winged Hawks delivered total number of prey items (response variable) per time period (block), number of large prey items per time period, and number of small prey items per time period equally throughout the day. We used multiple comparisons (Least Scientific Difference Means) of mean number of prey items (pooled, large, and small) to examine significant values ($\alpha = 0.05$) and determine which time periods differed with respect to number of prey items delivered (Sheskin 2000).

Nest Habitat Model. Areas used by broadwings for nesting at Río Abajo are valleys with tall forest bounded by limestone ridges and cliff walls, where pairs soar along their respective ridge tops (Delannoy and Tossas 2002). Forest vegetation along cliff walls and limestone ridges are used by resident broadwings for perching, but not for nesting (Hengstenberg and Vilella 2004). Our primary objective was to assess which stand-level variables best described a broadwing nest within the context of the surrounding habitat at Río Abajo Forest. Therefore, vegetation characteristics and structure around nest sites were measured at the end of the breeding season and following post-fledging dependency.

One nest used both in 2001 and 2002, was included once in the analyses. We described a nest site as all vegetation within a 0.04 ha plot (11.3-m radius) centered on the nest tree (Titus and Mosher 1981). We recorded habitat measurements on nine of ten occupied nests and nine nonuse sites using standard procedures (James 1971). We used a random numbers table to determine a distance and azimuth to travel from a particular nest site to an equivalent nonuse site. We constrained selection of random sites to forested area within a 400-m radius of the nest tree. All random sites were within the nest tree stand in valleys and side slopes. The closest tree to the plot center was chosen as the center point, and habitat variables were measured accordingly.

We recorded visual obscurity of the understory using a 2 m Nudds board (Nudds 1977). The board consisted of four 0.5 m sections with 30 orange and white squares. Nudds board measurements were taken from each cardinal direction at a distance of 10 m from center point. Percentage visual obscurity for the four cardinal directions was averaged for each 0.5 m section. We recorded altitude, aspect, percentage slope, and distance to the nearest rock wall, water, and man-made opening. All woody plants over 2 m tall according to species, diameter at breast height (DBH), height, and vertical stratification were recorded. Vertical structure was classified into three strata heights (1-understory, 2-midstory, 3-overstory). Nest heights were recorded directly with a measuring tape. Tree heights were measured either by clinometer or through visual estimation. We tested for differences in height between clinometer readings and visual estimations using a two-sample *t*-test (SAS Institute 1999). We used a spherical densitometer to collect four readings of canopy cover from each cardinal direction at a distance of 5 m from center point. We calculated a mean to estimate percentage overstory canopy cover.

Because of the paucity of information on nest site characteristics of Broad-winged Hawks in Puerto Rico (U.S. Fish and Wildlife Service 1997), we decided to record as much information as possible. We measured all variables considered biologically relevant to woodland raptors (Titus and Mosher 1981). We tested habitat variables for normality using a Kolmogorov-Smirnov Goodness-of-Fit Test (Sheskin 2000). As data were normally distributed, we then used two-sample *t*-tests to identify variables that differed between nest sites and random sites. Uncorrelated significant variables were selected for the variable selection model (see Table 1 for variables considered). Logistic regression analysis and AIC modeling was used to determine which variables best discriminate a Broad-winged Hawk nest site from a random site (PROC LOGISTIC; SAS Institute 1999).

To develop broadwing-habitat nest site relationships, we utilized a two model approach (variable selection and model selection). For both microhabitat analyses, an information-theoretic approach was used for model selection and inference (Burnham and Anderson 2002). We used Akaike's information criterion (AIC_c), delta AIC (Δ_i), and Akaike's ranking weight (w_i) to determine the best model.

Because of the small number of nest sites ($N = 9$), we recognized the variable selection model may produce biased results (Milliken and Johnson 1984). Therefore, we conducted an alternative AIC model selection approach to assess which biologically-relevant variables best described Broad-winged Hawk nest sites. This alternative analysis models the particular nest sites without use of stand-level comparisons (nest site versus random site) as in the variable selection model.

For the alternative model selection, we chose 10 explanatory variables from a list of 27 microhabitat variables (Table 1) based upon literature review and personal field experience (Titus and Mosher 1981, Delannoy and Tossas 2002). Variables chosen were: aspect, slope, road, rock wall, DBH, canopy cover, Nudds 2, midstory number of stems, overstory number of stems, and canopy height (Table 2). Nest or center tree height was excluded because it is significantly correlated with DBH. Best model selection was based on criteria stated by Burnham and Anderson (2002).

RESULTS

Breeding Behavior and Territorial Defense. From January to March of 2001 and 2002, we observed 158 courtship display flights by known pairs. Most (68%) aerial displays occurred 0917–1107 H ($\bar{x}$ = 1012 H). Across two breeding seasons, we documented courtship display behavior in 26 pairs throughout the Río Abajo Forest and surrounding private lands. Of the eleven pairs identified in 2001, occupied nests were located for six of these. In 2002, courtship behavior was observed by 8 of the 11 pairs recorded in 2001.

We observed 25 territorial interactions between Broad-winged Hawks and intruding Red-tailed Hawks. Broad-winged Hawks displaced Red-tailed Hawks 84% of the time when an intruding Red-

Table 1. Nest habitat characteristics (mean ± SD, range) measured within 0.04 ha of Broad-winged Hawk nest and random sites in Rio Abajo Forest, Puerto Rico, 2001 and 2002.

	Nest Site (9)		Random Site (9)	
Habitat Characteristics	Mean ± SD	Range	Mean ± SD	Range
Altitude (m)	235.7 ± 58.0	(150–330)	219.9 ± 62.7	(126–320)
Aspect	204.9 ± 105.1	(32–340)	192.7 ± 108.8	(12–334)
Slope (%)	46.0 ± 19.0	(18–88)	30.1 ± 24.3	(0–85)
Distance to water (m)	194.1 ± 127.1	(37–450)	174.1 ± 120.7	(3–370)
Distance to road or trail (m)	68.6 ± 35.5	(25.8–135.0)	40.8 ± 42.8	(3.5–133.0)
Distance to cliff wall (m)*	41.1 ± 19.0	(13–75)	71.8 ± 30.2	(35–137)
Nest or center tree height (m)*	22.2 ± 7.7	(16.0–35.1)	12.8 ± 5.2	(6.5–22.0)
Nest or center tree DBH (cm)*	46.1 ± 15.6	(23.0–74.5)	25.2 ± 13.5	(6.9–42.5)
Nest height (m)	16.3 ± 5.6	(10.0–25.9)		—
Percentage nest height	73.5 ± 6.7	(58.8–81.3)		—
Canopy cover (%)	85.2 ± 5.8	(72–91)	81.3 ± 6.0	(70–88)
Nudds 0.5 m (%)	90.1 ± 11.5	(63.7–100.0)	75.9 ± 17.6	(53.8–97.5)
Nudds 1.0 m (%)	75.8 ± 14.2	(59.6–97.5)	59.5 ± 25.4	(21.6–87.6)
Nudds 1.5 m (%)*	74.4 ± 14.8	(51.3–95.9)	55.7 ± 18.0	(25.8–77.7)
Nudds 2.0 m (%)*	77.1 ± 9.9	(63.7–92.6)	52.9 ± 24.5	(15.9–83.5)
Midstory species richness	11.1 ± 5.6	(3–18)	12.0 ± 4.8	(7–21)
Midstory # of stems	35.8 ± 16.7	(10–58)	58.6 ± 34.2	(18–124)
Midstory stem DBH 1–4.9 cm	15.9 ± 12.7	(1–36)	27.4 ± 21.7	(0–65)
Midstory stem DBH 5–8.9 cm	9.0 ± 6.1	(2–19)	16.0 ± 14.1	(2–50)
Midstory stem DBH ≥ 9	10.9 ± 5.3	(7–22)	16.3 ± 8.3	(4–33)
Overstory species richness	3.1 ± 2.0	(1–6)	3.4 ± 1.9	(2–7)
Overstory # of stems	10.2 ± 5.0	(3–17)	7.9 ± 5.1	(2–16)
Overstory stem DBH ≤ 25.9 cm	3.3 ± 2.9	(0–9)	3.0 ± 3.9	(0–10)
Overstory stem DBH 26–49.9 cm	5.6 ± 3.2	(2–11)	4.2 ± 3.5	(0–12)
Overstory stem DBH ≥ 50 cm	1.3 ± 1.4	(0–5)	0.7 ± 0.9	(0–2)
Basal area m^2/ha	31.8 ± 13.6	(14.2–53.4)	28.2 ± 14.0	(9.0–56.7)
Canopy height (m)	17.9 ± 2.8	(14.4–23.4)	16.6 ± 4.3	(13–26)

* Significant *t*-test ($P < 0.05$).

tailed Hawk entered an occupied territory (p_1 = 21/25 = 0.84, P = 0.009, 2-tailed test). In every aerial encounter, the Red-tailed Hawk was the intruding species. All aerial encounters involved adult birds of both species. Aerial displays involving one Broad-winged Hawk and one Red-tailed Hawk occurred 72% of the time. However, Broad-winged Hawk pairs flew in unison 28% of the time to defend their territory against Red-tailed Hawks.

Displays varied from "high-intensity flights" with intruders to "low-intensity flights" between pairs. During displays both birds circled together in close proximity and in the same general direction with the male broadwing flying above the female. During low-intensity flights, adults soared upward on widespread wings and fanned tails. In high-intensity displays, the adults would alternate between wing flaps and soaring. When the male reached the top of the flight, he performed undulating dives or dipping flight (Wiley and Wiley 1981, Brown and Amadon 1989), consisting of a series of 2–7 shallow dives made toward the female. Most other displays ended with the birds diving straight back with cupped wings at high speeds into the canopy, known as parachuting (Wiley and Wiley 1981, Goodrich et al. 1996).

Altitude gained varied among displays; generally the longer the flight, the higher the altitude obtained. Flights ranged from about 50 m above the tree canopy to elevations over 450 m. Courtship display flights lasted 60–900 sec ($\bar{x}$ = 334.7 ± 191.5 sec). Cartwheeling behavior or sky dancing (Goodrich et al. 1996) was only observed three times by three different pairs, in which the male was flying on top of the inverted female with their talons exposed. The birds proceeded to tumble with semi-locked talons at high speeds until they reached the forested canopy, where they quickly released their

Table 2. Model selection: parameters (K), relative AIC_c, Delta AIC (Δ_i), Akaike Weights (w_i), χ^2 Goodness-of-Fit statistic, P-value, and percent correct classification for Broad-winged Hawk nests in Rio Abajo Forest, Puerto Rico, 2001–02).

MODEL SELCTION	K	AIC_c	Δ_i	W_i	χ^2	P-VALUE	PERCENT
DBH + Canheight + Cliffwall + Overstems	4	20.057	0.000	0.304	10.953	0.027	77.8
DBH	1	21.362	1.305	0.158	6.613	0.010	66.7
Cliffwall	1	22.309	2.252	0.099	5.283	0.022	72.2
DBH + Canheight + Cliffwall	3	22.391	2.334	0.095	9.009	0.029	72.2
Nudds 2	1	22.399	2.342	0.094	5.762	0.016	61.1
DBH + Canheight	2	22.957	2.900	0.071	7.167	0.028	66.7
Aspect + DBH + Cliffwall	3	23.928	3.871	0.044	8.569	0.036	72.2
DBH + Canopy cover	2	24.619	4.562	0.031	6.765	0.034	61.1
Road + Cliffwall	2	25.591	5.534	0.019	5.582	0.061	72.2
Cliffwall + DBH	2	25.591	5.534	0.019	8.493	0.014	72.2
Midstems	1	26.050	5.993	0.015	3.018	0.082	55.6
Slope	1	26.974	6.917	0.010	2.346	0.126	66.7
Road	1	27.192	7.135	0.009	2.211	0.137	55.6
Canopy cover	1	27.435	7.378	0.008	1.977	0.160	55.6
Nudds 2 + Midstems + Overstems	3	27.961	7.904	0.006	8.146	0.043	61.1
Overstems	1	28.484	8.427	0.005	1.023	0.312	59.0
Midstems + Overstems	2	28.628	8.571	0.004	3.486	0.175	50.0
Canheight	1	28.862	8.805	0.004	0.650	0.420	38.9
DBH + Canheight + Cliffwall + Aspect	4	29.070	9.013	0.003	9.047	0.060	66.7
Aspect	1	29.458	9.401	0.003	0.066	0.797	0.0
Aspect + Slope	2	30.340	10.283	0.002	2.395	0.302	72.2

talon lock, swooped up, and dispersed upward in separate directions.

Territorial flights were elicited by the presence or vocalizations from intruding Red-tailed Hawks and juvenile Broad-winged Hawks in the vicinity of the residents' territory. Flights varied in intensity and depended on the intruding species and its proximity to the nest. Generally, males were first to fly and confront the intruder (Wiley and Wiley 1981). Adults used alarm vocalizations to warn their mate of an intruding bird. During these displays, adults used stuttered and whistle squeal vocalizations (Burns 1911). Stuttered and whistle squeals vocalizations were used in high-intensity displays. When Red-tailed Hawks were detected, Broad-winged Hawks responded quickly with rapid-pursuit flights. Resident birds circled and soared to an altitude above the intruding bird and repeatedly dived at it. The resident male continued to dive at the intruder until the intruder departed the territory. In some cases, the resident bird extended its talons during its dives. In one instance, a male broadwing locked talons with an intruding Red-tailed Hawk; once the intruder left the area, the resident male silently dove or "parachuted" back to its territory.

Dipping flight, or undulating display (Wiley and Wiley 1981, Brown and Amadon 1989), was a common behavior used in all intense intruder interactions in which the resident bird was successful at chasing the Red-tailed Hawk. Territorial confrontations between conspecific neighbors were less intense than toward Red-tailed Hawks. From the radiotelemetry study, a radio of a juvenile Broad-winged Hawk (5167) was found and all the feathers were plucked (D. Hengstenberg and F. Vilella unpubl. data). The cause of mortality was determined to be a Red-tailed Hawk, which had been observed numerous times in the same area as the juvenile broadwing.

Perched intruders were generally attacked by a slower supplantation flight (Wiley and Wiley 1981) or a dive in which the intruder typically fled the area. If the intruder remained, the residents then circled above and used low angled dives until the intruder departed (Wiley and Wiley 1981).

Nesting Biology. We found 10 nests during our study in Río Abajo Forest. Onset of incubation was

Table 3. Broad-winged Hawk nests monitored during the breeding seasons 2001 and 2002, Rio Abajo Forest, Puerto Rico.

REPRODUCTIVE VARIABLES	2001	2002	BOTH YEARS
Number of nests found	6	7	13
Occupied nests	6	4	10
Failed nests	1	2	3
Successful nests	5	2	7
Proportion successful nests	0.83	0.50	0.70
Mayfield nest success	0.81	0.51	0.67
Number of nestlings	7	3	10
Number fledged	6	2	8
Nestling loss	0.14	0.33	0.20
Fledglings per nest	1.2	1	1.2

from 28 February–21 March in 2001 and from 6–16 March in 2002. Hatching occurred from 9–20 April in 2001 and from 6–17 April in 2002. In 2001, six juveniles fledged at 35–39 d between 2–25 May, and two juveniles fledged at 35–36 d from 21–22 May in 2002. Three nests failed during the study (Table 3). Two of the failed nests were attributed to heavy rains. The third nest was depredated by a Red-tailed Hawk.

For 2001 and 2002, nest survival for the incubation and nestling periods was 0.67 (Table 3). The probability of surviving from nest initiation through fledging was 0.81 in 2001 and 0.51 in 2002. For both years, the probability of nest survival during the incubation period was 1.0. ($N = 10$). The number of fledglings per successful nest was 1.20 in 2001, 1.0 in 2002, and 1.14 for both years combined (Table 1).

During the egg stage, females spent the majority of time incubating. However, our results differ from the available information (Raffaele 1989, U.S. Fish and Wildlife Service 1997), as we documented males engaged in all nesting duties, including incubation. In some instances, males were observed continuously incubating for >4 hr and overnight. Adult Broad-winged Hawks frequently brought green vegetation, especially *Trichilia hirta,* to the nest. During incubation, vegetation may act as a buffer between nest branches and eggs. Raptors may use fresh greenery for concealment, to reduce odors, and to avoid ectoparasites (Wimberger 1984, Sibley 2001).

Nest Monitoring and Prey Delivery. We recorded 5534 min of nest observations during the incubation stage and 8825 min through the nestling stage. During the incubation period, females incubated approximately 53% of the time and males 23%. We observed both male and female Broad-winged Hawks incubating overnight. The nest was not attended 15%, and an unknown adult incubated 9% of the time. During the nestling period, the nest was not attended 69% of the time, females attended 17%, and males attended 14% of the time. As the nestlings matured, the female spent less time at the nest (Lyons and Mosher 1987).

Prey deliveries away from the nest were relatively common, with either member of the pair initiating solicitation calls (Goodrich et al. 1996). The delivering adult, usually the male, would vocalize back and forth until the incubating female flew off the nest to where the male was perched (<50 m from nest) to obtain the prey item. While one adult was eating, the other would fly to the nest and brood. Most prey deliveries during the nestling stage occurred during the early morning to mid-afternoon period.

We observed 60 prey items delivered to 7 of 10 monitored nests during the brood-rearing periods of 2001 and 2002 (Table 4). Prey consisted of 35% rats (*Rattus* spp.), 27% lizards, 17% birds, 12% macroinvertebrates, 7% unidentified prey, and 3% snakes. Pooled prey items (large and small) varied among the four time periods ($F_{3,27} = 4.01$, $P = 0.024$). More prey was delivered to nests during early morning to mid-afternoon than early evening. Daily prey deliveries were distributed as follows: 38% early morning, 40% late morning to mid afternoon, 17% mid to late afternoon, and 5% late afternoon to early evening. However, neither the number of small prey items ($F_{3,27} = 2.83$, $P = 0.068$), nor the number of large prey items ($F_{3,27} = 2.80$, $P = 0.067$) brought to nest sites, differed over the course of the day. The earliest prey delivery was recorded at 0856 H, and the latest prey delivery was observed at 1846 H. We calculated a mean prey delivery rate of 0.38 prey (SE = 0.08) items per chick per hour (range = 0.14–0.80).

Nesting Habitat. All nests were within 50 m of a rock wall. Nests sites were generally found on southwest facing slopes ($\bar{x} = 204°$). Distance among nests averaged 838.5 m (SE = 79.98, range = 200–1455 m) in 2001 and 793.0 m (SE = 91.87, 411–1231 m) in 2002. Distance did not vary between years ($t_{30} = 0.362$, $P = 0.720$). There was no difference amongst visual estimations and clinometer readings of nest tree heights when compared

Table 4. Observed prey items delivered to Broad-winged Hawk nests or consumed in Rio Abajo Forest, Puerto Rico, 2001–02.

COMMON NAME	TAXONOMIC NAME	OBSERVED NO. OF PREY	PERCENT
Puerto Rican giant centipede	*Scolopendra alternans*	4	6.7
Puerto Rican arboreal millipede	*Orthocricus arboreus*	3	5.0
Melodius coqui	*Eleutherodactylus wightmanae*	1	1.7
Common coqui	*Eleutherodactylus coqui*	3	5.0
Common anole	*Anolis cristatellus*	2	3.3
Banded anole	*Anolis stratulus*	1	1.7
Yellow-breasted anole	*Anolis gundlachi*	2	3.3
Small green anole	*Anolis evermanni*	1	1.7
Orange dewlap anole	*Anolis krugi*	1	1.7
Snake anole	*Anolis pulchellus*	1	1.7
Green giant anole	*Anolis cuvieri*	2	3.3
Common gecko	*Spaherodactylus macrolepis*	2	3.3
Puerto Rican boa	*Epicrates inoratus*	1	1.7
Ground snake	*Arrhyton exiguum*	1	1.7
White-winged Dove	*Zenaida asiatica*	1	1.7
Bananaquit	*Coereba flaveola*	6	10.0
Puerto Rican Bullfinch	*Loxigilla portoricensis*	3	5.0
Common mouse	*Mus musculus*	12	20.0
Roof rat	*Rattus rattus*	7	11.7
Norway rat	*Rattus norvegicus*	2	3.3
Unidentified prey items	—	4	6.7
Total prey items	—	60	100

to actual tape-measured heights ($P = 0.25$). Nest tree height averaged 22.3 ± 7.7 m (range = 16.0–35.1 m) and nest height averaged 16.3 ± 5.6 m (range = 10.0–25.9 m). Nest tree DBH averaged 46.1 ± 15.6 m (range = 23.0–74.5 cm). Dimensions for the two nests measured were: 0.79 m (long diameter) by 0.52 m (short diameter) by 0.61 m (depth), and 0.46 m (long) by 0.31 m (short) by 0.61 m (depth). Nest cup depth measured 1.27 and 2.54 cm, respectively. Within nest site vegetation plots we recorded 13 species of overstory trees, but only four tree species were used as nest trees. Nests were in maría, Honduras mahogany, moca, and guaraguao trees.

Of 27 microhabitat variables measured, five differed between nests and random sites (Table 1). Nest sites were closer to cliff walls ($t_{16} = 2.578$, $P = 0.020$), had greater tree height ($t_{16} = -3.020$, $P = 0.008$), larger DBH ($t_{16} = -3.048$, $P = 0.008$), and denser understories at 1.5 m ($t_{16} = -2.409$, $P = 0.028$) and 2.0 m ($t_{16} = -2.742$, $P = 0.015$) than random sites.

Logistic regression produced a best nest site model containing two variables: DBH (parameter = 0.1800, SE = 0.0965, $\chi^2_1 = 3.4814$, $P = 0.062$), and Nudds 2 m (parameter = 0.1297, SE = 0.0865, $\chi^2_1 = 2.2512$, $P = 0.134$). This variable combination correctly classified Broad-winged Hawk nests 83.3% of the time (Table 5). The best AIC model for nest sites contained DBH (parameter = 1.2853, SE = 1.5429, $\chi^2_1 = 0.694$, $P = 0.405$), canopy height (parameter = 5.5472, SE = 7.5492, $\chi^2_1 = 0.5399$, $P = 0.540$), distance to rock wall (parameter = −0.4281, SE = 0.8384, $\chi^2_1 = 0.2607$, $P = 0.610$), and overstory stems (parameter = 2.6233, SE = 3.5889, $\chi^2_1 = 0.5343$, $P = 0.465$). These four variables correctly classified nests 77.8% of the time (Table 2).

DISCUSSION

Albeit our small sample of nests, phenology was similar across both years, with the onset of incubation beginning in late February and juveniles fledging by the end of May. The post-fledging dependency period lasted 4–8 wk after the juveniles left the nest. During the first 2–3 wk post-fledging, juveniles frequently returned to the nest to receive

Table 5. Variable selection of Broad-winged Hawk nest sites in Rio Abajo Forest, Puerto Rico, 2001–02. Significant parameters (K), relative AIC (AIC_c), Delta AIC (Δ_i), Akaike Weight (w_i), Goodness-of-Fit statistic (χ^2), P-value, and percent correct classification.

VARIABLE SELECTION	K	AIC_c	Δ_i	W_i	χ^2	P-VALUE	PERCENT
DBH + Nudds 2	2	16.774	0.000	0.551	10.754	0.005	83.3
Cliffwall + DBH	2	19.386	2.612	0.149	8.493	0.014	72.2
Cliffwall + DBH + Nudds 2	3	19.630	2.856	0.132	11.553	0.009	83.3
DBH	1	21.362	4.588	0.056	6.613	0.010	66.7
Cliffwall + Nudds 2	2	21.770	4.996	0.045	8.595	0.014	83.3
Cliffwall	1	22.309	5.535	0.035	5.283	0.022	72.2
Nudds 2	1	22.399	5.625	0.033	5.762	0.016	61.1

prey deliveries from the adults and to roost for the night.

Broad-winged Hawk nests in Puerto Rico averaged 1.1 young per nest attempt and 67% nest success. Our estimate is almost double what Delannoy and Tossas (2002) reported (0.66 fledglings/nest) for Broad-winged Hawk nests in Río Abajo from 1994 to 1996. However, our estimates of nest success and young per nest attempt were slightly lower compared to Broad-winged Hawk studies in North America (Armstrong and Euler 1983, Crocoll 1984, Rosenfield 1984).

The number of fledglings per successful nest and overall nest success was greater in 2001 than in 2002. Lower nest success in 2002 may have been attributed to rain events that occurred in April of 2002. Two nest sites were abandoned within the same week of heavy rain in April 2002. Santana and Temple (1988) reported lower success of Red-tailed Hawks nesting in the eastern Luquillo Mountains rainforest region during extensive rainy periods. Similarly, severe rainfall was suggested as a cause of nest failures of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus vennator*) in the Luquillo Mountains (Snyder and Wiley 1976) and in forests of the central mountain range of the island (Delannoy and Cruz 1988).

April and May are important months to nestling survival. During this time period, Broad-winged Hawks are brooding partially feathered nestlings. In 2001, total precipitation from April and May was 44.2 cm. Conversely, April–May precipitation in 2002 was 54.4 cm. April rains in 2002 coincided with the presence of recently-hatched chicks or young nestlings and may have caused nest abandonment and hypothermia of young at the two failed nests.

At Río Abajo Forest, Broad-winged Hawks foraged primarily on rats, lizards, and small birds (Table 4). The Broad-winged Hawk is an opportunistic feeder who forages on a wide variety of prey (Rush and Doerr 1972, Keran 1978). However, our inability to detect a daily pattern of prey deliveries may have been a result of our small sample of nests and prey delivery observations.

Prey size or type exploited at Río Abajo Forest may be a function of seasonality (wet vs. dry), as changing weather conditions may produce differences in dietary patterns (Grubb 1977, Stinson 1980). In tropical environments such as Puerto Rico, rain may limit foraging opportunities (Foster 1974). We observed Broad-winged Hawks at Río Abajo Forest were less active during periods of rain.

There was no difference in the spatial distribution of nest sites between years, suggesting Broad-winged Hawks may maintain territories year round. These clusters of nests (Fig. 1) are bounded by limestone ridges and cliff walls, where pairs soar along their respective ridge tops. This may have some advantages. Pairs may be better able to detect intruding Red-tailed Hawks. Vigilance may contribute to greater survival of nesting birds (Alcock 1993).

Breeding Broad-winged Hawks were aggressive and successfully deterred intruding Red-tailed Hawks from their nesting territories. Delannoy and Tossas (2002) speculated similar nest-site requirements between Broad-winged Hawks and Red-tailed Hawks could lead to aggressive encounters. However, we found no evidence of nesting by Red-tailed Hawks within the closed canopy forests of Río Abajo. By and large, Broad-winged Hawk courtship and territory defense behavior in Puerto Rico was similar to that of the Ridgway's Hawk (*Buteo*

ridgwayi) in moist limestone forests of the Dominican Republic (Wiley and Wiley 1981).

Territory occupancy seemed relatively stable between years. The year-round residency and site fidelity of Broad-winged Hawks in the moist limestone region of Puerto Rico may be indicative of long-term pair bonds (Griffin et al. 1998). Like other tropical raptors (Mader 1982, Griffin et al. 1998), the subspecies in Puerto Rico seems to exhibit high site fidelity (73%, $N = 11$).

Our results from radio-marked breeding birds (D. Hengstenberg and F. Vilella unpubl. data) suggest Broad-winged Hawks tend to nest in the same stand or nearby from one year to the next (Keran 1978). We observed courtship behavior in 15 additional pairs, but found no evidence of nests or nest building. This may suggest that while some pairs may hold nesting territories, they do not necessarily build a nest or lay eggs every year, as has been documented in other raptors (Steenhof 1987).

Five nests constructed in maría trees were placed atop termite nests in the main crotch of the tree. Broad-winged Hawks nesting in North America sometimes place their nest on top of old bird and squirrel nests (Goodrich et al. 1996).

Distance to cliff wall, tree height and DBH, Nudds board 1.5 m, and Nudds 2.0 m differed between nest and random sites. Variables DBH and Nudds 2 m best classified nest sites, suggesting that Broad-winged Hawks at Río Abajo Forest may prefer large trees and dense understories (Table 5). Also, Broad-winged Hawks in North America avoided smaller trees and selected large DBH trees (Titus and Mosher 1987). At Río Abajo Forest, nest sites had denser understories than random sites. Dense understories may be related to prey availability for adults. These dense understories may offer fledglings protection from predators and greater foraging opportunities of prey. Radio-marked adults and juveniles were frequently observed hunting in the dense understory around their nest sites. Foraging habitat studies have suggested Broad-winged Hawks select sites with high prey availability (Steblein 1991). However, further research is required to better understand the relationships between Broad-winged Hawks in Río Abajo Forest and prey populations.

Model selection procedures for nests (site specific) yielded a four-variable model in which DBH, canopy height, cliff wall, and overstory stems correctly classified nest sites (Table 2). This suggests closeness to karst cliff walls and canopy height may be additional predictors of Broad-winged Hawk nest habitat, in addition to basal area (i.e., DBH) and understory cover.

Nest tree height averaged 22.2 m, whereas canopy heights of nest plots averaged 17.9 m and random sites averaged 16.6 m, suggesting Broad-winged Hawks select emergent trees for their nests. Our results coincide with nest site characteristics of North American broadwings (Goodrich et al. 1996). Delannoy and Tossas (2002) reported a mean nest tree height of 27.0 m and a mean canopy height of 15.7 m. On average, nest heights in Puerto Rico were taller than nest heights reported from North America (Burns 1911, Matray 1974, Titus and Mosher 1981, Armstrong and Euler 1983, Rosenfield 1984). This may reflect the relative lengths of trees in tropical versus temperate forests (Fedorov 1966).

Broad-winged Hawk nest sites were located within 50 m of a cliff wall. In the karst region, cliff walls are very abundant. Cliff walls may offer nest sites with adequate protection from the elements (wind, rain, and sun), intruding predators, provide vantage points, and facilitate reduction in energy requirements when searching for thermal updrafts. Nests sites were generally found on slopes facing southwest ($\bar{x} = 204°$). This nest placement may help protect the nests from the prevailing easterly winds. Broad-winged Hawk nest sites in a limestone forest may be described as occurring in mature closed-canopy overstory stands sheltering a thin midstory, a dense understory, and in close proximity to a cliff wall.

Conservation and persistence of the breeding population of Río Abajo Forest may depend on management of the existing forest stands used by Broad-winged Hawks. Further research is required in Río Abajo Forest to increase sample sizes of nest sites and validate the broadwing-habitat relationships revealed by our habitat model. Moreover, variance estimates of parameters from our study will provide baseline information needed to calculate sample sizes for future research. We suggest additional studies to quantify broadwing habitat in other localities of the karst region and to develop habitat models at multiple spatial scales.

At Río Abajo Forest, managers should limit disturbance within valleys used by broadwings during the critical nest initiation and incubation periods (i.e., February to April). Based on our preliminary results on habitat relationships, silvicultural prac-

tices within Río Abajo Forest that promote maintenance of canopy emergent trees and dense understories may improve habitat conditions for nesting pairs as well as fledglings during their dependence period. Moreover, Broad-winged Hawks readily used plantation tree species such as maría and Honduras mahogany for nest sites. We recommend the DNER Forest Service encourage surrounding private landowners to engage in agroforestry practices using these fast-growing plantation species. Additionally, programs for private lands that promote maintenance and enhancement of forest cover (e.g., USFWS Partners for Wildlife) should be brought to the attention of the landowners adjoining Río Abajo Forest.

In an attempt to establish a second wild population, releases of captive-reared Puerto Rican Parrots are scheduled for 2006 (U.S. Fish and Wildlife Service 1999). Available information suggests Puerto Rican Parrots may exceed the size of avian prey taken by Broad-winged Hawks (Snyder and Kepler 1987). At Río Abajo, 61% of prey deliveries to nests were rodents and *Anolis* lizards (Table 4). Forest songbirds (e.g., Puerto Rican Bullfinch [*Loxigilla portoricensis*] and Bananaquit [*Coereba flaveola*]) were the avian prey taken (Table 4).

In contrast, Red-tailed Hawks are known parrot predators (White et al. 2005). However, our results indicated resident Broad-winged Hawks chased off intruding Red-tailed Hawks effectively in Río Abajo Forest. Owing to the likely negative relationship between these sympatric *Buteos,* resident Broad-winged Hawks in Río Abajo may indirectly provide some degree of protection to released parrots from predation by excluding intruder Red-tailed Hawks. However, research is required to examine the relationship between spatial overlap of parrots and broadwings and the likelihood of Red-tailed Hawk predation on released parrots.

Other studies have reported some avian species select nest sites close to more aggressive species that regularly attack or mob predators (Durango 1949, Clark and Robertson 1979, Wiklund 1979, Dyrcz et al. 1981, Norrdahl et al. 1995). The Woodpigeon (*Columba palumbus*) benefits from nesting in association with Eurasian (northern) Hobbies (*Falco subbuteo*; Bogliani et al. 1999).

Nevertheless, both the Puerto Rican Parrot and Broad-winged Hawk are listed as endangered (U.S. Fish and Wildlife Service 1997, 1999). Therefore, a co-management approach will be required to ensure habitat management activities for one species are not done at the expense of the other. We recommend parrot habitat management activities (i.e., deployment of artificial cavities) should be limited to the nonbreeding season (August–December) to minimize disturbance to Broad-winged Hawk nesting pairs and post-fledging dependent juveniles.

Ultimately, the future of both these endangered species rests on the ability to disseminate research results to forest managers and policymakers. This information in turn will help to guide the protection and conservation of the karst forest region of Puerto Rico, as further forest fragmentation will impact severely the recovery of both the broadwing and the parrot. Multiagency efforts are underway to acquire and protect a significant portion (≥30 000 ha) of forest in the moist karst region of Puerto Rico (Lugo et al. 2001). Broad-winged Hawks do not limit their activities to the Río Abajo Forest boundaries, and their fate in the surrounding private lands may be uncertain. Therefore, DNER forest managers should work proactively with the surrounding land owners to promote land-use practices to conserve and to enhance existing forest cover. Future patterns of land use around the forest boundary may indirectly and directly affect the ability of the Río Abajo Forest to function as an effective conservation unit for the Broad-winged Hawk.

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RAPTOR ABUNDANCE AND DISTRIBUTION IN THE LLANOS WETLANDS OF VENEZUELA

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ABSTRACT.—The Llanos of Venezuela is a 275 000-km^2 freshwater wetland long recognized as an important habitat for waterbirds. However, little information exists on the raptor community of the region. We conducted raptor surveys in the Southwestern and Western Llanos during 2000–02 and detected 28 species representing 19 genera. Overall, areas of the Llanos that we sampled contained 52% of all raptor species and more than 70% of the kites, buteos, and subbuteos known to inhabit Venezuela. Regional differences in the mean number per route for four of the 14 most common species, the Crested Caracara (*Caracara plancus*), Black-collared Hawk (*Busarellus nigricollis*), American Kestrel (*Falco sparverius*), and Osprey (*Pandion haliaetus*), were significant ($P < 0.0018$) in relation to the wet or dry seasons. Of the 14 less common species, six were detected in only one season (wet or dry). The Southwestern and Western regions of the Llanos support a rich raptor community composed primarily of nonmigratory wetland-dependent and upland-terrestrial species.

KEY WORDS: *Neotropics; Venezuela; Llanos; savanna; wetlands; roadside surveys.*

DISTRIBUCIÓN Y ABUNDANCIA DE RAPACES EN HUMEDALES DE LOS LLANOS DE VENZUELA

RESUMEN.—Los llanos de Venezuela constituyen un humedal de agua dulce de 275 000 km^2 que ha sido tradicionalmente reconocido como un ambiente importante para las aves acuáticas. Sin embargo, existe poca información sobre la comunidad de rapaces de la región. Realizamos censos de aves rapaces en el sudoeste y el oeste de los llanos entre 2000 y 2002 y detectamos 28 especies que representaron 19 géneros. En total, las áreas de los llanos que censamos contuvieron el 52% de todas las especies de rapaces y más del 70% de los elanios, buteos y subbuteos que habitan en Venezuela. Las diferencias regionales en el número medio por ruta para cuatro de las 14 especies más comunes, *Caracara plancus, Busarellus nigricollis, Falco sparverius* y *Pandion haliaetus,* fueron significativas ($P < 0.0018$) con relación a las estaciones húmeda y seca. De las 14 especies menos comunes, seis fueron detectadas en una sola estación (húmeda o seca). Las regiones del sudoeste y del oeste de los llanos albergan una rica comunidad de aves rapaces compuesta primariamente por aves no migratorias que dependen de humedales y de especies terrestres de lugares elevados.

[Traducción del equipo editorial]

South America comprises 12% of the world's land surface, yet supports 28% of all raptors (Bierregaard 1998). Most South American raptors do not appear threatened globally, but more information is needed to confirm current assessments and appropriately address threats (Bierregaard 1998, Bildstein et al. 1998). Community level raptor research in South America has been primarily focused in forest habitats (e.g., Thiollay 1984, Thiollay 1989, Alverez et al. 1996, Manosa and Pedrocchi 1997, Manosa et al. 2003); thus, little is known about the raptor populations within the ex-

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tensive savanna and grassland regions of the continent. Raptor surveys in nine South American countries during 1979 detected the greatest number of species in the savannas, mixed riparian forests, pastures, and open areas of interior Venezuela (Ellis et al. 1990), indicating that these areas are important habitats for South American raptors. Furthermore, Neotropical raptors of open land and savanna habitats are currently threatened by habitat loss, including wetland depletion and landscape homogenization (Alvarez-Lopez and Kattan 1995).

In Venezuela, the savannas of the interior are part of an extensive (275 000 km^2) wetland complex called the Llanos. The Llanos cover approximately 31% of Venezuela (Mittermeier et al. 2003) and are located in the latitudinal region characterized by the greatest avian endemism in the Northern Hemisphere (Bibby et al. 1992). Between 32–36 nonmigratory and North American migratory raptor species use some or all of the Llanos (Ferguson-Lees and Christie 2001, Hilty 2003). Although the natural history, biology, and habitat associations of some of these species have been studied locally (Mader 1981, 1982, Beissinger et al. 1988, Balgooyen 1989, Kirk and Currall 1994), community based, landscape-level surveys are lacking.

Our objective was to document and compare the species richness, relative abundance, and distribution of nonmigratory and migratory raptors in the savannas of the Southwestern and Western regions of the Venezuelan Llanos. We also compared these population parameters between the distinct wet and dry seasons that characterize the Llanos.

STUDY AREA

Venezuela supports 1381 species of birds (Hilty 2003) and is considered a globally important region of biodiversity in part due to its rich avifauna (Mittermeier and Mittermeier 1997, Myers et al. 2000). The Venezuelan Llanos is located between ca. 6–9°N and 63–71°W and is bordered by the Coastal Cordillera to the north, the Orinoco Delta and Guiana Shield to the east and southeast, Colombia to the south and southwest, and by the Andes Mountains to the northwest.

Annual rainfall in the Venezuelan Llanos ranges from 90–180 cm (Silva and Moreno 1993), with most rain falling and widespread flooding occurring from April through November (Cole 1986). In contrast, the late November–late April dry season typically is rain free (Troth 1979).

The Venezuelan Llanos is divided into three general areas: western, central, and eastern (Huber and Alcaron 1988). Covering 90 000 km^2, the western area comprises 35% of the freshwater wetland in Venezuela and spans north and west of the Orinoco River from ca. 69–71°W and 6–9°N (Bulla et al. 1990). This area is relatively flat, with elevation ranging from sea level at the Orinoco River to 155 m near the foothills of the Andes. The western area is further divided into two distinct regions known as the Southwestern and Western Llanos (Fig. 1; Huber and Alcaron 1988).

The Southwestern Llanos includes the vast open–savanna–wetland habitats that extend from the Meta and Orinoco rivers northwest to the agricultural–savanna–forest mosaic habitats of the Western Llanos. The Southwestern Llanos is characterized by poor soils, savanna habitats with small patches of trees, gallery forest, and extensive wet season flooding that renders the region largely unsuitable for agriculture (Huber and Alcaron 1988).

The Western Llanos encompasses the alluvial plains bordered by the foothills of the Andes and extends southeast to the open savannas of the Southwestern Llanos. This region is characterized by fertile soils and partial flooding that support agricultural production and native forests dominated by tree species similar to those of the Amazon basin (Huber and Alcaron 1988, Silva and Moreno 1993).

METHODS

Sampling Design. We surveyed raptors along the sparse network of roads accessible during both the wet and dry seasons in the Southwestern and Western Llanos (Fig. 1) Despite limitations inherent in roadside surveys (Millsap and LeFranc 1988, Bunn et al. 1995), such counts can be used to survey relative raptor abundance, community composition, and habitat associations across large landscapes (Woffinden and Murphy 1977, Thiollay 1978, Ellis et al. 1990, Sorley and Andersen 1994, Seavy and Apodaca 2002). However, roadside surveys in open habitats may be inadequate for detecting small and uncommon raptor species unless surveys incorporate frequent and regular stops (Whitacre and Turley 1990). Therefore, we used the North American Breeding Bird Survey model (Droege 1990) to establish stationary surveying points along road routes.

We placed 50 survey routes along roads where the overall distribution of survey routes was dictated by accessibility of roads during the wet season (Fig. 1). Each route was 22.5 km long with 16 sample points spaced 1.5 km apart (Jensen 2003: Appendix A). Each sample point was surveyed by a 2-person surveying team for 3 min to the right and left side of the road for a total of 6 min/point. All raptors were tallied within a 500-m radius as measured by rangefinder binoculars. Except for the King Vulture (*Sarcoramphus papa*), we did not tally Cathartid vultures. Scientific and common names of birds follow Ferguson-Lees and Christie (2001).

Raptors were surveyed during rainless periods of the day, primarily from 0700–1200 H, and never later than 1400 H. Surveys were conducted over ca. 6-wk periods twice each year between August 2000 and March 2002 The 6-wk periods coincided with the end of the wet (August–October) and dry seasons (January–March). We surveyed 27 routes in the wet season of 2000, 39 in the

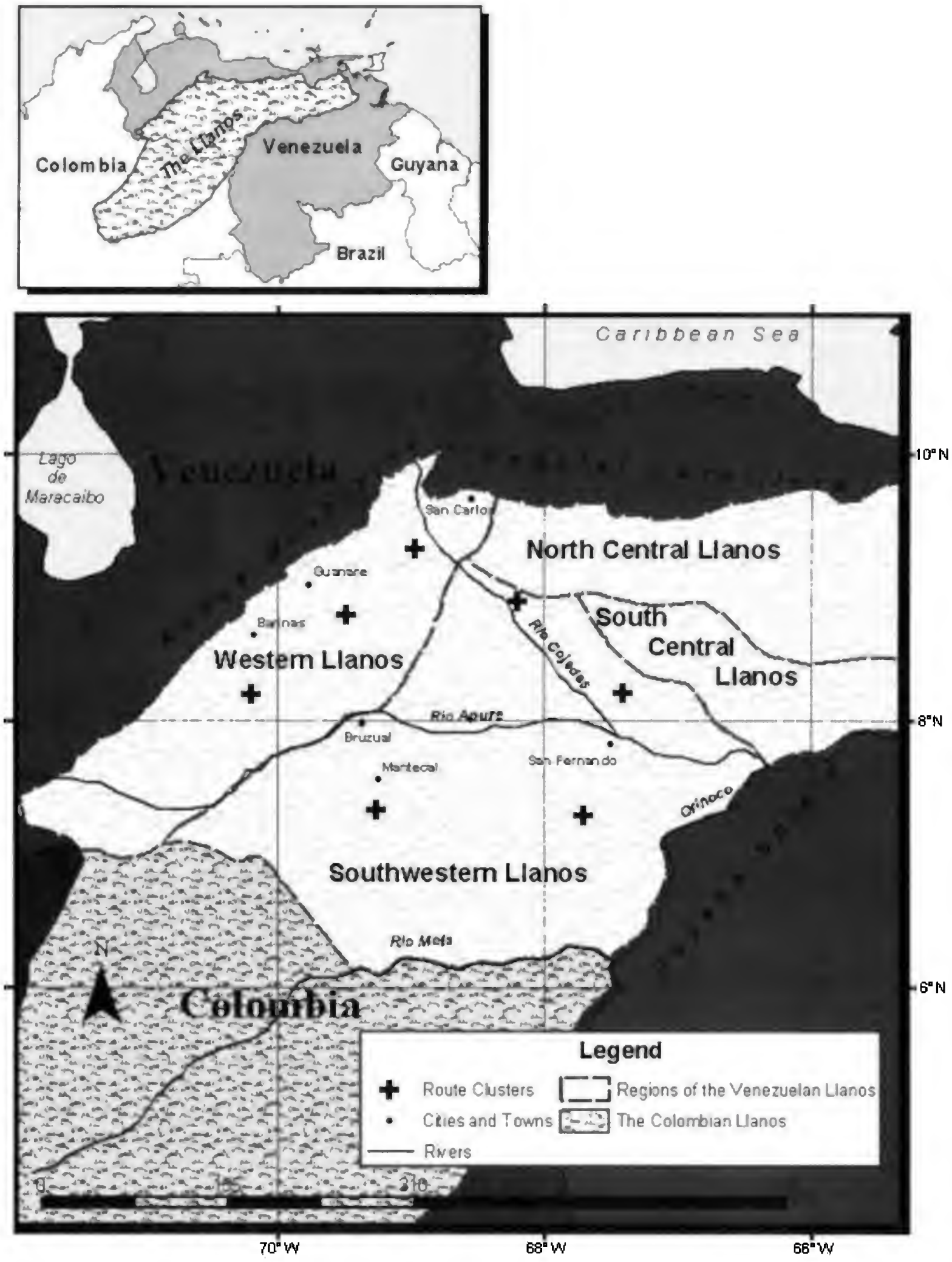

Figure 1. Study area map of the raptor survey during wet seasons 2000 and 2001 and dry seasons 2001 and 2002 in the Southwestern and Western Llanos of Venezuela. Route clusters are areas where groups of survey routes containing sample points are located.

dry season of 2001, 50 in the wet season of 2001, and 50 in the dry season of 2002.

Analysis. We calculated the total number of individuals detected on all surveys, as well as species totals, percent composition, and frequency of detection. We classified percent composition into four species abundance classes: Very common (10–26% of all individuals detected), Common (3–5%), Uncommon (1–2%), and Rare (<1%). We used EstimateS Version 6.0b1 software (Colwell 2000) to generate a species accumulation curve to evaluate the probability that our 2-yr 50-route roadside survey design was adequate for documenting all detectable raptor species.

We then calculated the mean number of individuals per species per route (mean number per route) by year, season, and region to investigate annual changes in abundance between the 2000 and 2001 wet seasons and the 2001 and 2002 dry seasons for each region. For this comparison we used the 27 routes surveyed during the first survey visit (wet season 2000) and resurveyed for the duration of the survey (2001 and 2002): Southwestern Llanos (15 routes) and Western Llanos (12 routes). Rare abundance class species were detected in numbers too low to meet the underlying assumptions for a *t*-test and were omitted from all subsequent statistical tests. For the 14 most common species, we used paired *t*-tests to evaluate four hypothesis (Ho_1: mean number per route Southwestern Llanos wet season 2000 = mean number per route Southwestern Llanos wet season 2001; Ho_2: mean number per route Southwestern Llanos dry season 2001 = mean number per route Southwestern Llanos dry season 2002; Ho_3: mean number per route Western Llanos wet season 2000 = mean number per route Western Llanos wet season 2001; Ho_4: mean number per route Western Llanos dry season 2001 = mean number per route Western Llanos dry season 2002). Differences were considered significant at $P < 0.10$ because we were interested in large-scale broad patterns. However, we used the Bonferroni Method to control for inflated experimentwise type I error rate resulting from simultaneous multiple comparisons (Beal and Khamis 1991). For all analysis, Bonferroni corrected significance for 56 comparisons was determined at ($P < 0.0018$).

We then combined data from both years to investigate seasonal and regional differences in species numbers, species diversity, community composition, and mean number per route for each species. During the 2-yr study, 50 routes were surveyed (Southwestern Llanos 28 routes, Western Llanos 22 routes). We surveyed 27 routes during both survey years (wet season 2000 and dry season 2001) and an additional 23 routes during the second survey year (wet season 2001 and dry season 2002). To standardize the number of individuals detected on the 27 routes surveyed over 2-yr, we averaged the number of individuals per survey point across survey years for each species. We then combined this 27-route average with the data from the 23 routes surveyed only during the second survey year to yield 50 total routes. Combining the data using this method preserved the majority of data collected, accounted for variation in numbers of individuals detected for each species on routes replicated over survey years, and preserved data from routes surveyed only during the second year.

We calculated species numbers and Simpson's Inverse Diversity Index ($D = 1/\Sigma\, pi^2$) for the wet and dry seasons within each region (Hayek and Buzas 1996). We also calculated Jaccard's Coefficient of Community Similarity to estimate the percent overlap between communities in both seasons and regions (Magurran 1988). Again, we used EstimateS version 6.0b1 software (Colwell 2000) to generate species accumulation curves for each regional and seasonal dataset to evaluate the probability that the number of routes surveyed in each region for each season were adequate for documenting all detectable raptor species.

To investigate seasonal and regional differences in numbers for each species, we first calculated the mean numbers per route for each region and season. To compare seasonal differences in mean numbers per route for the 14 most abundant species, we used paired *t*-tests to evaluate two hypothesis (Ho_1: mean number per route Southwestern Llanos wet seasons = mean number per route Southwestern Llanos dry seasons; Ho_2: mean number per route Western Llanos wet seasons = mean number per route Western Llanos dry seasons). For the same 14 species, we also used 2-sample *t*-tests to evaluate regional differences in mean numbers per route (Ho_1: mean number per route Southwestern Llanos wet seasons = mean number per route Western Llanos wet seasons; Ho_2: mean number per route Southwestern Llanos dry seasons = mean number per route Western Llanos dry seasons). The 14 rare abundance class species are presented only as present or absent for each region and season.

RESULTS

General Patterns. We counted 5735 raptors representing 28 species and 19 genera (Table 1). The four most abundant species, Crested Caracara (*Caracara plancus*), Yellow-headed Caracara (*Milvago chimachima*), Savanna Hawk (*Buteogallus meridionalis*), and Roadside Hawk (*Buteo magnirostris*), comprised 72% of all individuals and were seen on 98–100% of all routes. Four additional species were classified as common and together comprised 15% of all individuals. These were the Black-collared Hawk (*Busarellus nigricollis*), White-tailed Hawk (*Buteo albicaudatus*), Snail Kite (*Rostrhamus sociabilis*), and American Kestrel (*Falco sparverius*). Six additional species were uncommon and represented 10% of all detections. They were the Aplomado Falcon (*Falco femoralis*), Great Black Hawk (*Buteogallus urubitinga*), White-tailed Kite (*Elanus leucurus*), Crane Hawk (*Geranospiza caerulescens*), Laughing Falcon (*Herpetotheres cachinnans*), and Osprey (*Pandion haliaetus*). Fourteen additional species comprised the remaining 3%. Species classified as common were detected on 52–84% of all routes, whereas uncommon species were detected on 44–78% routes. The 14 rare species were detected on

Table 1. Species detected during raptor surveys in the Southwestern and Western Llanos of Venezuela during wet seasons in 2000 and 2001 and dry seasons in 2001 and 2002. Species are listed in order of relative abundance based on percent composition. English common names and taxonomy follow Ferguson-Lees and Christie (2001).

Relative Abundance Class[a]	Species	Status[b]	Total Number	Percent Composition	Frequency Occurrence (%)[c]
Very common	Creasted Caracara (*Caracara plancus*)	R	1473	26	100
	Yellow-headed Caracara (*Milvago chimachima*)	R	1061	19	100
	Savanna Hawk (*Buteogallus meridionalis*)	R	1005	18	98
	Roadside Hawk (*Buteo magnirostris*)	R	604	11	98
Common	Black-collared Hawk (*Busarellus nigricollis*)	R	269	5	84
	Snail Kite (*Rostrhamus sociabilis*)	R	226	4	68
	American Kestrel (*Falco sparverius*)	R/NAM	183	3	52
	White-tailed Hawk (*Buteo albicaudatus*)	R	155	3	72
	Aplomado Falcon (*Falco femoralis*)	R	113	2	78
Uncommon	Great Black Hawk (*Buteogallus urubitinga*)	R	110	2	58
	White-tailed Kite (*Elanus leucurus*)	R	137	2	70
	Crane Hawk (*Geranospiza caerulescens*)	R	74	1	56
	Laughing Falcon (*Herpetotheres cachinnans*)	R	70	1	44
	Osprey (*Pandion haliaetus*)	NAM	66	1	48
Rare	King Vulture (*Sarcoramphus papa*)	R	41	0.7	24
	Harris's Hawk (*Parabuteo unicinctus*)	R	36	0.5	28
	Grey-lined Hawk (*Buteo nitidus*)	R	27	0.5	28
	Zone-tailed Hawk (*Buteo albonotatus*)	R	19	0.3	32
	Slender-billed Kite (*Rostrhamus hamatus*)	R	19	0.3	16
	Bat Falcon (*Falco rufigularis*)	R	16	0.3	24
	Plumbeous Kite (*Ictinia plumbea*)	R	9	0.2	14
	Hook-billed Kite (*Chondrohierax uncinatus*)	R	5	0.08	10
	Long-winged Harrier (*Circus buffoni*)	R	5	0.09	6
	Common Black Hawk (*Buteogallus anthracinus*)	R	5	0.09	10
	Peregrine Falcon (*Falco peregrinus*)	NAM	5	0.09	8
	Short-tailed Hawk (*Buteo brachyurus*)	R	5	0.09	6
	Grey-headed Kite (*Leptodon cayanensis*)	R	3	0.05	4
	Pearl Kite (*Gampsonyx swainsonii*)	R	3	0.05	6

[a] Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%, Uncommon = 1–2%, Rare = <1%.

[b] Status: R = nonmigratory population, NAM = North American migratory population, R/NAM = nonmigratory and North American migratory populations.

[c] Frequency of occurrence: the percent of routes on which a species was detected.

≤32% of all routes. There were three species of North American migrants: Osprey, American Kestrel, and Peregrine Falcon (*Falco peregrinus*). The Osprey and Peregrine Falcon combined comprised 1.2% of all individuals seen. In contrast, the American Kestrel comprised 3%, having both nonmigratory and migratory populations (Hilty 2003). At least one of these three species was seen at least once on 82% of routes.

The species accumulation curve indicated the number of routes surveyed over the two survey years was adequate for documenting all species detectable by roadside point count surveys in the study area (Fig. 2). Specifically, all 28 species were detected with 34 routes (68% of all routes surveyed).

Yearly Comparisons. Among the 14 most common species there were no regional or seasonal differences ($P > 0.0018$) in mean number per route between survey years (Table 2).

Regional and Seasonal Patterns. The greatest number of species, 25, was detected in the Southwestern Llanos during the wet season and in the Western Llanos during the dry season (Fig. 3). Although species numbers were equal between regions, diversity was higher in the Western Llanos

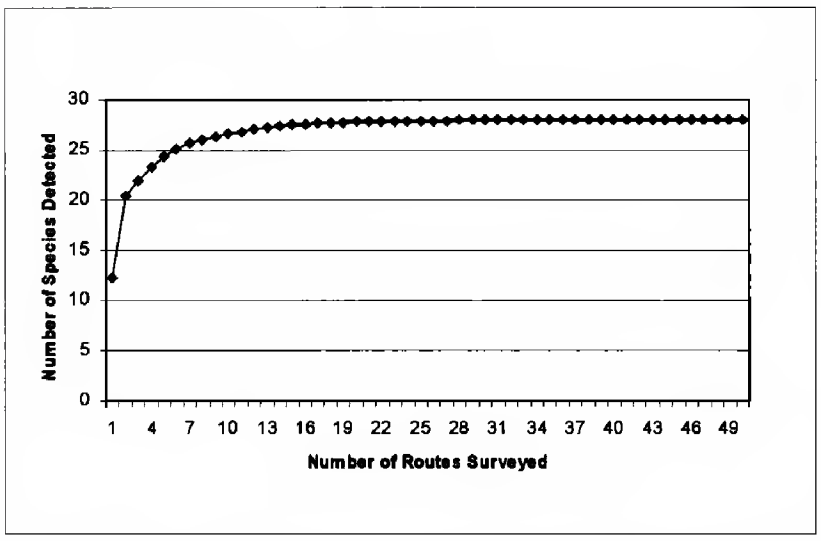

Figure 2. Species accumulation graph of raptor species detected on 50 survey routes in the Southwestern and Western Llanos of Venezuela during the wet seasons in 2000 and 2001 and dry seasons 2001 and 2002.

during both seasons. Species accumulation curves indicated the number of routes surveyed during each season was adequate to detect the majority of species for both regions (Fig. 4).

The raptor community (Jaccard's Coefficient of Community Similarity) in the Southwestern versus Western Llanos differed by 12%, both in the wet and dry seasons. For seasons combined, 25 species were detected in each region, of which 22 species were shared between regions. The seasonal changes in community composition within regions (26%) were greater than the regional differences within the wet and dry season (12%).

Four of the 14 most common species exhibited regional differences ($P < 0.0018$) in mean number per route in relation to the wet or dry seasons (Table 3). The Crested Caracara ($P < 0.001$) and Osprey ($P < 0.001$) were more numerous in the Southwestern Llanos than the Western Llanos during the wet season. The Black-collared Hawk ($P = 0.001$) was more numerous in the dry season in the Southwestern Llanos than the Western Llanos, whereas the American Kestrel ($P = 0.001$) was more numerous in the dry season in the Western Llanos than the Southwestern Llanos.

Of the 14 rare species, six were detected only during one season or region (Table 4). The Peregrine Falcon and Grey-headed Kite were seen only in the dry season, and the Pearl Kite and Slender-billed Kite were seen only in the wet season. The Common Black Hawk was detected only in the Southwestern Llanos in the wet season, and the Plumbeous Kite was detected only in the Western Llanos in the dry season.

DISCUSSION

General Findings. The savannas of the Southwestern and Western Llanos of Venezuela are particularly rich in raptors, supporting 52% (32 of 61) of all regularly occurring migrant and resident species found in Venezuela (Hilty 2003). Indeed, during our 2-yr study of the Venezuelan Llanos, these regions included 55% of all hawk species (10 of 18), 70% (7 of 10) of kite species, 67% (4 of 6) of vulture species, and 50% (3 of 6) of the regularly occurring North American migratory species (Hilty 2003). However, although the Llanos supported species assemblages equivalent to all other Venezuelan life zones for most raptors, we did not detect any of the eight eagle species that occur in Venezuela.

Except for the three common Cathartid species we did not count, we detected 24 of 27 resident species expected to occur in the Llanos (Hilty 2003). We did not detect three uncommon forest-dwelling raptors thought to occur in the region: the Collared Forest-Falcon (*Micrastur semitorquatus*), Bicolored Hawk (*Accipiter bicolor*), and Ornate Hawk Eagle (*Spizaetus ornatus*). We likely failed to see these species because of the inherent difficulty of detecting forest-dwelling species from roadside surveys (Millsap and LeFranc 1988).

Of the three North American migrant species we detected, two occur year-round in the Llanos. The American Kestrel occurs year-round in the Llanos because there are nonmigratory and migratory populations (Hilty 2003). Although the Osprey population is wholly migratory, the Osprey occurs year-round in the Llanos because first-year birds reaching the Llanos remain for at least 18 mo (Martell et al. 2001, Hilty 2003).

North American migratory species not seen during surveys were the Northern Harrier (*Circus cyaneus*), Broad-winged Hawk (*Buteo platypterus*), Swainson's Hawk (*B. swainsoni*), and Merlin (*Falco columbarius*). However, one Merlin was detected in the Llanos, but not on survey routes. Historical sightings of the Swainson's Hawk and Northern Harrier in the Llanos are considered accidental (Hilty 2003), and satellite-tracking of Swainson's Hawks confirms that their migrations to and from Argentina occur along the central and eastern slopes of the Andes (Fuller et al. 1998). The Broad-winged Hawk is thought to winter in portions of the Llanos west and north of our study area (Hilty 2003).

Table 2. Relative abundance class, species, and mean number of individuals (± SE) detected per route (mean/route) during raptor surveys in the Southwestern and Western Llanos of Venezuela during the wet seasons in 2000 and 2001 and the dry seasons in 2001 and 2002.

Relative Abundance Class[a]	Species	Southwestern Llanos				Western Llanos			
		Wet (N = 15)		Dry (N = 26)		Wet (N = 15)		Dry (N = 26)	
		2000	2001[b]	2001	2002	2000	2001	2001	2002
Very common	Crested Caracara	11.27 ± 2.88	11.53 ± 2.38	12.26 ± 2.60	14.04 ± 1.78	1.75 ± 0.63	2.83 ± 0.49	5.31 ± 1.24	5.00 ± 1.00
	Yellow-headed Caracara	5.07 ± 1.30	5.80 ± 1.10	5.22 ± 0.66	7.00 ± 0.92	4.58 ± 1.12	6.33 ± 1.09	8.92 ± 1.71	9.54 ± 1.99
	Savanna Hawk	2.47 ± 0.58	4.80 ± 0.97	6.19 ± 1.17	6.48 ± 1.18	1.00 ± 0.44	1.08 ± 0.53	10.92 ± 3.71	7.77 ± 1.99
	Roadside Hawk	2.07 ± 0.79	2.60 ± 0.88	2.41 ± 0.53	3.74 ± 0.80	1.83 ± 0.60	3.33 ± 0.66	3.38 ± 0.81	3.00 ± 0.60
Common	Black-collared Hawk	1.13 ± 0.41	2.33 ± 0.55	2.07 ± 0.53	2.93 ± 0.58	0.17 ± 0.11	0.42 ± 0.23	0.46 ± 0.22	0.39 ± 0.18
	Snail Kite	4.40 ± 2.63	3.73 ± 1.27	0.96 ± 0.29	0.89 ± 0.37	0.17 ± 0.17	1.50 ± 0.68	0	0.31 ± 0.13
	American Kestrel	0	0.13 ± 0.09	0.22 ± 0.10	0.22 ± 0.11	1.92 ± 0.74	2.33 ± 1.29	2.31 ± 0.74	3.54 ± 1.23
	White-tailed Hawk	1.40 ± 0.38	1.73 ± 0.47	0.07 ± 0.27	1.00 ± 0.26	0.25 ± 0.18	0.33 ± 0.33	1.08 ± 0.45	0.92 ± 0.37
Uncommon	Aplomado Falcon	0.73 ± 0.23	1.13 ± 0.39	0.41 ± 0.15	1.11 ± 0.36	0.50 ± 0.26	0.75 ± 0.28	0.54 ± 0.18	0.54 ± 0.18
	Great Black Hawk	0	0.53 ± 0.24	0.89 ± 0.24	1.11 ± 0.40	0	0.17 ± 0.17	0.15 ± 0.15	0.31 ± 0.18
	White-tailed Kite	0.33 ± 0.13	0.33 ± 0.19	0.26 ± 0.10	0.41 ± 0.15	1.25 ± 0.41	1.50 ± 0.56	1.77 ± 0.55	1.46 ± 0.39
	Crane Hawk	0.33 ± 0.21	0.27 ± 0.18	0.30 ± 0.12	0.78 ± 0.18	0.08 ± 0.08	0.08 ± 0.08	0.23 ± 0.17	0.23 ± 0.12
	Laughing Falcon	0.07 ± 0.07	0.27 ± 0.19	0.04 ± 0.04	0.19 ± 0.13	0.42 ± 0.26	0.33 ± 0.26	0.54 ± 0.27	0.39 ± 0.21
	Osprey	0.87 ± 0.39	0.73 ± 0.23	0.30 ± 0.12	0.48 ± 0.22	0	0	0.15 ± 0.15	0.39 ± 0.18

[a] Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%; Uncommon = 1–2%.

[b] All comparisons were not significant ($P > 0.0018$).

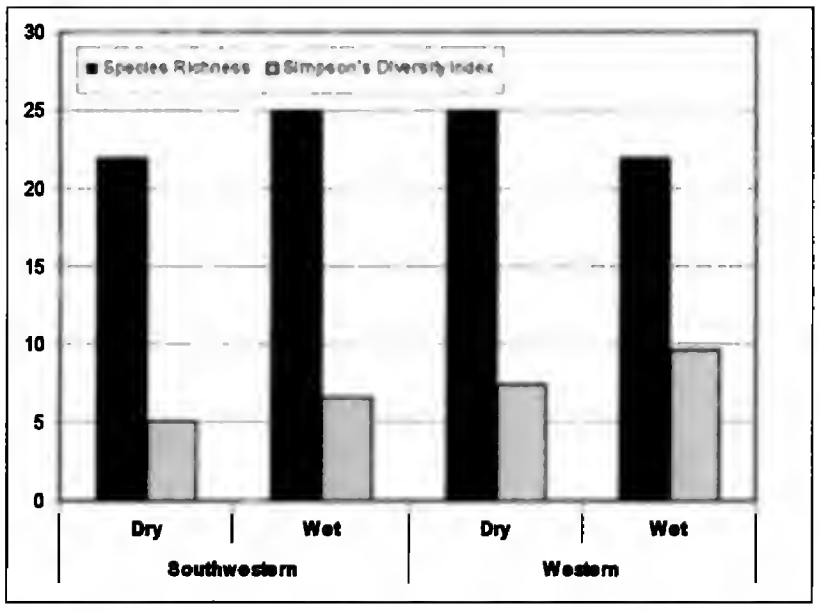

Figure 3. Raptor species numbers and diversity in the Southwestern and Western Llanos of Venezuela for combined years during the wet season (2000 and 2001) and the dry season (2001 and 2002).

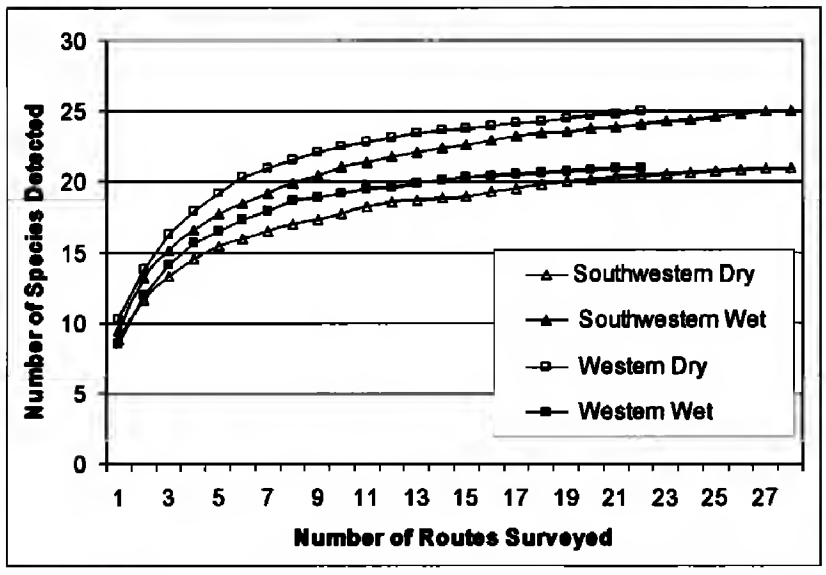

Figure 4. Species accumulation graphs for raptors detected in the Southwestern and Western Llanos of Venezuela for combined years during the wet seasons (2000 and 2001) and the dry seasons (2001 and 2002).

Overall, the Southwestern and Western regions of the Llanos lacked the eagle diversity characteristic of African savannas (Thiollay 1978). Nonetheless, these Llanos regions supported numbers of raptor genera (21) similar to those found in the seasonally-flooded savannas and agricultural-forest mosaic habitats of Kidepo Valley National Park of Uganda (22; Thiollay 1978). Consequently, migratory species in the Southwestern and Western Llanos only comprise a small portion of the raptor community (7%), whereas migratory species account for 33% of the raptor community in Kidepo Valley National Park of Uganda.

Table 3. Relative abundance of species and mean number of individuals (± SE) detected per route (mean/route) during raptor surveys for combined years in the wet (2000 and 2001) and the dry season (2001 and 2002) in the Southwestern and Western Llanos of Venezuela.

Relative Abundance Class[a]	Species	Status[b]	Southwestern (N = 28)		Western (N = 22)	
			Wet[c]	Dry[c]	Wet[c]	Dry[c]
Very common	Crested Caracara	R	10.21 ± 1.37[d]	13.80 ± 1.88	2.98 ± 0.88[d]	6.00 ± 1.62
	Yellow-headed Caracara	R	6.09 ± 0.70	6.70 ± 0.74	5.21 ± 0.97	8.05 ± 1.25
	Savanna Hawk	R	4.45 ± 0.63	6.34 ± 1.06	3.16 ± 0.76	12.70 ± 3.92
	Roadside Hawk	R	3.25 ± 0.62	3.59 ± 0.76	5.18 ± 0.81	5.41 ± 0.80
Common	Black-collared Hawk	R	2.36 ± 0.53	2.73 ± 0.55[D]	0.52 ± 0.21	0.66 ± 0.20[D]
	Snail Kite	R	3.00 ± 0.94	0.93 ± 0.35	0.73 ± 0.22	0.23 ± 0.09
	American Kestrel	R/NAM	0.25 ± 0.13	0.23 ± 0.10[D]	2.21 ± 0.76	2.37 ± 0.57[D]
	White-tailed Hawk	R	1.41 ± 0.24	0.82 ± 0.18	0.48 ± 0.24	0.68 ± 0.17
Uncommon	Aplomado Falcon	R	0.61 ± 0.17	0.84 ± 0.20	0.57 ± 0.13	0.60 ± 0.16
	Great Black Hawk	R	0.84 ± 0.30	1.21 ± 0.37	0.59 ± 0.19	0.43 ± 0.18
	White-tailed Kite	R	0.32 ± 0.09	0.39 ± 0.12	1.48 ± 0.40	1.50 ± 0.32
	Crane Hawk	R	0.30 ± 0.10	0.61 ± 0.14	0.27 ± 0.11	0.55 ± 0.19
	Laughing Falcon	R	0.23 ± 0.12	0.18 ± 0.13	0.93 ± 0.27	1.09 ± 0.38
	Osprey	NAM	0.93 ± 0.21[d]	0.38 ± 0.14	0[d]	0.28 ± 0.11

[a] Relative abundance class: Very common = 10–26% of all individuals detected; Common = 3–5%, Uncommon = 1–2%.
[b] Status: R = resident species, NAM = North American migratory species, R/NAM = resident and North American migratory population.
[c] Means denoted by "d" differed ($P < 0.0018$) between regions for the wet season. Means denoted by "D" differed ($P < 0.0018$) between regions for the dry season. All other comparisons were not significant ($P > 0.0018$).

Table 4. Rare species detected during raptor surveys for combined years in the wet (2000 and 2001) and the dry season (2001 and 2002) in the Southwestern and Western Llanos of Venezuela.

Relative Abundance Class[a]	Species	Status[b]	Southwestern (N = 28)		Western (N = 22)	
			Wet	Dry	Wet	Dry
Rare	King Vulture	R	X		X	X
	Harris's Hawk	R	X	X	X	X
	Gray-lined Hawk	R	X	X	X	X
	Zone-tailed Hawk	R	X	X	X	X
	Slender-billed Kite	R	X		X	
	Bat Falcon	R	X	X	X	X
	Plumbeous Kite	R				X
	Hook-billed Kite	R	X	X	X	X
	Long-winged Harrier	R	X	X		X
	Common Black Hawk	R	X			
	Peregrine Falcon	NAM		X		X
	Short-tailed Hawk	R	X		X	X
	Grey-headed Kite	R		X		X
	Pearl Kite	R	X		X	

[a] Relative abundance class: Rare = <1% of all individuals detected.
[b] Status: R = nonmigratory populations, NAM = North American migratory population.

Regional and Seasonal Patterns. The Western Llanos was characterized by higher levels of raptor diversity. This region underwent a period of extensive deforestation prior to 1825, followed by forest regeneration through 1950, and another period of deforestation by 1975 (Veillon 1976). Forest exploitation cycles, coupled with agricultural activity and year-round water sources, have resulted in a dynamic mosaic of forest, savanna, agricultural, pasture, and early successional habitats that likely account for the high raptor diversity in this region.

Overall, raptor communities in the Southwestern and Western Llanos were similar. However, varying vegetation cover types, large-scale flooding, and the availability of year round water sources during the dry season almost certainly influence the raptor community. For example, Balgooyen (1989) reported the American Kestrel preferred the forest-agriculture mosaic habitats in the Llanos. Our data indicated this pattern was pronounced in the dry season, when American Kestrel numbers increased in the Western Llanos, likely due to the arrival of wintering North American migrants. Furthermore, several examples of seasonal influences are apparent in the Southwestern Llanos, where flooding of savanna and gallery forest is extensive in the wet season, but also where wetland complexes persist throughout the year. The higher numbers of the Black-collared Hawk in this region during the dry season were likely explained by the presence of year-round wetland complexes. Similarly, the higher numbers of Osprey in the Southwestern Llanos versus Western Llanos during the wet season indicated that Osprey used both regions during the dry season, but first-year birds spent the wet season in the Southwestern Llanos, where flooding was extensive. Therefore, the year-round availability of wetland complexes and the extensive inundation of savanna in the wet season likely explains why these aquatic-dependent species are more abundant in this region.

Raptor Distribution. Our results on the relative abundance and distribution of the 14 most common species in our study were consistent with previous findings. However, 4 of 14 less common species were not expected to occur in the Llanos, or there was little information on their distribution and seasonal occurrence: Common Black Hawk (5 individuals), Pearl Kite (6), Plumbeous Kite (9), and Short-tailed Hawk (5). The Pearl Kite was reported as scarce or absent in the Llanos (Hilty 2003), but was detected in greater numbers than many species considered uncommon residents. Although the distribution of the Short-tailed Hawk was previously unknown in the Llanos (Hilty 2003), we detected this species in low numbers throughout the study area. Our observation that the Plumbeous Kite was absent during the wet season sug-

gests the Llanos population was similar to those of Central America, Mexico, and Trinidad. All of these raptors migrate southward in August and September and return north to breed in February and March (Ferguson-Lees and Christie 2001).

Conservation Implications. The rich raptor community of the Southwestern and Western Llanos is comprised of wetland-dependent and upland-terrestrial species, both nonmigratory and migratory, of which several appear seasonally nomadic and may depend on both regions as they move in and out in response to the wet and dry seasons. This pattern suggests that, at least in part, the diverse raptor community in the region owes its origins to a combination of a large landscape with a substantial seasonal influx of water and the forest-agricultural mosaic that creates a temporally and spatially diverse mix of habitats.

The Harris's Hawk (*Parabuteo unicinctus*), Savanna Hawk, and White-tailed Hawk are now absent from the Cauca Valley in Columbia as a result of landscape homogenization and wetland depletion (Alvarez-Lopez and Kattan 1995). We commonly detected the Savanna Hawk and White-tailed Hawk, and to a lesser extent the Harris's Hawk, throughout the Southwestern and Western Llanos, which suggests large-scale landscape homogenization and wetland degradation are not yet occurring in these regions. In contrast, because hawk-eagles may be less tolerant of human alterations on the landscape than many other raptors (Burnham et al. 1994), the Ornate Hawk-Eagle may have been affected by historical deforestation and subsequent lack of suitable habitats in these regions. However, with the exception of the Ornate Hawk-Eagle, the raptor community in the Llanos may represent a community model for Neotropical savanna–forest–agricultural regions.

Importantly, additional studies on the raptor community in the Llanos are required to better understand abundance patterns and seasonal fluctuations of raptors. Furthermore, research is needed to evaluate local areas where deforestation, intensive agriculture, and man-made impoundments are currently expanding, which may be useful for assessing the long-term stability of the current raptor community. Finally, comparisons between the Llanos and other Neotropical wetland–savanna complexes, such as the Brazilian Pantanal, will help determine the scope and representation of our findings.

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A COMPARISON OF BREEDING SEASON FOOD HABITS OF BURROWING OWLS NESTING IN AGRICULTURAL AND NONAGRICULTURAL HABITAT IN IDAHO

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ABSTRACT.—Through analysis of regurgitated pellets and prey remains collected at nests between 2001–02, we characterized diet composition of western Burrowing Owls (*Athene cunicularia hypugaea*) in the Snake River Birds of Prey National Conservation Area (NCA) of southwestern Idaho. We hypothesized that diet differs between owls nesting in agricultural and nonagricultural habitat, because at least one important prey species, montane voles (*Microtus montanus*), occurs predominately in the former. From 859 pellets, we identified 7402 prey items representing 23 species, and identified 403 prey remains of 19 species. Invertebrates dominated the diet in numbers of prey, whereas rodents contributed the greatest biomass. Montane voles, which were not present in pellets in nonagricultural areas, represented the greatest percent biomass of pellets in agricultural areas. Invertebrates (predominately Gryllidae) also were more abundant in diets of owls nesting in agricultural habitat. Pellets of owls nesting in agricultural areas had greater species richness, whereas pellets from nonagricultural areas had greater species evenness and broader food-niche breadths. Finally, we estimated food-niche breadth of Burrowing Owls in the NCA to be broader than previously reported.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *agriculture*; *food habits*; *food-niche*; *Idaho.*

UNA COMPARACIÓN DE LOS HÁBITOS ALIMENTICIOS DE INDIVIDUOS NIDIFICANTES DE *ATHENE CUNICULARIA* EN AMBIENTES AGRICOLAS Y NO AGRICOLAS EN IDAHO

RESUMEN.—A través del análisis de egagrópilas y de restos de presas recolectados en nidos en 2001 y 2002, caracterizamos la composición de la dieta de *Athene cunicularia hypugaea* en el Área Nacional de Conservación de Aves de Presa Snake River, sudoeste de Idaho. Nos planteamos la hipótesis de que la dieta difiere entre las lechuzas que nidifican en ambientes agrícolas y no agrícolas, debido a que al menos una de las especies de presa importantes, *Microtus montanus,* se encuentra predominantemente en las áreas agrícolas. De un total de 859 egagrópilas, identificamos 7402 ítems de presas correspondientes a 23 especies, e identificamos 403 restos de presas provenientes de 19 especies. Los invertebrados dominaron la dieta en términos del número de presas, mientras que los roedores representaron la mayor biomasa. *Microtus montanus* no estuvo presente en las egagrópilas de las áreas no agrícolas y representó el mayor porcentaje de biomasa en las egagrópilas de las áreas agrícolas. Los invertebrados (predominantemente Gryllidae) también fueron abundantes en las dietas de las lechuzas que nidificaron en los ambientes agrícolas. Las egagrópilas de las lechuzas que nidificaron en las áreas agrícolas presentaron mayor riqueza de especies, mientras que las provenientes de las áreas no agrícolas presentaron mayor equidad y nichos alimenticios más amplios. Finalmente, estimamos que el nicho alimenticio de *A. c. hypugaea* en el área silvestre de conservación estudiada es más amplio de lo que había sido informado previamente.

[Traducción del equipo editorial]

Agricultural practices historically have provided many different types of wildlife habitat, including shelterbelts, hedgerows and fencerows, cultivated fields, and fields in rotation. Although some species nest, seek cover, and forage in these habitats, many wildlife populations have declined significantly in areas of agricultural conversion (Carlson 1985, Murphy 2003). In fact, there is mounting evidence that converting natural landscapes into agricultural use can affect a wide array of wildlife populations through erosion, exposure to herbicides and pesticides, and destruction of nesting and cover habitat (Carlson 1985, Jahn and Schenck 1991, Gervais et al. 2000). These effects may be

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amplified by the shift from small-scale farming practices to large-scale monoculture farming seen throughout the United States and Canada (Peterjohn 2003).

Western Burrowing Owls (*Athene cunicularia hypugaea*) are listed as Endangered in Canada and several western U.S. states, and their populations are declining in many areas (e.g., James and Espie 1997, Clayton and Schmutz 1999, Klute et al. 2003). These owls suffer deleterious effects from agricultural practices (James and Fox 1987, Haug et al. 1993, Bellocq 1997, Gervais et al. 2000) and, in Canada, often avoid agricultural fields (Haug and Oliphant 1990, Clayton and Schmutz 1999). However, throughout some portions of their western U.S. range, Burrowing Owls associate with agriculture (Rich 1986, DeSante et al. 2004, Moulton et al., in press), and they are the only raptor species that shows significant affinity for agriculture in southern Idaho (Leptich 1994). Rich (1986) suggested that proximity to montane voles (*Microtus montanus*) in farmlands could explain some of this habitat selection. Moulton et al. (in press) confirmed that owls did not nest in agricultural areas because of decreased nest predation or increased availability of nesting sites but noted that prey consumption was greater in agricultural areas.

If Burrowing Owl nesting distributions can be affected by prey, as Rich (1986) and Moulton et al. (in press) hypothesize, then diet composition may differ for owls occupying agricultural and nonagricultural areas. Thus, the objective of our study was to examine breeding season food habits of Burrowing Owls in the Snake River Birds of Prey National Conservation Area (NCA), where Burrowing Owls inhabit both agricultural and nonagricultural areas. Specifically, we tested the hypotheses that (1) diets of owls in agricultural areas contain more montane voles than those in nonagricultural habitats and (2) because of influences of agricultural practices, diet diversity and food-niche breadths differ. We predicted that Burrowing Owls nesting in agricultural habitats would have greater prey diversity and broader food-niche breadths than owls nesting in nonagricultural habitats. Finally, we compared our food-niche breadth estimates with those of a previous study (Marti et al. 1993) on raptor food habits in the NCA.

METHODS

We studied Burrowing Owls nesting within and near the NCA in southwestern Idaho during 2001–02. This area was once representative of a typical shrub-steppe community dominated by large expanses of big sagebrush (*Artemesia tridentata wyomingensis*; Hironaka et al. 1983) and other shrubs, and scattered perennial bunchgrasses. However, disturbances, such as range fires, military training, grazing, and off-road vehicle use, have helped convert much of the area to exotic annual grasslands dominated by cheatgrass (*Bromus tectorum*), tumble mustard (*Sisymbrium altissimum*), and other non-native species (Hironaka et al. 1983). Surrounding areas also contained scattered residential homes, paved and dirt roads, a military training area, and public lands managed by the Bureau of Land Management. Cattle and sheep graze much of the area, especially during winter. Irrigated agricultural fields (primarily alfalfa, sugar beets, and mint) constituted <5% of the NCA and were located primarily along its margins (USDI 1996). For the purpose of this study, we considered Burrowing Owl nests that were within 1 km of an irrigated agricultural field, to be in "agricultural" habitat (hereafter agricultural nests). Agricultural nests were located in the natural vegetation surrounding agriculture fields rather than in the irrigated portions where crops grew. However, adult owls frequently hunted within these fields and perched on fence posts adjacent to them (Moulton et al. in press). "Nonagricultural" habitat was the term we used to categorize nests that were greater than 3 km from irrigated fields (hereafter nonagricultural nests). Because this distance exceeded the typical foraging range of Burrowing Owls (Haug and Oliphant 1990, Rosenberg and Haley 2004), we are almost certain that owls from nonagricultural nests were not collecting prey from or near irrigated fields. Nonagricultural areas were generally disturbed shrublands and grasslands much like that in the agricultural areas, but there were no crops or irrigation nearby

Diet Composition. Regurgitated pellets are reliable indicators of the diet of Burrowing Owls (Marti 1974), although amphibians and reptiles can be underrepresented in pellets (Thomsen 1971, Haug 1985). Similarly, prey remains alone do not provide reliable information regarding overall diet composition, as many prey items consumed by Burrowing Owls are too small to cache (such as small insects). But, remains provide better information than pellets concerning amphibians and reptiles in the diet. Therefore, to determine diet composition, we both documented prey remains at nests and collected and analyzed regurgitated pellets.

Pellet Collection and Analysis. We collected regurgitated pellets from tunnel entrances, perches, and nearby mounds within 20 m of nest burrows every 3–10 d from hatching through 25 d post-hatch (May–June). For nests at which we collected more than 20 pellets (29 of 51 nests; 22 agricultural, 7 nonagricultural), we analyzed a random sample of 20 pellets per nest. For all other nests, we analyzed all collected pellets (11.2 ± 1.0 [SE] pellets per nest, range = 4–19).

We analyzed and quantified remains of each pellet using standard procedures (Marti 1987) and by comparing prey species to a museum collection at Boise State University. Skulls, jaws, dentition patterns, head capsules, pronota, elytra, legs, scales and other distinguishing body parts helped identify prey.

Prey Remains. Owls in this study nested in artificial burrows deployed for other studies (Smith and Belthoff 2001, Belthoff and Smith 2003, Brady 2004, Moulton et al. in press), which provided access to nest chambers,

where we found most prey remains. We could therefore document cached and uneaten prey remains at all occupied nests and adjacent satellite burrows (non-nest burrows used by owls for roosting, cover, and caching prey). We quantified prey remains each time we excavated an artificial burrow (2–5 visits per nest) between hatching and 25 d post-hatch.

Biomass Estimation. We determined biomass of representative mammalian, avian, and amphibian prey using Smith and Murphy (1973) and Steenhof (1983). Biomass of invertebrate prey species was determined using our own estimates obtained from captured live specimens (Moulton 2003) and values reported in Smith and Murphy (1973) and Olenick (1990).

Statistical Analysis. Because we obtained prey remains from only two nonagricultural nests, we did not include data from prey remains in diversity calculations described below or in statistical comparisons; instead, pellet data provided all information used for these calculations and comparisons. We determined each prey type as a percent of total prey items per nest (percent number) and percent biomass per nest.

We determined food-niche breadth for agricultural and nonagricultural nests by calculating the reciprocal of Simpson's index (Simpson 1949). We calculated dietary evenness using the Alatalo (1981) modification of Hill's (1973) index: $F = (N_2 - 1)/(N_1 - 1)$.

To determine if differences in diets existed between owls nesting in each habitat, we compared percent number and percent biomass of each prey taxa (vertebrates), class (invertebrates), or order (invertebrates) per nest using Wilcoxon's ranked sums tests (Zar 1999). If there were differences between habitats in taxa/order of prey, we then compared species (vertebrates) or families (invertebrates) of that taxa/order. Because we made multiple comparisons of prey categories, we adjusted alpha levels using sequential Bonferroni corrections (Rice 1989).

To determine if diet diversity differed between agricultural and nonagricultural nests, we compared food-niche breadth (Simpson's index), species richness (number of species in the diet), and dietary evenness (Alatalo's index) using Wilcoxon's ranked sums tests. Statistical analyses were performed using JMPIN V.5 (SAS Institute, Inc., Cary, NC), and evaluated at an alpha level of 0.05 unless otherwise noted. Throughout, we present means with their standard errors.

RESULTS

Pellet Remains. We analyzed 602 regurgitated pellets from 34 agricultural nests and 257 pellets from 19 nonagricultural nests. From these, we identified 7402 prey items representing 23 different prey species.

Overall pellet composition. Invertebrates were the most frequent prey in pellets, representing 93% of prey items; however, they represented only 23% of biomass (Table 1). Conversely, vertebrates (rodents, birds, and herpetofauna) comprised 7% of prey items, but 77% of biomass.

Coleopterans (beetles) and Orthopterans (crickets, grasshoppers) were the most common invertebrates in pellets, constituting 47% and 32% of total prey, respectively (Table 1). Of Coleopterans, ground beetles (Carabidae) and darkling beetles (Tenebrionidae) were most common (33% and 22% of Coleopteran prey items, respectively). Orthopteran prey remains were predominately Gryllidae (crickets), which constituted 73% of Orthopteran prey items.

Rodents were the most common vertebrates in pellets and represented 97% of vertebrates detected and 73% of overall prey biomass (Table 1). Pocket mice (*Perognathus parvus*) and deer mice (*Peromyscus maniculatus*) were the most abundant rodents (37% and 25%, respectively), but montane voles represented the greatest biomass (18%).

Habitat variation. Invertebrates were the most frequent prey in pellets for both agricultural and nonagricultural nests, representing 95% and 90% of total prey items, respectively (Table 2). Vertebrate prey (mostly rodents) represented the greatest percent biomass in both agricultural (76%) and nonagricultural (79%) nests.

Coleopterans were the most common invertebrates in both habitats (Table 2). However, Arachnids contributed the greatest biomass (52%) of invertebrates in nonagricultural nests, and Orthopterans contributed the greatest biomass (52%) of invertebrates in agricultural nests. Of rodent species found in pellets, deer mice and pocket mice were most common in agricultural and nonagricultural nests, respectively. Pocket mice also contributed the greatest biomass of rodents at nonagricultural nests, but montane voles contributed the greatest biomass of rodents at agricultural nests. Only owls at agricultural nests preyed on montane voles (Table 2).

Agricultural and nonagricultural nests did not differ in percent biomass of vertebrates or invertebrates (Table 3). However, agricultural nests had a greater percent number of invertebrates, and nonagricultural nests had a greater percent number of vertebrates. Pellets from agricultural nests had greater percent number and percent biomass of montane voles (Table 4). Nonagricultural nests had greater percent number and biomass of pocket mice (Table 4). Among invertebrates, Arachnids and Orthopterans differed between habitats (Table 3). Solpugida (windscorpions) and Acrididae occurred in greater percent number and biomass in pellets of nonagricultural nests, while Gryllidae occurred in greater number and biomass in pellets at agricultural nests (Table 5).

For all nests combined, food-niche breadth was

Table 1. Mean (±SE) percent number and percent biomass per nest of prey items detected in pellets collected at 53 Burrowing Owl nests in southwestern Idaho, 2001–02.

PREY CATEGORY	PERCENT NUMBER	PERCENT BIOMASS
Mammals	6.7 ± 0.7	72.9 ± 2.5
Spermophilus mollis	0.2 ± 0.1	10.2 ± 3.4
Thomomys townsendii	0.2 ± 0.1	12.4 ± 3.5
Perognathus parvus	2.5 ± 0.6	12.5 ± 2.5
Dipodomys ordii	0.6 ± 0.2	9.4 ± 2.4
Reithrodontomus megalotis	0.1 ± 0.1	0.3 ± 0.1
Peromyscus maniculatus	1.7 ± 0.4	11.1 ± 2.5
Mus musculus	0.2 ± 0.1	1.2 ± 0.5
Microtus montanus	0.9 ± 0.2	13.2 ± 2.8
Rodent—unidentified[a]	0.4 ± 0.1	2.7 ± 0.7
Birds—unidentified[b]	0.2 ± 0.1	2.2 ± 0.8
Reptiles and Amphibians[c]	<0.1 ± 0.1	1.9 ± 1.2
Arachnids	13.8 ± 1.9	6.3 ± 1.0
Scorpionida	5.8 ± 1.0	3.5 ± 0.9
Solpugida	8.0 ± 1.5	2.8 ± 0.5
Orthopterans	31.6 ± 3.2	9.6 ± 1.6
Acrididae	2.9 ± 0.6	0.7 ± 0.1
Gryllidae	23.2 ± 3.5	7.7 ± 1.7
Unknown Orthoptera	5.5 ± 0.9	1.2 ± 0.2
Dermapterans (Forficulidae)	0.4 ± 0.2	0.2 ± 0.1
Homopterans (Cicadidae)	0.1 ± 0.1	0.1 ± 0.1
Coleopterans	47.0 ± 2.6	6.8 ± 0.7
Carabidae	15.7 ± 2.2	1.9 ± 0.3
Scarabidae	7.5 ± 1.3	1.1 ± 0.2
Silphidae	8.0 ± 1.4	1.1 ± 0.2
Tenebrionidae	10.6 ± 1.9	2.3 ± 0.4
Coleoptera—unidentified	5.3 ± 1.2	0.5 ± 0.1
Total vertebrates	6.9 ± 0.7	77.0 ± 2.1
Total invertebrates	93.1 ± 0.7	23.0 ± 2.1

[a] Mouse species: likely *P. parvus, R. megalotis, P. maniculatus,* or *M. musculus.*
[b] Likely *Eremophila alpestris* or *Sturnella neglecta.*
[c] Includes *Bufo woodhousei, Phrynosoma platyrhinos,* and unknown snake species.

4.22 ± 0.22 (N = 53). Nonagricultural (N = 19) nests had greater species evenness than agricultural (N = 34) nests (0.76 ± 0.03 versus 0.60 ± 0.02; Z = 3.89, P < 0.001) and broader food-niche breadth (5.21 ± 0.33 versus 3.67 ± 0.25; Z = 3.24, P = 0.001). However, agricultural nests had higher species richness (11.82 ± 0.40 versus 9.79 ± 0.54; Z = −2.69, P = 0.007).

Prey Remains. We recorded cached and other uneaten prey remains at 43 nests (N = 41 agricultural, N = 2 nonagricultural) and documented 403 prey items representing 19 species (Table 6). Because we had so few nonagricultural nests, we made no comparisons between habitats and pooled data from all nests for descriptions of prey remains.

Although common in pellets, invertebrate prey remains were uncommon in nest burrows (N = 50 individual invertebrate prey items). The majority of prey remains in both percent number (87.6%) and percent biomass (99.7%) were vertebrates, most of which were rodents. Of rodent species, montane voles were most common by number (36%), and pocket gophers represented the greatest biomass (50%).

Although rare in pellets, we occasionally found herpetofauna (N = 38) and birds (N = 18) cached in burrows. Woodhouse's toads (*Bufo woodhousei*) were the most common (92%) herpetofauna in nest burrows. All toads were in nests adjacent to agricultural fields. Burrowing Owl nestlings were the most common (50%) cached avian prey item

Table 2. Mean (±SE) percent number and percent biomass per nest of prey items detected in pellets of Burrowing Owls nesting in agricultural (N = 34) and nonagricultural (N = 19) habitats of southwestern Idaho, 2001–02.

	AGRICULTURAL		NONAGRICULTURAL	
PREY	PERCENT NO.	PERCENT BIOMASS	PERCENT NO.	PERCENT BIOMASS
Mammals	4.9 ± 0.8	70.7 ± 3.1	10.1 ± 1.1	76.9 ± 4.1
Spermophilus mollis	0.1 ± 0.1	5.3 ± 4.1	0.5 ± 0.2	0.2 ± 0.1
Thomomys townsendii	0.4 ± 0.1	1.9 ± 4.1	—	—
Perognathus parvus	0.7 ± 0.6	4.9 ± 2.6	5.6 ± 0.8	26.0 ± 3.4
Dipodomys ordii	0.4 ± 0.2	4.9 ± 2.8	1.2 ± 0.3	17.5 ± 3.8
Peromyscus maniculatus	1.4 ± 0.5	10.5 ± 3.1	2.1 ± 0.7	12.3 ± 4.2
Mus musculus	0.2 ± 0.1	1.9 ± 0.6	—	—
Microtus montanus	1.4 ± 0.3	20.6 ± 3.1	—	—
Birds—unidentified[a]	0.1 ± 0.1	2.3 ± 1.0	0.3 ± 0.1	2.0 ± 1.3
Reptiles and Amphibians[b]	0.1 ± 0.1	2.8 ± 1.5	0.1 ± 0.1	0.3 ± 2.0
Arachnida	6.7 ± 1.7	3.7 ± 1.1	26.5 ± 2.3	10.9 ± 1.4
Scorpionida	3.3 ± 1.1	2.0 ± 1.0	10.3 ± 1.5	6.0 ± 1.4
Solpugida	3.4 ± 1.6	1.7 ± 0.6	16.2 ± 2.1	4.9 ± 0.8
Orthoptera	40.0 ± 3.5	12.7 ± 1.9	16.7 ± 4.7	4.0 ± 2.6
Acrididae	1.8 ± 0.8	0.5 ± 0.2	4.9 ± 1.0	1.1 ± 0.2
Gryllidae	34.8 ± 3.5	11.4 ± 1.9	2.3 ± 4.7	1.0 ± 2.5
Coleoptera	47.6 ± 3.2	7.5 ± 0.8	46.1 ± 4.3	5.7 ± 0.1
Carabidae	21.4 ± 2.4	2.7 ± 0.4	5.5 ± 3.2	0.7 ± 0.5
Scarabidae	5.6 ± 1.5	1.0 ± 0.3	10.9 ± 2.0	1.3 ± 0.4
Silphidae	5.1 ± 1.7	0.9 ± 0.3	13.2 ± 2.3	1.4 ± 0.4
Tenebrionidae	11.1 ± 2.3	2.5 ± 0.6	9.6 ± 3.1	1.9 ± 0.7
Total vertebrates	5.0 ± 0.8	75.8 ± 2.6	10.3 ± 1.1	79.1 ± 3.5
Total invertebrates	95.0 ± 0.8	24.2 ± 2.6	89.7 ± 1.1	20.9 ± 3.5

[a] Likely *Eremophila alpestris* or *Sturnella neglecta*.
[b] Includes *Bufo woodhousei, Phrynosoma platyrhinos,* and unknown snake species.

we found. These Burrowing Owl nestlings all were individuals from nests other than the nest in which we found them. Whether they wandered into the nest on their own and subsequently starved or were killed or were taken directly from their nest is unknown. We suspect that adults tending nearby nests preyed upon these nestlings because they frequently were too young to have wandered into nests other than their own.

DISCUSSION

The NCA supports one of the highest densities of breeding raptors in the world (Marti et al. 1993), and many previous studies have examined food habits of nesting raptors there (e.g., Marks and Marks 1981, Marks and Doremus 1988, Marti 1988, Steenhof and Kochert 1988). However, dietary habits and trophic relationships of Burrowing Owls remain the least well-understood of raptors breeding in the NCA (Marti pers. comm.). Thus, our study filled an important knowledge gap in raptor ecology within the NCA. Our study found: (1) no one species dominated the vertebrate component of Burrowing Owl diets, unlike owls in other regions; (2) diets differed by habitat, most notably that montane voles and crickets were important prey for agricultural nests, but they were not part of the diet for nonagricultural nests; and (3) the food-niche breadth of Burrowing Owls in the NCA is broader than previously estimated.

Burrowing Owl Diet in the NCA. Burrowing Owls are considered opportunistic predators (Gleason and Craig 1979, Green et al. 1993, Haug et al. 1993), and the wide variety of prey owls consumed in our study area is consistent with this notion. Similar to studies in Colorado (Marti 1974), Saskatchewan (Haug 1985), and the Idaho National Engineering Laboratory (INEEL) in Idaho (Gleason and Craig 1979), invertebrates represented approximately 90–95% of prey items in regurgitated pellets, but they constituted only 20–30% of biomass of prey. In contrast, Olenick (1990), in

Table 3. Mean (±SE) percent number and percent biomass per nest of vertebrate (taxa) and invertebrate (class/order) prey detected in pellets of Burrowing Owls nesting in agricultural (N = 34) and nonagricultural (N = 19) habitats of southwestern Idaho, 2001–02.

Prey Category	Habitat		Z[a]	P-value
	Agricultural	Nonagricultural		
Percent Number				
Mammal	4.9 ± 0.8	10.1 ± 1.1	3.01	0.003*
Bird	0.1 ± 0.1	0.3 ± 0.1	0.22	0.823
Reptile and Amphibian	0.1 ± 0.1	0.1 ± 0.1	−0.38	0.701
Arachnid	6.7 ± 1.7	26.5 ± 2.3	4.98	<0.001*
Orthopteran	40.0 ± 3.5	16.7 ± 4.7	−3.61	<0.001*
Coleopteran	47.6 ± 3.2	46.1 ± 4.3	−0.29	0.774
Total vertebrates	5.0 ± 0.8	10.3 ± 1.1	3.05	0.002*
Total invertebrates	95.0 ± 0.8	89.7 ± 1.1	−3.05	0.002*
Percent Biomass				
Mammal	70.7 ± 3.1	76.9 ± 4.1	1.03	0.303
Bird	2.3 ± 1.0	2.0 ± 1.3	0.02	0.988
Reptile and Amphibian	2.8 ± 1.5	0.3 ± 2.0	−0.51	0.613
Arachnid	3.7 ± 1.1	10.9 ± 1.4	4.12	<0.001*
Orthopteran	12.7 ± 1.9	4.0 ± 2.6	−3.24	0.001*
Coleopteran	7.5 ± 0.8	5.7 ± 0.1	−0.99	0.321
Total vertebrates	75.8 ± 2.6	79.1 ± 3.5	0.96	0.340
Total invertebrates	24.2 ± 2.6	20.9 ± 3.5	−0.96	0.340

[a] Data were compared using Wilcoxon's ranked sums tests.

* Significant based on sequential Bonferroni corrections adjusted from an original alpha level of 0.05 for a total of 16 comparisons

Table 4. Mean (±SE) percent number and percent biomass per nest of rodent species detected in pellets of Burrowing Owls nesting in agricultural (N = 34) and nonagricultural (N = 19) habitats of southwestern Idaho, 2001–02.

Prey Species	Habitat		Z[a]	P-value
	Agricultural	Nonagricultural		
Percent Number				
Spermophilus mollis	0.1 ± 0.1	0.5 ± 0.2	1.83	0.067
Thomomys townsendii	0.4 ± 0.1	0.0 ± 0.1	−2.72	0.007
Perognathus parvus	0.7 ± 0.6	5.6 ± 0.8	4.23	<0.001*
Dipodomys ordii	0.4 ± 0.2	1.2 ± 0.3	1.67	0.095
Peromyscus maniculatus	1.4 ± 0.5	2.1 ± 0.7	−1.43	0.153
Mus musculus	0.2 ± 0.1	0.0 ± 0.1	−2.25	0.025
Microtus montanus	1.4 ± 0.3	0.0 ± 0.4	−4.32	<0.001*
Percent Biomass				
Spermophilus mollis	5.3 ± 4.1	0.2 ± 0.1	1.86	0.063
Thomomys townsendii	1.9 ± 4.1	0.0 ± 5.4	−2.72	0.007
Perognathus parvus	4.9 ± 2.6	26.0 ± 3.4	4.00	<0.001*
Dipodomys ordii	4.9 ± 2.8	17.5 ± 3.8	1.79	0.073
Peromyscus maniculatus	10.5 ± 3.1	12.3 ± 4.2	−1.05	0.294
Mus musculus	1.9 ± 0.6	0.0 ± 0.8	−2.25	0.025
Microtus montanus	20.6 ± 3.1	0.0 ± 4.2	−4.32	<0.001*

[a] Data were compared using Wilcoxon's ranked sums tests.

* Significant based on sequential Bonferroni corrections adjusted from an original alpha level of 0.05 for a total of 14 comparisons

Table 5. Mean (±SE) percent number and percent biomass per nest of Arachnid orders and Orthopteran families detected in pellets of Burrowing Owls nesting in agricultural (N = 34) and nonagricultural (N = 19) habitats of southwestern Idaho, 2001–02.

Prey Order/Family	Habitat		Z[a]	P-VALUE
	Agricultural	Nonagricultural		
Percent Number				
Arachnida				
Scorpiones	3.3 ± 1.1	10.3 ± 1.5	2.22	0.026
Solpugida	3.4 ± 1.6	16.2 ± 2.1	4.04	<0.001*
Orthoptera				
Acrididae	1.8 ± 0.8	4.9 ± 1.0	2.81	0.005*
Gryllidae	34.8 ± 3.5	2.3 ± 4.7	−5.43	<0.001*
Percent Biomass				
Arachnida				
Scorpiones	2.0 ± 1.0	6.0 ± 1.4	1.72	0.086
Solpugida	1.7 ± 0.6	4.9 ± 0.8	3.68	<0.001*
Orthoptera				
Acrididae	0.5 ± 0.2	1.1 ± 0.2	2.38	0.017*
Gryllidae	11.4 ± 1.9	1.0 ± 2.5	−5.26	<0.001*

[a] Data were compared using Wilcoxon's ranked sums tests.

* Significant based on sequential Bonferroni corrections adjusted from an original alpha level of 0.05 for a total of four comparisons each for Arachnida and Orthoptera.

southeastern Idaho, reported that invertebrates represent only 60% of the number of prey items and less than 3% of the biomass, and owls in the Imperial Valley, California, feed almost exclusively on invertebrates (York et al. 2002).

Although invertebrates generally constitute a large percentage of prey Burrowing Owls consume, the orders and families that are most common in the diet vary among regions. For example, Coleopterans were the most abundant invertebrate species in our study, as well as in Colorado (Marti 1974), Washington (Green et al. 1993), and Oregon (Green et al. 1993), whereas Jerusalem crickets (*Stenopelmatus* spp.) were the most important invertebrate prey species, in terms of biomass, for Burrowing Owls in Oregon (Green et al. 1993), California (Thomsen 1971), and southeastern Idaho (Gleason and Craig 1979).

Vertebrates accounted for most of the biomass in our study, but no one vertebrate species dominated the diet. Percent biomass of montane voles (17%), pocket mice (16%), pocket gophers (16%), and deer mice (14%) were similar. In contrast, *Microtus* sp. were the predominant vertebrate prey item in Montana (Holt et al. 2001) and represented 80% of biomass in owl diets in southeastern Idaho (Olenick 1990), and pocket mice dominated rodent prey in Oregon (97%; Green 1983). This lack of a dominant vertebrate prey may indicate a diverse prey base in our study area (Moulton et al. in press).

Agricultural versus Nonagricultural Nests. Comparisons of pellet remains from Burrowing Owl nests in agricultural and nonagricultural areas revealed different prey composition, species richness, species evenness, and food-niche breadth. Although both habitats had similar biomass of vertebrates, nonagricultural areas had greater numbers of rodent prey. In contrast, owls nesting adjacent to agricultural fields in southeastern Idaho had a higher proportion of rodents in their diet than those nesting in more natural areas (Gleason 1978). Agricultural nests had a higher proportion of invertebrates than nonagricultural nests, which resulted from the high numbers of crickets present in pellets from agricultural nests. Crickets were rare in pellets of owls nesting in nonagricultural habitats. Moulton et al. (in press) reported greater prey consumption by Burrowing Owls nesting near agricultural fields in the NCA; this difference primarily resulted from greater invertebrate prey in agricultural habitats. While some have suggested

Table 6. Percent number, percent biomass, and total number of cached and other uneaten prey remains documented at 43 Burrowing Owl nests in southwestern Idaho, 2001–02.

PREY CATEGORY	PERCENT NO.	PERCENT BIOMASS	TOTAL NO.
Mammals	73.70	87.67	297
Sylvilagus nuttallii	0.25	1.03	1
Thomomys townsendii	10.91	44.73	44
Dipodomys ordii	11.41	13.01	46
Perognathus parvus	2.48	0.77	10
Mus musculus	2.98	1.17	12
Mouse species[a]	18.86	5.86	76
Microtus montanus	26.80	21.10	108
Birds	4.47	8.09	18
Eremophila alpestris	0.25	0.09	1
Sturnus vulgaris	0.74	1.22	3
Sturnella neglecta	0.50	0.41	2
Passerine sp.[b]	0.25	0.15	1
Athene cunicularia—juv.	2.23	4.16	9
A. cunicularia—adult	0.25	1.03	1
Raptor sp.[c]	0.25	1.03	1
Amphibians	8.68	3.60	35
Bufo woodhousei	8.68	3.60	35
Reptiles	0.74	0.29	3
Pituophis catenifer	0.74	0.29	3
Scolopendromorpha	0.50	0.00	2
Arachnids	10.92	0.34	44
Scorpiones	10.67	0.33	43
Solpugida	0.25	0.01	1
Orthopterans	0.50	0.01	2
Acrididae	0.25	0.00	1
Gryllidae	0.25	0.00	1
Total vertebrates	87.59	99.65	353
Total invertebrates	12.41	0.35	50
Total			403

[a] Likely *P. parvus, R. megalotis, P. maniculatus,* or *M. musculus.*
[b] Likely *Eremophila alpestris* or *Sturnella neglecta.*
[c] Small juvenile hawk or Prairie Falcon (*Falco mexicanus*).

that Burrowing Owls associate with irrigated agriculture because of the high abundance of montane voles (Gleason 1978, Rich 1986), presence of high numbers of invertebrate prey in the diet of owls in agricultural habitat may indicate an overlooked importance of invertebrate prey to breeding Burrowing Owls in these areas.

Agricultural nests also had greater species richness than nonagricultural nests. Common rodent species in agricultural habitats, such as montane voles, were not in pellets of nonagricultural nests and likely were not available in that habitat type. However, nonagricultural nests had greater species evenness than agricultural nests. This greater species evenness likely contributed to our finding that diets of owls nesting in nonagricultural areas had a broader food-niche (i.e., greater diversity), as Simpson's diversity index can be greatly influenced by species evenness.

Narrower food-niche breadths of Burrowing Owls nesting near agricultural fields may indicate a more specialized diet. As MacArthur and Pianka (1966) proposed, one expects a species to specialize when prey availability is high (i.e., a productive environment), and thus search time is low. A species will generalize in unproductive environments

where search times are high. Therefore, if owls in agricultural areas exhibit more specialized diets relative to owls in nonagricultural areas, we propose that owls nesting in agricultural areas are experiencing greater prey availability. This is consistent with suggestions by previous researchers (Gleason 1978, Rich 1986, Moulton et al. in press) that Burrowing Owls associate with agriculture because of increased prey. However, further research is needed to determine if the narrower food-niche breadth of owls in agricultural areas results from greater prey availability, where owls can be selective, or lower prey diversity.

Food-niche Breadth of Burrowing Owls in the NCA. Prior to our study, Burrowing Owls in the NCA were thought to have a very narrow food-niche breadth compared to other raptor species breeding there. Marti et al. (1993) estimated food-niche breadth of Burrowing Owls to be only 2.43, which was the narrowest food-niche breadth of all 12 raptor species studied. In contrast, food-niche breadth of Burrowing Owls in our study was 4.22 $\pm$ 0.22, which ranks Burrowing Owls seventh in terms of food-niche breadth (first being the broadest). This disparity may be explained in part by smaller sample sizes in Marti et al. (1993) combined with different levels of identification; that is, the 1993 study identified invertebrate prey to order, whereas we identified invertebrates to family when possible. Because this difference in prey level identification would only affect the food-niche breadth estimates of a species whose diet has a large invertebrate component, only Burrowing Owl estimates likely would be affected.

Compared to other raptors breeding within the NCA, our study estimated food-niche breadths of Burrowing Owls to be similar to Golden Eagles (*Aquila chrysaetos*; 4.07) and Long-eared Owls (*Asio otus;* 4.79; Marti et al. 1993). However, Burrowing Owl diet composition is more similar to American Kestrels (*Falco sparverius),* which also frequently prey on invertebrates (Marti et al. 1993). In fact, Burrowing Owls and American Kestrels are the only two raptor species in the NCA for which invertebrate prey comprises >1% of the diet (in terms of biomass: 23% and 5%, respectively).

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RED-TAILED HAWK DIETARY OVERLAP WITH NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, ARIZONA

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ABSTRACT.—We determined food habits of Red-tailed Hawks (*Buteo jamaicensis*) for comparison with published information for Northern Goshawks (*Accipiter gentilis*) to evaluate potential competition on the Kaibab Plateau, Arizona. We collected prey remains and pellets from 42 Red-tailed Hawk nests at the end of the nesting season between August–October 1998–2001, and opportunistically from below nest trees during site visits, May–July 2000–01. We identified 478 prey items, including 17 mammal, 7 bird, and 2 reptile species. Prey species frequency did not vary among years ($P = 0.3$), across habitat types ($P = 0.8$), or by collection technique ($P = 0.4$). Annual food niche breadth for Red-tailed Hawks averaged 0.57. Published mean niche breadth for Northern Goshawks was 0.32, supporting that Red-tailed Hawks were feeding generalists, while Northern Goshawks were more specialized. However, 48% of Red-tailed Hawk diet on the Kaibab Plateau consisted of species comprising a major portion of the documented diet of Northern Goshawks, including Nuttall's cottontail (*Sylvilagus nuttallii*), golden-mantled ground squirrel (*Spermophilus lateralis lateralis*), rock squirrel (*S. variegates grammurus*), and Northern Flicker (*Colaptes auratus*). Because raptor communities with high dietary overlap and lack of prey partitioning show food-limited nesting success, greater agnonistic behavior, and territoriality, Red-tailed Hawks could be negatively affecting Northern Goshawks on the Kaibab Plateau.

KEY WORDS: *Red-tailed Hawk*; Buteo jamaicensis; *Northern Goshawk*; Accipiter gentilis; *competition*; *diet*; *food habits*; *food niche breadth*; *foraging*.

SOBRELAPAMIENTO DE LA DIETA DE *BUTEO JAMAICENSIS* Y *ACCIPITER GENTILIS* EN LA MESETA DE KAIBAB, ARIZONA

RESUMEN.—Determinamos la dieta de *Buteo jamaicensis* en la planicie de Kaibab, Arizona y la comparamos con información publicada sobre *Accipiter gentilis* con la finalidad de evaluar la posible existencia de competencia entre estas dos especies. Recolectamos restos de presas y egagrópilas de 42 nidos de *B. jamaicensis* al final de la temporada reproductiva entre agosto y octubre de 1998–2001, y de forma oportunista debajo de árboles de anidación durante visitas a la zona de estudio realizadas entre mayo y julio de 2000 y 2001. Identificamos 478 tipos de presas, incluyendo 17 especies de mamíferos, 7 de aves y 2 de reptiles. La frecuencia de las especies de presa no varió entre años ($P = 0.3$), tipos de hábitat ($P = 0.8$) y técnicas de colecta ($P = 0.4$). La amplitud anual del nicho alimentario de *B. jamaicensis* promedió 0.57. Registros publicados indican que la amplitud del nicho alimentario de *A. gentilis* es 0.32, lo cual sugiere que *B. jamaicensis* es una especie generalista, mientras que *A. gentilis* es más especializada. Sin embargo, el 48% de la dieta de *B. jamaicensis* en la planicie de Kaibab consiste de especies que forman la mayor parte de la dieta documentada para *A. gentilis*, entre las que se encuentran *Sylvilagus nuttallii, Spermophilus lateralis lateralis, S. variegates grammurus* y *Colaptes auratus*. Debido a que las comunidades de rapaces que presentan un alto grado de superposición en su dieta y en las que no hay repartición de presas muestran un bajo éxito de anidación debido a falta de alimento,

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un mayor comportamiento antagónico y mayor territorialidad, *B. jamaicensis* podría estar afectando negativamente a *A. gentilis* en la planicie de Kaibab.

[Traducción del equipo editorial]

Fire suppression, timber harvesting, and livestock grazing over the past 100 yr have caused changes in southwestern forests, including those on the Kaibab Plateau in northwestern Arizona (e.g., Weaver 1951, Cooper 1960, Covington and Moore 1994). Decreasing the quality and quantity of climax forest can favor habitat generalists (Carey 1984) such as Red-tailed Hawks (*Buteo jamaicensis*), which may out compete species dependent on late successional forests, such as Northern Goshawks (*Accipiter gentilis*; Andersen et al. 2003). Creation of 259-ha buffer zones on the plateau by the Kaibab National Forest, although maintaining the quality of old-growth for nesting sites, does not ensure sufficient quantity or quality of old-growth forest beyond these protected areas (Reynolds et al. 1992). Red-tailed Hawks often nest in abandoned Northern Goshawk nests after timber harvesting (Crocker-Bedford 1990). Beyond old-growth-managed buffer zones, open areas may favor the hunting style, and thus, increase foraging habitat of Red-tailed Hawks more than Northern Goshawks. Exploring the potential relationship between these two species facilitates a better understanding of how upper level avian predators have adjusted to human-caused alterations in southwestern forest ecosystems. Further, this understanding could aid resource managers in maintaining a viable Northern Goshawk population on the Kaibab Plateau.

Competition occurs when use or defense of a resource by one individual reduces the availability of that resource to other individuals (Gill 1990). Interspecific competition occurs when individuals of coexisting species require a resource that is in limited supply relative to their needs such that survival or reproduction of at least one species is decreased (Ricklefs and Schluter 1993). On the Kaibab Plateau, Red-tailed Hawks and Northern Goshawks, based on their proximity and similar habitat use, could be competing for nest sites, foraging areas, or prey, despite potential partitioning resulting from morphological and behavioral differences between species (Ballam 1984, Squires and Reynolds 1997). In this study, we focused on determining the diet of Red-tailed Hawks for comparison with published information on Northern Goshawks to evaluate potential overlap. We hypothesized that Red-tailed Hawks and Northern Goshawks, because of their close proximity and use of similar nesting and foraging habitat, could also be using the same prey species, creating the potential for competition.

STUDY AREA

The Kaibab Plateau, on the North Rim of the Grand Canyon, is located in northwestern Arizona within the Kaibab National Forest. The plateau encompasses 2980 km^2 above 1830 m elevation. Our study area was confined to 1732 km^2 above the 2075 m contour to be consistent with concurrent long-term Northern Goshawk research on the plateau (Reynolds et al. 1994). Goshawk and Red-tailed Hawk nest sites are interspersed throughout this study area. Vegetation on the plateau consists of ponderosa pine (*Pinus ponderosa*) forest between 2075–2500 m; mixed-conifer forest (ponderosa pine, Douglas-fir [*Pseudotsuga menziesii*], white fir [*Abies concolor*], blue spruce [*Picea pungens*], and quaking aspen [*Populus tremuloides*]) between 2500–2650 m; and Engelmann spruce-subalpine fir (*Picea engelmannii-Abies lasiocarpa*) forest between 2650–2800 m (Rasmussen 1941, White and Vankat 1993)

METHODS

Prey Remains and Pellet Identification. We collected prey remains and regurgitated pellets from all known occupied Red-tailed Hawk nests (N = 21, 24, 32, 11 for 1998–2001, respectively), from below and in the nest, at the end of the nesting season, August–October 1998–2001, and opportunistically during the nesting season, May–July 2000–01. Collections from each nest were separated by >3 d, and end-of-season samples were collected >30 d after previous collections. We treated each collection of pellets and prey remains from an occupied nest as one sample for that nest site. We assumed prey species identified in each sample had been consumed since the last sample and represented new prey.

To identify prey, we separated samples into bones/fragments, feathers, and hair. Bones and feathers were identified to the lowest taxon possible, through comparison with S. Bayard's reference prey collection stored at the Rocky Mountain Research Station, Fort Collins, CO. We identified hairs using keys (Williams 1938, Stains 1958, Moore et al. 1974) and by comparing hairs directly with samples from the Northern Arizona University, Department of Biological Sciences' collection and the private collection of H.E. Graham (Flagstaff, AZ U.S.A.). The characteristics we considered included color banding, shape, presence of a hair shield, and configuration of a medulla if present (Moore et al. 1974).

Determining diet via indirect means requires cautious interpretation because of inherent biases associated with each method (Lewis et al. 2004); however, identification of a prey species in pellets and prey remains is an absolute indication of presence. Therefore, we recorded one occurrence whenever a species was found in a sample.

We then pooled samples across years for each nest and summed the number of times a prey species occurred. This provided a conservative estimate of the relative importance of prey species consumed by Red-tailed Hawks at each nest. We also calculated the total number and percent of nests at which each prey species occurred.

Prey Species Dissimilarity. Dyer (1978) developed a linear statistical analysis for comparing species dissimilarity that can be used in conjunction with any species dissimilarity index and is designed for data sets that involve both multiple species and multiple environmental variables. Total species dissimilarity is divided into components with one component being assigned to each environmental variable or interaction of environmental variables:

$$D_{ij} = \beta_0 + \beta_1\delta_{ij}^{(1)} + \beta_2\delta_{ij}^{(2)} + \ldots + \beta_m\delta_{ij}^{(m)} + e_{ij},$$

where D_{ij} is the (dis)similarity between observations i and j, $\delta_{ij}^{(1)}$ is a known function of i and j which corresponds to the ith environmental variable or interaction, β_1 is an unknown parameter which represents the contribution of the ith environmental variable or interaction to the total dissimilarity, and e_{ij} is an error term with an expected value of 0.

We used this linear model with the Jaccard dissimilarity index (Krebs 1998) to estimate whether the species identified in prey remains and pellets of Red-tailed Hawks varied among years (1998–2001), vegetation types (ponderosa pine only, mixed conifer with pine dominant, or mixed conifer only), or collection techniques (end of season samples from nest or opportunistic samples collected from below nest trees during nesting season). Jaccard's index is specifically designed for presence-absence data, and because, by definition, rare species are typically absent, rare species have little influence on the value of the index (Krebs 1998). The Jaccard dissimilarity index (D_{ij}) is calculated by:

$$D_{ij} = a/(a + b + c)$$

where a is the number of binary characteristics present in sample i and sample j, b is the number present only in i, and c is the number present only in j. We estimated Dyer's model using the Jaccard index. We used permutation methods (Edington 1995) to estimate a significance level (P-value) for each environmental variable. Statistical tests were significant if $P < 0.05$.

Niche Breadth. Niche breadth and niche overlap are widely applied to analysis of foraging and community ecology to estimate competition (Greene and Jaksic 1983). Niche breadths were calculated according to Levins' (1968) equation:

$$\beta = \frac{1}{\sum p_i^2} \quad \text{for } i = 1 \text{ to } n$$

where p_i is the proportion of Red-tailed Hawk nests with the ith taxon present. The value of β varies from 1 to n, where n is the number of taxa. If prey taxa occur equally among all nests, then $\beta = n$. Niche-breadth values were standardized and converted to a fraction ranging from 0 to 1 by the equation:

$$\beta_{standard} = (\beta - 1)/(n - 1).$$

To calculate niche breadth, we created a prey species list based on pooled prey species present across all occupied Red-tailed Hawk nests by year. This yielded a separate food niche breadth measure for each of the four study years. We also calculated a 95% confidence interval for Red-tailed Hawk niche breadth on the Kaibab Plateau for comparison with calculated niche breadths for Northern Goshawks from other studies.

RESULTS

Pellet and Prey Remain Analysis. Considering each visit's collection of pellets and prey remains as one discreet sample, we obtained 140 prey samples (N = 80 end of nesting season, 1998–2001; N = 60 opportunistic during nesting season, 2000–01), consisting of 1–10 collections from 42 nests ($\bar{x}$ = 3.3). We identified 478 prey items, including at least 17 mammal, seven bird, and two reptile species (Table 1). The number of species at any one nest site ranged from 1–6. For all 4 yr combined, mammals represented 72% of Red-tailed Hawk diet and birds represented 27% (Table 1). Only two reptile species were identified; they did not contribute greatly to the overall diet (<1%). Six species accounted for 67% of prey by frequency of occurrence: Nuttall's cottontail (*Sylvilagus nuttallii*, 17.6%), Kaibab squirrel (*Sciurus aberti kaibabensis*, 7.7%), rock squirrel (*Spermophilus variegatus grammurus*, 10.0%), golden-mantled ground squirrel (*S. lateralis lateralis*, 10.3%), Northern Flicker (*Colaptes auratus*, 10.7%), and Steller's Jay (*Cyanocitta stelleri*, 10.3%; Table 1). Rare occurrences of porcupine (*Erethizon dorsatum*), coyote (*Canis latrans*), and mule deer (*Odocoileus hemionus*) comprised <2% of overall Red-tailed Hawk diet.

Dissimilarity Measures and Niche Breadth. Prey species frequency identified from pellet and prey remains did not vary among years (P = 0.3), across habitat types (P = 0.8), or by collection technique (P = 0.4). Dietary niche breadth for Red-tailed Hawks pooled across nests for each year was 0.58 in 1998, 0.52 in 1999, 0.51 in 2000, and 0.65 in 2001. The mean and 95% confidence interval for Red-tailed Hawks niche breadth for all four years combined was 0.57 ± 0.11. Calculated food niche breadths for Northern Goshawks for Arizona and several other western states did not fall within our confidence interval for Red-tailed Hawks (Table 2). Dietary overlap between the Red-tailed Hawk during this study and a Northern Goshawk diet from Boal's (1993) earlier study in the same area was 55% (number of common species/sum of species recorded for both raptors).

Table 1. Frequency of prey species in 140 samples (478 identified prey items) of pellets and prey remains collected from 42 Red-tailed Hawk nests, May–October 1998–2001, on the Kaibab Plateau, Arizona, U.S.A.

PREY SPECIES	FREQUENCY (N = 478)	PERCENT FREQUENCY	NEST OCCURRENCE (N = 42)	PERCENT NEST OCCURRENCE
Nuttall's cottontail (*Sylvilagus nuttallii*)	84	17.6	36	85.7
Golden-mantled ground squirrel (*Spermophilus lateralis*)	49	10.3	26	61.9
Rock squirrel (*Spermophilus variegatus grammurus*)	48	10.0	29	69.0
Kaibab squirrel (*Sciurus aberti kaibabensis*)	37	7.7	21	50.0
Chipmunk (*Eutamias* sp.)	27	5.6	20	47.6
Northern pocket gopher (*Thomomys talpoides*)	22	4.6	21	50.0
Long-tailed vole (*Microtus longicaudus*)	17	3.6	17	40.5
Red squirrel (*Tamiasciurus hudsonicus*)	15	3.1	13	31.0
Mouse (*Peromyscus* sp.)	13	2.7	9	21.4
Shrew (*Sorex* sp.)	11	2.3	10	23.8
Black-tailed jackrabbit (*Lepus californicus*)	8	1.7	8	19.0
Long-tailed weasel (*Mustela frenata arizonensi*)	5	1.0	5	11.9
Mule deer (*Odocoileus hemionus*)	5	1.0	5	11.9
Plains pocket mouse (*Perognathus flavescens*)	3	0.6	2	4.8
Porcupine (*Erethizon dorsatum*)	2	0.4	2	4.8
Ringtail (*Bassariscus astutus*)	1	0.2	1	2.4
Coyote (*Canis latrans*)	1	0.2	1	2.4
Northern Flicker (*Colaptes auratus*)	51	10.7	28	66.7
Steller's Jay (*Cyanocitta stelleri*)	49	10.3	26	61.9
Clark's Nutcracker (*Nucifraga columbiana*)	13	2.7	10	23.8
Unknown bird	8	1.7	7	16.7
Common Raven (*Corvus corax*)	3	0.6	3	7.1
Western Bluebird (*Sialia mexicana*)	1	0.2	1	2.4
Hairy Woodpecker (*Picoides villosus*)	1	0.2	1	2.4
Common Nighthawk (*Chordeiles minor*)	1	0.2	1	2.4
Unknown snake	3	0.6	2	4.8
Mountain short horned lizard[a] (*Phrynosoma douglassi*)	0	0.0	0	0.0

[a] Mountain short horned lizard was positively identified as a prey species during observations, but was not found in the prey collections.

Table 2. Food niche breadth of nesting Northern Goshawks calculated from prey remains collected in Arizona and other western states.

LOCATION	NUMBER OF NESTS	FOOD NICHE BREADTH	SOURCE
Arizona	20	0.29	Boal and Mannan (1994)
California	114	0.41	Bloom et al. (1986)
New Mexico	8	0.36	Kennedy (1991)
Oregon	4	0.38	Reynolds and Meslow (1984)

DISCUSSION

Our results on the Kaibab Plateau were consistent with Red-tailed Hawks being feeding generalists and preying primarily upon rabbits (*Sylvilagus* spp.), black-tailed jackrabbits (*Lepus californicus*), and ground squirrels (*Spermophilus* spp; Preston and Beane 1993); however, Northern Flickers and Steller's Jays were also frequent in this diet analysis. Previous observation and prey remains analyses for Northern Goshawks on the plateau indicated goshawks also preyed mostly upon rabbits and hares, tree and ground squirrels, Northern Flickers, and Steller's Jays (Boal and Mannan 1994, Kaufmann et al. 1994, and Reynolds et al. 1994). Bosakowski and Smith (1992) found that in eastern forests, competition between accipiters and buteos is usually minimized by a difference in prey selection, with buteos typically having a higher proportion of mammals in their diet, and accipiters more avian prey.

Red-tailed Hawks frequently exhibit switching behavior, which is the capability to utilize whichever species is most abundant at the time (Steenhof and Kochert 1988). Predators that are generalists often have weak and variable prey preferences and will exhibit switching behavior, while specialists with strong or consistent preferences do not (Murdoch 1969). The wider niche breadth of Red-tailed Hawks on the Kaibab Plateau indicated weaker preferences compared to the narrower niche breadth of Northern Goshawks.

Red-tailed Hawks and Northern Goshawks frequently occupy similar nesting habitat on the Kaibab Plateau. Both species tend to nest in larger trees ($\bar{x}$ DBH = 68.3–72.5 cm) and mid-slope in drainages ($\bar{x}$ slope position = 0.36–0.37; LaSorte et al. 2004). Because they also nest in close proximity (<2000 m apart, USDA Forest Service, North Kaibab Ranger District unpubl. data), we suggest that they may also be utilizing the same foraging habitat. Unfortunately, pellets and prey remains do not provide insight into any spatial or temporal partitioning of prey by these two species. However, our research clearly shows Red-tailed Hawks are preying upon many of the same species utilized by Northern Goshawks. Thus, we believe the potential for competition exists. We further hypothesize that the more generalist nature of Red-tailed Hawk diet and nesting habitat, in combination with the deterioration of late-successional forest habitat and concurrent creation of openings on the Kaibab Plateau, may tend to exacerbate any potential conflict. We suggest that additional research should be implemented to examine this potential competition, better quantify numbers of prey in both species' diets, and determine potential effects on such competition on Northern Goshawk management alternatives.

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BAT PREDATION BY LONG-EARED OWLS IN MEDITERRANEAN AND TEMPERATE REGIONS OF SOUTHERN EUROPE

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ABSTRACT.—We described spatial and temporal variation in bat consumption by Long-eared Owls (*Asio otus*) at a coastal site of eastern Spain and examined the importance of bats in the diet of this raptor in nine temperate and 21 Mediterranean localities of southern Europe. In our study site in Spain, bats accounted for 2% of prey items, which is the largest percentage so far reported for the species. The vast majority of bats were *Pipistrellus* spp. Bat predation occurred in all seasons, but was significantly higher in spring and summer. The temporal pattern of bat predation was unrelated to temporal variation in the consumption of rodents, the dominant prey in the diet. Although a consistent increase in bat intake only in years of rodent scarcity predicts an aggregation of occurrences over time, bat occurrence during 31 successive seasons was not different from a random sequence. Pellets containing bat remains originated mainly from one communal roosting site. Bat remains appeared in pellets from five of 16 nests, accounting for 17% of prey items on average. In southern Europe, bats occurred in 38% of diets in the Mediterranean region, while they were absent in diets from adjacent temperate localities. Our results suggest that Long-eared Owls prey on bats rarely and opportunistically in Mediterranean sites, but also that bat aggregations could be a locally important food source for some individual owls during certain periods.

KEY WORDS: *Long-eared Owl;* Asio otus; *Chiroptera; diet; Mediterranean basin; trophic plasticity.*

PREDACIÓN DE MURCIÉLAGOS POR EL BÚHO CHICO EN REGIONES TEMPLADAS Y MEDITERRÁNEAS DEL SUR DE EUROPA

RESUMEN.—Describimos la variación espacial y temporal en el consumo de murciélagos por parte del búho Chico *Asio otus* en una localidad costera del este de España, y examinamos la importancia de los quirópteros en la dieta de esta rapaz en 30 localidades del sur de Europa, 9 de clima templado y 21 de clima mediterráneo. En nuestra área de estudio, los quirópteros constituyeron el 2% de las presas ingeridas, cifra que representa el mayor consumo conocido para la especie. Casi todos los murciélagos consumidos fueron a *Pipistrellus* spp. Su predación se produjo en todas las estaciones, pero fue significativamente más alta en primavera y verano. El patrón temporal de predación de murciélagos no estuvo relacionado con la variación temporal en el consumo de roedores, la presa dominante en la dieta. El incremento en el consumo de murciélagos sólo en años en los que los roedores son escasos predice una agregación temporal de las apariciones. Sin embargo, la presencia de murciélagos en la dieta a lo largo de 31 estaciones sucesivas no difirió de una secuencia aleatoria. La mayor parte de las egagrópilas que contuvieron murciélagos procedieron del dormidero comunal. Encontramos restos de quirópteros en cinco de los 16 nidos muestreados, donde constituyeron en promedio el 17% de las presas. En Europa meridional, los murciélagos aparecieron en el 38% de las dietas de la región mediterránea, pero en ninguna de las dietas de la región templada adyacente. Nuestros resultados indican que *A. otus* consume murciélagos con baja frecuencia y de forma oportunista en la región mediterránea, pero también sugieren que las agrupaciones de quirópteros pueden ser una fuente de alimento localmente importante para algunos individuos durante periodos concretos.

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Throughout the boreal and temperate regions of Europe, Long-eared Owls (*Asio otus*) prey almost exclusively upon microtine rodents (Herrera and Hiraldo 1976, Lundberg 1979, Marks et al. 1999). As a result, owl numbers decrease locally with declining vole (*Microtus* spp.) populations and, at larger spatial scales, owls may use nomadic or irruptive movements to track peaks in vole abundance (Lundberg 1979, Korpimäki 1985, Hanski et al. 1991). Such a numerical response is a trait of specialist predators that may be explained in part by low availability of alternative prey (Weber et al. 2002) and by high predictability of vole population peaks in such ecosystems (Korpimäki 1985). However, Long-eared Owls seem to depend less on rodents at lower latitudes (Bertolino et al. 2001), especially in Mediterranean regions (García and Cervera 2001) which feature lower environmental predictability, resulting in strong seasonal and annual fluctuations in the abundance of rodents and other prey (Blondel and Aronson 1999). Indeed diet diversification with decreasing latitude may be a general pattern in nocturnal raptors (Herrera and Hiraldo 1976, Mikkola 1983, Korpimäki and Marti 1995) and other predators (Revilla and Palomares 2002, Clavero et al. 2003), suggesting that specialization may not always reflect species-specific constraints in physiology or morphology, but behavioral flexibility (Futuyma and Moreno 1988, Martín et al. 1995).

Bats have regularly been reported, albeit in small amounts, as prey of a variety of diurnal and nocturnal raptors (e.g., Baker 1962, Ruprecht 1979, Barclay et al. 1982). Long-eared Owls are no exception. For example, in the British Isles, this species was the second most important bat predator among raptors (Speakman 1991). In this paper, we describe the pattern of bat consumption by Long-eared Owls during an 8-yr period in a Mediterranean site with good habitat for bats in terms of roost (buildings) and food availability (insects in rice fields and other flooded areas). We also review European studies of Long-eared Owl diet in the Mediterranean basin and the adjacent temperate zone to examine the geographical pattern of predation on bats. We predicted that occurrence of bats in the Mediterranean sites would be higher than in temperate sites of similar latitude because (1) rodent abundance undergoes pronounced seasonal and annual fluctuations, and owls must search for alternative prey and (2) the season of bat activity is longer, and bat average abundance higher, in warmer Mediterranean environments (Avery 1985, Altringham 1996).

METHODS

We studied food habits of Long-eared Owls in Devesa de l'Albufera, one Mediterranean coastal site near Valencia city, Spain (39°21′N, 0°19′W). The owl habitat is a mosaic of pine forest (*Pinus halepensis*) with dense understory and open areas, mostly dunes and mesic interdune depressions (Costa et al. 1982). This forested landscape is highly disturbed (many buildings and regular recreational activities) and surrounded by a large expanse of rice fields. From November 1995 to June 2003, we collected owl pellets from beneath roost and nest sites on a monthly basis. We identified prey remains and, for each pellet, determined occurrence and minimum number of individuals of prey species. Using these data, we analyzed spatio-temporal fluctuations in bat predation. For analysis of seasonal variation in bat consumption, seasons were defined as winter (January–March), spring (April–June), summer (July–September), and fall (October–December).

We carried out the biogeographic comparison of bat predation using data from 30 diet studies from southern Europe (Table 1). Each study area was assigned to the Mediterranean or the temperate climate region according to Emberger et al. (1963; Fig. 1). We excluded northern temperate localities to avoid diets almost completely dominated by voles. For diets containing bats, we used Spearman correlation analysis to test the hypothesis that proportion of bats decreased with increasing latitude and altitude.

RESULTS AND DISCUSSION

Bat Consumption in Devesa de l'Albufera, Coastal Spain. We collected 2012 pellets that contained 6210 prey items. Pellets containing bat remains originated mainly from a communal roosting site (60%) and also near 16 nest sites, where we recorded successful owl reproduction. Bats accounted for 2% of prey items (Table 1), which is the largest percentage thus far reported for Long-eared Owls (Marti 1976, Mikkola 1983; Table 1). Of 126 bats, 124 were pipistrelle bats (*Pipistrellus* spp; Table 2). Bat remains occurred in all seasons, but predation on bats was significantly higher during the peak of bat activity and abundance in spring and summer ($G = 47.3$, df = 3, $P < 0.001$; Fig. 2). In our study area, the first flights of young pipistrelle bats take place between mid-July and mid-August (D. Almenar and M. Monsalve pers. comm.), and during the initial 2 wk their flight skills are less than those of adults (Blanco 1998). Thus, the combination of the annual peak in abundance associated with the emergence of young bats and their relatively higher vulnerability, associated with their reduced flight capability, may help to

Table 1. Long-eared Owl diet composition in 30 localities of southern Europe. Each locality is assigned to a climatic region either Mediterranean or temperate. The percentage of bats, rodents, and other prey are calculated on the total number of prey individuals. Numbers assigned to each study area are the same as in Fig. 1.

STUDY	COUNTRY	CLIMATIC REGION[a]	NO. OF PREY	PERCENT BATS	PERCENT RODENTS	PERCENT OTHER PREY	SOURCE
1	Spain	M	874	0.00	86.61	13.26	Alegre et al. 1989
2	Spain	M	232	0.00	96.10	3.90	Delibes et al. 1984
3	Spain	M	6929	0.04	90.70	9.20	Araújo et al. 1974
4	Spain	M	3726	0.00	92.60	7.30	San Segundo 1988
5	Spain	M	3185	0.03	78.50	21.50	Veiga 1980
6	Spain	M	255	0.00	96.50	2.80	López-Gordo et al. 1977
7	Spain	M	804	0.00	72.60	27.40	Amat and Soriguer 1981
8	Spain	M	6210	2.03	52.77	45.20	This study
9	Spain	M	6249	0.08	89.00	10.70	Corral et al. 1979
10	France	M	368	0.00	58.40	39.13	Kayser and Sadoul 1996
11	Italy	M	494	0.00	90.08	9.72	Gerdol and Perco 1977
12	Italy	M	121	0.00	95.87	4.13	Gerdol and Perco 1977
13	Italy	M	103	0.00	54.37	45.63	Gerdol et al. 1982
14	Italy	M	1157	0.00	93.52	6.49	Casini and Magnani 1988
15	Italy	M	181	0.00	97.24	2.76	Capizzi et al. 1998
16	Italy	M	338	0.30	98.20	1.50	Plini 1986
17	Italy	M	1787	0.00	81.60	18.50	Guidoni et al. 1999
18	Italy	M	201	0.00	95.10	5.00	Capizzi and Luiselli 1996
19	Italy	M	—	0.11	70.70	28.40	Sublimi and Scalera 1991
20	Italy	M	234	≤1.40	93.60	5.00	Sarà 1990
21	Greece	M	961	0.30	87.90	11.70	Alivizatos and Goutner 1999
22	Italy	T	1787	0.00	81.60	18.40	Bertolino et al. 2001
23	Italy	T	1836	0.00	85.52	14.44	Galeotti and Canova 1994
24	Italy	T	519	0.00	83.63	16.37	Mezzavilla 1993
25	Italy	T	655	0.00	93.44	6.56	Malavasi 1995
26	Italy	T	593	0.00	90.58	9.42	Aloise and Scaravelli 1995
27	Italy	T	98	0.00	79.59	20.40	Riga and Capizzi 1999
28	Slovenia	T	10991	0.00	95.48	4.52	Tome 2003a
29	Romania	T	1268	0.00	88.18	11.82	Marariu et al. 1991
30	Switzerland	T	4639	0.00	99.23	0.77	Roulin 1996

[a] M = Mediterranean and T = temperate region.

explain the high occurrence of bats in summer samples. The relative importance of bats in the diet varied by year ($G = 79.3$, df = 6, $P < 0.001$; Fig. 2). In our study area and other Mediterranean environments, rodent populations typically show annual minima during summer, especially during warm years (Blondel and Aronson 1999). Although owl consumption of rodents roughly follows availability (Fig. 3), bat predation was unrelated to the proportion of rodents in the summer diet ($r_s = 0.048$, $N = 8$, $P = 0.911$; Fig. 3). This suggests that bats are not specifically sought as an alternative prey. The hypothesis that bats are taken only in years of marked rodent scarcity also predicts a clumped occurrence of bats in the diet over the 8 study yr. However, bat occurrence during 31 successive seasons did not differ from a random sequence (runs test, Zar 1984; $Z = 0.726$, $P = 0.233$; Fig. 3).

Bat remains occurred in 42 pellets (2.1%). In 27% of these, bats were the only prey item, with 2–8 individuals per pellet. In 62% of pellets, bats occurred together with other prey, but accounted for ≥50% of prey items in each sample. The distribution of the number of individual bats per pellet was aggregated (did not fit a Poisson distribution with $\lambda = 0.055$, $\chi^2 = 42.62$, df = 1, $P < 0.001$; only pellets with bats, $\lambda = 2.643$, $\chi^2 = 13.23$, df = 3, $P = 0.004$). These results suggested that bats were clumped when captured. Pipistrelle bats are

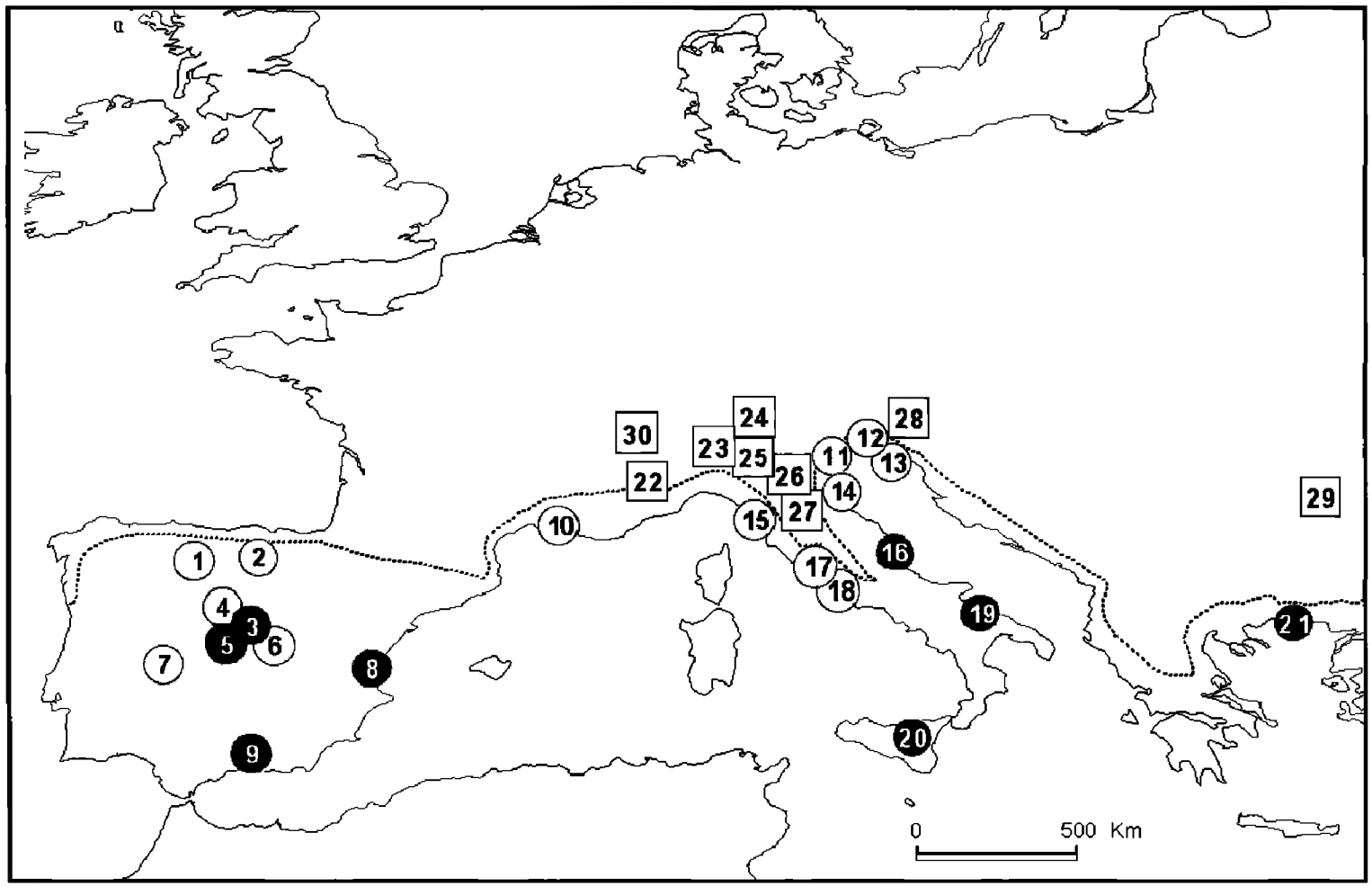

Figure 1. Localities where Long-eared Owl diet was studied in southern Europe. The broken line separates the temperate (squares) and the Mediterranean localities (circles) following Emberger et al. (1963). Black circles indicate sites where bat predation has been recorded. Numbers correspond to study numbers in Table 1.

Table 2. Bat species in the diet of Long-eared Owls in the Mediterranean region of Europe. Seasons when predation occurred and the range of body mass (g) are also shown. Body masses are from Palomo and Gisbert (2002). Study number and location are as in Table 1 and Fig. 1.

Species	Body Mass (g)	Season	Source	Study
Greater horseshoe bat (*Rhinolophus ferrumequinum*)	14.6–31.6	Winter	Alivizatos and Goutner 1999	21
		All seasons	This study	8
Greater mouse-eared bat (*Myotis myotis*)	21.0–35.0	Winter–Spring	Corral et al. 1979	9
		Fall	Sublimi and Scalera 1991	19
Lesser mouse-eared bat (*Myotis blythii*)	18.0–29.5	Spring–Summer	Veiga 1980	5
Whiskered bat (*Myotis mystacinus*)	4.0–8.0	All seasons	Plini 1986	16
Myotis spp.		Winter	Alivizatos and Goutner 1999	21
Pipistrellus spp.	3.5–10.0	All seasons	This study	8
Serotine bat (*Eptesicus serotinus*)	14.0–33.0	Winter–Spring	Corral et al. 1979	9
Brown long-eared bat (*Plecotus auritus*)	6.8–12.0	Spring–Fall	Araújo et al. 1974	3
Schreibers' bat (*Miniopterus schreibersii*)	10.1–20.8	All seasons	This study	8
European free-tailed bat (*Tadarida teniotis*)	22.0–54.0	Winter	Alivizatos and Goutner 1999	21

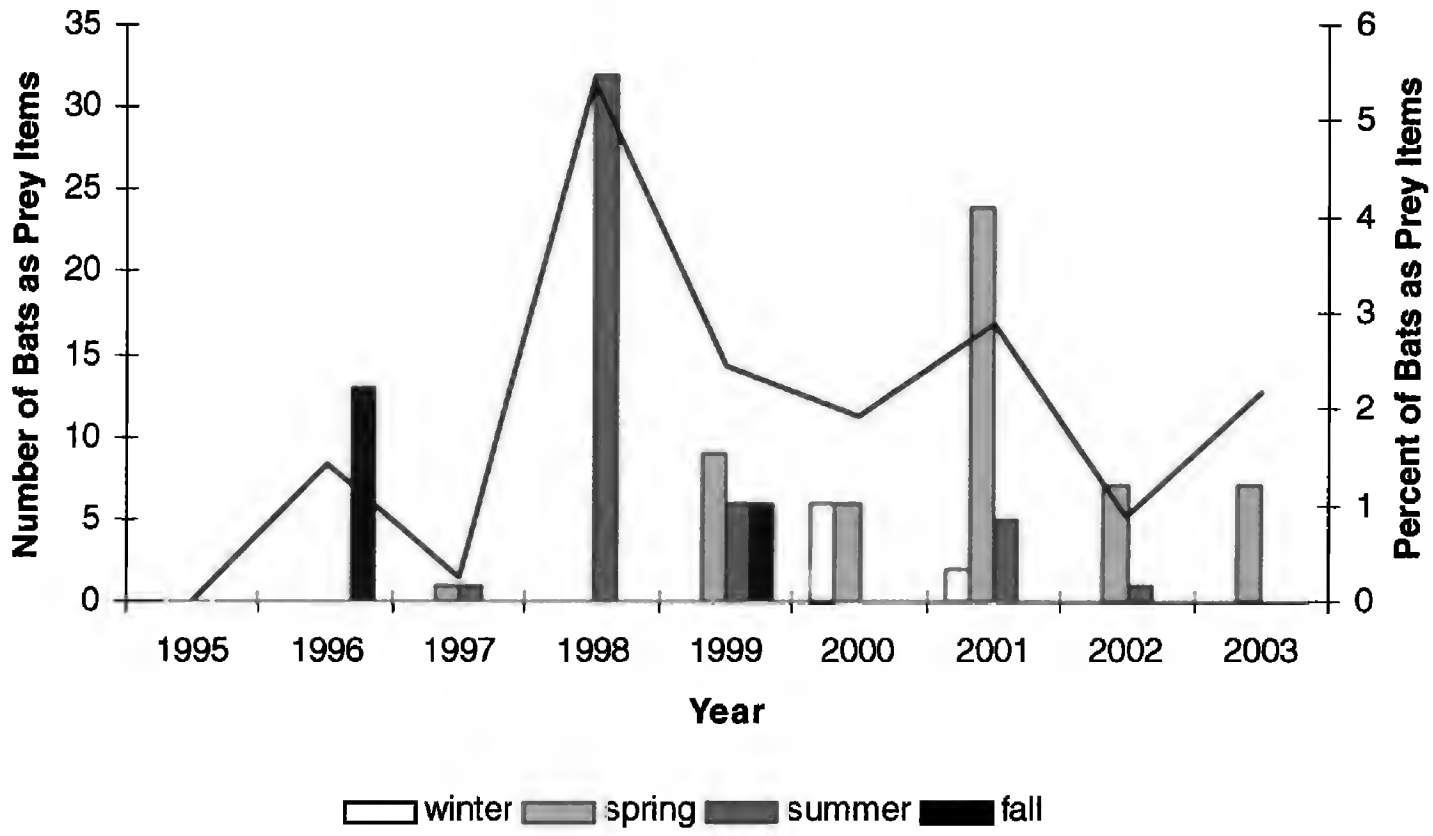

Figure 2. Temporal variation in the number of individuals taken by Long-eared Owls (bars) and in the percent of bats in terms of the total number of prey items (line) in Devesa de l'Albufera between 1996 and 2003.

very abundant in the study area and roost in colonies, often in buildings. Long-eared Owls could capture them at emergence as pipistrelle bats leave the roosts in large groups, but return as single individuals or in small groups and much more spaced over time. Although pipistrelle bats do not gather while foraging over large rice fields, they can form large aggregations when feeding along

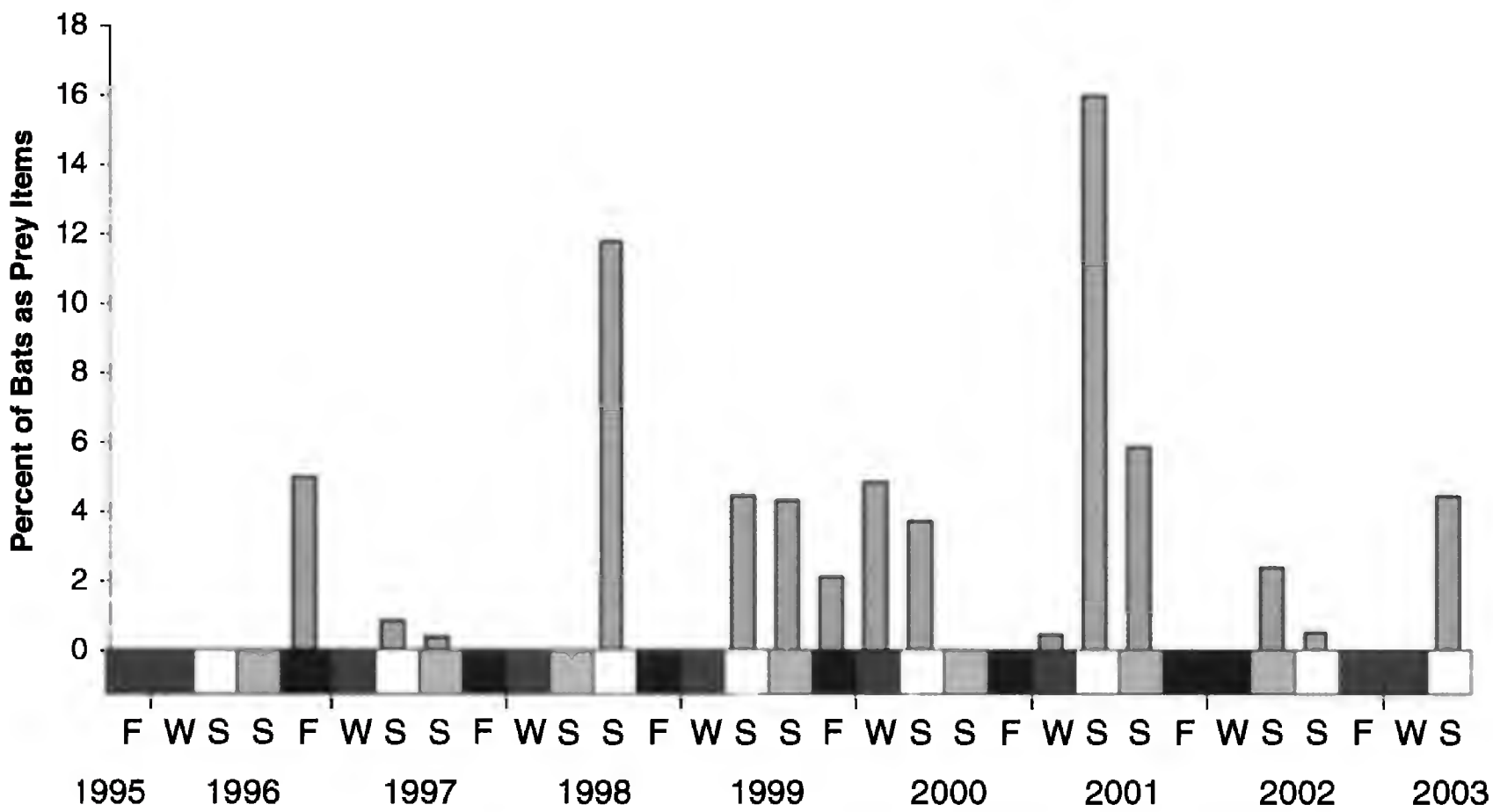

Figure 3. Seasonal variation in the percent (on the total number of prey items) of bats taken by Long-eared Owls in Devesa de l'Albufera between 1995 and 2003. Below the bars and for each year, shading intensity of cells indicates the ranked percentage of rodents in the diet, from the highest (dark) to the lowest importance (light) in the seasonal diet.

drainage channels or near street lamps (Blake et al. 1994), and the owls could hunt them there as well. Predation by nocturnal raptors on predictable accumulations of bats has been previously documented (Barclay et al. 1982, Fenton et al. 1994, Hoetker and Gobalet 1999).

The spatial distribution of bat remains during the owl breeding season was not random. Bat remains appeared in pellets from only five ($N = 205$ prey items) of 16 nests sampled. The mean percentage of bats per positive nest sample was 17.6 ± 13.0% (SD) of prey items. Only in one owl nest did bats account for <11% of prey, and the maximum observed was 37%. These figures make less plausible the idea of an opportunistic capture of bats as a result of accidental encounters (Ruprecht 1979). Our results were consistent with the hypothesis of individual differences in ability to catch bats or with individual knowledge of the location of pipistrelle colonies, which may be more profitable to exploit than solitary bat species if the emergence of large numbers of bats increases hunting success (Fenton et al. 1994). Even small-sized pipistrelle bats (body mass = 7.5 g) could be a profitable prey for Long-eared Owls if available in large quantities. The biomass of 8 pipistrelle bats (60 g; the maximum number of bats found per pellet) may satisfy two thirds of the daily energy needs (93.3 g for a 280 g owl; Wijnandts 1984), perhaps with little energy expenditure during foraging.

Biogeographic Pattern. We considered 21 diets for the Mediterranean region (34 410 prey items) and nine diets in the adjacent temperate region (22 386 prey items; Fig. 1). In the Mediterranean region, 38% of diets included bats as prey, whereas bats did not occur in any diet for the temperate region (Table 1). These differences in bat occurrence were significant ($G = 6.885$, df = 1, $P = 0.009$). Even excluding our study in coastal Spain, where we found an unusually high quantity of bat remains, the mean proportion of bats in the Mediterranean diets was significantly higher than in the diets of adjacent temperate sites (Mann-Whitney U-test, $Z = 1.98$, $P = 0.048$). In the Mediterranean region, the overall importance of bats in the diet of Long-eared Owls (0.43% of prey-items) was at least twice as high as in other geographical areas. But the large number of bats in the diet of owls in our study area was very influential in this comparison. In fact, omitting our results from eastern Spain, bats only represent 0.06% of prey items found in the combined diets from the Mediterranean region, which is similar to figures found elsewhere. In the diets from North America (23 888 prey items) and temperate Europe, plus Iraq, reviewed by Marti (1976), bats did not occur. In later reviews, Mikkola (1983) and Speakman (1991) found that bats accounted for <0.20% of prey items in Europe (67 805 prey items) and 0.05% in the British Isles (12 870 prey items).

In the studies we reviewed, bat predation was restricted to latitudes 37–43°N and altitudes 0–1400 m. Differences between localities in bat occurrence in the diet could not be attributed to a decline in bat species richness northwards, as species richness is almost constant at latitudes 35–50°N in Europe, which encompass all localities in Figure 1 (Pérez-Barbería 1991, Mitchell-Jones et al. 1999). However, bat abundance increases with decreasing latitude and altitude (Pérez-Barbería 1991, Kunz and Fenton 2003). Moreover, following the temporal pattern of insect availability, bats in Mediterranean environments show an extended activity season (Avery 1985, Altringham 1996, Blondel and Aronson 1999). Indeed, bat predation occurs in all seasons (Table 2). If an extended period of activity and a higher abundance were indicators of increased availability of bats for owls, we would expect increasing bats in the diet with decreasing latitude and altitude. We found no such correlations (latitude, $r_s = -0.05$, $P = 0.91$; altitude, $r_s = -0.45$, $P = 0.26$), but these analyses were based on small sample sizes ($N = 8$ diets containing bats).

Long-eared Owls preyed on nine of 29 bat species present in southern Europe (Mitchell-Jones et al. 1999; Table 2). Speakman (1991) suggests that large bat species would be more profitable prey than small ones, and therefore selected by raptors. However, Long-eared Owls consumed a variety of bat species, very different in body size, and there was no bias toward large species (Table 2). All the bat species that owls consumed, except *Tadarida teniotis*, forage low in open areas (Altringham 1996), just as Long-eared Owls do (Mikkola 1983, Tome 2003b) while hunting terrestrial prey on the wing (Marks et al. 1999). Excluding our results in coastal Spain, in Mediterranean environments, mean bat intake per diet, standardized as bats per 1000 prey items, was 3.4 individuals, suggesting that predation is in most cases opportunistic (Ruprecht 1979). Comparable results have been obtained for Barn Owls (*Tyto alba*; Pérez-Barbería 1991), which are regarded as opportunistic predators of bats.

We conclude that bat aggregations could be a

locally important food source for some individual owls during certain periods, as exemplified by the population of Devesa de l'Albufera. More generally, this evidence supports the view that Long-eared Owls may show substantial trophic plasticity, in contrast to their widespread recognition as a rodent specialist. In other words, their trophic response may be context-dependent rather than imposed by morphological or behavioral constraints that typically affect all populations across the range of true specialists.

At the geographical scale, bat abundance does not seem to reflect bat availability for Long-eared Owls, maybe because hunting strategies for preferred prey such as rodents are not compatible with a regular exploitation of flying bats. Accordingly, bats occur in a number of diets across the Mediterranean region, but their contribution remains largely irrelevant.

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Differential Effectiveness of Playbacks for Little Owls (*Athene noctua*) Surveys Before and After Sunset

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Most nocturnal owls respond to broadcast of conspecific recordings, and this technique may be used to study their behavior (Galeotti and Pavan 1993, Galeotti et al. 1997), to map territories (Finck 1990, Lane et al. 2001), to identify individuals (Galeotti and Sacchi 2001, Delport et al. 2002), or to study population trends (Exo and Hennes 1978, Martínez and Zuberogoitia 2004). Several factors affecting the effectiveness of playback techniques or spontaneous vocalizations have been identified, including response distance (Proudfoot et al. 2002), season (Zuberogoitia and Campos 1998), weather (Lengane and Slater 2002), gender, and social status (Appleby and Redpath 1997). However, only a few studies have investigated systematically how these factors influence playback methodology (McGarigal and Fraser 1985, Redpath 1994, Centili 2001). When comparing the accuracy of sampling using spontaneous owl vocalizations or conspecific playbacks, several authors demonstrated that sampling error increases when using spontaneous calls (McGarigal and Fraser 1985, Haug and Didiuk 1993, Redpath 1994). However, for Eurasian Eagle-Owl (*Bubo bubo*), passive auditory surveys provide better results than surveys based on broadcast calls (Penteriani and Pichera 1991, Martínez and Zuberogoitia 2002).

The Little Owl (*Athene noctua*) is a territorial species widely distributed in Palearctic regions. This small raptor inhabits a wide variety of semi-open areas, from steppes and stony semideserts to farmlands and open woodlands, and villages and urban areas (Cramp 1985). Little Owls prey on insects, small mammals, and birds, and hunt both during diurnal and nocturnal hours (Negro et al. 1990). Researchers have surveyed Little Owls by listening to spontaneous vocalizations or by playing typical calls to provoke the territorial vocalization after sunset (Finck 1990, Exo 1992, Mastrorilli 1997, Zuberogoitia and Campos 1998, Verwaerde et al. 1999, Pirovano and Galeotti 1999) or before sunset (Martínez and Zuberogoitia 2004). Territorial defense is performed mostly by males, which are more vocal than females (Mikkola 1983, Finck 1990, Zuberogoitia and Campos 1998).

Here, we examine the effectiveness of the playback method to detect Little Owls before or after sunset. Specifically, we tested whether broadcast before or after sunset would elicit the greater response frequency and whether duration of playback affected the Little Owl response rate. We also offer some suggestions to improve the survey methodology.

Study Area and Methods

We conducted the study in Clot de Galvany Council Natural Park (southeastern Spain, Province of Alicante). The study area (ca. 650 ha.) was characterized by a mosaic of shrubs, saline grasslands, and mixed forest, interspersed with extensive abandoned arboreal cultures such as almond and olive trees. The area exhibits a semiarid Mediterranean climate (Sancho and López 2002).

Between 19 April–17 May 2002 (the courtship and territorial defense period; Mikkola 1983, Finck 1990), we surveyed twice (before and after sunset) for Little Owls at 14 permanent stations during five sessions (10 d). Each day, survey stations were sampled with three different "survey" experiments, seven before and seven after sunset. The first survey was made 2 hr before sunset (1900–2100 H). The second survey was done 2 hr after sunset (2130–2330 H). These survey experiments were: (1) Spontaneous Calls: the observer listened for 2 min, registering the response rate (number of different Little Owls heard); (2) First Playback: after the spontaneous calls trial, a territorial intrusion was simulated by broadcasting territorial calls of Little Owl for 2 min using a

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cassette-player. Then, the observer listened for 1 min, recording the response; (3) Second Playback: after the first playback (1 min later), a new territorial intrusion was simulated by broadcasting territorial calls for 2 min by using a cassette-player. The observer listened for 1 min, recording the total response rate (response rate of first and second playback). The sequence of stations surveyed was reversed every other visit. To reduce the number of Little Owls that could be potentially counted twice, the distances between survey stations were at least 500 m (Finck 1990, Exo 1992, Centili 2001). To avoid differences associated with possible bias in sound direction, we always used the same cassette-player (power: 4 watts, Sony WN-FX 195, Barcelona, Spain), placed on the ground with the loudspeakers directed upwards. To minimize the potential of lower response rates (i.e., owls becoming less responsive because they habituated to our broadcasts), we used territorial male calls from five different individual owls (Roché 1996, SEO 1998, Llimona et al. 2002). We did not conduct experiments on windy or rainy days.

Because data were not normally distributed, we used nonparametric tests for statistical analysis (Zar 1996). To avoid pseudoreplication, we used the mean of response rate for each survey station. Statistical analyses were carried out using the SPSS statistical package (SPSS for Windows 1999). Two-tailed *P*-values were used throughout and statistical significance was set at $P < 0.05$.

RESULTS

Before sunset, spontaneous Little Owl calls were heard at only two stations (Table 1). In contrast, Little Owls were detected after sunset by spontaneous calls at nine stations (Table 1). As expected, more Little Owls sang spontaneously after sunset than before (Kruskal-Wallis test, $\chi^2 = 10.39$, df = 1, $P < 0.001$). Numbers of Little Owls detected by passive auditory surveys were significantly lower than those detected by playback surveys, both before and after sunset (Fig. 1). These differences were shown in both the comparison with the first playback (before sunset: $\chi^2 = 22.07$, df = 1, $P < 0.001$; after sunset: $\chi^2 = 19.84$, df = 1, $P < 0.001$), and the second playback (before sunset: $\chi^2 = 28.17$, df = 1, $P < 0.001$; after sunset: $\chi^2 = 25.73$, df = 1, $P < 0.001$). Playback surveys detected more individuals after sunset than before (first playback before vs. after sunset: $\chi^2 = 6.83$, df = 1, $P < 0.001$; second playback before vs. after sunset: $\chi^2 = 4.51$, df = 1, $P = 0.03$), but there were no differences between the two playback experiments within each period (first playback vs. second playback before sunset: $\chi^2 = 0.55$, df = 1, $P = 0.46$, first playback vs. second playback after sunset: $\chi^2 = 0.03$, df = 1, $P = 0.87$; Fig. 1).

DISCUSSION

Our results strongly suggest that nocturnal broadcast surveys were the most effective method for surveying Little Owls, both for detecting presence and counting individuals or territories (Zuberogoitia and Campos 1998, Verwaerde et al. 1999, Centili 2001, van Nieuwenhuyse et al. 2002). These results are in accordance with similar studies with other owls: Barred Owl (*Strix varia*; McGarigal and Fraser 1985), Tawny Owl (*Strix aluco*; Redpath 1994), Burrowing Owl (*Athene cunicularia*; Haug and Didiuk 1993), Ferruginous Pygmy-Owl (*Glaucidium brasilianum*; Proudfoot and Beasom 1996), and Long-eared Owl (*Asio otus*; Martínez et al. 2002).

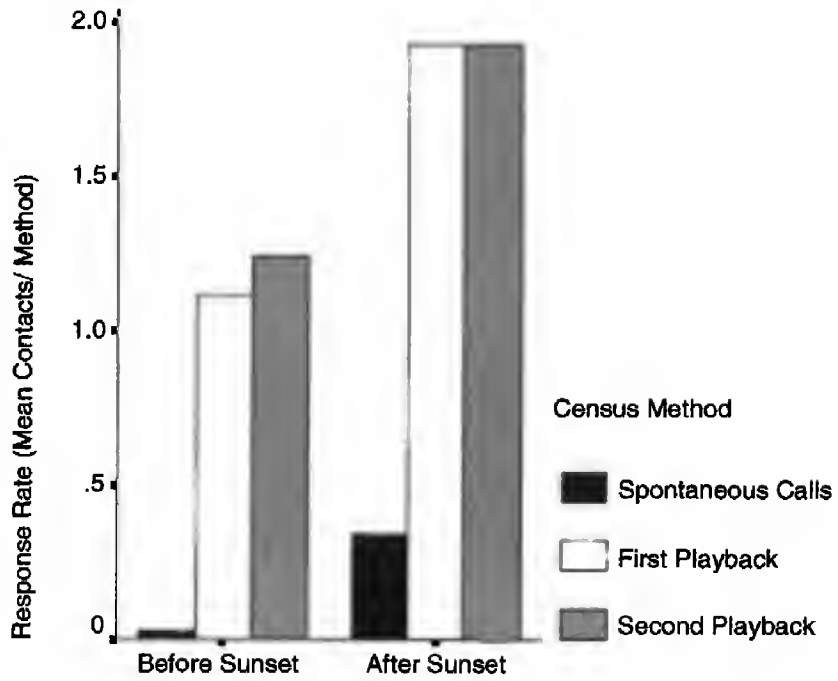

Figure 1. Call rates (calling means for Little Owls per survey station) detected without using playback (spontaneous calls), using first and second playback both before and after sunset.

Interestingly, our study indicated that Little Owls responded at a similar rate in the first and the second playback (before and after sunset). The fact that our first playback experiment, broadcasting for 2 min, elicited a similar number of owls as when both playbacks were included, suggested that 2 min of continuous playback was sufficient for detecting Little Owls, which was a shorter period than that used in other studies of this species (5 min, Zuberogoitia and Campos 1998; 4 min, Verwaerde et al. 1999; 3 min, Centili 2001).

Detection rate of Little Owls after sunset was less variable and higher than before sunset (Table 1, Fig. 1). Thus, before sunset, surveys may underestimate the number of breeding Little Owls in an area. However, the use of playback before sunset would be useful in finding territories and nests because individuals might be observed when calling at perches (Martínez and Zuberogoitia 2004, pers. obs.).

Estimating the breeding density of owl species is an important part of population studies, and comparisons are widely used to assess the abundance of a species across years and geographical areas. Biased estimates of breeding pair density are misleading and prevent comparisons between studies. Thus, increased efficiency of survey methods and knowledge of potential error is necessary. Our results suggest broadcasting 2 min of conspe-

Table 1. Mean call rates (number of different owls calling at each survey station/number of trials ±SD) of Little Owls at Clot de Galvany Park, Alicante Province, Spain. Data were obtained during five visits/survey station; protocol included recording spontaneous calls followed by playback of conspecific calls.

	Before Sunset			After Sunset		
Station	Spontaneous Calls	First Playback	Second Playback	Spontaneous Calls	First Playback	Second Playback
1	0	1.00 ± 1.00	0.80 ± 0.84	0.20 ± 0.45	1.60 ± 1.14	2.20 ± 1.48
2	0	0.60 ± 0.89	0.60 ± 0.89	0.20 ± 0.45	1.60 ± 0.89	1.40 ± 1.34
3	0	1.00 ± 0.71	2.20 ± 0.83	0	3.40 ± 0.34	3.20 ± 0.84
4	0	0.60 ± 0.55	0.20 ± 0.45	0.20 ± 0.45	1.00 ± 1.00	0.60 ± 0.89
5	0	1.00 ± 0.00	1.00 ± 0.00	0	1.00 ± 0.71	0.80 ± 0.45
6	0	2.20 ± 0.84	2.00 ± 1.58	0.80 ± 1.60	2.40 ± 0.89	3.20 ± 0.84
7	0.20 ± 0.45	0.80 ± 0.45	1.00 ± 0.71	0.40 ± 0.55	1.89 ± 0.84	1.40 ± 0.55
8	0.20 ± 0.45	1.60 ± 1.14	1.80 ± 0.84	0.80 ± 0.84	2.20 ± 0.84	2.60 ± 0.55
9	0	1.80 ± 0.84	2.00 ± 0.00	0.40 ± 0.89	2.60 ± 1.14	2.20 ± 1.30
10	0	1.60 ± 0.89	1.00 ± 0.71	0	1.40 ± 0.55	1.20 ± 1.30
11	0	0.40 ± 0.89	0.60 ± 0.55	0.40 ± 0.55	0.80 ± 0.45	1.00 ± 1.41
12	0	2.00 ± 1.22	2.00 ± 1.41	0	3.00 ± 0.71	3.00 ± 0.71
13	0	0.60 ± 0.55	1.20 ± 1.10	0.60 ± 0.89	1.60 ± 1.34	1.40 ± 1.34
14	0	0.40 ± 0.89	1.00 ± 1.22	0	2.60 ± 0.89	2.80 ± 0.45
Total	0.03 ± 0.01	1.10 ± 0.62	1.24 ± 0.64	0.29 ± 0.29	1.94 ± 0.79	1.93 ± 0.92

cific songs just after sunset elicits vocal responses effectively from resident Little Owls.

DIFERENTE EFFECTIVIDAD DEL PLAYBACK PARA CENSAR MOCHUELO EUROPEO (*ATHENE NOCTUA*) ANTES Y DESPÚES DEL ANOCHECER

RESUMEN.—Los búhos son difíciles de contar pues son poco conspicuos, tienen hábitos nocturnos y duante el día permanecen perchados en sitios ocultos. La reproducción de vocalizaciones previamente grabadas ha sido considerada un modo eficiente para determinar la presencia de estas sigilosas rapaces. En este estudio examinamos la efectividad y precisión de la reproducción de vocalizaciones para detectar individuos de la especie *Athene noctua*. Los censos en los que se reprodujeron llamados espontáneos fueron menos eficientes que aquellos en los que se reprodujeron vocalizaciones coespecíficas pregrabadas. La tasa de detección luego del atardecer fue mayor y menos variable que la tasa previa al atardecer. Esto sugiere que los censos nocturnos con vocalizaciones podrían ser el método más efectivo para detectar la presencia de *A. noctua* y para contar los individuos y territorios de esta especie.

[Traducción del equipo editorial]

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KING VULTURES (*SARCORAMPHUS PAPA*) FORAGE IN MORICHE AND CUCURIT PALM STANDS

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Feeding on palm fruit, particularly drupes of the African oil palm (*Elaeis guineensis*), has been documented for several Old World species of birds of prey (Thiollay 1978, Barlow 2004). In the New World, fruits of the imported African oil palm have been consumed by the Turkey Vulture (*Cathartes aura ruficollis;* Pinto 1965), Yellow-headed Caracara (*Milvago chimachima;* Haverschmidt 1962), and Black Vulture (*Coragyps atratus;* Haverschmidt 1947, Pinto 1965, Elias and Valencia 1982). Both vulture species, as well as the Crested Caracara (*Caracara cheriway*), consume flesh of coconuts (*Cocos nucifera;* Haverschmidt 1947, Crafts 1968), and fruits of palms (*Mauritia flexuosa* and *Desmoncus* sp.) have been found in stomach contents of the Black Caracara (*Daptrius ater;* Haverschmidt 1962). American Black Vultures also feed on sweet potatoes (McIlhenny 1945) and avocado (Röhl 1949) when carrion is scarce, and Turkey Vultures ingest leaves, seeds, and bark of cottonwood trees (*Populus* spp.), apparently as casting material (Davis 1983). No published data were found on ingestion of plant matter by King Vultures (*Sarcoramphus papa*), but residents at Hato Las Nieves, Venezuela reported that the species consumes fruits of the moriche (*Mauritia flexuosa*) and cucurit (*Attalea maripa*) palms when carrion is scarce (Y. Carbonell and A. Mendoza pers. comm.). The observations reported in this paper were gathered in an attempt to verify these claims.

STUDY AREA AND METHODS

My observations were part of a long-term study (1994–2000) on the abundance, population structure, movement patterns, and foraging strategies of King Vultures in the Serranía de la Cerbatana, Estado Bolívar, Venezuela The study was conducted in the southeastern part of the massif at Hato Las Nieves (Sabana Nueva: 6°34′80″N, 66°12′17″W), a ranch located ca. 125 km south of Caicara del Orinoco. The valley of Las Nieves, ca. 20 km long (northwest-southeast) and 9 km wide, is dominated by lowland shrub savanna, mainly 220–260 m above sea level. The bordering mountains reach elevations of 1600 m to the west and 1880 m to the north (Cerro de la Cerbatana). The moriche palms (*Mauritia flexuosa*) can be found scattered in the gallery forests or in stands (morichales; see González Boscán 1987) in the seasonally inundated areas of the valley. The moriche fruits, 3–7 cm long, ovate to globular and having an oily mesocarp (Borgtoft Pedersen and Balslev 1990), fall to the ground when almost ripe and accumulate in the water among fallen fronds and debris. Cucurit palms (*Attalea maripa* = *Maximiliana regia*) occur as stands within the gallery forests on dry terrain. The fruits, ovate, 5–7 cm long, are also rich in oil (Braun 1997). The observations reported here took place during the rainy season, which lasts April through October or November. The study periods (24 June–24 July 1994, 26 June–14 August 1995, 28 May–14 July 1996, 30 June–18 August 1997) were set up to coincide with the fruiting season reported locally for both palm species. Observations were carried out daily, generally from 0615–1900 H. The length of each monitoring period (up to 5 hr) depended on weather, logistics, and whether or not the King Vultures were present in the valley. The number of sample days for each study period varied from 29–50 d, with the afternoon of arrival and morning of departure being counted if observations were carried out (Table 1). I used 10× binoculars and observed from outcrops and other high points.

RESULTS

In all four years, moriche and cucurit fruit production took place earlier than expected and little remained by mid-July. Both palm species suffered from drought in 1995 and 1996. A mean of 2.1 ± 1.1 (SD) King Vultures (range = 1–4) foraged in four different morichales (N = 7 occurrences), and 3.4 ± 1.0 (range = 2–4) foraged (N = 7 occurrences) in two of the cucurit stands, primarily during the 1994 and 1995 field seasons (Table 1). This activity was most often carried out by two adults together (N = 5) or three adults and an immature (N = 6), presumed to be the local birds. Eleven of the 14 occurrences took place when the vultures had not fed on livestock carcasses (natural mortality, including jaguar [*Panthera onca*] predation) or inedible parts of slaughtered animals for 2–3 wk. Four bouts in the cucurit stands (August 1995) followed presumed feeding on the remains of jaguar-killed native wildlife.

On 27 June 1994, at 0947 H, four American Black Vultures flew from the western morichal. As I approached, I sighted an adult King Vulture perched low at the edge of the palm stand and another adult on the ground near-

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Table 1. Mean number of King Vultures per study period (1994–97) seen foraging in moriche and cucurit palm stands and number of occurrences at Hato Las Nieves, Venezuela. Number of days the vultures fed on livestock carcasses and total days of observation are given.

Study Period	Number of King Vultures $\bar{x} \pm$ SD (range)	Frequency		Number of Days	
		Moriche	Cucurit	Livestock Carcasses	Observation
1994	2.2 ± 1.0 (1–4)	3	3	15	29
1995	3.3 ± 1.3 (1–4)	3	4	11	50
1996	3.0 ± 0 (3)	1	0	26	48
1997	0	0	0	15	49

by at the base of the only fruiting moriche in the area. This bird, with head down, just out of sight, seemed to be nibbling on something. When both birds flew to nearby palms, I could see that their crops were extended. Their flight attracted a Turkey Vulture that walked around the area but did not feed. At the site, I found one unripe moriche fruit with half the mesocarp freshly scraped off longitudinally on one side, the marks clearly imprinted on the nut, and a large piece of overripe mesocarp from another fruit. No debris, no carrion, and no live animals were present. I concluded that the King Vulture had consumed the missing pulp, but this would not explain crop extension. The next day after the rains stopped (1620 H), I observed an adult sunning in the main cucurit stand. As I penetrated into the gallery forest, I came across another King Vulture rummaging in the litter at the base of a cucurit palm. The debris contained no animal matter, only cucurit fruits, whole or rotting or partially eaten, pieces of mesocarp, and clean kernels. Several wedged-capped capuchin monkeys (*Cebus olivaceus*) were in the stand. Two days later (30 June 1994), two adults were observed in a morichal at ca. 1100 H and in a cucurit stand in the afternoon, and the following day three adults and an immature were in the same cucurit stand at mid-day. Capuchin monkeys were present both days. The last sighting in 1994 took place on 7 July, 2 d after the vultures had consumed a dead horse. At 0737 H an adult was again perched low at the edge of a morichal. It was raining hard (1000 H) when I found the adult foraging under the only fruiting moriche in the area. The bird flushed upon seeing me, but then returned to the morichal again, weaving in and out of the vegetation and foraging on the ground as I tracked it for ca. 90 min. Moriche fruits were present in the areas where the bird had foraged. I found no carrion or live animals. The vulture's crop was extended, indicating it had ingested food while in the morichal.

On 28 June 1995, at 0722 H, two adult King Vultures and an American Black Vulture perched at the edge of a morichal. An hour later another adult King Vulture and an immature joined them, and one of the first adults flew to the ground near a palm with fruit. When I investigated, I found several fruits with the mesocarp wholly or partially scraped off. No carrion was present, but a medium-sized savanna tortoise (*Geochelone carbonaria*) was in the area and could have been feeding on the fruits earlier. Later (1157 H), I located the immature bird feeding at the base of another fruiting moriche. Again, the mesocarp on several fruits had been freshly scraped off. No debris or carrion was found, and no live animals were nearby. I concluded that the King Vulture had eaten the pulp. Two days later, at 0740 H, an adult perched in the gallery forest north of the central camp, and at 0913 H I found it foraging on the ground among the few palms that remained of a remnant morichal. No carrion was present. On 29 July 1995, 8 d after a carcass had been consumed, two adults suddenly flew up from one of the gallery-forest floors (1645 H) in an area that had fruiting moriche, but I was unable to investigate further. Then, on 5–6 and 9–10 August 1995, three adults and an immature, presumed to be the same birds as above, were sighted in a cucurit stand. Eight Turkey Vultures were also present. The King Vultures perched within the upper strata of the canopy of the broad-leafed trees, occasionally going to the top of the trees to sun or dry, and spent the mornings in the stand. A troop of ca. 30 wedge-capped capuchin monkeys, with many females transporting infants, was foraging there on the first two days. The area was strewn with large pieces of bark and fallen branches. On the last 2 d, fewer capuchins were present, but were seen with a pair of red-howler monkeys (*Alouatta seniculus*). I found no remains of carrion.

On 8 June 1996 at 0913 H, 4 d after the vultures had eaten livestock carrion, I came upon two adult King Vultures and an immature resting on a low shrub at the edge of a morichal and next to a fruiting moriche palm. Three American Black Vultures were feeding on the ground at the base of the palm. The crop of one King Vulture was slightly extended. I found no carrion and no live animals, only palm fruits lacking part of the mesocarp and showing signs of having been scraped. I concluded that both vulture species had been feeding on the fruits. This was the only time the King Vultures were observed to forage in a morichal in 1996, but very few moriche palms were

fruiting (≤10% in the major stands). No foraging took place in the cucurit stands, but only two cucurit palms had fruit, although fermenting drupes were found at the base of others. Livestock carrion was abundant (Table 1), and jaguars were in the area.

The King Vultures were not seen foraging in the palm stands in 1997, even though more moriche and cucurit were fruiting than in 1996. A small troop of capuchin monkeys was present twice in the study area, and domestic carrion was not often available (Table 1), as most livestock had been removed from the valley. The vultures picked over the debris at former carcass sites on 12 d and followed a jaguar. This feline was known to have come through the valley on four occasions, and the King Vultures presumably fed on the remains of kills on native wildlife at or near Las Nieves on 5 d.

DISCUSSION

My observations support the claims that the King Vultures at Hato Las Nieves eat fruits of the moriche palm, particularly when carrion is scarce. Eating moriche fruits may partially compensate the lack of carrion, 100 g of fresh pulp having 10.5 g of fat and 3.0 g of protein, but the fruits could have been ingested for their vitamin-mineral content (see González Boscán 1987, Borgtoft Pedersen and Balslev 1990). From the remains of the fruits found at the feeding sites, I conclude that the mesocarp was scraped off longitudinally, but judging from the size of extended crops of some vultures, some fruits, probably the smaller ones, may have been swallowed whole. Both feeding techniques are used by the Palm-nut Vulture (*Gypohierax angolensis*) when consuming drupes of the African oil and *Raphia* palms, the ingested kernels being regurgitated later (Thiollay 1978). Only once in my observations was a potential fallen-fruit consumer present—a tortoise. My observations also lend support to claims that American Black Vultures eat *Mauritia* fruits (Y. Carbonell and A. Mendoza pers. comm.). Moriche fruit-eating appears to be an activity carried out by vultures local to the study area; however, because northwestern Bolívar state is one of the few areas in the Venezuelan Guayana that has a high concentration of morichales (see González Boscán 1987), moriche fruit-eating by King Vultures could be more widespread than at Hato Las Nieves.

On the other hand, I was not able to confirm that King Vultures eat cucurit fruits, although their consumption is plausible considering the oil content of the mesocarp (Braun 1997). Whenever the King Vultures foraged in the cucurit stands, wedge-capped capuchin monkeys were also present, which suggests that a foraging association may exist between the two species. The monkey troops were also attended by the Turkey Vultures. Raptor-monkey associations usually involve opportunistic feeding on flushed invertebrates, particularly insects (e.g., Fontaine 1980), and sometimes on vertebrates displaced by the movements of monkey troops (e.g., arboreal snakes: Zhang and Wang 2000).

How could King Vultures benefit from associating with *Cebus* monkeys? Is it only to profit from occasional primate mortality? Although 55% of the wedge-capped capuchin's diet consists of plant matter, particularly ripe fruits, invertebrates are searched out by peeling off loose bark, digging into rotting material and sifting through leaf debris on the ground (Robinson 1986). Perhaps the King Vultures benefit from larvae that are exposed or fall to the ground while the troop forages; vultures are known to scoop up maggots from decomposing carcasses (Houston 1988). Of greater interest is the occasional predatory behavior of the capuchins on vertebrates. For example, the viscera of lizards may be eaten but the muscular part left, and the remains of captured frogs discarded (Robinson 1986). In *Cebus capucinus,* after wrestling with an *Iguana* sp., a monkey managed to break off 30–40 cm of the iguana's tail, stripped some meat from it, and dropped the rest (Baldwin and Baldwin 1977). By following wedge-capped capuchin monkeys, the vultures could glean the remains of discarded vertebrate prey. However, eating moriche fruit or monitoring monkeys did not seem to be as beneficial as picking over the scattered remains of former carcasses and following jaguars to consume the remains of kills. These observations illustrate some opportunistic feeding strategies used by King Vultures.

SARCORAMPHUS PAPA FORRAJEA EN MORICHALES Y EN GRUPOS DE PALMAS DE CUCURTO

RESUMEN.—Este trabajo se realizó durante las épocas lluviosas desde finales de junio de 1994 hasta mediados de agosto de 1997 en la Serranía de la Cerbatana, Hato Las Nieves, Estado Bolívar, Venezuela. Los datos recolectados sostienen las afirmaciones del personal del hato de que *Sarcoramphus papas* come frutos de la palma moriche (*Mauritia flexuosa*), principalmente cuando escasea la carroña. Una media de 2.1 individuos de *S. papa* (rango = 1–4) forrajearon en los morichales (N = 7 avistamientos). No pude confirmar las afirmaciones de que *S. papa* come también frutos de la palma de cucurito (*Attalea maripa*). Los frutos de ambas especies de palma contienen aceite. En mis observaciones, una media de 3.4 individuos (rango = 2–4) se encontraron vigilando tropas del mono capuchino *Cebus olivaceus* que habían venido a forrajear a los rodales de cucuritos. Sugiero que *S. papa* podría asociarse con los monos para aprovechar los invertebrados que espantan, como las larvas de insectos, los restos de vertebrados que capturan y ocasionalmente los cadáveres de monos.

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FAMILY BREAK UP, DEPARTURE, AND AUTUMN MIGRATION IN EUROPE OF A FAMILY OF GREATER SPOTTED EAGLES (*AQUILA CLANGA*) AS REPORTED BY SATELLITE TELEMETRY

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KEY WORDS: *Greater Spotted Eagle*; Aquila clanga; *departure*; *family break up*; *migration*; *satellite telemetry.*

The transition of birds of prey to independence is difficult to study (Brown and Amadon 1968), as both old and young birds stray ever further from the nest site toward the end of the post-fledging period. We know of no study concerning a raptor species in which the departure on migration, the break up of the family, and subsequent migration have been investigated by satellite tracking. Here, we report on a case concerning Greater Spotted Eagles (*Aquila clanga*). Available information on this species is limited, but Ivanov et al. (1951) and Dementiev and Gladkov (1951) believed that Greater Spotted Eagle families departed as a unit on migration.

In the closely related Lesser Spotted Eagle (*Aquila pomarina*), both adults migrated separately, as determined by satellite telemetry (Meyburg et al. 2006). The offspring in this species, which were not tracked with satellite telemetry, normally leave before the parent birds. However, in some cases, the females leave before the young (Meyburg et al. 2006). Satellite telemetry has so far been used to track one adult Greater Spotted Eagle (Meyburg et al. 1995a).

As part of a long-term research program in northeastern Poland (Mizera et al. 2001), we are endeavoring to raise the level of knowledge, and thereby, the protection of the Greater Spotted Eagle by making use of the available technology (i.e., satellite telemetry) to investigate the species' migration and wintering habits.

METHODS

In 1996, an entire family of Greater Spotted Eagles was fitted with satellite transmitters (Platform Transmitter Terminals, PTTs) in the Biebrza river valley of northeastern Poland. The eagle nest was located in a National Park protecting the largest peatlands in Central Europe, including 15 547 ha of forests, 18 182 ha of agricultural land, and 25 494 ha of wetlands—the Biebrza marshes. More than 70 natural and semi-natural plant associations have been documented in the Biebrza valley. The most dominant forest associations include black alder (*Alnus glutinosa*), swampy birch (*Betula pubescens*), and peat coniferous forests (*Salici-Betuletum*). Frequent anthropogenic ecosystems found in the valley are pastures, cultivated grounds and urbanized areas. One of the greatest threats to the park is human modified drainage patterns, which causes the invasion of marshes by shrubs and trees. Active conservation measures have been applied to stop further succession and maintain more natural intermediate successional stages. A broad public awareness campaign is in place to encourage the adoption of organic farming, as 45% of the park is privately owned. The eagle nest was built in dense humid alder (*Alnus glutinosa*) and birch (*Betula* spp.) forest.

We used the dho gaza method (Hamerstrom 1963, Clark 1981, Bloom 1987) with a Eurasian Eagle Owl (*Bubo bubo*) to trap the adults. By this method, the eagles "attacked" the live eagle owl, tethered to a perch and got entangled in the dho gaza net. We used transmitters supplied by Microwave Telemetry, Inc. (Columbia, MD U.S.A.) with a mass of 60 g. They were fitted as backpacks, using Teflon ribbon (Bally Ribbon Mills, Bally, PA U.S.A.) to attach them to the bird. The young fledgling eagle was equipped with a battery-powered transmitter with a mass of 60 g and a temperature sensor. To ensure as long a life as possible, this radio was programmed to operate only at intervals of 4 d and then for only 10 hr. The adult birds were fitted with solar-powered PTTs These were programmed to be in continuous operation, provided the level of light was sufficient to generate power for the transmitter.

All location data were analyzed individually and entered into databases. We used the computer program

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Mapit (Allison 1997) to plot locations, which were provided by Service Argos, Inc. (Toulouse, France), measure distances between locations, and trace the migration routes. This program is an integrated global mapping and digital display system, which computes the great-circle distance between one point and another, while dynamically displaying both great-circle and constant-compass-bearing (rhumb) lines. Great-circle distances are physically the shortest distances on a globe.

RESULTS

Three eagles in the family broke up when leaving the breeding territory. The female was the first to depart (19 September 1996), at least 2 or 3 d before her young. The male was the last to leave (26 September 1996), 1 wk after the female. Whereas the adults headed straight for the Bosphorus (Fig. 1), the 1687 km covered by the young bird terminated in Albania, where this eagle apparently perished at the end of October. The young probably left on 21 or 22 September 1996, and the male was present on 23 September, but only made minimal migration progress by midday on 26 September 1996 (Table 1). Due to the programming of its transmitter (operation of 4 d) the progress of the young could not be determined as accurately as that of the two adults. The date of departure of the young eagle was assessed from the first locations away from the nest, providing an average estimate of speed and distance from the breeding territory during the first stages of its migration (Table 1, 2). On average, this eagle flew only 57 km per day. This young eagle may have covered the first 257 km up to the first location away from the nest in more than 4 or 5 d, and thus, have left the breeding area before 21 or 22 September.

The young bird set off from the breeding territory in a southwesterly direction (Fig. 1). The eagle remained in Poland until at least 4 October, while the female and male were located in the country for the last time on 19 and 26 September, respectively. The female reached the Bosphorus on 14 October and the male on 22 October. The young bird apparently met its death in southern Albania, ca. 70 km south of Tirana and 13 km north of Ballesh. All the data from its transmitter (temperature and no change of location) after 26 October indicate mortality. The transmitter was transmitting signals until 13 July 1997. However, it is also possible, but much less likely, that the eagle lost or removed the transmitter.

DISCUSSION

In birds of prey, the transition to independence is difficult to study as toward the end of the post-fledging period, both old and young birds stray ever further from the nest site. Direct observation does not account adequately for local movements of raptors as they begin the departure process. Nevertheless, a number of studies concerning eagles and other raptors (e.g., Alonso et al. 1987, Morvan and Dobchies 1990, Bahat 1992, Bustamante 1995, Real et al. 1998, Rafanomezantsoa 2000) have been published during recent years.

Table 1. The departure of the Greater Spotted Eagle family from the nest site in 1996 was determined by satellite telemetry.

	ID-NUMBER	DATE AND TIME (GMT) OF LAST LOCATION AT NEST	DATE AND TIME (GMT) OF FIRST MIGRATION LOCATION	DISTANCE FROM NEST SITE TO FIRST MIGRATION LOCATION	DATE OF DEPARTURE	REMARKS
Male	16864	23 Sept at 0117 H	26 Sept at 1037 H	46 km	Probably 26 Sept (AM)	This bird could have left in the morning of 23 Sept, as midday (local time) of 26 Sept it was 46 km away from the nest site. However, based on its mean migration speed, it most likely left the morning of 26 Sept.
Female	19628	18 Sept at 1817 H	20 Sept at 0047 H	193 km	19 Sept	The bird could not have left on 18 Sept.
Offspring (male)	19626	17 Sept at 1034 H	26 Sept at 0044 H	257 km	Probably on 21 or 22 Sept	This eagle could have left the breeding area as early as 17 Sept, but this is unlikely given its mean daily distances covered.

Figure 1. The autumn migration of the three Greater Spotted Eagles in Europe determined by satellite telemetry in 1996; dates of arrival at selected points en route are indicated.

Table 2. The outward migration of the juvenile Greater Spotted Eagle (see Fig. 1) 1996 was determined by satellite telemetry.

BEGINNING AND END OF EACH STAGE[a]	LENGTH OF THE DIFFERENT STAGES IN km	DURATION OF EACH STAGE (days)	MEAN LENGTH OF DAILY FLIGHT DISTANCES	COUNTRIES TRANSVERSED
ca 21/22 Sept 26 Sept: 0044 H	257 km	?	?	Poland
26 Sept: 0044 H 30 Sept: 1134 H	Roosting	4.5	—	Poland
30 Sept: 1134 H 4 Oct: 1534 H	242 km	4.5	54 km/day	Poland
4 Oct: 1720 H 9 Oct: 0005 H	76 km	4	19 km/day	Poland and Slovakia
9 Oct: 0547 H 13 Oct: 0600 H	329 km	4	82 km/day	Slovakia and Hungary
13 Oct: 0600 H 17 Oct: 1327 H	202 km	4.5	45 km/day	Hungary and Croatia
17 Oct: 1738 H 22 Oct: 0109 H	361 km	4	90 km/day	Bosnia - Herzegovina
22 Oct: 0109 H 26 Oct: 0619 H	220 km	4	55 km/day	Montenegro and Albania

[a] Each migration stage was 4 d, based on the duty cycle of the satellite transmitter. Location data provided by Argos Service, Inc (Toulouse, France).

Dementiev and Gladkov (1951) and Ivanov et al. (1951) believed that Greater Spotted Eagle families departed together on migration. We know of no study in the literature on this species, or any other raptor, in which the dates of departure on migration, the break up of the family, and their combined or separate migrations have been investigated by satellite telemetry. The family of Greater Spotted Eagles studied here clearly broke up when leaving the breeding territory.

We also have studied a pair of the closely-related Lesser Spotted Eagle using this method over several years. The members of this pair migrated separately in 1997–98 and 1998–99 and overwintered ca. 1000 km apart both years in southern Africa (Meyburg et al. 2006). However, in this case, the offspring were not tracked.

REGISTRO DE LA RUPTURA FAMILIA, PARTIDA Y MIGRACIÓN DE OTOÑO DE UNA FAMILIA DE AQUILAS MOTEADAS (*AQUILA CLANGA*) EN EUROPA USANDO TELEMETRÍA SATELITAL

RESUMEN.—Ambos adultos y el polluelo de una famila de *Aquila clanga* fueron estudiados mediante telemetría satelital en el noreste de Polonia para determinar la fecha de inicio de su migración, la disolución de la familia y sus patrones de migración combinados e independientes. La familia se disolvió al abandonar el territorio de cría. La hembra fue la primera en partir, el inmaduro lo hizo alrededor dos o tres días más tarde y el macho partió una semana después de la hembra. Los adultos se dirigieron directo al Bósforo. El inmaduro recorrió 1687 km hasta Albania, donde aparentemente murió a fines de octubre.

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SEASONAL PATTERNS OF COMMON BUZZARD (*BUTEO BUTEO*) RELATIVE ABUNDANCE AND BEHAVIOR IN POLLINO NATIONAL PARK, ITALY

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KEY WORDS: *Common Buzzard*; Buteo buteo; *relative abundance*; *roadside surveys.*

Nest-site selection and habitat use have been described in the Common Buzzard (*Buteo buteo*) by several authors (e.g., Penteriani and Faivre 1997, Krüger 2002, Lõhmus 2003, Bustamante and Seoane 2004, Sergio et al. 2005), but few studies have documented annual variations in the abundance and habitat associations of this species (Meunier et al. 2000).

We conducted monthly roadside surveys of Common Buzzards in a mountainous area of southern Italy. Although roadside surveys have well-known limitations (e.g., Andersen et al. 1985, Fuller and Mosher 1987, Millsap and LeFranc 1988, Viñuela 1997), they remain a useful technique for monitoring local abundance and distribution of raptors (Fuller and Mosher 1987, Ellis et al. 1990). Because roadside surveys are easy to conduct, they can be carried out at frequent intervals. Here, we present results from monthly roadside surveys of Common Buzzards. Using these data, we examine habitat associations, describe seasonal patterns of Common Buzzard behavior and abundance and, in particular, discuss the effectiveness of roadside surveys to monitor changes in abundance.

METHODS

The Common Buzzard (hereafter buzzard) surveys were conducted from October 2000–September 2001 in Pollino

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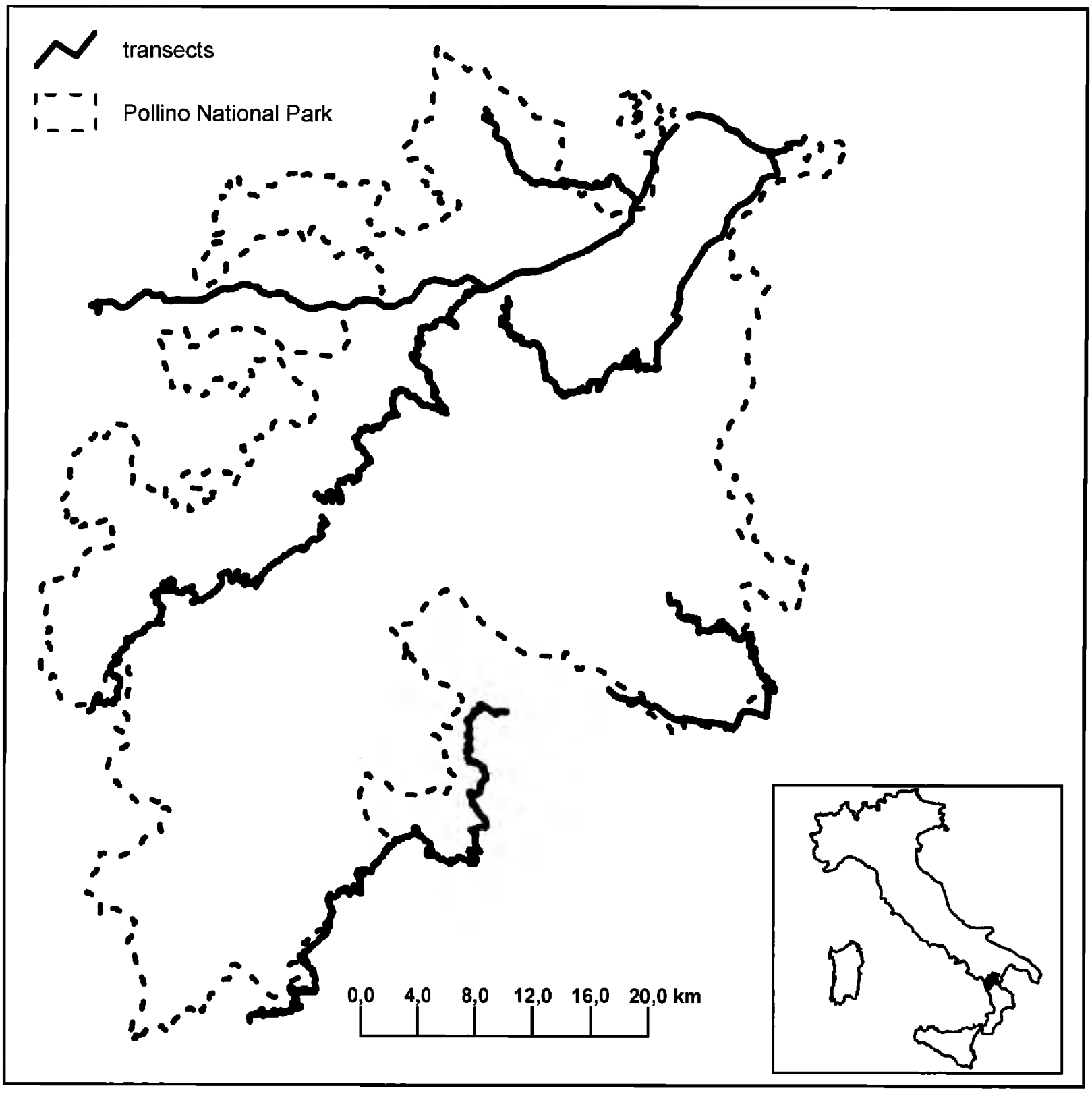

Figure 1. Locations of seven routes (thick dark lines) used for roadside surveys in Pollino National Park, southern Italy, in 2000–01 (thin lines indicate the boundaries).

National Park (39°58′N, 16°08′E), a 1821 km^2 area located in the southern Italian Apennines (Fig. 1). The elevation ranges from 170–2266 m. The land uses include farmlands and oak woods (*Quercus ilex, Q. pubescens, Q. cerris*) in the northern section of the park and grassland and beech woods (*Fagus sylvatica*) in the southern portion. Over the study period, the mean monthly temperature was 14.5°C, with a mean of 28.8°C during July–September and 9.7°C during October–February. The annual rainfall in the 12 mo of the survey was 841 mm.

We surveyed buzzards along seven paved roads (Fig. 1) selected randomly with restrictions (Caughley and Sinclair 1994). Specifically, we rejected routes adjoining those roads previously chosen. Each road was surveyed once each mo, during the third or fourth wk of the mo and only on calm and clear days. We did not sample on days with snow, rain, fog, or strong winds. Each month, the routes were surveyed over 4 d by means of two cars, each one with a driver and two observers. All surveys were conducted in the morning (0900–1200 H), typically the best time to count raptors (Robbins 1981). We drove at a speed of 40–45 km/hr and stopped the car to confirm each sighting. For each buzzard detected, we recorded if it was flying or perched and if it was alone or with other buzzards. Also, we discounted any buzzard that may have represented a re-sighted bird.

We calculated the relative abundance as the number of buzzards seen per 100 km sampled. For abundance computations we excluded the stretches of roads lined by trees within tunnels, forests, or villages. Therefore, al-

Table 1. Number of Common Buzzards recorded along seven routes in Pollino National Park (southern Italy, 2000–01). For computation of relative abundance, we used the survey length obtained discounting the stretches of roads lined by trees or passing through tunnels, forests, or villages.

Routes	Length (km) of Routes	Survey Length (km) of Routes	Monthly Mean ±SD of Relative Abundance
1	57.8	40.4	11.2 ± 1.8
2	18.3	18.3	10.2 ± 2.0
3	44.4	28.9	6.7 ± 2.0
4	47.3	34.0	12.7 ± 2.7
5	38.5	38.3	7.7 ± 1.6
6	43.8	24.2	20.1 ± 5.7
7	65.1	53.6	9.3 ± 1.2

though the total road length was 315.2 km, we considered for analysis only 237.6 km (survey km in Table 1).

For the analysis of buzzard habitat associations, we reported the sightings as presence/absence in a 1 × 1 km UTM grid. We created a 1 km buffer on both sides of each route and we considered only buzzards observed inside this buffer. We analyzed the habitat associations within this buffer using the Corine Land Cover 1:100 000 digital map (Legend level 3, Ministero dell'Ambiente e del Territorio—Ente Parco), identifying 10 land cover types which we then pooled into four general vegetation cover types: (1) arable land (cultivated areas regularly plowed and generally under a rotation system), (2) heterogeneous agricultural areas (areas principally occupied by agriculture, interspersed with natural areas), (3) forests, and (4) shrub or herbaceous vegetation (Table 2). In each 1 × 1 km grid cells or portions of a cell included inside the buffer, we calculated the surface of each cover type by means of a Geographical Information System (GIS) analysis (Geomedia Professional 2002). Buzzard habitat associations were analyzed in four periods: February–April (courtship), May–July (incubation and nesting), August–September (post-fledging), and October–January (winter). Although observers recorded the number of individual buzzards sighted, we only considered their presence/absence in each grid cell.

We used the Friedman repeated measures analysis of variance (F_r) to detect any difference in the relative abundance among months and among periods. Using the same test, we evaluated if the number of flying or perched buzzards varied among months or periods. We used the Kruskal-Wallis test to detect any difference in the relative abundance among routes and the Mann-Whitney U test to ascertain whether flying buzzards were observed more frequently than perched buzzards. We used the arcsin-transformation to convert the proportion of sightings composed of buzzard groups. The Kolmogorov-Smirnov one-sample test (Z) was used to examine if the distribution of relative frequencies was uniform. Finally, we used a stepwise logistic regression to deter-

Table 2. Summary of logistic regression models exploring relationships between habitat types and Common Buzzard presence during four periods (Pollino National Park, southern Italy, 2000–01).

	Courtship		Incubation and Nesting		Post-fledging		Winter	
	P[a]	Exp (B)[b]	P	Exp (B)	P	Exp (B)	P	Exp (B)
Arable land	0.46	0.52	0.82	1.25	0.36	3.01	0.89	1.11
Heterogeneous agricultural areas	0.87	1.10	0.74	1.29	0.46	2.21	0.70	1.29
Forests	0.66	1.29	0.80	1.19	0.34	0.31	0.57	0.69
Shrub or herbaceous vegetation	0.83	1.14	0.53	1.60	0.20	3.79	0.80	0.84

[a] P = statistical significance of the Wald statistic, a chi-square distribution used to ascertain if a variable is a significant predictor of the outcome (presence or absence of buzzards; Field 2000).

[b] Exp (B) = indicator of the change in odds (probability of an event occurring divided by the probability of that event not occurring) resulting from a unit change in the predictor (Field 2000).

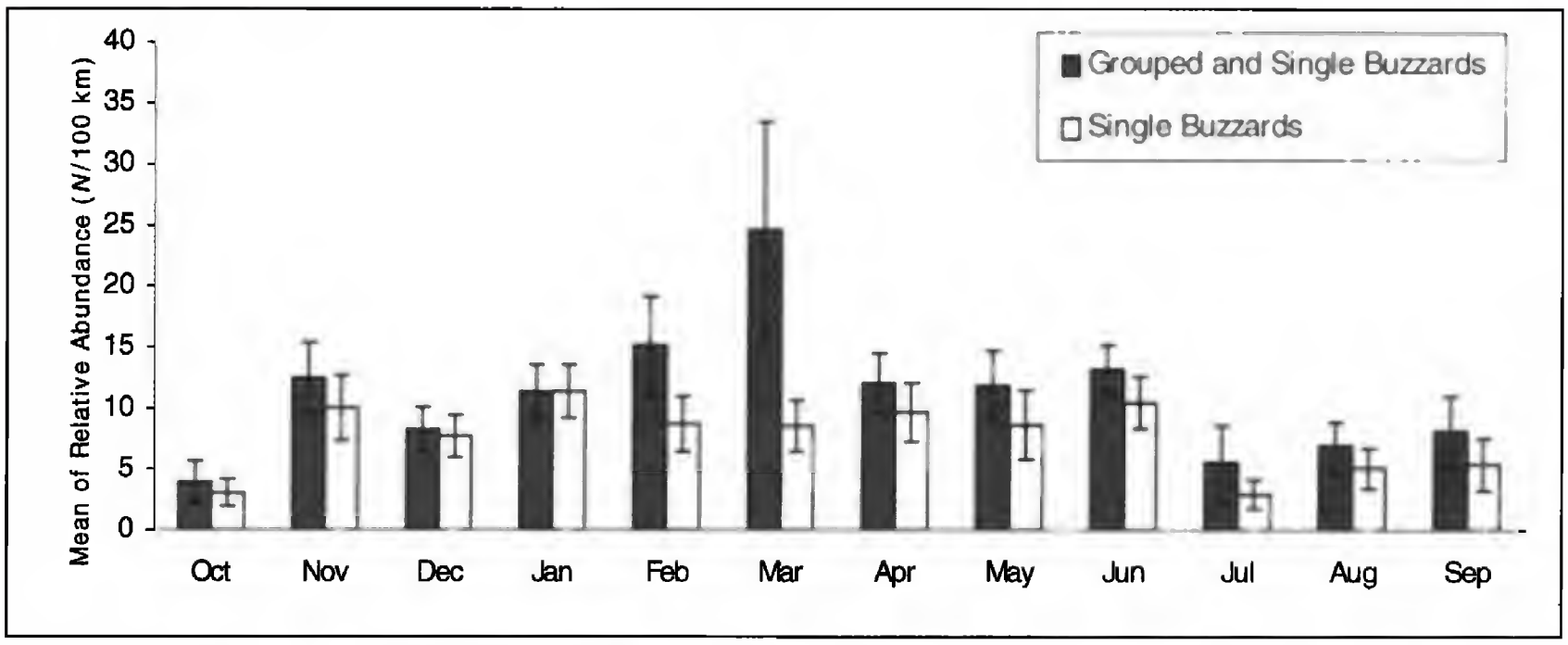

Figure 2. Monthly mean ±SD of the relative abundance of Common Buzzards recorded along seven routes in Pollino National Park, southern Italy (2000–01). The dark columns show the relative abundance calculated considering both grouped and single individuals; the white columns are the relative abundance calculated based on single individuals only.

mine whether the probability of detecting buzzards varied among the four cover types in each of the periods. Means are presented ±SD. The nonparametric tests were from Siegel and Castellan (1988), and the logistic regression analysis followed Field (2000). All of the statistical tests were performed with SPSS 10.0 (SPSS 2000).

RESULTS

During the study period, we recorded 328 buzzard sightings. The mean relative abundance per roadside survey was 11.1 ± 4.4 (N = 84) buzzards/100 km (Table 1). Buzzard abundance varied among months (F_r = 23.1; df = 11; $P < 0.05$; Fig. 2) and, marginally, among periods (F_r = 7.6; df = 3, P = 0.054). In particular, a post-hoc multiple comparisons test showed that the abundance was greater during the courtship period than in the other three periods and in the incubation-nesting period than in the winter ($P < 0.05$ for all comparisons). However, the relative abundance estimates showed a high variation for all periods (17.2 ± 11.9 for courtship, 10.2 ± 5.0 for incubation and nesting, 7.2 ± 4.3 for post-fledging, and 9.0 ± 2.4 for winter).

We found no difference (χ^2 = 10.3; df = 6; P = 0.11) in abundance among routes, although the survey routes crossed different land cover types. We detected more buzzards flying (87.2%) than perched (12.8%; U = 1.5; N = 24; $P < 0.0001$). The number of perched buzzards did not vary among months (F_r = 15.6; df = 11; $P >$ 0.05), whereas the number of flying buzzards did (F_r = 21.0; df = 11; $P < 0.05$) (Fig. 3). In addition, the number of flying buzzards varied among periods (F_r = 10.8; df = 3; $P < 0.05$); during courtship, flying buzzards were more numerous than in all other periods (Multiple Comparison test $P < 0.05$).

Most buzzards detected (67.4%, N = 221) were alone, while 23.2% (N = 76) were paired and 9.4% (N = 31) were in larger groups, with a mean group size of 3.9 ± 0.6 individuals. The proportion of sightings composed of a group of buzzards showed a uniform distribution throughout the year, ranging from 0.4 in July to 0.0 in January (Z = 1.5; N = 12; $P > 0.05$).

No land cover variable entered the stepwise logistic regression discriminating between grid cells with or without buzzards, in any of the four periods of the year (Table 2).

DISCUSSION

The relative abundance of the study population was relatively stable throughout the year, apart from a peak during the courtship period (February–April). A possible explanation is that during the courtship period, many young buzzards return to their natal area. A high tendency for philopatric movements among dispersers has been recorded both in Common Buzzards (Walls and Kenward 1998) and other raptors (e.g., Ferrer 1993, Newton et al. 1994, Carter 2001). A second explanation for the observed increase in relative abundance may be linked more to buzzard behavior and detectability than to variations in actual population density. During courtship, buzzards participate in more aerial displays than in other periods, and are thus more detectable. This explanation is supported by the higher proportion of flying buzzards recorded during the courtship period, particularly in March, when all the detected individuals were flying (Fig. 3).

The decrease in relative abundance during the incubation and nesting periods is probably related to the fact

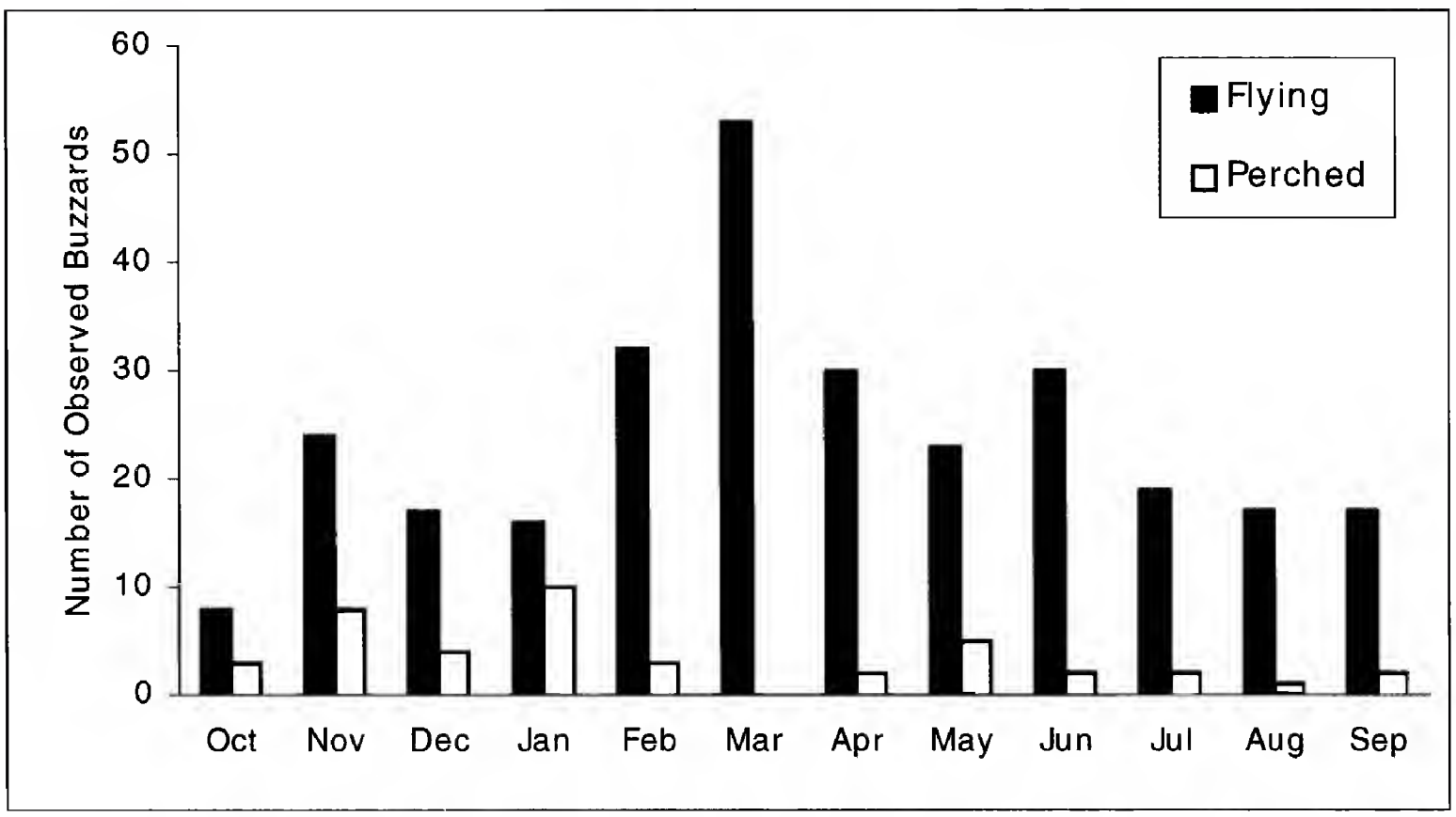

Figure 3. Total number of flying and perched Common Buzzards observed per month during vehicle surveys conducted at Pollino National Park, southern Italy in 2000–01.

that half of the breeding population were tending nests or were close to their nests most of the time. However, contrary to expectations, during the post-fledging period, when flying young join the adult population, the relative abundance was not higher than that estimated during the other periods. This could be caused by the relatively inconspicuous behavior of fledged buzzards that often are perched in the immediate neighborhood of the nest for several weeks after fledging (Tubbs 1974, Tyack et al. 1998). Moreover, because most natal dispersal usually occurs in the autumn (Picozzi and Weir 1976, Walls and Kenward 1998), it is possible that our survey methods underestimated fledged young during the post-fledging period.

In our study, buzzards did not show a preference for any land cover type during any periods of the year. This is supported by lack of variation among the seven roadside surveys, although these routes crossed different habitats. This lack of association with cover type may be due to the buzzard's high plasticity and varied diet (Cramp and Simmons 1979, Sergio et al. 2002). However, Sánchez-Zapata and Calvo (1999), Krüger (2002), and Sergio et al. (2005) found that buzzard breeding sites were linked to some landscape characteristics, particularly forest cover. There are three possible explanations for this discrepancy in results. First, the previous studies examined the relationship between habitat characteristics and nesting sites, while we examined the association of individual locations with land cover type. Second, we recorded buzzards when in flight or perched, whether they were hunting or involved in other activities. Finally, the disagreement could be related to the coarse scale of our landscape analysis. However, Sánchez-Zapata and Calvo (1999) found a linkage between buzzard nest sites and some landscape characteristics using a coarse-scale (1. 200 000) land use map.

In summary, our results showed that the relative abundance of a raptor population recorded by road counts may be sensitive to temporal behavioral changes, which ultimately affect detectability, thus biasing a potential assessment of seasonal variations in numbers. For this reason, roadside surveys would be a coarse method to monitor intra-annual population changes, or to compare the relative abundance recorded in different years, unless the data are collected in the same time period or season. On the other hand, we suggest further investigation into whether roadside surveys can be a useful tool for long-term monitoring of a population when comparing the same months in different years.

PATRONES ESTACIONALES EN LA ABUNDANCIA RELATIVA Y EL COMPARTAMIENTO DE *BUTEO BUTEO* EN EL PARQUE NACIONAL POLLINO, ITALIA

RESUMEN.—Se estudió la abundancia relativa de una población de *Buteo buteo* a lo largo de 12 meses en el Parque Nacional Pollino (sur de Italia) para comparar datos entre meses y para determinar las asociaciones de hábitat Realizamos censos mensuales en carreteras a lo largo de siete rutas (total = 315 km). La media anual de aves detectadas fue de 11.1 ± 4.4 individuos/100 km, aunque este valor varió significativamente entre meses. Esta varia-

ción probablemente reflejó la actividad de vuelo de *B. buteo* y no las fluctuaciones en el número de individuos durante el año, ya que la mayoría de los registros tuvieron lugar durante el período de cortejo. Con base en nuestros resultados, sugerimos que los censos realizados para esta especie a lo largo de carreteras son más efectivos durante el período reproductivo que en otras épocas, cuando los individuos realizan vuelos elevados con menor frecuencia. Finalmente, la presencia y la distribución de *B. buteo* dentro del parque no se asociaron con el tipo de cobertura del suelo.

[Traducción del equipo editorial]

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NEW NESTING RECORD AND OBSERVATIONS OF BREEDING PEREGRINE FALCONS IN BAJA CALIFORNIA SUR, MÉXICO

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KEY WORDS: *Peregrine Falcon;* Falco peregrinus; *nesting record; Baja California; México.*

The Baja California peninsula has been an area where resident Peregrine Falcons (*Falco peregrinus*) were common in the past (Bancroft 1927, Banks 1969). Historical records of their presence in the region were published by Bryant in 1889 (see Grinnell 1928). Detailed accounts of nesting territories for the peninsula and Gulf of California islands were made by Banks (1969), Anderson (1976), and Porter et al. (1988). According to Banks (1969), prior to 1967, 54 known peregrine locations accounted for approximately 66 nest sites in this region. Porter et al. (1988) identified 67 eyries in this area in 1976–84. As in other parts of the world from the late 1960s to the early 1980s, the peninsular Peregrine Falcon population declined, likely due to the impact of organochlorine pesticides (Kiff 1988). However, published data show that recovery began by the late 1980s (Porter et al. 1988, Castellanos et al. 1997).

Historical nesting territories were mainly located on sea cliffs of the western side of the state of Baja California, from Tijuana to Santa Catarina, and on islands along both coasts of the peninsula (Banks 1969, Porter et al. 1988, Castellanos et al. 1997, Ruiz-Campos and Contreras-Balderas 2000). A small number of inland territories were also known (Banks 1969, Castellanos et al. 1997). However, no nesting pair has ever been reported on Bahía Magdalena region, which is located on the west coast of the peninsula (Fig. 1). Here, we provide the first report of Peregrine Falcons nesting in this area. Our finding extends the breeding range of this species to an area of the Baja California peninsula lacking suitable natural nesting sites. We also report on the reproductive output of this pair.

METHODS

We observed the nest from vantage points 100–200 m from the metal tower, where the peregrine nest was located. We monitored activities around the nesting area, and with the help of binoculars and a spotting scope, recorded the behavior and attendance of adults at the nest. During each observation period, we registered the contents in the nest, the birds' activities, time, the number of interactions between birds, and disturbance events that occurred.

RESULTS AND DISCUSSION

On 25 January 2004, we found a pair of Peregrine Falcons at 25°05′21″N and 112°04′41″W in Santa Elenita, a remote, abandoned industrial port 7 km north of Adolfo López Mateos in Bahía Magdalena, Baja California Sur, México. Both birds displayed activities (mutual roosting, cooperative hunting excursions, courtship flights) suggesting they were a territorial pair. The same day we sighted another single adult Peregrine Falcon 7.5 km south of Santa Elenita. After our finding, we visited Santa Elenita between February to mid-October to monitor the pair's reproductive status (20 hr 25 min of observation in 9 d between 1000–1600 H). The port is a concrete platform about 30 m wide by 120 m long located in a mangrove estuary. Above this platform there are four metal towers and a central crane 40 m tall. The crane has a metal horizontal arm about 30 m long oriented northeast to southwest (Fig. 2). The peregrine pair nested on an old Osprey (*Pandion haliaetus*) nest at the extreme southwestern end of the arm (Fig. 2). On the opposite side was another Osprey nest. A small fishing camp near the platform was operating daily during the study.

On 28 February, we saw another single bird (male Peregrine Falcon, by relative size) approaching the nest. Both males "fought," and after the interaction and the intruder left, the nesting male copulated with the female. On 18 March, we found the female incubating eggs. From 8–28 May, three nestlings were observed in the nest, and they began to fly in late June. On 22 July, we observed the parents and one of the fledglings. The adults were still on the territory on 1–4 and 11–15 October.

The tower was shared with an Osprey pair during the entire study period. However, both pairs showed tolerance despite their proximity. Daily and incidental human disturbance at the base of the towers was relatively intense (22 events or 1.08 events/hr, including small boats, people, cars, and motocross traffic); however, the peregrine nest was not deserted and breeding was successful. Peregrine response to disturbance occurred more frequently when other birds approached to within about 20

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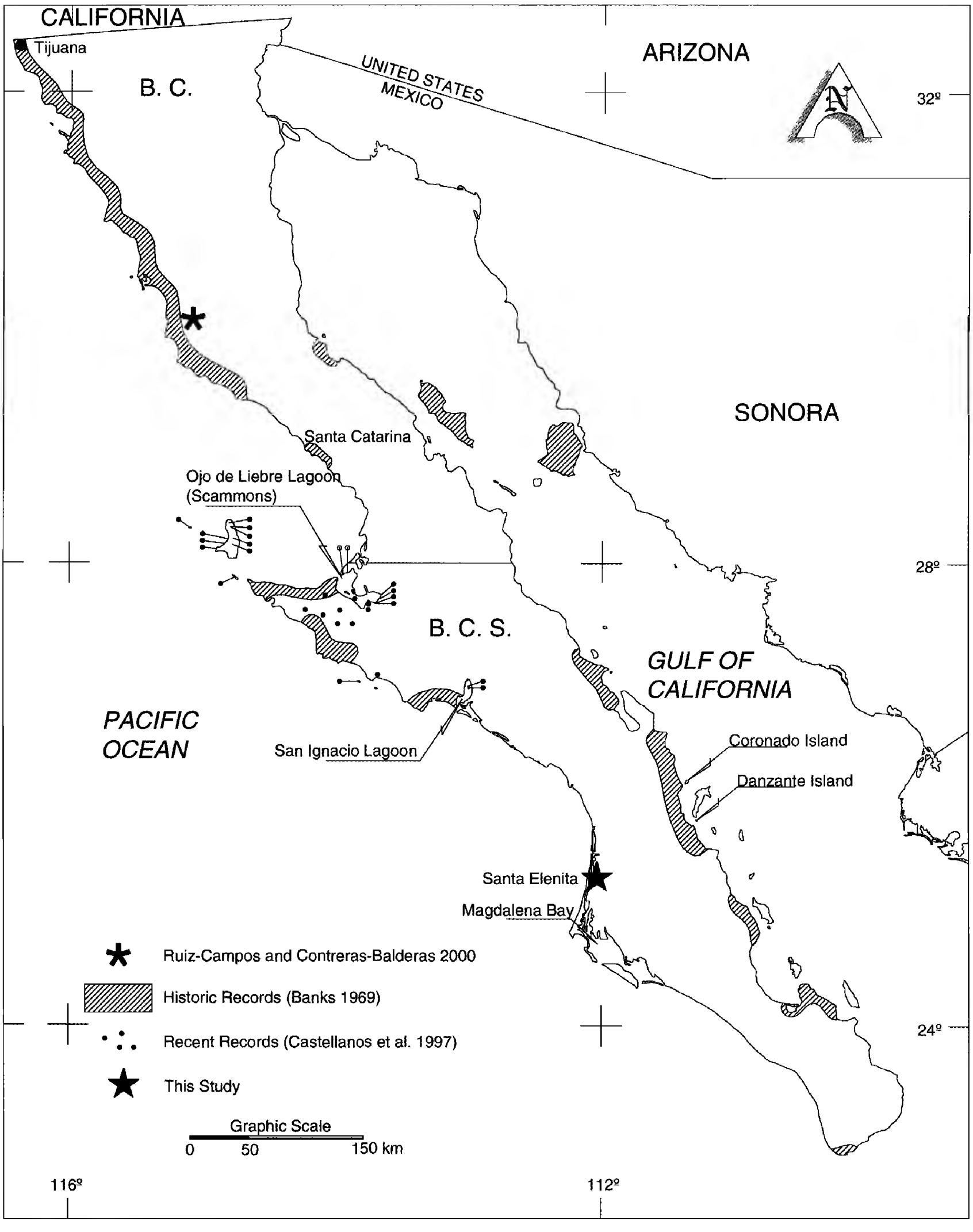

Figure 1. Current and historical distribution of nesting territories of Peregrine Falcon in Baja California Sur, México

Figure 2. View of Santa Elenita mangrove estuary in Bahía Magdalena, B. C. S., México, and Peregrine Falcon (a) and Osprey (b) nesting sites.

m of the nest. We observed 16 interactions (0.79 events/hr), including eight with Magnificent Frigatebirds (*Fregata magnificens*), four with Ospreys, three with Common Ravens (*Corvus corax*), and one with a gull (*Larus* sp.). Peregrines made territorial attacks or cacking-calls in all interactions.

Breeding dates and the number of nestlings and fledglings reared by this pair were similar to those reported for other areas on the western coast of the peninsula (Porter et al. 1988, Castellanos et al. 1997). Previous reports (Castellanos et al. 1997) also show the number of nestlings and fledglings produced by pairs on the western side of the peninsula are greater than those along the Gulf of California. Reasons for this higher productivity are unknown. However, it may be an indication of a healthier environment; the west coast of the peninsula is a relatively low organochlorine pesticide-polluted area in North America (total DDT concentration levels on Osprey eggs between 5–311 ppm lipid basis; Spitzer et al. 1977).

The southwest coastline of the peninsula is quite different from the northwestern coast. The terrain is relatively flat and covered by sparse desert shrubs. The lack of suitable natural nesting sites such as sea cliffs, ledges on vegetated slopes, and high trees precludes establishment of breeding pairs in spite of a variety and abundance of shore birds and waterfowl. The Santa Elenita towers provided an opportunity for this nest-site-limited species to breed.

Future conservation of Peregrine Falcon south of the U.S.A. should be focused on protection of the natural landscape (Temple 1988). This strategy is on course in México. In 1972, the islands in the Gulf of California were protected as wildlife refuges. In 1988, the entire central west coast, including the small islands and Lagunas Ojo de Liebre and San Ignacio, was declared a biosphere reserve. These refuges preserve prime Peregrine Falcon breeding range with low human impact.

NUEVO REGISTRO DE ANIDACION Y OBSERVACIONES DE HALCONES PEREGRINES REPRODUCTORES EN BAJA CALIFORNIA SUR, MÉXICO

RESUMEN.—Encontramos una pareja reproductiva y dos adultos no reproductivos de *Falco peregrinus* en Bahía Magdalena, en la costa suroeste de Baja California Sur, México. El nido estaba localizado en una torre metálica en un puerto abandonado. La anidación fue exitosa y tres volantones abandonaron el nido. Nuestro hallazgo amplía el rango de anidación conocido en la península.

[Traducción de los autores]

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LETTERS

J. Raptor Res. 39(4):476–477

A PREVIOUSLY UNDESCRIBED VOCALIZATION OF THE NORTHERN PYGMY-OWL

Vocalizations of the Northern Pygmy-Owl (*Glaucidium gnoma*) were summarized by Holt and Peterson (2000, The Birds of North America, No. 494, Philadelphia, PA U.S.A.). The known repertoire of adult vocalizations consists of: the "toot song," which functions as the primary song for both sexes; the "trill call," which often accompanies the "toot song" and for which a function is not yet known; and the "chitter call," which accompanies prey deliveries and certain interactions between breeding adults. Also, a "chatter call" used during copulation was described by Righter (1995, *Colo. Field Ornithol. J.* 29:21–23). Here, I describe a previously undocumented vocalization of the Northern Pygmy-Owl.

As part of an ongoing study of Northern Pygmy-Owls in northern Montana, I have radio-tracked 11 (between one and five annually) owls since 2001. Owls were tracked before, during, and after the nesting season. Periods of behavioral observation were intermittently conducted in durations ranging from ca. 15 min to 4 hr. On three occasions, I observed a "*weet*" vocalization, which somewhat resembled a single note of the "toot song," but was slightly prolonged with a "screeching" quality and a slight upward bend in pitch. In abruptness and duration, this call superficially resembled the sudden, high-pitched alarm calls of some Spermophilus ground squirrels, but was deeper in pitch and slightly more hollow sounding. The most similar avian call that I am familiar with is the *ksew* call of the Northern Saw-whet Owl (*Aegolius acadicus*; Cannings 1993, The Birds of North America, No. 42, Washington DC, U.S.A.). However, that call is lower in pitch, descending, and usually repeated in a brief series, while the *weet* call I describe here was a single ascending note. Proudfoot and Johnson (2000:7, The Birds of North America, No. 498, Philadelphia, PA U.S.A.) describe an alarm call of the congeneric Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) as "short and sharp with upward inflection, *pee weet*, repeated at irregular intervals." Although I am unfamiliar with the Ferruginous Pygmy-Owl alarm call, this describes accurately the Northern Pygmy-Owl vocalization I observed, except that the former consists of two syllables and the latter only one.

On 21 July 2003, while observing a Northern Pygmy-Owl family group, I first observed an adult male give the "*weet*" call. A few seconds later an adult Northern Goshawk (*Accipiter gentilis*) flew within 50 m of the family group and disappeared. On 1 July 2004 at 0936 H, while observing a family group with recently fledged young, I observed both the adult male and adult female give the *weet* call. A Northern Goshawk appeared and perched briefly in the same stand as the family group a few seconds after the calls. In that instance, the male gave the call first and was followed by the female. The female then repeated the call one more time just before the goshawk entered the stand The female's call was slightly higher pitched to a degree approximately equivalent to the difference in pitch of the "toot song" between the sexes (Holt and Peterson 2000, pers. obs.). At 1003 H, during the same observation period on 1 July 2004, a Northern Goshawk flew through an opening adjacent to the stand in which the family group (same stand and same family group as the previous observation) was located. Both adults gave *weet* calls, and both repeated the calls after 5–10 sec. In that instance, several of the seven fledglings had been calling actively before the adults gave the *weet* calls. The fledglings' calls immediately ceased after the *weet* calls were given, but resumed less than 30 sec later, at which time the goshawk was no longer visible to me. I am not certain whether any of the Northern Goshawks in these instances were aware of the owls. Twice the goshawks simply flew past, and the one time a goshawk perched nearby, it quickly left the perch when it apparently became aware of my presence. The contexts of these observations suggest that the function of the *weet* call is an alarm call. During a Northern Pygmy-Owl study in Washington, A. Giese (unpubl. data) observed what was likely the call described here, and likewise suspected its function as an alarm call. The call was given several times during a 1.5 hr period by an adult female in the presence of fledged young. The young generally ceased vocalizing after the call was given. Unlike the calls I observed, however, that female vocalized in bouts of 3–4 calls at a time.

Interestingly, I have observed instances in which Northern Pygmy-Owls might have been expected to give alarm calls, but did not give the *weet* call. I observed a domestic dog in close proximity (<5 m) to a group of fledgling and adult owls perched low on branches on two occasions in 2004 and heard no calls. When banding young owls or climbing nest trees to check nests, I have observed adults give short versions of the toot song, trill calls, and display agitated behavior (e.g., rapid tail twitching, perching close to and staring at the human intruder). However, I have not heard the *weet* call I describe here in those situations. On 7 May 2001, I observed a Northern Goshawk pass

within 5 m of a solitary nonbreeding Northern Pygmy-Owl perched with prey. The owl watched the goshawk intently, but gave no call.

If the *weet* call was indeed an alarm call, these observations suggested that it may be associated specifically with avian predators, as the mammalian (dog and human) observations I described did not elicit the call. Additionally, the observation of the solitary owl failing to give a *weet* call suggests that it may be used only when fledglings or mated owls are present. Alarm calls are well documented for many strigids (e.g., Ferruginous Pygmy-Owl, Proudfoot and Johnson 2000; Great Gray Owl, *Strix nebulosa,* Bull and Duncan 1993, The Birds of North America, No. 41, Philadelphia, PA U.S.A.; Long-eared Owl *Asio otus,* Marks et al. 1994, The Birds of North America, No. 133, Philadelphia, PA U.S.A.) and are often given in response to threats to nests and fledged young. However, further study is needed to better understand the causes and contexts of this and other Northern Pygmy-Owl vocalizations.

I am grateful to the many individuals who have volunteered their time to conduct fieldwork during this study. Private contributions have helped make this ongoing study possible. The Conservation Research Foundation, Marmot's Edge Conservation, the Owl Research Institute, and the Rocky Mountain Ranger District of the Lewis and Clark National Forest have generously provided assistance with various parts of this project as well. A. Giese and G Proudfoot provided criticism and field observations that improved the manuscript.—**Graham G. Frye (e-mail address: ggfrye@rmf-inh.org) Rocky Mountain Front Institute of Natural History, P.O. Box 186, Choteau, MT 59422 U.S.A.**

Received 12 August 2004; accepted 18 June 2005
Associate Editor: Ian G. Warkentin

BOOK REVIEW

J. Raptor Res. 39(4):478–479

Hawks and Owls of Eastern North America. By Donald S. Heintzelman. 2004. Rutgers University Press, Piscataway, NJ U.S.A. viii + 203 pp., 5 color plates, numerous black and white photos. ISBN 0-8135-3350-3. Cloth, $29.95.—Donald Heintzelman's original purpose with this volume was to prepare a second edition of his earlier work, Hawks and Owls of North America (1979, Universe Books, New York, NY U.S.A.). However, this book restricts coverage to the raptors of eastern North America, which is loosely defined as birds east of the Mississippi River, except for parts of Minnesota and Ontario. The volume begins with six chapters dealing with general topics: Introduction to Raptor Ecology, Hawk Migrations, Owl Migrations and Invasions, Raptor Conservation, Citizen Scientists, and Recreational Raptor Watching; and follows with eight chapters of raptor species accounts mostly in taxonomic order, beginning with Ospreys (*Pandion halieatus*) and ending with Northern Saw-whet Owls (*Aegolius acadicus*). For the most part, the book is nicely illustrated with a selection of outstanding black and white photos.

I found the introductory chapter, "An Introduction to Raptor Ecology," to be well out of date. In the preface, Heintzelman acknowledges that this chapter includes substantial portions of the text from his 1979 contribution. Upon reading this chapter, it is clear that many of the ideas expressed reflect antiquated ecological opinions and speculations of the 1960s and early 1970s. Statements such as, Northern Goshawks (*Accipiter gentilis*) are beneficial to Ruffed Grouse (*Bonasa umbellus*) populations, that raptors control numbers of prolific rodents, and raptors maintain a delicate and effective ecological balance between predator and prey, without presentation of supporting data or sources are made freely throughout this short chapter.

The subsequent introductory chapters, although brief, provided easier reading and were based on more-current information. The chapter on Raptor Conservation reported a series of interesting and relatively-recent anecdotes. However, when discussing habitat degradation and loss, Heintzelman emphasizes the "ambitious, long-term restoration" effort of the Lehigh Gap Restoration Project, which has a goal of restoring 750 acres of woodland on the Kittatinny Ridge in Pennsylvania. From a raptor perspective, restoring ca. 3 km^2 of deciduous woodland habitat is extremely trivial and will likely have little impact on the population of any raptor. I am familiar with several other governmental and private (e.g., the Nature Conservancy) land acquisition/habitat restoration programs that involve many thousands of hectares that are much more likely to have substantial population impacts on several species of raptors. I would have liked to have seen Heintzelman discuss some of these major habitat restoration efforts, perhaps in addition to smaller isolated projects that he has personally spear-headed.

Some minor distractions for me were the provision of selective contact information. Although most major raptor conservation organizations were mentioned in the volume, contact information was only provided for a select few. Perhaps, in this day and age in which an interested person can quickly obtain contact information by googling the name of an organization, this is not necessary. But, why provide detailed contact information (postal address, e-mail address, phone numbers) for a few selected organizations, and no information for others?

Probably more bothersome for a professional ornithologist using this volume is the style of not citing references in the text. Although most chapters are reasonably-well researched and supported with references, albeit selectively, all references are included in the back of the volume listed alphabetically by chapter. Thus, when you encounter a statement in a given chapter, identifying the responsible source is exceedingly difficult. Also, the supporting sources represent a very mixed bag in which some very current and important studies are mentioned and cited, while most of the references are from state journals and generally represent novel anecdotes.

Although I found most of the material presented in the species accounts to be accurate, I ran across several reported "facts" that in my opinion,

amounted to unsubstantiated and rather far-reaching speculations. Some examples include a statement that evidence supports that mated pairs of Rough-legged Hawks (*Buteo lagopus*) perch together on their wintering grounds; statements or implications that several species of raptors covered in the volume relatively commonly exhibit cooperative hunting; that Gyrfalcons (*Falco rusticolus*) are faster than Peregrine Falcons (*F. peregrinus*); and that the food habits of several small raptors include large birds and mammals, such as waterfowl (Anatidae), grouse (Tetraoninae), raccoons (*Procyon lotor*), woodchucks (*Marmota monax*), and hares (*Lepus* spp.). The latter is true, although most of these relatively large preys are taken rarely and most likely involve very-young animals or carrion. This clarification is generally not included and the way accounts are worded, the text implies that such large prey are just as commonly taken as small rodents. The layout of the book, with citations lumped by chapter, makes tracking down the specific sources for these far-reaching speculations and implications nearly impossible. As a scientist, I found this aggravating.

Besides my mild complaints indicated above, the species accounts were concise and informative. Within each account, the known longevity record for each species is reported, which I found to represent an interesting anecdote. Each account is illustrated with one or more high-quality black and white photos of the featured species. For the most part, the volume is well-edited and I found only a few typographical errors scattered about the text.

Generally, I feel this volume would make an excellent primer for an amateur or beginning student interested in North American birds of prey. The presentation of the basic natural history and promotion of recreational hawk watching to the beginning student of birds is clearly the intended target of this publication. I would recommend this volume to a high school or underclass university student that expresses an interest in raptors. Also, this book would make an excellent resource for local public libraries throughout eastern North America.—**James C. Bednarz, Department of Biological Sciences, Arkansas State University, P.O. Box 599, Jonesboro, AR 72467 U.S.A.**

J Raptor Res. 39(4):480–483

JOURNAL OF RAPTOR RESEARCH
INFORMATION FOR CONTRIBUTORS

The *Journal of Raptor Research* (JRR) publishes original research reports and review articles about the biology of diurnal and nocturnal birds of prey. All submissions must be in English, but contributions from anywhere in the world are welcome. Manuscripts are considered with the understanding that they have not been published, submitted or accepted for publication elsewhere. Manuscripts are subjected to peer review for evaluation of their significance and soundness, and edited to improve communication between authors and readers. Decisions of the editor are final.

Material is published as feature articles, short communications (usually not longer than four printed pages), and letters (see recent issue of the JRR for examples). Submissions that adhere closely to the JRR's format greatly enhance the efficiency and cost of the editorial and publishing processes. Author's efforts in this regard are deeply appreciated by the editorial staff.

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JOURNAL OF RAPTOR RESEARCH

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(*check items and submit with manuscript*)

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J Raptor Res. 39(4):484–491

Index to Volume 39

Prepared By Autumn A. Farless

The index includes references to general topics, common names, keywords, and authors. Reference is also made to book reviews and letters. Taxa other than raptors are included where referenced by authors.

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THE JOURNAL OF RAPTOR RESEARCH

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NUMBER 4

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Raptor Research Foundation, Inc.

Grants and Awards

For details and additional information visit:
http://biology.boisestate.edu/raptor/grants%20and%20awards.htm

Awards for Recognition of Significant Contributions

The **Tom Cade Award** is a non-monetary award that recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. The **Fran and Frederick Hamerstrom Award** is a non-monetary award that recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Submit nominations for either award to: Dr. Clint Boal, Texas Cooperative Fish and Wildlife Research Unit, BRD/USGS, Texas Tech University, 15th Street & Boston, Ag Science Bldg., Room 218, Lubbock TX 79409-2120 U.S.A.; phone: 806-742-2851; e-mail: cboal@ttu.edu

Awards for Student Recognition and Travel Assistance

The **James R. Koplin Travel Award** is given to a student who is the senior author and presenter of a paper or poster to be presented at the RRF meeting for which travel funds are requested. Application deadline: due date for meeting abstract. Contact: Dr. Patricia A. Hall, 5937 E. Abbey Rd., Flagstaff, AZ 86004; phone: 520-526-6222 U.S.A.; e-mail: pah@spruce.for.nau.edu

The **William C. Anderson Memorial Award** is given to both the best student oral and poster presentation at the annual RRF meeting. The paper cannot be part of an organized symposium to be considered. Application deadline: due date for meeting abstract, no special application is needed. Contact: Rick Gerhardt, Sage Science, 319 SE Woodside Ct., Madras, OR 97741 U.S.A; phone: 541-475-4330; email: rgerhardt@madras.net

Grants

Application deadline for all grants is February 15 of each year; selections will be made by April 15.

The **Dean Amadon Grant** for up to $1000 is designed to assist persons working in the area of systematics (taxonomy) and distribution of raptors. The **Stephen R. Tully Memorial Grant** for up to $500 is given to support research and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Agency proposals are not accepted. Contact for both grants: Dr. Carole Griffiths, 251 Martling Ave., Tarrytown, NY 10591 U.S.A.; phone: 914-631-2911; e-mail: cgriff@liu.edu

The **Leslie Brown Memorial Grant** for up to $1400 is given to support research and/or the dissemination of information on African raptors. Contact: Dr. Jeffrey L. Lincer, 9251 Golondrina Drive, La Mesa, CA 91941, U.S.A.; e-mail: JeffLincer@tns.net