THE
JOURNAL
OF
RAPTOR RESEARCH

CONTENTS

****

A RAPTOR SURVEY IN THE BRAZILIAN ATLANTIC RAINFOREST

SANTI MAÑOSA AND VITTORIO PEDROCCHI

Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona,
Avinguda Diagonal 645,
08028 Barcelona, Catalonia, Spain

ABSTRACT.—We give the results of a raptor survey conducted in August 1994 in the Porque Estadual Intervales, a well preserved area of Atlantic rainforest in southeastern Brazil. Point counts were more effective than transect counts. Ten species of raptors were detected. The presence of a pristine population of Mantled Hawks (*Leucopternis polionota*), Black Hawk-eagles (*Spizaetus tyrannus*) and Ornate Hawk-eagles (*S. ornatus*), gives to the area a remarkable interest for the conservation of birds of prey in Brazil. We also observed Turkey Vultures (*Cathartes aura*), Black Vultures (*Coragyps atratus*, Tiny Hawks (*Accipiter superciliosus*), Roadside Hawks (*Buteo magnirostris*), Short-tailed Hawks (*Buteo brachyurus*), Yellow-headed Caracaras (*Milvago chimachima*), Collared Forest-falcon (*Micrastur semitorquatus*) and possibly Grey-headed Kites (*Leptodon cayanensis*).

KEY WORDS: *Atlantic rainforest; birds of prey; Brazil.*

Sequimiento de Rapaces en la Selva Atlántica de Brasil

RESUMEN.—Se dan los resultados de un seguimiento de rapaces efectuado en agosto de 1994 en el Parque Estadual Intervales, una zona bien preservada de selva atlántica del sureste de Brasil. Los censos puntuales se mostraron más eficaces que los censos lineales. Se detectaron 10 especies seguras de rapaces. En particular, destaca la presencia de una población saludable de busardo blanquinegro *Leucopternis polionota*, águila-azor negra *Spizaetus tyrannus* y águila-azor galana *S. ornatus*, lo cual dota a este área de un notable interés para la conservación de aves de presa en Brasil. Se observaron también el aura gallipavo *Cathartes aura*, el zopilote negro *Coragyps atratus*, el gavilancito americano *Accipiter superciliosus*, el busardo caminero *Buteo magnirostris*, el busardo colicorto *Buteo brachyurus*, el caracara chimachima *Milvago chimachima*, el halcón-montés collarejo *Micrastur semitorquatus*, y posiblemente el milano cabecigrís *Leptodon cayanensis*.

[Traducción Autores]

The Brazilian Atlantic rainforest is considered among the areas of highest avian endemism in South America (Cracraft 1985). However, less than 8% of the original forest is left, and the remaining forest patches are small and isolated from one another (Fonseca 1985, Alburquerque 1995, Fundaçao SOS Mata Atlântica 1995). Birds of prey can be good ecological indicators of the conservation value of these patches, because some species require large amounts of well-preserved habitat to survive, while others increase in human-altered habitats. Although some species are threatened by habitat fragmentation and destruction (Thiollay 1985), difficulties faced when studying rainforest raptors (Thiollay 1989) limit the information needed to design good conservation strategies. Several monitoring and research programs are being conducted in the Neotropical region to fill this gap (Thiollay 1989, Vannini 1989, Whitacre and Thorstrom 1992), but the Atlantic rainforest has received little attention. In this paper, we present the results of a pilot survey conducted in an Atlantic rainforest area of southeastern Brazil from 1–12 August
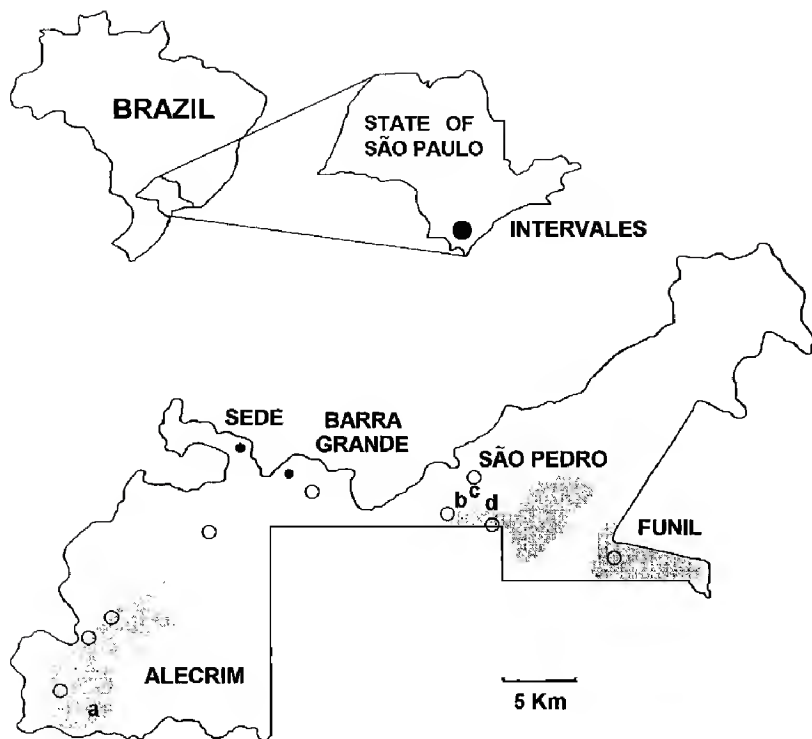
Figure 1.   Map of the Parque Estadual Intervales, showing the location of the areas covered by transect counts (shaded), the location of the point counts (a, b, c, d) and the possible location of Mantled Hawk breeding territories (O). The location of the Parque Estadual Intervales Information Center (Sede) and Barra Grande station are also shown.

1994 to provide baseline data for future monitoring and conservation programs.

STUDY AREA AND METHODS

The survey was conducted in the Parque Estadual Intervales, a natural reserve comprised of 383 km² of continuous mature and secondary Atlantic rainforest (Fig. 1). The reserve is situated at the southeastern portion of the State of São Paulo, 80 km from the coast (24°20'S, 48°15'W), and is part of a mountain range about 900 km long known as Serra do Mar. The Parque Estadual Intervales, together with neighboring protected and private land (Parque Estadual Turístico do Alto Ribeira-Petar, Estação Ecólogica de Xitué and Parque Estadual de Carlos Botelho), constitutes a 1168 km² area of well-preserved habitat. The area receives as much as 2500 mm of annual rainfall, concentrated mainly between November–March. The reserve is not hunted, and the palmito Euterpe edulis, one of the main components of the forest, is no longer being exploited. The forest covers all the reserve, except small openings around hamlets and guard stations. Mature or nearly mature forest communities cover 40% of the reserve, 40% is covered by old secondary forest, and 20% by young secondary forest found mainly along the roads and around inhabited areas (J.C. Guix pers. comm.). Areas around the Parque Estadual Intervales are agricultural land and grassland.

Three areas within the reserve were surveyed (Fig. 1). The Alecrim area ranging from 150–600 m elevation consisted of old secondary forest and included a small hamlet surrounded by pastures and crops. The São Pedro area (350–860 m elevation) was covered by mature and

old secondary forest. The Funil area (40–150 m elevation) was covered by old secondary forest on the hill slopes and young secondary forest on the lowest areas near to agricultural areas. For a detailed account of plant communities found in Intervales see Guix et al. (1992).

Raptor counts were conducted using transect and point count methods. No playback techniques (Whitacre and Thorstrom 1992) were used. We conducted 68 transect surveys on foot with the aim of recording monkeys, toucans, guans and birds of prey. Although transects were not specifically designed to count raptors, they allowed us to obtain an index of detections/km for several species. Transect lengths ranged from 1–22 km, but most were 2–3 km long ($\bar{x}$ = 4.3 km, SD = 4.0). Except the longest transect that required a full day to complete, most surveys were conducted just after dawn or before dusk and lasted for 1.5–2 hr. The spatial arrangement of the transects was determined by the distribution of foot paths laid out by the guard staff to survey the reserve, but we felt it was representative of all the area. Transect counts were conducted by teams of 2–6 people. The weather was variable between counts, from clear to slightly rainy.

Point counts followed the method described by Whitacre et al. (1992). Counts were conducted in clear and calm weather by two observers from elevated points of the landscape, with a view angle of 60°–145°, and an unbounded view radius of at least 1 km. We selected points along the main tracks, offering good visibility of different rainforest areas. One count (a) was conducted from a midslope road in the Alecrim area and the other three (b, c, d) were conducted in the São Pedro area. Counts in the São Pedro area were done from the top of emergent trees that were about 2 km apart and gave unobstructed views of three different valleys. Counts were initiated 2.5–4.5 hr after dawn and lasted for 3–4 hr. The counting period was divided into 5 min intervals. For every interval, all raptors seen were recorded. Using this method, we obtained a list of species, the minimum number of groups and individuals observed and the proportion of 5-min intervals in which a species was recorded.

RESULTS AND DISCUSSION

On 68 transects, we walked a total of 290 km and made observations for 121 hr. We recorded birds of prey on 15 occasions (0.12 contacts/hr) for a total of 26 individuals of five different species. Raptors were observed on only 12 (17%) of the transects (Table 1). Mantled Hawks (Leucopternis polionota) were observed in the Alecrim area along the Pilões-Formoso river, between Alecrim and Sede. One pair was observed 6 km from Alecrim and another three hawks were observed simultaneously 8 km further along the river. In both cases, the birds were heard calling and were observed perching in small forested areas. We concluded that at least three or four pairs of Mantled Hawks inhabited the 14 km of the Pilões-Formoso river valley that we surveyed (Fig. 1).

Table 1. Summary of the results of transect counts in Brazilian Atlantic rainforest. Each figure corresponds to the number of individuals in one group. Numbers in brackets represent numbers of individuals counted on the same transect.

	ALECRIM	SÃO PEDRO	FUNIL
# of transects	31	27	10
Total length (km)	121	137	32
Habitat type	Old[a]	Mature[b]	Young[c]
Leucopternis polionota	(2,1)(1)(2)(1,1)	—	(1)
Buteo brachyurus	—	(1)	—
Buteo magnirostris	(1)	—	—
Cathartes aura	(1)(1)(1)	—	—
Coragyps atratus	(7)(2,3)	—	—

[a] Old secondary forest.
[b] Mature or nearly mature forest.
[c] Young secondary forest.

We conducted four point counts totalling 14.5 hr of observation and 174 5-min census intervals. Five raptor observations, involving 19 individuals of four raptor species (0.34 contacts/hr), occurred during three of the point counts. Of the 174 5-min census intervals, Black Vultures (*Coragyps atratus*) were seen during seven (4%), Mantled Hawks during 28 (16%), Tiny Hawks (*Accipiter superciliosus*) during one (0.6%) and Ornate Hawk-eagles (*Spizaetus ornatus*) during one (0.6%). At point count b, a pair of Mantled Hawks was recorded flying and perching in a small area of the forest for more than half the observation period and a single Mantled Hawk was observed flying over the forest at point count c (Table 2, Fig. 1).

Between counts, we also recorded a Black Hawk-eagle (*Spizaetus tyrannus*) flying over the São Pedro region, and a Collared Forest-falcon (*Micrastur semitorquatus*) and a possible Gray-headed Kite (*Leptodon cayanensis*) in the Funil area. Yellow-headed Caracaras (*Milvago chimachima*) were frequently seen in the Sede area in open habitats within the boundary of the reserve. One Mantled Hawk was recorded in the Barra Grande area near Sede and a second was seen next to the São Pedro station (Fig. 1).

No raptors were observed during a large proportion of the transect counts and, overall, they yielded fewer observations per unit time than did point counts. Although foot surveys detected some

Table 2. Summary of the results of the four raptor point counts, totalling 14.5 hr (174 5-min intervals) conducted in Brazilian Atlantic rainforest. For each species and count, the proportion of time intervals in which the species was seen, and the number of groups and individuals (groups, individuals) observed, are given. Habitat types are the same as in Table 1.

	POINT A	POINT B	POINT C	POINT D
Area	Alecrim	S. Pedro	S. Pedro	S. Pedro
Elevation	455 m	615 m	615 m	500 m
Date	2 Aug	9 Aug	9 Aug	10 Aug
Solar time (H)	0915–1300	0930–1330	1030–1330	0900–1245
Type	Road	Tree	Tree	Tree
Habitat type	Old	Mature	Mature	Mature
Duration	225 min	240 min	180 min	225 min
# intervals	45	48	36	45
Coragyps atratus	13%(2,9)	2%(1,4)	—	—
Leucopternis polionota	—	56%(1,2)	3%(1,1)	—
Accipiter superciliosus	—	—	3%(1,2)	—
Spizaetus ornatus	—	—	3%(1,1)	—

species not recorded on point counts, these would have also probably been detected if more point counts had been conducted. Except in the Alecrim area, where the transect followed a road with good views, the foot surveys were inside the forest where viewing raptors proved difficult due to dense vegetation. In fact, most species found during the transect surveys were not typical forest raptors (*Buteo*, *Cathartes*, *Coragyps*), and were seen above the canopy or in openings next to the road or hamlets. Although an extra amount of time and effort was needed to find good census trees and to climb them, the point count method allowed us to standardize the counts. However, secretive forest-dwelling raptors also escaped detection in our point surveys, probably because no playback techniques were used.

Of the species recorded in Intervales, records of Mantled Hawks were most important due to the fact that there is very little information on this Atlantic rainforest endemism. Its breeding range extends along the Atlantic coast of Brazil from Bahia to eastern Uruguay and Paraguay (del Hoyo et al. 1994). Mountain habitats upon which this species relies have quickly disappeared because of deforestation. For this reason, the Mantled Hawk, which was listed as a species of unknown status (Thiollay 1985, IUCN 1990), is now listed as an endangered (Thiollay 1994) or near-threatened (Collar et al. 1992, del Hoyo et al. 1994) species. All Mantled Hawks we observed were in adult plumage and their calling behavior suggested that the second half of the winter or dry season corresponded to the early portion of its nesting season in this area. This species was also reported in four out of the seven São Paulo State Atlantic rainforest areas visited by Willis & Oniki (1981), in the Serra do Tabuleiro on Santa Catarina State (Alburquerque 1995), and in different areas of disturbed and undisturbed habitats in Rio Grande do Sul, where it is reported as rare (Alburquerque 1986).

The Black Hawk-eagle and Ornate Hawk-eagle are typical large rainforest raptors. The Ornate Hawk-eagle has a higher preference for mature forests than the Black Hawk-eagle. Both species were found in the São Pedro area, which is the most remote of the sites we surveyed and the one with the least amount of disturbed forest habitats.

The Tiny Hawk and the Collared Forest-falcon were new records for the Intervales area and for the Atlantic mountain rainforest of the São Paolo State (Guix et al. 1992, Willis and Oniki 1981). If we include the Barred Forest-falcon (*Micrastur ruficollis*) which was recorded during previous surveys (Guix et al. 1992), 12 species of raptors have now been reported in the Parque Estadual Intervales. A total of only 15 species was found during an extensive ornithological survey of seven Atlantic rainforest areas of São Paulo State (Willis and Oniki 1981). Since no more than 20 diurnal raptor species are possible in the region (del Hoyo et al. 1994), we concluded that the Parque Estadual Intervales still contains a raptor community representative of the Atlantic rainforest and the area deserves protection from further fragmentation and destruction.

LITERATURE CITED

ALBURQUERQUE, J.L.B. 1986. Conservation and status of raptors in southern Brazil. *Birds of Prey Bull.* 3:88–94.
———. 1995. Observations of rare raptors in southern Atlantic rainforest of Brazil. *J. Field Ornithol.* 66:363–369.
COLLAR, N.J., L.P. GONZAGA, N. KRABBLE, A. MADROÑO-NIETO, L.G. NARANJO, T.A. PARKER AND D.C. WEGE. 1992. Threatened birds of the Americas. The ICBP/IUCN Red Data Book. ICBP, Cambridge, UK.
CRACRAFT, J. 1985. Historical, biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Pages 49–84 *in* P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely and F.G. Buckley [EDS.], Neotropical ornithology. Ornith. Monog. 36. AOU, Washington, DC U.S.A.
DEL HOYO, J., A. ELLIOT AND J. SARGATAL [EDS.]. 1994. Handbook of the birds of the world, Vol. 2. New World vultures to guineafowl. Lynx Edicions, Barcelona, Spain.
FONSECA, G.A.B. 1985. The Vanishing Brazilian Atlantic Forest. *Biol. Conserv.* 34:17–34.
FUNDAÇAO SOS MATA ATLÂNTICA. 1995. Mata atlântica ameaçada. *Bol. Especial SOS Mata Atlântica.*
GUIX, J.C., A.A.J. TABANEZ, A.N. SILVA, C. LOPEZ, C. MARTINEZ, E. MATHEU, F.L. DE SOUZA, K.R. PISCIOTTA, N. BRADBURY AND W.G. PORTILHO. 1992. Viagem de re-

conhecimento científico a algumas áreas desconheci-
das da Fazenda Intervales, Estado de São Paulo, dur-
ante o período de 04 a 16 outubro de 1991. *Grupo
Estud. Ecol. Ser. Doc.* 4:38–94.

IUCN. 1990. IUCN red list of threatened animals. IUCN,
Gland, Cambridge, UK.

THIOLLAY, J.M. 1985. Falconiforms of tropical rain forest:
a review. Pages 155–165 *in* I. Newton and R.D. Chan-
cellor [EDS.], Conservation studies on raptors, Vol. 5.
ICBP Tech. Publ., Cambridge, UK.

———. 1989. Censusing of diurnal raptors in a primary
rain forest: comparative methods and species detect-
ability. *J. Raptor Res.* 23(3):72–84.

———. 1994. A world review of tropical forest raptors.
Current trends, research objectives and conservation
strategy. Pages 231–239 *in* B.U. Meyburg and R.D.
Chancellor [EDS.], Raptor conservation today. Pica
Press, Berlin, Germany.

VANNINI, J.P. 1989. Neotropical raptors and deforesta-
tion: notes on diurnal raptors at finca El Faro, Quetz-
altenango, Guatemala. *J. Raptor Res.* 23(2):27–38.

WHITACRE, D.F. AND R.K. THORSTROM [EDS.]. 1992. Proy-
ecto Maya: Uso de aves rapaces y otra fauna como
indicadores del medio ambiente, para el diseño y ma-
nejo de áreas protegidas y para fortalecer la capacidad
local para la conservación en América Latina. The
Peregrine Fund, Inc., Boise, ID U.S.A.

———, L.E. JONES AND J. SUTTER. 1992. Censos de aves
rapaces y de otras aves en el bosque tropical: mejoras
hechas a la metodología. Pages 43–56 *in* D.F. Whitacre
and R.K. Thorstrom [EDS.], Proyecto Maya: Uso de
aves rapaces y otra fauna como indicadores del medio
ambiente, para el diseño y manejo de áreas protegidas
y para fortalecer la capacidad local para la conserva-
ción en América Latina. The Peregrine Fund, Inc.,
Boise, ID U.S.A.

WILLIS, E.O. AND Y. ONIKI. 1981. Levantamento preli-
minar de aves en treze áreas do estado de São Paulo.
Rev. Brasil. Biol. 41:121–135.

BREEDING DENSITY AND LANDSCAPE-LEVEL HABITAT SELECTION OF COMMON BUZZARDS (*BUTEO BUTEO*) IN A MOUNTAIN AREA (ABRUZZO APENNINES, ITALY)

VINCENZO PENTERIANI

Laboratoire d'Ecologie, Université de Bourgogne, Batiment "Mirande," B.P. 138, 21004 Dijon Cédex, France and *Stazione Romana Osservazione e Protezione Uccelli (S.R.O.P.U.), c/o Oasi Naturale W.W.F. "Bosco di Palo", 00055 Ladispoli, Rome, Italy*

BRUNO FAIVRE

Laboratoire d'Ecologie, Université de Bourgogne, Batiment "Mirande," B.P. 138, 21004 Dijon Cédex, France

ABSTRACT.—The breeding density and landscape-level habitat selection of Common Buzzards (*Buteo buteo*) was studied from 1989–93 in a mountain area of Abruzzo Apennines (central Italy). Analysis of landscape features was based on circular plots (2.5 km diameter) centered on occupied nest trees. A total of 32 Common Buzzard nesting territories were identified within a 387 km² area (8.3 pairs/100 km², mean nearest-neighbor distance 2.5 km). The average altitude of the nest sites was 1399 m above sea level and 73.1% were oriented NE. Stepwise discriminant function analysis showed significant differences between nesting ($N = 17$) and control sites ($N = 15$) based on four landscape variables: relief index, distance from forest edge, distance from paved road and distance from valley bottom. Results suggest that Common Buzzards select nesting areas in the eastern portion of forests which are distant from roads but close to valley bottoms, in rugged areas of irregular morphology.

KEY WORDS: *Common Buzzard; habitat selection; landscape-level; breeding density;* Buteo buteo.

Densidad de cría y selección niveles de paisaje hábitat en *Buteo buteo*

RESUMEN.—La delicadeza de cría y nivel del paisaje, selección del hábitat del *Buteo buteo* fue estudiado de 1989–93 en un área de montaña de Abruzzo Apennines (central Italy). Análisis del elementos del paisaje estuvo basado en lugares círculos (2.5 km diámetro) centrado en nidos de árbol ocupados. Un total de 32 *B. buteo* territorios de nido fueron identificados dentro de 387 km2 área, (8.3 pares/100 km², media cerca-vecino distancia 2.5 km). El altitud regular de los nidos fue 1399 m arriba del mar y 73.1% fueron orientados NE. Una función discriminante de pasos enseño un análisis con diferencias significas entre nidos ($N = 17$) y sitios de control ($N = 15$) basados en cuatro paisajes variados: relevo indicie, distancia de la orilla del bosque, distancia del camino pavimentado y distancia del fondo del valle. Resultados Sugieren que el *B. buteo* selecciona áreas de nidos en lugares este en el bosque donde están muy lejos de caminos pero mas cerca al fondo del valle, en áreas toscas de morfología irregular.

[Traducción de Raúl De La Garza, Jr.]

Nest-site preferences have been described for the Common Buzzard (*Buteo buteo*) (Tubbs 1967, Glutz von Blotzheim et al. 1971, Tubbs 1974, Arce Velasco 1987, Taylor et al. 1988), but few studies have attempted to quantitatively determine the factors involved in nest-site selection at a landscape level (Newton et al. 1982, Jedrzejewski et al. 1988, Kostrzewa 1989, Hubert 1993, Hohmann 1994, Graham et al. 1995, Cerasoli and Penteriani 1996). All of these studies have analyzed nest-site selection at a microhabitat level (nest-tree characteristics and stand structure) without considering the pos-

sible effects of landscape structure. In this paper, we present a landscape-level analysis of Common Buzzard nest sites, which was conducted to identify the landscape determinants of nest-site selection.

METHODS

A population of Common Buzzards was studied from 1989–93 in a mountain area of central Italy (Abruzzi Apennines). The study covered a 387 km² area of beech (*Fagus sylvatica*) forest (typical of the Apennine massifs of the Abruzzi region) that covers the National Park of Abruzzi and the Sirente mountains. Elevation of the area ranges from 1000–2340 m. The landscape has a distinct mosaic structure with large woodland areas and reforest-

ed tracts of *Pinus nigra*, cropland, pastures and fallow land from 1000–1800 m elevation.

Occupied nests were located by systematic foot searches of the area prior to leafout. We also used playbacks of recorded Common Buzzard calls during the months of March–April (prelaying period) and June–July (nestling and fledgling periods) (Cerasoli & Penteriani 1992). Areas where a pair of Common Buzzards was observed during the breeding period, but no nest was found, were classified as possible nesting territories (Jedrzejewski et al. 1994). A number of nesting territories were identified by observing adults carrying nesting material, by noting where the displays of males ended with steep dives into the woods (Picozzi and Weir 1974) and from alarm calls of adults and shrill calls of the fledged young.

We used the nearest-neighbor distance method (Newton et al. 1977) to estimate nesting density. Regularity in nest-site spacing was computed with a G-test (Brown & Rothery 1978). Landscape-level analysis of habitat selection only considered those Common Buzzard nest sites where nests had been located. Moreover, all nest sites that changed during the study period due to road building, cutting of forest tracts or changes in farming were excluded from the analysis. Analysis of landscape features was based on circular plots centered on the occupied nest tree. These plots had a diameter equal to the mean distance between neighboring nest sites. Each nest site was characterized using a set of 23 variables: slope exposure, elevation, eight variables describing patch composition of the landscape (percentage of woodlands, pastures, fallow land, fallow land with trees, rocks, crops, crops with trees and built-up patches), three variables for horizontal heterogeneity (number of ecotones, number of different habitats calculated on two orthogonal axes from the plot center and patch interspersion index [habitat changes/plot area] x 100, calculated on two orthogonal axes from the plot center; Baxter and Wolfe 1972), two variables for vertical heterogeneity (maximum difference in elevation and relief index calculated as the sum of the number of contour lines crossed by two orthogonal axes from the plot center; Janes 1985, Litvaitis et al. 1994), and eight variables for distance of nest sites from surrounding landscape components (forest opening, forest edge, valley bottom, built-up area, paved road, pathways, cliffs, permanent water). The number of ecotones, number of habitats and the interspersion relief indexes were sampled on two straight lines oriented N-S and W-E along the plot diameters. Areas of each of the different habitats were determined on the basis of land use maps to a scale of 1:25 000. For each nest site, one control plot was established where we measured the same variables as in nest site plots, except for slope exposure and elevation to estimate landscape selection. Each control plot was centered around a random point located between nest-site plots. To qualify as control plot, the plot had to lie within a forested area. Plots which did not have woodland areas or which had only young plantation areas (where Common Buzzards do not nest) were not included in our analysis (Hubert 1993, Jedrzejewski et al. 1994).

Landscape characteristics of nest-site and control plots were compared by using a stepwise discriminant function analysis (DFA, Sokal and Rohlf 1981). We used the 5% level of significance for including variables in each step

of the analysis. The classification of the described sites, obtained with DFA, was tested with Kappa statistic (Titus and al. 1984). The robustness of the nest-site selection model was tested with a jack-knife procedure. We used a chi-square test to analyze the selection of nest-site slope exposure.

RESULTS

Nest-site Density. A total of 26 known and 6 suspected Common Buzzard nesting territories were identified within the 387 km² study area, for a density of 8.3 pairs/100 km². Mean distance between nesting territories averaged 2.5 km (range = 1.62–4.12 km, SD = 0.54). Within woodland areas, Common Buzzard nesting sites were spaced regularly, as shown by the G-test (G = 0.96).

Landscape-level Habitat Selection. The average altitude of buzzard nest sites was 1399 m above sea level (range 1150–1550 m, SD = 131.87). Analysis of nest exposure (N = 26) showed that 73.1% (N = 19) were oriented NE (χ^2 = 33.69, df = 3, P = 0.001), 3.8% (N = 1) S and SE, and 19.3% (N = 5) SW.

The DFA showed significant differences (P < 0.05) between nesting (N = 17) and control sites (N = 15) based on the four landscape variables relief index, distance from forest edge, distance from paved road and distance from valley bottom (Table 1). We obtained correct classification for 14 of the control sites (93.3%) and 16 of the Common Buzzard nesting sites (94.1%). Conversely, there was one misclassified control site (7%) and one misclassified nesting site (6%). This classification is 87% better than random (Kappa = 0.874, Z = 4.946, P < 0.0001). The jack-knife classification showed the robustness of the model with 88.2% of the nesting sites and 93.3% of the control sites correctly classified.

DISCUSSION

Common Buzzard nesting density decreases from 8.3 pairs/100 km² in the mountain areas of the Apennines, to 19.7 pairs/100 km² in the hills in the piedmont, to 32 pairs/100 km² in woodlands of low-altitude areas (Manzi and Pellegrini 1989, Manzi et al. 1991). Low nesting densities at higher altitudes is likely due to the scarcity of prey as evidenced by the lower density of birds in high mountain areas (36 pairs/10 ha; Bernoni 1995) than in piedmont (59.2 pairs/10 ha; Pandolfi and Taferna 1991) and plain areas (158 pairs/10 ha; Bernoni et al. 1989). The average nearest-neighbor distance of 2.5 km was also relatively high when

Table 1. Sample means and standard deviations of landscape habitat variables measured at control and nest sites of the Common Buzzard. Significant differences determined by Stepwise Discriminant Function Analysis.

	NESTING SITES ($N = 17$)	CONTROL PLOTS ($N = 15$)
Woodland patches (%)	54.5 ± 22.9	40.2 ± 25.3
Pasture patches (%)	24.1 ± 16.1	19.8 ± 11.3
Fallow patches (%)	6.5 ± 5	9.4 ± 5.8
Fallow patches with trees (%)	3.9 ± 4.1	7 ± 7.9
Rocky patches (%)	4.8 ± 6.5	7.1 ± 7.7
Cropland patches (%)	2.7 ± 2.9	3.5 ± 5.6
Cropland patches with trees (%)	3.5 ± 8.5	12.4 ± 14.7
Built-up patches (%)	0 ± 0	0.6 ± 1.3
Number of ecotones	9.8 ± 4.1	16 ± 4.5
Number of habitats	15.5 ± 5.6	20 ± 5.2
Interspersion index	11 ± 2.4	10.5 ± 2.1
Maximum difference in elevation (m)	395.1 ± 165.7	468.3 ± 121.5
Relief index	47.2 ± 12.5	23.2 ± 9.7*
Distance from forest opening (m)	267.6 ± 155.3	179.3 ± 140.9
Distance from nearest forest edge (m)	269.1 ± 239.22	509.3 ± 383.4*
Distance from valley bottom (m)	983.8 ± 487.7	1438.3 ± 845.8*
Distance from built-up area (m)	2827.9 ± 1738.8	2236.7 ± 1049.7
Distance from nearest paved road (m)	1592.6 ± 1224.4	753.3 ± 610.6*
Distance from footpath (m)	613.2 ± 632.1	120 ± 88.2
Distance from cliffs (m)	1376.5 ± 706.8	1128 ± 486.8
Distance from permanent water (m)	1560.3 ± 959.5	885.3 ± 443.2

* $P < 0.05$.

compared with the values of 0.87 and 1.13 km (Newton et al. 1982) 1.04 km (Jedrzejewski et al. 1994) and 1.9 km (Graham et al. 1995) in other areas of Europe.

Our landscape level analysis showed that Common Buzzards did not select habitat at random at a landscape level, as the majority of nest sites (94.1%) and control sites (93.3%) were correctly classified. These results suggest that Common Buzzards select nest sites in the eastern part of forests that are situated on northern slopes. The tendency to use northern slopes may simply be due to the fact that NE facing slopes support the tallest beech trees, but it may also be related to the fact that these slopes provide cooler temperatures and less sunlight, as well as a denser canopy cover that may increase nest protection.

The Common Buzzard is an area-sensitive species that requires forested habitats which are distant from roads but close to valley bottoms in rugged areas (Robbins et al. 1989). The choice of nest sites which are far from paved roads has also been corroborated by Kostrzewa (1989). Nesting close to valley bottoms may be due to the fact that most pasture and crop lands are found there, both of which are favorite hunting grounds for Common Buzzards. Reliance on open areas for foraging may also explain why Common Buzzard nest sites are often near forest edges (Tubbs 1974, Knuwer & Loske 1980, Weir and Picozzi 1983, Goszczynski 1985, Jedrzejewski et al. 1988, Kostrzewa 1989, Hubert 1993, Hohmann 1994, Graham et al. 1995). Open areas may also be needed because they facilitate courtship behavior. Development of higher temperatures and upward thermal air currents over open habitats (Cone 1962, Jedrzejewski et al. 1988, Cerasoli and Penteriani 1996) may enhance courtship flights when pair-bonding takes place in the early part of the nesting season. Nest-site selection near forest edges may also be attributed to ease of access to nests and to a need for an unobstructed view of the surrounding landscape (Roché 1977, Hubert 1993).

tion of Abruzzi National Park provided the logistic support for this work: we thank especially the Director, Franco Tassi and Cinzia Sulli.

Literature Cited

Arce Velasco, L.M. 1987. Biología y ecología del Ratonero Común en la región Astur-Leonesa. Mercantil-Asturias, S.A., Spain.

Baxter, W.L. and C.W. Wolfe. 1972. The interspersion index as a technique for evaluation of Bobwhite Quail habitat. *Proc. Natl. Bobwhite Quail Symp.* 1:158–165.

Bernoni, M., L. Ianniello and P. Plini. 1989. Censimento dell'avifauna nidificante in un bosco deciduo dell'Italia centrale. *Avocetta* 13:25–29.

Bernoni, M. 1995. Il metodo del mappaggio in una faggeta del Parco Nazionale d'Abruzzo. *Avocetta* 19: 131.

Brown, D. and P. Rothery. 1978. Randomness and local regularity of points in a plane. *Biometrica* 65: 115–122.

Cerasoli, M. and V. Penteriani. 1992. Effectiveness of censusing woodland birds of prey by playback. *Avocetta* 16:35–39.

———— and ————. 1996. Nest-site and aerial meeting point selection, nesting density and reproduction of Common Buzzrads. *J. Raptor Res.* 30:130–135.

Cone, C.D., Jr. 1962. Thermal soaring in birds. *Am. Sci.* 50:180–209.

Glutz von Blotzheim, U.N., K.M. Bauer and E. Bezzel. 1971. Handbuch der Vögel Mitteleuropas, Vol. 4. Frankfurt am Main, Germany.

Goszczynski, J. 1985. The effect of structural differentiation of ecological landscape on the predator-prey interactions. Publ. Warsaw Agric. Univ. SGGW-AR, Warsaw (In Polish with English summary).

Graham, I.M., S.M. Redpath and S.J. Thirgood. 1995. The diet and breeding density of Common Buzzards (*Buteo buteo*) in relation to indices of prey abundance. *Bird Study* 42:165–173.

Hohmann, U. 1994. Status specific habitat use in the Common Buzzard (*Buteo buteo*). Pages 359–366 in B.-U. Meyburg and R.D. Chancellor [Eds.], Raptor conservation today. Proc. IV World Conference on Birds of Prey and Owls. WWGBP/The Pica Press, Berlin, Germany.

Hubert, C. 1993. Nest-site habitat selected by Common Buzzard (*Buteo buteo*) in southwestern France. *J. Raptor Res.* 27:102–105.

Janes, S.W. 1985. Habitat selection in raptorial birds. Pages 159–188 in M.L. Cody [Ed.], Habitat selection in birds. Academic Press, London, UK.

Jedrzejewski, W., B. Jedrzejewska and M. Keller. 1988. Nest-site selection by the buzzard (*Buteo buteo* L.) in the extensive forests of eastern Poland. *Biol. Conserv.* 43:145–158.

————, A. Szymura and B. Jedrejewska. 1994. Reproduction and food of the buzzard (*Buteo buteo*) in re-

lation to the abundance of rodents and birds in Bialowieza National Park, Poland. *Ethol. Ecol. & Evol.* 6: 179–190.

Knuwer, H. and K.H. Loske. 1980. Zur frage des habitatanspruche des Mausebussards (*Buteo buteo*) bei der Horstplatzwahl. *Vögelwelt* 101:18–30.

Kostrzewa, A. 1989. Nest habitat separation in three European raptors: *Accipiter gentilis, Buteo buteo* and *Pernis apivorus*—a multivariate analysis. Pages 553–559 in B.-U. Meyburg and R.D. Chancellor [Eds.], Raptors in the modern world. Proc. III World Conference on Birds of Prey and Owls. WWGBP/The Pica Press, Berlin, Germany.

Litvaitis, J.A., K. Titus and E.M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pages 254–274 in T.A. Bookhout [Ed.], Research and management techniques for wildlife and habitats, 5th ed. The Wildlife Society, Bethesda, MD U.S.A.

Manzi, A. and M.R. Pellegrini. 1989. Dati sulla biologia riproduttiva della Poiana (*Buteo buteo*) in un'area della fascia collinare abruzzese. *Avocetta* 13:109–114.

————, M.R. Pellegrini, M.S. Pellegrini, V. Penteriani and F. Pinchera. 1991. Distribuzione e consistenza delle popolazioni di alcune specie di *Accipitriformes* e *Falconiformes* nidificanti nella regione Abruzzo. Pages 363–366 in M. Fasola [Ed.], Atti II Seminario Italiano Censimenti Faunistici dei Vertebrati. Suppl. Ric. Biol. Selvaggina, XVI: 1–820.

Newton, I., M. Marquiss, D.N. Weir and D. Moss. 1977 Spacing of Sparrowhawk nesting territories. *J. Anim. Ecol.* 46:425–441.

————, P.E. Davis and J.E. Davis. 1982. Ravens and buzzards in relation to sheep-farming and forestry in Wales. *J. Appl. Ecol.* 19:681–706.

Pandolfi, M. and G. Taferna. 1991. Censimento del popolamento di Passeriformi di un bosco di conifere e di uno di latifoglie dell'Italia centrale. Pages 375–378 in M. Fasola [Ed.], Atti II Seminario Italiano Censimenti Faunistici dei Vertebrati. Suppl. Ric. Biol. Selvaggina, XVI: 1–820.

Picozzi, N. and D. Weir. 1974. Breeding biology of the buzzard in Spaced. *Breadboards* 67:199–210.

Robbins, C.S., D.K. Dawson and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildl. Monogr.* 103:1–33.

Roché, J. 1977. Un recensement de buses en plaine de Saône: quelques données concernant la nidification. *Jean-le-Blanc* 16:48–63.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd ed. W.H. Freeman and Co., New York, NY U.S.A.

Taylor, K., R. Hudson and G. Horne. 1988. Buzzard breeding distribution and abundance in Britain and Northern Ireland in 1983. *Bird Study* 35:109–118.

Titus, K., J.A. Mosher and B.K. Williams. 1984. Chance-corrected classification for use in discrimi-

nant analysis: ecological applications. *Amer. Midland Nat.* 111:1–7.

TUBBS, C.R. 1967. Population study of buzzards in the new forest during 1962–66. *Brit. Birds* 60:381–395.

————. 1974. The buzzard. David & Charles Limited, Devon, UK.

WEIR, D. AND N. PICOZZI. 1983. Dispersion of buzzards in Spaced. *Brit. Birds* 76:66–78.

VARIATIONS IN BREEDING BALD EAGLE RESPONSES TO JETS, LIGHT PLANES AND HELICOPTERS

Teryl G. Grubb

*USDA Forest Service, Rocky Mountain Forest and Range Experiment Station,
2500 S. Pine Knoll Dr., Flagstaff, AZ 86001 U.S.A.*

William W. Bowerman

Gale Gleason Environmental Institute, Lake Superior State University, Sault Ste. Marie, MI 49783 U.S.A.

Abstract.—We analyzed 3122 observations of military jets, light planes and helicopters for three levels of response (none, alert, flight) by breeding Bald Eagles (*Haliaeetus leucocephalus*) at 13 occupied nests in Arizona and six in Michigan, 1983–85 and 1989–90, respectively. Helicopters elicited the greatest frequency of response (47%), followed by jets (31%) and light planes (26%). Frequency of response (23–61%) and frequency of flight (2–13%) both increased through the nesting season from February to June. Distance from eagle to aircraft, duration of overflight and number of aircraft and/or passes were the most important characteristics influencing eagle responses to pooled and individual aircraft types. Classification tree (CART) models for individual aircraft types provide dichotomous keys of distance and secondary variables affecting associated response rates, and should facilitate evaluating aircraft-specific impacts. Our analyses indicate a categorical exclusion of aircraft within 600 m of nest sites would limit Bald Eagle response frequency to 19%.

Key Words: *Bald Eagle*; Haliaeetus leucocephalus; *disturbance; aircraft; behavior; Arizona; Michigan; modeling; classification trees.*

Variaciones en crías de águilas en reacción ha aviones militar, aviones ligeros y helicópteros

Resumen.—Nosotros analizamos 3122 observaciones de avión militar, avión ligero y helicóptero para tres niveles de reacción (nada, alerta, volar) de águilas (*Haliaeetus leucocephalus*) de cría en 13 nidos ocupados en Arizona y seis en Michigan, 1983–85 y 1989–1990, respectivamente. Helicópteros le sacaron la reacción con mas frecuencia (47%), seguido por avión militar (31%) y avión ligeros (26%). La frecuencia de reacción (23–61%) y frecuencia de volar (2–13%) aumentaron durante la temporada de poner nidos de febrero ha junio. Distancia de águilas al avión, tiempo en viento, y numeros de aviones y/o pases eran los mas importantes característicos influyendo la respuesta de águilas ha grupos o solos tipos de aviones. Modelos (CART) con clasificación tres para aviones solos proporcionan llaves dicotomías de distancia y variables secundarias afectando respuestas asociadas, y debe facilitar la evaluación de impactos specíficos de aviones. Nuestra análisis indica una exclusión categórico de aviones dentro de 600M de nidos debe limitar la respuesta de frecuencia ha (19%) en águilas.

[Traducción de Raúl De La Garza, Jr.]

Aircraft come into contact with breeding raptors in essentially two nonexclusive ways: first, as a potentially disturbing form of ambient human activity (Smith et al. 1988) and second, as a research/management tool specifically focused on nest overflights to survey breeding populations and monitor reproductive success (Fuller and Mosher 1987). For effects on breeding Bald Eagles (*Haliaeetus leucocephalus*), aircraft have been addressed either passively as part of broader disturbance studies (e.g., Grubb and King 1991, McGarigal et al. 1991) or actively as part of an evaluation of the aircraft type

used in the reported study (e.g., Fraser et al. 1985, Watson 1993). However, comparative response data on the three common types of aircraft affecting breeding Bald Eagles and other raptors (low-level military jet fighters, light planes and helicopters) are scarce (Smith et al. 1988, Watson 1993) and have not been collected within the context of a single study.

Our research specifically focused on variation in breeding Bald Eagle responses to the three common types of aircraft. It represented a collation and extension of previously described Bald Eagle/

human disturbance research in Arizona (Grubb and King 1991) and Michigan (Grubb et al. 1992). Although these studies showed aircraft to elicit the lowest response of the five disturbance groups evaluated (vehicle 52–74%, pedestrian 45–72%, aquatic 46–53%, noise 38–54%, aircraft 29–33%), the authors noted any potentially disturbing activity, in excess or under the right conditions, can alter normal behavior or induce nesting failure. However, activities that may not cause nest failure can still detrimentally impact eagles. Low-level overflights have caused Bald Eagles to attack (Fyfe and Olendorff 1976) or avoid (Fraser et al. 1985) the aircraft, or depart the area entirely (Grubb and King 1991), all of which are energetically costly and behaviorally disruptive. In Arizona, the death of a nestling was attributed to frequent helicopter flights <30 m off a cliff nest; this unusual activity kept the adults away for long periods and significantly reduced prey deliveries (L.A. Forbis pers. comm.).

Thus, our standardized assessment of nonfailure-producing effects of the three common aircraft types on Bald Eagle responses should facilitate evaluation of potential aircraft disturbances and encourage disturbance-specific breeding area management.

STUDY AREA

The central Arizona study area was located in Gila, Maricopa and Yavapai counties, primarily along the Salt and Verde River drainages. The area is characterized by clustered mountain ranges and desert basins, with elevations of 500–1500 m (Chronic 1983). All nest sites were associated with riparian vegetation consisting of cottonwood-willow (*Populus fremontii-Salix goodingii*) and mixed broadleaf (*Platanus wrightii, Fraxinus pennsylvanica, Alnus oblongifolia*) series amid prevailing Sonoran desertscrub-Arizona upland or palo verde-mixed cacti (*Cercidium* spp.-*Opuntia* spp.) series (Brown 1982). Most eagle nests were located on 50–100-m cliffs.

The Michigan study area was located in the northern lower peninsula along the Au Sable River in Alcona, Iosco, Oscoda and Otsego counties, and the Manistee River in Manistee County. Terrain was flat to rolling with occasional hills; elevation range was 200–400 m. Vegetation was predominantly continuous mixed hardwood forest of aspen (*Populus grandidentata* and *P. tremuloides*), oak (*Quercus rubra* and *Q. alba*), maple (*Acer rubrum* and *A. saccharum*) and birch (*Betula papyrifera*), with interspersed conifer stands of white (*Pinus strobus*), red (*P. resinosa*) and jack (*P. banksiana*) pine. All eagle nests were in trees, mostly white pine.

METHODS

Because of federal threatened and endangered species restrictions, we observed Bald Eagle responses to passing aircraft opportunistically, with no manipulative experimentation nor direct control of aircraft. We could not govern the number or distribution of aircraft among nest sites, through the breeding seasons, or across years. Nor could we effectively address apparent variation in responsiveness by nest site because of differing numbers, types and timing of aircraft (Table 1). Therefore, after testing for differences in the Arizona and Michigan data sets, we combined observations to maximize sample size for analysis and modeling of response trends. Arizona data ($N = 2848$) were collected during the 1983–85 breeding seasons in the vicinity of 13 Bald Eagle nest sites. Michigan data ($N = 274$) were collected during the 1989–90 breeding seasons around six nest sites. Data collection techniques were identical in both states. The combined sample of 19 nest sites represented ≥45 free-flying Bald Eagles from two populations over five breeding seasons (Table 1).

For seasonal analyses, Michigan data were standardized to Arizona data on the basis of incubation dates; one month was subtracted from Michigan dates to integrate the later breeding season into the predominant sample. For general application beyond these two populations, February to early-March was considered the incubation period; mid-March to May, the nestling period; and early June, the fledging period.

As an alternative to unattainable cause-and-effect testing, we monitored variations in Bald Eagle response severity (none, alert/agitated, flight) and response frequency (% none/any) as aircraft overflights occurred. Alert behavior included head turns, vocalizations and increased movements on or between perches. Grubb and King (1991) and Grubb et al. (1992) detail data collection procedures and analytical methods.

We classified aircraft into three generic types: low-flying, military jet fighters; civilian, propeller-driven, light planes; and helicopters, civilian or military, mostly single-rotor. For all aircraft events within 2000 m of nest sites and less than approximately 305 m overhead (1000 ft, estimated), we recorded distance-from-affected-eagle-to-aircraft (m), duration-of-overflight (min), number-of-units-per-event (aircraft and/or passes overhead), visibility-of-aircraft-to-affected-eagle (none/any), and position-relative-to-affected-eagle (above/below). Distance-to-aircraft was approximated by plotting flight paths on topographic maps and measuring distances to reference eagles. Visibility was based on eagle and aircraft positions relative to obscuring vegetation and terrain features.

Medians were used in summary statistics to represent central tendencies because of skewness in data caused by a preponderance of nearby, short-duration overflights. Frequencies, descriptive statistics, and nonparametric k-sample median and goodness-of-fit tests using the chi-square statistic were calculated with SPSS/PC+ 4.0 (Norusis 1990). We used notched box and whisker plots (Chambers et al. 1983, STSC 1991) to evaluate the relationship between distance-to-aircraft and response severity.

We developed classification and regression tree (CART) models to assess variations in response frequency associated with pooled aircraft (all three types combined with no type distinction), pooled aircraft including aircraft type as a separate variable and for each aircraft type

Table 1. Sample distribution by nest site, minimum number of Bald Eagles, years of data, aircraft type, nesting season month and associated variability in frequency of Bald Eagle response for 3122 observations of military jet fighters, light planes and helicopters near 19 occupied nest sites in Arizona (nests 1–13) and Michigan (nests 14–19), 1983–85 and 1989–90, respectively.

Nest Site	BEs	Yrs	% Response Frequency[a] (N for Aircraft Type)				% Response Frequency[a] (N for Month)				
			Pooled	Jets	Planes	Helos	Feb	Mar	Apr	May	Jun
1	≥2	3	37 (108)	20 (5)	31 (90)	85 (13)	27 (77)	40 (15)	67 (9)	100 (7)	– (0)
2	≥2	3	34 (79)	33 (3)	27 (55)	52 (21)	39 (36)	33 (27)	27 (15)	0 (1)	– (0)
3	≥2	3	44 (188)	57 (14)	38 (143)	64 (31)	33 (49)	40 (89)	62 (50)	– (0)	– (0)
4	≥2	3	51 (215)	28 (40)	55 (122)	60 (53)	40 (126)	69 (58)	65 (23)	63 (8)	– (0)
5	4	1	90 (39)	– (0)	93 (28)	82 (11)	– (0)	50 (2)	96 (28)	78 (9)	– (0)
6	≥3	3	20 (1286)	20 (215)	11 (631)	34 (440)	11 (493)	12 (396)	31 (194)	41 (116)	61 (87)
7	≥2	3	62 (24)	– (0)	58 (12)	67 (12)	77 (13)	46 (11)	– (0)	– (0)	– (0)
8	≥4	3	62 (21)	– (0)	78 (9)	50 (12)	20 (5)	83 (6)	100 (1)	68 (9)	– (0)
9	≥2	3	24 (345)	28 (168)	10 (150)	74 (27)	42 (48)	46 (74)	8 (185)	36 (36)	50 (2)
10	≥2	3	53 (49)	36 (14)	59 (17)	61 (18)	62 (8)	72 (18)	28 (18)	50 (4)	100 (1)
11	≥4	2	90 (39)	93 (14)	86 (21)	100 (1)	86 (7)	88 (25)	100 (2)	100 (5)	– (0)
12	≥2	2	44 (390)	45 (97)	36 (234)	73 (59)	10 (40)	63 (91)	41 (134)	45 (125)	– (0)
13	≥3	2	40 (65)	17 (18)	40 (30)	65 (17)	39 (49)	64 (11)	– (0)	– (0)	– (0)
14	2	1	53 (17)	64 (11)	0 (3)	67 (3)	50 (2)	50 (2)	70 (10)	0 (3)	– (0)
15	2	1	30 (10)	25 (4)	33 (6)	– (0)	– (0)	50 (4)	25 (4)	0 (2)	– (0)
16	1	1	0 (1)	0 (1)	– (0)	– (0)	– (0)	0 (1)	– (0)	– (0)	– (0)
17	1	1	100 (1)	– (0)	100 (1)	– (0)	– (0)	– (0)	– (0)	100 (1)	– (0)
18	2	1	50 (10)	100 (2)	38 (8)	– (0)	– (0)	43 (7)	67 (3)	– (0)	– (0)
19	≥2	2	29 (235)	32 (173)	9 (34)	36 (28)	– (0)	33 (73)	28 (120)	26 (42)	– (0)
19	≥45	3	32 (3122)	31 (779)	26 (1594)	47 (749)	23 (953)	34 (910)	33 (801)	44 (368)	61 (90)

[a] Response frequency (%) = number of responses divided by number of events times 100%.

(California Statistical Software, Inc. 1985; Grubb and King 1991). Classification analysis provides predictive, discriminant models in the form of nonparametric, dichotomous keys (Brieman et al. 1984; Verbyla 1987). For each level (branch) of the model, CART selects the independent (splitting) variable, and the point within its range, that best separate (classify) remaining data into classes of the dependent variable (response in our case). This process of tree growing continues until all data are classified.

Only the classification tree aspects of CART were used in our analyses. The first split in each tree separated the higher response, left side of the models from the lower response, right side. Each variable used in CART was ranked for its splitting ability by assigning the first (primary) splitting variable a value of 100% and expressing the relative value of secondary variables as a percentage of the primary variable.

Cross-validation provided an estimate of classification accuracy (predictability) for each tree on a scale of 0.00–1.00 (Brieman et al. 1984, Verbyla 1987). For this procedure, CART randomly divides the data into 10 subsets, develops a classification tree with nine subsets, estimates tree accuracy by applying it to the withheld subset, then repeats the process until all 10 subsets have been withheld. Averaging results of the 10 mini-tests yields an overall estimate of classification accuracy for the tree developed from the full data set (Steinberg and Colla 1992).

RESULTS

Frequencies for none, alert and flight responses did not differ between state populations of Bald Eagles (Arizona—68, 28, and 4% and Michigan—69, 26, and 5%, respectively; $\chi^2 = 1.19$, $P = 0.55$). Although median distance-to-aircraft for alert response varied between Arizona and Michigan (350 and 500 m, respectively; $\chi^2 = 10.57$, $P < 0.01$), median distances for no response (750 and 800 m; $\chi^2 = 1.45$, $P = 0.23$) and flight response (both 200 m; $\chi^2 < 0.01$, $P = 0.96$) were similar. When "state" was added as an independent variable to the CART analyses, it was not included in the resulting models; state location had no discriminatory value for partitioning Bald Eagle responses to aircraft.

Our combined sample consisted of 51% light planes, 25% military jets and 24% helicopters ($N = 3122$, Table 2). Median number-of-aircraft and

Table 2.   Comparison of disturbance and response characteristics among three types of aircraft for 3122 occurrences within 2000 m of 13 occupied Bald Eagle nests in Arizona and six in Michigan, 1983–85 and 1989–90, respectively.

TYPE	DISTURBANCE				NO RESPONSE		ANY RESPONSE	
	FREQUENCY (NO. OF EVENTS)	MEDIAN NO. PER EVENT	MEDIAN DISTANCE (m)	MEDIAN DURATION (min)	FREQUENCY (%)[a]	MEDIAN DISTANCE (m)	FREQUENCY (%)[a]	MEDIAN DISTANCE (M)
Military jets	779	1	500	1	69	600	31	400
Light planes	1594	1	700	1	74	850	26	400
Helicopters	749	1	420	1	53	700	47	250
Total sample	3122	1	600	1	68	800	32	333

[a] Response frequency (%) = number of responses divided by number of events times 100%.

duration (min) were similar for all aircraft types. Helicopters occurred at the closest median distance and had the highest response rate, followed by jets, then light planes. All three types typically occurred closer than the median no-response distance, yet overall response rate was only 32%. Response frequencies at individual nest sites were highly variable but at the 12 sites where all three

Figure 1.   Notched box and whisker plot of median distance to aircraft (military jets, light planes and helicopters) for three levels of response severity for breeding Bald Eagles at 19 occupied nests in Arizona and Michigan, 1983–85 and 1989–90, respectively. Boxes cover middle 50% of data. Tops of boxes indicate the distance within which 75% of recorded responses occurred. Whiskers indicate range but do not exceed 1.5 times box length. Stars represent outlying observations. Box width is proportional to sample size. Center lines are medians, with position indicating skewness. Notches are width of 95% confidence intervals for pairwise comparisons.

aircraft occurred, helicopters consistently elicited the highest response (Table 1).

Median distance-to-aircraft varied among different levels of response severity, with closer proximity resulting in greater response ($P = 0.05$, Fig. 1). Response frequencies for each type of aircraft also varied at each response level (Fig. 2). Helicopters had the lowest rate of no response ($\chi^2 = 292, P < 0.01$) and the highest rates of alert response ($\chi^2 = 124, P < 0.01$) and flight response ($\chi^2 = 11.55, P < 0.01$). Median distance for flight response was 200 m for all three aircraft types, although frequency of flight from helicopters was more than three times that from jets and planes.

As the nesting season progressed, Bald Eagles responded both more frequently and more severely with more flight. The frequencies of alert and flight responses increased from February to June
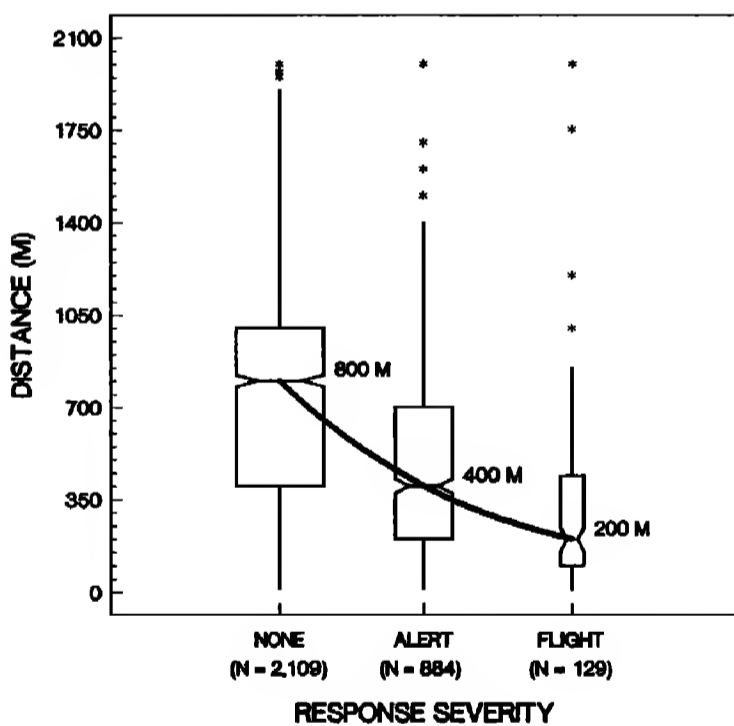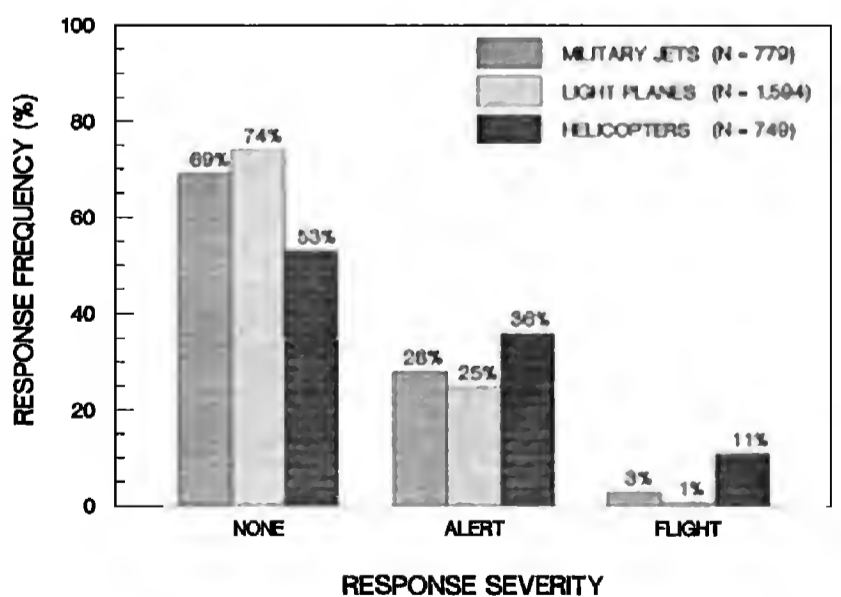

Figure 2.   Differing response frequencies among three types of aircraft for three levels of response severity for breeding Bald Eagles at 19 occupied nests in Arizona and Michigan, 1983–85 and 1989–90, respectively.
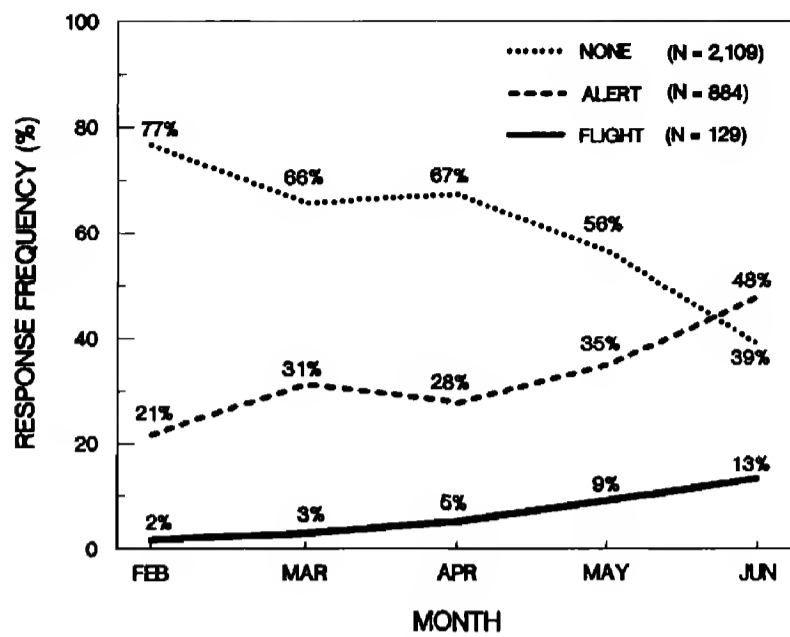
Figure 3. Monthly variations in response frequency for three levels of response severity for breeding Bald Eagles at 19 occupied nests in Arizona and Michigan, 1983–85 and 1989–90, respectively.

$(\chi^2 = 448$ and 1904, respectively; $P < 0.01$), with a compensatory decrease in no-response $(\chi^2 = 6969, P < 0.01$; Fig. 3). Seasonal changes in aircraft proximity appeared to have little effect on Bald Eagle responsiveness. Distance-to-pooled-aircraft decreased through the nesting season $(\chi^2 = 115, P < 0.01$; Table 3), but median distance-to-aircraft eliciting response did not fluctuate significantly be-

tween February and May (median $= 350$ m; $\chi^2 = 3.65, P = 0.30$).

Although sample sizes became smaller as the nesting season progressed, responsiveness to pooled and individual aircraft types started relatively low during incubation (February), leveled at a higher plateau during the nestling period (March–May) and increased to the highest levels after fledging (June, Table 3). May and June data also indicated that the consistently higher response to helicopters was more a function of aircraft type than distance. In May, when the median distance to both jets and helicopters was 500 m, eagle responses were 37% and 52%, respectively. In June, light planes and helicopters both occurred at 200 m, yet eagle responses were 45% and 84%, respectively.

Frequency of eagle response increased as the frequency of aircraft decreased. Nest site No. 6 had >1200 recorded aircraft overflights, six sites had between 100–400 and 12 sites had <100 (Table 1). Response frequencies for these three groups were 20, 38 and 55%, respectively $(\chi^2 = 545, P < 0.01$). Yet, the median distance-to-aircraft-eliciting-response was similar between nest groups: alert response, 300–400 m $(\chi^2 = 2.25, P = 0.32)$ and flight response, 150–200 m $(\chi^2 = 1.82, P = 0.40)$.

In the CART pooled aircraft model (Fig. 4), dis-

Table 3. Monthly variation[a] in sample sizes, response rates and median distances for 3122 military jet fighters, light planes and helicopters near 19 occupied Bald Eagle nest sites in Arizona and Michigan, 1983–85 and 1989–90, respectively.

	FEB	MAR	APR	MAY	JUN
Military jets					
N	199	209	255	86	30
Median distance (m)	600	500	600	500	300
% Response	23	38	27	37	53
Light planes					
N	515	503	403	144	29
Median distance	850	700	700	600	200
% Response	20	26	28	40	45
Helicopters					
N	239	198	143	138	31
Median distance	500	400	440	500	200
% Response	30	50	55	52	84
Pooled aircraft					
N	953	910	801	368	90
Median distance	800	600	600	500	250
% Response	23	34	33	44	61

[a] On the basis of incubation dates, Michigan data were standardized to Arizona data by subtracting one month.
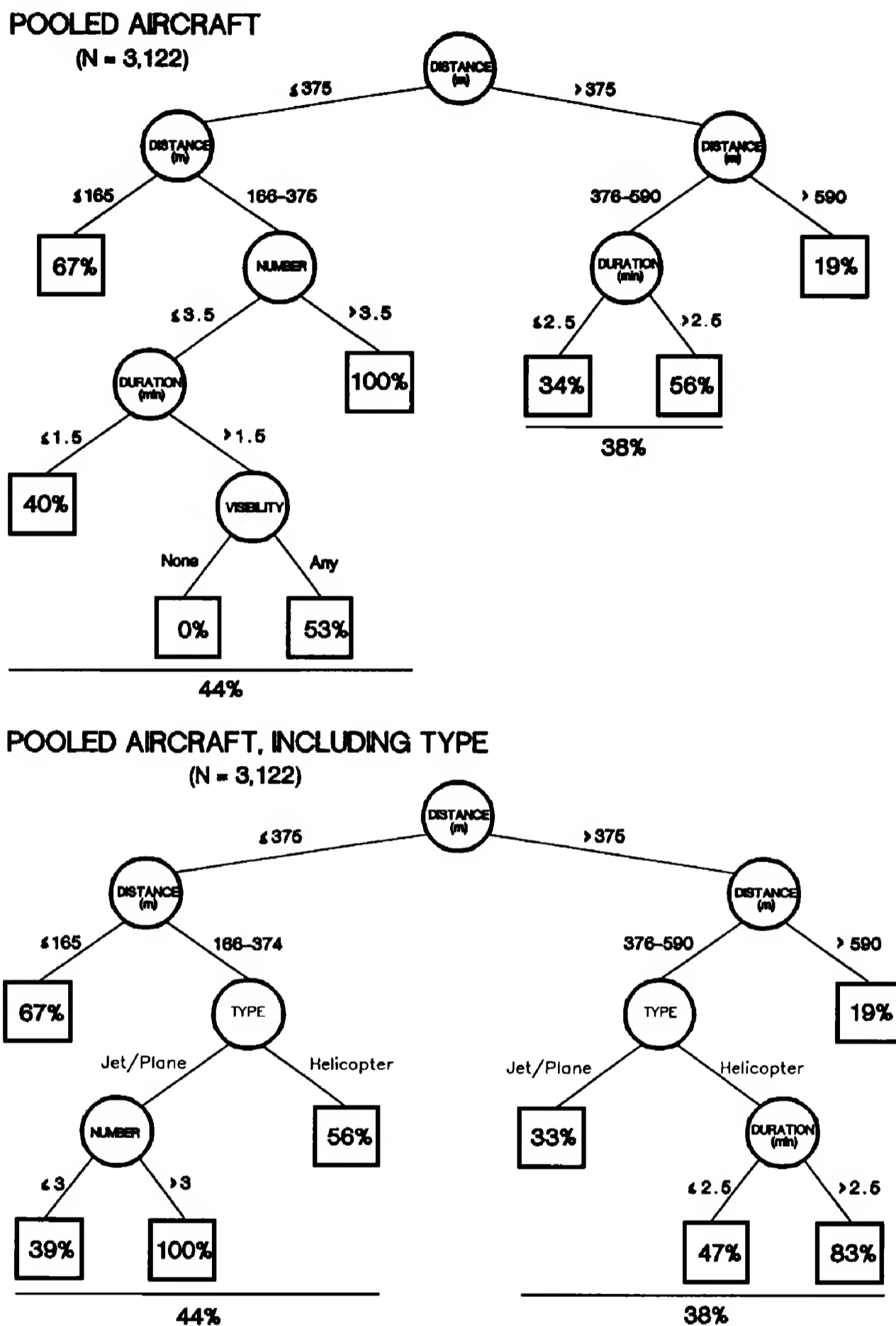
Figure 4. Classification tree (CART) models, with associated eagle response frequencies, for pooled and pooled-within-type aircraft disturbance near breeding Bald Eagles at 19 occupied nests in Arizona and Michigan, 1983–85 and 1989–90, respectively.

tance was the primary and secondary splitting variable, followed by number, duration, and visibility on the left (high-response) side of the tree, and duration alone on the right (low-response) side. When aircraft type was included as a variable in the pooled tree, it entered the model at the tertiary level, after the two distance splits. Type influenced response rates in the midrange distances (166–590 m), with helicopters partitioned from and showing greater response rates than jets and planes. Re-
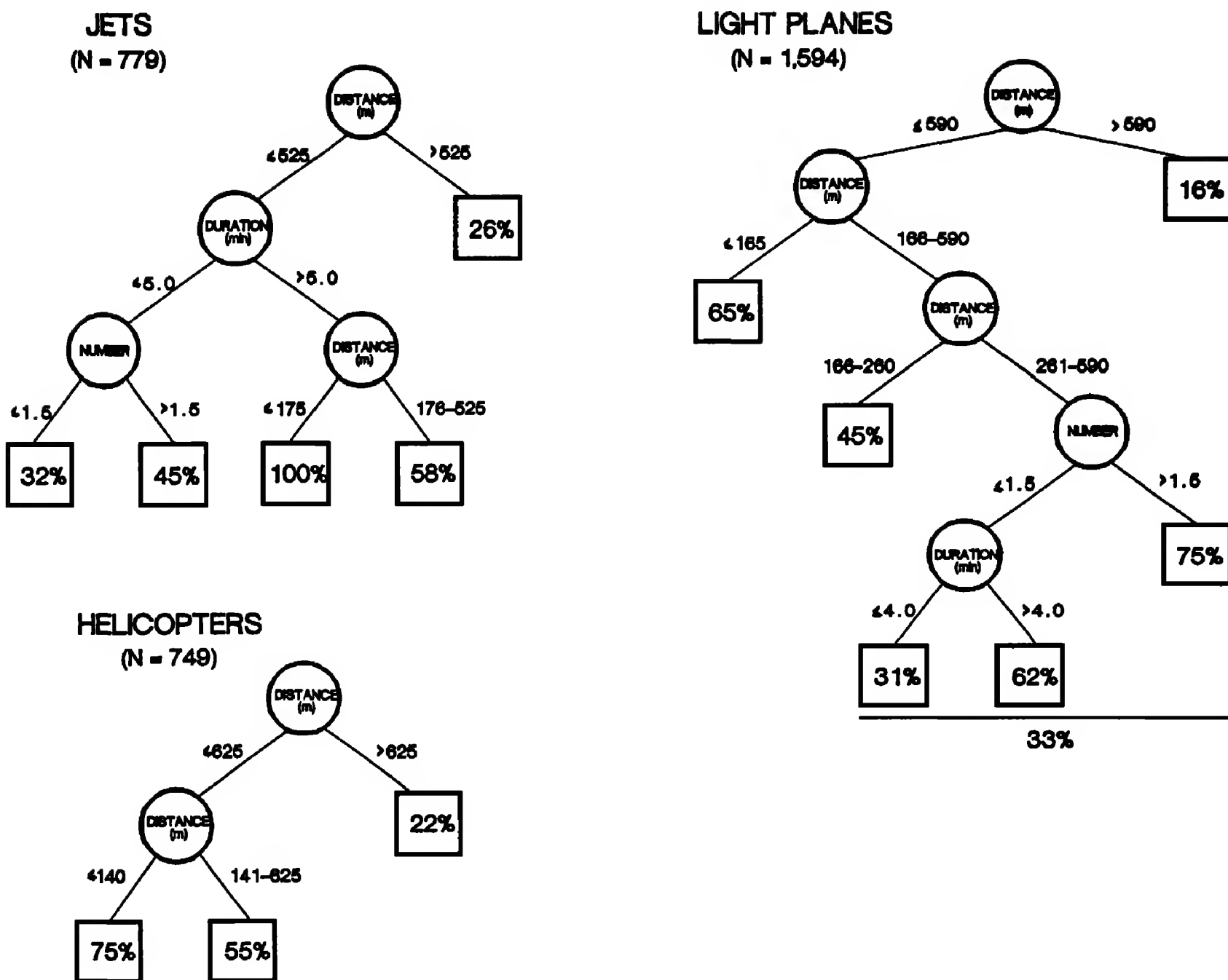
Figure 5. Classification tree (CART) models, with associated eagle response frequencies (%), for military jet, light plane and helicopter disturbance near breeding Bald Eagles at 19 occupied nests in Arizona and Michigan, 1983–85 and 1989–90, respectively.

sponse rates for both models were 67% at ≤165 m, 44% at 166–375 m, 38% at 376–590 m, and 19% at >590 m (χ^2 = 4179, P < 0.01). Estimated accuracy for the pooled and pooled-with-type models was 0.63.

Although CART-generated, initial splitting distances increased from jet fighters, through light planes, to helicopters, the low-response side of individual models showed light planes causing the least response at greater distances (16%) and jets the highest (26%, Fig. 5). For jets, short overflight duration (≤5 min) and single aircraft appeared to mitigate the effect of proximity within 525 m, whereas longer duration within 175 m caused certain response. Calculated response rates based solely on distance were 52% at ≤175 m, 37% at

176–525 m and 26% at >525 m (χ^2 = 398, P < 0.01); the first two rates differ from the CART model because of the incorporation of duration and number within 525 m. Jet model accuracy was estimated at 0.60.

Light planes within 165 m elicited 65% response regardless of any other factors; between 166–260 m, response rate dropped to 45%. Response rates at 261–590 m and at >590 m were 33% and 16%, respectively (χ^2 = 3888, P < 0.01). Between 261–590 m, >1 plane or pass/event or >4 min duration caused response greater than or equal to close proximity events. Response to helicopters simply decreased as distance increased: 75% at ≤140 m, 55% at 141–625 m, and 22% at >625 m (χ^2 = 399, P < 0.01). Accuracy estimates for the light plane

Table 4. Relative importance[a] of independent (splitting) variables in CART analyses for three types of aircraft disturbance, treated separately and pooled with/without type included as a variable.

| | DISTURBANCE | | | | | |
VARIABLE	POOLED	POOLED WITH TYPE	JETS	PLANES	HELICOPTERS	OVERALL RANKING
Distance	100	100	100	100	100	1
Duration	28	36	61	26	35	2
Type	–	24	–	–	–	–
Number	17	–	39	14	6	3
Visibility	7	8	5	8	8	5
Position	6	8	11	10	8	4

[a] Standardized so primary splitting variable = 100% and secondary variables are expressed as a percentage of the primary variable.

and helicopter models were 0.61 and 0.70, respectively.

CART modeling verified distance as the most critical determinant between response and no-response associated with aircraft (Table 4). Duration-of-overflight was a consistent second and number-of-units-per-event third. Both duration and number appeared nearly twice as important for responses to jets as for the other types of aircraft. Number had the least effect on response to helicopters. Overall, position and visibility affected eagle responses to aircraft very little. When included in the pooled model, aircraft type was ranked third behind distance and duration.

DISCUSSION

These results are necessarily qualified by the fact that sample data were not evenly or randomly distributed across the various parameters measured or among nest sites. Thus, the distribution of sample data should be considered when interpreting or applying our results. For example, repeated aircraft observations on many of the same eagles may have reduced the observed variability, frequency and/or severity of response. However, inherent limitations are at least partially mitigated by the size of the data set, the number of eagles and nest sites involved, the duration of the study and the standardization of aircraft and response measurements among types.

Greater stimuli typically result in Bald Eagles reacting farther away (Grubb et al. 1992). Thus, helicopters might be expected to cause eagle responses at greater distances than light planes. The relatively low median response distance for helicopters compared to other aircraft was more likely a result of proximate flights than an indication of

breeding eagle tolerance. Helicopters, because of their enhanced maneuverability, and military jets, because of the nature of low-level fighter training, tended to follow drainages and contours (where nests were located) more closely than light planes, especially in the rugged canyon terrain of Arizona. At very close range, the consistent 200 m, calculated median flight distance for all three aircraft and the pooled-with-type CART model, which did not include aircraft type before 166 m, indicate proximity outweighs type. Comparable minimum splitting distances in each of the type models (jets 175 m, planes 165 m and helicopters 140 m) support this conclusion.

In their review of responses to aircraft by 14 raptor species, Smith et al. (1988) found the impact of low-level military jets to be brief and insignificant. In our study, jets and helicopters occurred at similar distances from nest sites. Yet, jets and light planes elicited comparable response rates at identical response distances. The fact that helicopters caused much greater response, and that CART split jets and planes from helicopters in the modeling process, argues for type differences. Also, the CART model for helicopters included no other variables than distance, suggesting a stimulus of sufficient magnitude that secondary characteristics did not influence response. Distances within the model were consistent with Platt (1977), who recorded helicopter overflights at ≤160 m altitude disturbing all adult Gyrfalcons (Falco rusticolus) and overflights >600 m disturbing none of the five pairs tested. Our data confirm the traditional view that helicopters are the most disturbing type of aircraft (Watson 1993).

Bald Eagles appeared least responsive to aircraft

early in the nesting season, as indicated by both their lower response rate and tendency to remain at or near nests without flying. Increasing response rates, especially for flight, later in the season suggest adults were more frequently flushed as their nest attendance requirements diminished. Watson (1993) noted presence of young nestlings led to reduced adult response. He also found eagles with small young were more reluctant to flush in adverse weather, and eagles were disturbed at higher rates when no young were in the nest. Decreasing sample size over time is partially attributable to reduced adult presence near nests, which typically declines as nestlings mature (Bowerman 1991).

Grubb and King (1991) concluded breeding Bald Eagles in Arizona may have become habituated to aircraft, and in Michigan habituation was also evidenced at one nest site near a military air base (Grubb et al. 1992). Our current analysis of the combined data set indicates variability among nest sites, with an inverse relationship between frequency of air traffic and frequency of eagle response. If habituation occurs with repeated exposure, then our results may underestimate Bald Eagle response at nest sites with limited air traffic and overestimate at sites with a high frequency of aircraft.

The relative importance of CART splitting variables indicates that managing distance, duration and number of aircraft overflights could effectively minimize impacts on breeding Bald Eagles. The higher values for duration and number with jets may be a result of the tendency for military jets to fly in groups of two or more, as well as the proximity of the one Michigan nest (No. 19) to an Air National Guard, air-to-ground firing range where repeated overflights were common (Grubb et al. 1992). The relative importance of type in the pooled-with-type model validates using individual aircraft models to refine distance and potential management considerations.

Cross-validation indicates our CART aircraft models should correctly predict breeding eagle response for two of every three aircraft events. Model accuracy might be improved through controlled experimentation and by the addition and/or refinement of independent variables, including consideration of specific eagle activity (Grubb and King 1991, McGarigal et al. 1991, Watson 1993) and weather conditions (Schueck and Marzluff 1995) at the time of overflight. Significance and intensity of prestimulus eagle behavior, as well as

time of the year (e.g., breeding versus nonbreeding season) may also be important factors (Smith et al. 1988).

Management plans for nesting Bald Eagles typically include restrictive buffer zones, limiting human activity within 400 m of nest sites (Grier et al. 1983). Plans may also include restrictions associated with key habitat areas such as used for foraging and perching (Isaacs and Silvosky 1981). Aircraft are typically precluded from flying within these restriction zones. CART primary splits at 525, 590, and 625 m for jets, planes and helicopters and a secondary split at 590 m on the pooled model, resulting in 19–26% response, suggest that aircraft would best be categorically excluded from within 600 m of nest sites and key habitat areas during the breeding season.

When such a categorical limitation is impractical, our CART models indicate if duration and number of aircraft and/or passes are limited to <5 min and one, respectively, jet fighters within 200 m of nest sites would cause relatively low expected eagle response (<33%). Light planes within 275 m, if limited to <4 min duration and one plane or pass/overflight, would cause 31% expected response. Avoiding helicopter overflights within 600 m of nest sites would result in a 22% expected response. However, given the advantages and therefore inevitable continued closer use of helicopters for raptor surveys (Watson 1993, Ewins and Miller 1995), we recommend these surveys be flown at maximum distance (>150 m) and minimum duration (<1 min), with only one overhead pass. Whenever possible, surveys are better conducted with light planes, because they typically cause minimal disturbance to breeding Bald Eagles (Fraser et al. 1985).

State University, USDA Forest Service and EARTH-
WATCH, Inc.

LITERATURE CITED

BRIEMAN, L., J.H. FRIEDMAN, R.A. OLSHEN AND C.J. STONE.
    1984. Classification and regression trees. Wadsworth
    & Brooks, Monterey, CA U.S.A.
BOWERMAN, W.W., IV. 1991. Factors influencing breed-
    ing success of Bald Eagles in upper Michigan. M.A.
    thesis, Northern Michigan Univ., Marquette, MI
    U.S.A.
BROWN, D.E. [ED.]. 1982. Biotic communities of the
    American Southwest–United States and Mexico. Desert
    Plants 4:1–342.
CALIFORNIA STATISTICAL SOFTWARE, INC. 1985. CART
    (TM). California Stat. Software, Inc., LaFayette, CA
    U.S.A.
CHAMBERS, J.M., W.S. CLEVELAND, B. KLEINER AND J. TU-
    KEY. 1983. Graphical methods for data analysis. Dux-
    bury Press, Boston, MA U.S.A.
CHRONIC, H. 1983. Roadside geology of Arizona. Moun-
    tain Press Publ., Missoula, MT U.S.A.
EWINS, P.J. AND M.J.R. MILLER. 1995. Measurement error
    in aerial surveys of Osprey productivity. J. Wildl. Man-
    age. 59:333–338.
FRASER, J.D., L.D. FRENZEL AND J.E. MATHISEN. 1985. The
    impact of human activities on breeding Bald Eagles
    in north-central Minnesota. J. Wildl. Manage. 49:585–
    592.
FULLER, M.R. AND J.A. MOSHER. 1987. Raptor survey
    techniques. Pages 37–65 in B.A. Giron-Pendleton,
    B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor
    management techniques manual. Nat. Wildl. Fed.,
    Washington, DC U.S.A.
FYFE, R.W. AND R.R. OLENDORFF. 1976. Minimizing the
    dangers of nesting studies to raptors and other sen-
    sitive species. Canadian Wildl. Serv. Occas. Paper 23.
GRIER, J.W., J.B. ELDER, F.J. GRAMLICH, N.F. GREEN, J.V.
    KUSSMAN, J.E. MATHISEN AND J.P. MATTSSON. 1983.
    Northern states Bald Eagle recovery plan. U.S. Fish &
    Wildl. Serv., Washington, DC U.S.A.

GRUBB, T.G. AND R.M. KING. 1991. Assessing human dis-
    turbance of breeding Bald Eagles with classification
    tree models. J. Wildl. Manage. 55:500–511.
———, W.W. BOWERMAN, J.P. GIESY AND G.A. DAWSON.
    1992. Responses of breeding Bald Eagles to human
    activities in northcentral Michigan. Can. Field-Nat
    106:443–453.
ISAACS, F.B. AND G. SILVOSKY. 1981. Bald Eagle manage-
    ment on the Fremont National Forest, Lakeview, Or-
    egon. USDA For. Serv., Fremont Nat. For., Supervi-
    sor's Office, Lakeview, OR U.S.A.
MCGARIGAL, K., R.G. ANTHONY AND F.B. ISSACS. 1991. In-
    teractions of humans and Bald Eagles on the Colum-
    bia River estuary. Wildl. Monogr. 115.
NORUSIS, M.J./SPSS, INC. 1990. SPSS/PC+ 4.0 Base
    Manual and Statistics 4.0. SPSS, Inc., Chicago, IL
    U.S.A.
PLATT, J.B. 1977. The breeding behavior of wild and cap-
    tive Gyrfalcons in relation to their environment and
    human disturbance. Ph.D. dissertation, Cornell Univ.,
    Ithaca, NY U.S.A.
SCHUECK, L.S. AND J.M. MARZLUFF. 1995. Influence of
    weather on conclusions about effects of human activ-
    ities on raptors. J. Wildl. Manage. 59:674–682.
SMITH, D.G., D.H. ELLIS AND T.H. JOHNSON. 1988. Rap-
    tors and aircraft. Pages 360–367 in R.L. Glinski, B.
    Giron-Pendleton, M.B. Moss, M.N. LeFranc, Jr., B.A.
    Millsap and S.W. Hoffman [EDS.], Proceedings of the
    southwest raptor management symposium and work-
    shop. Nat. Wildl. Fed., Washington, DC U.S.A.
STEINBERG, D. AND P. COLLA. 1992. CART: a supplemen-
    tary module for SYSTAT. SYSTAT, Inc., Evanston, IL
    U.S.A.
STSC, INC. 1991. Statgraphics reference manual, version
    5. STSC, Inc., Rockville, MD U.S.A.
VERBYLA, D.L. 1987. Classification trees: a new discrimi-
    nation tool. Can. J. For. Res. 17:1150–1152.
WATSON, J.W. 1993. Responses of nesting Bald Eagles to
    helicopter surveys. Wildl. Soc. Bull. 21:171–178.

PRODUCTIVITY OF GOLDEN EAGLES WEARING BACKPACK RADIOTRANSMITTERS

JOHN M. MARZLUFF[1] AND MARK S. VEKASY[1]
Greenfalk Consultants, 8210 Gantz Avenue, Boise, ID 83709 U.S.A.

MICHAEL N. KOCHERT AND KAREN STEENHOF
*U.S. Geological Service, Biological Resources Division, Forest and Rangeland Ecology Science Center,
Raptor Research Field Station, 970 Lusk Street, Boise, ID 83706 U.S.A.*

ABSTRACT.—We examined the association between the presence of backpack radiotransmitters and Golden Eagle (*Aquila chrysaetos*) reproduction (percentage of occupied territories producing young, and number of nestlings produced) over three years. The association between radio-tagging and nesting success and the number of nestlings produced varied significantly among years. A negative association with tagging was observed in one of three years, which coincided with low prey (jackrabbit) populations and a cold spring. However, small sample size and breeding by subadults may confound this result.

KEY WORDS: *Aquila chrysaetos; Golden Eagle; productivity; radio-tagging; weather.*

La productividad de águilas (*Aquila chrysaetos*) con radio emisora

RESUMEN.— Nosotros examinamos la asociación entre la presencia de un radio ajustado en la espalda y la reproducción (porcentaje de territorio ocupado tenido jóvenes, y numeros de pajaritos producidos) de la águila (*Aquila chrysaetos*) por tres años. La asociación entre marcando con el radio y el desarrollo de nidos y los numeros de pajaritos producidos variado mucho entre clases de edad. Una asociación negativa con marcando fue observado uno de los tres años, que coincido con poblaciones bajas de presa y una primavera fría. Sin embargo, muestras pocas y reproducción mínima de subadultos puede confundir resultados.

[Traducción de Raúl De La Garza, Jr.]

Effects of radio-tagging on behavior should be considered before making inferences about an animal's biology (Wanless 1992, Hiraldo et al. 1994). Radio-tagging may have little effect (Vekasy et al. 1996), or may adversely affect condition and behavior by abrading skin, influencing time budgets, decreasing foraging efficiency, increasing metabolic costs or causing desertion of eggs or nestlings (Gessaman and Nagy 1988, Massey et al. 1988, Hooge 1991, Foster et al. 1992). Effects may vary year to year with weather and prey abundance (Peitz et al. 1993, Vekasy et al. 1996).

We examined reproductive responses of Golden Eagles (*Aquila chrysaetos*) wearing backpack radiotransmitters in the Snake River Birds of Prey National Conservation Area (NCA) from 1991–94. Our objective was to determine the influence of radio-tagging on reproduction and identify other factors that may have interacted with radio-tagging to either increase or decrease the magnitude of the effect.

METHODS

Throughout the course of this study 27 Golden Eagles were captured and 15 were radio-tagged (Table 1). Our sample during winter 1991–92 included eight eagles at seven nesting areas (sections of cliffs or powerlines where nests are found each year, but where no more than one pair has ever bred at one time). Both members of the pair were tagged at one site. In 1992–93 our sample increased by two nesting areas where we tagged the male of one pair and the female of the other pair. We also radio-tagged two additional birds in our original seven areas in 1992–93; a female after her mate's transmitter failed, and a male where we had previously trapped and radio-tagged the female. Our sample size was reduced by two nesting areas during winter 1993–94, when we found one female dead of unknown cause, and we failed to locate one male. Captured eagles were weighed and measured, and we determined sex using weight and footpad length and observations of copulation (Edwards and Kochert 1986).

Golden Eagle control nesting areas consisted of all oc-

---

[1] Present address: College of Forest Resources, University of Washington, Seattle, WA 98195 U.S.A.

Table 1.   Golden Eagle territories where birds were radio-tagged and productivity was studied during 1991–94 breeding seasons in the Snake River Birds of Prey National Conservation Area.

| TERRITORY | NUMBER OF EAGLES | | INDIVIDUALS USED IN ANALYSES | | | YEARS USED IN ANALYSES | | | |
	CAP-TURED	INSTRU-MENTED	SEX	AGE	CAPTURE DATE	1991	1992	1993	1994
A—Black Butte	2	1	M	Ad	12 Nov 91		—	—	—
B—Beercase	2	2	M	Ad	18 Jan 92		—	—	—
C—Wildhorse	2	2	F	Ad	14 Oct 91		—	—	—
			M	Ad	16 Dec 92			—	—
D—PP&L 119	5	4	M	Ad	19 Feb 91	—	—	—	
			F	Ad	23 Oct 92		—	—	—
			M	Subad	11 Mar 94				—
E—Pole 369	0[a]	0[a]	F	Subad	17 Dec 91			—	
F—Grand View	2	2	F	Subad	17 Dec 91	—			
			M	Ad	24 Oct 92		—	—	—
G—Ogden	1	1	M	Ad	14 Dec 92		—	—	—
H—Beecham	1	1	M	Ad	22 Nov 91	—	—	—	—
I—Cabin	12	2	F	Ad	06 Dec 91	—	—	—	—
	—	—	M	Ad	12 Apr 94				—
Total	27	15							

[a] Individual moved from Grand View Sand Cliff territory to Pole 369 territory.

cupied nesting areas in the NCA with known nesting outcomes and without radio-tagged adults (1992, N = 23; 1993, N = 19; 1994, N = 21). A nesting area was considered "occupied" if we observed territorial activity, courtship, brood rearing activity, eggs, young or conspicuous field sign (e.g., whitewash at a roost). Control and treatment nesting areas were interspersed along the Snake River Canyon.

We attached transmitters as backpacks using a Teflon® ribbon harness (after Buehler et al. 1995). Details of harness construction and fitting are found in Vekasy et al. (1996). A transmitter with harness weighed 75 g, less than 3% body weight for males ($\bar{x}$ = 3691.5 g, SE = 98.9, N = 10), and less than 2% body weight for females ($\bar{x}$ = 4412.5 g, SE = 133.4, N = 4).

We observed Golden Eagle nesting areas from a helicopter two or three times throughout the season to determine occupancy and egg laying, and number of nestlings ≥51 d old (brood size). We surveyed nesting areas from the ground when we could not determine these parameters by helicopter. We considered pairs as nonlaying if there was no evidence that eggs were laid and a bird was not seen in an incubating posture on a nest. The presence of one member of a pair in incubating posture, or eggs or young in a nest was considered a nesting attempt. Nesting attempts were considered successful if at least one nestling reached 80% of fledging age (Steenhof 1987), or approximately 51 d.

We classified degree of exposure at each nest site when possible. Nest shading was classified as the percent of a nest in shade between 1200 H and sunset. Nests were classified as shaded if >25% of a nest was shaded, inter-mediate if 6–25% was shaded and exposed if ≤5% was shaded.

We observed nesting areas with radio-tagged eagles once every one to two weeks to assess behavior and habitat use during foraging. One observer remained in the canyon near the nest while the other was positioned outside the canyon to follow an eagle by vehicle during forays. We did not follow and observe eagles in control areas.

We used a three-factor (treatment, year, nesting success) log-linear model to test for the effect of radio-tagging (treatment) on nesting success (number of pairs successful/occupied territory) among years. We used a one-factor (treatment) ANOVA with a repeated measure (year) to test for differences between the number of young produced by control and radio-tagged pairs at occupied nesting areas. We used a repeated-measure ANOVA because the same eagles were monitored each year. We used a two-factor (year and treatment) ANOVA to analyze the brood size of successful control and radio-tagged eagles. Sample sizes were too small to use the repeated measures ANOVA for brood size, and treating the data as independent may have inflated the significance of this test.

Small sample sizes of radio-tagged and control eagle nests made conventional significance tests of shading differences suspect, so we analyzed differences in shade characteristics between radio-tagged and control eagle nests using permutation tests (Manly 1991; StatXact software) on each year separately. Nests classified as shaded or intermediate were combined and compared to exposed nests.

We used a one factor (treatment) ANOVA to compare the historical likelihood of nesting successfully between treatment and control nesting areas. Historical likelihood of successful nesting (number of years successful/all years occupied) during 1970–91 was calculated for nine treatment territories and 19 control areas. For this calculation, we excluded controls with more than five consecutive vacancies between 1970–91, or consecutive vacancies in 1992 and 1993 because such nesting areas were also avoided during radio-tagging. This is a conservative bias that excludes extremely unproductive control territories because such territories would not have been selected for radio-tagging. We also excluded one control nesting area with a radio-tagged male present from 1975–80. At nesting areas with past research disturbances, we excluded cases where productivity might have been influenced, including treatment of nestlings for parasites, placement of shade devices and trapping and radio-tagging of adults.

RESULTS

Over all years, tagged and control eagles had similar nesting success (39% of 23 tagged and 51% of 63 control nests were successful). However, differences in nesting success between radio-tagged and control eagles varied significantly among years (3-way interaction of treatment, year and fate: G_2 = 5.82, P = 0.054, Fig. 1). Radio-tagged eagles had similar nesting success compared to control eagles in 1992, but success of radio-tagged eagles was much lower than control eagles in 1993. In 1994, radio-tagged eagles had slightly higher nesting success than control eagles.

The timing of failures varied among years. In 1992, all seven radio-tagged pairs laid and hatched eggs (100%). In 1993, eight of nine (88.9%) tagged eagles laid eggs and four (50%) hatched eggs. In 1994, six of seven (85.7%) tagged pairs laid eggs and four (66.7%) hatched eggs. The percentage of nonlaying control and radio-tagged pairs, respectively, was 17.4% (N = 4) and 0.0% (N = 0) in 1992, 10.0% (N = 2) and 11.1% (N = 1) in 1993, and 38.1% (N = 8) and 14.3% (N = 1) in 1994.

Number of fledglings produced in occupied territories was associated with tagging and year ($F_{2,22}$ = 5.07, P = 0.016). Radio-tagged eagles produced fewer fledglings than control eagles in 1993, but their productivity was the same or slightly higher during 1992 and 1994 (Fig. 1). Combining radio-tagged and control eagles, brood size did not vary among years ($F_{2,35}$ = 2.04, P = 0.15).

The degree of shading at nests did not differ between radio-tagged and control eagles. Between 1992 and 1994, control and treatment groups had similar proportions of exposed nests (1992, 36.8%, N = 19, 28.6%, N = 7; 1993, 38.9%, N = 18, 62.5%, N = 8; 1994, 38.5%, N = 13, 40.0%, N = 5; G_2 = 1.15, P = 0.56).

Historical nesting success of treatment and control territories did not differ ($F_{1,26}$ = 0.003, P = 0.95). The nesting success between 1971–91 was 50.2% (N = 9) for treatment territories and 49.8% (N = 19) of control territories.

DISCUSSION

Decreased Golden Eagle productivity (nesting success, fledglings per occupied territory and brood size) was associated with the presence of a radiotransmitter, but this was significant during only the 1993 breeding season. This is in contrast to Prairie Falcons (*Falco mexicanus*), which carried similar transmitters without negative effects on productivity (Vekasy et al. 1996). The stress of capture did not appear to inhibit nesting success, as most eagles were captured in the winter of 1991–92, and no radio-tagging association with success was apparent during the 1992 breeding season. Male eagles captured at two nesting areas in 1993 both had mates that laid eggs, but both were unsuccessful. One female captured in both 1993 and 1994 did not lay eggs in either year. Effects of capture and handling may be more evident when coupled with other year-dependent stresses. The timing of capture within a winter or the sex of the bird tagged may also influence effects, but our sample size is too small to quantify this.

Golden Eagle productivity appears to be related to jackrabbit density. The variable effect of radio-tagging on productivity in eagles may be related to the dynamics of prey population fluctuations. The strongest association between tagging and success occurred during a precipitous decline in jackrabbit densities (1992–93). We detected no association between tagging and success during a slight recovery from low jackrabbit densities (1993–94) or during years of high jackrabbit densities (1991–92). Radio-tagged eagles may be especially sensitive to changes in prey densities. During periods of low prey densities, foraging opportunities may be reduced, and transmitter loads can decrease maneuverability (Gessaman and Nagy 1988) and may decrease foraging success.

Weather and nest shading may have interacted with low prey populations to reduce radio-tagged eagle nesting success in 1993. Although nest shading did not differ significantly between treatment
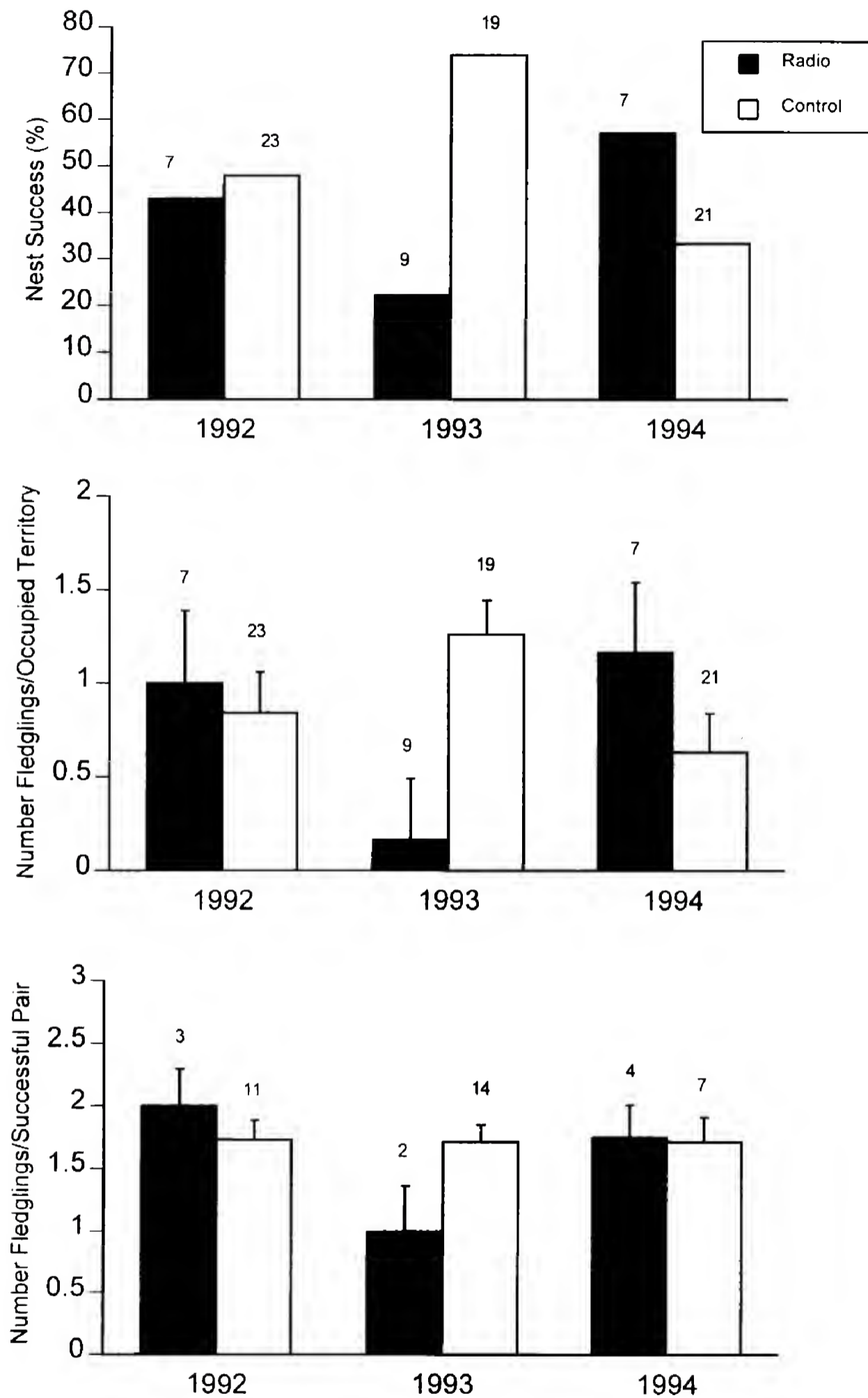
Figure 1.   Radio-tagged and control Golden Eagle nesting success for all occupied nesting areas and mean (±SE) number of fledglings (nestlings ≥51 d old) per occupied territory and per successful pair. Sample sizes (numbers of pairs) are given above error bars.

and control nests, treatment nests in 1993 had the highest percentage of exposed nests (62.5%). Aside from having the lowest prey densities during our study, the spring of 1993 was also very cool and wet (NOAA 1993). Wet weather has been associated with poor foraging success in raptors (Adamcik et al. 1979, Kostrzewa and Kostrzewa 1990), and low prey and poor foraging conditions may disproportionately reduce foraging success of radio-tagged eagles compared to controls. Females we studied left the nest unattended while males were absent and may have left more frequently or for greater durations because of food stress. This may leave eggs and small chicks exposed and could decrease their survival during extreme weather conditions (Mosher and White 1976).

Small sample size may have had the greatest influence on whether or not we detected an effect of radio-tagging on Golden Eagles. We attempted to reduce some of the bias associated with small sample size by comparing historical nesting success between treatment and control territories. However, a slight change in the composition of our sample can have large effects. For example, two radio-tagged pairs had subadult mates in 1993, and both were unsuccessful. Steenhof et al. (1983) found that pairs of Golden Eagles with at least one subadult member had lower nesting success compared to adult pairs. If the age composition of pairs in 1993 had been different or both pairs with subadults had been successful, we may not have detected any difference in nesting success between radio-tagged and control eagles.

LITERATURE CITED

ADAMCIK, R.S., A.W. TODD AND L.B. KEITH. 1979. Demographic and dietary responses of Red-tailed Hawks during a snowshoe hare fluctuation. Can. Field-Nat. 93: 16–27.

BUEHLER, D.A., J.D. FRASER, M.R. FULLER, L.S. McALLISTER AND J.K.D. SEEGAR. 1995. Captive and field tested radio attachment techniques for Bald Eagles. J. Field Ornithol. 66:173–180.

EDWARDS, T.C. AND M.N. KOCHERT. 1986. Use of body weight and length of footpad as predictors of sex in Golden Eagles. J. Field Ornithol. 57:317–319.

FOSTER, C.C., E.D. FORSMAN, E.C. MESLOW, G.S. MILLER, J.A. REID, F.F. WAGNER, A.B. CAREY AND J.B. LINT 1992. Survival and reproduction of radio-marked adult Spotted Owls. J. Wildl. Manage. 56:91–95.

GESSAMAN, J.A. AND K.A. NAGY. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. Condor 90:662–668.

HIRALDO, F., J.A. DONÁZAR AND J.J. NEGRO. 1994. Effects of tail-mounted radio-tags on adult Lesser Kestrels J Field Ornithol. 65:466–471.

HOOGE, P.N. 1991. The effects of radio weight and harnesses on time budgets and movements of Acorn Woodpeckers. J. Field Ornithol. 62:230–238.

KOSTRZEWA, A. AND R. KOSTRZEWA. 1990. The relationship of spring and summer weather with density and breeding performance of the buzzard, goshawk, and kestrel. Ibis 132:550–559.

MANLY, B.F.J. 1991. Randomization and monte carlo methods in biology. Chapman and Hall, London.

MASSEY, B.W., K. KEANE AND C. BOARDMAN. 1988. Adverse effects of radio transmitters on the behavior of nesting Least Terns. Condor 90:945–947.

MOSHER, J.A. AND C.M. WHITE. 1976. Directional exposure of Golden Eagle nests. Can. Field-Nat. 90:356–359.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1993. Local climatic data: Monthly summary, Nat. Weather Service, Boise, ID. Nat. Climatic Data Center, Asheville, NC U.S.A.

PEITZ, P.J., G.L. KRAPU, R.J. GREENWOOD AND J.T. LOKEMOEN. 1993. Effects of harness transmitters on behavior and reproduction of wild Mallards. J. Wildl. Manage. 57:696–703.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pp. 157–170 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.W. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.

———, M.N. KOCHERT AND J.H. DOREMUS. 1983. Nesting of subadult Golden Eagles in southwestern Idaho. Auk 100:743–746.

WANLESS, S. 1992. Effects of tail-mounted devices on the attendance behavior of Kittiwakes during chick rearing. J. Field Ornithol. 63:169–176.

VEKASY, M.S., J.M. MARZLUFF, M.N. KOCHERT, R.N. LEHMAN AND K. STEENHOF. 1996. Influence of radio transmitters on Prairie Falcons. J. Field Ornithol. 67:680–690.

CRESTED CARACARA FOOD HABITS IN THE CAPE REGION OF BAJA CALIFORNIA, MEXICO

RICARDO RODRÍGUEZ-ESTRELLA AND LAURA B. RIVERA RODRÍGUEZ
*Centro de Investigaciones Biológicas del Noroeste, km 1 Carr. San Juan de la Costa,
El Comitán, La Paz 23000 B.C.S., Mexico*

ABSTRACT.—The diet of the Crested Caracara (*Caracara plancus*) in the Cape region of Baja California, Mexico was studied by analyzing 195 pellets collected beneath 10 occupied nests in 1990 and recording prey brought to two nests containing young in 1990–91. Our results showed that Crested Caracaras fed opportunistically on mammals (mainly lagomorphs), reptiles (mainly iguanas and snakes), carrion of domestic animals such as cattle and dogs, and invertebrates (mainly Coleoptera and Orthoptera). The caracaras' ability to kill live prey was denoted both by the high frequency of reptile and bird remains in pellets, and by the high frequency of remains of recently killed birds, lizards and hares that were carried to nests. Our observations at nests indicated that Crested Caracaras killed as much as 63% of vertebrate prey in pellets, while invertebrates may all have been captured alive. Numerically, live prey comprised about 88% of the diet of caracaras in the Cape region. In terms of ingested biomass, lagomorphs (both carrion and killed prey), reptiles (both carrion and killed iguanas, snakes) and carrion of cattle, represented the most important food sources. We discuss the importance of slaughterhouses, henhouses and garbage dumps for young caracaras in the Cape region.

KEY WORDS: *Caracara plancus; Crested Caracara; food; Baja California, Mexico.*

Hábitos alimenticios de Caracara plancus en la región del Cabo, Baja California, México

RESUMEN.—La dieta del caracara común (*Caracara plancus*) fue estudiada en la región del Cabo, Baja California, México, analizando 195 egagrópilas colectadas bajo 10 nidos activos en 1990 y registrando las presas traídas a dos nidos conteniendo 3 y 1 pollos en 1990 y 1991, respectivamente. El caracara es una rapaz oportunista que se alimenta principalmente de lagomorfos, iguanas, culebras, carroña de animales domésticos, e invertebrados (coleópteros y ortópteros). De acuerdo a nuestras observaciones en nidos y al análisis de egagrópilas, estimamos que los caracaras cazaron el 63% de los vertebrados, mientras que los invertebrados fueron todos cazados. Por lo tanto, en términos de frecuencia, las presas vivas representaron alrededor de 88% de la dieta, aunque fueron lagomorfos y reptiles (presas y carroña de ambos grupos), y la carroña de ganado quienes proveyeron la mayor biomasa. Se discute sobre la importancia de los mataderos, granjas avícolas y basureros en la dieta de los jóvenes caracaras en la región del Cabo.

[Traducción Autores]

Among caracaras, the Crested Caracara (*Caracara plancus*) is the species with the widest distribution in America, ranging from Florida, Texas and southern Arizona, through most of Mexico, particularly in deserts and tropical areas (Peterson and Chalif 1973), south to Tierra del Fuego (Brown and Amadon 1968). In spite of its wide distribution, very little is known on the ecology and feeding habits of this species. Currently, studies on its breeding ecology are being carried out in different areas of its distribution (Texas, Dickinson and Arnold 1996; Mexico, Rodríguez-Estrella et al. unpubl. data; Florida, J. Morrison pers. comm.; Argentina, A. Travaini pers. comm.). The Crested Caracara is described to be opportunistic but largely carrion-feeding raptor (Sherrod 1978, Johnsgard 1990), although it may hunt living prey and steal food from other birds (Bent 1938, Hamilton 1981, Whitacre et al. 1982, Rodríguez-Estrella and Rivera 1992). Descriptions of its diet have been largely anecdotical and few quantitative data have been published on variation in feeding habits throughout its range (Bent 1938, Haverschmidt 1947, Sprunt 1954, Glazener 1964, Brown and Amadon 1968, Richmond 1976, Layne et al. 1977, Kilham 1979, Thiollay 1980, Mader 1981, Whitacre et al. 1982, Lyons 1988, Wallace and Temple 1987, Palmer 1988, Yosef and Yosef 1992, Dickinson 1995).

Here, we present information on the diet of a population of Crested Caracaras during the breeding season in the Cape region of Baja California, Mexico.

STUDY AREA

We studied caracaras in the xerophylous scrub vegetation of the Cape region of Baja California (109°60'-111°45'W, 25°45'N). The vegetation is characterized by cardón (*Pachycereus pringlei*), dagger cactus (*Stenocereus gummosus*), mesquite (*Prosopis articulata*), palo verde (*Cercidium microphyllum*), Adam's tree (*Fouquieria diguetii*), plum tree (*Cyrtocarpa edulis*), copal (*Bursera* spp.), lomboy (*Jatropha cinerea*) and cholla (*Opuntia cholla*). The elevation of the area ranges from 0–250 m. This zone is characterized by a mean annual precipitation of 150.6 mm, a winter rainy season and an annual temperature range between 22.1–23.4°C.

METHODS

The breeding season of the Crested Caracara in the Cape region extends from February–August. We collected pellets and prey remains during the breeding season of 1990, particularly in April, May, June and July. Feeding habits were determined by analyzing 195 fresh and whole pellets collected in and around 10 occupied nests. As Chi-square tests did not detect significant differences in the type of prey appearing in pellets from all nests ($P > 0.05$), we pooled all data. Pellets from nests located near henhouses were eliminated from the analysis to avoid an overrepresentation of carrion in the diet. For identification, we compared remains of skulls, bones, hairs, scales, feathers and invertebrates with known reference specimens at the Centro de Investigaciones Biológicas del Noroeste (CIBNOR, Mexico). Prey remains in pellets were identified to the closest possible level of taxonomic resolution. Food-niche breadth was estimated using the Levins (B) index (Krebs 1989). Numbers of prey species were used for computation of niche breadth.

As it was not possible to determine whether mammalian and reptilian prey represented in the pellets were captured alive or collected as carrion by caracaras, we made observations from a blind at a nest one day ($N_1 = 675$ min) and at a second nest for seven days ($N_2 = 3102$ min) to determine the proportion of prey types transported to the nest by adults that were freshly-killed (Richmond 1976, Mader 1981). Nest 1, containing three young near fledging age, was observed on 16 May 1991 and all prey adults brought to the nest were recorded. In 1992, we made similar observations at nest 2 which contained one young approximately two wk old. We observed prey deliveries at this nest from 25 September–21 October, when the young caracara fledged. We analyzed our data in terms of ingested biomass. If a prey item was heavier than 500 g, we considered that the prey was probably consumed as carrion. Mean prey weights were obtained from specimens trapped in the field and from those stored at CIBNOR.

Additionally, the number and age (immature, adult; Clark and Wheeler 1987) of caracaras feeding on carrion at slaughterhouses, henhouses and garbage sites were recorded (Rodríguez-Estrella 1996). Whenever caracaras were found feeding on roadkills, we recorded the species on which they were feeding.

RESULTS

Crested Caracaras preyed on a broad variety of vertebrates and invertebrates (B = 6.3). Prey species richness was over 60 species (Table 1). The most important prey in terms of numbers were insects (mainly Orthoptera and Coleoptera) which represented 68% of the prey items identified (Table 1, $N = 2152$). In terms of biomass, mammals (mainly *Lepus* and *Sylvilagus*) and reptiles (spiny-tailed iguana [*Ctenosaura hemilopha*], and snakes) were the most important prey (almost 80% of ingested biomass, Table 1). We considered that small mammals, birds, small to medium reptiles, and insects, were preyed upon by caracaras as live prey because we recorded caracaras both carrying recently killed items to the nest (Table 2) and killing those prey. Whether mammals and reptiles >500 g appearing in pellets were captured alive and carried to the nests remains unknown, but our observations of prey transported to nests by adults made this seem doubtful. At nest 1, adults delivered one mouse, five birds, one spiny-tailed iguana, one piece of a lagomorph and one unidentified lizard. None of these were >500 g. At nest 2, one kangaroo rat (*Dipodomis merriami*), two woodrats (*Neotoma lepida*), one bird, five lizards, one snake and several pieces of apparently freshly-killed hares and rabbits, none of which were >500 g, were delivered (Table 2). We also observed adult caracaras hunting, pursuing and killing live prey on six occasions: two White-winged Doves (*Zenaida asiatica*), two Inca Doves (*Columbina passerina*) and two spiny-tailed iguanas. Again none of these prey were >500 g.

Adult, but especially immature caracaras were frequently recorded feeding on carrion at henhouses, slaughterhouses and garbages dumps (Rodríguez-Estrella 1996). Most roadkills where caracaras fed were of hares ($N = 20$), cows ($N = 10$), horses ($N = 5$), small reptiles ($N = 5$), small mammals ($N = 5$) and domestic dogs ($N = 3$). Caracaras also fed on maggots (*Cochliomyia macellaria*) at carcasses, adding up to 150 items that one adult ate in 5 min. Caracaras tended at times to follow tractors in fields being plowed catching grasshoppers and small mammals killed by plow.

DISCUSSION

The Crested Caracara in the Cape region is an opportunistic raptor feeding on mammals (mainly

Table 1. Diet of the Crested Caracara in the Cape region of Baja California, Mexico in 1990 as determined from 195 pellets collected at nests. Totals show the number of individuals per group and the ingested biomass in grams. Asterisks indicate that computing weights were a maximum of 500 g.

SPECIES	WEIGHT (g)	% FREQ.[1]	% BIOM.	% APPEAR.[2]
Mammalia				
Lepus californicus	500*	3.6	21.9	39.5
Sylvilagus auduboni	500*	2.4	14.8	26.7
Ammospermophilus leucurus	102	0.8	1.0	9.2
Thomomys umbrinus	103	0.8	1.0	8.7
Chaetodipus arenarius	26.0	0.3	0.1	3.6
Dipodomys merriami	42.0	0.3	0.1	3.1
Peromyscus eva	13.8	0.4	0.1	4.1
Peromyscus sp.	13.0	0.05	tr*	0.5
Neotoma lepida	148	0.3	0.5	3.1
Unidentified rodents	25.0	0.8	0.2	8.7
Canis latrans	500*	0.1	0.9	1.5
Spilogale putorius	500*	0.05	0.3	0.5
Total[3]		213	71 959.1	
Aves				
Falco sparverius	93	0.05	0.05	0.5
Callipepla californica	189.5	0.1	0.2	1.0
Zenaida asiatica	152.9	0.8	1.6	9.2
Columbina passerina	38	0.1	tr*	1.0
Geococcyx californianus	210	0.2	0.5	2.1
Melanerpes uropygialis	54	0.4	0.2	4.1
Colaptes auratus	82	0.1	0.1	1.0
Myiarchus cinerascens	27.4	0.2	0.1	2.1
Aphelocoma coerulescens	84	0.4	0.4	4.1
Campylorhynchus brunneicapillus	49	0.05	tr*	0.5
Phainopepla nitens	25.4	0.05	tr*	0.5
Cardinalis cardinalis	43	0.05	tr*	0.5
Icterus cucullatus	31.8	0.3	0.1	3.1
Polioptila californica	6	0.05	tr*	0.5
Carpodacus mexicanus	21	0.3	0.1	3.6
Passer domesticus	22.4	0.05	tr*	0.5
Unidentified birds	25	3.0	0.9	32.2
Total		131	7606.4	
Reptilia				
Callisaurus draconoides	23.9	0.1	tr*	1.5
Ctenosaura hemilopha	500*	1.9	11.9	21.5
Dipsosaurus dorsalis	60.7	0.6	0.4	6.7
Phrynosoma coronatum	36	1.9	0.8	20.5
Sceloporus hunsakeri	52.5	0.1	0.1	1.5
Sceloporus licki	16.5	0.9	0.2	10.8
Sceloporus monserratensis	17	0.5	0.1	5.6
Sceloporus zosteromus	29.5	0.1	0.05	1.5
Cnemidophorus maximus	24.9	1.2	0.4	13.3
Lampropeltis getulus	229	0.1	0.4	1.5
Masticophis flagelum	300	0.6	2.2	6.7
Pituophis melanoleucus	280	0.2	0.8	2.5
Salvadora hexalepis	170	0.2	0.4	2.1
Crotalus enyo	500*	0.2	1.1	1.5
Crotalus ruber	500*	0.4	2.3	4.1
Unidentified reptiles	25	0.2	0.1	2.6

Table 1.   Continued.

SPECIES	WEIGHT (g)	% FREQ.[1]	% BIOM.	% APPEAR.[2]
Unidentified snakes	500*	2.7	16.8	28.7
Total	263		67 038.1	
Invertebrata				
Arachnida	0.5	0.05	tr*	0.5
Theraphosidae	5.0	0.05	tr*	0.5
Scorpionidae	2.0	0.6	tr*	6.2
Solifugae	0.5	0.2	tr*	0.5
Chilopoda	2.0	0.1	tr*	0.5
Coleoptera	0.5	0.7	tr*	7.2
Carabidae	0.37	0.7	tr*	5.1
Scarabaeidae	0.5	0.5	tr*	3.1
Tenebrionidae #1	0.5	10.9	0.06	40.0
Tenebrionidae #2	0.13	4.3	tr*	20.5
Cerambycidae	1.0	0.3	tr*	2.1
Orthoptera	0.75	0.2	tr*	1.5
Gryllidae	1.0	29.9	0.4	37.9
Acrididae	2.0	11.8	0.3	26.7
Tettigonidae	1.0	0.2	tr*	1.5
Dermaptera				
Formiculidae	0.5	3.1	tr*	9.2
Hymenoptera	0.5	0.4	tr*	2.6
Odonata	1.0	0.05	tr*	0.5
Diptera	0.5	0.05	tr*	0.5
Unidentified	1.0	4.1	0.05	22.6
Total		1466	1470.4	
Unidentified carrion	500*	3.7	15.6	40.5
Total		79	27 300.0	
GRAND TOTAL		2152	175 374.0	

* tr < 0.05% of total prey biomass.
[1] Total number of individuals of each prey type × 100 divided by the grand total number of prey.
[2] Number of occurrences of each prey type × 100 divided by the total number of pellets; because of this, the sum of frequencies may be above 100.
[3] Total number and biomass per group

lagomorphs), reptiles (mainly iguanas and snakes), carrion of domestic animals such as cattle and dogs, and invertebrates (mainly Coleoptera and Orthoptera). Its opportunism is evidenced not only by the breadth of its food niche, but also by the fact that as many as nine prey species can be found in a single pellet. The caracara's ability to kill live prey is denoted by the high frequency of mobile prey including reptiles and birds that appear in pellets and are brought to nests, apparently having been captured alive. Its predatory ability is also demonstrated by the six captures we observed of live prey (doves and lizards) and observations of active prey pursuit and capture elsewhere (Richmond, 1976, Layne et al. 1977, Whitacre et al. 1982).

We were not certain as the proportion of lagomorphs that were taken as carrion or live prey but,

according to our direct observations, we estimated that caracaras killed about 63% of vertebrate prey in pellets (considering conservatively that 35% of lagomorphs were captured as live prey). We assumed that all invertebrates were all captured as live prey. Based on our numerical analysis of the diet, we felt that live prey represented 88% of the diet of caracaras in the Cape region. However, in terms of ingested biomass, lagomorphs (both carrion and killed prey), reptiles (both carrion and killed spiny-tailed iguana and snakes) and carrion of cattle, represented the most important food sources. In Texas, Dickinson (1990) found that the majority of the caracara's diet at nest sites consisted of live-caught prey (61%), with carrion comprising 39%.

Crested Caracaras in Baja California fed nest-

Table 2.   Prey items brought to nests of the Crested Caracara in the Cape region, Baja California, Mexico.

PREY	NUMBER	NOTES
Nest 1, 16 May 1991		
Mammals		
Lepus californicus	1	1 piece of leg
Unidentified rodent	1	complete item
Birds		
Zenaida asiatica	1	complete item
Carpodacus mexicanus	1	complete item
Unidentified bird	3	20–30 g, complete
Reptiles		
Ctenosaura hemilopha	1	complete item
Unidentified lizard	1	complete item
Total items	9	
Rate/day	9	
Rate/hour	0.80	
Nest 2, 25 September–21 October 1992		
Mammals		
Sylvilagus audubonii	2	1 leg, 1 head
Lepus californicus	12	8 pieces of legs, 2 heads
Dipodomys merriami	1	complete item
Neotoma lepida	2	complete item
Birds		
Unidentified bird	1	20–30 g, complete
Reptiles		
Cnemidophorus sp.	3	complete item
Sceloporus sp.	2	complete item
Unidentified snake	1	ca. 100 g fresh snake
Total items	24	
Rate/day	5	
Rate/hour	0.46	

lings mainly with vertebrate prey captured alive, as observed in studies elsewhere (Richmond 1976, Mader 1981), but proportions of prey groups differed. Levy (1988), analyzing 30 pellets collected beneath a nest in Arizona, found that 26% of the pellets contained scales of *Phrynosoma* lizards, 93% contained arthropod remains, and seldom were hairs of lagomorphs identified. Dickinson (1990) reported that invertebrate prey brought to the nests accounted for only 3% of items.

Immature caracaras seem to depend mainly on carrion and invertebrates during the postfledging period as evidenced in our observations that most immatures foraged near slaughterhouses, hen-houses, garbage sites (Rodríguez-Estrella 1996) and cultivated areas rather than in natural areas. Carrion in human refuse areas is a predictable source of food and cultivated areas attract high

numbers of invertebrates (mainly Orthoptera). Thus, these feeding areas are probably important for young caracaras in the Cape region. Indeed, what appeared to be family groups of two adults and one to three young were commonly observed during the postfledging period feeding on human refuse sources and agricultural areas (35.1%, N = 74 group observations). We had the impression that adults lead juveniles to predictable food sources. Additional studies on feeding behavior of immature and adult caracaras during the post-fledging period deserve further attention in order to better understand the process by which juveniles learn to find predictable food sources.

ACKNOWLEDGMENTS

LITERATURE CITED

BENT, A.C. 1938. Life histories of North American birds of prey, Part 2. U.S. Natl. Mus. Bull. # 170.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. McGraw-Hill Book Co., New York, NY U.S.A.

CLARK, W.S. AND B.K. WHEELER. 1987. A field guide of hawks of North America. Houghton Mifflin Co., Boston, MA U.S.A.

DICKINSON, V.M. 1990. Breeding biology and behavior of the Crested Caracara in Texas. M.S. thesis, Texas A&M Univ., College Station, TX U.S.A.

———. 1995. Red imported fire ant predation on Crested Caracara nestlings in South Texas. Wilson Bull. 107: 761–762.

——— AND K.A. ARNOLD. 1996. Breeding biology of the Crested Caracara in South Texas. Wilson Bull. 108: 516–523.

GLAZENER, W.C. 1964. Note on the feeding habits of the caracara in South Texas. Condor 66:162–163.

HAMILTON, K.L. 1981. Caracara kleptoparasitizes marsh hawk. Southwestern Nat. 26:440.

HAVERSCHMIDT, F. 1947. The Black Vulture and the caracara as vegetarians. Condor 49:210.

JOHNSGARD, P.A. 1990. Hawks, eagles and falcons of North America. Smithsonian Institution Press, Washington, DC U.S.A.

KILHAM, L. 1979. Caracara courtship behavior. Raptor Res. 13:17–19.

KREBS, C.J. 1989. Ecological methodology. Harper Collins Publ. New York, NY U.S.A.

LAYNE, J.M., F.E. LOHNER AND C.E. WINGARNER. 1977. Birds and mammal predators of the Cattle Egret in Florida. Florida Field Nat. 5:1–4.

LEVY, S.H. 1988. Status and distribution of the Crested Caracara Polyborus plancus audubonii Cassin 1865 in Arizona. Tech. Rep. Arizona Game and Fish Department, Phoenix, AZ U.S.A.

LYONS, J. 1988. The uncommon caracara. Texas Parks and Wildlife 46:8–11.

MADER, W.J. 1981. Notes on nesting raptors in The Llanos of Venezuela. Condor 83:48–51.

PALMER, R.S. 1988. Handbook of North American birds, Vol. 5. Yale Univ. Press, New Haven, CT U.S.A.

PETERSON, R.T. AND E.D. CHALIF. 1973. A field guide to Mexican birds. Houghton Mifflin Co., Boston, MA U.S.A.

RICHMOND, A.R. 1976. Feeding of nestlings by the caracara in Costa Rica. Wilson Bull. 88:667.

RODRÍGUEZ-ESTRELLA, R. 1996. Response of Common Black Hawks and Crested Caracaras to human activities in Mexico. Pages 356–363 in D.M. Bird, D. Varland and J.J. Negro [EDS.], Raptors in human landscapes. Academic Press, London, UK.

RODRÍGUEZ-ESTRELLA, R. AND L.B.R. RIVERA. 1992. Kleptoparasitism and other interactions of Crested Caracara in the Cape region, Baja California, Mexico. J. Field Ornithol. 63:177–180.

SHERROD, S.K. 1978. Diets of North American falconiformes. Raptor Res. 12:49–121.

SPRUNT, A.P., JR. 1954. Audubon's caracara. Florida Nat. 27:99–101.

THIOLLAY, J.M. 1980. Strategies d'exploitation par les rapaces d'un ecosysteme herbacé Neotropical. Alauda 48:221–253.

WALLACE, M.P. AND S.A. TEMPLE. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290–295.

WHITACRE, D., D. UKRAIN AND G. FALXA. 1982. Notes on the hunting behavior and diet of the Crested Caracara in northeastern Chiapas and Tabasco, Mexico. Wilson Bull. 94:565–566.

YOSEF, R. AND D. YOSEF. 1992. Hunting behavior of Audubon's Crested Caracara. J. Raptor Res. 26:100–101

REMARKABLE SAKER FALCON (*FALCO CHERRUG*) BREEDING RECORDS FOR MONGOLIA

DAVID H. ELLIS
U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708-4019 U.S.A.

MERLIN H. ELLIS
Institute for Raptor Studies, HC 1, Box 4420, Oracle, AZ 85623

PU. TSENGEG
Mongolian State University, Ulaanbaatar—46, P.O. Box 137, Ulaanbaatar, Mongolia

ABSTRACT.—During 1994–95 surveys, we located over 80 Saker Falcon (*Falco cherrug*) breeding sites in Mongolia. Over half of the sites had features that were in some way remarkable or previously unde-scribed in the scientific literature. Ten were on utility poles, two on bridges, three on abandoned build-ings and one was on a truck tire on a pole. Seven sites were very near buzzard nests and two more were in buzzard nests that were used the same season. Five sites were on cliff tops accessible by walking. Four were on very short cliffs, two were on broken/sloping cliffs and one was at the base of a cliff. Five were on the tops of stone pillars. Six were in very short elm trees. Nest composition was also sometimes remarkable: one was a suspended uric acid (excrement) platform without underlying support, three were trash nests and two were composed largely of bones.

KEY WORDS: *Saker Falcon*; Falco cherrug; *proximal nesting; Mongolian birds; nesting situations; Upland Buz-zard*; Buteo hemilasius.

Falco cherrug registros de crías en Mongolia

RESUMEN.—Durante estudios en 1994–95, nosotros localizamos arriba de 80 *Falco cherrug* sitios de cría en Mongolia. Arriba de medio de los sitios tenían elementos que estabán en una manera extraordinario e nunca antes describido en la literatura científica. Diez estabán en postes, dos en puentes, tres en edificios abandonados y uno en una llanta de camioneta en un poste. Siete sitios fueron cerca de nidos de *Buteo buteo*, y dos mas estabán en los nidos de *Buteo buteo* que estabán usadas esa misma temporada. Cinco sitios estabán en precipicios accesible por caminando. Cuatro estabán en precipicios cortos, dos estabán en precipicios quebrados/inclinado y uno estaba en el base del precipicios. Cinco estabán en el cumbre de columnas de pierda. Seis estabán en árboles muy cortos. Composición de nidos también a veces estaba extraordinario: uno estaba suspendido en ácido uric plataforma sin soporte por de bajo, tres nidos eran de basura y dos estabán componida por mayoría de huesos.

[Traducción de Raúl De La Garza, Jr.]

The Saker Falcon (*Falco cherrug*) normally nests on cliffs (short and tall) and in tall trees (Brown and Amadon 1968, Cade 1982). Other species of large falcons are known to occasionally breed on man-made structures (Newton 1979) and one species, the Peregrine Falcon (*F. peregri-nus*), regularly does so, at least in some parts of its range. Remarkably, in the eastern Sahara Des-ert, the Lanner Falcon (*F. biarmicus*) has been reported to breed in such odd situations as in abandoned motor vehicles and on the ground next to fuel cans (Goodman and Haynes 1989). The only published record of a saker possibly nesting on a man-made structure is Baumgart's (1978) reference to a pair that he believed "bred on a ruin" (Baumgart 1980).

During 1994–95 surveys across Mongolia, we lo-cated over 80 saker nests. At 78 of these sites, pairs were breeding the year of our visit. This paper summarizes unusual aspects of these breeding sites. We previously reported saker productivity us-ing data from these samples (Ellis et al. 1995). In

234

Table 1. Features of Saker Falcon nests on man-made structures in Mongolia, 1994–1995.

SUPPORT TYPE	NUMBER NESTS	NEST HEIGHT (STRUCTURE HEIGHT) IN m
Powerline monopod	1	14 (23)
Telephone monopod	1	7 (8)
Powerline bipod	2	8 (9), 7 (8)
Powerline tripod	6	9 (11), 8 (10), 8 (9), 6 (8), 8 (9), 9 (9)
Bridges	2	1.4 (2.3), 2.0 (2.9)
Abandoned buildings	3	5 (7), 3.1 (3.1), 5 (6)
Truck tire on metal pole	1	11 (11)

the only previous study of saker breeding in Mongolia, Baumgart (1978) found several pairs, most of which were believed breeding in the montane forests near Ulaanbaatar.

METHODS

From May–July 1994 and 1995, our survey team, using 4-wheel drive vehicles, traversed 10 781 km in two survey loops beginning in Ulaanbaatar and extending into extreme northwestern Mongolia (1994) and extreme eastern Mongolia (1995). Inasmuch as improved roads are almost nonexistent except near Mongolia's largest cities, our meandering route was largely determined by the presence of potential raptor nesting habitat on the horizon.

At each site, we measured over 20 descriptive parameters. Most measurements were taken directly from taped segments of climbing ropes or using tape measures. Longer distances were estimated from photographs by proportional comparisons with humans of known height or segments of the cliff or other supports of known height or length. Access to powerpole tops was obtained by first shooting a tethered (nylon, monofilament fish line) arrow over a cross arm, hoisting a climbing rope attached to the monofilament, then using conventional climbing ascenders to scale the rope. Poles with ground wires were not scaled. Horizontal measurements were sometimes taken by pacing distances between nest sites. Long distance estimates are believed to be within 5% of their true value. Distances of 10 m or less are accurate to the nearest 2 cm.

RESULTS

We found 10 nests on power or telephone support structures (Table 1). Most of these were constructed by Upland Buzzards (*Buteo hemilasius*), Ravens (*Corvus corax*) or perhaps Black Kites (*Milvus migrans*). Only a small proportion of the poles in Mongolia are used by raptors because pole configurations usually will not support their nests. We found a few fallen nests below poles and more than 100 Upland Buzzard nests on the ground immediately adjacent to utility poles. Sakers never preempted these ground nests. Remarkably, the buzzards were able to fledge young even in areas

where foxes (*Vulpes vulpes* and *Cynalopex corsac*) and wolves (*Canis lupus*) were believed to be common. The utility pole nests were in central and eastern Mongolia and were found only where trees and cliffs were absent. There are records of sakers nesting on utility pylons in Hungary (Bagyura et al. 1994) and a single record for the Lipetsk Region, south of Moscow, Russia (V.M. Galushin, pers. comm.).

Six saker nests were in truly remarkable situations. Two were on very low railroad bridges. One of these was only 1.4 m above water. A second was 2 m above the ground (Fig. 1). Three were on buildings. Two of these were in windows and one was on a rooftop only 3.1 m above ground. One nest was on a truck tire on top of a pipe at the edge of an abandoned Russian military post. All of these unusual nesting situations (Table 1) were in eastern Mongolia and far from sizeable cliffs or forests.

Although we frequently saw Saker Falcons chasing Upland Buzzards, we found seven situations where nests of the two species were in close proximity. Although Dementiev and Gladkov (1951) mention sakers nesting near other raptors, our observations in Mongolia suggest that sakers rarely nest within 200 m of buzzards. At the five exceptional sites, sakers were nesting 4.4–50 m from Upland Buzzards ($\bar{x}$ = 36 m). The most unusual of these nests was only 4.4 m from, and directly above, a buzzard nest (Fig. 2) containing 2 large fledglings. With the oldest saker nestling about 26 days of age, the female spent very little time on the nest except when feeding. From her roost, a Buddhist shrine 250 m away, she harried the buzzards when they came within 200 m of the nest. However, once on its nest, the buzzard could remain unmolested even when the falcon was on hers.

We found two sites where Saker Falcons had nested in nests that were later that same year re-

Figure 1. A saker nest 2 m from the ground on an active railroad trestle.

furbished by Upland Buzzards. At one of these, we found two saker eggs (one dimpled but sloshy and a second egg crushed and being consumed by dermestid larvae) beneath about 10 cm of recently added sticks. At the second nest, we found large, bright (not faded) eggshell fragments beneath about the same depth of sticks. The lack of fresh whitewash at egg level in both nests suggested that neither pair of sakers had hatched or fledged young.

Sakers also occasionally nested near eagles, but not nearly as close as to Upland Buzzards. We found two Steppe Eagle (Aquila nipalensis) nests, each approximately 1.5 km from saker nests. The nearest occupied Golden Eagle (Aquila chrysaetos) nest containing one nestling was estimated to be within 200 m of a saker brood, occupying one of the eagle's alternate nests.

Most Saker Falcon cliff nests are placed in inaccessible niches. However, we found five nests placed at the very tops of cliffs (Table 2). All of

these were approachable from above by walking, with no climbing or descending required. These sites were sometimes beside an emergent boulder, but each nest could be easily entered by a wolf, and the eggs in one had been burned in a grass fire.

At four other sites, the nests were inaccessible, but the cliffs were very short (<6.5 m high, Table 2). Two other nests were on sloping or broken cliffs that were accessible from above, below, and/or the side. The most accessible scrape was on bare soil at the very base of a tiny, sloping cliff. It had nonetheless fledged at least two young just prior to our visit.

Five saker nests were on stone columns with little or no shade for either the brooding adult or the nestlings (Fig. 3). All of these pillars were steep enough to require climbing, but only the two tallest were secure from mammalian predators.

Although falcons do not build nests (Ellis 1993), one of our saker sites seems to violate this rule

Figure 2. A cliff top Saker Falcon nest with an Upland Buzzard nest 4.4 m below.

Table 2. Features of Saker Falcon nests on very short or broken cliffs.

LOCATION OF NEST	NUMBER NESTS	NEST HEIGHT (CLIFF HEIGHT) IN m
On accessible cliff top	5	8 (9), 3.1 (3.4), 3.7 (3.7), 5.5 (5.5), 5.2 (5.8)
On cliff face	4	3.0 (5.8), 4.0 (4.9), 4.1 (6.3), 3.2 (4.7)
On sloping or broken cliff	2	2.1 (2.7), 2.4 (2.7)
At cliff base	1	0.0 (ca 3)

(Fig. 4). It consisted of an unsupported uric acid (excrement) platform wedged into a crevice. A twig clinging to its underside evidenced that it was once underlain and supported by a stick nest.

Many saker nests contained trash collected by the previous occupants. In three of these, trash items were conspicuously important in their composition and long stringers of wire, twine, or cloth dangled from the rim. On the open steppe where few natural building materials are available other than grass, raptors of several species routinely use cast off clothing, machine parts, wire, bones, and tools as nesting material. In one Upland Buzzard nest, we even found paper money.

Dementiev and Gladkov (1951) previously reported a Saker Falcon nest in an elm tree (*Ulmus* sp.) in Mongolia. We found six instances of Saker Falcons using small elms in southeastern Mongolia. These were 2.7–4.0 m above the ground in elms ranging from 4.9–8.5 m tall. All of these were stick nests probably built by either Black Kites or Upland Buzzards. All but one tree provided a closed canopy, shading the nest.

Figure 3. A nest on a short, broad, unshaded pillar in southeastern Mongolia.

Figure 4.   This nest is an unsupported uric acid platform, formerly underlain with a stick nest.

DISCUSSION

Saker Falcons are now known to breed in a wide variety of situations in Mongolia. Many of these were previously unreported for the saker and some are new for any large falcon. Probably the most remarkable structural supports were the two very low, railroad trestles and the elevated tire. From a behavioral viewpoint, the nest only 4.4 m from a buzzard nest was most remarkable. The saker's adaptability in using a wide range of breeding situations is, no doubt, a response to favorable prey populations in areas lacking large trees and cliffs.

ACKNOWLEDGMENTS

LITERATURE CITED

BAGYURA, J., L. HARASZTHY AND T. SZITTA. 1994. Methods and results of Saker Falcon *Falco cherrug* management and conservation in Hungary. Pages 391–395 *in* B.-U. Meyburg and R.D. Chancellor [EDS.], Raptor conservation today. WWGBP/The Pica Press, London, UK.

BAUMGART, W. 1978. Concerning plumage status, and migration of breeding eastern Saker Falcons. [In German]. *Mitt. Zool. Mus. Berlin* 54 (Suppl., Ann. Orn. 2): 145–166.

———. 1980. Der Sakerfalke. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world, Vol. 2. McGraw-Hill, NY U.S.A.

CADE, T.J. 1982. The falcons of the world. Comstock/ Cornell Univ. Press, Ithaca, NY U.S.A.

DEMENTIEV, G. AND N.A. GLADKOV [EDS.]. 1951. Birds of the Soviet Union, Vol. 1. Gosudarstvennoe Izdatel'stvo "Sovetskaya Nauka", Moskva. Translated from Russian by the Israel Program for Scientific Translations, 1966 (Vol. 1), Jerusalem, Israel.

ELLIS, D.H. 1993. Do falcons build nests? *J. Raptor Res.* 27:217.

————, M.H. ELLIS AND PU. TSENGEG. 1995. Productivity of Saker Falcons (*Falco cherrug*) in Mongolia. Pages 117–130 *in* Proc. Specialist Workshop, Middle East Falcon Research Group, Abu Dhabi, U.A.E.

GOODMAN, S.M. AND C.V. HAYNES, JR. 1989. The distribution, breeding season, and food habits of the lanner from the eastern Sahara. *Natl. Geogr. Res.* 5:126–131.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

SPATIAL INCIDENCE OF BARRED OWL (*STRIX VARIA*) REPRODUCTION IN OLD-GROWTH FOREST OF THE APPALACHIAN PLATEAU

J. CHRISTOPHER HANEY[1]

Wildlife Technology Program, School of Forest Resources, The Pennsylvania State University, DuBois, PA 15801 U.S.A.

ABSTRACT.—Barred Owl (*Strix varia*) occurrence and breeding were evaluated in old-growth forest using Poisson and binomial models constructed with seven spatially-explicit parameters derived from territorial density. Reproduction was evidenced by owl chicks heard inside cavity nests or being fed by adults in old-growth deciduous (beech-maple, oak-hickory) and old-growth mixed forest types (hemlock-white pine-deciduous). Barred owls nested on 64% of 11 relatively small (6–33 ha) study plots. Probabilities of obtaining this many cases of breeding or occurrence by chance alone were extremely low in all model executions, ranging to as little as $P = 1.6 \times 10^{-7}$. Compared to managed forests, old-growth forests used by breeding owls typically had higher snag densities and basal areas, large (≥ 45 cm dbh) eastern hemlock (*Tsuga canadensis*), some large live trees 50–100 cm dbh, and reduced understories. Among old-growth stands, vertical ($P = 0.06$) and horizontal complexity ($P < 0.01$) of the canopy differed significantly between areas used and not used for breeding. As in other *Strix*, I infer that spatial juxtaposition of structural features in late successional forest favors localizing reproductive effort within a small subset of the owl's home range. Older forest provides large cavities for nesting, a dense canopy for thermoregulation and protection from mobbing, and sparse ground cover that may facilitate prey detection and capture. All of these structural features are enhanced by life history characteristics of eastern hemlock.

KEY WORDS: *Barred Owl; Strix varia; reproduction; breeding season habitat; habitat use; eastern old-growth; Pennsylvania.*

Incidencia espacial de Búhos (*Strix varia*) reproducción en bosques viejos en el Appalachian Plateau

RESUMEN.—Ocurrencia y crianza del Búho (*Strix varia*) fueron evaluados en bosque de crecimiento-viejo usando modelos Poisson y binomial construidos con siete parámetros explícitos derivados de densidad territorial. Reproducción fue indicado por búhos chicos oídos dentro de la cavidad de nidos o por los adultos dándoles de comer en crecimiento-viejo de bosques de hoja caduca (beech-maple, oak-hickory) y bosque mixtos de crecimiento-viejo (hemlock-white pine-deciduous). Búhos estabán en nidos en 64% de 11 lugares de estudio relativamente pequeños (6–33 ha). Probabilidades de obteniendo tantas situaciones de cría y ocurrencias por chanza sola eran muy bajas en modelo executaciones, desde tan poco come $P = 1.6 \times 10^{-7}$. Comparado con bosques manejados, bosques de crecimiento-viejo usados por búhos que crían típicamente tenían densidades altas y áreas (basal), grandes (≥ 45 cm dbh) *Tsuga canadensis*, unos árboles grandes 50–100 cm dbh, y vegetación reducidas por de bajo. Dentro de áreas de bosques de crecimiento-viejo, vertical ($P = 0.06$) y complexidad horizontal ($P < 0.01$) del dosel vario mucho entre áreas usadas y áreas no usadas para cría. Como en otras *Strix*, Yo digo que espacial yuxtaposición de elementos estructurad en bosques sucesional tardes hace favor de localizar esfuerzos reproductivo dentro de un lugar chico en el arreo de los búhos. Bosques maduros mantienen cavidades grandes para nidos, un dosel denso para reglamentación termal y protección de una multitud, y un suelo disperso que puede facilitar detección de presa y captura. Todos estos elementos estructurad mejoran los característicos históricos de la vida del *Tsuga canadensis*.

[Traducción de Raúl De La Garza, Jr.]

Mature and structurally-complex forest is a common feature of breeding habitat in North American *Strix* owls. Affinities for old-growth forest are more widely recognized in the Northern (*S. occidentalis caurina*, Forsman et al. 1984), California (*S. o. occidentalis*, Gutiérrez et al. 1992) and Mexican Spotted Owls (*S. o. lucida*, Ganey and Balda 1994), but Great Gray (*S. nebulosa*) and Barred Owls (*S.*

varia) have also been linked with late successional forests with large-diameter trees (Elody and Sloan 1985, Allen 1987, Bull et al. 1988). Extensive tracts of old-growth containing eastern hemlock (*Tsuga canadensis*) were identified as important Barred Owl habitat a century ago (Bolles 1890, Eifrig 1907).

Barred Owls have been chosen as a management indicator species in several eastern national forests (USDA 1985, 1986), and are classified as threatened in some states (Bosakowski 1994). Concern for this species has increased because of its sensitivity to anthropogenic disturbance, including forest fragmentation, and because such land-use practices may indirectly erode integrity of its habitat via increasing competition with the more disturbance-tolerant Great Horned Owl (*Bubo virginianus*) (Morrell and Yahner 1994, Laidig and Dobkin 1995).

Generally an uncommon nocturnal predator, the Barred Owl occurs at low densities (one territory per 2.5–6.5 km^2; Nicholls and Fuller 1987, Bosakowski et al. 1989). Populations can be monitored by broadcasts of conspecific recordings (McGarigal and Fraser 1985, Mosher et al. 1990), but playback may elicit little response from Barred Owls during incubation and early chick rearing (Devereux and Mosher 1984, Laidig and Dobkin 1995). Objectives of this study were to develop and test statistical models that would evaluate Barred Owl use of breeding sites in old-growth forest using passive sampling at spatial scales less than the size of the home range and to describe structural attributes and habitat configuration in the general vicinity of breeding sites (Hunter et al. 1995).

METHODS

Study Areas. Potential study areas on the Appalachian Plateau physiographic province in western and northcentral Pennsylvania (Fig. 1) were first screened by consulting inventories of locations, forest type, management regime and size of remaining old-growth forests (Mickalitis 1956, Erdman and Wiegman 1975, Smith 1989). Because a major criterion for plot selection was a size sufficient to contain the minimum recommended area for a Breeding Bird Census (BBC) in forested habitat (10 ha, Lowe 1995), the smallest sites (26%, $N = 51$) were excluded from consideration. Two or more study plots were established in each of the three largest consolidated tracts of mixed old-growth forest in Pennsylvania: Cook Forest State Park (>200 ha); Tionesta Scenic and Research natural areas (1675 ha) and Heart's Content, Allegheny National Forest (60 ha).

Aerial photos and detailed maps of stand ages were used visually to establish eleven 10–18 ha plots away from
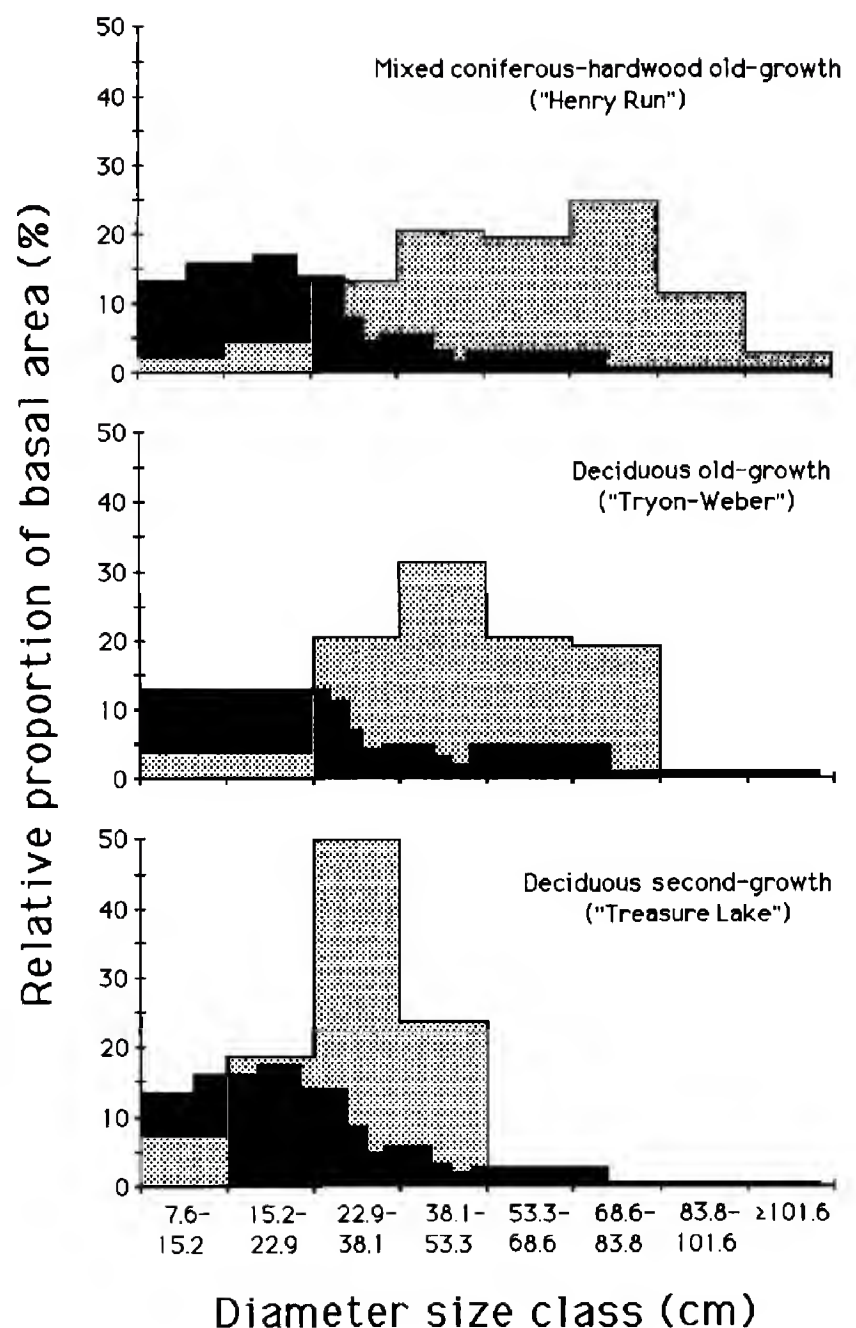
Figure 1.   Characteristic diameter size-class distributions of old-growth mixed, old-growth deciduous, and young, previously-harvested deciduous forest. Black histograms represent regional averages for all size classes as calculated with data from the relevant regional unit as summarized in Alerich (1993); different widths to histograms reflect varying size-class intervals for which data were available. Stippled histograms represent the size distributions of trees observed on plots in this study.

roads, rights-of-way, habitat edges and extensive windthrows, and in areas where vegetation age and composition were relatively uniform. Due to limited availability, small size of potential study areas and other logistical constraints, random selection of study plots within sites was not feasible. Nevertheless, all plots were chosen without prior knowledge of the presence of Barred Owls. Variable extent and shape of old-growth forest remnants also necessitated study plots of different sizes; plot shapes were usually square or rectangular. Combined area of all study plots used in this study was approximately 4% of the total old-growth known to remain in Pennsylvania (Haney 1996).

Compared to nearby managed forests, old-growth sites

ın this study possessed stand ages older than the average age at which disturbances interrupt succession (200–300 yr), basal areas 30–73 m²/ha, large (70–100 cm dbh) live and dead trees, canopy cover ≥90% and a primary mode of disturbance by windthrow. Eastern hemlock made up 37–70% of the canopy at mixed forest sites; codominant canopy trees included various hardwoods and occasionally a few eastern white pine (*Pinus strobus*). All three large old-growth study sites were embedded in mostly unfragmented landscapes with extensive forest cover (≥3000 ha, Fig. 1).

Internal structure of mixed old-growth sites has never been altered substantially (Hunter 1989). Each site is dominated by very old forest. No extensive cutting has ever been conducted and stand ages (based on coring) are generally >300 yr. There is some evidence of historical fire in both Cook Forest and Heart's Content, but not in Tionesta (Hough 1936). American chestnut (*Castanea dentata*) was never prevalent (≤10% canopy) or widespread at study sites (Hough and Forbes 1943, Abrams and Ruffner 1995) except for Heart's Content, where it was once the third most common canopy species (Lutz 1930). On the other hand, there has been an eight-fold reduction in total area of this forest type on the northern Appalachian Plateau since presettlement times (Abrams and Ruffner 1995).

Due to the regional rarity of deciduous old-growth (Erdman and Wiegman 1975, Smith 1989), only small sites with this forest type were available, and two plots did not meet the minimum preferred size for BBCs. Although possessing large trees, pit-and-mound topography, considerable coarse woody debris (CWD) and other elements of old-growth, the four smaller deciduous old-growth sites were probably cut selectively sometime late ın the 19th or early 20th century. Deciduous plots were located in fragmented landscapes; all were bordered on two or more sides by fields, roads and other open areas. Three sites were in glaciated northwestern Pennsylvania where original forest was beech-maple (*Fagus-Acer*). The fourth deciduous plot was dominated by a mixture of hardwoods, including hickory (*Carya*), oaks (*Quercus*) and maples.

Two 15-ha plots were also established in 40–60-yr-old managed forest on the Appalachian Plateau. Prior to cutting, compositions and basal areas of canopy trees on these plots were similar to the mixed old-growth forest. Further details on the vegetation, exact locations and topographic setting of study plots can be found in *J. Field Ornithol.* 65(Suppl.):73–74, 88–93, and 66(Suppl.):53–54, 56–59, 70–71, 82–88.

Data Collection. Barred Owls and nest sites were detected during repeated (7–10) visits to each study plot while territory mapping for BBCs during the 1993–94 breeding seasons; from one to three additional visits per plot were undertaken to measure vegetation. Each mapping visit, lasting from 1.5–4.0 hr, involved slowly walking established census lines ≤100 m apart and delineating bird territories within gridded plots at 25–50 m resolution. Order of visitation (date and time of day, whether dawn, mid-morning or dusk) was randomized. Two visits at dusk were generally made on each plot. All BBC visits were conducted between 22 April–5 July, a period coin-

ciding with incubation, brooding and prefledging of the Barred Owl (Johnsgard 1988).

Reproduction was determined by beak clapping, hissing and food-begging calls of young from within nest trees, or observations of stationary, prefledging juveniles outside nests begging from or being fed by adults. Adult owls often flushed from daytime roosts and gave nonelicited calls during visits, but adult presence alone was not considered evidence of reproduction.

Data Attributes and Model Construction. Study plots (Table 1) were quite small relative to home ranges recorded for Barred Owls (86–370 ha, Nicholls and Warner 1972); techniques appropriate for other birds, such as the BBC, are usually unsuitable for wide-ranging and secretive raptors (Fuller and Mosher 1981). Over spatial scales at which field work was conducted, occurrence of Barred Owl nests would be unexpected even if plots happened to be fortuitously located within an owl territory. This was not necessarily the case as plots were located solely on the basis of their old-growth chararacteristics On the other hand, two or more plots that were close together might be situated within a single territory and thus not represent independent sample units.

These elements of the field sampling required developing a statistical approach that addressed explicitly each of the data attributes mentioned above. Thus, I chose a simple probability approach for testing occupancy of habitats by Barred Owls. Binomial models better account for frequency of occurrence in a set of samples (e.g., "incidence," Wright 1991), and similar approaches have been applied to other studies of *Strix* owls (Azuma et al. 1990, Gutiérrez 1994). The general null hypotheses tested were that Barred Owl reproduction and territorial occupancy did not occur in old-growth forest more than expected by chance.

Given a documented upper limit of approximately 370 ha for the home range (Nicholls and Warner 1972), only distances ≥1.0 km (the approximate radius of a circle having area 370 ha) could certainly be supposed to contain biologically-independent territories. Plots separated by distances less than 1000 m were therefore combined into a single unit, ultimately reducing sample size from 15 to 11 (Table 1). This interval to independence was of the same order used in other studies where the survey scale matched movement distances by the species (Bosakowski et al. 1987, Laidig and Dobkin 1995).

Modeling was approached as follows: if owl nests are located randomly within a hypothetical home range of area B, and plot A represents some fraction of this area, then let $\hat{p} = A/B$. The variable $\hat{p}$ is the binomial for the likelihood that reproductive effort will be localized in area A (= positive incidence), and is expected to be quite small, except for plots of moderately large size (e.g., $\hat{p} = 0.10$ if $A = 10$ ha and $B = 100$ ha). Values for A were derived from plot sizes used in the study, including plots combined due to spatial proximity (Table 1). Parameter values for B were obtained from the literature: minimum, mean and maximum home range (Nicholls and Warner 1972), and mean annual and mean summer home range (Elody and Sloan 1985).

Probabilities of owl reproduction on a particular plot were estimated by dividing its area, A, by each of the parameter values available for B. For plots studied both

Table 1. Cumulative (observed) probabilities ($\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$) of the likelihood of Barred Owl reproduction in sample plots during a 2-yr period in eastern old-growth forests. The subsample ($N = 11$ plots) includes four pairs of plots that were combined due to spatial proximity (see Methods). Final probabilities indicate the likelihood of obtaining as many instances of owl reproduction as were actually observed across all plots. Seven different estimates of Barred Owl home range size or density were used to develop probabilities.

	PLOT						
	MIXED CONIFEROUS-DECIDUOUS						
PARAMETER	SWAMP[a] 15 ha	SENECA[a] 15 ha	CATHE-DRAL/HILL-SIDE[a] 33.2 ha	HENRY RUN 15 ha	TIONESTA I,II[a] 24 ha	TIONESTA III,IV 24 ha	HC I,II 22 ha
BBC area (0.0095/ha)	0.2451[b]	0.2451	0.4326	0.1430	0.3529	0.7712	0.2097
BBC incidence (0.1413)	0.2532	0.2532	0.4417	0.1487	0.3627	0.7620	0.2182
Mean home range (229 ha)[c]	0.1207	0.1207	0.2448	0.0645	0.1851	0.8968	0.0946
Min. home range (86 ha)[c]	0.2880	0.2880	0.4740	0.1744	0.4024	0.7209	0.2558
Max. home range (369 ha)[c]	0.0778	0.0778	0.1634	0.0405	0.1213	0.9351	0.0595
Mean annual home range (282 ha)[e]	0.1007	0.1007	0.2077	0.0532	0.1557	0.9149	0.0780
Mean summer home range (118 ha)[e]	0.2219	0.2219	0.4044	0.1271	0.3240	0.7966	0.1864

[a] Plot studied during both breeding seasons (1993, 1994).
[b] Final probability based on multiplication rule, i.e., the product of all cumulative probabilities of owl reproduction across all plots.
[c] Nicholls and Warner (1972).
[d] Exact probabilities are 1.6 and 7.4 $\times$ 10^{-7} for maximum and mean annual home range parameters, respectively.
[e] Elody and Sloan (1985).

years, the probability of finding reproduction in one, neither or both study years is given by the binomial expansion: p^2, q^2, or $2\hat{p}\hat{q}$, where $\hat{q} = 1 - \hat{p}$ (e.g., the probability that a plot will not have owl breeding; = negative incidence). Because in no plot was reproduction detected in both years, nor did any plot studied for two years fail to have reproduction in one of the years, in practice only $\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$ gave cumulative plot probabilities. The fact that no plot had nests or fledgings in both years, and plots studied for two years had a nest or fledgings in at least one year, mitigated against violating the independence assumption for binomial trials (Snedecor and Cochran 1980).

In addition to home range size, two other estimates of $\hat{p}$ based on published BBCs were available. The first ($\hat{p}$ = 0 0095/ha) was calculated by dividing the total number of owl territories by the total area of all study plots in a sample of 92 BBCs (J. Field Ornithol. 64[Suppl.] and 65[Suppl.]). These 92 BBCs originated solely from within the species' range and consisted of all available plots from potential habitat (completely vegetated plots in upland forest). The second estimate ($\hat{p}$ = 0.1413) was derived by taking the proportion of the 92 BBCs on which entire or partial Barred Owl territories were registered. Note that neither BBC estimate for $\hat{p}$ necessarily implies that reproduction occurred; rather, it is a measure of territorial occupancy.

Statistical Analyses. Each of five home range- and two BBC-based parameter values for $\hat{p}$ was used to calculate a plot-specific probability of reproduction for either one

or two years; that is, the product of plot area with $\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$. Each of the seven parameter values was subsequently used to compute a final cumulative probability of reproduction using the binomial multiplication rule (e.g., the product of probabilities in a specified series of events such as owl reproduction in independent plots). Use of different parameter values for $\hat{p}$ acted as a sensitivity analysis in executions of the binomial model to allow examining whether results were solely the consequence of parameter outliers.

In a second approach, I used a two-sample test of proportions (Snedecor and Cochran 1980) to evaluate the probability of obtaining the observed number of Barred Owl territories in old-growth. If $\hat{p}_1$ is the probability of territorial occupancy in the sample of old-growth plot-years (where $N_1 = 15$), and $\hat{p}_2$ is the probability of territorial occupancy in a sample of BBCs ($N_2 = 92$ plot-years), then the test statistic for differences between two sample proportions is given by the normal deviate, Z, where:

$$Z = \hat{p}_1 - \hat{p}_2 / \sqrt{\hat{p}\cdot\hat{q}(1/N_1 + 1/N_2)},$$

and $\hat{p}$ and $\hat{q}$ are the joint probabilities across all BBCs ($N = 107$) of finding and not finding owls, respectively.

Reproduction by Barred Owls at spatial scales employed in this study should be rare, a condition for which the Poisson distribution is well-suited. I calculated the expected number of reproductive events (nests or owl fledgings) in $r = 11$ trials (number of combined plots) using the highest, most conservative parameter value

Table 1. Extended.

PLOT				
DECIDUOUS				
PRINCE GALLITZIN 10.3 ha	ERIE I 6 ha	ERIE II 7.5 ha	TRYON-WEBER 9.8 ha	FINAL P
0.9023	0.9428	0.9285	0.0929	0.000109[b]
0.8984	0.9405	0.9256	0.0967	0.000129
0.9559	0.9742	0.9678	0.0419	0.000002
0.8808	0.9302	0.9128	0.1134	0.000247
0.9723	0.9838	0.9797	0.0264	<0.000001[d]
0.9637	0.9787	0.9734	0.0346	<0.000001[d]
0.9131	0.9492	0.9364	0.0826	<0.000064

available ($p = 0.1413$, Table 1). If owl reproductive events are distributed randomly with average incidence, p, the number of events expected in a sample of size C is a Poisson variable with mean pC (Snedecor and Cochran 1980). If there are more incidences of owl reproduction than expected, the Poisson model will be a poor fit and the null hypothesis of randomness will be rejected. Expected values for the number of reproductive events ≥ 1 were figured with the Poisson expression:

$$\Sigma \; P(r) = (p^r/r!)e^{-p}, \quad \text{for all } r > 0,$$

and where $e = 2.71828$, the base of natural logarithms (Snedecor and Cochran 1980). Expected values were then compared to those actually observed using a χ^2 test for goodness-of-fit.

Although I provide exact probability values (P) for model runs, these estimates are biased (albeit conservatively so). For example, if any plot was actually outside an owl home range, values of p based on area would be inflated, increasing the likelihood of falsely accepting the null hypothesis of no effect of old-growth on owl reproduction. Such bias acts to increase the final absolute value of P. Although this increases risk of Type II error, I was more concerned in these analyses with making false conclusions regarding Barred Owl use of old-growth. Thus, P values should be considered as upper limits on the real chance of committing a Type I error. To guard against Type II error resulting from small sample sizes, inferences were considered significant at $\alpha = 0.10$. When available, I provide observed significance levels (Forbes 1990).

Vegetation Measurement. On the basis of breeding, I poststratified plots to compare vegetation characteristics of forest stands used and not used by owls. Canopy composition and shrub stem density on all plots were estimated at randomly-drawn points with 0.04 ha circular subplots (James and Shugart 1970); sample size for circular subplots was set uniformly at one per ha of total plot size (4%). Canopy height was measured at each subplot with a clinometer. Canopy foliage (leaf) cover was

estimated with a concave spherical densiometer (Lemmon 1957) based on the average of measurements from four cardinal directions. Systematic transects were used to estimate size, total elliptical area and frequency of treefall gaps (Runkle 1985); 10 m $\times$ 50 m randomly-chosen rectangular plots were used to measure snag type and density, and type, volume and biomass of downed CWD (Tyrrell and Crow 1994).

RESULTS

Incidence of Reproduction. During both years, Barred Owls nested on 7 of 15 (47%) original plots, or 7 of 11 (64%) combined plots (those ≤ 1000 m apart). Nests ($N = 1$) or prefledging juveniles ($N = 6$ instances) were recorded on "Seneca" and "Tionesta I/II" in 1993, and "Swamp," "Hillside/Cathedral," "Henry Run," "Heart's Content I/II" (HC I) and "Tryon-Weber" in 1994 (Table 1). The single nest detected was in a live eastern hemlock with a broken top. Five of 6 sets of juveniles (1–3 individuals per brood) were also being fed in large, old hemlocks. Reproduction occurred on more of the combined plots dominated by mixed conifer-hardwood old-growth (86%) than plots dominated by deciduous old-growth (25%; $Z = 2.033$, $P = 0.05$).

Adult owls were recorded as visitors, or had partially-overlapping territories, on other plots and/or during other years: "Hillside/Cathedral" in 1993, and "Seneca," "Tionesta I/II" and "Erie II" in 1994. In none of these instances was reproduction confirmed, although it could have occurred nearby in similar forest surrounding most plots.

Model Results. With the first model, some parameter values for p gave significant incidences of reproduction on single plots within a single year. Reproductive incidence on the "Tryon-Weber" plot alone was significant for all but the minimum home range parameter ($p > 0.10$). Greater than expected reproduction in a single year also occurred when the model was executed with parameter maximum home range (5 plots), mean home range and mean annual home range (3 plots), BBC area, BBC incidence, and mean summer home range (1 plot). No plot had a significantly greater than expected incidence of reproduction within a single year when the model was executed with the minimum home range parameter.

Observed number of reproductive events in old-growth was highly unlikely due to chance alone (Table 1). No final cumulative probability with the binomial model exceeded $P = 0.000247$, and one cumulative probability (using the model parameter

Table 2. Comparison of observed and expected number of breeding incidences by Barred Owls in some eastern old-growth forest. Expected numbers were generated with a Poisson model of rare events in 11 trials (plots).

Breeding Incidences	Expected	Observed
0	9.551	4
≥1	1.449	7
Total	11.000	11

maximum home range) fell to $P = 1.6 \times 10^{-7}$. When all plots were analyzed jointly, each parameter value for p gave a highly significant final result, giving no indication that results came from outliers (extreme values) in model parameters.

Other statistical models gave similar results. There were more incidences of reproduction than expected under the Poisson model ($\chi^2 = 24.47$, $P < 0.0001$; Table 2). Based on a two-sample test of proportions, there were also more occurrences of territory occupancy in plots located in old-growth (80%) compared to younger, managed forests (14%; $Z = 5.63$, $P < 0.0001$).

Vegetation Characteristics. Relative to the entire regional landscape, diameter size distributions of canopy trees were different in old-growth plots used for breeding (Fig. 1). Both mixed and deciduous old-growth plots had more diverse diameter size classes in canopy trees, and were skewed toward trees in larger size classes. Most plots used by owls had at least some very large trees (70–100 cm dbh). No evidence of owl reproduction or of territorial occupancy was found in younger forest. Power to detect avoidance of this habitat type was very low, however. Analyses indicated that with the binomial model $N \geq 12$ 15-ha plots would be required to detect whether owls used younger forest less than expected.

Canopy complexity created by tree-fall gaps distinguished old-growth sites used and not used for breeding (Table 3). Owls bred where on average such canopy gaps opened up 8% of the stand; no breeding was observed where less than 5% of the stand was in tree-fall gaps. No significant differences were detected in the size class distributions of canopy gaps (Kolmogorov-Smirnov $\chi^2 = 3.34$, maximum difference 0.133, $P = 0.361$; Fig. 2).

Table 3. Comparison of forest structure at old-growth sites used and not used for breeding by Barred Owls.

Structural Characteristic	Breeding ($N = 7$)			Not Breeding ($N = 9^a$ or 10)			Comparison			
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	Z^b	U	U'	P^b
Tree stems (per ha)	499	50.4	348–644	473	41.6	317–697	−0.342	31.5	38.5	0.732
Basal area (m²/ha)	38	2.7	30–49	42	4.1	31–73	−0.441	30.5	39.5	0.659
Hemlock basal area (m²/ha)	17	3.2	<1–25	12	4.1	0–30	−0.587	29	41	0.557
Canopy height (m)	30	2.0	21–34	29	1.8	20–37	−0.532	26.5	36.5	0.595
Range canopy height (m)	14	1.5	10–20	11	1.9	6–24	−1.865	14	49	0.062
Variation canopy height (CV)	16	1.9	11–25	12	1.2	8–19	−1.747	15	48	0.081
Canopy gaps (%)	8	1.0	5–13	4	0.8	0–9	−2.733	7	63	0.006
Mean canopy gap size (m²)	116	34.7	37–301	159	71.5	0–728	−0.489	30	40	0.625
Largest canopy gap (m²)	430	107	133–915	658	253	0–2261	−0.195	33	37	0.845
Foliage cover (%)^c	96	1.1	92–99	97	0.7	93–99	−0.401	31	39	0.689
Snag stems (per ha)	32	5.6	12–54	42	6.0	20–73	−0.977	25	45	0.329
Snag basal area (m²/ha)	4	1.2	1–9	4	0.9	1–8	−0.683	28	42	0.495
Snag volume^d (m³/ha)	48	13.5	3–100	51	21.8	4–222	−0.586	29	41	0.558
Volume CWD^e (m³/ha)	152	47.8	20–408	142	57.9	8–612	−0.586	29	41	0.558
Biomass CWD (10³ kg/ha)	27.5	6.6	2.8–58.4	28.2	12.1	1.3–124.6	−0.781	27	43	0.435
Shrub stems (10³/ha)	4.8	2.7	0.2–20.7	5.9	2.5	1.2–24.6	−0.688	25	38	0.491

[a] Some missing data for one plot.
[b] Mann-Whitney U-test corrected for ties.
[c] Relative cover; high canopy cover in this study mitigated against potential positive biases found in some forest stands measured with densiometers (see Cook et al. 1995).
[d] Volume estimates based on decay classes defined in Cline et al. (1980), Tyrrell and Crow (1994).
[e] CWD = coarse woody debris; biomass of downed tree boles estimated as a function of decay class (Tyrrell and Crow 1994).

Table 4. Number of samples[a] (as a function of plot size, in ha) required to detect significantly more incidences (= positive incidence) of breeding by Barred Owls than expected by chance.

| | | ALPHA LEVEL | | | | | | | | |
| | | $\alpha = 0.10$ | | | | | $\alpha = 0.05$ | | | | |
PARAMETER	PLOT SIZE =	5	10	15	20	25	5	10	15	20	25
BBC area		1	1	2	2	2	1	2	2	2	3
BBC incidence[b]		2	2	2	2	2	2	2	2	2	2
$\bar{x}$ home range		1	1	1	1	2	1	1	2	2	2
Min. home range		1	2	2	2	2	2	2	2	3	3
Max. home range		1	1	1	1	1	1	1	1	1	2
$\bar{x}$ ann. home range		1	1	1	1	1	1	1	1	2	2
$\bar{x}$ summer home range		1	1	2	2	2	1	2	2	2	2

[a] Number of samples in a binomial model based on differences in spatial scales between plot size and owl activity (see text).
[b] Number of samples is derived from a frequency-based parameter rather than a scale difference (see text).
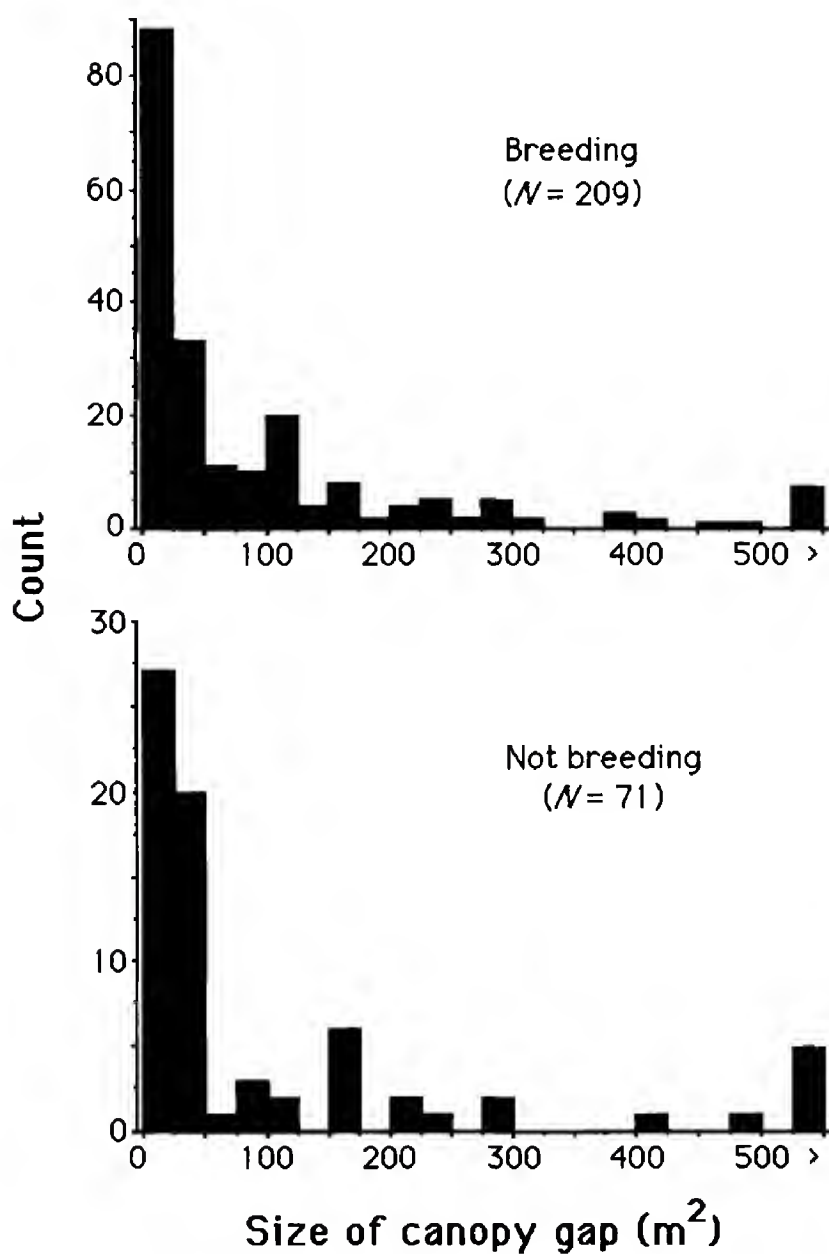

Figure 2. Canopy gap size-distributions in areas used and not used for breeding by Barred Owls (*Strix varia*).

Rather it was spatial arrangement of the canopy gaps (e.g., interspersion throughout the stand) that characterized breeding areas. Breeding sites on average also had an increase of approximately 25% in variability of canopy height (Table 3).

Plots with breeding owls were more likely to contain large ($\geq$45 cm dbh) hemlock snags than plots not used for breeding (Fig. 3). Some plots on which owls bred had snags >100 cm dbh. Breeding owls were also more likely to use stands with higher densities of large snags (all tree species) and greater total snag basal area (all tree species).

Understory at breeding sites was generally sparse. Most plots on which Barred Owls bred had fewer shrubs and sapling trees (stems $\leq$7.6 cm dbh). Out of 15 original old-growth study plots, nine were used by owls for either breeding, roosting or foraging, and seven of these (78%) had shrub densities <3000 stems/ha. Conversely, 67% of old-growth plots where neither breeding, roosting or foraging was detected had shrub densities >3000 stems/ha.

Most other vegetation measurements exhibited little difference between old-growth areas used and not used by breeding owls (Table 3). For example, average tree diameter in all plots used for breeding ($\bar{x} = 31.7$ cm dbh, SD = 5.1, range = 24.4–38.5, $N = 7$) was not different than average tree diameter in plots not used ($\bar{x} = 33.9$ cm, SD = 6.9, range = 23.9–44.5, $N = 10$; Mann-Whitney U-test, Z corrected for ties = -0.684, $P = 0.4943$).
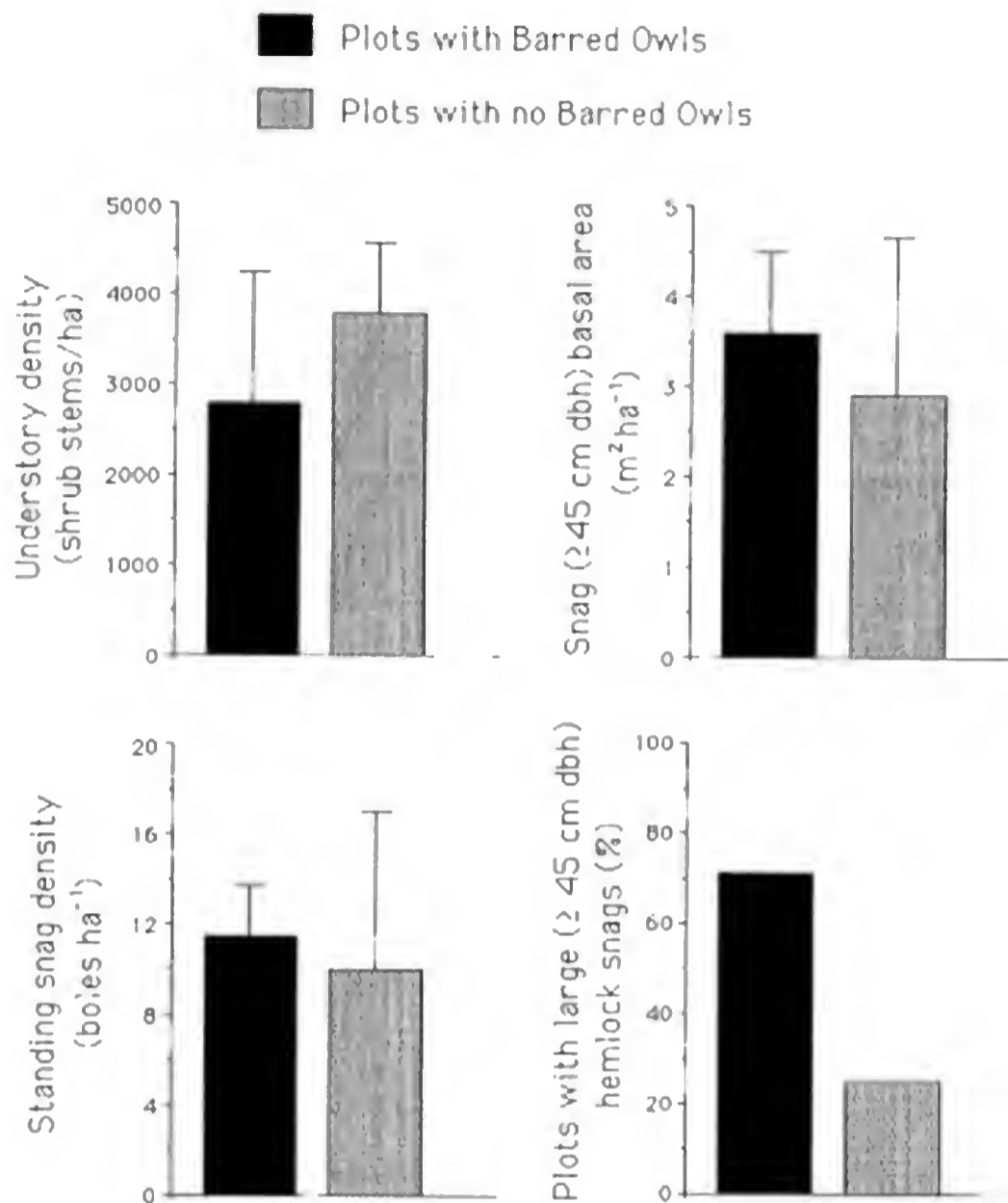
Figure 3.   Vegetation of forested plots with Barred Owl reproduction compared to plots without reproduction. Bars indicate +1 SE.

DISCUSSION

Scale and Type of Habitat Use. Barred Owl breeding was strongly linked to patches of old-growth hemlock-hardwood forest on the northern Appalachian Plateau. Given this owl's low density, such a large number of breeding events in a relatively small sample was not expected. At plot sizes ranging from 5–25 ha, however, and regardless of the home range parameter chosen, no more than 3 plots are required to detect greater-than-expected incidence of reproduction if all plots are used for nesting (Table 4).

Except at Tionesta, breeding territories of the size typically recorded for the species (Nicholls and Warner 1972, Elody and Sloan 1985) were unlikely to have been situated entirely within late successional forest; remnant patches of old-growth in this region are usually smaller than Barred Owl territories (Haney 1996). In silvicultural terms, the spa-

tial scale of habitat use observed in this study corresponds to the stand level. Specifically, Barred Owl use of breeding habitat was detected over scales on the order of 1–10s ha and horizontal distances of 10s–100s m.

These scales correspond to an activity center within the home range. Because habitat use of *Strix* owls is quite scale-sensitive (Carey et al. 1992, Hunter et al. 1995), use or selection at the level of nests or territories may differ. Further study might reveal whether microhabitat at nest sites used by Barred Owls is similar to their North American congeners (Seamans and Gutiérrez 1995) via comparison of nest to random sites (Buchanan et al. 1993), whether at landscape levels Barred Owl territories are smaller in or adjacent to old-growth (Carey et al. 1990) and whether territorial occupancy occurs in proportion to the availability of different seral stages. Habitat use is likely to vary also as a func-

tion of demography (sex, age), social organization (population, pair, individual; Carey et al. 1992) and activity type (foraging, roosting, or nesting; Ganey and Balda 1994).

Barred Owls and Old-growth. Forest contiguity and age both influence habitat use by Barred Owls (Bosakowski 1994, Laidig and Dobkin 1995). Hunter et al. (1995) found that fragmentation adjacent to nest sites influenced habitat selection of Spotted Owls. In contrast, several other studies cited by Hunter et al. (1995) found seral stage heterogeneity to be similar between random sites and areas used by *Strix* owls. Barred Owls prefer mature to young forest in patches of similar size (McGarigal and Fraser 1984). The preference for old-growth is not a regional artifact. In a follow-up study >800 km away, territorial occupancy and breeding by Barred Owls occurred in old-growth ($\geq$200 yr) hemlock-hardwood forest more than expected by chance ($P \leq 0.017$ in all model executions; $N = 3$ plots [12–27 ha each] dispersed across three Southern Appalachian national forests).

Seeming inconsistencies in owl use of forested habitats may arise if all areas studied happen to meet a threshold of suitability. For example, although I did not find average tree diameter to differ between sites used and not used for breeding, my comparisons were restricted largely to old-growth, and thus all sites may have contained adequate features. Barred Owls avoid forests with average tree diameters $\leq$15 cm (Bosakowski et al. 1987). Average diameter for all forests in my study region was 20 cm (weighted mean, based on Alerich 1993); all sites where I detected breeding owls had average tree diameters $\geq$30 cm. Despite trees $\geq$50 cm dbh making up <2% of all stems on the northern Appalachian Plateau (Alerich 1993), some trees in this size class characterized each site used by Barred Owls in this study (Devereux and Mosher 1984).

Barred Owls are thought to prefer mature forest, including old-growth, due to greater availability of nest sites, because lower stem densities in the understory facilitate unimpeded visibility and travel-ways for foraging, or because dense canopies provide protection from mobbing (Nicholls and Warner 1972, McGarigal and Fraser 1984, Bosakowski 1994). Dense canopies also foster thermally-neutral microclimates for some *Strix* owls (Barrows 1981). Since all of these structural characteristics were evident on sites studied here, and I did not measure availability, it was not possible to identify which fac-

tor(s) were actually selected. Compared to younger forest, older forest provides other *Strix* owls with their preferred prey type, size, or abundance (Thrailkill and Bias 1989, Waters and Zabel 1995, Zabel et al. 1995). Barred owls usually have diverse diets (Bosakowski and Smith 1992), but the prey base in eastern old-growth would be worthy of detailed study.

Breeding sites were located where the canopy was more complex. These areas had more vertical variation in tree heights and greater horizontal patchiness and internal edge created by tree-fall gaps. Small openings that are interspersed throughout the stand yet still near breeding sites may facilitate foraging by adults who must satisfy both their own dietary needs as well as provision chicks. Thus, spatial juxtaposition of diverse ecological characteristics may enhance suitability of old-growth habitat for Barred Owls.

Any use of older forest by Barred Owls could have implications for conservation of the Northern Spotted Owl. Barred Owls have displaced (Sharp 1989) and interbred (Hamer et al. 1994) with Northern Spotted Owls during the past few decades in the Pacific Northwest. Although the former species has been implicated as more adaptable, throughout much of eastern North America the Barred Owl is the more specialized large owl (Laidig and Dobkin 1995), and its populations are impacted negatively by forest alterations detrimental to Northern Spotted Owls, such as fragmentation and seral truncation (Bosakowski 1994). I suggest that recent overlap in the ranges of *Strix* owls stems at least in part from their broadly-similar habitat requirements.

Management Considerations. As a codominant canopy tree (Rogers 1978), eastern hemlock plays a key role in providing habitat for Barred Owls. The "eastern hemlock" or "hemlock-white pine-hardwood" region (Nichols 1935) once stretched from the Great Lakes, St. Lawrence River Valley and New England south through the Southern Appalachians. Apparent antibiotic properties of hemlock litter (Rogers 1978) and canopy shading both tend to suppress understory vegetation, maintaining a rather open ground layer that may benefit foraging owls. After acheiving old-growth conditions at 275–300 yr (Tyrrell and Crow 1994), hemlocks tend to have snapped tops, broken limbs, cavity inclusions and other signs of decadence that furnish ample sites for nests as well as perches suitable for sit-and-wait foraging. Dense groves of hem-

lock also attract certain hawks, corvids and squirrels, all of which construct bulky nests occasionally appropriated by Barred Owls (Johnsgard 1988). Hemlock decomposes more slowly than most hardwoods (Harmon et al. 1986), so snags suitable as nest sites tend to persist for long periods.

Because hemlock tends to grow well in shade (Rogers 1978), it ensures a continuous supply of replacement canopy dominants, thereby exploiting low-intensity disturbances typical of late-seral communities (Runkle 1982, Ward and Parker 1989). Hemlock's longevity ($\approx$800 yr; Loehle 1988) and low frequency of catastrophic stand disturbance ($\approx$1200 yr; Canham and Loucks 1984, Frelich and Lorimer 1991) would, historically, have tended to provide large areas of owl habitat. On the northern Appalachian Plateau alone, presettlement beech-hemlock forest covered 2.4 million ha (Bjorkblom and Larson 1977). Management practices that promote stand development or allow expanded coverage of large hemlock (Farr and Tyndall 1992) are thus likely to benefit Barred Owls.

The Barred Owl's utility as a management indicator species is predicated on an affinity for older forest (USDA 1985, 1986). High breeding incidence in the very old stands studied here suggests that merely extending the rotation ages of timber harvests to $\approx$110 yr (the criterion for "old-growth" in many eastern forests) may not in itself provide optimal habitat for Barred Owls. Further research is needed on Barred Owl abundance, habitat use and reproduction across the full spectrum of stand ages representative of eastern forests.

ACKNOWLEDGMENTS

LITERATURE CITED

ABRAMS, M.D. AND C.M. RUFFNER. 1995. Physiographic analysis of witness-tree distribution (1765–1798) and present forest cover through north central Pennsylvania. Can. J. For. Res. 25:659–668.

ALERICH, C.R. 1993. Forest statistics for Pennsylvania— 1978 and 1989. USDA For. Serv. Res. Bull. NE-126.

ALLEN, A.W. 1987. Habitat suitability index models: Barred Owl. USDI Fish Wildl. Serv. Biol. Rep. 82.

AZUMA, D.L., J.A. BALDWIN AND B.R. NOON. 1990. Estimating the occupancy of Spotted Owl habitat areas by sampling and adjusting for bias. USDA For. Serv. Gen. Tech. Rep. PSW-124.

BARROWS, C.W. 1981. Roost selection by Spotted Owls· an adaptation to heat stress. Condor 83:302–309.

BJORKBLOM, J.C. AND R.G. LARSON. 1977. The Tionesta Scenic and Research natural areas. USDA For. Serv. Gen. Tech. Rep. NE-31.

BOLLES, F. 1890. Barred Owls in captivity. Auk 7:101–114

BOSAKOWSKI, T. 1994. Landsat reveals negative effect of forest fragmentation on Barred Owl distribution. Records of New Jersey Birds 20:66–70.

———— AND D.G. SMITH. 1992. Comparative diets of sympatric nesting raptors in the eastern deciduous biome. Can. J. Zool. 70:984–992.

————, R. SPEISER AND J. BENZINGER. 1987. Distribution, density, and habitat relationships of the Barred Owl in northern New Jersey. Pages 135–143 in Proceedings, biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Winnipeg, Manitoba, Canada.

————, R. SPEISER AND D.G. SMITH. 1989. Forest owl populations of the Pequannock Watershed. Records of New Jersey Birds 15:2–8.

BUCHANAN, J.B., L.L. IRWIN AND E.L. McCUTCHEN. 1993. Characteristics of Spotted Owl nest trees in the Wenatchee National Forest. J. Raptor Res. 27:1–7.

BULL, E.L., M.G. HENJUM AND R.S. ROHWEDER. 1988. Nesting and foraging habitat of Great Gray Owls. J. Raptor Res. 22:107–115.

CANHAM, C.D. AND O.L. LOUCKS. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803–809.

CAREY, A.B., J.A. REID AND S.P. HORTON. 1990. Spotted Owl home range and habitat use in southern Oregon Coast Ranges. J. Wildl. Manage. 54:11–17.

————, S.P. HORTON AND B.L. BISWELL. 1992. Northern Spotted Owls: influence of prey base and landscape character. Ecol. Monogr. 62:223–250.

CLINE, S.P., A.B. BERG AND H.M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Washington. J. Wildl. Manage. 44:773–786.

COOK, J.G., T.W. STUTZMAN, C.W. BOWERS, K.A. BRENNER AND L.L. IRWIN. 1995. Spherical densiometers pro-

duce biased estimates of forest canopy cover. *Wildl. Soc. Bull.* 23:711–717.

DEVEREUX, J.G. AND J.A. MOSHER. 1984. Breeding ecology of Barred Owls in the central Appalachians. *Raptor Res.* 18:49–58.

EIFRIG, G. 1907. American goshawk (*Accipiter atricapillus*) versus man and Barred Owl. *Auk* 24:437–438.

ELODY, B.J. AND N.F. SLOAN. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radio-telemetry. *Jack-Pine Warbler* 63:3–8.

ERDMAN, K.S. AND P.G. WIEGMAN. 1975. Preliminary list of natural areas in Pennsylvania. Western Pennsylvania Conservancy, Pittsburgh, PA U.S.A.

FARR, P.M. AND R.W. TYNDALL. 1992. Expansion of an eastern hemlock forest in Maryland. *Castanea* 57:190–195.

FORBES, L.S. 1990. A note on statistical power. *Auk* 107:438–439.

FORSMAN, E.D., E.C. MESLOW AND H.M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87.

FRELICH, L.E. AND C.G. LORIMER. 1991. Natural disturbance regimes in hemlock-hardwood forest of the Upper Great Lakes region. *Ecol. Monogr.* 61:145–164.

FULLER, M.R. AND J.A. MOSHER. 1981. Methods of detecting and counting raptors: a review. *Stud. Avian Biol.* 6:235–246.

GANEY, J.L. AND R.P. BALDA. 1994. Habitat selection by Mexican Spotted Owls in northern Arizona. *Auk* 111:162–169.

GUTIÉRREZ, R.J. 1994. Changes in the distribution and abundance of Spotted Owls during the past century. *Stud. Avian Biol.* 15:293–300.

———, J. VERNER, K.S. MCKELVEY, B.R. NOON, G.N. STEGER, D.R. CALL, W.S. LAHAYE, B.B. BINGHAM AND J.S. SENSER. 1992. Habitat relations of the California Spotted Owl. Pages 79–98 in J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutiérrez, G.I. Gould, Jr. and T.W. Beck [EDS.], The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133, USDA For. Serv., Albany, CA U.S.A.

HAMER, T.E., E.D. FORSMAN, A.D. FUCHS AND M.L. WATERS. 1994. Hybridization between Barred and Spotted owls. *Auk* 111:487–492.

HANEY, J.C. 1996. Policy aspects of old-growth forest reserves in the eastern U.S. Pages 41–62 in S.K. Majumdar, E.W. Miller and F.J. Brenner [EDS.], Forests—a global perspective. The Pennsylvania Academy of Science, Phildelphia, PA U.S.A.

HARMON, M.E., J.F. FRANKLIN, F.J. SWANSON, P. SOLLINS, S.V. GREGORY, J.D. LATTIN, N.H. ANDERSON, S.P. CLINE, N.G. AUMEN, J.R. SEDELL, G.W. LIENKAEMPER, K. CROMACK AND K.W. CUMMINS. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:772–783.

HOUGH, A.F. 1936. A climax forest community on East

Tionesta Creek in northwestern Pennsylvania. *Ecology* 17:9–28.

——— AND R.D. FORBES. 1943. The ecology and silvics of Pennsylvania high-plateau forests. *Ecol. Monogr.* 13:299–320.

HUNTER, J.E., R.J. GUTIÉRREZ AND A.B. FRANKLIN. 1995. Habitat configuration around Spotted Owl sites in northwestern California. *Condor* 97:684–693.

HUNTER, M.L. 1989. What constitutes an old-growth stand? *J. For.* 88:33–35.

JAMES, F.C. AND H.H. SHUGART. 1970. A quantitative method of habitat description. *Am. Birds* 24:727–736

JOHNSGARD, P.A. 1988. North American owls. Smithsonian Inst. Press, Washington, DC U.S.A.

LAIDIG, K.J. AND D.S. DOBKIN. 1995. Spatial overlap and habitat associations of Barred Owls and Great Horned Owls in southern New Jersey. *J. Raptor Res.* 29:151–157.

LEMMON, P.E. 1957. A new instrument for measuring forest overstory density. *J. For.* 55:667–668.

LOEHLE, C. 1988. Tree life history strategies: the role of defenses. *Can. J. For. Res.* 18:209–222.

LOWE, J.D. 1995. Resident bird counts 1994. *J. Field Ornithol.* 66(Suppl.):3–4.

LUTZ, H.J. 1930. Vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. *Ecology* 11:1–29.

MCGARIGAL, K. AND J.D. FRASER. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. *J. Wildl. Manage.* 48:1393–1398.

——— AND ———. 1985. Barred Owl responses to recorded vocalizations. *Condor* 87:552–553.

MICKALITIS, A.B. 1956. Virgin timber tracts in Pennsylvania. *Pennsylvania Forests* 36:35–36.

MORRELL, T.E. AND R.H. YAHNER. 1994. Habitat characteristics of Great Horned Owls in southcentral Pennsylvania. *J. Raptor Res.* 28:164–170.

MOSHER, J.A., M.R. FULLER AND M. KOPENY. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. *J. Field Ornithol.* 61:453–461.

NICHOLS, G.E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology* 16:403–422.

NICHOLLS, T.H. AND D.W. WARNER. 1972. Barred Owl habitat use as determined by radiotelemetry. *J. Wildl. Manage.* 36:213–224.

——— AND M.R. FULLER. 1987. Territorial aspects of Barred Owl home range and behavior in Minnesota. Pages 121–128 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDS.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

ROGERS, R.S. 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and post-settlement history. *Can. J. Bot.* 56:843–854.

RUNKLE, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533–1546.

———. 1985. Comparison of methods for determining

fraction of land area in treefall gaps. *For. Sci.* 31:15–19.

SEAMANS, M.E. AND R.J. GUTIÉRREZ. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. *Condor* 97:944–952.

SHARP, D.V. 1989. Range extension of the Barred Owl in western Washington and first breeding record on the Olympic Peninsula. *J. Raptor Res.* 23:179–180.

SMITH, T.L. 1989. An overview of old-growth forests in Pennsylvania. *Nat. Areas J.* 9:40–44.

SNEDECOR, G.W. AND W.G. COCHRAN. 1980. Statistical methods, seventh edition. Iowa State Univ. Press, Ames, IA U.S.A.

THRAILKILL, J. AND M.A. BIAS. 1989. Diets of breeding and nonbreeding California Spotted Owls. *J. Raptor Res.* 23:39–41.

TYRRELL, L.E. AND T.R. CROW. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to stand age. *Ecology* 75:370–386.

U.S. DEPARTMENT OF AGRICULTURE. 1985. Jefferson National Forest land and resource management plan. USDA For. Serv., Land Management Planning, Roanoke, VA U.S.A.

———. 1986. Allegheny National Forest land resource management plan. USDA For. Serv., Eastern Region, Warren, PA U.S.A.

WARD, J.S. AND G.R. PARKER. 1989. Spatial dispersion of woody regeneration in an old-growth forest. *Ecology* 70:1279–1285.

WATERS, J.R. AND C.J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. *J. Wildl. Manage.* 59:858–866.

WRIGHT, D.H. 1991. Correlations between incidence and abundance are expected by chance. *J. Biogeogr.* 18: 463–466.

ZABEL, C.J., K. MCKELVEY AND J.P. WARD. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–439.

HABITAT ASSOCIATIONS OF THE BARRED OWL IN THE BOREAL FOREST OF SASKATCHEWAN, CANADA

KURT M. MAZUR[1]
Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2 Canada

PAUL C. JAMES
Saskatchewan Environment and Resource Management, 3211 Albert Street, Regina, Saskatchewan S4S 5W6 Canada

MICHAEL J. FITZSIMMONS
Parks Canada, Prince Albert National Park, P.O. Box 100, Waskesiu Lake, Saskatchewan S0J 2Y0 Canada

GIDO LANGEN
Prince Albert Model Forest Association, Inc., 77-11th Street West, Prince Albert, Saskatchewan S6V 7G3 Canada

RICHARD H.M. ESPIE
*Department of Veterinary Anatomy, Western College of Veterinary Medicine, 52 Campus Drive,
University of Saskatchewan, Saskatoon, Saskatchewan S7N 5B4 Canada*

ABSTRACT.—Little information exists regarding Barred Owl (*Strix varia*) habitat requirements in the boreal forest. During 1993, we located Barred Owls through call-playback surveys in the boreal forest of central Saskatchewan, Canada. We analyzed habitat found within 1.5 km and 3.0 km radius circles centered on 25 Barred Owl locations, 100 random locations and 275 survey locations. We compared habitat found within random circles to that found at survey and owl locations. Habitat at survey locations differed from random locations for four habitat types, indicating a habitat bias of road-based surveys. Barred Owls were found associated with old mixed-wood forest, old deciduous forest and water, and avoided young forest and treed muskeg. As in other portions of its range, the Barred Owl is associated with old forest in boreal forest.

KEY WORDS: Strix varia; Barred Owl; boreal forest; habitat association; Saskatchewan.

Asociaciones de hábitat en búhos (*Strix varia*) en bosques boreal en Saskatchewan, Canada

RESUMEN.—Poca información existe con respecto de requisitos de hábitat para búhos (*Strix varia*) en bosques boreal. Durante 1993 nosotros localizamos búho con llamadas recordadas en el bosque boreal de el centro Saskatchewan, Canada. Nosotros analizamos hábitat dentro 1.5 km y 3.0 km radio círculos centrados en 25 lugares de 25 búhos, 100 lugares al azar y 275 lugares de encuesta. Nosotros comparamos el hábitat dentro los círculos al azar con los de encuesta y lugares de búho. Hábitat en lugares de encuesta eran diferentes a lugares al azar para cuatro tipos de hábitat, indicando una tendencia de hábitat de encuesta con caminos. Búhos fueron encontrados dentro de bosque variables, bosque de hoja caduca y agua y evitaba bosque jóvenes. Como en otras lugares de la pradera, el búho esta asociado con bosques viejos en bosques boreal.

[Traducción de Raúl De La Garza, Jr.]

Habitat associations of Barred Owls (*Strix varia*) have been quantified for only a portion of their range, primarily the northeastern U.S. (Nicholls and Warner 1972, Devereux and Mosher 1984, Elody and Sloan 1985, Bosakowski et al. 1987, Laidig and Dobkin 1995). In this region, Barred Owls typically occupy large contiguous tracts of mature to old-growth hardwood and mixed hardwood/softwood forests. Some authors have also suggested a need for swamps and an association with water

---

[1] Present address: Grassland and Forest Bird Project, Box 24, 200 Saulteaux Cresc., Winnipeg, MB R3J 3W3 Canada.

(Bent 1961, Bosakowski et al. 1987, Dunbar et al. 1991, Laidig and Dobkin 1995). Its relatively narrow habitat requirements have resulted in its adoption as a forest-management indicator in the southern Appalachians (Bosakowski 1994). During this century, the Barred Owl is believed to have expanded its range into boreal forests to the western montane forests of Canada and the U.S. (Houston 1959, Taylor and Forsman 1976, Boxall and Stepney 1982, Sharp 1989, Dunbar et al. 1991). In the western portion of their range, Barred Owls were found in association with old-growth and mature coniferous and mixedwood forests and riparian zones (Hamer 1988, Dunbar et al. 1991). Van Ael (1996) reported Barred Owls in northwestern Ontario to be found in association with unfragmented mixed-wood forests. Records from the western boreal forest suggest a relationship with old forests, but this relationship has yet to be quantified (Boxall and Stepney 1982, Pinel et al. 1991). Our objective was to identify which habitat in the boreal forest of Saskatchewan Barred Owls were associated with, and to compare this to the available habitat.

STUDY AREA

This study was conducted in the southern boreal forest of Saskatchewan, Canada (53°35′–54°15′N, 105°05′–106°45′W). The 400 000-ha study area encompassed the Prince Albert Model Forest including a portion of Prince Albert National Park. The dominant tree species in the study area included trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*). Habitats included pure deciduous, mixed coniferous/deciduous and pure coniferous forest, muskeg and shrub lands. Elevation ranged from 490–698 m. The topography is gently rolling, interspersed with numerous lakes and creeks. The climate is boreal continental, with an average annual precipitation of 40.1 cm; 28.1 cm as rain and 12.0 cm as snow. July and January temperatures average 17.6°C and −19.7°C, respectively, with annual extreme temperatures of 36.1°C and −48.3°C (Environment Canada Parks 1986). A portion of the study area is currently being commercially harvested for wood pulp and lumber. Approximately half of the study area is located within the boundaries of Prince Albert National Park.

METHODS

Barred Owl locations were estimated through nocturnal call-surveys from 28 April–28 May 1993. Call-surveys were restricted to randomly-selected, vehicle-accessible roads, and were conducted between one half hour after sunset and one half hour prior to sunrise. Call-survey stops were spaced 1 km apart. Thirteen survey routes, totalling 275 call-survey stops, were each surveyed once.

These call-survey stops represented the survey locations Territorial calls of a male and a female Barred Owl were broadcast using a 12-watt battery powered tape recorder with 4 directional speakers (MTC Electronics), set approximately 1.5 m above the ground. Surveyors remained at each survey stop for 8 min consisting of an initial 1 min listening period prior to broadcast, followed by a 2 min broadcast, and concluding with a 5 min post-broadcast listening period. McGarigal and Fraser (1985) and Mosher et al. (1990) found that 70–80% of Barred Owls detected during the post-broadcast listening period responded within 5 min of the end of the broadcast period. Surveys were not conducted during periods of precipitation or when wind speed exceeded 15 km/hr as reported by Environment Canada, or scored 3 or greater on the Beaufort scale.

At each survey stop where owls responded, we recorded the following parameters: the apparent direction to the owl (to the nearest degree), number and sex of owls responding, time for owl to respond and if the owl(s) was observed. Owl locations were determined by triangulation from at least two consecutive survey stops, or by direct observation of the owl, in which case the survey location was used as the *owl location*. One hundred random locations were generated throughout the study area, in order to compare available habitats. These random locations did not include locations on water surfaces.

We characterized habitat within 1.5 and 3.0 km radius circles (706 and 2827 ha, respectively) centered on 25 owl locations, 100 random locations and 275 survey locations. Of the 25 owl locations where habitat was characterized, seven represented a pair of owls and 18 represented a single owl. Area of overlap of adjacent circles were intersected with Thiessen polygons and the overlap divided between the two circles to prevent double counting of any habitat area. Therefore, overlapping circles had a reduced area as the overlapping area was divided between the two circles.

Although previous studies used smaller circles as an estimate of the area used by Barred Owls (Laidig and Dobkin 1995), radiotelemetry data from 14 adult Barred Owls revealed that annual home ranges (95% MCP) of Barred Owls in our study area ranged from 692–2489 ha ($\bar{x} = 1361$ ha) (Mazur 1997). We therefore chose circles of 1.5 and 3.0 km radius which more closely approximated the area used by Barred Owls in this region. The circles do not represent an owl's home range, but rather provide an area with which an owl is likely to be associated.

We used the 1993 forest inventories for Prince Albert National Park (Padbury et al. 1978) and Saskatchewan Northern Provincial Forest (Lindenas 1985) to classify the available habitat into 12 types (Table 1). The proportional coverage of each habitat within each circle was calculated using an ARC/INFO geographic information system (GIS). As the data did not conform to a normal distribution we used nonparametric statistics (Zar 1996) We tested for differences between habitat associated with owl and random, and survey and random locations for both 1.5 and 3.0 circles using the Mann-Whitney U-test (Zar 1996).

Table 1. Habitat classification of the Prince Albert National Park study area by habitat cover type and age.

HABITAT TYPE	COVER VEGETATION DESCRIPTION
Deciduous[1]	Trembling aspen +/or balsam poplar +/or white birch (<20% conifer)
Mixed-wood[1]	Combination of deciduous and coniferous species: trembling aspen, balsam poplar, white birch, white spruce, black spruce, jack pine, balsam fir (≥20% conifer, ≥20% deciduous)
Coniferous[1]	White spruce +/or black spruce +/or jack pine +/or tamarack +/or balsam fir (<20% deciduous)
Treed Muskeg	Black spruce +/or tamarack, excessive moisture and retarded tree growth
Open	Cut over, burn over, flooded land, sand, clearing, open muskeg, herbs, shrubs
Water	Lakes, rivers, creeks

[1] Could occur in three age classes: young (<50 years), mature (50–79 years) and old (80+ years).

RESULTS

Survey Locations versus Random Locations.
Habitat composition surrounding survey locations (e.g., habitat adjacent to roads) was found to differ from habitat composition found at random locations (e.g., habitat throughout the study area) (Figs. 1a and 1b). Significant differences were found between the proportions of two habitat types within the 1.5 circles and four habitat types within the 3.0 circles. Survey 1.5 circles were found to have significantly less mature conifer ($z = -5.23$, $P = 0.000$) and treed muskeg ($z = -5.06$, $P = 0.000$) than did random 1.5 circles (Fig. 1a). Within survey 3.0 circles, there were significantly more mature deciduous ($z = -2.09$, $P = 0.025$), and significantly less mature mixed-wood ($z = -3.07$, $P = 0.001$), mature conifer ($z = -4.79$, $P < 0.001$), and treed muskeg ($z = -4.10$, $P < 0.001$) compared to random 3.0 circles (Fig. 1b).

Owl Locations versus Random Locations. Barred Owls were associated with habitat types in different proportions than expected from the available habitat. Habitat composition of owl 1.5 and 3.0 circles differed from random 1.5 and 3.0 circles for four habitat types within the 1.5 km circles and six habitat types within the 3.0 km circles (Figs. 2a and 2b). Within the 1.5 circles, owl locations were found to have significantly higher proportions of old mixed-wood ($z = -3.53$, $P < 0.001$) than random circles, and significantly lower proportions of young mixed-wood ($z = -1.87$, $P = 0.038$), young conifer ($z = -2.27$, $P = 0.011$) and treed muskeg ($z = -3.24$, $P = 0.001$) than random circles (Fig. 2a). Within the 3.0 circles, owl locations were found to have significantly higher proportions of old deciduous ($z = -2.39$, $P = 0.014$), old mixed-

wood ($z = -2.29$, $P = 0.021$) and water ($z = -3.82$, $P < 0.001$) and significantly lower proportions of young mixed-wood ($z = -2.36$, $P = 0.012$), young conifer ($z = -2.44$, $P = 0.010$) and treed muskeg ($z = -3.30$, $P < 0.001$) than random circles (Fig. 2b).

DISCUSSION

Our results indicated that Barred Owls were not randomly distributed relative to the available habitat. Owls showed a greater than expected association with old deciduous forest, old mixed-wood forest and water, and an avoidance of young forest and treed muskeg. This agrees with what has been recorded previously in the boreal forest (Boxall and Stepney 1982, Van Ael 1996). Barred Owls are cavity-nesting owls, requiring relatively large trees (Johnsgard 1988). In Maryland, Devereux and Mosher (1984) reported an average diameter at breast height (dbh) of 61 cm for Barred Owl nest trees. Similarly, in our study area Barred Owl nest trees average 47 cm dbh. Old mixed-wood forest is likely the only forest type in the boreal setting that provides an adequate density of large diameter (>40 cm dbh) trees (Lee et al. 1995). The old mixed-wood forest is the most structurally and species diverse habitat type in the boreal forest (Stelfox 1995). Therefore, prey diversity and abundance is likely high in this habitat. The positive association with water has also been documented in the past (Sutton and Sutton 1985, Bosakowski et al. 1987, Pinel et al. 1991). In some areas suitable habitat for Barred Owls is largely restricted to wet areas (Devereux and Mosher 1984). In our study area, the forest was largely continuous, with available habitat in both upland and lowland areas. We
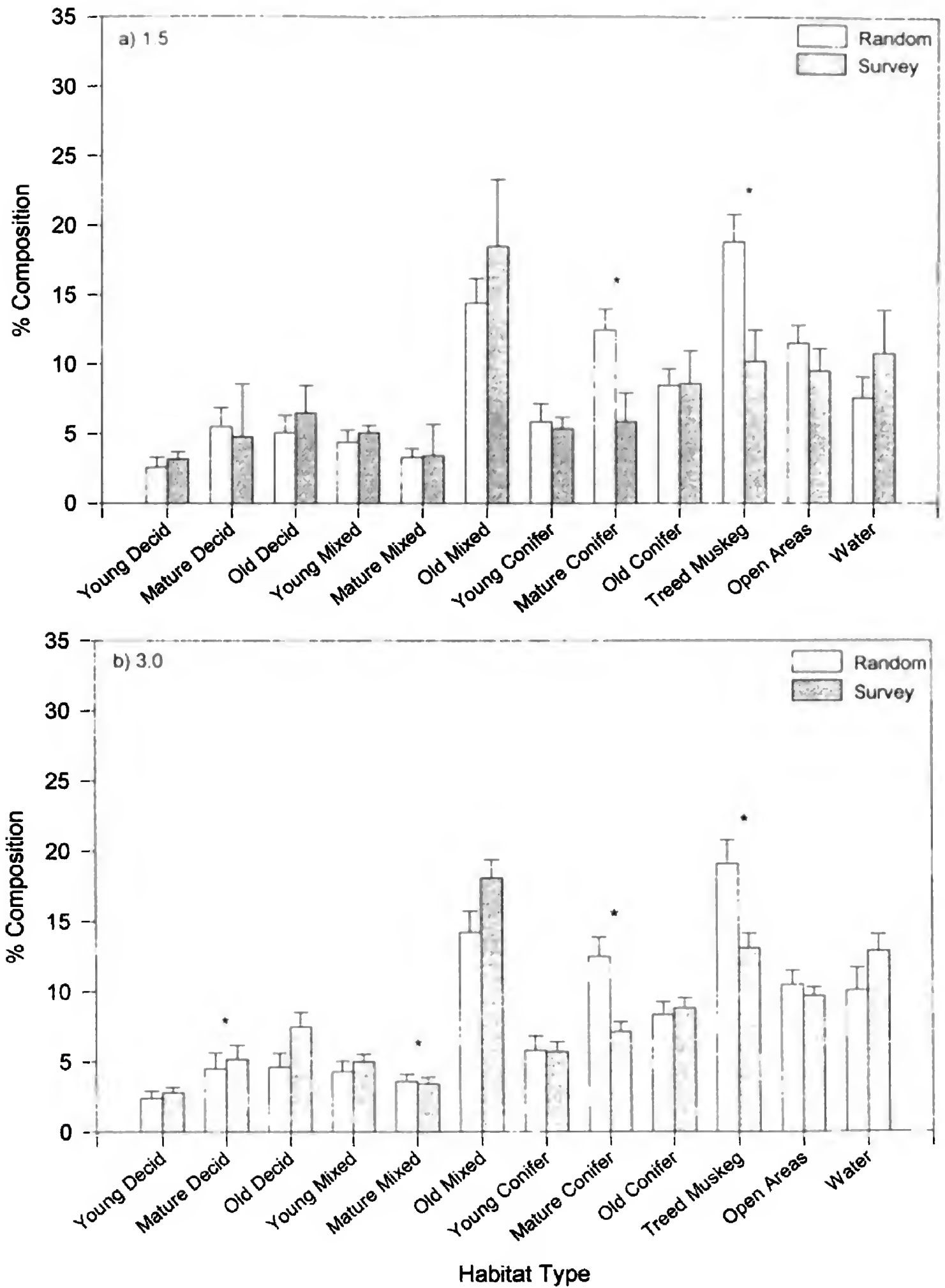
Figure 1.   Comparison of mean percent habitat composition (±SE) within (a) 1.5 km radius circles (706 ha) and (b) 3.0 km radius circles (2827 ha), centered on 100 random and 275 survey locations. Significant difference * (P < 0.05).
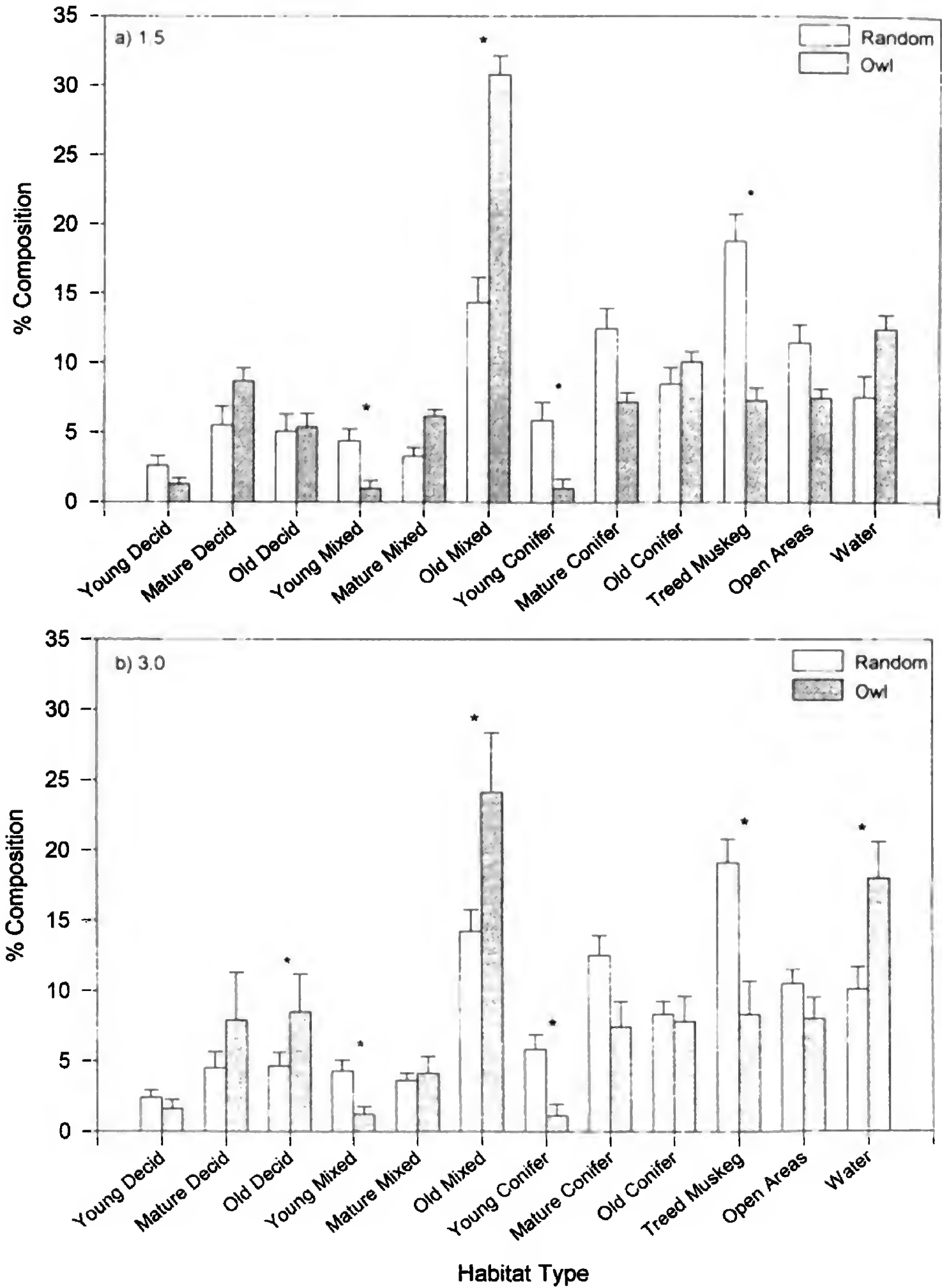
Figure 2.   Comparison of mean percent habitat composition (±SE) within (a) 1.5 km radius circles (706 ha) and (b) 3.0 km radius circles (2827 ha), centered on 100 random and 25 owl locations. Significant difference * (P < 0.05).

found Barred Owls in both upland and lowland areas.

Habitat associated with survey locations was found to be representative of the habitat within the study area, with the exception of four habitat types. Typically, roads were built on higher areas, avoiding low-lying muskeg and wetlands. This was evident as the percentage of treed muskeg associated with survey locations was significantly lower than that of random locations. We suggest that when comparing habitat use to availability, habitat adjacent to roads presents an available habitat bias, and therefore comparisons between habitat use and random habitat should be made.

Habitat characterization of circles centered on owl locations contained biases making them not entirely representative of owl home ranges. Owls detected may have moved toward the tape playback, or the owl may have been detected calling from the periphery of its home range. However, Lehmkuhl and Raphael (1993) supported the use of circles as surrogates for home ranges in the analysis of habitat pattern associations of Spotted Owls (*Strix occidentalis*) in Washington. Few differences in habitat composition were apparent between 1.5 km circle comparisons and 3.0 km circle comparisons. However, the smaller circles would present a more conservative estimate of the area that the owl likely uses. Given that the 3.0 circle approximates the maximum Barred Owl home range size, this larger circle size may include large areas of unused habitat.

Our findings show that in the boreal forest, like other regions, Barred Owls are associated with old forest, in this case old mixed-wood forest. This species appears to have the potential to serve as a biological indicator for the management of old mixed-wood forest in the boreal forest (James 1993). Knowledge of the Barred Owl's specific habitat and area requirements would allow for management of an adequate quantity of old mixed-wood forest, therefore sustaining this highly species diverse habitat.

Literature Cited

Bent, A.C. 1961. Life histories of North American birds of prey. Part II. U.S. Natl. Mus. Bull. 167.

Bosakowski, T., R. Speiser and J. Benzinger. 1987. Distribution, density, and habitat relationships of the Barred Owl in northern New Jersey. Pages 135–143 *in* R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [Eds.], Biology and conservation of northern forest owls. USDA For. Serv. Gen. Tech. Rep. RM-142, Fort Collins, CO U.S.A.

Bosakowski, T. 1994. Landsat reveals negative effect of forest fragmentation on Barred Owl distribution. *Records of New Jersey Birds* 20:66–70.

Boxall, P.C. and P.H.R. Stepney. 1982. The distribution and status of the Barred Owl in Alberta. *Can. Field-Nat.* 96:46–50.

Devereux, J.G. and J.A. Mosher. 1984. Breeding ecology of Barred Owls in the central Appalachians. *Raptor Res.* 18:49–58.

Dunbar, D.L., B.P. Booth, E.D. Forsman, A.E. Hetherington and D.J. Wilson. 1991. Status of the Spotted Owl, *Strix occidentalis*, and the Barred Owl, *Strix varia*, in southwestern British Columbia. *Can. Field-Nat.* 105: 464–468.

Elody, B.I. and N.F. Sloan. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. *Jack-Pine Warbler* 63:3–8.

Environment Canada Parks. 1986. Prince Albert National Park resource description and analysis. Environment Canada Parks, Prairie and Northern Region, Winnipeg, Canada.

Hamer, T.E. 1988. Home range size of the Northern Barred Owl and Northern Spotted Owl in western Washington. M.S. thesis, Western Washington Univ., Bellingham, WA U.S.A.

Houston, C.S. 1959. First records of the Barred Owl in Saskatchewan. *Blue Jay* 17:94.

James, P.C. 1993. Oldgrowth and owls: what have we learned? Pages 70–79 *in* D.H. Kuhnke [Eds.], Birds in the boreal forest. Proceedings of a workshop held 10–12 March in Prince Albert, Saskatchewan. Forestry Canada, Edmonton, Alberta, Canada.

Johnsgard, P.A. 1988. North American owls. Smithsonian Institution Press, Washington, DC U.S.A.

Laidig, K.J. and D.S. Dobkin. 1995. Spatial overlap and habitat associations of Barred Owls and Great Horned Owls in southern New Jersey. *J. Raptor Res.* 29:151–157.

Lee, P.C., S. Crites, M. Nietfeld, H. Van Nguyen and J.B. Stelfox. 1995. Changes in snags and down woody material characteristics in a chronosequence of aspen mixedwood forests in Alberta. Pages 49–61 *in* J.B. Stelfox [Ed.], Relationship between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta,

and Canadian Forest Service (Project No. 0001A), Edmonton, Alberta, Canada.

LEHMKUHL, J.F. AND M.G. RAPHAEL. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.* 57: 302–315.

LINDENAS, D.G. 1985. Forest inventory interpretation and mapping manual. Forestry Branch, Saskatchewan Parks and Renewable Resources, Regina, Saskatchewan, Canada.

MAZUR, K.M. 1997. Spatial habitat selection by Barred Owls in the boreal forest of Saskatchewan, Canada. M.S. thesis, Univ. Regina, Regina, Saskatchewan, Canada.

MCGARIGAL, K. AND J.D. FRASER. 1985. Barred Owl responses to recorded vocalizations. *Condor* 87:552–553.

MOSHER, J.A., M.R. FULLER AND M. KOPENY. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. *J. Field Ornithol.* 61:453–461.

NICHOLLS, T.H. AND D.W. WARNER. 1972. Barred Owl habitat use as determined by radiotelemetry. *J. Wildl. Manage.* 36:213–224.

PADBURY, G.A., W.K. HEAD AND W.E. SOUSTER. 1978. Biophysical resource inventory of the Prince Albert National Park, Saskatchewan. Saskatchewan Institute of Pedology, Publ. S185, Saskatoon, Saskatchewan, Canada.

PINEL, H.W., W.W. SMITH AND C.R. WERSHLER. 1991. Alberta birds, 1971–1980. Vol. 1. Non-passerines. Provincial Museum of Alberta, Natural History Occasional Paper No. 13., Edmonton, Alberta, Canada.

SHARP, D.U. 1989. Range extension of the Barred Owl in western Washington and first breeding record on the Olympic Peninsula. *J. Raptor Res.* 23:179–180.

STELFOX, J.B. [ED.]. 1995. Relationship between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta and Canadian Forest Service (Project No. 0001A), Edmonton, Alberta, Canada.

SUTTON, C.C. AND P.T. SUTTON. 1985. The status and distribution of Barred Owl and Red-shouldered Hawk in southern New Jersey. *Cassinia* 61:20–29.

TAYLOR, A.L. AND E.D. FORSMAN. 1976. Recent range extension of the Barred Owl in western North America, including the first records for Oregon. *Condor* 78:560–561.

VAN AEL, S.M. 1996. Modelling Barred Owl habitat in northwestern Ontario. M.S. thesis, Lakehead Univ., Thunder Bay, Ontario, Canada.

ZAR, J.H. 1996. Biostatistical analysis. Third Edition. Prentice Hall, Inc., NJ U.S.A.

THE WINTER ROOSTING BEHAVIOR OF EASTERN SCREECH-OWLS IN CENTRAL KENTUCKY

TARA A. DUGUAY, GARY RITCHISON AND JEFFREY P. DUGUAY[1]
Department of Biological Sciences, Eastern Kentucky University,
Richmond, KY 40475 U.S.A.

ABSTRACT.—The winter roosting behavior of Eastern Screech-owls (*Otus asio*) in central Kentucky was examined from October 1993–March 1994. Eleven owls used 69 roost sites 563 times, with 29 boxes used 308 times, 25 cavities used 226 times and 15 limbs used 29 times. Most natural cavities were in black locusts (*Robinia pseudoacacia*), southern red oaks (*Quercus falcata*) and snags; boxes were located in 15 different species of trees. All conifer limb roosts were in eastern redcedars (*Juniperus virginiana*). Frequent use of boxes and cavities during winter is probably the result of owls seeking favorable microclimates and concealment from predators. Screech-owls roosted in conifers more frequently when temperatures were above freezing and in boxes and cavities more frequently on days with rain, drizzle, or snow, supporting the conclusion that roosting owls seek favorable microclimates. Owls used each roost site an average of seven times. Female screech-owls were more likely to use boxes and males more likely to use cavities and conifer limbs. The suitability of boxes as potential nest sites may be one reason for their frequent use as roost sites by females.

KEY WORDS: *Eastern Screech-owl*; Otus asio; *roosting behavior*; *cavities*; *winter*.

La conducta de búhos (*Otus asio*) en centro Kentucky durante el tiempo de percha en el invierno

RESUMEN.—La conducta de búhos (*Otus asio*) durante el invierno en el tiempo de percha en centro Kentucky fue examinado en Octubre 1993–Marzo 1994. Once búhos usaron 69 sitios de percha 563 veces, con 29 cajas usadas 308 veces, 25 cavidades usadas 226 veces y 15 ramas usadas 29 veces. Las mas natural cavidades fueron en *Robinia pseudoacacia, Quercus falcata* y tocones, y cajas fueron localizadas en 15 diferente especies de árboles. Las ramas de coniferos para percha estabán en *Juniperus virginiana*. La frecuencia de uso de cajas y cavidades durante el invierno es probablemente el resulto de búhos buscando microclimas favorable y lugares para esconderse de depredadores. Búhos estabán en percha en coniferos con mas frecuencia cuando temperaturas estabán arriba de helando y en cajas y cavidades con mas frecuencia en días con lluvia, llovizna y nieve, soportando la conclusión que búhos en percha buscan microclimas favorables. Búhos usaron cada sitio de percha un normal de siete veces. Hembras eran mas probable usar cajas y machos eran mas probable usar cavidades y ramas de coniferos. La conveniencia de cajas como sitios de nido puede ser una razón para su uso con regular como sitios de percha para hembras.

[Traducción de Raúl De La Garza, Jr.]

Many aspects of the behavior and ecology of Eastern Screech-owls (*Otus asio*) have been examined (e.g., Van Camp and Henny 1975, Belthoff and Ritchison 1989, Gehlbach 1994), including their roosting behavior. Belthoff and Ritchison (1990a) monitored adult and juvenile screech-owls during the summer (May–July) in central Kentucky and found that vines (or branches covered to varying degrees with vines), cedars and open limbs of deciduous trees were used as roost sites. These sites apparently provided concealment from predators and favorable microclimates (Belthoff and Ritchison 1990a). Smith et al. (1987) reported that use of roost sites by screech-owls varied with season, with open limbs used during the summer and cavities used more often during the fall, winter and spring. Other investigators have also noted that screech-owls use cavities for roosting (Merson et al. 1983, Gehlbach 1994).

Although previous work has shown that screech-owls use different types of roost sites (e.g., open limbs and cavities), less is known about the environmental factors that influence selection of roost

sites or about features of roost sites that might be important in roost-site selection by screech-owls. The objective of our study was to examine roost-site selection by Eastern Screech-owls during late fall and winter (October–March) in central Kentucky. Specifically, we examined characteristics of roost sites used by screech-owls, possible relationships between certain environmental conditions and roost-site selection, and compared frequently used sites with little used and unused sites in an attempt to determine which features might be important in roost-site selection.

METHODS

The roosting behavior of screech-owls was monitored from 11 October 1993–19 March 1994 at the Central Kentucky Wildlife Management Area, 17 km southeast of Richmond, Kentucky. This area consists of small deciduous woodlots and thickets interspersed with cultivated fields and old fields (Sparks 1990, Sparks et al. 1994). Beginning on 11 October, owls were captured from nest boxes and fitted with radiotransmitters (Wildlife Materials, Carbondale, Illinois). Radio-marked owls were located at least four times each week. Each time owls were located, we noted the temperature (above or below 0° C) and categorized sky conditions as clear or partly cloudy, overcast or overcast with precipitation.

Each roost site was categorized as either a natural cavity, deciduous limb, conifer limb or nest box. For limb roosts, we noted tree species, roost height, tree height, diameter at breast height (dbh), roost orientation (position of owl relative to main bole), distance from main bole, distance from nearest permanent water and distance from the edge of the woodlot. For cavities and boxes, we noted tree species, tree height, dbh and diameter at cavity height, distance from nearest permanent water and distance from the edge of the woodlot. Characteristics were also measured for all boxes and accessible cavities, including cavity entrance dimensions (height and width), cavity depth (total and from bottom of cavity to entrance), inside diameter (distance from entrance to back wall) and entrance orientation. Tree, roost and cavity heights were determined with a clinometer.

To determine which features of natural cavities might influence roost-site selection, we compared the characteristics of 14 frequently used (≥8 times) cavities with 14 cavities in which owls were not observed roosting. To select unused cavities, we conducted 14 random line transects through woodlots used by our radio-tagged owls and chose the first cavity detected within 10 m on either side of the transect. Unused cavities selected for comparison with used cavities had to be large enough to permit entry by screech-owls (opening >8 cm in height and width).

For both used and unused natural cavities, we measured the previously listed cavity characteristics plus characteristics of vegetation surrounding the tree (James and Shugart 1970). For trees >8 cm dbh located within a 0.04 ha circular plot centered on the cavity tree, we recorded tree species, dbh and height. Shrub density and height were estimated by making two perpendicular transects

within the plot and counting and measuring the diameter and height of all woody stems <8 cm dbh within 1 m of each transect. Percent tree canopy and ground cover were estimated by sampling 10 points along transects in each of the four cardinal directions from the roost tree Percent understory cover was measured along the same transects using the line-intercept method (Brower et al 1977).

All analyses were performed using the Statistical Analysis System (SAS Institute 1989). Because we made repeated observations of the same owls, repeated measures analysis of variance was used to compare characteristics (roost height, tree height, dbh and distance to edge and water) of different types of roosts (conifer limb, natural cavity and nest box). Multivariate analysis of variance was used to compare characteristics of used and unused cavities, characteristics of little used and frequently used cavities and characteristics of cavities used by males and females. Cavity entrance orientation was analyzed using circular statistics to test the null hypothesis that orientation was random. Wilcoxon rank sum tests (which correspond to Mann-Whitney U-tests; SAS Institute 1989) were used to examine possible differences in the roosting behavior of males and females. Chi-square goodness-of-fit tests were used to examine differences in frequency of use of the various types of roosts over time (months) and with different environmental conditions (temperature, wind velocity and sky conditions). Results are presented as mean ±1 SD.

RESULTS

We monitored roosting behavior of 11 radio-marked owls (3 males and 8 females). Sex was determined by observations of behavior either during previous breeding seasons (for previously banded owls) or the following season. Only two radio-marked owls were paired. The female of this pair was only monitored for 14 days and, therefore, no comparison of the roosting behavior of these owls was possible. Female and male owls were monitored for an average of 96.8 ± 48.9 days and 131.7 ± 22.7 days, respectively. Overall, owls used 69 different roosts 563 times. We located an average of 51.2 ± 19.9 roosts per owl ($\bar{x}$ = 47.5 ± 22.4 for females; $\bar{x}$ = 61 ± 4.6 for males). Six boxes and five natural cavities were used at different times by two owls (either by each member of a pair or owls with adjacent ranges). We located an average of 93.8 ± 53.0 roosts each month, ranging from 33 in October to 189 in December.

Variation among Roost Types. The 69 roost sites included 29 boxes, 25 natural cavities and 15 limbs. Fourteen limb roosts were in conifers and one was in a deciduous tree. The deciduous limb roost was only used twice and is not considered further. Owls used boxes 308 times, natural cavities 226 times and conifer limbs 27 times.

Conifer roost trees were located closer to the edge of woodlots than trees with boxes and natural cavities ($F_{2,12} = 5.14$, $P = 0.02$). Conifer roosts were a mean distance of 5.31 ± 4.57 m from edges while boxes and natural cavities averaged 18.89 ± 11.94 m and 18.81 ± 20.75 m, respectively, from edges. We found no differences among roost types in mean distance from water ($F_{2,12} = 0.51$, $P = 0.61$), with mean distances ranging from 69.5 ± 77.6 m for boxes to 107.2 ± 127.9 m for conifers. Roost height (e.g., the height of owls in conifers or the height of the cavity entrance for boxes and natural cavities) did not vary among the three sites ($F_{2,10} = 0.51$, $P = 0.62$), with mean heights of 5.7 ± 2.4 m for conifers, 5.9 ± 1.5 m for boxes and 6.2 ± 2.3 m for cavities.

The mean diameter (height) of box and cavity entrances differed ($F_{1,6} = 51.7$, $P = 0.0004$) as did the mean depth (distance from the top of the cavity to the bottom) ($F_{1,6} = 9.98$, $P = 0.0196$), with natural cavities being deeper ($\bar{x} = 90.6 ± 75.5$ cm for cavities vs. 41.1 ± 13.74 cm for boxes) and having taller entrances ($\bar{x} = 20.4 ± 12.5$ cm for cavities vs. 8.2 ± 1.6 cm for boxes). In addition, differences in the mean cavity depth (distance from the bottom of the entrance hole to the bottom of the cavity) and the mean width of cavity entrances approached significance (cavity depth: $F_{1,6} = 5.32$, $P = 0.06$; cavity entrance width: $F_{1,6} = 3.55$, $P = 0.11$). No differences were found either in the diameter of trees at the level of the cavity ($F_{1,6} = 0.14$, $P = 0.72$) or in the diameter of the cavity ($F_{1,6} = 0.28$, $P = 0.62$).

The 29 boxes used by roosting screech-owls were located in 15 species of trees, with most in sycamores (*Platanus occidentalis*). The 25 natural cavities used by owls were in 12 species of trees. Most natural cavities were in black locusts (*Robinia pseudoacacia*), snags and southern red oaks (*Quercus falcata*). All 14 conifer roosts were in eastern redcedars (*Juniperus virginiana*).

Variation among Individuals and Between Sexes. The 11 owls used an average of 7.2 ± 3.9 different roost sites (range = 4–18). We found no correlation between the number of roost sites used and the number of days that an owl was located (Spearman rank correlation; $r_s = 0.4$, $P = 0.22$). Each roost site was used an average of 7.0 ± 11.6 times (range = 1–66).

We found no difference between males and females in the mean number of different roost sites used ($z = 1.34$, $P = 0.18$; $\bar{x} = 10.7 ± 6.4$ for males
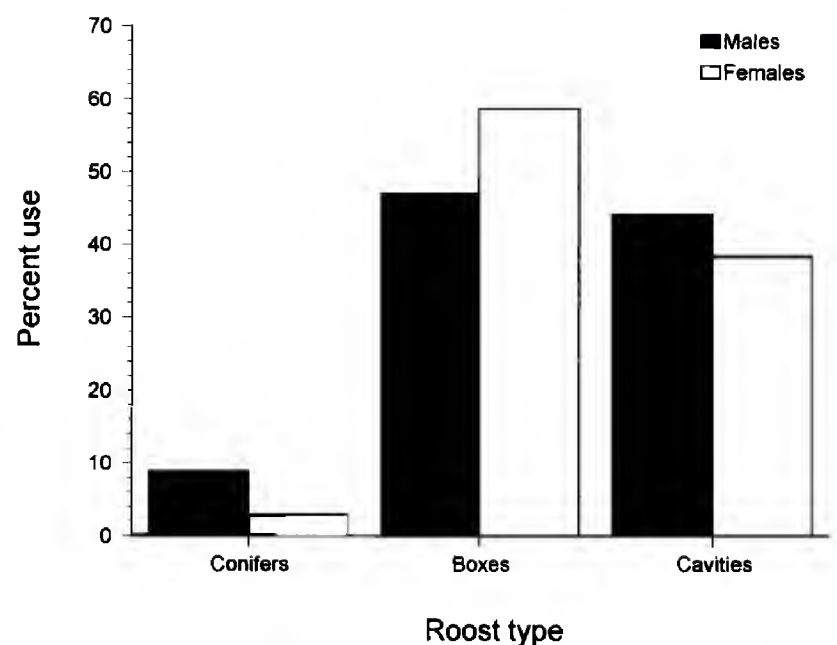

Figure 1. Use of different roost types by male and female Eastern Screech-owls.

and 6.0 ± 1.9 for females) or the mean number of times that particular roost sites were used ($z = 1.08$, $P = 0.28$; $\bar{x} = 5.7 ± 7.9$ times for males and 7.9 ± 13.7 times for females). Males and females differed in the use of different roost types ($\chi^2 = 13.1$, df = 2, $P = 0.001$). Females were more likely to use boxes while males were more likely to use conifers and natural cavities (Fig. 1).

Dimensions of roost trees and natural cavities used by males and females did not differ (Wilk's Lambda = 0.41, F = 1.63, $P = 0.24$). Although there was no overall difference (i.e., multivariate) between natural cavities used by males and females, the mean height of cavities above ground (one-way ANOVA; $F_{1,16} = 6.24$, $P = 0.024$) and the mean diameter (height) of entrances (one-way ANOVA; $F_{1,16} = 7.63$, $P = 0.014$) used by males and females did differ. The mean height of natural cavities was 4.68 ± 1.97 m ($N = 11$) for males and 7.40 ± 1.89 m for females ($N = 13$). For cavity entrances, the mean diameter (height) was 28.13 ± 14.15 cm for males ($N = 8$) and 14.25 ± 6.60 cm for females ($N = 10$).

Variation among Months. Use of conifer limbs, boxes and natural cavities varied among months ($\chi^2 = 20.2$, df = 10, $P = 0.028$). Conifers were used more often in February and March (Fig. 2). Use of boxes was greatest in November and lowest in February while use of natural cavities was greatest in December and lowest in March (Fig. 2).

Environmental Conditions and Roosting Behavior. Owls used boxes and natural cavities more on overcast days and days with precipitation (drizzle,
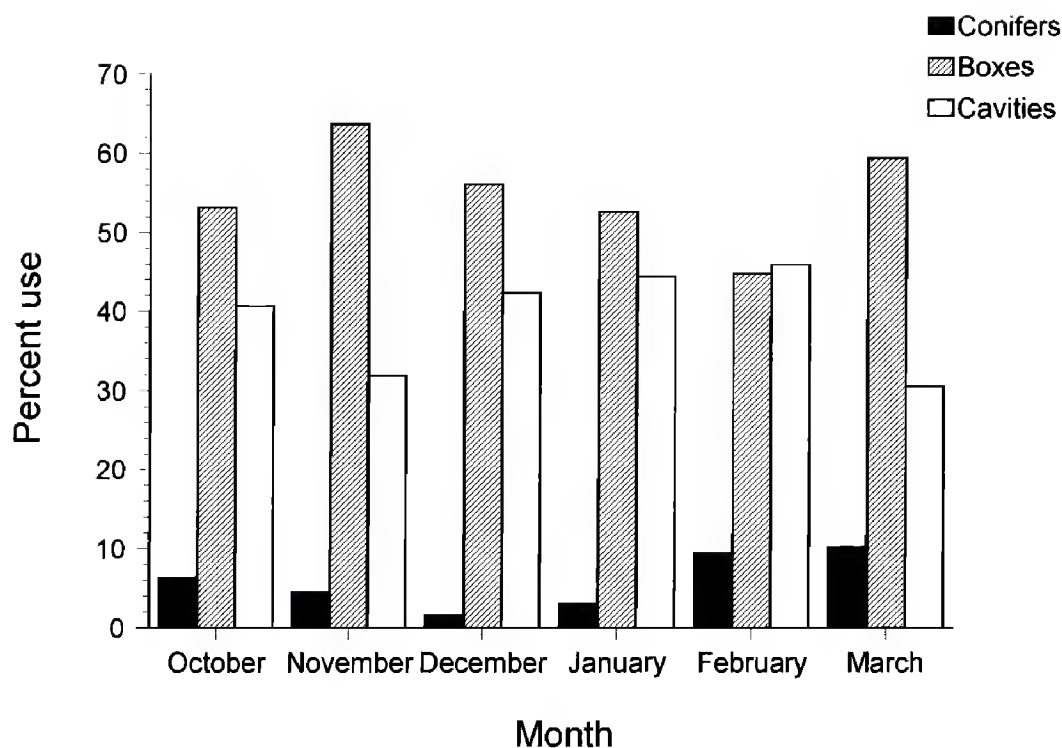
Figure 2. Variation in use of different roost types among months.

rain or snow; χ^2 = 12.3, df = 4, P = 0.015; Fig. 3). Owls were more likely to use conifers on clear or partly cloudy days (Fig. 3). Natural cavities were used more when temperatures were below freezing, and conifers were used more when temperatures were above freezing (χ^2 = 8.14, df = 2, P = 0.017).

Characteristics of Used versus Unused Natural Cavities. We found no differences between used and unused sites either in the dimensions of roost

trees and cavities (Wilk's Lambda = 0.60, F = 1.24, P = 0.34) or in the characteristics of surrounding vegetation (Wilk's Lambda = 0.79, F = 0.53, P = 0.83). The mean entrance orientation (direction) of used and unused roost cavities/boxes was 174 degrees (r = 0.438) and 354 degrees (r = 0.149), respectively. Neither sample exhibited significant directionality (Rayleigh's z-test; used: z = 2.69, $P >$ 0.05; unused: z = 0.27, P > 0.5). Similarly, there was no significant difference between used and un-
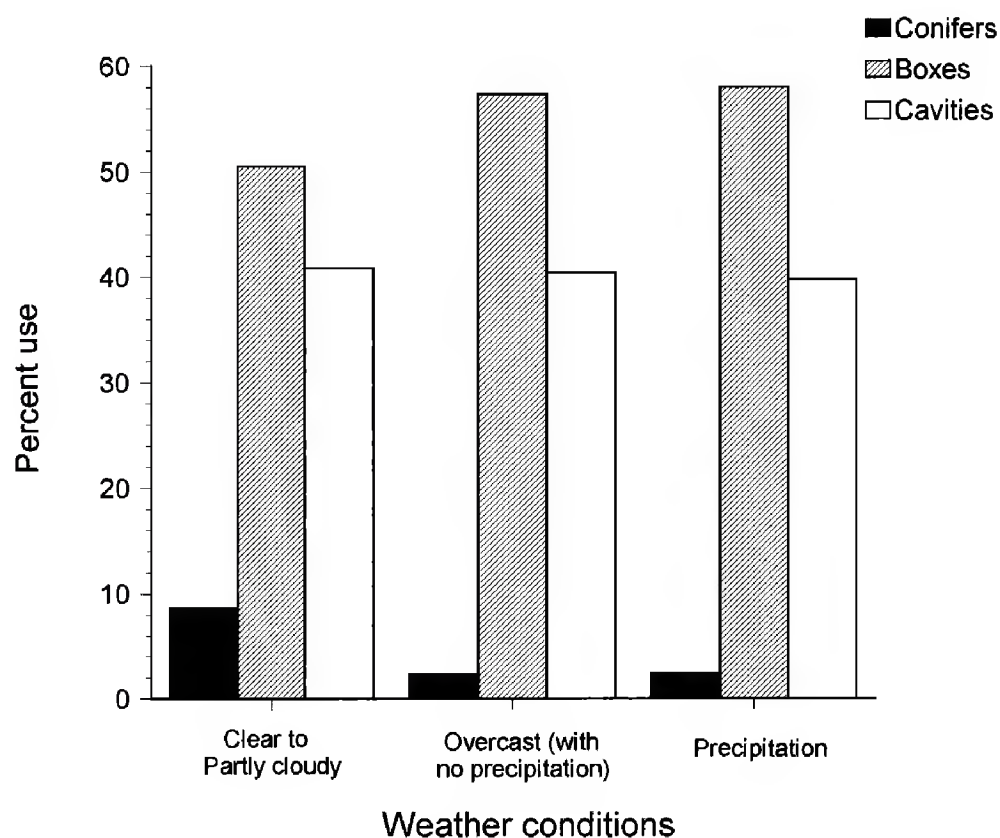

Figure 3. Variation in use of different roost types with different weather conditions.

used sites in mean entrance orientation (Watson's test; U2 = 0.068, $P > 0.5$).

Characteristics of Frequently Used versus Infrequently Used Natural Cavities and Boxes. For natural cavities, roost tree and cavity means for frequently used ($N \geq 8$) and infrequently used ($N \leq 7$) sites did not differ (Wilk's Lambda = 0.75, F = 1.18, $P = 0.34$). Similarly, for natural cavities and roost boxes combined, roost tree and cavity means for frequently and infrequently used sites did not differ (Wilk's Lambda = 0.76, F = 1.36, $P = 0.23$).

DISCUSSION

Screech-owls in our study used nest boxes and natural cavities more frequently than open limbs during the period from October–March. In contrast, Belthoff and Ritchison (1990a) found that screech-owls in the same study area roosted almost exclusively in open sites during summer (May–July). Previous investigators have also reported seasonal changes in types of roosts used (Smith et al. 1987, Gehlbach 1994). The shift from open sites in summer to boxes and cavities in winter is probably the result of owls seeking favorable microclimates and better concealment from predators. Hayward and Garton (1984) found that Western Screech-owls (*Otus kennicottii*) roosted only in conifers during late winter and early spring (prior to leaf out) and suggested that concealment was the most important factor in roost-site selection. These authors suggested that screech-owls roosted in cavities "only when sufficient protective cover for concealment is not available" and further noted that cavity-roosting owls would be protected from aerial predators but might be vulnerable to predation by arboreal mammals (Hayward and Garton 1984). Roosting in conifers might provide adequate concealment from hawks and other owls plus the opportunity to escape approaching mammalian predators (Hayward and Garton 1984).

Gehlbach (1994) found that use of boxes by screech-owls during December in central Texas corresponded significantly to mean air temperature and suggested that thermoregulation was the primary factor in roost-site selection. Further, he (1994) observed three male screech-owls during the period from November–February and found that mean ambient temperatures were lower when these males were in boxes and higher when in conifer roosts (junipers). Similarly, we found that ambient temperatures were usually above freezing when screech-owls used conifers for roosting, and

that owls were more likely to use conifers in February and March when temperatures are beginning to increase.

Eastern Screech-owls in our study roosted in boxes more than in natural cavities. Availability may have been one reason for the greater use of boxes. However, differences in microclimate may have been another factor, i.e., screech-owls may have used boxes more frequently during winter to reduce thermoregulatory costs (see McComb and Noble 1981).

We found that the height of roost sites in conifers did not differ from the height of the entrance holes of boxes and cavities used by roosting owls. Gehlbach (1994) reported similar results and found that open roosts were an average of 3.8 m high while entrances of boxes and cavities were an average of 3.1 m high.

The height of roost sites might be influenced by the risks of predation. For example, Nilsson (1984) found a lower rate of predation on nest cavities located higher in trees for six species of birds and Albano (1992) found that Carolina Chickadees (*Parus carolinensis*) nesting in lower cavities suffered higher rates of predation. Thus, screech-owls may not use roost sites below some minimum height because of the increased risk of predation. In addition, Gehlbach (1994) suggested that screech-owls refrain from using very high roost sites, possibly because such sites may be more exposed to the elements and flying up to higher roosts would require more energy (Collias and Collias 1984, Korol and Hutto 1984).

Individual screech-owls used an average of more than seven different roost sites during our study. Smith et al. (1987) observed that "an owl may use a roost site for several days . . . then move to a new site." Merson et al. (1983) also reported that screech-owls used a variety of roost sites. Using different roost sites may reduce the chances of predation (Belthoff and Ritchison 1990a). Screech-owls in our study area sometimes lose boxes and cavities to other species such as eastern gray squirrels (*Sciurus carolinensis*) and southern flying squirrels (*Glaucomys volans*), and occasional reuse by owls might also reduce the chances that cavities will be usurped by these other species.

Screech-owls in our study used each roost site an average of seven times. Other investigators have reported the repeated use of certain roost sites by screech-owls (Merson et al. 1983, Smith et al. 1987, Gehlbach 1994) and other species of owls (e.g.,

Barrows 1981, Bosakowski 1984, Hayward and Garton 1984). In contrast, Belthoff and Ritchison (1990a) found that screech-owls usually did not use the same roost site on successive days during the post-fledging period (May–July), possibly indicating that many suitable sites are available (Belthoff and Ritchison 1990a). In contrast, reduced cover from leaf fall during the autumn months plus the possible need to use sites providing favorable microclimates limits the number of suitable roost sites available during the winter (Belthoff and Ritchison 1990a). Such limits may contribute to the repeated use of particular roost sites (boxes and cavities) during the winter.

We found differences in the roosting behavior of male and female screech-owls. In contrast, Belthoff and Ritchison (1990a) found no differences in the characteristics of open roost sites used by male and female screech-owls. At least two factors may have contributed to differences in the roosting behavior of males and females. First, the availability of the different types of roosts may have varied among the ranges of males and females. Second, the suitability of boxes or cavities used by female screech-owls may be based in part on their potential as nest sites. Perhaps as a result, cavities used by female screech-owls were higher and had smaller entrances than those used by males. As discussed previously, higher cavities suffer lower rates of predation and may be preferred by nesting females. In addition, nesting screech-owls may avoid cavities with large entrances (Belthoff and Ritchison 1990b) because cavities with smaller entrances will exclude some potential nest predators (Sonerud 1985).

We found no significant differences between characteristics of used and unused cavities or between frequently and infrequently used cavities, suggesting that screech-owls exhibit little selectivity in their choice of roost cavities. Smith et al. (1987) also reached this conclusion and, regarding the use of roost cavities by screech-owls, stated that "the sizes of both the cavity entrance and the interior were quite variable. . . ." Smith et al. (1987) also noted that the entrances of some roost sites were elongated slits while others were large openings created when the tops of trees or limbs had broken off.

In contrast, Belthoff and Ritchison (1990b) found that Eastern Screech-owls were selective in their use of nest cavities, perhaps because variation in the characteristics of nest cavities may influence

the risks of predation. The apparent tendency of screech-owls to be less selective in the use of roost cavities suggests that the risks of predation may be lower during the nonbreeding season. At least one group of potential predators, snakes, (Bent 1938) is either less active or not active during the nonbreeding season. In addition, nestling screech-owls are more vulnerable to predation than adults. Therefore, adult owls must select nest cavities that minimize the risks of predation. During the nonbreeding season, less vulnerable adults may not be as selective because they are better able to defend themselves and to escape from potential predators.

LITERATURE CITED

ALBANO, D.J. 1992. Nesting mortality of Carolina Chickadees breeding in natural cavities. *Condor* 94:371–382.

BARROWS, C. 1981. Roost selection by Spotted Owls: an adaptation to heat stress. *Condor* 83:302–309.

BELTHOFF, J.R. AND G. RITCHISON. 1989. Natal dispersal of Eastern Screech-owls. *Condor* 91:254–265.

———. 1990a. Roosting behavior of postfledging Eastern Screech-owls. *Auk* 107:567–579.

———. 1990b. Nest-site selection by Eastern Screech-owls in central Kentucky. *Condor* 92:982–990.

BENT, A.C. 1938. Life histories of North American birds of prey, Part 2. Smithsonian Inst. U.S. Natl. Mus. Bull. 170, Washington, DC U.S.A.

BOSAKOWSKI, T. 1984. Roost selection and behavior of the Long-eared Owl (*Asio otus*) wintering in New Jersey. *Raptor Res.* 18:137–142.

BROWER, J.E., J.H. ZAR AND C.N. VON ENDE. 1977. Field and laboratory methods for general ecology. Wm. C. Brown Publishers, Dubuque, IA U.S.A.

COLLIAS, N.E. AND E.C. COLLIAS. 1984. Nest building and bird behavior. Princeton Univ. Press, Princeton, NJ U.S.A.

GEHLBACH, F.R. 1994. The Eastern Screech Owl: life history, ecology, and behavior in the suburbs and countryside. Texas A&M Univ. Press, College Station, TX U.S.A.

HAYWARD, G.D. AND E.O. GARTON. 1984. Roost habitat selection by three small forest owls. *Wilson Bull.* 96: 690–692.

JAMES, F.C. AND H.H. SHUGART, JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727–736.

KOROL, J.J. AND R.L. HUTTO. 1984. Factors affecting nest site location in Gila Woodpeckers. *Condor* 86:73–78.

McComb, W.C. AND R.E. Noble. 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. *J. Wildl. Manage.* 45:284–289.

Merson, M.H., L.D. Leta AND R.E. Byers. 1983. Observations on roosting sites of screech-owls. *J. Field Ornithol.* 54:419–421.

Nilsson, S.G. 1984. The evolution of nest-site selection by hole-nesting birds: the importance of nest predation and competition. *Ornis Scand.* 15:167–175.

SAS Institute. 1989. SAS user's guide: statistics, 1989 ed. SAS Institute, Cary, NC U.S.A.

Smith, D.G., A. Devine AND R. Gilbert. 1987. Screech-owl roost site selection. *Birding* 19:6–15.

Sonerud, G.A. 1985. Risk of nest predation in three species of hole nesting owls: influence on choice of nest-

ing habitat and incubation behavior. *Ornis Scand.* 16: 261–269.

Sparks, E.J. 1990. The spatiotemporal ecology of adult and juvenile Eastern Screech-owls in central Kentucky. M.S. thesis, Eastern Kentucky Univ., Richmond, KY U.S.A.

——, J.R. Belthoff AND G. Ritchison. 1994. Habitat use by Eastern Screech-owls in central Kentucky. *J. Field Ornithol.* 65:83–95.

Van Camp, L. AND C.J. Henny. 1975. The screech-owl: its life history and population ecology in northern Ohio. N. Amer. Fauna No. 71, U.S. Fish and Wildl. Ser., Washington, DC U.S.A.

NUTRIENT CONTENT OF FIVE SPECIES OF DOMESTIC ANIMALS COMMONLY FED TO CAPTIVE RAPTORS

NANCY J. CLUM[1]
The Peregrine Fund, 566 W. Flying Hawk Lane, Boise, ID 83709 U.S.A.

MARIANNE P. FITZPATRICK AND ELLEN S. DIERENFELD
Department of Nutrition, Wildlife Conservation Society, 185th St. and Southern Blvd., Bronx, NY 10460 U.S.A.

ABSTRACT.—The objective of this work was to provide a basis for more informed evaluation of diet options with respect to the nutritional needs of captive raptors. We compared nutritional content of five domesticated species that are most commonly fed to captive raptors; quail (*Coturnix coturnix japonica*), chickens (*Gallus domesticus*), rats (*Rattus norvegicus*), mice (*Mus musculus*) and guinea pigs (*Cavia porcellus*). We measured proximate composition (moisture, lipid, protein, ash), vitamin A, vitamin E, copper, iron, zinc, magnesium, manganese, calcium and potassium. Significant species differences were found in lipid and in vitamins A and E, and differences approached significance in iron and manganese concentrations. Differences in nutrient content between species did not correspond to differences in nutrient levels of diets consumed by prey. All species contained adequate amounts of protein, lipid, vitamin A, calcium, magnesium and zinc. However, whole domesticated prey were potentially inadequate sources of vitamin E, copper, iron and manganese.

KEY WORDS: *body composition; minerals; nutrition; vitamins; raptor diet.*

Contentos de nutrimento para cinco especies de animales domesticos frecuentamente dados para comer ha rapaces captivos

RESUMEN.— El objetivo de este trabajo fue para proporcionar un base para una evaluación mas informada de opciones de dieta con respeto con la necesidad de alimentación de rapaces cautivas. Nosotros comparamos el contento de nutrimiento de cinco especie domesticadas que estén frecuentemente dadas de comer a rapaces cautivos: codorniz (*Coturnix coturnix japonica*), gallinas (*Gallus domesticus*), rata, (*Rattus norvigicus*), ratón (*Mus musculus*) y cobayo (*Cavia porcellus*). Nosotros medimos composición próximo (humedad, grasa, proteína, ceniza), vitamina A, vitamina E, cobre, fierro, zinc, magnesio, manganeso, calcio y potasio. Diferencia significas de especies fueron encontradas en grasa y en vitamina A y E y diferencias estabán significante en concentraciones de fierro y manganeso. Diferencias en alimento entre especie no correspondieron a diferente niveles de nutrimiento de dietas consumidas para la presa. Todos contienen suficiente cantidad de proteína, grasa, vitamina A, calcio, magnesio y zinc. Sin embargo, presa domesticada fueron pontenciamente insuficiente de vitamina E, cobre, fierro y manganeso.

[Traducción de Raúl De La Garza, Jr.]

The diets of most wild raptors consist of a wide variety of prey species (Palmer 1988). Of necessity, raptors maintained in captivity are usually fed a very limited array of domesticated species. The diet of captive birds is therefore artificial in both the type and variety of species consumed. Few studies have been done regarding the nutritional status of free-ranging birds, but the data that do exist suggest that wild birds may differ significantly from captive animals of the same species (Dierenfeld et al. 1989, Dierenfeld 1994). This is of concern to zoos, private breeders and conservation organizations that engage in captive propagation because nutritional status affects health (Gershwin et al. 1985, Sklan et al. 1995), growth (Lavigne et al. 1994a), reproduction (NRC 1984, Naber and Squires 1993) and longevity (Good and Gajjar 1986). Undernutrition can also have long-term effects (Bedi 1987, Grantham-McGregor 1987, Lavigne et al. 1994b), and can, therefore, potentially influence the viability of reintroduced populations.

[1] Present address: Environmental Science Program, DePaul University, 1036 West Belden Ave., Chicago, IL 60614.

For most individuals and organizations, no feasible alternative exists to feeding artificial diets. For financial and logistical reasons, options are usually restricted to prepared commercial diets or to one or more domesticated species. Relatively little information is available on the nutrient content of whole vertebrate prey (see Dierenfeld et al. 1994 for review) to facilitate comparison of dietary options. Furthermore, existing nutritional information focuses primarily on macronutrients such as lipid, protein, ash and fiber which are less likely to be limiting in the diet of captive animals than vitamins or minerals.

This study compares nutritional content of five domesticated species that are among the most commonly fed to captive raptors: quail (*Coturnix coturnix japonica*), chickens (*Gallus domesticus*), rats (*Rattus norvegicus*), mice (*Mus musculus*) and guinea pigs (*Cavia porcellus*). We measured proximate composition (moisture, lipid, protein, ash), vitamin A, vitamin E, copper (Cu), iron (Fe), zinc (Zn), magnesium (Mg), manganese (Mn), calcium (Ca) and potassium (K). These results provide the basis for a more informed evaluation of diet options with respect to the nutritional needs of captive raptors.

METHODS

Experimental Design. We analyzed five species of domesticated animals. Both male and female quail were analyzed, but only males of other species were used because females are typically retained for breeding stock at our facility. Birds ($N = 50$, each species) were raised from hatch to 6 wk of age in brooders. Mammals were raised in litters until weaning. Three individuals from each mammalian species (from different litters) were then randomly selected and placed together in new cages. Mice were raised to 12 wk, rats were raised to 11 wk and guinea pigs were raised to 10 wk in standard laboratory mammal cages. The following complete commercial products were fed, exclusively and *ad libitum*: quail, Purina Turkey Starter; chickens, Purina Meatbuilder; rats and mice, Purina Formulab Chow; guinea pigs, Purina Guinea Pig Chow (all manufactured by Purina Mills, St. Louis, MO U.S.A.).

Laboratory Analyses. Three individuals of each species (and each sex for quail) were ground separately. Feathers were removed from birds, as most raptors pluck their prey and the majority of feathers consumed are regurgitated in pellets; for this study we assume that nutrient intake from feather digestion is negligible. Guinea pigs were also decapitated as even the largest eagles held at our facility failed to consume the craniums of this species. Four samples were immediately taken from each individual; two for duplicate vitamin analyses and two for duplicate moisture, lipid, ash and mineral analyses. The remainder of the ground sample was frozen, and two

samples were taken at a later time for duplicate protein analyses. One sample was also taken from each type of feed fed to each species.

Moisture content was determined by drying samples to a constant weight in a vacuum oven at 60°C. Lipid content of dried samples was determined indirectly using Soxhlet extraction (Ellis 1984). Fat-free dry samples were ashed in a muffle furnace at 550°C for three days (Ellis 1984) to determine ash content. Protein content of thawed wet tissues was assayed by the Biuret method (Horwitz 1975); samples were corrected for any moisture loss during freezing by redrying a second set of samples. Tissue extraction and analyses of retinol and alpha- and gamma-tocopherol were modifications of the general methods of Taylor et al. (1976) as described in Douglas et al. (1994), using high performance liquid chromatography. Extraction of feed was performed according to the method described by Combs and Combs (1985). Vitamin A activity was calculated as 0.3 g all-trans retinol = 1 IU (Olson 1984). Vitamin E was calculated by summing alpha- and gamma-tocopherols, where 1 mg alpha-tocopherol = 1.1 IU and 1 mg gamma-tocopherol = 0.1 IU (Machlin 1984). Ashed samples were prepared for mineral analysis according to the method of Parker (1963). Ca, Cu, Fe, Zn, Mg and Mn levels were measured on a Perkin-Elmer atomic absorbance spectrometer.

Statistical Analyses. Species differences in nutrient content were analyzed using a one-way ANOVA in SYSTAT (Wilkinson 1990). Sex differences and comparisons between pairs of species were analyzed using the Mann-Whitney U-statistic or the Student's t-test. Comparisons among more than two species were analyzed with a Kruskal-Wallace test. Where the same test was performed on multiple dependent variables, critical P-values were corrected for multiple comparisons using a sequential Bonferroni method (Rice 1989). Significance was assigned at the level of (corrected) $P \le 0.05$.

RESULTS

Female quail were 17% heavier than male quail at 6 wk of age (mass$_{males}$ = 121.6 g, SE = 12.6, mass$_{females}$ = 146.5 g, SE = 8.9, t = 5.91, P = 0.00001). No sex differences were found in proximate composition, vitamin A and vitamin E content, or mineral levels (Table 1), although females had consistently higher levels of all vitamins and minerals (Sign test, z_c = 2.5, P = 0.008). Values for male and female quail were therefore combined in subsequent analyses.

Significant species differences were found in lipid (Table 2), vitamin A and vitamin E (Table 3) and differences approaching significance (adjusted $P < 0.06$) in Fe and Mn concentrations (Table 3). Lipid levels were lowest in mice and highest in guinea pigs and chickens. Mice were 10 times higher in vitamin A than rats (Mann-Whitney, U = 18.0, P = 0.02), the species containing the next highest vitamin A values. Rats, quail and chickens did not

Table 1. Mean nutritional content of whole male and female Japanese Quail.[a]

	MALE		FEMALE		P[b]
Moisture (%)	65.1	(3.1)	65.6	(1.8)	0.827
Protein (%DM)	64.9	(14.6)	71.6	(6.8)	0.524
Lipid (%DM)	33.2	(6.3)	26.3	(3.2)	0.050
Ash (%DM)	9.6	(1.3)	12.0	(1.7)	0.127
Retinol (IU/kg)	32 989	(10 951)	66 444	(30 525)	0.127
Alpha-tocopherol (IU/kg)	41.6	(13.3)	79.3	(0.4)	0.050
Calcium (mg/kg)	32 685	(4178)	43 615	(6561)	0.127
Copper (mg/kg)	2.66	(0.61)	3.02	(0.77)	0.827
Iron (mg/kg)	85.07	(7.93)	112.40	(33.94)	0.275
Magnesium (mg/kg)	578.6	(255.2)	752.7	(209.3)	0.513
Manganese (mg/kg)	6.61	(2.11)	8.45	(4.31)	0.513
Zinc (mg/kg)	55.01	(9.13)	54.30	(26.66)	0.827

[a] All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. $N = 3$, each sex
[b] Unadjusted P-values, Student's t-test. No comparisons significant following correction for multiple comparisons.

differ in vitamin A content (Kruskal-Wallace, $H = 0.641$, $P = 0.73$). Guinea pigs were 50% lower in vitamin A than chickens (Mann-Whitney, $U = 9.0$, $P = 0.05$), the species with the next lowest values. Guinea pigs also had vitamin E levels that were at least 50% lower than quail (Mann-Whitney, $U = 18.0$, $P = 0.02$); quail, mice and chickens were not significantly different in vitamin E content (Kruskal-Wallace, $H = 1.55$, $P = 0.46$). Rats were three times higher in vitamin E than mice (Mann-Whitney, $U = 9.0$, $P = 0.05$).

Chicken and quail were not significantly different in Fe content (Mann-Whitney, $U = 10.0$, $P = 0.80$) or Mn content (Mann-Whitney, $U = 15.0$, $P = 0.12$), but the avian species were significantly higher than the mammalian species in both Fe (Mann-Whitney, $U = 64$, $P = 0.04$) and Mn (Mann-Whitney, $U = 68$, $P = 0.02$). Within the mammals, mice contained more Fe than guinea pigs (Mann-Whitney, $U = 9.0$, $P = 0.05$) or rats (Mann-Whitney, $U = 9.0$, $P = 0.05$), but rats and guinea pigs did not differ from each other (Mann-Whitney, $U = 4.0$, $P = 0.827$). Guinea pigs and mice had sim-

ilar levels of Mn (Mann-Whitney, $U = 5.0$, $P = 0.275$) and were both higher in this nutrient than rats (Mann-Whitney, $U = 16.0$, $P = 0.05$). Differences in nutrient levels of feeds did not correspond to nutrient differences between species in any case (Table 4).

DISCUSSION

The differences between 6-wk male and female quail were not significant in this study; however, it is worth noting that females had consistently higher levels of most nutrients, as well as lower lipid levels, than males. We have also found that at 16 wk of age nutrient levels in male quail are unchanged relative to 6-wk old birds, but levels in female quail (mobilizing resources for egg production) have almost doubled (unpubl. data). These data suggest that sex differences in nutrient content may be detectable with larger samples sizes or at different ages.

With the exception of lipid content, little difference was observed in proximate composition among species. Our results are similar to published

Table 2. Proximate composition of whole domestic species.[a]

	QUAIL	CHICKEN	RAT	MOUSE	GUINEA PIG	P
Moisture (%)	65.4 (2.3)	67.7 (1.3)	64.3 (2.4)	66.9 (2.6)	69.3 (1.8)	0.075
Protein (%DM)	67.6 (11.4)	64.0 (15.1)	63.4 (14.3)	64.4 (20.8)	58.9 (14.9)	0.955
Lipid (%DM)	29.7 (5.9)	47.2 (5.3)	34.9 (5.2)	23.7 (8.8)	45.4 (11.0)	0.005[b]
Ash (%DM)	10.8 (1.9)	10.4 (2.0)	7.5 (2.1)	9.2 (1.6)	8.9 (0.6)	0.155

[a] All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. $N = 3$, each species
[b] P-value significant after correction for multiple comparisons.

Table 3. Vitamin and mineral content of whole domesticated species.[a]

	QUAIL		CHICKEN		RAT		MOUSE		GUINEA PIG		P
Retinol											
(IU/kg)	49 716	(27 504)	35 588	(15 309)	68 244	(23 220)	657 344	(196 887)	19 989	(3000)	<0.00001[b]
Alpha-tocopherol											
(IU/kg)	60.4 (29.8)		61.4 (5.6)		210.5 (68.7)		74.4 (18.2)		29.8 (0.9)		0.00013[b]
Calcium											
(mg/kg)	38 150	(7748)	24 546	(2864)	22 856	(4636)	32 076	(6185)	29 458	(4458)	0.01841
Copper											
(mg/kg)	2.8 (0.7)		2.7 (0.1)		1.3 (0.4)		3.8 (0.2)		6.0 (4.2)		0.04781
Iron											
(mg/kg)	98.7 (31.6)		97.6 (10.2)		43.0 (3.9)		76.4 (0.4)		51.9 (6.8)		0.00675
Magnesium											
(mg/kg)	665.6 (229.5)		535.9 (71.3)		247.3 (134.9)		431.9 (54.2)		637.3 (39.6)		0.02099
Manganese											
(mg/kg)	7.5 (3.2)		11.0 (1.2)		2.9 (0.9)		5.3 (1.7)		6.6 (0.5)		0.00688
Zinc											
(mg/kg)	54.7 (17.8)		74.1 (21.1)		35.0 (10.0)		44.0 (5.7)		64.4 (23.7)		0.09748

[a] All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. $N = 3$, each species
[b] P-values significant after correction for multiple comparisons.

values for these species, which range between 55–68% for water content, 43–66% (DM) for protein content and 7–10% (DM) for ash content (Medway 1958, Lepore and Marks 1971, Brisbin and Tally 1973, Bird and Ho 1976, Thonney et al. 1984, Lavigne et al. 1994a). Lipid content appears to be the most variable component of proximate composition ranging between 19–49% (Lepore and Marks 1971, Brisbin and Tally 1973, Bird and Ho 1976, Perrigo and Bronson 1983, Thonney et al. 1984, Lavigne et al. 1994a), but there is no consistent

pattern of lipid content with respect to species, as might be expected with a labile body component.

Vitamin and mineral content in this study were much more variable than proximate composition. Although few comparative data are available, species differences in vitamin A and vitamin E content have also been found by Douglas et al. (1994), and species differences in mineral content appear to be present in the results of Bird and Ho (1976) and Lavigne et al. (1994a), although no statistical analysis of these data was presented. The pattern of

Table 4. Composition of commercial diets and relation between diet and body composition[a].

	TURKEY STARTER	MEAT-BUILDER	FORMULAB CHOW	GUINEA PIG CHOW	P[b]
Moisture (%)	9.3	7.7	8.9	9.4	0.900
Lipid (%)	1.1	4.2	2.0	2.4	0.192
Protein (%)	20.4	18.3	15.2	16.1	0.274
Ash (%)	7.0	5.8	7.6	8.4	0.270
Vitamin A (IU/kg)	3500	4500	6133	29 733	0.282
Vitamin E (IU/kg)	11.8	4.2	14.8	15.9	0.730
Calcium (mg/kg)	17 079	12 584	13 762	15 124	0.085
Copper (mg/kg)	18.7	14.5	13.4	14.1	0.872
Magnesium (mg/kg)	1285.1	1218.5	1068.0	1757.4	0.202
Iron (mg/kg)	161.9	154.6	239.6	290.4	0.855
Manganese (mg/kg)	76.4	78.2	16.3	54.7	0.520
Zinc (mg/kg)	127.3	124.4	99.8	90.4	0.058

[a] All data except moisture content presented on a dry matter basis. $N = 1$, all diets.
[b] Unadjusted P-values for regression of diet composition on body composition.

species differences in these studies, however, is not consistent with the pattern that we observed. For example, we observed rats to be generally low in mineral content, while Bird and Ho (1976) did not. Also, our values for vitamin E were up to 50% greater, and our values for vitamin A were up to two times greater than those of Douglas et al. (1994). Variation in nutritional content can result from differences in diet (Thonney and Ross 1987, Dierenfeld et al. 1989, Clum et al. 1996), genetics (Lepore and Marks 1971), age (Brisbin and Tally 1973, Bird and Ho 1976, Thonney and Ross 1987, Douglas et al. 1994) or sex, all of which have been demonstrated to cause significant changes in proximate composition and/or vitamin and mineral content. Diet formulation in particular has almost certainly changed over the two decades that these studies encompass, and may, therefore, be a significant source of variation. Manner and length of storage can also affect nutrient levels, particularly of vitamins, which are more labile than minerals or proximate composition. Storage may have caused the observed differences in vitamin levels between our study and that of Douglas et al. (1994), as their animals were purchased frozen from breeders whereas ours were freshly killed.

Our study suggests that species differences in nutritional content are not readily predictable. Comparative work on digestive efficiency of birds of prey has shown that the Common Buzzard (*Buteo buteo*), a generalist species, has high efficiency on a wider variety of prey than the Peregrine Falcon (*Falco peregrinus*), a specialist species (Barton and Houston 1993). Such variation in the ability to extract nutrients may partially explain the food preferences of birds in captivity. However, the prey that has the closest physical resemblance to wild prey does not necessarily bear the closest nutritional resemblance for the reasons mentioned above. If different species require prey with different nutritional content as Barton and Houston (1993) have suggested, then it is necessary to provide prey that are not only taxonomically acceptable, but nutritionally compatible for optimal breeding.

Generally, when authors allude to food quality or nutritional content they are referring to proximate composition. Although lipid content of prey may be of critical energetic importance in wild birds (Blem 1990) and does have the ability to limit egg number (Drobney 1980), lipid reserves are unlikely to be a limiting factor in the energetics or reproduction of captive birds that experience both

lower energy demands and more regular access to food. A greater potential problem in captivity is egg and chick viability, which is not limited by lipid and protein reserves, but can be severely affected by vitamin and mineral content of food (NRC 1984, Naber and Squires 1993).

All prey analyzed in this study met known requirements of domestic mammalian carnivores for vitamin A, Ca, Mg and Zn (vitamin A, 2440–10 000 IU/kg; Ca, 0.4–1.2%; Mg, 0.04–0.1%; Zn, 30–50 mg/kg; NRC 1985, 1986, Robbins 1983). Copper levels were inadequate in all species except guinea pigs, Fe was below recommended levels in rats and guinea pigs and Mn was lower than suggested in rats (Cu, 5.0–7.3 mg/kg; Fe, 60–100 mg/kg; Mn, 5–10 mg/kg; NRC 1982, 1985, 1986). Manganese deficiency has recently been documented in captive raptor chicks fed exclusively rats (C. Sandfort, pers. comm.). Although all species except guinea pigs met recommended levels of vitamin E for mammalian carnivores (20–80 IU/kg, NRC 1982, 1985, 1986), it has been suggested that raptors may require up to 10 times more vitamin E to protect against deficiencies (Calle et al. 1989, Dierenfeld et al. 1989). Other differences between nutrient requirements for domestic mammalian carnivores and nondomestic avian carnivores may exist.

LITERATURE CITED

BARTON, N.W.H. AND D.C. HOUSTON. 1993. A comparison of digestive efficiency in birds of prey. *Ibis* 135. 363–371.

BEDI, K.S. 1987. Lasting neuroanatomical changes following undernutrition in early life. Pages 1–49 *in* J. Dobbing [ED.], Early nutrition and later achievement. Academic Press, London, U.K.

BLEM, C.R. 1990. Avian energy storage. Pages 59–113 *in* D. Power [ED.], Current Ornithology, Vol. 7. Plenum Press, New York, NY U.S.A.

BIRD, D.M. AND S.K. HO. 1976. Nutritive values of whole-animal diets for captive birds of prey. *Raptor Res.* 10. 45–49.

BRISBIN, I.L., JR. AND L.J. TALLY. 1973. Age-specific

changes in the major body components and caloric value of growing Japanese quail. *Auk* 90:624–635.

CALLE, P.P., E.S. DIERENFELD AND M.E. ROBERTS. 1989. Serum alpha-tocopherol in raptors fed vitamin E-supplemented diets. *J. Zoo Wildl. Med.* 20:62–67.

CLUM, N.J., M.P. FITZPATRICK AND E.S. DIERENFELD. 1996. Effects of diet on nutritional content of whole prey. *Zoo Biol.* 15:525–537.

COMBS, S.D. AND G.F. COMBS, JR. 1985. Varietal differences in the vitamin E content of corn. *J. Agric. Food Chem.* 36:815–817.

DIERENFELD, E.S. 1994. Vitamin E in exotics: effects, evaluation and ecology. *J. Nutr.* 124:2579S–2581S.

————, C.E. SANDFORT AND W.C. SATTERFIELD. 1989. Influence of diet on plasma vitamin E in captive Peregrine Falcons. *J. Wildl. Manage.* 53:160–164.

————, N.J. CLUM, E.V. VALDES AND S.E. OYARZUN. 1994. Nutrient composition of whole vertebrate prey: a research update. Proc. Assoc. Zoo Aquaria Conf., Atlanta, GA U.S.A.

DOUGLAS, T.C., M. PENNINO AND E.S. DIERENFELD. 1994. Vitamins E and A, and proximate composition of whole mice and rats used as feed. *Comp. Biochem. Physiol.* 107A:419–424.

DROBNEY, R.D. 1980. Reproductive bioenergetics of wood ducks. *Auk* 97:480–490.

ELLIS, R.L. 1984. Meat and meat products. Pages 431–443 *in* S. Williams [ED.], Official methods of analysis. Association of Official Analytical Chemists, Inc., Arlington, VA U.S.A.

GERSHWIN, M.E., R.S. BEACH AND L.S. HURLEY. 1985. Nutrition and immunity. Academic Press, San Diego, CA U.S.A.

GOOD, R.A. AND A.J. GAJJAR. 1986. Diet, immunity and longevity. Pages 235–250 *in* M.L. Hutchinson and H.N. Munro [EDS.], Nutrition and aging. Academic Press, San Diego, CA U.S.A.

GRANTHAM-MCGREGOR, S. 1987. Field studies in early nutrition and later achievement. Pages 128–174 *in* J. Dobbing [ED.], Early nutrition and later achievement. Academic Press, London, U.K.

HORWITZ, W. [ED.] 1975. Official methods of analysis of the Association of Official Analytical Chemists. Assoc. Off. Analyt. Chem., Washington, DC U.S.A.

LAVIGNE, A.J., D.M. BIRD, D. LACOMBE AND J.J. NEGRO. 1994a. Growth of hand-reared American Kestrels I. The effect of two different diets and feeding frequency. *Growth Dev. Aging* 58:191–201.

————. 1994b. Growth of hand-reared American Kestrels II. Body composition and wingloading of fledglings hand-fed two different diets. *Growth Dev. Aging* 58:203–209.

LEPORE, P.D. AND H.L. MARKS. 1971. Growth rate inheritance in Japanese quail. 4. Body composition following four generations of selection under different nutritional environments. *Poult. Sci.* 50:1191–1193.

MACHLIN, L.J. 1984. Vitamin E. Pages 99–146 *in* L.J. Machlin [ED.], Handbook of vitamins: Nutritional, biochemical and clinical aspects. Marcel Dekker, Inc., New York, NY U.S.A.

MEDWAY, W. 1958. Total body water in growing domestic fowl by antipyrine dilution technic. *Proc. Soc. Exp. Biol. Med.* 99:733–735.

NABER, E.C. AND M.W. SQUIRES. 1993. Vitamin profiles of eggs as indicators of nutritional status in the laying hen: diet to egg transfer and commercial flock survey. *Poult. Sci.* 72:1046–1053.

NATIONAL RESEARCH COUNCIL. 1982. Nutrient requirements of minks and foxes. National Academy Press, Washington, DC U.S.A.

————. 1984. Nutrient requirements of poultry. National Academy Press, Washington, DC U.S.A.

————. 1985. Nutrient requirements of dogs. National Academy Press, Washington, DC U.S.A.

————. 1986. Nutrient requirements of cats. National Academy Press, Washington, DC U.S.A.

OLSON, J.A. 1984. Vitamin A. Pages 1–44 *in* L.J. Machlin [ED.], Handbook of vitamins: nutritional, biochemical and clinical aspects. Marcel Dekker, Inc., New York, NY U.S.A.

PALMER, R.S. 1988. Handbook of North American birds. Vols. 4 and 5. Yale Univ. Press, New Haven, CT U.S.A.

PARKER, H.E. 1963. Magnesium, calcium and zinc in animal nutrition. *Atomic Absorption Newsletter* 2:23.

PERRIGO, G. AND F.H. BRONSON. 1983. Foraging effort, food intake, fat deposition and puberty in female mice. *Biol. Reprod.* 29:455–463.

RICE, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.

ROBBINS, C.T. 1983. Wildlife feeding and nutrition. Academic Press, Orlando, FL U.S.A.

SKLAN, D., D. MELAMED AND A. FRIEDMAN. 1995. The effect of varying dietary concentrations of vitamin A on immune response in the turkey. *Br. Poult. Sci.* 36:385–392.

TAYLOR, S.L., M.P. LAMBEN AND A.L. TAPPEL. 1976. Sensitive flourometric method for tissue tocopherol analysis. *Lipids* 11:530–538.

THONNEY, M.L. AND D.A. ROSS. 1987. Composition of gain of rats fed low or high protein diets and grown at controlled rates from 80 to 205 grams. *J. Nutr.* 117:2135–2141.

————, A.M. OBERBAUER, D.J. DUHAIME, T.C. JENKINS AND N.L. FIRTH. 1984. Empty body component gain of rats grown at different rates to a range of final weights. *J. Nutr.* 114:1777–1786.

WILKINSON, L. 1990. SYSTAT: The system for statistics. Systat, Inc., Evanston, IL U.S.A.

SHORT COMMUNICATIONS

JUVENAL PLUMAGE CHARACTERISTICS OF MALE SOUTHEASTERN AMERICAN KESTRELS
(*FALCO SPARVERIUS PAULUS*)

KARL E. MILLER
Department of Wildlife Ecology and Conservation, University of Florida, P.O. Box 110430, Gainesville, Florida 32611 U.S.A.

JOHN A. SMALLWOOD
Department of Biology, Montclair State University, Upper Montclair, NJ 07043 U.S.A.

KEY WORDS: *American Kestrel; Falco sparverius; Florida; aging; plumage pattern.*

Determining ages of American Kestrels (*Falco sparverius*) can be problematic. The first prebasic molt in American Kestrels is incomplete; juvenal body plumage is replaced in the late summer or early fall of the hatching year, while juvenal remiges and rectrices are retained. However, some males retain a few too many juvenal body feathers through the first prebasic molt (Smallwood 1989). Retention of juvenal body feathers was common in male American Kestrels (*F. s. sparverius*) wintering in southern Florida; of 18 males known to be immature because of distinctive fault bar patterns (Hamerstrom 1967, Smallwood 1989), four retained their juvenal body plumage after the first prebasic molt was completed and four others were undergoing delayed body molt as late as November (J. Smallwood, unpubl. data). Thus, a substantial portion of immature male American Kestrels can be aged after the first prebasic molt.

Many sources have reported that heavy streaking on the breast and dark barring on the anterior dorsum are diagnostic characters of the juvenal plumage of male American Kestrels (Parkes 1955, Bird and Palmer 1988, Smallwood 1989, Wheeler and Clark 1995). In his key for age and sex determination of American Kestrels, Smallwood (1989) used the absence of bars on the "upper one-third to one-half of back" as a diagnostic character to distinguish males in basic plumage from hatching-year males.

Existing keys for aging American Kestrels are based on *F. s. sparverius*. Little has been published about the biology of the Southeastern American Kestrel (*F. s. paulus*), which breeds in Florida and the southern portions of South Carolina, Georgia, Alabama, Mississippi and Louisiana (Smallwood 1990). This nonmigratory race underwent a marked decline in recent decades (Hoffman and Collopy 1988) and is currently listed as threatened in Florida (Collopy 1996). The objective of this study was to examine the plumage characteristics of male Southeastern American Kestrel nestlings in northcentral Florida and to compare them to those observed throughout the better studied portion of the species' range.

STUDY AREA AND METHODS

We examined the plumage characteristics of nestling male Southeastern American Kestrels in Levy County, Florida, during May–July 1994 and May 1995. Nestlings ranged in age from 14–27 d at the time of banding, but some nestlings younger than 17 d of age were not sufficiently feathered to include in our analysis. Therefore, we characterized the juvenal plumage of nestlings ≥17-d old. We defined the "back" of the kestrel as the area extending from the rump to the nape, including the interscapular region (U.S. Fish and Wildlife Service 1980). Each nestling was classified as belonging to one of four categories based on a visual assessment of the extent of barring on its back: (1) barring restricted to the posterior third of the back, (2) barring extending beyond the lower one-third but not beyond the lower one-half of the back, (3) barring extending throughout the lower two-thirds of the back or (4) barring extending throughout the entire back or nearly so.

RESULTS AND DISCUSSION

We examined 33 male nestlings from 20 nest boxes. Mean age of the nestlings examined was 22.4 d. Fifteen (45%) of 33 male nestlings lacked the diagnostic barring on the anterior half of the dorsum. Several had no barring at all. Only nine males (27%) had barring throughout the entire dorsum as indicated in couplet 2A of the key (Smallwood 1989). Moreover, brood mates did not share the same barring pattern; of 11 nests containing at least two males, only four nests had brood mates belonging to the same dorsal plumage category.

Bloom (1973) stated that immature birds of either sex in southern California could not be distinguished from adults by feathering. However, most authors reported that juvenal males had heavy streaking on the breast and

dark barring on the anterior dorsum, whereas males in basic plumage had immaculate to lightly spotted upper breasts (Parkes 1955, Bird and Palmer 1988, Smallwood 1989, Wheeler and Clark 1995). We found that the amount of streaking on the breast was variable in male nestlings as has been observed in juvenal plumage of *F. s. sparverius*. In contrast, we found that nearly half of the male nestlings we examined in our study area lacked the dark barring on the anterior dorsum diagnostic in *F. s. sparverius*. We recommend both characters be assessed in determining age in *F. s. paulus*.

RESUMEN.—Nosotros comparamos los característicos del plumaje de pajaritos machos *Falco sparverius paulus* en el norte centro de Florida con esos observados durante todo el estudio de la especies pradera. 15 (45%) de 33 machos pequeños les faltaba la barra en el parte anterior de la espalda que ha estado reportando como diagnóstico para *F. s. sparverius*. Muchos no tenían barras. Nosotros recomendemos que una variada de plumaje este valorada en determinando edad en *F. s. paulus*.

[Traducción de Raúl De La Garza, Jr.]

LITERATURE CITED

BIRD, D.M. AND R.S. PALMER. 1988. American Kestrel (*Falco sparverius*). Pages 253–290 *in* R.S. Palmer [ED.], Handbook of North American birds, Vol. 5, Diurnal raptors (Part 2). Yale Univ. Press, New Haven, CT U.S.A.

BLOOM, P.H. 1973. Seasonal variation in body weight of sparrow hawks in California. *West. Bird Bander* 48:17–19.

COLLOPY, M.W. 1996. Southeastern American Kestrel. Pages 211–218 *in* J.A. Rodgers, H.W. Kale and H.T. Smith [EDS.], Rare and endangered biota of Florida, Vol. V, Birds. Univ. Presses of Florida, Gainesville, FL U.S.A.

HAMERSTROM, F. 1967. On the use of fault bars in aging birds of prey. *Inland Bird-Banding News* 39:35–41.

HOFFMAN, M.L. AND M.W. COLLOPY. 1988. Historical status of the American Kestrel (*Falco sparverius paulus*) in Florida. *Wilson Bull.* 100:91–107.

PARKES, K.C. 1955. Notes on the molts and plumages of the sparrow hawk. *Wilson Bull.* 67:194–199.

SMALLWOOD, J.A. 1989. Age determination of American Kestrels: a revised key. *J. Field Ornithol.* 60:510–519.

———. 1990. Kestrel and Merlin. Pages 29–37 *in* B.A. Giron Pendleton [ED.], Proc. of the southeast raptor management symposium. Natl. Wildl. Federation, Washington, DC U.S.A.

U.S. FISH AND WILDLIFE SERVICE. 1980. North American bird banding manual, Vol. II (revised edition). U.S Government Printing Office, Washington, DC U.S.A

WHEELER, B.K. AND W.S. CLARK. 1995. A photographic guide to North American raptors. Academic Press, London, UK.

DOUBLE BROODING BY AMERICAN KESTRELS IN IDAHO

KAREN STEENHOF AND BRIT E. PETERSON
Snake River Field Station, Forest and Rangeland Ecosystem Science Center, Biological Resources Division, U.S. Geological Survey, 970 Lusk Street, Boise, ID 83706 U.S.A.

American Kestrels (*Falco sparverius*) sometimes raise two broods in a single nesting season in captivity (Porter and Wiemeyer 1970, 1972), and double brooding by wild kestrels has been recorded in Florida and Central Missouri (Howell 1932, Toland 1985). Evidence for double brooding elsewhere, however, has been mainly circumstantial (Stahlecker and Griese 1977, Black 1979, Sutton 1979), and there have been no reports of double brooding by kestrels north of 40° latitude. During a long-term study of kestrel nest box occupancy, productivity and site fidelity, we confirmed that a pair of kestrels successfully

raised two broods in southwestern Idaho (43° N, 116° W) during a single breeding season.

In 1996, we captured the same marked pair of adults at two different nest boxes, both of which had young that reached fledging age. We captured the female on an incomplete set of three eggs at the first box on 25 March and captured the male in a mist net (Steenhof et al. 1994) placed by the same box on 17 May. We banded five young from this box on 17 May. Ages of the young at banding ranged from 15–25 d, based on a comparison with a photographic aging key (Griggs and Steenhof 1993). We recaptured the female on 18 June in a box with six eggs, 800 m from the first box. We caught the same male in this box on 28 June with three eggs and three young. We banded five 22- to 26-d-old young from this box on 23 July. We assume that all 10 young fledged from the boxes because we found no dead young in or below the boxes during subsequent checks.

Both members of the pair were at least 2-yr-old in 1996, and both had nested successfully in the area in 1995. The female was first captured on 5 February 1995 on a balchatri midway between her two 1996 nesting efforts. In 1995, she raised young in the same box where she raised her second brood in 1996. The male was first captured as a breeding adult in 1995, paired with a different female at a box approximately 1.7 km from his nearest 1996 nesting attempt.

The distance between nesting efforts in Idaho (800 m) was much greater than the distances in Missouri (0–300 m, Toland 1985), possibly due to fewer available nesting sites in Idaho. Both boxes used in Idaho were mounted on boards attached to fenceposts in open agricultural and rangeland habitats. There were no nest boxes or natural cavities nearer either box. The second clutch size (6 eggs) in Idaho was bigger than any recorded in Missouri, and in contrast to Toland's (1985) findings, the second clutch in Idaho was larger than the first clutch (5 eggs).

The estimated hatching dates of young produced by the pair that raised two broods in 1996 were 24 April and 28 June. During our 11-yr study, estimated hatch dates have been as early as 17 April and as late as 24 July ($\bar{x}$ = 25 May, SD = 18.5 d, N = 247). We have identified five broods with earlier hatch dates than the first brood of the pair that raised two broods and 10 broods with later hatch dates than their second brood, for all years combined. In 1996, the first brood of the renesting pair was the second earliest nesting effort in our study area, and the second brood was the second latest. The individuals that raised two broods in 1996 probably only raised one brood each in 1995 because their 1995 nesting chronology was closer to the long-term mean. The male's 1995 brood hatched on 14 June, and the female's hatched on 11 May.

Whether a pair will attempt to raise two broods in a single season likely depends on food availability, weather conditions and nesting experience. Both food availability and prior nesting experience may have increased the

likelihood of successful double brooding in 1996. Prey remains in the two nest boxes consisted mainly of voles (*Microtus* spp.), and our subjective observations indicated that voles were unusually abundant in 1996. Both members of the renesting pair in Idaho had successfully bred in the area the prior year. As in Toland's (1985) study, double brooding may be possible only for early breeders in Idaho. The climate in southwestern Idaho provides just enough time for kestrels to raise two broods. Henny and Brady (1994) found that permanent residents nest earlier than migrant kestrels in the Pacific Northwest. The female that raised two broods in our area was known to have spent at least part of one winter near her nesting territory.

Although this was the first and only documented case of double brooding during our 11-yr study, it may have occurred before. We would have missed other cases of double brooding if kestrels used natural nest sites in trees that we did not monitor for one of their nesting attempts. We also might have missed cases if we did not capture and/or mark both adults during one of their nesting efforts. In 1996, we knew the identities of 63% of the males and 93% of the females nesting in boxes; the proportions of unidentified individuals were higher during the first 7 yr of our study. The fact that kestrels used different boxes for nesting makes it difficult to confirm double brooding if the parents are not individually marked. It also raises doubts about some suspected cases of double brooding reported in the literature. The presence of a second clutch in the same box does not constitute evidence for renesting by a particular individual or pair (Sutton 1979). During our study, we knew the identity of females in five "renestings" following failures during incubation. In three cases, females whose clutches failed during incubation moved to other boxes. In two other situations, a new female nested in the same box where a different female had failed during incubation.

American Kestrels probably require a minimum of 120 d to raise two broods successfully: at least 5 d for each laying period, 27 d for each incubation period and 30 d for each brood-rearing period (Porter and Wiemeyer 1972). In southwestern Idaho, kestrels begin laying eggs as early as mid-March, and young have fledged as late as early to mid-August, a window of approximately 150 d. Theoretically, pairs with young that hatch earlier than 15 May could produce a second brood, and broods with hatch dates later than 15 June could be second broods. In our 11-yr study, 31% of broods hatched on or before 14 May, suggesting that almost one-third of the population nests early enough to produce two broods. However, only 15% of broods hatched after 15 June, indicating that at least half of the early nesters do not produce a second brood. In addition, some of the late broods represent pairs that nest late for other reasons, including renesting after failures during incubation. During our study, we knew of six renestings following failures, only two of which were successful. The young from these nesting at-

tempts hatched on 15 and 19 June, 9–13 d earlier than the second brood from the double brooding pair. If we assume conservatively that only those broods with hatch dates after 28 June (the hatch date of the second brood we confirmed) were second broods, then approximately 4% of the kestrel pairs in southwestern Idaho raise second broods. Continued monitoring of marked adults should provide more insight about the frequency of double brooding in northern latitudes.

RESUMEN.—Una pareja marcada de *Falco sparverius* crió dos nidadas de cinco en una temporada en dos cajas de nidos diferentes en el sur oeste de Idaho. Los dos padres tenían el mínimo de dos años y tenían éxito con nidos en el lugar antes. Las dos crías eran primera y la mas tarde en la área de estudio, pero sospechamos que hasta 4% de parejas en el sur oeste de Idaho crían dos crías cada temporada.

[Traducción de Raúl De La Garza, Jr.]

LITERATURE CITED

BLACK, E.A. 1979. American Kestrel possibly two-brooded in central Oklahoma. *Bull. Okla. Ornithol. Soc.* 12: 29–30.

GRIGGS, G.R. AND K. STEENHOF. 1993. Photographic guide for aging nestling American Kestrels. Unpubl. rep., Raptor Res. Tech. Asst. Cen., U.S. Dept. Interior, Bur. Land Manage., Boise, ID U.S.A.

HENNY, C.J. AND G.L. BRADY. 1994. Partial migration and wintering localities of American Kestrels nesting in the Pacific Northwest. *Northwestern Naturalist* 75:37–43

HOWELL, A.H. 1932. Forida bird life. Florida Department of Game and Freshwater Fish, Tallahassee, FL U.S.A.

PORTER, R.D. AND S.N. WIEMEYER. 1970. Propagation of captive American Kestrels. *J. Wildl. Manage.* 34:594–604.

——— AND ———. 1972. Reproductive patterns in captive American Kestrels (sparrow hawks). *Condor* 74:46–53.

STAHLECKER, D.W. AND H.J. GRIESE. 1977. Evidence of double brooding by American Kestrels in the Colorado high plains. *Wilson Bull.* 89:618–619.

STEENHOF, K., G.P. CARPENTER AND J.C. BEDNARZ. 1994. Use of mist nets and a live Great Horned Owl to capture breeding American Kestrels. *J. Raptor Res.* 28: 194–196.

SUTTON, G.M. 1979. Is the American Kestrel two-brooded in Oklahoma? *Bull. Okla. Ornithol. Soc.* 12: 30–31.

TOLAND, B.R. 1985. Double brooding by American Kestrels in central Missouri. *Condor* 87:434–436.

Received 6 September 1996; accepted 10 May 1997

FIRST NEST RECORD OF THE BARE-SHANKED SCREECH-OWL (*OTUS CLARKII*)

PAULA L. ENRÍQUEZ ROCHA[1] AND J. LUIS RANGEL-SALAZAR[1]
Programa Regional en Manejo de Vida Silvestre, Universidad Nacional, Apartado 1350-3000, Heredia, Costa Rica

JOE T. MARSHALL
National Museum of Natural History, 10th & Constitution Ave. N.W., Washington, DC 20560 U.S.A.

Most New World tropical forest raptors are poorly known, especially those restricted in distribution and

[1] Present address: Depto. Ecología y Sistemática Terrestre, ECOSUR, Apartado Postal 63, 29290 San Cristóbal de Las Casas, Chiapas, México.

habitat. An estimated one-half of Neotropical raptors, their nests, eggs and voices have never been described (Thiollay 1985). Most of the world's owl species occur in the tropics and their ecology and biology are little known (Clark et al. 1978).

Costa Rica contains 9.9% (17 species) of the 172 owl species (Monroe and Sibley 1993). The Bare-shanked Screech-owl (*Otus clarkii*) is a resident from the central mountains of Costa Rica (Central Cordillera, Talamanca

Cordillera), Panamá (W Chiriquí, Veraguas and Darién) through NW Colombia (Cerro Tacarcuna in NW Chocó) (AOU 1983). It has been recorded in the highlands of Monteverde, Poás Volcano, Tapantí, Chirripo, Cerro de la Muerte, Cerro Chompipe and Villa Mills (Stiles and Lewis 1980). It is the only species of the genus *Otus* that inhabits cloud forest and humid forest at high altitudes (900–2350 m) in Costa Rica (Slud 1964). Its numbers are unknown, but it has been reported to be uncommon or rare in Costa Rica (Stiles and Skutch 1989). Almost no information is available on its breeding biology and nests remain undescribed (Wetmore 1968, Stiles and Skutch 1989). The only previous evidence of breeding by Bare-shanked Screech-owls in Costa Rica comes from the presence of brood patches on museum specimens (Stiles and Skutch 1989). In this paper, we describe what we consider to be the first Bare-shanked Screech-owl nest located in the mountains of central Costa Rica.

From 15–17 April 1994, we heard and observed what appeared to be a breeding pair of Bare-shanked Screech-owls in a pasture near the Tapantí Hotel, approximately 71 km south of Cartago City, Provincia de San José, Costa Rica (9° 35'N, 83° 45'W). It is close to Tapantí National Park and above Cerro de la Muerte at the top of the northwest Talamanca Cordillera with an elevation of 2490 m. Mean annual temperature in the area is 6°C and mean annual precipitation is 6500 mm. Typical vegetation is cloud forest and subalpine paramo, and includes oaks, bromeliads, orchids, mosses and ferns.

On 15 April 1994 at 1900 H, we heard a deep whistled *huu-huu-huu* much like the typical call of a Bare-shanked Screech-owl. When it stopped, we imitated the call and a small owl flew to a mossy branch approximately 5 m away from us. We identified the owl to be an adult Bare-shanked Screech-owl and recorded its calls that night. On the morning of the next day, a search of two isolated trees nearby failed to locate any roosting owls or any sign that owls had recently used the trees. However, at about one-half hour after sunset, we observed an adult female Bare-shanked Screech-owl flying and a male perched and calling in the two trees. We distinguished the female by her higher pitched call (Fig. 1). At approximately 1830 H, the female flew to a nest in a live oak (*Quercus copeyensis*). A fork in the trunk created a natural cavity where the bird nested. The tree had a dbh (diameter at breast height) of 65 cm and was 23 m tall. The nest was 3.3 m high and the cavity was 35 cm long and 64 cm wide.

On 17 April 1994, we observed a single nestling covered with down in the cavity that we estimated to be approximately 3-wk-old (Fig. 2). No nesting material was found but the nestling was on a large clump of moss. Habitat surrounding the nest tree consisted of scattered, tall oaks laden with epiphytes. Ground cover consisted of meadow grasses.

Both parents brought food to the nestling. We were unable to identify the prey that were delivered, but the items appeared to be large insects such as orthopterans

and coleopterans. Many *Otus* species are mainly insectivorous (Ross 1969). Several times, the female flew from the nest to capture insects on the ground and returned quickly to give the food to the nestling. Occasionally the male perched on a lamp from which it caught insects. No pellets were found below the nest and we did not search for pellets inside the nest in order to avoid disturbance to the nest.

Otus is the largest genus in the order Strigiformes, and Monroe and Sibley (1993) list 46 species for this genus Marshall (1967) lists seven species of *Otus* occupying North and Middle America where they overlap without interbreeding. Most of them live in the world's tropical regions, except in Australasia, and many restricted populations of screech owls are now endangered species (Hekstra 1973). Our observations indicate that Bare-shanked Screech-owls probably breed from middle February (egg laying) through early May (fledging) in the Tapantí region. We estimated the breeding chronology based on Flammulated Owl (*Otus flammeolus*) in Colorado (Reynolds and Linkhart 1987). These findings are comparable with those reported by Stiles and Skutch (1989).

In view of limited geographic distribution of the Bare-shanked Screech-owl and its unknown breeding status, more information is needed on its nesting biology, nesting density and habitat affinities to address questions concerning its possible management and conservation Currently habitat loss is a major problem that threatens all raptor populations, and cloud forest habitats in central Costa Rica have been affected seriously by developments related to the dairy industry on highlands. Based on our limited knowledge of the breeding biology of the Bare-shanked Screech-owl, it may actually be the development of dairy farms which increase the numbers of isolated trees and lampposts for feeding. Any useful conservation strategy for the protection of Bare-shanked Screech-owls should at least protect woodlots as potential breeding sites.

RESUMEN.—Reportamos el primer registro de anidación de la Lechucita Serranera (*Otus clarkii*), encontrado en las tierras altas de Costa Rica. El nido se localizó en un árbol de encino (*Quercus copeyensis*) a una altura de 3.3 m en una cavidad natural con las siguientes dimensiones: 35 cm de largo y 64 cm de ancho. El nido contenía un pollo con una edad estimada de 3 semanas. Ambos padres alimentaban al pollo con insectos del orden coleóptera y ortóptera. No encontramos egagrópilas dentro ni fuera del nido. Se necesita más información sobre densidad poblacional y aspectos ecológicos para la Lechucita Serranera. Sin embargo, para establecer estrategias de conservación para esta especie, es importante incluir la protección de lotes arbolados para su reproducción.
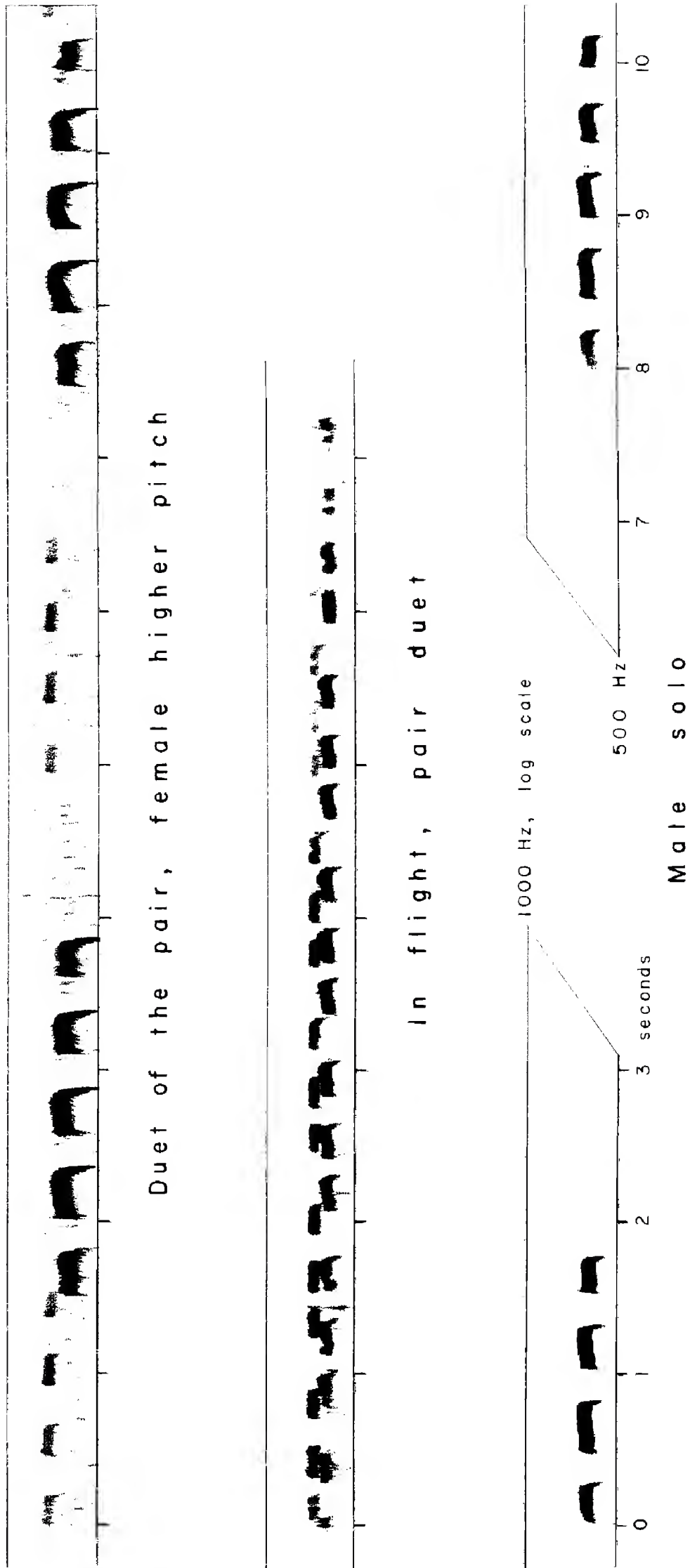
[Traducción de Autores]

Figure 1. Three kinds of Bare-shanked Screech-owl calls digitally recorded over 14 min the night of 15 April 1994 near the Tapantí Hotel, approximately 71 km south of Cartago City, Provincia de San José, Costa Rica: a) duet of the pair, female higher pitch, b) pair duet in flight, and c) male solo.

Figure 2. The nest and nestling of the Bare-shanked Screech-owl pair near the Tapantí Hotel, Costa Rica.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds, 6th edition. AOU, Smithsonian Inst., Washington, DC U.S.A.

CLARK, R.J., D.G. SMITH AND L.H. KELSO. 1978. Working bibliography of owls of the world. Washington DC, Natl. Wild. Fed. Sci. Tech. Publ. No. 1.

HEKSTRA, G.P. 1973. Scops and Screech owls. Pages 94–155 in J.A. Burton [ED.], Owls of the world. Eurobook Limited, The Hague, Netherlands.

MARSHALL, J.T. 1967. Parallel variation in North and Middle American Screech-owls. Western Foundation of Vertebrate Zoology. Monogr. 1. Los Angeles, CA U.S.A.

MONROE, B.L. AND C.G. SIBLEY. 1993. World checklist of birds. Yale Univ. Press, New Haven, CT U.S.A.

REYNOLDS, R.T. AND B.D. LINKHART. 1987. The nesting biology of Flammulated Owls in Colorado. Pages 239–248 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H.

Hamre [EDS.], Biology and conservation of northern forest owls. Winnipeg, Manitoba, Canada.

ROSS, A. 1969. Ecological aspect of the food habits of insectivorous Screech-owls. Proceedings of the Western Foundation of Vertebrate Zoology Vol. 1, No. 6. Los Angeles, CA U.S.A.

SLUD, P. 1964. The birds of Costa Rica, distribution and ecology. Bull. American Mus. Nat. Hist., Vol. 128. New York, NY U.S.A.

STILES, G. AND T.J. LEWIS. 1980. Locational check-list of the birds of Costa Rica. Costa Rica Expeditions, San José, Costa Rica.

———— AND A. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY U.S.A.

THIOLLAY, J.M. 1985. Falconiforms of tropical rain forest: a review. Pages 155–165 in I. Newton and R.D. Chancellor [EDS.], Conservation studies on raptors. ICBP Tech. Publ. No. 5. Paston Press England Ltd., London, UK.

WETMORE, A. 1968. The birds of the Republic of Panama. Smithsonian Misc. Coll., Vol. 150, Part 2. Washington, DC U.S.A.

THE SUMMER DIET OF THE LITTLE OWL (*ATHENE NOCTUA*) ON THE ISLAND OF ASTIPALAIA (DODECANESE, GREECE)

FRANCESCO M. ANGELICI AND LEONARDO LATELLA
Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza,"
viale dell'Università 32, I-00185 Roma, Italy

LUCA LUISELLI
Dipartimento di Biologia Animale e dell'Uomo,
Università di Roma "La Sapienza," via A. Borelli 50, I-00161 Roma, Italy

FRANCESCO RIGA
Istituto Nazionale della Fauna Selvatica, via Ca' Fornacetta 9,
I-40064 Ozzano dell'Emilia (Bologna), Italy

Widespread and easy to study taxa are ideal models for analyses of life-history divergence, because they permit comparisons that are not confounded by genetically-coded divergence in other morphological, behavioral and ecological traits (Luiselli et al. 1996a, 1996b). The problem, however, is to find species whose life history traits have been adequately studied in different portions of their range. In general, Palearctic owls have a great deal of potential in this area because several aspects of their biology such as food habits have been studied in detail (Herrera and Hiraldo 1976, Cramp 1985). The exception to this is the Mediterranean Islands, especially islands in the Aegean and East Mediterranean Seas, where virtually nothing is known concerning the food habits of owls (Uttendörfer 1952, Niethammer 1989). In particular, the diet of the Little Owl (*Athene noctua*) is little known. There are some dietary data available for islands in the western Mediterranean (Contoli et al. 1988, Lo Verde and Massa 1988) but nothing is known about what Little Owls eat in the Aegean and East Mediterranean Seas.

In the present paper, we report detailed information on the summer diet of the Little Owl from a Mediterranean island of Dodecanese, Greece.

STUDY AREA AND METHODS

Data were collected in late June 1990 on Astipalaia, an island of Dodecanese, Greece (36°30'–36°36'N, 26°14'–26°30'E, Fig. 1). The island is mainly mountainous (highest elevation, 506 m) with calcareous soils on the eastern and exterior western sides, and arenaceous and schistous soils in the remaining parts. The vegetation is poor, and characterized by chaparral with spiny shrubs, olive-groves, orchards, vineyards and cereal growings. Detailed faunistic studies for Astipalaia have already been done (Angelici et al. 1990, 1992). The island is inhabited by two species of owls, the Little Owl and Barn Owl (*Tyto*

alba). We recently reported the first records of Barn Owls on the island (Angelici et al. 1992).

Owl pellets were collected in abandoned buildings and at a few rocky sites. The collected material was identified in the laboratory. Small mammals and reptiles were identified by skull and mandibular remains, and arthropods by chitinous exoskeleton remains. We counted, in the most parsimonious way possible, the frequency of occurrence of each prey species in the diet. Although it was not possible to identify *Crocidura* remains to species level, we assumed they all belonged to *C. suaveolens*, a species widespread in the Dodecanese islands (Niethammer 1989).

Statistical analyses were performed by a STATISTICA (version 4.5, 1993) for Windows PC package, with α set at 5%. All data were checked for homoscedasticity before statistical analyses and normalized if necessary. If this procedure also failed in obtaining a normal distribution, nonparametric tests were used. Dietary diversity was assessed by applying Simpson's (1949) and Levins' (1968) formulas to the numerical frequency of occurrence of the various prey types in the pellets.

RESULTS

We collected a total of 33 complete and an undetermined number of incomplete Little Owl pellets, containing 1068 prey remains. Excluding the incomplete pellets from the analysis, the mean number of prey per pellet was 23.3. Little owls preyed on both vertebrates (0.56% of the total number of prey eaten) and invertebrates (99.44%) (Table 1). Contingency-table analysis showed that Little Owls fed on invertebrates significantly more frequently than on vertebrates ($\chi^2 = 1044.135$, df = 1, $P < 0.00000001$). All invertebrates eaten were insects, and most of them were earwigs (*Forficula lurida*) which accounted for over 70% of the total number of prey items ingested. Little Owls preyed significantly more often on earwigs than on all the other prey categories combined ($\chi^2 = 251.24$, df = 1, $P < 0.000000001$). Moreover, the mean number of earwigs per pellet was statistically higher than that of any other prey type in the diet (paired *t*, in all cases $P < 0.00001$). Beetles (belonging mainly to the
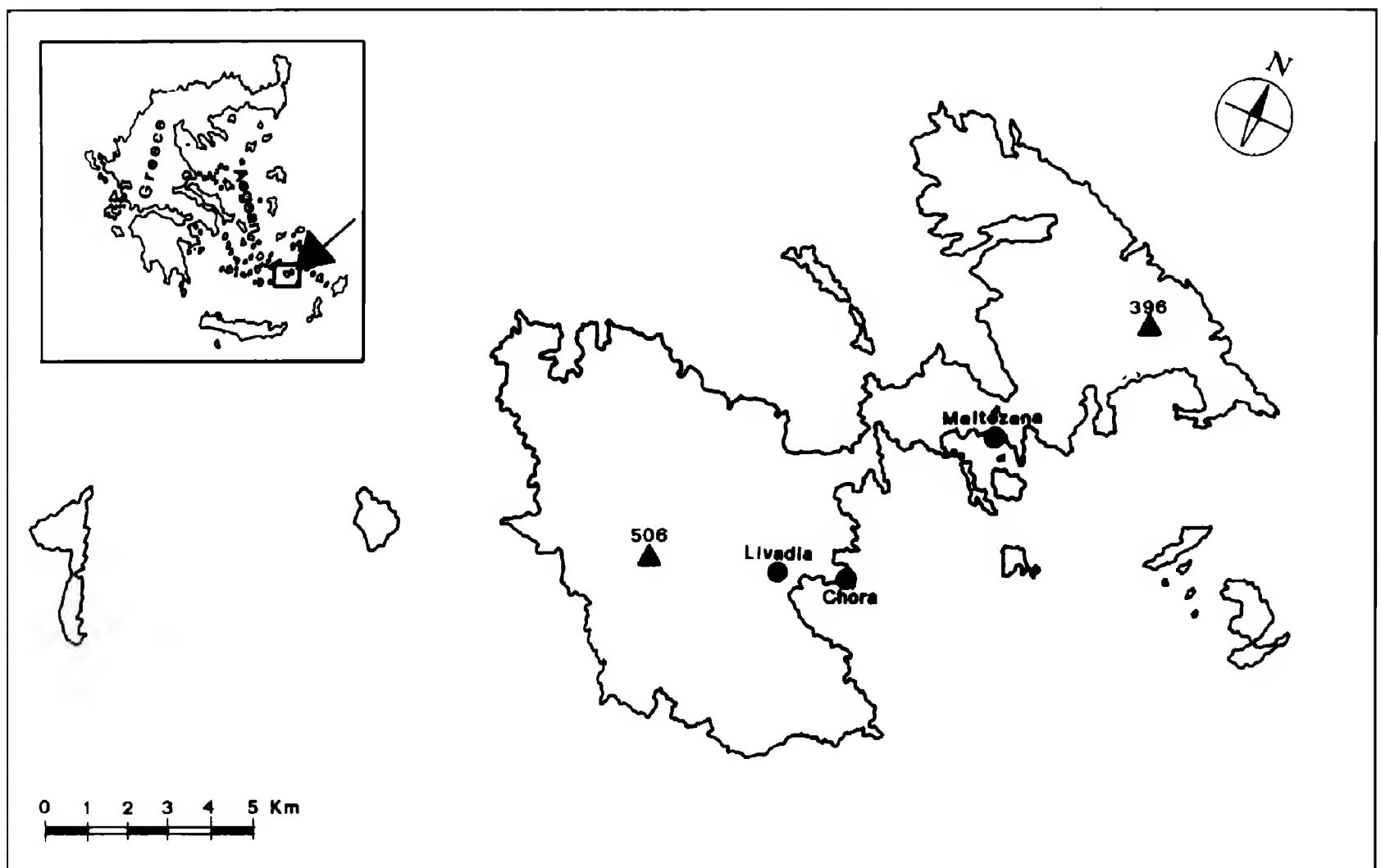
Figure 1. Location of Astipalaia Island (Dodecanese, Greece). Symbols: black triangles = high points in elevation; black circles = villages or towns.

family Tenebrionidae) were also frequently eaten (18.16% of the total number of prey items eaten). Some ants were eaten, all of them winged forms. Little Owls preyed occasionally also on small vertebrates (lizards, birds and shrews).

Dietary diversity was relatively low either using Levins' index (L = 0.094) or Simpson's index (B = 1.751).

DISCUSSION

Our data show the summer diet of Astipalaia Little Owls consists almost entirely of insects. This finding is consistent with Mikkola's (1983) suggestion that the proportion of insects in the diet of the Little Owl increases from the central European regions to the Mediterranean regions due to the lower availability of microtine rodents in the Mediterranean. An apparent exception has been shown in Sicily, where *Microtus savii* is widespread and is frequently preyed upon (16.4% of the total number of prey items) by Little Owls (Lo Verde and Massa 1988).

Our data collection was restricted to the summer season so it is not surprising that Little Owls would be eating large numbers of insects like earwigs which were readily available. Earwigs have been cited as important prey for Little Owls in other areas, including Denmark (Cramp 1985). The Little Owl diet on Astipalaia is probably greatly affected by seasonal fluctuations in the availability of various types of prey (Cramp 1985, Arias 1994). Therefore we feel that anal-

ysis of prey remains collected over an entire year would show a larger proportion of small mammals in the diet. We were surprised that we did not find remains of murids of the genus *Mus* in the Little Owl diet. These small-sized rodents (on average 17 g in mass) are the most common small mammal in Astipalaia (Angelici et al. 1992) and are frequent prey species for Little Owls elsewhere (Arias 1994). It is likely that Little Owls on Astipalaia become more dependent on murids later in the season when insects are not as abundant (Zerunian et al. 1982).

RESUMEN.—Los costumbres de comida del Búho (*Athene noctua*) fue estudiado durante el verano en la Isla de Astipalaia, una isla árida en Dodecanese, Grecia donde la ecología de este especies todavía esta completamente sin conocer. Un total de 1068 pedazos de presa fueron colectados. La dieta de búho consiste casi totalmente de insectos, especialmente tijeretas (*Forficula lurida*). Escarabajos y hormigas con halas también fueron frecuentemente comidas. Vertebrados casi nunca fueron cazados y muy pocos ratones chicos del genio *Mus*, que estaban muy abundante en los labores, casi nunca fueron cazados.

[Traducción de Raúl De La Garza, Jr]

Table 1. Summer diet of the Little Owl on Astipalaia Island (Dodecanese, Greece).

PREY TYPE	N	% N
Vertebrata		
Reptilia		
Podarcis erhardii	3	0.28
Aves		
Passer domesticus	1	0.09
Mammalia		
Crocidura sp.	2	0.19
Arthropoda		
Insecta		
Dermaptera		
Forficula lurida	793	74.25
Orthoptera		
Tettigonidae	42	3.93
Coleoptera		
Tenebrionidae	94	8.80
Curculionidae	9	0.84
Cerambicidae	7	0.66
Scarabeoidae	1	0.09
Carabidae	44	4.12
undetermined	39	3.65
Hymenoptera		
Formicidae	33	3.09

comments on the manuscript. This paper is the contribution No. 226 of the "Ricerche zoologiche delle Università di Roma nel vicino Oriente."

LITERATURE CITED

ANGELICI, F.M., M. CAPULA AND F. RIGA. 1990. Notes on the herpetofauna of Astipalaia island (Dodecanese, Greece). *Brit. Herp. Soc. Bull.* 34:31–33.

———, F. PINCHERA AND F. RIGA. 1992. First record of *Crocidura* sp. and *Mus domesticus* and notes on the mammals of Astipalaia Island (Dodecanese, Greece). *Mammalia* 56:159–161.

ARIAS, J.M. 1994. Nota sobre alimentacion de mochuelo (*Athene noctua* L., Aves: Strigiformes). *Doñana, Acta Vertebrata* 21:183–185.

CONTOLI, L., G. ALOISE AND M.G. FILIPPUCCI. 1988. Sulla diversificazione trofica di Barbagianni *Tyto alba* e Civetta *Athene noctua* in rapporto al livello diagnostico delle prede. *Avocetta* 12:21–30.

CRAMP, S. [ED.]. 1985. The birds of the western Palearctic, Vol. IV. Oxford Univ. Press, Oxford, UK.

HERRERA, C.M. AND F. HIRALDO. 1976. Food-niche trophic relationships among European owls. *Ornis Scand.* 7:29–41.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ U.S.A.

LO VERDE, G. AND B. MASSA. 1988. Abitudini alimentari della civetta (*Athene noctua*) in Sicilia. *Naturalista sicil.* 12 (suppl.):145–149.

LUISELLI, L., M. CAPULA AND R. SHINE. 1996a. Food habits, growth rates and reproductive biology of grass snakes *Natrix natrix* (Colubridae) in the Italian Alps. *J. Zool. (Lond.)* 240: in press.

———, ——— AND ———. 1996b. Reproductive output, costs of reproduction and ecology of the smooth snake (*Coronella austriaca*) in the eastern Italian Alps. *Oecologia* 106:100–110.

MIKKOLA, H. 1983. Owls of Europe. T. & A.D. Poyser, Calton, U.K.

NIETHAMMER, J. 1989. Gewöllinhalte der Schleiereule (*Tyto alba*) von Kos und aus Südwestanatolien. *Bonn. Zool. Beitr.* 40:1–9.

SIMPSON, E.H. 1949. Measurement of diversity. *Nature* 163:688.

UTTENDÖRFER, O. 1952. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. Eugen Umer, Stuttgart, Germany.

ZERUNIAN, S., G. FRANZINI AND L. SCISCIONE. 1982. Little Owls and their prey in a Mediterranean habitat. *Boll. Zool.* 49:195–206.

HOME RANGE, HABITAT USE AND NATAL DISPERSAL OF BLAKISTON'S FISH-OWLS

YUKO HAYASHI

Laboratory of Applied Zoology, Faculty of Agriculture, Hokkaido University, 060 Sapporo, Japan

KEY WORDS: *Blakiston's Fish-owl;* Ketupa blakistoni; *radio-telemetry; home range; habitat use; natal dispersal; inbreeding.*

Blakiston's Fish-owls (*Ketupa blakistoni*) occur in southeastern Russia (Amurland and Ussuriland, Sakhalin and southern Kuril Islands), northeastern China and northern Japan (northeastern Hokkaido) (Voous 1988, Brazil and Yamamoto 1989). Although this species was once widely distributed throughout Hokkaido, it now occurs very locally (Brazil and Yamamoto 1989) and the present population is estimated at 80–100 individuals (Brazil and Yamamoto 1989) and with no more than 20 breeding pairs (Clark and Mikkola 1989). This species is highly dependent on riparian forest (Burton 1973) and loss of suitable habitat could be contributing to its decline. However, there is no information available on the home range and habitat use of this species. Here, I report the results of a study aimed at describing the home range size, habitat use and dispersal behavior of young Blackiston's Fish-owls.

STUDY AREA AND METHODS

The study area (43°23'N, 143°20'E) was in the National Forest Agency and located on the upper Tokachi River in eastern Hokkaido, Japan. Approximately half of the study area consisted of a conifer forest plantation consisting of Sakhalin spruce (*Picea glehnii*), Japanese larch (*Larix leptolepis*) and eastern white pine (*Pinus strobus*). The other half included two types of natural forest. One consisted of mixed coniferous forest, mainly Yezo spruce (*Picea jezoensis*), Sakhalin fir (*Abies sachalinensis*) and broad-leaved tree species, such as Mongolian oak (*Quercus mongolica*), painted maple (*Acer mono*) and basswood (*Tilia japonica*) at higher elevations, and the other type consisted of broad-leaved forest dominated by Japanese poplar (*Populus maximowiczii*) and alder *(Alnus* spp.) which occurred along streams at lower elevations. Most of the ground cover was dwarf bamboo (*Sasa nipponica*).

Blakiston's Fish-owls were first observed breeding in the study area in 1986 and, thereafter, the same pair successfully fledged young four times from 1987–91 (*N* = 9 fledglings). Since 1985, the Environmental Agency of Japan supplemented the food supply of this pair by stocking a pond with fish to prevent possible starvation of the owls, especially in winter. This pond has become a major feeding area for the owls. In 1987, both adult owls and

one of the two young born in 1986 were mist netted and individually color banded. Since 1987, all fledglings have also been color marked for individual identification.

To study movements, two young owls, one male and one female, raised in the study area were captured in mist nets near the stocked pond on 27 and 30 January 1992, respectively. Radio-transmitters were attached to the tail according to Kenward (1978), with some modifications. Radios were trimmed to fit the rectrix shaft and attached to the ventral surface with stainless-steel wire and epoxy glue. Antennas were 260 mm in length. They were fastened to the feather shaft using fishing trace wire, and the ties were sealed with epoxy resin.

Owls were tracked using Yaesu FT-290mkII receivers. When tracking, a car-mounted whip antenna was used to determine the general location of an owl. A more precise location was then determined using a three-element hand-held Yagi antenna. Bearings were taken from at least three different sites. If the resulting error polygons were larger than 1 ha, the location was not used. For each owl, locations were determined once in the daytime around noon and three or four times (with an interval of more than 2 hr) during the night. The minimum convex polygon method (MCP, Mohr 1947) was used to calculate home range sizes. Mean error distance of the directional bearings from the test transmitters was 46.8 m (SD = 29.0, range = 0–125, *N* = 12).

Habitat types in the study area were identified using topographic maps (Geographical Survey Institute) and timber-type maps (National Forest Agency) and categorized as: (1) mixed forest (evergreen coniferous and deciduous broad-leaved trees), (2) coniferous plantation (deciduous and evergreen), (3) young broad-leaved forest, (4) artificial (forest roads, houses and electric powerline right-of-ways) and (5) water area (streams and lake). The 13.3 km^2 study area was surrounded by mountain ridges so an aerial survey was also conducted to obtain dispersal data.

RESULTS AND DISCUSSION

One radio-tagged owl (90M) was a male that fledged from the nest in 1990. He stayed within his natal area for one yr, disappeared in late April 1991, and returned on 6 November 1991. He was captured and radio-tagged on 27 January 1992. After radio-tagging, he stayed within 400 m of the capture site for two d. He then traveled upstream 6.9 km and then returned to the capture site where he stayed for the next month. I calculated his home range to be 6.1 km^2 (*N* = 11 locations) during the month of February. After that, he disappeared. On 25

Table 1. Compositions of the habitat components in the study area and home range, and of the actual habitat used by one female Blakiston's Fish-owl.

| VEGETATION CATEGORY | STUDY AREA | | HOME RANGE | | RADIO LOCATIONS | | | |
	PERCENT COVERAGE	EXPECTED NUMBERS	PERCENT COVERAGE	EXPECTED NUMBERS	DAY	NIGHT	TOTAL	
	%	n	%	n	n			%
Mixed forest	60.4	66.7	70.0	79.7	29	55	84	77.1
Coniferous plantation	36	39.8	21.1	24.0	8	7	15	13.8
Young broad-leaved forest	0.8	0.9	2.5	2.7	5	5	10	9.1
Artificial	1.5	1.6	2.3	2.6	0	0	0	0
Water area	1.3	—	4.1	—	0	0	0	0
Total	100.0	109	100.0	109	42	67	109	100.0

June (3.5 mo later), the transmitter signal was found 18.7 km west of the capture site during an aerial search of the study area and the radio, which had fallen off, was recovered on 15 July in the same location. On 28 July, I found 90M roosting at the side of a stream 2.5 km from the point where the radio had been recovered. He was not located again after that.

The other owl (86F), a female that fledged from the nest in 1986, was radio-tagged on 30 January 1992. For two yr, she had remained within the natal nesting area before disappearing in March 1988. She returned to her natal area on 16 November 1988 and spent the next winter there, after which she again disappeared in March 1989 and was absent for two yr. Two mo after the disappearance of this owl's mother (this probably occurred sometime in October 1991), she returned to the natal area and mated with her father in December 1991. She laid two eggs in early March 1992 and incubated until early April, during which time she stayed in the nest almost continuously except for one or two short trips away from the nest (<200 m) for 2–20 min. In early April, she deserted the nest before the eggs hatched.

I did not radio-track 86F egg-laying and incubation periods but, from 30 January–19 May (when the radio fell off), I obtained 109 locations for this owl on 49 different days. Her total home range size was 4.1 km². During the prelaying period (from February–March), the home range was 0.3 km² ($N = 20$ locations). This area included the nest and the small area immediately around the nest. After the nest failed, the home range increased in size to 3.6 km² in April ($N = 51$ locations) but decreased again in May to 2.8 km² ($N = 38$ locations).

Use of the home range by 86F appeared to be affected by the location of water. Her most distant location was 462.5 m from water and it was only about one third of the way to the edge in the study area. Daytime roost sites averaged significantly farther from water ($\bar{x} = 139.29$ m, SE $= 18.36$, $N = 42$ locations) than did nighttime roosts ($\bar{x} = 88.99$ m, SE $= 13.35$, $N = 67$ locations; Mann-Whit-

ney U-test, $U = 1010.5$, $P < 0.05$) indicating that she tended to hunt around streams and lakes at night.

The distribution of habitats also affected use of the home range by 86F. All telemetry locations were in the three forest types (mixed forest, conifer forest plantation and young broad-leaved forest), and she was never found using either the open water or artificial habitat categories. Because there was no significant difference in habitat use between day and night ($\chi^2 = 2.51$, df $= 2$, $P > 0.05$), all locations were pooled when habitat use was compared to availability within the overall study area and home range (Table 1). Because the area of young broad-leaved forest was small (0.8% of whole study area), locations in this category were combined with locations in the mixed forest category. Owl 86F used mixed forest more often than expected based on its availability within the study area (two-tailed binomial test, $P < 0.01$) and within the home range ($P < 0.05$).

Because use of mixed forest was possibly related to the fact that a stream was located adjacent to the area of mixed forest in the home range, I compared the number of locations in mixed forest that were within 100 m of water ($N = 58$ locations) to the expected number of locations in mixed forest based on the availability of this habitat category ($N = 41$ locations) and found the difference in use to again be significant (two-tailed binomial test, $P < 0.01$). Therefore, I concluded that the owl selected both the stream and its surrounding mixed forest habitat.

In Hokkaido, heavy timber cutting from the late 1950s to early 70s has converted most native forests into conifer forest plantations. Obviously this caused a loss of habitat and thus reduced the number of Blakiston's Fish-owls in the area. The father-daughter mating observed in my study was probably inevitable due to the small size of the fish-owl population. A daughter returning to the parental home range after a long absence (22 mo) suggests that she could not find a potential mate nor adequate habitats elsewhere.

RESUMEN.—El tamaño de la pradera, uso de hábitat y el comportamiento de dispersión de *Ketupa balkistoni* fueron

estudiados en el norte este de Hokkaido, Japon en 1992. Este especie cría de febrero–mayo, durante el tiempo, dos individuales (macho y hembra) fueron observados por uso de radio-telemetro. Una hembra formo una pareja con su padre que había perdido su pareja tres meses antes. Su pradera calculado por el método mínimo convexa polígono (MCP) fue 0.3 km² antes de poner, poniendo y tiempos de incubación. Ella dejo el nido antes que los huevos salieron de cascarón. 3.6 km² en abril y bajo ha 2.8 km² en mayo. La pradera total medida durante el tiempo de observación fue 4.1 km². Ella prefería usar bosques mixtos con ríos. El macho joven se movía en un área amplia después que estaba marcado, y se fue del área de nacimiento.

[Traducción de Raúl De La Garza, Jr.]

LITERATURE CITED

BRAZIL, M.A. AND S. YAMAMOTO. 1989. The status and distribution of owls in Japan. Pages 389–401 in B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. WWGB: Berlin, London and Paris.

BURTON, J.A. 1973. Owls of the World. A & W Visual Library.

CLARK, R.J. AND H. MIKKOLA. 1989. A preliminary revision of threatened and near threatened nocturnal birds of prey of the world. Pages 371–388 in B.-U. Meyburg and R.D. Chancellor [EDS.], Raptors in the modern world. WWGB: Berlin, London & Paris.

KENWARD, R.E. 1978. Radio transmitters tail-mounted on hawks. Ornis Scand. 9:220–223.

MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37: 223–249.

VOOUS, K.H. 1988. Owls of the northern hemisphere. William Collins Sons & Co. Ltd., London, UK.

Received 20 June 1996; accepted 3 May 1997

LETTERS

NEST DEFENSE AND MOBBING BEHAVIOR OF ELF OWLS

Avian mobbing has been defined as when birds of one or more species assemble near a predator, change perch locations frequently and emit loud vocalizations (E. Curio 1978, *Z. Tierpsychol.* 48:175–183). Predator mobbing is the most widely distributed avian response to predators (A.F. Skutch 1976, Univ. Texas Press, Austin, TX U.S.A.; Curio 1978; I.G. McLean and G. Rhodes 1991, *Current Ornithol.* 8:173–211), and has been the subject of numerous studies (Curio 1978; McLean and Rhodes 1991), but little information exists on nocturnal mobbing by either diurnal or nocturnal species. Such behavior may be rare among diurnal species. For example, Common Terns (*Sterna hirundo*) will group mob Black-crowned Night Herons (*Nycticorax nycticorax*) during diurnal periods but flee from them at night (D.A. Shealer and S.W. Kress 1991, *Colonial Waterbirds* 14:51–56).

Nocturnal species, such as owls, may be more likely to engage in nocturnal mobbing behavior, but accounts of owls mobbing natural predators are rare. Screech-owls (*Otus* spp.) will make vocal and physical attacks on squirrels, snakes, domestic cats and humans (A.C. Bent 1938, Pt. 2. U.S. Natl. Mus. Bull. 170; F.R. Gehlbach 1994, Texas A&M Univ. Press, College Station, TX U.S.A.), and we have captured Western Screech-owls (*O. kennicottii*) in a dho-gaza trap (P.H. Bloom et al. 1992. *J. Raptor Res.* 26:167–178) baited with a Great Horned Owl (*Bubo virginianus*) after dark. Also, Gehlbach (1994) observed a male Eastern Screech-owl (*O. asio*) among a flock of songbirds mobbing a black ratsnake (*E. obsoleta*) in daylight. Martin (1973, *Condor* 75:446–456) reported adult Burrowing Owls (*Speotyto cuniculana*) from territories as far away as 300 m approaching and aiding a resident pair in mobbing a Great Horned Owl.

The Elf Owl (*Micrathene whitneyi*) is the smallest Strigiform (P.M. Walters 1981, *North Am. Bird Bander* 6:104–105). They are territorial but will sometimes nest in close proximity (10 m) to one another (J.D. Ligon 1968, Misc. Pub. Mus. Zool., Univ. Mich. No. 136, Ann Arbor, MI U.S.A.; M.S. Goad and R. W. Mannan 1987, *Condor* 89:659–662). If their nest is approached by a human, Elf Owls may make scolding vocalizations, fly closely by and possibly even strike the intruder (Ligon 1968). However, Elf Owls are little studied and virtually no information is available on their defensive behavior toward natural predators. Herein, we report the defensive behaviors of Elf Owls toward two different predators. The dates of the observations correspond with late incubation and early nestling stages for Elf Owls (Ligon 1968). Thus, we suggest these observations are examples of mobbing as a nest-defense behavior.

On 20 June 1995, at approximately 1950 H, we observed a 91–106 cm long gopher snake (*Pituophis melanoleucus*) climbing a honey mesquite tree (*Prosopis velutina*) at our field station 1.6 km south of Fairbank, Arizona, in the San Pedro Riparian Conservation Area. We knew from adult vocalizations that Elf Owls had been nesting in the tree but we had not located their nest cavity. The snake was approximately 5.5 m above the ground when we visually located an Elf Owl making scolding *cheeur* vocalizations (Ligon 1968) from its perch in the canopy of the tree. Moments later a second Elf Owl flew from a cavity as the snake approached the entrance. When the snake entered the cavity with its head and 8–10 cm of its body, we heard the trilling vocalizations of nestling Elf Owls. By this time it was dark and all further observations were made with the aid of flashlights. Both adult Elf Owls repeatedly changed perches within the canopy of the tree and continued vocalizing, but did not approach the snake when it was in the cavity. After 12–15 min, the snake withdrew from the cavity and began to descend the tree. The Elf Owls increased their vocalization rate and made repeated passes at it, striking its head at least four times. The strikes were powerful enough to propel the snake's head 5–10 cm sideways. The snake stopped at a main crotch of the tree where it was relatively protected from the Elf Owls. The vocalizations of the owls gradually subsided, and we ended our observations at 2022 H. The snake was no longer in the tree when we checked at 0430 H the next morning.

Both owls made flights at the snake, but we could not determine if only one or both had actually struck the snake. During the attacks, a third Elf Owl, presumably from a known adjacent territory, flew to the mesquite and also vocalized. The third owl repeatedly changed perch locations within the canopy but we were unable to determine if it also attacked the snake. Despite being a very territorial species (Ligon 1968), there was no indication of intraspecific aggression between the Elf Owls; all aggression appeared directed toward the snake. We did not observe the defensive wing drooping postures Elf Owls use during intraspecific territorial interactions (Ligon 1968), but this may have been due to the owls' small size and the poor light conditions.

We observed a similar incident in which several Elf Owls attacked a Great Horned Owl. At dusk (approximately 1930 H) on 21 June 1993, we tethered a Great Horned Owl to a perch in our campsite in a riparian woodland near

Aravaipa Creek, Arizona. Almost immediately at least six Elf Owls began vocalizing from dispersed locations around our campsite and at least four of them began making low passes at the Great Horned Owl. Before we could relocate the horned owl to a protected enclosure, it was struck once in the head by an Elf Owl.

Some nocturnal behaviors may not be well known or understood, not because they are rare, but because they are difficult to observe. This may change with the increased availability of night vision equipment (P. Henson and J A Cooper 1994, *Auk* 111:1013–1018). Currently, observations of nocturnal behaviors are likely to be sporadic and anecdotal, and therefore unreported. Such information, however, may help in understanding a species biology. For example, other researchers have observed group mobbing by Elf Owls (F.R. Gehlbach, pers. comm.; B.A. Millsap, pers. comm.), but there are no published reports of the behavior. Our observations, and those of other researchers, suggest that Elf Owls will join together in mobbing and that they can be physically aggressive when defending their nests against predators.

We thank A. Duerr, T.S. Estabrook and R.L. Spaulding for assisting with the observations. We also thank T. Brush, F.R. Gehlbach, R. Glinski, P. Hardy, B.A. Millsap, G. Proudfoot and H.A. Snyder for sharing their observational information concerning mobbing by small owls. This manuscript benefitted from the constructive reviews of F.R. Gehlbach, C. Marti, B.A. Millsap and an anonymous reviewer.—**Clint W. Boal, Brent D. Bibles and R. William Mannan, School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721 U.S.A.**

GRIFFON VULTURES (*GYPS FULVUS*) INGESTING BONES AT THE OSSUARIES OF BEARDED VULTURES (*GYPAETUS BARBATUS*)

Some African vultures overcome the calcium deficiency in their diets by ingesting bone fragments, and are dependent on the presence of large predators to supply them (Mundy and Ledger 1976, *S. Afr. J. Sci.* 72:106–110; Mundy 1982, The comparative biology of southern African vultures, Vulture Study Group, Johannesburg, South Africa; Richardson et al. 1986, *J. Zool. Lond.* 210:23–43). Because of the lack of large mammalian carnivores in the Iberian Peninsula, vultures apparently satisfy their calcium needs by ingesting small bone fragments from carcasses (König 1975, *Ardeola* 21:219–224) or small pieces of limestone (Fernández 1975, *Ardeola* 22:29–54; Elosegi 1989, *Acta Biol. Mont.* 3, Série documents de Travail). This note reports several observations of Griffon Vultures (*Gyps fulvus*) making use of bone splinters obtained from Bearded Vulture (*Gypaetus barbatus*) ossuaries, where large bones are deliberately dropped onto rock slabs (Boudoint 1976, *Alauda* 44:1–21).

Field work was carried out in the meridional Prepyrenees (northeast of Spain), an area of isolated calcareous massifs described by Riba et al. (1976, Geografia física dels Països catalans, Ketres, Barcelona, Spain). The data were collected while we were monitoring several Bearded Vulture pairs between 1991–95 at eight ossuaries located in five different nesting areas (Heredia 1991, Pages 78–89 *in* R. Heredia and B. Heredia [EDS.], El quebrantahuesos *Gypaetus barbatus* en los Pirineos, ICONA, Madrid, Spain) selected at random. All ossuaries had Griffon Vulture colonies nearby (<1 km). We made 126 visits to the nesting areas during the nestling period from February–August.

Griffon and Bearded Vultures interacted at ossuaries in all five nesting areas. Occasionally, Griffon Vultures explored ossuaries when there had been no previous occurrence of bone drops, but more often they were observed at ossuaries after Bearded Vultures had dropped bones. Over a 6-d-period, we observed groups of one to seven Griffon Vultures ($\bar{x}$ = 2.62, SD = 1.99, N = 21) visiting the sites. During a total of 75 bone droppings, Griffon Vultures immediately descended to the ossuaries on 13 occasions (17.3 %) in numbers ranging from one to five individuals ($\bar{x}$ = 2.30, SD = 1.63, N = 30).

On five occasions, Griffon Vultures attempted to pirate bone fragments from Bearded Vultures. Once, when an immature Bearded Vulture was dropping a bone, a Griffon Vulture flew in quickly and ingested small bone fragments next to the place where the impact had occurred before the Bearded Vulture could land. Twice, we observed griffons trying to overtake Bearded Vultures in flight to recover dropped bones, without success. Once, after a Bearded Vulture had perched next to the bone it had dropped, three Griffon Vultures attacked it and seized a large bone fragment which they then proceeded to fight over and ingested. We also saw a Bearded Vulture drop a bone and, once on the ground, five Griffon Vultures attacked the Bearded Vulture forcing it to flee with the prey.

We also observed three Griffon Vultures inside a Bearded Vulture nest that had been used in the previous breeding

season. One of them spent 30 min pecking an old sheep or goat bone. Occupation of Bearded Vulture nests by Griffon Vultures is frequent in the Pyrenees (Fernández and Donázar 1991, *Bird Study* 38:42–44; Donázar, pers. obs.).

Our observations suggest that Griffon Vultures living near Bearded Vultures benefit from this association because Bearded Vultures provide a source of calcium. The Griffon Vulture, like other species that eat mainly soft parts of carcasses (Brown 1976), is subject to a lack of calcium because his diet contains only 0.01 % of this element (Houston 1978, *J. Zool. Lond.* 186:175–184). The Bearded Vulture, a species that in the last century was spread over a large part of the Iberian Peninsula mountains (Hiraldo et al. 1979, El quebrantahuesos *Gypaetus barbatus* (L.), Monografías 22, ICONA, Madrid, Spain), may have also facilitated the spread of Griffon Vultures as the distribution of both species was extensively coincident in much of the southern Palaearctic (Elosegi 1989, *Acta Biol. Mont.* 3, Série documents de Travail).

We thank S. Mañosa for many helpful suggestions and criticism for the manuscript's improvement. We also thank J.A. Donázar, D.C. Houston and S.R. Wilbur for their review and comments on the manuscript. This study was supported by the Departament d'Agricultura, Ramaderia i Pesca de la Generalitat de Catalunya.—**Joan Bertran[1] and Antoni Margalida, GEPT (Grup d'Estudi i Proteccío del Trencalòs), Ap. 43, E-25520 El Pont de Suert (Lleida), Spain.**

---

[1] Present address: Grases, 14–18. entlo 1a, 08004 Barcelona, Spain.

A GOLDEN EAGLE EATS WILD CANADA GOOSE EGGS

Golden Eagles (*Aquila chrysaetos*) prey primarily upon medium-sized rodents, hares, birds and ungulates (S.K. Carnie 1954, *Condor* 56:3–12; Boeker and Ray 1971, *Condor* 73:463–467; M.N. Kochert 1972, M.S. thesis, Univ. of Idaho, Moscow, ID U.S.A.; P.A. Johnsgard 1990, Hawks, eagles, and falcons of North America, Smithsonian Inst. Press, Washington, DC U.S.A.). Although they are known to exploit a great variety of prey items throughout their holarctic range, eggs have not been reported as a food item (A.C. Bent 1961, Life histories of North American birds of prey, Dover Publications, Inc., New York, NY U.S.A.; Dement'ev and Gladkov 1966, Birds of the Soviet Union, Israel Program for Scientific Translations, Israel; Brown and Amadon 1968, Eagles, hawks, and falcons of the world, County Life Books, London, UK; Beecham and Kochert 1975, *Wilson Bull.* 87:506–513; Matchett and O'Gara 1987, *J. Raptor Res.* 21:85–94; Palmer 1988, Handbook of North American birds, Yale Univ. Press, New Haven, CT U.S.A.).

We observed a Golden Eagle raid a Canada Goose (*Branta canadensis*) nest and eat two eggs on 4 April 1995 in Hell's Canyon National Recreation Area in western Idaho. At 1150 H, an adult Golden Eagle (gender unknown) flushed a Canada Goose off a ground nest located on an island in the Snake River. The eagle landed near the nest, walked to the nest and broke open the eggs by grasping an egg in its foot and placing all of its weight on the egg until, after two to four attempts, it broke. The eagle ate the contents of the egg (stage of embryonic development was unknown) and then broke and ate the second egg. The pair of geese that had been displaced from the nest and four other pairs of nearby geese gave alarm calls during our observations, but never approached the eagle. Two Black-billed Magpies (*Pica pica*) followed the eagle to the nest and scavenged eggshell fragments while the eagle consumed the contents. The eagle finished eating both eggs at 1206 H and then spent the next 5 min walking and hopping around the island, possibly searching for more eggs. The magpies followed the eagle on the ground until 1211 H when the eagle flew 50 m downstream and perched on a talus slope. The Canada Goose pair returned to their depredated nest at 1430 H.

Although Golden Eagles have not been previously observed eating eggs, we speculate that depredation on goose eggs in Hell's Canyon may not be uncommon. Perhaps Golden Eagles in Hell's Canyon eat eggs when more typical prey for this region (black-tailed jackrabbits, *Lepus californicus*) are rare. In contrast, Golden Eagles nesting 128 km upstream of Hell's Canyon in the Snake River Birds of Prey National Conservation Area, where black-tailed jackrabbits were abundant and an important prey species (Steenhof and Kochert 1988, *J. Anim. Ecol.* 57:37–48), have not been observed to prey upon goose eggs, even though Canada Geese occasionally nest nearby (W. Bodie, pers. comm.).

This study was funded by the Idaho Power Company. Toni Holthuijzen, Mary McFadzen, Brian Herting and Mike Kochert made constructive comments on the manuscript. Toni Holthuijzen translated the German papers. James

TWO PLUMBEOUS KITES (*ICTINIA PLUMBEA*) CAPTURE SWALLOW

The Plumbeous Kite (*Ictinia plumbea*) is a common but poorly studied raptor of the neotropics, ranging from Mexico to northern Argentina and Paraguay (L. Brown and D. Amadon 1968, Eagles, hawks and falcons of the world, McGraw-Hill Book Co., New York, NY U.S.A). This species feeds mainly on insects (A.F. Skutch 1947, *Condor* 49:25–31; F. Haverschmidt 1962, *Condor* 64:154–158), but vertebrates, including birds and bats, make up a small percentage of its diet (N.E. Seavy et al. 1994, *J. Raptor Res.* 29:65–66). Likewise, birds, including swallows and swifts, and bats have been recorded as prey items for the similarly insectivorous Mississippi Kite (*Ictinia mississippiensis*) (J.W. Parker 1988, pgs. 166–186 *in* R.S. Palmer [ED.], Handbook of North American birds, Vol. 4, Yale Univ. Press, New Haven, CT U.S.A.). We know of no published accounts, however, of either species capturing small birds by tandem hunting.

On 6 June 1994, we were observing a Plumbeous Kite nest in Tikal National Park, Petén, Guatemala. The nest contained one 21-d-old nestling. Both adults were perched approximately 100 m from the nest in a large cedro (*Cedrela mexicana*) tree. The area between the adults and the nest was a large open plaza covered with short grass. At 0659 H, one of the kites flew from its perch passing within 1 m of a flying Northern Rough-winged Swallow (*Stelgidopteryx serripennis*). The swallow flew down and away and the kite dived unsuccessfully again on the fleeing swallow, which at this point was no more than 1–2 m above the ground. On a third dive, the kite again missed, and the swallow took cover, perching in the short grass. As this kite was making a fourth dive, the second adult kite also dived from its perch toward the grounded swallow. As the first kite dived, the swallow flushed and was caught by the second kite in its feet no more than 2 m above the ground. The first kite followed the second kite for a short distance and then returned to perch in the cedro. The second kite flew to the nest and fed the swallow to the nestling.

Cooperative hunting can allow raptors to take larger or more elusive prey with increased success compared to solo hunting (D.P. Hector 1986, *Ethology* 73:247–257; J.C. Bednarz 1988, *Science* 239:1525–1527). Based on the social foraging classes defined by Ellis et. al. (1993, *Bioscience* 43:14–20), our observation qualifies as either "pseudocooperative hunting" (group attacks by a variable number of individuals on large or elusive quarry, without division of labor or sharing of prey, though success is enhanced) or "cooperative pair hunting" (involving only two birds, clear division of labor and at least limited prey sharing).

Tandem hunting occurred only once during 127 foraging attempts we observed from perches. Most attempted prey captures were directed at insects. In comparison, 29% (102 of 349) of all Aplomado Falcon (*Falco femoralis*) foraging attempts observed by Hector (1986, *Ethology* 73:247–257) involved pursuit by two falcons. Of these tandem hunts 66% were directed at birds and only 2% at insects. Though probably not important in the pursuit and capture of insects and other small prey, tandem hunting may allow the Plumbeous Kite to increase success in occasional attacks on elusive prey such as birds.

BOOK REVIEW

EDITED BY JEFFREY S. MARKS

The Golden Eagle. By Jeff Watson. 1997. T. & A.D. Poyser, London, U.K. xx + 374 pp., 76 figures, 73 tables, 6 appendices, color frontispiece. ISBN 0-85661-099-2. Cloth, $49.95.—This long-awaited volume from T. & A.D. Poyser originates in Scotland, where Golden Eagles (*Aquila chrysaetos*) have been studied for many years. In *The Golden Eagle,* Jeff Watson combines details of his own research on Golden Eagles in Scotland with information from studies of Golden Eagles and other *Aquila* eagles conducted throughout the world. Using this approach, Watson provides a comprehensive review of the ecology of the Golden Eagle and a general overview of the ecology of *Aquila* eagles. A tremendous amount of general and technical information is presented in the text and accompanying figures, tables and appendices; however, the book is relatively easy to read. Most chapters begin with an introductory statement and conclude with a brief summary. Each chapter is illustrated with beautiful black-and-white drawings by Keith Brockie and wash landscapes by Donald Watson. Two color plates, one by each artist, appear at the beginning of the book.

In his acknowledgments and opening chapter, Watson reflects on his experiences writing this book. As I read the book, I was struck with a great appreciation for how much work went into gathering, compiling and organizing the information for it; I think that readers will quickly gain a similar appreciation. Seton Gordon once said "I cannot imagine anyone studying the ways of the eagle without admiring the nobility of the bird." Jeff Watson's admiration, knowledge and enthusiasm for Golden Eagles come across loud and clear throughout the book.

Chapter 2 presents a review of field characteristics, reversed sexual size dimorphism, taxonomy and general ecology of Golden Eagles. The distribution of the Golden Eagle is reviewed in Chapter 3, and Watson introduces readers to the Scottish

Highlands in Chapter 4. Most of Watson's work was conducted in the Scottish Highlands, an area rich in contemporary and historical Golden Eagle research and conservation. This chapter provides a good background for discussions of Watson's research in Scotland through the rest of the book.

In Chapter 5, Watson describes the hunting behavior of Golden Eagles. This chapter is informative, despite the scarcity of studies on this subject. Descriptions of the food habits of Golden Eagles and other species of *Aquila* are presented in Chapter 6. The long-standing issue of Golden Eagles and livestock is discussed at the end this chapter. Chapter 7 focuses on nesting sites of Golden Eagles, including descriptions of nest structures, nest types, nest elevations, nest orientation, use of alternative nest sites and interactions with other species at nesting sites. I was surprised that interactions between nesting Gyrfalcons (*Falco rusticolus*) and Golden Eagles in western Canada (Platt 1989) were not mentioned in this chapter.

In Chapter 8, entitled "Ranging Behavior," Watson describes home ranges and territories of Golden Eagles based primarily on observational studies from Europe and North America. A brief discussion on the ranging behavior of nonbreeding birds as determined using radiotelemetry is also presented. Watson also briefly discusses variation in home range size, competition with other species, communal roosting and ranging behavior of migratory *Aquila*. Chapter 9 begins with an overview of the mechanisms driving nest spacing and density of breeding birds. Using data from Scotland, Watson discusses the relationship between breeding densities and food supply. He also discusses winter densities of migratory Golden Eagles in North America.

Current population estimates and trends of Golden Eagle populations are addressed in Chapter 10. The strong point of this chapter is the review of the historical and current status of Golden Eagles in Europe. The weakest point is Watson's North America population size estimate. Watson suggests that a total population estimate of 50,000

to 70,000 individual Golden Eagles in North America would "appear reasonable"; however, I would argue that insufficient data are available to make a continent-wide population estimate.

Chapter 11, entitled "The Pre-breeding Season" begins with a description of Golden Eagle behavior in winter, and continues with descriptions of territorial flights, nest building, courtship, mating and unusual mating systems. Chapter 11 concludes with a discussion on faithfulness to mates in Golden Eagles. Watson reminds readers that without empirical data, testing the assumption that Golden Eagles form lifelong pair bonds is difficult.

The breeding season is covered in Chapters 12 and 13. In Chapter 12, Watson describes Golden Eagle eggs and reviews nesting phenology, clutch size, replacement clutches, incubation period, behavior of adults during incubation and reasons why pairs fail to lay eggs. He also examines the relationship between latitude and median egg-laying dates. Watson states that "in the most northerly populations of Alaska and Siberia (65–70°N) laying does not commence until the first 10 days of May." This contradicts several published studies that documented mean laying dates for Golden Eagles in arctic Alaska and Canada from mid- to late April (Ritchie and Curatolo 1982, Poole and Bromley 1988, Young et al. 1995). In Chapter 13, Watson draws heavily on studies conducted in the western United States to describe activities associated with the nestling period. A review of the postfledgling period and time to independence is presented in Chapter 14. Few studies have focused on the behavior and activities of Golden Eagles from the time they leave the nest to the time they are recruited into the breeding population. Watson reviews the available information and is quick to point out that more study is needed to describe this portion of the Golden Eagle's life cycle.

In Chapter 15, Watson examines the factors that influence breeding performance of Golden Eagles, including food and weather. At the end of the chapter, Watson asks why Golden Eagles in North America typically breed more successfully than those in Scotland and includes an interesting analysis of the relationship between dietary breadth and reproductive performance. Based on an analysis using data from 24 studies, Watson suggests that breeding success is likely to be high when eagles can specialize on one or two types of prey in the "optimal size range." This is an interesting suggestion. Given the limitations of determining food

habits of Golden Eagles using prey remains collected at nests, however, more studies are needed before general conclusions regarding the dietary breadth of Golden Eagles can be made.

Patterns of molt and age-specific plumage characteristics are reviewed in Chapter 16. In Chapter 17, Watson discusses the movement and migration of Golden Eagles and other *Aquila* eagles using data collected through banding and telemetry studies in Europe and North America. Chapters 18 and 19 cover mortality and threats to Golden Eagles, respectively. In the first part of Chapter 18, Watson discusses the difficulty of estimating mortality rates of Golden Eagles using banding and marking studies. The major causes of Golden Eagle mortality are covered in detail in Chapter 18. The take-home message of this chapter is that most known Golden Eagle deaths in Europe and North America are attributable to humans. In Chapter 19, Watson lists the known threats to Golden Eagles including direct persecution by humans, unintentional human disturbance, pesticides and pollutants, power poles and land-use changes. Watson also describes the effects of large-scale afforestation of the Golden Eagle population in Scotland and the relationship between Golden Eagles and grazing animals. The last part of the chapter will be interesting to anyone managing lands where grazing animals and Golden Eagles interact.

Chapter 20, entitled "Conservation," is a good follow-up to the previous chapter. Watson addresses the various management and educational tools used for countering the threats outlined in Chapter 19. In Chapter 21, Watson draws on information from Europe, North America and central Asia to describe relationships between Golden Eagles and humans and to describe how these relationships have changed over time. Historically, Golden Eagles held high status in all three geographic areas. With the introduction of firearms, however, many eagles in Europe and North America were persecuted. Watson ends this chapter on a positive note and hopes that "some of the empathy for the natural world which was implicit in so many traditional societies, will be rekindled and embraced again by people in the so-called 'developed world.'"

In the closing chapter, Watson provides "food for thought" and makes recommendations for future Golden Eagle research. These recommendations include learning more about the distribution of Golden Eagles in the eastern Palearctic and re-

mote areas of northern North America and describing ranging behavior of nonbreeding and migratory Golden Eagles. In closing, Watson stresses the need to understand how land-use changes affect Golden Eagle populations. This is a worldwide concern that should be addressed sooner rather than later.

The 22 Chapters are followed by six appendices that provide additional information on the distribution and ecology of the genus *Aquila*, the Scottish Highland landscape, calculating dietary breadth, assessing food supply, calculating nearest-neighbor distances and densities and the scientific names of plants and animals mentioned in the book.

Overall, I enjoyed the book very much. The illustrations by Donald Watson (Jeff Watson's father) and Keith Brockie are superb. *The Golden Eagle* contains an enormous amount of technical and general information. At times, however, I felt that Watson tried to cover too much territory, that some of his statements were too general and that some of his statistical analyses were based on insufficient data to draw conclusions. Despite these minor

shortcomings, *The Golden Eagle* contains a wealth of information on Golden Eagle ecology, and I highly recommend it to anyone interested in raptors. Raptor bibliophiles will want this book for their libraries, and the book also is a must for public and university libraries.—**Carol L. McIntyre, National Park Service, P.O. Box 74680, Fairbanks, AK 99707 U.S.A. and Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331 U.S.A.**

LITERATURE CITED

PLATT, J.B. 1989. Gyrfalcon courtship behavior and early breeding behavior on the Yukon North Slope. *Sociobiology* 15:43–69.

POOLE, K.G. AND R.G. BROMLEY. 1988. Interrelationships within a raptor guild in the central Canadian Arctic. *Can. J. Zool.* 66:2275–2282.

RITCHIE, R.J. AND J.A. CURATOLO. 1982. Notes on Golden Eagle productivity and nest site characteristics, Porcupine River, Alaska, 1979–1982. *Raptor Res.* 16:123–127.

YOUNG, D.D., JR., C.L. MCINTYRE, P.J. BENTE, T.R. MCCABE AND R.E. AMBROSE. 1995. Nesting by Golden Eagles on the North Slope of the Brooks Range in Northeastern Alaska. *J. Field Ornithol.* 66:373–379.

ABSTRACTS OF PRESENTATIONS MADE AT THE ANNUAL MEETING OF THE RAPTOR RESEARCH FOUNDATION, INC., HELD AT GAINESVILLE, FLORIDA, 1986

THE IMPACT OF FALCONRY ON WILD RAPTOR POPULATIONS
PREFACE

ROBERT KENWARD. *Institute of Terrestrial Ecology, Furzebrook Road, Wareham, Dorset BH20 5AS U.K.*

At the 1986 annual conference of the Raptor Research Foundation held in Gainesville, Florida, Jim Mosher organized a mini-symposium to consider the impact of falconry on wild raptor populations, as the basis for a position statement. An ad-hoc committee including Jim Mosher (Chair), Jim Brett, Robert Kenward and Ian Newton prepared a draft position statement that was modified at the annual conference in St. Paul, Minnesota in 1988, and was then approved by a postal vote of the membership early in 1989. The six expanded abstracts that follow provide pointers to further literature on each of the main issues of the position statement.

A publication that is long in gestation risks being overtaken by events. Nevertheless, the conclusions of the position statement have so far been strengthened rather than contradicted. After three further years of data from a Prairie Falcon (*Falco mexicanus*) harvest study, D.E. Runde (pers. comm., see too Conway et al. 1995) was "comfortable that removal of 10–20% of nestlings is a safe sustainable yield." Radio-tagging has shown that banding can substantially overestimate first-yr mortality, and the resulting new models indicate that sustainable yields for some species could be more than 30% of the young (Kenward pp. 295–296). Three cases of hybrid falcons displacing normal peregrines breeding in Germany (H. Reilman pers. comm.) reinforce the position statement recommendation that such birds should at the least be imprinted on humans before being used in falconry.

LITERATURE CITED

CONWAY, C.J., S.H. ANDERSON, D.E. RUNDE AND D. ABBATE. 1995. Effects of experimental nestling harvest on Prairie Falcons. *J. Wildl. Manage.* 59:311–316.

CONTROLLED HARVEST OF NESTLING PRAIRIE FALCONS: A FIELD EXPERIMENT

DOUGLAS E. RUNDE.[1] *Wyoming Cooperative Fishery and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Box 3166, University Station, Laramie, WY 82071 U.S.A.*

Raptors have been removed from the wild for use in falconry for centuries, but sustainable levels of harvest have not been clearly demonstrated. As the recreational demand for raptors focuses primarily on the younger age classes (nestlings and juveniles), standard models for estimating maximum sustainable yield (MSY) are inappropriate. The MSY concept is based on density-dependent population growth models, which typically require a reduction in population size well below carrying capacity in order to stimulate maximal population growth and allow maximal levels of harvest. For raptors, a more appropriate goal is to maintain stable populations near carrying capacity while allowing conservative harvests.

One approach to estimating a sustainable yield (SY) for a raptor population is based upon a comparison of reproductive success and mortality. For the Prairie Falcon (*Falco mexicanus*), mean productivity (from 15 studies spanning more than 20 years) is 2.5 young pair^{-1} yr^{-1} (Runde 1987). A series of 15 survival schedules, derived from banding data, indicated that an average of 2.0 young pair^{-1} yr^{-1} are needed to maintain stable populations through time (Runde 1987). Theoretically then, an average surplus of 0.5 nestlings is produced by each breeding pair each year.

From this, a SY for a local Prairie Falcon population is easily calculated by dividing the number of breeding pairs by 2. To do so requires an estimate of breeding population size. However, it may be impractical to survey the population each year and then set harvest levels. If an estimate of the number of breeding territories, or maximum number of breeding pairs is available, then average breeding population size can be calculated. A conservative estimate of occupancy rate (based on 9 field studies) is 65% (Runde 1987). If previous surveys indicate that 100 breeding territories are present, then 65 pairs are expected to occupy territories and 32.5 surplus nestlings will be produced in an average year. Due to normal fluctuations in populations, this approach will lead to recommended harvest levels that are above SY in some years and below SY in others.

My approach is based upon life-table estimates of survival rates from band return data. Such estimates are unavoidably suspect due to many potential sources of bias (Burnham and Anderson 1979). Thus, a field test of this approach was proposed and an experimentally-controlled harvest of nestling Prairie Falcons in southwestern Wyoming was begun in 1982. A 2420 km^2 study area was divided into a harvest area (with 20–26 breeding pairs) and an adjacent control area (with 45–55 pairs).

[1] Present address: Florida Game and Fresh Water Fish Commission, 620 South Meridian Street, Tallahassee, FL 32399 U.S.A.

Table 1.   Summary of nestling Prairie Falcon removals in SW Wyoming, 1982–86.

YEAR	NUMBER REMOVED	HARVEST RATE (%)	PRODUCTIVITY AFTER REMOVALS[1]
1982	4	9	1.95
1983	0	—	1.55
1984	10	18	1.88
1985	15	27	1.90
1986	13	28	1.70
Totals	42	18	1.80

[1] Number of young per occupied breeding territory.

Experimental harvest involved removing enough nestling falcons to reduce breeding success to below 2 young pair^{-1} each year (Table 1). Nestlings were fostered into nests far removed from the study area (>225 km to the east), and hacked at an artificial nest site in southeastern Montana. None were removed in 1983 as natural nest success was very low.

If harvest exceeds SY, a decline in the population may eventually result. Excessive harvesting may lead to a decline in falcons available to fill vacant nest sites, in which case the number of occupied territories should decline. Therefore, breeding territories in the harvest and control areas were monitored each year to compare trends in territory occupancy. To avoid biases due to the discovery of additional nesting territories, occupancy rates were calculated from a subset of sites visited every year.

Although there was no evidence of a change in population size from 1982–86, it is too early to draw firm conclusions. Effects of the harvest will be detectable only after falcons fledged during the experiment dominate the breeding population. Trapping of breeding adults indicated that the recruitment of these cohorts began in 1985. As annual mortality of adults has been low (13–19%) (Runde 1987), recruitment will be slow. Complete turnover of the breeding population will require about eight yr.

Immigration may compensate for reduced breeding success and maintain the population even if SY has been exceeded. In an attempt to measure immigration into the harvest area, an extensive banding program has been conducted. More than 500 nestling and 100 adult falcons have been banded in or near the study area. If immigration is high and there is no decline in numbers of breeding pairs, a precise level of sustainable harvest will not have been demonstrated. However, the presence of a harvestable surplus will be shown and the approach taken may be applicable on a local scale.

LITERATURE CITED

BURNHAM, K.P. AND D.R. ANDERSON. 1979. The composite dynamic method as evidence for age-specific waterfowl mortality. *J. Wildl. Manage.* 43:356–366.

RUNDE, D.E. 1987. Population dynamics and movement patterns of the Prairie Falcon (*Falco mexicanus*). Ph.D. dissertation, Univ. Wyoming, Laramie, WY U.S.A.

FALCONRY HARVEST IN THE UNITED STATES

JAMES A. MOSHER. *Savage River Consulting, 17811 Lappans Road, Fairplay MD 21733 U.S.A.*

Falconry, most simply defined, is the taking of game with the aid of a trained raptor. Many raptors used in falconry are birds taken from wild populations. There are numerous opinions about the sport or potential impacts on wild populations from this harvest. The purpose here is to present some data concerning raptor harvest, to put the harvest in perspective with regard to population numbers and to make some reasoned management recommendations. I believe that biologists and falconers alike will be drawn to similar conclusions by these data.   The data came from two sources. First, an unpublished report by Brohn in 1986 for the International Association of Fish and Wildlife Agencies (IAFWA) Nongame Wildlife Committee included summaries of numbers of falconers and of raptors harvested, based on survey responses from 42 states. Second, I summarized falconers' annual reports for 23 states covering the 1- or 2-yr reporting periods ending in 1986. Copies of these reports were kindly provided by Walter Steiglitz, Assistant Director for Refuges and Wildlife of the United States Fish and Wildlife Service (USFWS). In order to protect the privacy of the individuals, much information was obscured in these reports. Where this resulted in a range of possible values, I used the high estimate for numbers harvested, and the low estimate for numbers returned to the wild. Because so many Peregrine Falcons (*Falco peregrinus*) and Harris' Hawks (*Parabuteo unicinctus*) were captive bred, and that information was obscured on most reports, I excluded those species from the USFWS data. They are, however, included in the IAFWA data.

Brohn reported that 2 776 falconers harvested 737 raptors of 15 species from the wild during 1986. Of these raptors, 367 were returned to the wild, either intentionally or accidentally, for an estimated net annual harvest of 370 birds. My review of USFWS data from 23 states yielded 350 birds harvested, 66 released and 118 accidentally lost, for a net harvest of 166 birds from wild populations. The IAFWA survey gave a net harvest rate of 8.8 birds state^{-1} yr^{-1}, while the USFWS reports gave a net harvest rate of 7.3 birds state^{-1} yr^{-1}. Further, the USFWS reports record that 330 young birds (6.9 state^{-1} yr^{-1}) were produced by captive propagators during the 1985 reporting year. Even allowing for no benefit from raptors returning to the wild from any source, the maximum annual harvest is estimated between 15.2 and 17.5 birds in each state.

Almost 56% of all raptors harvested were Red-tailed Hawks (*Buteo jamaicensis*) or Prairie Falcons (*Falco mexi-*

canus), species certainly not threatened or endangered. Regionally, California reported the highest harvest, with 128 birds taken and 118 returned to the wild, giving a net loss of 100 birds from the wild.

G.S. Butcher, M.R. Fuller and J.L. Ruos (unpubl. data) found significant increases from the early 1970s to the early 1980s in Christmas Bird Count (CBC) numbers of Northern Goshawks (*Accipiter gentilis*), Red-tailed Hawks, Merlins (*Falco columbarius*), Prairie Falcons and Gyrfalcons (*Falco rusticolus*), using the most conservative data. Their estimates of continental population numbers, extrapolated from CBSs for Red-tailed Hawks and Prairie Falcons are 80 000 and 13 000, respectively, for winter 1982–83.

My estimates of density of breeding raptors in the eastern forests, based on complete censuses of 32 km² study areas distributed from Maryland to Minnesota, approximate to 1 pair of Broad-winged Hawks (*Buteo platypterus*) in 5 km² and 1 pair each in 25 km² of Red-shouldered Hawks (*Buteo lineatus*), Red-tailed Hawks and Cooper's Hawks (*Accipiter cooperii*). In the northeastern U.S., where these study areas are located, there are approximately 575 000 km² of forested land. Some of it is certainly not suitable breeding habitat for one or more of these species. Likewise, portions of the areas I censused did not provide suitable breeding habitat. If only half of the available forest land is occupied, these data can be extrapolated to over 10 000 breeding pairs of the least dense species and almost 60 000 pairs of Broad-winged Hawks.

International trade in raptors is also dwarfed by these numbers. The annual report of the convention on International Trade in Endangered Species (CITES) of wild fauna and flora for 1986 reports 213 468 birds imported to the U.S.A. Only 36 individuals were raptors of falconry interest, and 9 of them were for falconry. For the same period, 5684 birds were exported, which included 16 raptors (15 hybrid falcons and 1 Peregrine Falcon reexported to Canada). The total number of imports, including species not covered by CITES (all raptors are covered) was estimated to be more than 700 000.

In the light of these data, I agree with the IAFWA that the harvest of wild raptors by falconers has no significant biological impact on the resource. It does not seem that substantial expenditures of time and money by state and federal regulatory agencies are needed to protect raptor populations from falconry harvest. In fact, when captive propagation by falconers is considered, the net effect may be a gain rather than a loss for some species in some areas. As noted by the IAFWA, there is scope for simplification of regulations and a reallocation of federal and state funding priorities. The limited funds available for management of raptor populations would be far better spent on regional and national monitoring programs and for research on the impacts of land use changes.

In particular, I note that in the U.S. it would be consistent with other managed migratory bird populations to remove state barriers to harvesting raptors. In 1986,

Wisconsin required only a nonresident small game license to permit harvest by nonresident falconers. Reporting and banding requirements could be eliminated for all species except those of special concern. Internationally, experience in the U.S. supports the licensing of falconers based on demonstrated competency and experience, with possession limits based on the class of license. If standards of competency for falconers similar to the U.S. system were adopted internationally, noncommercial exchange of raptors might be permitted among licensed individuals of any countries adhering to such standards.

INFERRING SUSTAINABLE YIELDS FOR RAPTOR POPULATIONS

ROBERT E. KENWARD. *Institute of Terrestrial Ecology, Wareham, Dorset BH20 5AS U.K.*

Sustainable yield levels for raptors can be estimated in three main ways: (1) from data on populations harvested for falconry, (2) from data on stable populations in which a known proportion was killed by man and (3) by studying the dynamics of artificially depressed populations.

Ideally, harvest data should be obtained for at least 10 yr from populations where compensatory immigration can be discounted. The only such data are for Gyrfalcons (*Falco rusticolus*): records of nestlings which were taken from Iceland for four centuries would represent 25–50% of young from the present, saturated population (Cade 1968). More recently, an average 22% of Peregrine Falcon (*Falco peregrinus*) nestlings were taken from the Queen Charlotte Islands during five yr in the early 1960s (Blood 1968). There was no immediate marked population decline, but a slight downward trend would have been undetected in this short period. Similarly, the experimental 9–27% harvest of young Prairie Falcons (*Falco mexicanus*) in Wyoming seems to have caused no population decline (Runde 1987).

Although the proportion killed by man has ranged from 40–92% of recoveries in at least 27 banding studies (Newton 1979), this must partly reflect recovery bias: 47% of recovered Northern Goshawk (*Accipiter gentilis*) rings were from killed hawks on a Swedish island during 1975–85, but man caused only 36% of the deaths among 352 radio-tagged hawks in the same period (Kenward et al. 1993). To obtain a minimum estimate of man's impact, the number of birds killed can be expressed as a proportion of the number banded, and not just the recovered bands. In this case 14% of peregrines and 19–21% of goshawks were killed in Fennoscandia prior to 1962 (Nordstrom 1963, Höglund 1964), and 16% of North American Cooper's Hawks (*Accipiter cooperii*) during the 1930s (Henny and Wight 1972). The Fennoscandian goshawk population has remained large, with "best estimates" that about 30% were being killed in Finland (Haukioja and Haukioja 1970).

Data on increase rates for depressed raptor popula-

tions provide minimum estimates of sustainable yield, because the increase may stem from alleviation rather than removal of the depressive factors. Increase rates of 12% per annum in Britain and 16% in West Germany have been recorded for peregrines as a result of reduced persecution or pollution (Ratcliffe 1980, Newton 1988). In Holland, goshawk numbers increased by 19% annually during 1963–80 as organochlorine use was restricted (Marquiss 1981), and the reintroduced British goshawk population grew at an annual rate of 21% during 1964–80 (Thissen et al. 1981). The increases probably stemmed in part from breeding by birds which would not reproduce in saturated populations. Thus, 12% of goshawks bred in their first year in a German population where many adults were killed (Ziesemer 1983, Looft 1984), whereas none have in the Swedish island study (Kenward et al. 1991). If the German reproduction data are used in the Swedish population model, there is a 27% annual increase. Moreover, the Swedish females have a lower mortality than males, and thus a 1.67:1 excess in the adult population: removing 36% of young females would equalize the adult sex ratio.

These studies show that healthy peregrine and goshawk populations can sustain the removal of at least 10% of their young, and in some cases more than 20%. The same probably applies to many other raptor species. The impact of allotting native raptors for falconry is likely to be less than the gross take, because 50–93% may eventually be released or lost into the wild (Kenward 1974). This process can even benefit raptor conservation: it was a cheap and successful way to reestablish goshawks in Britain (Kenward et al. 1981, Marquiss 1981).

Healthy raptor populations can probably sustain at least a 10% harvest of juveniles, and in some cases perhaps more than 20%. The actual number of birds available from a given population would depend on the population's size, which should be monitored continuously to ensure that no decline results from the harvest. Since population monitoring is useful for raptor conservation, but costly, it may make more sense to encourage falconers to contribute to data collection, as the price for their harvest, than to channel their resources into the captive breeding of species which are unthreatened in the wild.

LITERATURE CITED

BLOOD, D.A. 1968. Population status of Peregrine Falcons in the Queen Charlotte Islands, British Columbia. *Can. Field-Nat.* 82:169–176.

CADE, T.J. 1968. The Gyrfalcon and falconry. *Living Bird* 7:237–240.

HAUKIOJA, E. AND M. HAUKIOJA. 1970. Mortality rates of Finnish and Swedish Goshawks (*Accipiter gentilis*). *Finn. Game Res.* 31:13–20.

HENNY, C.J. AND H.M. WIGHT. 1972. Red-tailed and Cooper's Hawks: their population ecology and environmental pollution. Patuxent Wildlife Research Center, MD U.S.A.

HÖGLUND, N. 1964. Der Habicht *Accipiter gentilis* in Fennoscandia. *Viltrevy* 2:195–270.

KENWARD, R.E. 1974. Mortality and fate of trained birds of prey. *J. Wildl. Manage.* 38:751–756.

———, M. MARQUISS AND I. NEWTON. 1981. What happens to goshawks trained for falconry. *J. Wildl. Manage.* 45:802–806.

———, V. MARCSTRÖM AND M. KARLBOM. 1991. The goshawk (*Accipiter gentilis*) as predator and renewable resource. *Gibier Faune Sauvage* 8:367–378.

———, ——— AND ———. 1993. Causes of death in radio-tagged Northern Goshawks. Pages 57–61 *in* P.T. Redig, J.E. Cooper, D.J. Remple and D.B. Hunter [EDS.], Raptor biomedicine. Univ. Press, Minneapolis, MN U.S.A.

LOOFT, V. 1984. Die Entwicklungen des Habichtbestandes (*Accipiter gentilis*) in Schleswig-Holstein 1968–1984. *Corax* 10:395–400.

MARQUISS, M. 1981. The goshawk in Britain—its provenance and current status. Pages 43–57 *in* R.E. Kenward and I.M. Lindsay [EDS.], Understanding the goshawk. Int. Assoc. Falconry Cons. Birds of Prey, Oxford, U.K.

NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Berkhamsted, U.K.

———. 1988. Regulation of peregrine populations. Pages 55–101 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White [EDS.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.

NORDSTROM, G. 1963. Einige Ergebnisse der Vogelberingung in Finnland in der Jähren 1913–1962. *Ornis Fenn.* 40:81–124.

RATCLIFFE, D. 1980. The Peregrine Falcon. T. & A.D Poyser, Berkhamsted, U.K.

RUNDE, D.E. 1987. Population dynamics and movement patterns of the Prairie Falcon (*Falco mexicanus*). Ph.D dissertation, Univ. Wyoming, Laramie, WY U.S.A.

THISSEN, J., G. MÜSKENS AND P. OPDAM. 1981. Trends in the Dutch Goshawk *Accipiter gentilis* population and their causes. Pages 28–43 *in* R.E. Kenward and I.M. Lindsay [EDS.], Understanding the goshawk. Int. Assoc. Falconry, Birds of Prey, Oxford U.K.

ZIESEMER, F. 1983. Untersuchungen zum Einfluss des Habichts (*Accipiter gentilis*) auf Populationen seiner Beutetiere. Beiträge zur Wildbiologie 2. G. Hartmann, Kronshagen, Germany.

COMMENTS ON HYBRIDIZATION IN RAPTORS

JIMMIE R. PARRISH[1] AND CLAYTON M. WHITE. *Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.*

[1] Present address: Avocet Consulting, Inc., 1065 East Canyon Road, Avon, UT 84328 U.S.A.

The concept of hybrid raptors has interest to both the evolutionary biologists (systematist), because of the implications of hybridization to the understanding of phylogenetic relationships, and also to the falconer, because of the blending of characteristics that hybrids may manifest, some of which may be particularly desirable in the sport. At the writing of this paper, hybrids in many combinations of species are a major source of raptors for the falconer. As a group, falconers thus have specific interest in the phenomenon, in part because the concept of producing hybrids has come under question by some environmentalists, conservationists, biologists and others.

A basic understanding of taxonomic concepts, as well as criteria defining hybridization, is critical to adequately address hybridization involving raptors. We defined these concepts as pertaining to avian populations in general. We then defined the species using the classical and time honored characteristic notion of reproductive discontinuity (Mayr 1970, Bush 1975), as outlining the limits of a species, recognizing that such a definition may become obsolete as more and more data and analyses, especially molecular data, are available. Within this context, however, hybridization is the mixing of "alien" genes from one Mendelian population to another (Sibley 1957, Rising 1983) in both natural and artificial schemes. The hybrid is then the offspring of a cross between genetically dissimilar (at some level) individuals or populations. The word hybrid may conjure bad connotations (Cade 1983) while the word "purebred" gives good feelings. Purebreds, however, are nothing but channeled mixtures of genotypes. We used examples of hybrids that may occur in stable hybrid zones in the wild, among such nonraptorial birds as flickers (*Colaptes* spp.), jays (*Cyanocitta* spp.) and meadowlarks (*Sturnella* spp.) (Rising 1983). We further explored the influence of the natural spread of "alien" genes throughout the range of a species; for example, the Mallard (*Anas platyrhynchos*) is reproducing with and swamping out genes in related species such as the American Black Duck (*Anas rubripes*) (Ankney et al. 1986) and Pacific Black Duck (*Anas superciliosa*). Important questions, as they applied to the above nonraptorial species, but also the raptorial species discussed, include: what constitutes hybrid vigor (heterosis)? What is the effect of a hybrid swarm? How is fecundity of a given taxon affected by hybridization? What other effects should be considered when introduction of a hybrid occurs in a population? Is the question of hybridization among wild raptors an important one?

Most of these questions are not easily answered. At present, some cannot be. A relative paucity of data exists for evaluating effects of hybridization among wild raptor populations. Therefore, we discussed the kinds of data needed to formulate effective management questions involving hybrid raptors. An early record suggested the natural cross between a male Northern Goshawk (*Accipiter gentilis*) and a female Common Buzzard (*Buteo buteo*) (Gray 1958). Recently, there are at least five cases of in-

trageneric natural hybrids in raptors: *Otus asio* x *Otus kennicotti*, *Buteo jamaicensis* × *Buteo buteo*, *Falco tinnunculus* × *Falco naumanni*, *Accipiter fasciatus* × *Accipiter novaehollandiae*, *Milvus milvus* × *Milvus migrans* and *Falco peregrinus* × *Falco mexicanus* (Marshall 1967, Wobus and Creutz 1970, Sylven 1977, Hollands 1984, Olsen and Olsen 1985, Bjilsma 1988, Oliphant 1991). Two other natural hybrids have been suggested. Ellis (1995) speculated, based primarily on plumage, that the so-called Altay falcon (*Falco altaicus* or *Falco cherrug*?) of the mountains of central Asia resulted from hybridization of *Falco cherrug* × *Falco rusticolus*. Seibold et al. (1993), based on DNA sequence data showing two distinct mitochondrial hyplotypes within the currently recognized *Falco cherrug*, suggested that one of the hyplotypes may have resulted from hybridization of *Falco cherrug* × *Falco peregrinus*. Any special circumstances surrounding each of these examples is briefly discussed.

Some of the most interesting hybrids are those produced in captive breeding situations. The list of species that have been bred in captivity often with artificial insemination, is, of course, considerable. Of 83 species of diurnal raptors successfully bred in captivity as of 1985, 23 were falcons, eight buteos and seven accipiters (Cade 1986). Currently, hybrids are commonplace within the falconry community (Haak 1980). Certain combinations of falcons seem to be better for the sport than either of the parental types and indeed, some types of hybridization may confer a certain evolutionary fitness over either parental species (Grant and Grant 1992). We do not have good data on all the hybrid falcons that have been produced nor the combinations (either species involved or whether a tri- or more hybrid cross), and thus not much of an assessment can be made. Some of the karyotype and chromosomal differences in parental species within large native North American *Falco* were discussed (Schmutz and Oliphant 1987).

The inevitable question concerns the fate of such hybrid raptors if lost to the wild. Since we now live in habitats that are highly modified, a sort of hybrid environment, the question of what fits best into the environment is moot. Hundreds of "exotic" raptors have been lost into the environment without any discernable long-lasting affects. For example, Saker Falcons have bred with Peregines (Stevens 1972) and yet sakers lost to the wild in North America seem never to show up again; their genes certainly do not seem to be represented in wild breeding native populations of other North American *Falco* unless the haplotype situation mentioned above could be detected. Certainly, genes modifying morphology are not evident. Some intrageneric hybrids, where one of the parents is an exotic species, may be of concern, however. *Buteo jamaicensis*, an exotic in the U.K., has mated in the wild with *Buteo buteo* and this could pose a problem in the future as with the Mallard × black duck example.

As with most other management-oriented questions, the answers to questions surrounding hybridization are

to be found within the natural realm only after some periods of observations. We can provide logical expectations on effects of artificial hybridization to wild raptor populations, and the affects seem to be of little consequence. In our discussion, particular emphasis was placed on taxa within the genus *Falco*.

LITERATURE CITED

ANKNEY, C.D., D.G. DENNIS, L.N. WISCHARD AND J.E. SEEB. 1986. Low genic variation between black ducks and Mallards. *Auk* 103:701–709.

BIJLSMA, R.G. 1988. Unidentified Kenyan kites—Hybrid Black × Red? *Gabar* 3:19–20.

BUSH, G.L. 1975. Modes of animal speciation. *Ann. Rev. Ecol. Syst.* 6:339–364.

CADE, T.J. 1983. Hybridization and gene exchange among birds in relation to conservation. Pages 288–309 *in* C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde and W.L. Thomas [EDS.], Genetics and conservation. The Benjamin/Cummings Publ. Co., Inc., Menlo Park, CA U.S.A.

————. 1986. Propagating diurnal raptors in captivity: a review. *Int. Zoo Yearb.* 24/25:1–20.

ELLIS, D.H. 1995. What is *Falco altaicus* Menzbier? *J. Raptor Res.* 29:15–25.

GRANT, P.R. AND B.R. GRANT. 1992. Hybridization of bird species. *Science* 256:193–197.

GRAY, A.P. 1958. Bird hybrids. A checklist with bibliography. *Commonw. Bur. Anim. Breed. Genet. Tech. Commun.* Edinburgh 13:1–390.

HAAK, B. 1980. Hybrid falcons. *J. N. Am. Falconers Assoc.* 18/19:74–83.

HOLLANDS, D. 1984. Eagles, hawks and falcons of Australia. Thomas Nelson Australia, Melbourne, Victoria, Australia.

MARSHALL, J.T., JR. 1967. Parallel variation in North and Middle American Screech-owls. Monog. No. 1, West. Found. Vert. Zool., Los Angeles, CA U.S.A.

MAYR, E. 1970. Populations, species and evolution. Harvard Univ. Press, Cambridge, MS U.S.A.

OLIPHANT, L.W. 1991. Hybridization between a Peregrine Falcon and a Prairie Falcon in the wild. *J. Raptor Res.* 25:36–39.

OLSEN, P.D. AND J. OLSEN. 1985. A natural hybridization of the Brown Goshawk (*Accipiter fasciatus*) and Grey Goshawk (*A. novaehollandiae*) in Australia, and a comparison of the two species. *Emu* 85:250–257.

RISING, J.D. 1983. The great plains hybrid zones. Pages 131–157 *in* R.F. Johnston [ED.], Current ornithology, Vol. 1. Plenum Press, New York, NY U.S.A.

SCHMUTZ, S.M. AND L.W. OLIPHANT. 1987. A chromosome study of Peregrine, Prairie and Gyrfalcons with implications for hybrids. *J. Hered.* 78:388–390.

SEIBOLD, I., A.J. HELBIG AND M. WINK. 1993. Molecular systematics of falcons (family Falconidae). *Naturwissenschaften* 80:87–90.

SIBLEY, C.G. 1957. The evolutionary and taxonomic significance of sexual selection and hybridization in birds. *Condor* 59:166–191.

STEVENS, R. 1972. B.P.I.E. No. 27. Peregrine Falcon-Saker cross. *Raptor Res.* 6:18–21.

SYLVEN, M. 1977. Hybridisering mellan glada *Milvus milvus* och brunglada *M. migrans* i Sverige 1976. *Vår Fågelvärld* 36:38–44.

WOBUS, U. AND G. CREUTZ. 1970. Eine erfolgreiche Mischbrut von Rot und Schwarzmilan (*Milvus milvus* × *Milvus migrans*). *Zool. Abh.* 31:305–313.

CONTRIBUTIONS OF REHABILITATION/EDUCATION PROGRAMS IN RAPTOR MANAGEMENT

PATRICK T. REDIG, GARY E. DUKE AND MARC MARTELL. *Raptor Research and Rehabilitation Program, 295 Animal Science/Veterinary Medicine Building, 1988 Fitch Avenue, St. Paul, MN 55108 U.S.A.*

The rise of rehabilitation of raptors has occurred concurrently with the increase in general efforts to manage and conserve raptors. Prior to the mid-1960s there was little evidence of rehabilitation being undertaken on any scale that might impact aspects of raptor management. Similarly, prior to 1970, there was a dearth of specific veterinary information available to be utilized in providing state-of-the-art medical care for raptors. Since then, a significant development in the number and scope of organizations for rehabilitating raptors and other wildlife has occurred among both lay and professional sectors. Many of these projects include public education and research, both basic and applied, among their objectives, so that the total impact of these efforts can potentially have a sizeable positive influence on the survival of raptors. Using data derived largely from the research and rehabilitation effort maintained at the University of Minnesota since 1974, we reached a number of conclusions. (1) Combined research and rehabilitation programs can provide effective means for detecting naturally occurring diseases and for assessing the importance of various causes of mortality among raptors. Fourteen years of data collected systematically show in general that the occurrence of natural disease is low in raptors, whereas the incidence of traumatic injuries from man-made factors constitutes the majority of the admissions. Among the latter, the greatest number of injuries arose from collisions with moving vehicles and powerlines. (2) Rehabilitation can result in complete recoveries with successful releases to the wild and subsequent survival. Data from banding records and telemetry studies show survival in excess of seven yr for some rehabilitated raptors and distances of more than 1000 miles traveled over the course of five mo following release. Data are also available which document successful nesting of released Bald Eagles (*Haliaeetus leucocephalus*), through the finding of color-marked feathers in and below occupied nests. The influence of these recovered birds on wild populations varies with the num-

bers involved, the number of wild birds present in a population and the effectiveness with which rehabilitated raptors are assimilated back into the wild. (3) Reintroduction and translocation projects for Bald Eagles and Peregrine Falcons (*Falco peregrinus*) have benefited by the rearing of young, and also through the assessment of health status and medical treatment of those that have become ill or injured during the release process. (4) Research into the utilization of crippled raptors for breeding purposes has produced positive results. Young of Bald Eagles and several owl species have been produced by crippled parents for release projects.

Other impacts of rehabilitation projects are farther reaching, but less measurable, than those mentioned above. Since 1980, 18 senior veterinary students have completed internships ranging from three wk to three mo at this program, and several have gone on to establish research and rehabilitation projects at other veterinary colleges. Additionally, raptor biologists from Spain, Mexico, France, England, Denmark, New Zealand and Israel have served internships during which they gained valuable experience in capture, restraint, blood sampling and other procedures that enhance their ability to gather field data about raptors. Further, the program now maintains an active list of more than 100 volunteers working in clinical, educational and public relations areas which not only further the immediate work of the program, but also provide the volunteers with lifetime experiences that will stimulate their understanding and make them effective communicators for raptor conservation in the future.

The most immeasurable thrust is in the area of public relations and education. Uncountable hundreds of thousands of people are being informed about the ongoing need for conservation of raptors and wildlife resources. Rehabilitation statistics indicate the effectiveness of such efforts. In the period 1972–75, 35% of the admissions to the program occurred due to projectile injuries; since 1981, 4% or fewer of admissions have come from projectile injuries. Additionally, public awareness of the need for eagle wintering habitat caused the reevaluation of an airport improvement project in St. Paul, MN that would have resulted in the felling or topping of trees on an island in the Mississippi that was used by Bald Eagles. This population of eagles was found by radio-tracking a rehabilitated bird that had recovered from a trap injury.

Influencing public policy and legislation are other arenas in which rehabilitation projects have had an impact. The current trend toward elimination of lead shot for waterfowl hunting has gained impetus from the realization that Bald Eagles are affected by lead poisoning, a fact that came to light from the admission of lead-poisoned eagles to rehabilitation facilities as well as the USFWS Health Laboratory in Madison. Additionally, several states in the Midwest have enacted legislation to eliminate the use of open-baited steel-jawed traps for small mammal trapping after recognizing the numbers of eagles admitted to rehabilitation projects that had been caught in traps.

The cost-effectiveness of rehabilitation is only measurable in terms of the number of benefits one is willing to apply against the actual medical costs of rehabilitation The Minnesota project computes a cost of about $75 per bird admitted to the clinic, amortized over a total admission of 4000 raptors in 14 yr. At an average release rate of 42%, the cost per released bird is about $150. Cost factors associated with other means of raptor management are not available, so direct comparisons cannot be made. However, given the wide array of benefits afforded raptors by the global efforts in conservation mediated through rehabilitation and education projects, we conclude that this area of endeavor is a viable and worthwhile tool for their management.

DEVELOPMENT OF CAPTIVE BREEDING AND RELEASE TECHNIQUES

TOM J. CADE AND MARTIN J. GILROY. *The Peregrine Fund, World Center for Birds of Prey, 5666 West Flying Hawk Lane, Boise ID 83709 U.S.A.*

Aldo Leopold (1933) began what can be called the "ecological tradition" in wildlife management, with its emphasis on habitat. Its principle is that the preservation and manipulation of all environmental factors that are necessary to support wildlife populations is more important than direct manipulation of the animals themselves. This approach has continued to the present date and is certainly the best policy whenever it can be pursued. The preservation of suitable habitats for birds of prey should be our paramount concern, as it is for all wildlife, since the more natural areas and ecosystems we can set aside and preserve in the unaltered state, the greater will be the abundance and diversity of raptors in the future. However, we all recognize that despite our best intentions and efforts, natural habitats of all sorts will continue to shrink in size and to deteriorate in their capacities to support a diversity of species, under the continuing influence of human population pressures and needs. Such passive preservation measures that aim to preserve the status quo are delaying actions at best, and alone will not suffice, simply because they will not occur on a large enough scale to take care of everything. Increasingly in the future, the strategy of biological conservation will need to combine strict habitat preservation with preservation of individual species, by using manipulative techniques (such as captive propagation and reintroduction) to help species to adjust and to survive in the increasingly human-dominated world.

PROPAGATION

It is curious that the captive propagation of raptors is a quite recent activity, given the long tradition of human involvement with these species in the sport of falconry and as tribal and national totems. The first Peregrine Falcon (*Falco peregrinus*) known to be raised from captive parents was produced as recently as 1942, and even as late as 1965 only

about 23 species of diurnal raptors had successfully been bred in captivity, mostly on a casual basis.

The situation has changed markedly in the last two decades. When it became evident in the late 1960s that many raptor populations in north temperate regions had suffered major declines, owing to DDT and related pesticides or to other forms of environmental degradation, an interest emerged (particularly among falconers) to perfect techniques of captive breeding for some of these species, especially the peregrine. More than a quarter of all falconiform species have now been bred in captivity. At least 12 species have produced more than 100 progeny in captivity since 1975, some having produced thousands; the number of peregrines produced worldwide certainly exceeds 5000. It is probably safe to conclude that most, if not all, diurnal birds of prey can be bred in captivity given sufficient knowledge of their needs and sufficient resources to carry out the work.

Among the explanations for these breakthroughs is the zealous nature of raptor breeders. Most of them are falconers, building on 3000 years of knowledge about handling and training hawks and falcons. A second factor contributing to the success of these projects has been the rapid and free exchange of information among breeders through organizations such as the Raptor Research Foundation, North American Falconers Association, the Hawk and Owl Trust and the British Falconers' Club, to name a few. Finally, much is owed to the application of basic scientific information on avian reproductive physiology and breeding behavior and ecology. A quick example is the now well-known development of human-imprinted "semen donors" for artificial insemination, solving infertility problems owing to incompatibilities between mates. A thorough review of captive propagation is available in Cade (1986).

REINTRODUCTION

Raptor reintroduction programs, which are often technically "restocking" in that the original population is not truly extinct, have employed three general methods: (1) fostering captive-bred or harvested wild young into the nests of conspecific surrogates, (2) cross-fostering into the nests of other species and (3) hacking by modifications of the traditional falconers' methods. Details are available in Sherrod et al. (1981), Cade et al. (1988) and Barclay and Cade (1983). As these techniques have been refined, there has been a rapid increase in the number of reintroduction programs for raptors.

If a program is to be successful, its goals need to be specifically stated, based on reproductive and survival data from similar projects or from natural populations in other parts of the species' range so that accurate projections of the required commitment can be made, in terms of birds, work, time and money. Such projects should not be started merely because it is now comparatively easy to do so, or is good publicity, or makes an agency available for federal funding. Experience to date indicates that the

establishment of self-sustaining populations in vacant range takes a lot of birds and a lot of time.

A concerted, cooperative, regional approach can maximize the return on species restoration efforts. Clustering release sites so as to saturate a region increases the likelihood of pair formation, and may be accomplished through cooperation of several states. Toward that end, an active, enthusiastic recovery team approach has worked well in the eastern peregrine reintroduction. Besides their role in coordinating the multitude of state and federal agencies that carry out this work, they have helped to expedite the regulatory burden and moderate the political aspects that accompany a large-scale program.

The cost of conducting raptor restoration programs in the coming decades will be high, since they are so labor intensive, especially when captive-produced birds are involved. Taking the Eastern Peregrine Recovery Program as a case in point, the Peregrine Fund has spent about $2.8 million to propagate and release peregrines in the eastern states. Figuring in the expense of cooperating agencies probably brings this cost to about $3.5 million, perhaps more, and this is but one of four regional recovery programs in the U.S. Though this may seem a staggering amount at first, it is not really that expensive relative to many of the other things people are willing to spend our public and private wealth to obtain. Compared to the $10 million one individual recently paid for a single untrained racehorse, or the $15 million purses of championship prize fights, or the billions of dollars spent on Star Wars technology, saving endangered species seems a bargain.

These costings underscore the need for sound economic projections in the planning stages of a reintroduction program, and the need for continued support for the duration of the program. Complete restoration may not be achieved until years after the initial enthusiasm of the program has waned. Moreover, the required support extends beyond money alone, to agency support. The success in establishing initial small populations can lead to an attitude of complacency, for example, so that states just entering a program become ineligible for the federal funds that got the program started. Government labs can become reluctant to analyze eggs to monitor the factors responsible for the species' original decline.

The involvement of the skilled private sector is one way of reducing some of the costs of reintroduction programs. Members of local bird clubs and individual falconers have helped survey and monitor falcons in the east. Many falconers have provided young for the peregrine recovery effort. Because of production problems at our facility in Boise in 1986, more than 15% of the birds released in the east were donated by private breeders. Others provided falcons for release in the Upper Mississippi region.

As natural environments become fragmented and degraded, it is up to those of us who care about these birds to convince the rest of humanity that they are worth the cost of saving. So long as people are willing to commit

the necessary time, effort and money, the creative use of management techniques like captive breeding and reintroduction can be made to work for particular species of concern. The future is not bleak, as some pessimists would have us think; rather, it is a challenge.

LITERATURE CITED

BARCLAY, J.H. AND T.J. CADE. 1983. Restoration of the Peregrine Falcon in the eastern United States. *Biol. Cons.* 1:3–40.

CADE, T.J. 1986. Using science and technology to reestablish species lost in nature. Pages 279–288 *in* E.O. Wilson [ED.], Biodiversity. National Academy Press, Washington DC U.S.A.

———, J.H. ENDERSON, C.G. THELANDER AND C.M. WHITE. 1988. Peregrine Falcon populations, their management and recovery. The Peregrine Fund Inc., Boise, ID U.S.A.

LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York, NY U.S.A.

SHERROD, S.K., W.R. HEINRICH, W.A. BURNHAM, J.H. BARCLAY AND T.J. CADE. 1981. Hacking: a method for releasing Peregrine Falcons and other birds of prey. The Peregrine Fund, Boise, ID U.S.A.

THE RAPTOR RESEARCH FOUNDATION, INC.
(FOUNDED 1966)

The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, letters to the editor, thesis abstracts and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 216 × 278 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (6th ed., 1983) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1990).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 27(4), and are available from the editor.

1997 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1997 annual meeting will be hosted by Georgia Southern University and will be held October 30 through November 2 at the Marriott Riverfront in Savannah, Georgia. Details about the meeting and a call for papers will be mailed to Foundation members in the spring of 1997. For more information, contact Michelle Pittman (912/681-5555, e-mail: meeden@gsvms2.cc.gasou.edu) or Steve Hein (912/681-0831) at Georgia Southern University.

RAPTOR RESEARCH FOUNDATION, INC., AWARDS
Recognition for Significant Contributions[1]

The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.

The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.

The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Dr. Petra Wood, West Virginia Cooperative Fish and Wildlife Research Unit, P.O. Box 6125, Percival Hall, Room 333, Morgantown, WV 26506-6125 U.S.A.** Deadline: established for conference paper abstracts.

The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants[2]

The **Stephen R. Tully Memorial Grant** for $500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Dr. Kimberly Titus, Alaska Division of Wildlife Conservation, P.O. Box 20, Douglas, AK 99824 U.S.A.** Deadline: September 10.

The **Leslie Brown Memorial Grant** for $500-$1,000 is given to support research and/or the dissemination of information on raptors, especially to individuals carrying out work in Africa. Contact: **Dr. Jeffrey L. Lincer, P.O. Box 1675, Valley Center, CA 92082 U.S.A.** Deadline: September 15.

[1] Nominations should include: (1) the name, title and address of both nominee and nominator, (2) the names of three persons qualified to evaluate the nominee's scientific contribution, (3) a brief (one page) summary of the scientific contribution of the nominee.

[2] Send 5 copies of a proposal (≤ 5 pages) describing the applicant's background, study goals and methods, anticipated budget, and other funding.