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SURVIVAL AND MOVEMENTS OF IMMATURE BALD EAGLES FLEDGED IN NORTHERN CALIFORNIA

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ABSTRACT.—We studied survival and movements of 13 radiotagged immature Bald Eagles (*Haliaeetus leucocephalus*) fledged in 1989 and 1990 from nests at Lake Britton in northcentral California. Initial observations were consistent with a previously-described postfledgling northward migration into Canada and Alaska. First-year eagles returned to northern California between January and May of the following year and moved extensively in the general region of northcentral California. Of the two cohorts, 10 birds were located within a year of fledging for a minimum first-year survivorship of 76.9%. Seven eagles returned to our study area. Five of these birds returned briefly to their natal territories. Three of 10 returning birds were not observed again in our study area but were recorded infrequently at distances of 50–190 km outside the study area. Two different movement patterns emerged within the 10 returning birds: five birds showed a high degree of affinity to the study area and five did not. In their second year of life, radiotagged immatures showed less affinity for our study area during late summer and fall. We could not determine if this disappearance indicated a regular or repeated migration, or merely an increased tendency to wander.

KEY WORDS: *Bald Eagle, Haliaeetus leucocephalus; movements; survival; mortality; radiotelemetry; California.*

Sobrevivencia y movimientos de juveniles de águilas calvas del norte de California

RESUMEN.—Estudiamos la sobrevivencia y movimientos de 13 águilas calvas juveniles (*Haliaeetus leucocephalus*) dotados de radiotransmisores nacidas en 1989 y 1990 en nidos del lago Britton en el centro-norte de California. Las observaciones iniciales fueron consistentes con la migración norte previamente descrita hacia Canadá y Alaska. El primer año las águilas regresaron al norte de California entre enero y mayo del año siguiente y se movilizaron extensivamente en la región centro-norte de California. De las dos cohortes, 10 aves fueron localizadas al año de haber nacido, para un mínimo de sobrevivencia del 76.9%. Siete águilas regresaron a nuestra área de estudio. Cinco de estas aves regresaron brevemente a sus territorios de natalidad. Tres de 10 aves que regresaron no fueron observadas nuevamente en nuestra área de estudio pero si infrecuentemente a distancias entre 50–190 km por fuera del área de estudio. Dos patrones distintos de movimientos emergieron a partir de las 10 aves que regresaron: cinco aves mostraron un alta afinidad al área de estudio y cinco no. En el segundo año de vida, los juveniles con radiotransmisores mostraron una afinidad menor al área de estudio durante el verano y el otoño. No pudimos determinar si esta ausencia indicó un repetido patrón de migración o si era una tendencia a deambular.

[Traducción de César Márquez]

Since Broley's (1947) pioneering studies of eaglet movements from Florida, various researchers have studied Bald Eagle (*Haliaeetus leucocephalus*) movements across North America (e.g., Southern 1963, Gerrard and Bortolotti 1988, McClelland et al. 1994). Studies of Bald Eagle movements have focused on migration of adults between breeding and wintering grounds (Gerrard et al. 1978, Hodges et al. 1987, McClelland et al. 1994), movements within breeding or wintering grounds (Buehler et al. 1991a, Gerrard et al. 1992, Garrett et al. 1993, Harmata and Stahlecker 1993) and movements of nestlings from their natal territories (Broley 1947, Gerrard et al. 1974, Harmata et al. 1985, Hunt et al. 1992, McClelland et al. 1996). Eagle movements may be affected by a wide variety of biotic and abiotic factors, including the age of birds, the distribution and behavior of various prey species or the prevailing environmental conditions such as climate, topography, and latitude.

Breeding Bald Eagles in North America include resident and migratory populations, or a combination, in which some birds are migratory and others remain on breeding territories in winter. Newton (1979) believed that residency is the preferred condition when prevailing environmental conditions, principally food supply, allow for year-round occupancy of a nesting territory. Milder winter climates in lower latitudes of North America appear to provide conditions necessary for residency, whereas harsh winters of northern latitudes induce breeding eagles to migrate south in search of dependable food supplies. Residency for breeding pairs appears the norm in California (Jenkins and Jackman 1993), southern Oregon, Florida and Chesapeake Bay, Maryland (Buehler et al. 1991a). Migratory breeding populations probably occur in most of the Canadian provinces (Gerrard et al. 1978, Gerrard and Hatch 1983) and Alaska. Sherrod et al. (1976, Alaska) and Swenson et al. (1986, Greater Yellowstone) provided two examples where some breeding eagles move in winter and others do not.

Available information now suggests, in general, that eaglets that hatch in the southern latitudes of North America migrate north, while those that hatch in northern latitudes migrate south. Broley (1947) first discovered a northward migration of Bald Eagle fledglings from their Florida nest sites. Immature Bald Eagles from Saskatchewan migrate south and move throughout the midwestern U.S. (Gerrard et al. 1974). Bald Eagles hatched in

Maine similarly moved south down the Atlantic seaboard (McCullough 1986). Five fledglings followed from our study area in northern California in the mid-1980s all migrated northward, and four of five continued to British Columbia or southeast Alaska (Hunt et al. 1992). Mabie et al. (1994) also reported a northern postfledging dispersal pattern of fledgling Bald Eagles from nests in Texas. Broley (1947) first suggested that these northward migrations allowed eaglets to reach runs of anadromous fish in rivers of the northern portion of the continent in summer and early fall.

In 1989 and 1990, we monitored the movements of two cohorts of six and seven nestlings, respectively, in our northern California study area. We assumed that these eaglets would undertake the previously discovered northward migration (Hunt et al. 1992) and made no attempt to follow them after their initial migration. Our objectives were to locate these birds following their return from their northern migration, determine first year survivorship and monitor movements into their second year of life.

STUDY AREA AND METHODS

The Pit River originates in Modoc County, drains much of northeastern California and is a major tributary of the Sacramento River system. The Pit River Study Area (PRSA) consists of 78 km of the Pit River in Shasta County. Lake Britton is the system's largest reservoir; it is approximately 13-km long and less than 1-km wide in most places, and has a surface area of approximately 520 ha. Lake Britton supported six occupied Bald Eagle nesting territories during the study period. Three additional small reservoirs, all less than 50 ha in surface area, are found downstream from Lake Britton; four Bald Eagle nesting territories occurred at these reservoirs.

Our study area included an intergradation of habitat types characteristic of Cascade and Sierra Nevada mountain regions. The area around Lake Britton is dominated by ponderosa pine (*Pinus ponderosa*) forest, which occurred as open stands ≤ 70 m in height (Holland 1986). Downstream from Lake Britton, the Pit River canyon, including the three downstream reservoirs, was dominated by Sierran mixed coniferous forest. This habitat was similar to ponderosa pine forest, but was denser, often slightly taller (75 m), and composed of several dominant species, including ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Libocedrus decurrens*) and sugar pine (*Pinus lambertiana*).

Nestlings were radiotagged in 1989 and 1990 backpack style with teflon ribbons over and under the wings, secured on the breast with one or more stitches of cotton thread. The thread was designed to eventually deteriorate, allowing the transmitter package to fall off in 3–5 yr. Transmitters weighed 65 g with a battery life expectancy of approximately 1000 d. All 13 nestlings were tagged in nests at Lake Britton at 8–10 wk of age. All

Table 1. Movements of 10 Bald Eagles radiotagged as nestlings at Lake Britton in 1989 and 1990.

BIRD	DATE RADIOTAGGED AS NESTLING	DATE OF FIRST DETECTION ^a	TOTAL NUMBER OF DETECTIONS	NUMBER OF DETECTIONS IN STUDY AREA	GREATEST DISTANCE (km) FROM STUDY AREA
JM25 ^b	19 May 89	6 Feb. 90	17	13	105NE
JM26	4 June 89	19 April 90	21	20	110NW
JF27 ^c	4 June 89	21 Feb. 90	2	1	115N
JM28	10 June 89	20 Feb. 90	25	24	80S
JM30	11 June 89	29 March 91	1	0	130NE
JF31	24 May 90	8 March 91	11	6	160S
JF32	24 May 90	8 Feb. 91	2	0	90SW
JM34	1 June 90	5 Jan. 91	2	0	190NE
JF36	7 June 90	29 March 91	2	1	135SW
JM37	9 June 90	23 May 91	38	25	50SW

^a Following initial migration.

^b Male.

^c Female.

eaglets were banded with standard USGS aluminum leg bands. Birds were sexed on the basis of morphometric measurements (Bortolotti 1984, Garcelon et al. 1985).

Radiotagged eagles were monitored weekly in the study area with a scanning receiver and hand-held two- and three-element Yagi antennae. Two-element antennae were mounted on the wing struts of a fixed-wing aircraft for covering larger geographic areas. We conducted weekly helicopter surveys from March 1983–December 1984 (Jenkins 1992) and again from July 1987–July 1991. The age of each observed eagle was classified as adult, near-adult, subadult or juvenile following age class descriptions of McCollough (1989). To assist in data interpretation, birds not appearing in adult plumage were grouped in a category called nonadults. In addition to weekly helicopter surveys, fixed-wing aircraft surveys were conducted in 1989–92 at about monthly intervals over northern California and southern Oregon, outside the Pit River study area.

RESULTS

Of the six fledglings radiotagged in 1989 at Lake Britton, four birds were located the following year and a fifth bird was located in 1991. Seven additional fledglings were radiotagged in 1990 and five of these were located in 1991. The survival rate was 76.9% (10 of 13) for the first year of life. Our survival rate is a minimum estimate, because it ignores possible transmitter loss or failure, the possibility that fledglings were missed on aerial surveys over northern California and southern Oregon or that some eagles never returned to the region.

All 13 radiotagged juvenile eagles departed the study area by 1 September of the fledging year. Of the four immature eagles from the 1989 cohort relocated in northern California in 1990, three were

first located in February and one in April (Table 1). A fifth bird from this cohort was first located in March 1991. Five of the seven nestlings from the 1990 cohort were subsequently located in 1991. The first of these birds was found in southern Oregon on 5 January 1991. Others from the 1990 cohort were first located in February, March, and May 1991 (Table 1). Returning birds wandered throughout our study area, northern California and southern Oregon during the subsequent monitoring period (Fig. 1).

Seven of the 10 surviving eagles actually (both cohorts) returned to parts of the PRSA. Five of these birds returned briefly to their natal territories and other locations on Lake Britton. Two of seven birds that returned to the PRSA also subsequently wandered distances over 100 km outside the PRSA (Table 1). Three juveniles that were frequently recorded in the PRSA after their initial migration disappeared for a time in the summer and fall of their second year of life but were recorded again in the PRSA a few months later. Three surviving fledglings were not recorded in the PRSA despite weekly helicopter and periodic ground surveys. These three birds were recorded infrequently at distances of 50–190 km from the PRSA. In previous studies, we recorded a marked juvenile Bald Eagle from the PRSA subsequently establishing a nesting territory. This eaglet, originally banded in our study area in 1983 at Lake Britton, later was trapped as a breeding adult on Shasta Lake in 1990, a distance of about 55 km southwest of Lake

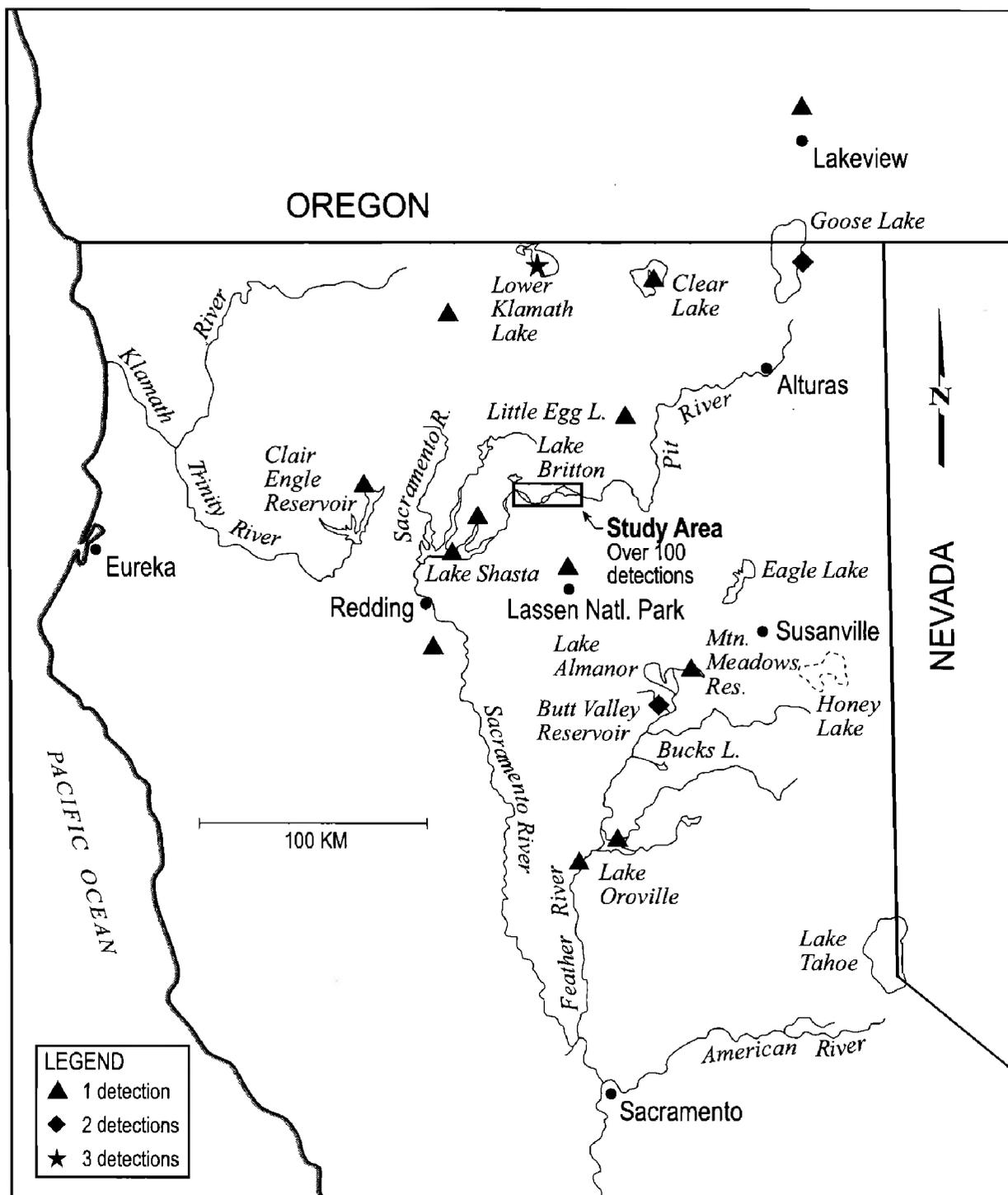


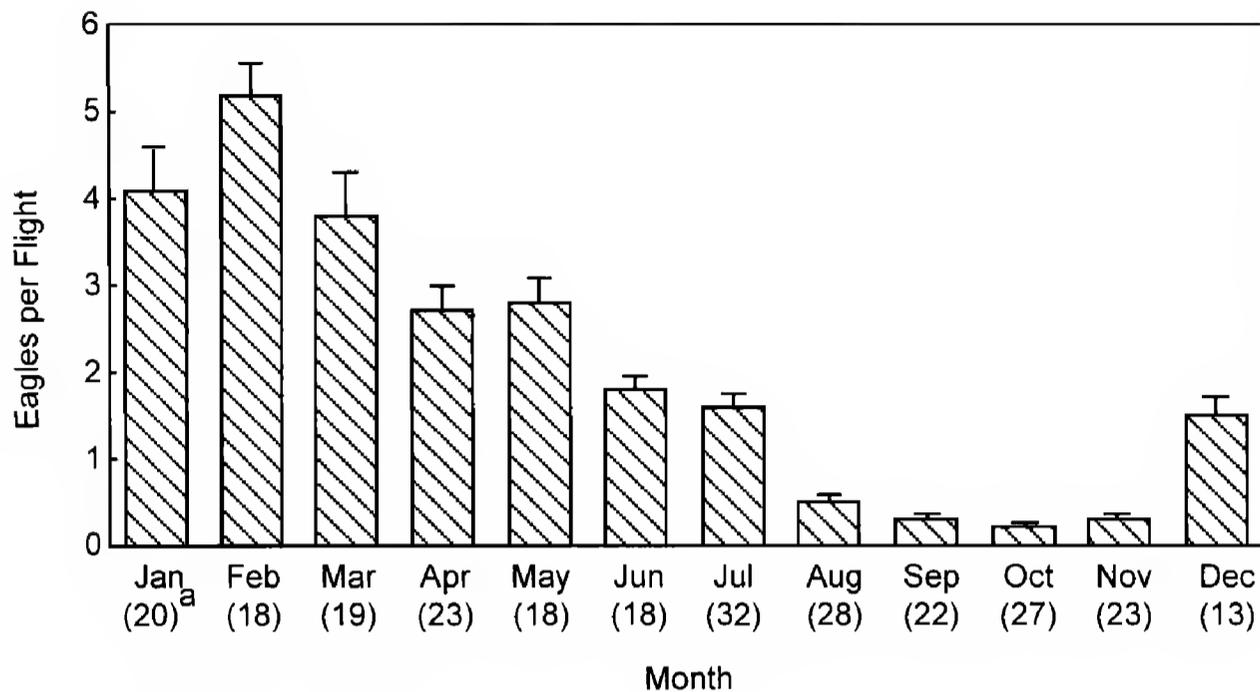
Figure 1. Locations throughout northern California of 10 radiotagged Bald Eagle nestlings fledged from nests at Lake Britton in 1989 and 1990.

Britton (Jenkins 1992). This is our only record of future breeding by a Bald Eagle fledged from our study area.

Based on weekly helicopter surveys, the total number of Bald Eagles recorded in nonadult plumage in the PRSA declined markedly during the late summer and fall but increased again beginning in December (Fig. 2). Three immature eagles radiotagged from PRSA nests visited the Klamath Basin in their second winter, about 100 air km from the PRSA. This area is one of the largest wintering congregations of Bald Eagles in the lower 48 states, supporting hundreds of migrant Bald Eagles which feed on migrating waterfowl.

DISCUSSION

McCullough (1986) estimated a minimum survival of first-year Bald Eagles in Maine of 54%, and a 73% survival for first-year birds when artificial feeding was provided. Gerrard et al. (1978) reported 37% first-year survival for 43 Bald Eagles wing-marked as juveniles in Saskatchewan. Sherrod et al. (1976) estimated that fewer than 10% of fledglings survived to breeding age on Amchitka Island, Alaska, and suggested that about 5.4% of the adult population died each year. Buehler et al. (1991b) recently estimated 100% survival for 39 radiotagged Bald Eagles through their first year of life in the Chesapeake Bay area. Similarly, Mc-



(a) Number of flights

Figure 2. Mean number (\pm SE) of nonadult (immature, subadult and near adult) Bald Eagles recorded in weekly helicopter surveys of the PRSA, 1983–84 and 1987–91, shown by month.

Clelland et al. (1996) reported 10 of 11 (91%) juvenile Bald Eagles fledged from nests at Glacier National Park, Montana, surviving their first winter.

Our estimated survival rate of 76.9% (10 of 13) suggested a high degree of juvenile survival for the PRSA Bald Eagle population. Our survival estimate was consistent with the present growth of the breeding population of Bald Eagles in California. A population model recently reported by Jenkins (1996) using this value and an empirically-derived annual adult survival value of 94.6% indicates a 6–7% increase in the California breeding population, which is consistent with observed population growth during the past 15 yr (Jenkins et al. 1994).

It was unclear whether subadult eagles migrated like fledglings in their second and subsequent years. The number of nonadult birds in the PRSA was low from June through late summer and fall. It seemed likely that subadults had less affinity to the PRSA at this time of year, but it was not clear if this involved a regular and repeated migration or simply an increased tendency to wander. The fact that radiotagged eagles were not detected during fixed-wing aircraft surveys of larger areas of northern California, suggested that immature eagles undertook extensive movements during this period.

Our data indicated the movements of immature Bald Eagles were highly nomadic and variable with only some fledglings returning to their natal areas.

The tendency of some birds to concentrate their movements around PRSA may have resulted from a sampling bias due to increased monitoring in the PRSA; subadult movements may have been even more extensive than indicated by our data. Extensive movements give subadults an opportunity to visit various water bodies across northern California and familiarize themselves with other breeding territories and potential habitat throughout the region.

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PREY OF NESTING BALD EAGLES IN NORTHERN CALIFORNIA

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ABSTRACT.—Inland nesting Bald Eagles (*Haliaeetus leucocephalus*) in northern California preyed on both native and introduced freshwater fish species, primarily brown bullhead (*Ameiurus nebulosus*), Sacramento sucker (*Catostomus occidentalis*), common carp (*Cyprinus carpio*) and tui chub (*Gila bicolor*). At most locations, eagles ate mainly fish; however, birds, principally American Coots (*Fulica americana*) and Mallards (*Anas platyrhynchos*), were more important than fish at sites isolated from large rivers. Fish species taken by eagles varied between major drainages: Sacramento sucker were most common in eagle diets at impoundments along the Pit River and the American River, catfish predominated on the Feather River and Trinity River drainages, and tui chub were the principal prey of eagles nesting in the Lahontan System. Mean standard lengths of common prey fishes ranged from 240 mm for brown bullhead to 510 mm for carp; Sacramento sucker prey averaged 393 mm standard length. Productivity of eagle pairs using mostly native fishes on the Pit River was nearly identical to that of pairs taking mostly introduced fishes on the Feather River. We recommended that resource managers consider prey species composition and fish prey sizes in management decisions affecting Bald Eagle breeding habitat. Important management factors affecting fish populations included dam construction and operation and nongame fish control.

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; *California*; *food habits*; *prey remains*.

Presas de *Haliaeetus leucocephalus* anidando en el norte de California

RESUMEN.—Las águilas calvas anidantes de tierras adentro en el norte de California depredaron a especies nativas e introducidas de peces de agua dulce. Principalmente *Ameiurus nebulosus*, *Catostomus occidentalis*, *Cyprinus carpio* y *Gila bicolor*. En casi todas las localidades las águilas se alimentan de peces; sin embargo las aves principalmente *Fulica americana* y *Anas platyrhynchos* fueron mas importantes que los peces en los sitios aislados de los grandes ríos. Las especies de peces consumidas por las águilas varió entre los mayores drenajes: *Catostomus occidentalis* fue el mas común en la dieta de las águilas a lo largo del Río Pit y Río American, los bagres predominaron en los drenajes de los ríos Feather y Trinity. *Gila bicolor* fue la presa principal de las águilas anidando en el sistema Lahontan. La media estandar longitudinal de las presas comunes osciló entre 240 mm para *Ameiurus nebulosus* hasta 510 mm para *Cyprinus carpio*; *Catostomus occidentalis* promedio 393 mm de longitud. La productividad de las parejas de águilas que utilizaron peces nativos en el Río Pit fue casi idéntica a otras parejas que consumieron peces introducidos en el Río Feather. Recomendamos a los manejadores de recursos considerar la composición de especies presa y los tamaños de peces presa en las decisiones de manejo que afectan los habitats de anidación de las águilas calvas. Algunos factores importantes de manejo que pueden afectar las poblaciones de peces incluyen la construcción y operación de represas así como también el control de especies que no son de pesca comercial.

[Traducción de César Márquez]

Numerous introductions of nonnative game fish have greatly altered species composition within California waterways (Moyle 1976a). Likewise, extensive habitat alterations, especially dam construction, river flow regulation and channelization, have tended to favor introduced species (Moyle 1976b). Nongame fish eradication programs and flow changes specifically benefit recreational fisheries. Decisions regarding such habitat alterations and management programs have rarely considered the prey of Bald Eagles (*Haliaeetus leucocephalus*) and other piscivorous birds (Dombeck et al. 1984). Even so, nesting populations of Bald Eagles in California have increased in the post-DDT era (Detrich 1986), and the number of occupied nesting territories now exceeds 140 (R.M. Jurek unpubl. data). Most pairs nest in highly modified habitats and feed on both native and introduced fishes (Detrich 1989, Hunt et al. 1992c).

In this paper, we examine the relationship of eagle diets to habitat and prey regimes now characterizing northern California rivers. By analyzing prey remains obtained during this and several other studies (Hunt et al. 1992b, Jenkins 1992, Jenkins et al. 1994), we were able to compare differences in prey utilization between various river drainages, assess the dietary importance of various native and introduced fish species and provide information relative to conservation and enhancement of prey populations in important eagle management areas.

STUDY AREA

We collected prey remains from Bald Eagle nests located within three major drainage basins in northern California, each containing a different composition of native fishes: the Sacramento-San Joaquin drainage, the Lahontan system, and the Klamath River drainage (Moyle 1976a). In our study, the principal rivers of the Sacramento-San Joaquin drainage system with nesting Bald Eagles were the Pit River (including the Fall River and its tributary, the Tule River), the McCloud River, the Sacramento River, the Feather River (including the North, Middle, and South forks), the American River, and the Eel River (Fig. 1). Study sites in the Lahontan system, which flows into the Great Basin, were along the Little Truckee River, the Susan River and Eagle Lake. Within the Klamath system, eagle territories were near the Lost River and along the Trinity River. More than 80% of the nesting territories in this study were near reservoirs; the remainder were on natural lakes. Adjacent riverine habitats were often accessible to the eagles. Most nest sites occurred in ponderosa pine (*Pinus ponderosa*) or mixed conifer forests at elevations ranging from 450–1800 m.

For comparative purposes, we divided Bald Eagle territories into subgroups based on their proximity to one another along a shared drainage or impoundment. We

also grouped pairs according to similarities of available fish fauna or aquatic habitat characteristics. For example, reservoirs designated as "Trout-managed" were stocked annually with hatchery salmonids (trout and salmon) and contained no significant populations of other prey fishes, although native catostomids (suckers) and cyprinids (minnows) were potentially available in nearby riverine habitats. We classified relatively small and isolated impoundments as "Basin Reservoirs," where there was no discernable watershed, or if they lay within an intermittent portion of a watershed.

METHODS

During 1983–92, we collected prey remains in and below nests, usually following dispersal of young and sometimes during the late nestling stage. Some sites were visited in multiple years and others only once during the study. From nest sites, we obtained bones, fur, feathers and fine nest lining, the latter containing fish scales and fine bones. We assembled a reference collection of common fish species in various size categories. We used reference bones and keys (Casteel 1976) and reference scales and scale keys (Lagler 1940, Casteel 1972) to identify the species and size of fish represented by each prey item found in the prey collections (Hunt et al. 1992c). For each fish species in our reference collection, we developed bone-length to standard-body-length regression equations for opercula, cleithra, crania, dentary and other species-diagnostic bones (McConnell 1952, Hansel et al. 1988). Using these equations, we calculated standard fish lengths (i.e., head to end of caudal peduncle) for each prey item and eliminated duplicate prey items by matching parts representing like-sized individuals falling within 95% confidence intervals. We determined the ages of fish scales by standard methods (i.e., counting annuli; Bagenal and Tesch 1978); we used length/annulus tables (Carlander 1969, 1977) to estimate size of fish represented only by scales. Since scales can only be aged and not assigned to individual fish numbers, we did not quantify fish prey from scales unless scales were the only remains for a particular species. In those cases, one fish was counted for each age represented. We calculated total weights for the selected (nonduplicate) prey items using length-to-weight equations from our reference fish and from Carlander (1969, 1977). From these total weights, we subtracted the weights of bones and scales plus 5% of the total weight (estimated unavailable or discarded biomass) to arrive at the edible biomass for each prey fish (Hunt et al. 1992c). For comparisons, we referred to "primary" prey fish species as those represented by $\geq 30\%$ of total prey numbers or biomass, and "important" prey fish species as those with 15–29% of numbers or biomass.

We identified nonfish remains by comparison with museum collections. Identifying mammal hair required keys (Adorjan and Kolenosky 1969, Moore et al. 1974) and microscopic examination. We calculated biomass for nonfish prey from standard mean weights (Burt and Grosenheider 1964, Steenhof 1983, Dunning 1984) minus 10% to account for bones and unavailable biomass. Large species (i.e., weighing > 5 kg) were assigned an arbitrary estimate of 2.5 kg biomass contribution, assuming that eagles obtained only a portion of each carcass.

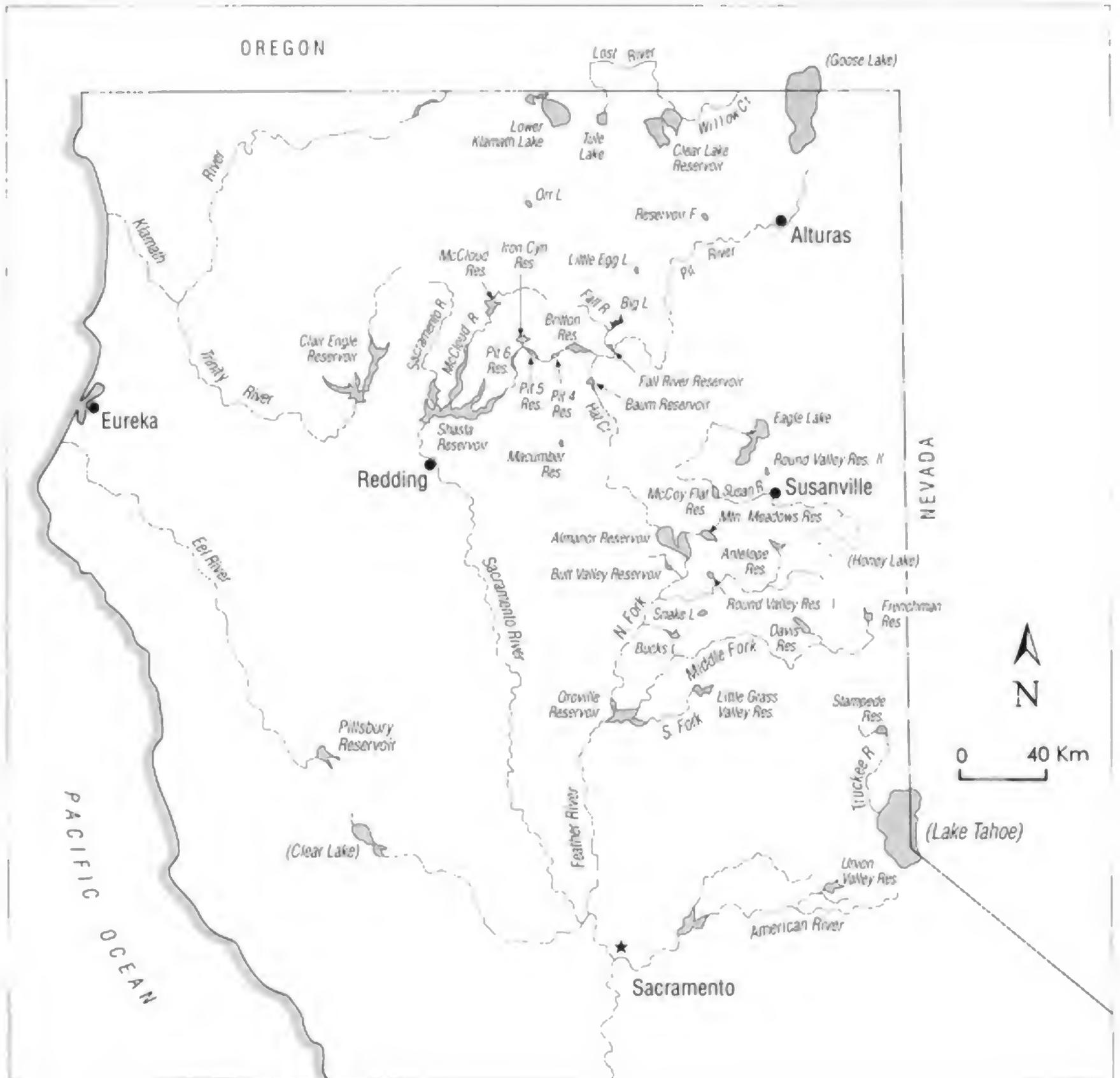


Figure 1. Location of the study area in northern California. Lakes indicated in parentheses were not included in the study.

Our analysis of prey use was biased in that it was based exclusively on prey remains. Previous studies comparing the analysis of Bald Eagle prey remains with observations of prey deliveries to the nest (Todd et al. 1982, Dugoni et al. 1986, Knight et al. 1990, Hunt et al. 1992a, 1992c, Grubb 1995) indicated that while prey remains tend to show all taxa used by eagles, in most cases small, soft-boned fish (e.g., trout) were underrepresented, and large, bony fish (e.g., carp and catfish) and birds were generally overrepresented in remains. The fish scale collections from nest linings helped mitigate this potential

bias. With a few exceptions and catfish which have no scales, the relative number of scales found in nests reflected our fish bone analysis (i.e., large numbers of scales accompanied large numbers of conspecific bones).

RESULTS

Diet. We identified 2351 individual prey items representing 1637 kg of biomass from 56 nesting territories in our study area (Table 1). Nesting Bald Eagles utilized 20 species of fish, 41 bird, 15 mam-

Table 1. Number of individuals and estimated biomass (kg) of prey identified from remains collected in and below 56 Bald Eagle nests in northern California from 1983–92.

SPECIES	NUMBER	(%)	BIOMASS	(%)
FISH (Osteichthyes)				
Brown bullhead (<i>Ameiurus nebulosus</i>) ^a	817	(34.8)	214.2	(13.1)
Sacramento sucker (<i>Catostomus occidentalis</i>)	285	(12.1)	290.3	(17.7)
Common carp (<i>Cyprinus carpio</i>) ^a	122	(5.2)	368.9	(22.5)
Tui chub (<i>Gila bicolor</i>) ^b	110	(4.7)	57.5	(3.5)
Hardhead (<i>Mylopharodon conocephalus</i>)	80	(3.4)	48.1	(2.9)
Trout (Salmonidae)	32	(1.4)	15.5	(0.9)
Sacramento squawfish (<i>Ptychocheilus grandis</i>) ^c	30	(1.3)	25.9	(1.6)
Channel catfish (<i>Ictalurus punctatus</i>) ^a	21	(0.9)	17.8	(1.1)
Crappie (<i>Pomoxis</i> spp.) ^a	19	(0.8)	3.6	(0.2)
Tule perch (<i>Hysterocarpus traski</i>)	15	(0.6)	0.6	(trace)
Sacramento blackfish (<i>Orthodon microlepidotus</i>)	14	(0.6)	26.5	(1.6)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	14	(0.6)	8.1	(0.5)
Largemouth bass (<i>Micropterus salmoides</i>) ^a	6	(0.3)	4.1	(0.2)
Sacramento perch (<i>Archoplites interruptus</i>) ^d	5	(0.2)	6.6	(0.4)
Tahoe sucker (<i>Catostomus tahoensis</i>)	5	(0.2)	6.5	(0.4)
Other sunfish (Centrarchidae) ^{a,e}	61	(2.6)	38.7	(2.4)
Other catfish (Ictaluridae) ^{a,f}	46	(2.0)	13.1	(0.8)
Unidentified minnows (Cyprinidae)	30	(1.3)	9.9	(0.6)
Unidentified trout/salmon (Salmonidae)	18	(0.8)	4.1	(0.2)
Unident. suckers (Catostomidae)	5	(0.2)	4.0	(0.2)
Other fish ^g	3	(0.1)	1.5	(0.1)
Subtotal fish	1738	(73.9)	1165.5	(71.2)
BIRDS (Aves)				
American Coot (<i>Fulica americana</i>)	120	(5.1)	69.3	(4.2)
Mallard (<i>Anas platyrhynchos</i>)	53	(2.3)	51.6	(3.2)
Western Grebe (<i>Aechmophorus occidentalis</i>)	25	(1.1)	33.2	(2.0)
Mountain Quail (<i>Oreortyx pictus</i>)	21	(0.9)	4.4	(0.3)
American Wigeon (<i>Anas americana</i>)	15	(0.6)	10.2	(0.6)
Northern Pintail (<i>Anas acuta</i>)	14	(0.6)	12.7	(0.8)
Gull (<i>Larus</i> spp.) ^h	17	(0.7)	7.7	(0.5)
Northern Shoveler (<i>Anas clypeata</i>)	12	(0.5)	6.6	(0.4)
Western Meadowlark (<i>Sturnella neglecta</i>)	12	(0.5)	1.1	(0.1)
Pied-billed Grebe (<i>Podilymbus podiceps</i>)	11	(0.5)	4.4	(0.3)
Cinnamon Teal (<i>Anas cyanoptera</i>)	11	(0.5)	3.8	(0.2)
Eared Grebe (<i>Podiceps nigricollis</i>)	10	(0.4)	2.7	(0.2)
Ruddy Duck (<i>Oxyura jamaicensis</i>)	9	(0.4)	4.4	(0.3)
Gadwall (<i>Anas strepera</i>)	8	(0.3)	6.6	(0.4)

Table 1. Continued.

SPECIES	NUMBER	(%)	BIOMASS	(%)
Band-tailed Pigeon (<i>Columba fasciata</i>)	8	(0.3)	2.8	(0.2)
Canada Goose (<i>Branta canadensis</i>)	7	(0.3)	21.2	(1.3)
Common Merganser (<i>Mergus merganser</i>)	7	(0.3)	9.3	(0.6)
Other puddle ducks (Anatinae) ⁱ	52	(2.2)	32.6	(2.0)
Unident. grebes (Podicipedidae)	26	(1.1)	17.3	(1.1)
Other diving ducks (Aythyinae) ^j	21	(0.9)	15.2	(0.9)
Other perching birds (Passeriformes) ^k	15	(0.6)	2.5	(0.2)
Other Anatidae ^l	10	(0.4)	18.7	(1.1)
Other birds ^m	39	(1.7)	34.5	(2.1)
Subtotal Birds	523	(22.3)	372.8	(22.8)
MAMMALS (Mammalia)				
Muskrat (<i>Ondatra zibethicus</i>)	13	(0.6)	13.7	(0.8)
Mule deer (<i>Odocoileus hemionus</i>)	10	(0.4)	25.0	(1.5)
Ground squirrels (<i>Spermophilus</i> spp.) ⁿ	10	(0.4)	2.7	(0.2)
Rabbits (Leporidae) ^o	8	(0.3)	9.4	(0.6)
Western gray squirrel (<i>Sciurus griseus</i>)	7	(0.3)	5.4	(0.3)
Other Sciuridae ^p	15	(0.6)	11.9	(0.7)
Other mammals ^q	25	(1.1)	30.6	(1.9)
Subtotal Mammals	88	(3.7)	98.7	(6.0)
REPTILES (Reptilia)				
Western pond turtle (<i>Clemmys marmorata</i>)	1	(trace)	0.2	(trace)
INVERTEBRATES				
Crayfish (Crustacea)	1	(trace)	0.1	(trace)
GRAND TOTAL	2351	(100.0)	1637.3	(100.0)

^a Introduced fish species in California.

^b Native to California, introduced into Almanor and Mtn. Meadows reservoirs.

^c Native to California, introduced into Eel River/Pillsbury Reservoir.

^d Native to California, introduced into Almanor Reservoir.

^e 45 unidentified, 10 bass (*Micropterus* spp.)^a, 4 sunfish (*Lepomis* spp.)^a, 1 smallmouth bass (*Micropterus dolomieu*)^a and 1 bluegill (*Lepomis macrochirus*)^a.

^f 20 bullheads (*Ameiurus* spp.)^a, 2 white catfish (*Ameiurus catus*)^a and 24 unidentified.

^g 1 American shad (*Alosa sapidissima*)^a, 1 golden shiner (*Notemigonus chrysoleucas*) and 1 unidentified fish.

^h Includes at least 2 California Gull (*Larus californicus*) and 2 Ring-billed Gull (*Larus delawarensis*).

ⁱ 4 Green-winged Teal (*Anas crecca*), 2 Wood Duck (*Aix sponsa*) and 46 unidentified.

^j 3 Common Goldeneye (*Bucephala clangula*), 3 Scaup (*Aythya* spp.), 2 Ring-necked Duck (*Aythya collaris*), 1 Redhead (*Aythya americana*), 1 Bufflehead (*Bucephala albeola*) and 11 unidentified.

^k 3 Steller's Jay (*Cyanocitta stelleri*), 2 Black-billed Magpie (*Pica pica*), 1 Common Raven (*Corvus corax*), 1 American Crow (*Corvus brachyrhynchos*), 1 blackbird (Emberizidae) and 7 unidentified.

^l 2 Snow Goose (*Chen caerulescens*), 1 Tundra Swan (*Cygnus columbianus*), 1 Greater White-fronted Goose (*Anser albifrons*), 1 goose (Anserinae) and 5 unidentified.

^m 4 Double-crested Cormorant (*Phalacrocorax auritus*), 2 Ring-necked Pheasant (*Phasianus colchicus*), 2 Western Screech-Owl (*Otus kennicottii*), 2 Belted Kingfisher (*Ceryle alcyon*), 2 Northern Flicker (*Colaptes auratus*), 2 Acorn Woodpecker (*Melanerpes formicivorus*), 1 Great Blue Heron (*Ardea herodias*), 1 Rock Dove (*Columba livia*), 1 pigeon (Columbidae), and 22 unidentified.

ⁿ At least 2 California ground squirrel (*Spermophilus beecheyi*) and 1 Belding's ground squirrel (*Spermophilus beldingi*).

^o 2 jackrabbits (*Lepus* spp.), 1 black-tailed jackrabbit (*Lepus californicus*) and 5 unidentified.

^p 2 yellow-bellied marmot (*Marmota flaviventris*), 1 chipmunk (*Tamias* sp.) and 12 unidentified.

^q 4 rodents (Rodentia), 3 voles (*Microtus* spp.), 2 raccoons (*Procyon lotor*), 2 ungulates (Artiodactyla), 1 domestic cow (*Bos taurus*), 1 striped skunk (*Mephitis mephitis*), 1 western spotted skunk (*Spilogale gracilis*), 1 broad-footed mole (*Scapanus latimanus*) and 10 unidentified.

Table 2. Mean standard length of fish species commonly selected as prey by nesting Bald Eagles in northern California as measured from prey remains collected at nests.

SPECIES	N	MEAN STANDARD LENGTH (mm)	RANGE (mm)	SE
Trout	18	321	185-498	24
Common carp	85	510	244-854	13
Hardhead	64	330	194-527	8
Sacramento squawfish	28	418	278-631	14
Tui chub	98	282	180-341	4
Sacramento sucker	228	392	131-587	4
Channel catfish	17	368	251-551	24
Brown bullhead	456	240	129-356	2

mal and one each of reptile and invertebrate species. Fish accounted for >70% of overall prey numbers and biomass, while birds contributed approximately 20% and mammals <10% to both number and biomass totals. Mean standard lengths of most commonly taken prey fishes were greater than 300 mm, except for tui chub and brown bullhead (Table 2). Common carp showed both the greatest mean length and the widest range of lengths.

Regional Differences in Prey Utilization. Bald Eagle food habits varied widely between drainage and habitat groups (Table 3). Both the numbers and biomass of fish ($\chi^2 = 383.3$, $df = 18$, $P < 0.001$; $\chi^2 = 415.8$, $df = 18$, $P < 0.001$), birds ($\chi^2 = 306.2$, $df = 18$, $P < 0.001$; $\chi^2 = 283.8$, $df = 18$, $P < 0.001$), and mammals ($\chi^2 = 77.6$, $df = 18$, $P < 0.001$; $\chi^2 = 105.3$, $df = 18$, $P < 0.001$) differed between 19 study locations as grouped in Table 3. Overall, fish dominated the diet (>50% of biomass and prey numbers) at most locations. Exceptions included Basin Reservoirs, Trout-managed reservoirs and Lost River, where birds and, to a lesser extent mammals, exceeded fish as prey.

Anatids were most prevalent in bird remains at the majority of sites; however, American Coots were more abundant in remains collected at the Lost River sites, Almanor, Butt Valley, and Pillsbury reservoirs. Gulls (Laridae) and grebes (Podicipedidae) were the predominant avian prey at Union Valley Reservoir and Lahontan sites, respectively.

All Bald Eagles nesting along the Pit River relied primarily on native Sacramento suckers (31-55% of prey biomass and 18-42% of prey numbers at all sites). Introduced ictalurids (catfish) were im-

portant only at Fall River Valley and Britton Reservoir nests (25% and 17% prey numbers, 14% and 8% biomass, respectively). Native cyprinids were important at all Pit River sites (17-22% prey numbers, 12-19% biomass) except Baum Reservoir (5% prey numbers, 4% biomass). Tui chub were the predominant native minnow taken in the Fall River Valley, and we found mostly hardhead in remains of cyprinids from nests along the rest of the Pit River drainage.

Native Sacramento blackfish and introduced common carp (38% and 34% biomass, 26% and 21% prey numbers, respectively) were the primary prey fish species of eagles at Shasta Reservoir. At the inflow of the North Fork Feather River to Oroville Reservoir, one eagle pair captured relatively large numbers of another native cyprinid, Sacramento squawfish (18% biomass, 15% prey numbers), although catfish were their primary prey (34% biomass, 37% prey numbers). A diversity of mostly introduced fish species populate both Shasta and Oroville Reservoirs.

Eagles nesting at reservoirs along all portions of the Feather River relied heavily on catfish (36-87% of prey individuals, 5-73% biomass for all sites). Common carp were the primary prey at Butt Valley Reservoir (86% biomass, 38% prey numbers), where catfish numbers were high (36% prey numbers), but their biomass (5%) was unimportant by comparison. With the exception of the Oroville Reservoir pair mentioned above, Feather River eagles captured very few native fishes. Although present throughout the Feather River system, Sacramento suckers were taken rarely, except at Oroville Reservoir (15% biomass and 14% prey numbers).

Table 3. Percent biomass of major prey groups and total number of prey items utilized by California breeding Bald Eagles as calculated from analysis of prey remains for 19 waterway territory groups.

WATERWAYS (N TERRITORIES)	TROUT	CARP	MIN- NOWS	SUCKERS	CAT- FISH	SUNFISH	OTHER FISH	TOTAL			N
								FISH	BIRDS	MAM- MALS	
Pit R.: Fall River Valley (3) ^a	1.5	3.3	12.4	30.5	13.9	4.4	0.0	66.0	25.1	8.9	178
Pit R.: Baum Res./Hat Cr. (1)	9.0	0.0	3.5	54.5	3.4	0.0	0.0	70.4	20.6	9.0	36
Pit R.: Britton Reservoir (6)	0.9	5.0	18.8	49.4	8.2	1.6	0.4	84.3	11.2	4.5	414
Pit R.: Pit 4, 5, 6 res. (4)	2.2	7.5	15.0	46.0	0.0	0.3	0.1	71.3	22.0	6.7	121
Shasta Reservoir (6) ^b	0.0	34.2	37.7	0.7	7.9	2.6	0.0	83.0	13.5	3.5	58
NFFR ^c : Oroville Reservoir (1)	1.3	9.1	18.3	14.9	34.4	5.1	0.0	83.1	16.9	0.0	52
NFFR: Mtn. Meadows Res. (2)	0.1	0.0	0.9	0.1	73.0	2.1	0.0	76.3	22.1	1.6	316
NFFR: Almanor Reservoir (4)	1.3	10.3	13.0	7.7	34.6	10.8	0.0	77.8	18.8	3.4	182
NFFR: Butt Valley Res. (2)	1.0	85.5	0.1	1.8	5.0	0.8	0.0	94.2	5.2	0.6	155
NFFR: East Fork (3) ^d	0.0	20.4	0.0	9.7	34.5	6.5	0.2	71.3	28.7	0.0	97
Middle Fork Feather R. (3) ^e	1.1	19.3	0.0	0.0	18.7	6.5	0.0	45.6	41.8	12.6	267
South Fork Feather R. (1) ^f	0.0	41.2	9.1	0.0	15.9	0.0	0.0	66.1	33.9	0.0	22
American River (1) ^g	0.6	0.0	0.0	47.8	0.0	17.6	0.0	66.0	27.0	7.0	28
Eel River/Pillsbury Res. (1)	1.9	3.6	31.6	27.9	0.0	18.2	0.0	83.1	7.4	9.5	37
Lahontan System (5) ^h	4.1	0.0	35.7	9.8	3.4	1.4	0.0	54.4	42.4	3.2	97
Trinity R./Clair Engle Res. (2)	1.8	0.0	0.0	9.1	57.6	10.4	0.0	78.9	18.8	2.3	72
Lost River (2) ⁱ	0.0	0.0	0.7	3.7	0.3	0.0	0.0	4.7	70.6	24.7	42
Basin Reservoirs (5) ^j	1.4	0.0	0.0	0.0	16.9	1.9	0.0	20.2	62.0	17.8	72
Trout-managed res. (4) ^k	9.8	0.0	0.3	4.4	0.0	0.2	0.9	15.6	63.0	21.4	103
All Sites (57)	1.7	22.5	10.3	18.4	15.0	3.2	0.1	71.2	22.8	6.0	2349

^a Fall R., Tule R., Big Lk., Fall R. Res.; ^b Sacramento R., McCloud R., Pit R.; ^c North Fork Feather R.; ^d Snake Lk., Round Valley Res I, Antelope Res.; ^e Davis Res., Frenchman Res.; ^f Little Grass Valley Res.; ^g Union Valley Res.; ^h Eagle Lk., Stampede Res.; ⁱ Clear Lk Res., Willow Cr., Lower Klamath Lk., Tule Lk.; ^j Orr Lk., Res. F, Little Egg Lk., Round Valley Res. II, McCoy Flat Res.; ^k McCloud Res., Iron Canyon Res., Macumber Res., Bucks Lk.

The most common cyprinid taken by eagles at Almanor Reservoir was the tui chub (13% biomass, 12% prey numbers), a species native to most areas and introduced into the reservoir.

Sacramento sucker was a primary prey of Bald Eagles nesting on two reservoirs along the American and Eel rivers: Union Valley and Pillsbury Reservoirs (48% and 28% biomass, 36% and 30% prey numbers, respectively). Sacramento squawfish, introduced into the Eel River, was also a primary prey fish at Pillsbury Reservoir (32% biomass, 35% prey numbers). Our examination of scales in nest linings suggested that both eagle pairs took more salmonids than indicated by the bone samples. Eagles at both reservoirs captured more centrarchids (sunfish) than other California eagles (both 18% biomass and 14% numbers). All centrarchids identified in this study were introduced; the only sunfish native to California and taken by eagles, the

Sacramento perch, was planted in Almanor Reservoir.

Within the Lahontan system, our studies focused principally on Eagle Lake (Table 3). The native tui chub was the primary prey of Lahontan eagles (36% biomass, 44% of prey individuals), and we found some use of native Tahoe suckers (10% biomass, 5% prey numbers). Birds, especially grebes, were also important (42% biomass, 41% numbers).

At Clair Engle Reservoir on the Trinity River, we identified catfish as the primary prey of nesting Bald Eagles (58% biomass, 72% prey numbers). Salmonids and centrarchids were probably underestimated in our analysis as evidenced by the relatively high numbers of their scales found in nest linings. Prey remains and scale samples indicated no use of native suckers.

In the Klamath Basin, Lost River Bald Eagles relied mostly on birds (i.e., American Coots; 71%

biomass, 76% of prey numbers) and mammals (25% biomass, 12% prey numbers). Fish, including native suckers and tui chub, were used infrequently (5% biomass, 12% numbers).

Like the eagles at Lost River, those nesting at Basin and Trout-managed reservoirs also captured many birds, mostly anatids (62% and 63% biomass, 53% and 57% prey numbers, respectively) and mammals. In addition, Basin and Trout-managed reservoir eagles exploited catfish (brown bullhead, 17% biomass and 33% numbers) and salmonids, respectively. Statewide, salmonids were important prey to Bald Eagles only at these Trout-managed reservoirs (18% prey numbers, 10% biomass) and at Baum Lake near a trout hatchery (14% numbers, 9% biomass). Also, salmonid use by eagles was likely even greater at these reservoirs, judging from the large number of scales collected. Bald Eagles captured hatchery-released trout, as evidenced by tag recoveries at Macumber Reservoir and Eagle Lake nests.

Prey Selection and Eagle Productivity. To evaluate the relative ecological benefit to eagles of exploiting mostly native versus mostly introduced prey fishes, we compared the productivity of all Bald Eagle pairs nesting on the Pit River with that of eagles nesting on the Feather River. Prey selection of fish groups differed significantly between drainages ($\chi^2 = 633.8$, $df = 5$, $P < 0.001$): Pit River eagles consumed mostly native suckers and native cyprinids while pairs on the Feather River took mostly introduced catfishes and carp. Mean productivity during 1983–92 on the Pit River ($\bar{x} = 0.93$ young/occupied year, $N = 121$ occupied years in 14 territories, $SE = 0.08$) was nearly identical to that on the Feather River ($\bar{x} = 0.95$ young/occupied year, $N = 112$ occupied years in 16 territories, $SE = 0.08$; $t = 0.11$, $df = 231$, $P = 0.46$). The annual success rates (successful years/occupied years, 1983–92) for the two areas were also similar: 55% ($N = 121$, $SE = 5\%$) on the Pit River and 60% ($N = 112$, $SE = 5\%$; $t = 0.68$, $df = 231$, $P = 0.25$) on the Feather River.

DISCUSSION

Fisheries. Like other populations of Bald Eagles (Swenson et al. 1986, Hunt et al. 1992a), those nesting in northern California exhibited a high degree of versatility in exploiting prey types that varied within and between drainage systems. Several studies have positively correlated the abundance of fish (measured by gill-netting) in open water hab-

itats (i.e., estuary, reservoir and natural lake) with the diets of Bald Eagles (Gerrard and Bortolotti 1988, Mersmann 1989, Vondracek et al. 1989, Hunt et al. 1992c). We, however, did not sample fish populations for this study. Fish predominated in the diets of eagles at most locations, except in the Lost River area and at Basin and Trout-managed reservoirs. These reservoirs tended to be isolated from major river drainages and, hence, from large standing populations of fish. Many Basin Reservoirs periodically underwent drawdowns (e.g., from drought) with a resultant loss of fish. Past irrigation farming practices adversely affected native sucker populations in the Lost River system (Moyle 1976a). At Trout-managed reservoirs, salmonid populations were usually nonsustaining and were stocked annually. In these areas with depleted or unstable fish populations, eagles relied more on birds.

Overall, native fishes contributed substantially to the diets of California's Bald Eagles where exotics were absent (e.g., Eagle Lake), within regulated and unregulated riverine habitats (Hunt et al. 1992c), and where circumstances or adaptations allowed native fish to compete with introduced species within reservoirs. For example, pool fluctuations and low retention time due to hydroelectric operations of the relatively narrow Pit River reservoirs discourage spawning success and skew optimum temperatures for introduced centrarchids that prey on native fishes (Vondracek et al. 1989). By interviewing local fisheries biologists, we learned that native prey fish populations were relatively uncommon in reservoirs where eagles captured mostly exotics (R. Decoto, R. Flint, P. Chappel pers. comm.). Our research does not reveal how habitat modifications and reductions in native fish populations have affected Bald Eagles in a historical perspective.

Bald Eagles in California readily exploit the large populations of introduced fishes in reservoirs, and, indeed, most pairs (74%) are associated with reservoirs (Detrich 1989). Despite the destructive effects of carp on aquatic systems (Moyle et al. 1987), the species provided the greatest caloric contribution to breeding eagles overall, although they were not found as prey at many locations. Introduced species can fill human-created niches unsuitable for native fishes and thus provide prey for eagles in otherwise unsuitable habitat. For example, bullheads endure low temperatures and reduced oxygen conditions associated with low water

levels (Moyle 1976a), an adaptation allowing them to persist in intermittent or widely fluctuating water bodies such as Mountain Meadows Reservoir. Annual stocking of salmonids at higher elevation, oligotrophic lakes (e.g., Bucks Lake) no doubt increases foraging opportunities for Bald Eagles.

Management Issues. Historically, Bald Eagle management activities focused on manipulating forest stands and restricting human activities at breeding sites (Dzus and Gerrard 1993). Bald Eagle prey species are now being considered more frequently when alterations to fish fauna or hydrological systems and wetlands are contemplated. For example, Hunt et al. (1992c) provided flow recommendations which benefitted both Bald Eagle foraging and trout fishing on the regulated Pit River.

There has been concern that efforts to convert to or restore salmonid fisheries by poisoning non-game fishes with rotenone may depress Bald Eagle productivity. Poisoning of Macumber Reservoir (1977) was followed by two years of no production for the single pair of nesting Bald Eagles, then succeeded by 14 years of reproduction averaging 1.3 young per occupied year. More recently at Reservoir F and Frenchman Reservoir, both eagle pairs were successful for the two years subsequent to rotenone treatment (R. Jurek, G. Studinski pers. comm.). Certain conditions were implemented to limit impacts of these treatments to nesting Bald Eagles, including timing eradication outside the breeding season and the immediate and continued generous stocking of salmonids following eradication. Waterbirds were also readily available to eagles to supplement their diet. If managed properly, salmonid restoration apparently has minimal impact on Bald Eagle productivity.

Both natural and human-related factors such as spawning stress, powerhouse tailrace kills, reservoir fluctuations stranding fish, hatchery trout releases and angling mortality contribute to carrion availability, which eagles habitually exploit (Hunt et al. 1992c, Stalmaster and Plettner 1992). We periodically observed substantial numbers of dead fish floating in reservoirs, including suckers at Britton Reservoir (Hunt et al. 1992c) and bullheads at Mountain Meadows Reservoir, where each species was prominent in the prey of eagles nesting at those respective sites. Prior to altering existing operations at water facilities, managers should consider potential impacts on carrion availability for Bald Eagles.

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BALD EAGLE RESPONSE TO BOATING ACTIVITY IN NORTHCENTRAL FLORIDA

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ABSTRACT.—I examined the effects of weekend and weekday boating activity on Bald Eagle (*Haliaeetus leucocephalus*) use of three lakes in northcentral Florida during 1988–89. On Lake Lochloosa, which had the highest number of boats of the three lakes, boating activity significantly reduced the numbers of all age classes of eagles using the lake ($P < 0.025$). Increased boating activity on Lake Wauberg was not related to use by eagles ($P = 0.06$) likely because boating activity was concentrated during midday while eagles typically foraged early and late in the day. On Newnan's Lake, the number of eagles observed also was not different between weekends and weekdays ($P = 0.20$). Weekend boating activity did not relate to perch use, habitat use, interactions or age distribution indicating no alteration of eagle behavior patterns. Flush distance did not vary between weekends and weekdays ($P = 0.96$), but did vary by month ($P = 0.0001$), with a greater flush distance during months with highest boating activity. Minimal flush distances ($\bar{x} = 53\text{m}$) and lack of measurable effects on behavior suggested that eagles in my study area were tolerant of boat disturbance.

KEY WORDS: *Bald Eagle, Haliaeetus leucocephalus; boat disturbance, Florida; human activity.*

Respuesta de *Haliaeetus leucocephalus* a actividades de canotaje en el centronorte de Florida

RESUMEN.—Examiné los efectos de canotaje durante los fines de semana y durante la semana en águilas calvas (*Haliaeetus leucocephalus*) en tres lagos del centronorte de Florida durante 1988–89. En el lago Lochloosa el cual tiene el mayor número de botes de los tres lagos, las actividades de canotaje redujeron significativamente los números de todas las clases de edad de las águilas que utilizaron el lago ($P < 0.025$). El incremento en el canotaje del lago Wauberg no fué relacionado con el uso por parte de las águilas ($P = 0.06$), debido a que las actividades de canotaje se concentraron durante el medio día, mientras que las águilas forrajeaban temprano en la mañana o tarde durante el día. En el lago Newnan, el número de águilas observadas no fué diferente entre los fines de semana y entre semana ($P = 0.20$). Las actividades de canotaje durante el fin de semana no estuvieron relacionadas con la utilización de perchas, uso de habitat, interacciones o distribución de edades lo que indicó que no hubo alteraciones en los patrones de comportamiento de las águilas. Las distancias a las cuales las águilas levantaban el vuelo no variaron entre fines de semana y entre semana ($P = 0.96$), pero sí entre meses ($P = 0.0001$), con una mayor distancia de levantamiento de vuelo durante los meses con mayor canotaje. La distancia de levantamiento de vuelo mínima ($\bar{x} = 53\text{ m}$) y la falta de efectos medibles en el comportamiento sugieren que las águilas en mi estudio son tolerantes a la perturbación de los botes.

[Traducción de César Márquez]

Boating activity can modify foraging patterns of Bald Eagles (*Haliaeetus leucocephalus*) by reducing or even precluding use of foraging areas (Steenhof 1976, Stalmaster and Newman 1978, Knight and Knight 1984, Chester et al. 1990, McGarigal et al. 1991, Brown and Stevens 1997). McGarigal et al. (1991) concluded that boating activities restrict use of certain foraging areas by breeding eagles and ultimately may affect productivity. Since Bald Eagles are easily disturbed when foraging (Grubb and King 1991) and adults are more sensitive to distur-

bance than younger eagles (Stalmaster and Newman 1978), increasing recreational use of lakes in Florida may pose problems for breeding eagles. In addition, the dense eagle population in Florida that exists in close proximity to high levels of human activity provided an opportunity to determine if eagles habituate to human activity.

I conducted a study to examine the effects of boating activity on the use of lake shorelines by Bald Eagles and addressed the following objectives: (1) to determine if the number of Bald Eagles ob-

Table 1. Mean number of Bald Eagles and boats on weekend (WE) and weekday (WD) counts on shoreline surveys of three lakes in northcentral Florida, 1988 and 1989.

LAKE	YEAR	N ^a	NUMBER OF EAGLES				NUMBER OF BOATS			
			\bar{x} WE (RANGE)	\bar{x} WD (RANGE)	<i>t</i>	<i>P</i>	\bar{x} WE (RANGE)	\bar{x} WD (RANGE)	<i>t</i>	<i>P</i>
Lochloosa	1988	10	3.2 (0-10)	6.1 (1-10)	-3.36	0.005	28.7 (4-50)	5.8 (4-31)	4.06	0.005
	1989	10	6.9 (0-11)	10.6 (3-20)	-2.38	0.025	17.9 (12-24)	7.8 (3-16)	5.37	0.005
Newnans	1988	12	4.2 (1-11)	5.3 (1-9)	-0.95	0.20	18.5 (5-36)	11.5 (2-23)	5.02	0.005
	1989	12	8.2 (3-20)	8.3 (2-14)	-0.19	0.30	8.6 (2-16)	5.5 (0-13)	2.94	0.01
Wauberg	1988	10	2.5 (1-6)	4.2 (0-11)	-1.66	0.06	6.7 (1-19)	3.5 (0.10)	1.61	0.06
	1989	14	5.6 (1-11)	6.1 (1-11)	-0.43	0.25	12.8 (2-32)	4.7 (0-8)	3.08	0.01

^a N = number of paired surveys.

served on a shoreline differed between high and low boat use days, (2) to determine if differences existed in response to boat disturbance by different age classes of eagles, (3) to determine if distance perched from the shoreline or distance flushed by a boat differed between high and low boat use days, and (4) to determine if differences in activity, habitat use, perch use, or interactions occurred between high and low boat use days.

STUDY AREA AND METHODS

Data on effects of boating activity on eagles were obtained at Lochloosa, Newnans, and Wauberg lakes in Alachua County, Florida. Lochloosa and Newnans lakes are large fishing lakes in the region and the majority of boating activity involved fishing from stationary boats. Wauberg is a small lake with restricted access for gasoline-powered boats but heavily used for recreational activities, primarily canoeing, sailboating, and occasionally fishing from small boats equipped with electric motors (Wood 1992). Newnan's Lake is a hyper-eutrophic lake of 2433 ha (Shannon and Brezonik 1972) with a mean depth of 1.5 m (maximum = 4.0 m). Lake Lochloosa is a 2235 ha meso-eutrophic lake with a mean depth of 2.9 m. Lake Wauberg is a 101-ha eutrophic lake with a mean depth of 3.8 m (maximum = 5.2 m). The lakes are rimmed primarily with baldcypress (*Taxodium distichum*) and hardwood swamps with adjacent pine (*Pinus* spp.) forests.

Lakes were surveyed every 2 wks on Sundays and Mondays from 28 February-9 May 1988, and on Sundays and Tuesdays from 11 December 1988-4 April 1989, to compare days with high human use (Sundays) to low-use days (weekdays). On Newnans and Lochloosa lakes, we surveyed a route of approximately 7 km from a johnboat by driving slowly (about 3-5 knots) approximately 100 m from the shoreline. Because Wauberg Lake is much smaller, we surveyed the entire shoreline from an anchored boat at the center of the lake. Each sampling day was divided into morning, midday, and late-day and a sampling schedule was devised so that each lake rotated through these periods throughout the season. On a given sampling day, we conducted 6 surveys; 2 successive surveys were conducted on a lake before moving to the next lake. We began the first survey shortly after dawn, and

finished the last of 6 surveys near dusk. We began each of the 6 surveys at the same time on the two paired sample days.

Data recorded for each eagle observed included location, age class, activity, habitat, perch type, distance perched from edge, interactions, and with whom the interaction occurred. Age classes were based on plumage characteristics (McCullough 1989) and included adults (all white head and tail), late subadults (some brown in head and tail), early subadults (no white in head or tail), immatures (first year eagles), subadults (birds that could not be classed as early or late), and unknowns. Locations of eagles and boats were plotted on topographic maps. In 1989, the distance from our boat at which a perched eagle flushed was estimated with periodic verification using a Lietz range finder.

I first determined the sample size needed to test the hypothesis that boating activity was reducing eagle use of lakeshores using the prespecified variance method (Gilbert 1987:51-52). Data were analyzed separately for 1988 and 1989 for each lake with a paired difference *t*-test to avoid problems with temporal changes in eagle and boat abundance.

I used a *t*-test to examine the effect of boating activity on the distance eagles perched from the edge of the shoreline and on the estimated flush distance. Analysis of variance was used to examine month and age variations in flush distance. I used χ^2 contingency tests (Winkler and Hays 1975: 825-829) to examine the distributions for age of eagles observed, habitat use, perch types, activity, and interactions on weekends versus weekdays.

RESULTS

On Lochloosa Lake, boats were more abundant on weekends than on weekdays in both years (Table 1), while more eagles were observed on weekdays than on weekends. The maximum number of boats generally was greater in 1988, while the highest maximum number of eagles occurred in 1989. Likewise on Newnans Lake, boats were more abundant on weekends than on weekdays in both years (Table 1), although the mean difference was not as large in 1989. The number of eagles observed

Table 2. Mean distance (m) Bald Eagles were perched from the edge of the shoreline (1988 and 1989) and flush distance (1989) on weekdays (WD) and weekends (WE) during shoreline surveys of Lochloosa, Newnans, and Wauberg lakes in northcentral Florida.

VARIABLE	<i>N</i> ^a	\bar{x}	SE	RANGE	<i>t</i>	<i>P</i>
Distance to edge						
WD	256	5.6	0.56	0-50	-2.52	0.01
WE	193	8.5	0.99	0-75		
Flush distance						
WD	32	53.9	12.32	5-200	0.05	0.96
WE	27	52.9	12.73	5-200		

^a *N* = number of Bald Eagle observations.

was not significantly different on weekdays than on weekends in either year. Maximum counts of boats were lower on Newnans Lake in 1989 compared to 1988, but maximum counts of eagles were higher. Fewer boats may affect a smaller portion of the shoreline available to eagles. On Lake Wauberg, there was no difference in the number of boats or eagles observed on weekends versus weekdays in 1988 (Table 1). In 1989, more boats were observed on weekends, but the number of eagles observed did not differ.

Of 816 eagles observed, the majority (47.9%) were adults. The age distribution of eagles sighted on weekends did not differ from that on weekdays ($\chi^2 = 4.01$, $P = 0.55$). Weekend boating activity, therefore, was related to eagle numbers regardless of age class. Eagles perched farther from the shoreline edge on weekends (Table 2) when boating activity was higher than on weekdays with less boating activity, although the difference was only 3 m.

Of 517 eagle sightings in 1989, eagles flushed in response to our boat in 59 instances. Flush distance did not differ between weekends and weekdays (Table 2), but differed by month (Table 3; $F = 10.46$, $P = 0.0001$). Eagles were flushed by boats at a greater distance in January and February, when boating activity typically increased with winter tourism. Flush distance did not differ by age class ($F = 1.23$, $P = 0.32$).

During the shoreline surveys, I identified five types of perches: snags, pines, cypress, hardwoods, and palms. There was no difference in the distribution of eagles using these perch types on weekends (high boat use days) compared to weekdays ($\chi^2 = 5.74$, $P = 0.33$). The majority of the 489

Table 3. Number of flushes (*N*) and mean estimated flush distance (m) by month for Bald Eagles sighted on shoreline surveys of Lochloosa, Newnans and Wauberg lakes in northcentral Florida, 1989. Means with the same letter are not significantly different (Waller-Duncan K-ratio *t*-test).

MONTH	<i>N</i>	\bar{x}	SE	RANGE
December	5	5 B	0.0	5-5
January	13	80 A	21.9	5-200
February	20	99 A	14.2	5-200
March	5	5 B	0.0	5-5
April	13	5 B	0.0	5-5
May	3	5 B	0.0	5-5

sightings of perched birds occurred in cypress (51.9%) or hardwood (21.1%) trees.

I also distinguished six habitat types used by eagles: cypress, hardwood, pinewoods, marsh, lake, and developed (Wood 1992). Eagles used these habitats in the same proportion on weekends as on weekdays ($\chi^2 = 3.85$, $P = 0.57$). The most frequently used habitat was cypress (46%). Pinewoods (22%) and lake (21%) also were commonly used habitats but only 21 (3%) eagles occurred in developed habitats.

Six categories of interactions were observed and involved 332 sightings of eagles: chasing or being chased (31%), perched together (44%), flying together (20%), and stooping on, hitting, and talon locking (5%). Because of small sample sizes, stooping on, hitting, and talon locking were combined into one category for analysis purposes. Boating activity did not change the distribution of eagles engaged in the various interactions ($\chi^2 = 3.56$, $P = 0.31$).

DISCUSSION

Boat and eagle numbers were negatively related on Lochloosa Lake with boat use highest on weekends and eagle use highest on weekdays. On Newnans Lake, the mean difference in the number of boats was not as large as that observed for Lochloosa Lake, particularly in 1989. The small difference in boating activity between weekends and weekdays, although significantly different, may not have been a true measure of boating effects on eagles because of the overall low number of boats present. On Newnans Lake, the maximum number of boats counted on the 7-km segment of shoreline (1988 = 36, 1989 = 16) was much less than on

Lochloosa Lake (1988 = 50, 1989 = 24). There may be a threshold number of boats required on a lake before eagles avoid an area. In contrast, McGarigal et al. (1991) reported a reduction in the use of highly used foraging areas in response to a single stationary boat.

No relationship was detected between boat and eagle numbers on Lake Wauberg. Because this lake is used primarily for recreational activities other than fishing (sailing and canoeing), boat disturbance is concentrated during early afternoon with little disturbance in the early morning and late evening. This allowed eagles to forage undisturbed on the lake for several hours when foraging by eagles generally reaches a peak (Mersmann 1989). Further, Lake Wauberg has restricted access for boats powered with gasoline engines, so disturbance created by a fishing boat is less than that on other lakes. The type of boat and timing of boating activity both can affect response by eagles (Grubb and King 1991, Grubb et al. 1992, Stalmaster and Kaiser 1998).

Human disturbance could at times alter behavior patterns or differentially affect individual age classes (Stalmaster and Newman 1978). In my study, boating activity did not affect eagle activity, perch use, habitat use, interactions, or the age distribution of eagles observed. Thus, eagles likely were not displaced from preferred perching or foraging areas and were not differentially affected by age class.

In my study, flush distance did not differ between weekends and weekdays. In contrast, Stalmaster and Kaiser (1998) found shorter flush distances on weekends. I generally found that when eagles responded to boat disturbance the primary response was to avoid the lakes. Similarly, Steenhof (1976) and McGarigal et al. (1991) found that it was more common for eagles to entirely avoid areas where boats were present. I found no difference in flush distance between age classes. Knight and Knight (1984) and Buehler et al. (1991) reported no age-specific differences in flush distance, whereas Stalmaster and Kaiser (1998) detected longer flush distances by subadults. Stalmaster and Newman (1978) reported that adults were more sensitive to disturbance than younger eagles and preferred areas with lower human activity.

Mean flush distance of 53 m was less than that reported in other studies (Knight and Knight 1984: 152 m; Buehler et al. 1991: 175 m in summer and

265 m in winter; McGarigal et al. 1991: 197 m; Stalmaster and Kaiser 1998: 111–293 m). Buehler et al. (1991) suggested that the difference in winter and summer flush distances observed on the Chesapeake Bay might be a difference in response by the northern migrant eagles inhabiting the Chesapeake in the winter, compared to the southern migrants and Chesapeake eagles present in summer. Because flush distance in my study was very low, particularly after high boat disturbance in January and February, it is possible that eagles habituated to boat disturbance in Florida which contributed to the low summer flush distance observed on the Chesapeake Bay. Knight and Knight (1984) reported a decreased tendency for eagles to flush in response to a canoe, but could not conclusively attribute the response to habituation. Stalmaster and Kaiser (1998) found decreased flush responses over the winter season, but no change in flush distances suggesting some habituation to disturbance.

In summary, boating activity reduced the number of eagles using the shoreline on only one of the three lakes studied, did not influence flush distance, and increased the distance perched from the shoreline by only 3 m. Thus, at this time, there was no evidence that recreational boating activity negatively affected eagle use of these lakes. The minimal flush distances and the lack of measurable effects on eagle behavior and activity patterns suggested that many of these birds may have become habituated to boating disturbance, although they still show some avoidance behavior.

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THE GOLDEN EAGLE (*AQUILA CHRYSAETOS*) IN THE BALÉ MOUNTAINS, ETHIOPIA

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ABSTRACT.—We studied Golden Eagles (*Aquila chrysaetos*) in the afro-alpine area (elevation 3500–4000 m) of the Balé Mountains in Ethiopia. We monitored seven territories from 1–5 successive years for a total of 26 territory-years. Home ranges varied from only 1.5–9 km², the smallest size recorded for the species. This was probably due to the abundance of prey, mainly hares and grass rats, that made up 50% and 30% of prey, respectively. Despite this, productivity of these Golden Eagles was quite low averaging only 0.28 young per occupied territory ($N = 25$). This was due to a large number of unmated territorial adults and poor breeding performance by pairs (0.4 young per pair per year, $N = 17$). The high density and frequent interspecific interactions with Verreaux's Eagles (*Aquila verreauxii*) were key factors affecting the dynamics of this Golden Eagle population. The unusual coexistence of these two closely related species was a novel component of the rich predator guild in the area that included five other wintering or resident eagle species. This richness was related to the high density of rodents and lagomorphs, a characteristic of the Ethiopian afro-alpine ecosystem.

KEY WORDS: *Golden Eagle*; *Aquila chrysaetos*; *Verreaux's Eagle*; *afro-alpine habitats*; *Ethiopia*; *prey abundance*; *interspecific competition*; *productivity*.

El águila dorada (*Aquila chrysaetos*) en las montañas Balé de Etiopía

RESUMEN.—Estudiamos el águila dorada (*Aquila chrysaetos*) en el área afro-alpina (elevación 3500–4000 m) de las montañas Balé en Etiopía. Monitoreamos siete territorios de 1–5 años continuos para un total de 26 territorios/año. Los rangos de hogar variaron entre 1.5–9 km². Los más pequeños reportados para la especie. Esto probablemente debido a la abundancia de presas, principalmente liebres y ratas de pastizales, las cuales representan el 50% y el 30% de las presas respectivamente. A pesar de esto la productividad de las águilas fue muy baja con un promedio de 0.28 juveniles por territorio ocupado ($N = 25$). Esto se debió al gran número de adultos territoriales sin pareja y al pobre desempeño reproductivo de las parejas (0.4 juveniles por pareja por año, $N = 17$). La alta densidad y las frecuentes interacciones intraespecíficas con las águilas Verreaux (*Aquila verreauxii*) fueron factores que afectaron la dinámica de esta población de águilas doradas. La inusual coexistencia de estas dos especies estrechamente relacionadas es un componente novedoso de la estructura de depredadores en el área que incluye otras cinco especies migratorias o residentes de águilas. Esta riqueza estuvo relacionada con la alta densidad de roedores y lagomorfos, una característica del ecosistema afro-alpino Etíope.

[Traducción de César Márquez]

The recent discovery of a Golden Eagle (*Aquila chrysaetos*) population in Ethiopia (Clouet and Barrau 1993) has provided a unique opportunity to study this species in a new biogeographical area. The population occurs in the Balé Mountains located in the southern part of the Ethiopian high plateau, east of the Rift Valley. It occurs at the afro-

alpine region which supports the largest mountain moorland and grassland habitat on the continent. This rich and unique ecosystem (Dorst and Roux 1972, Hillman 1986) supports an avian community dominated by a predator-scavenger guild (Clouet et al. 1995). The Golden Eagle is part of a unique assemblage of eagle species and coexists with the

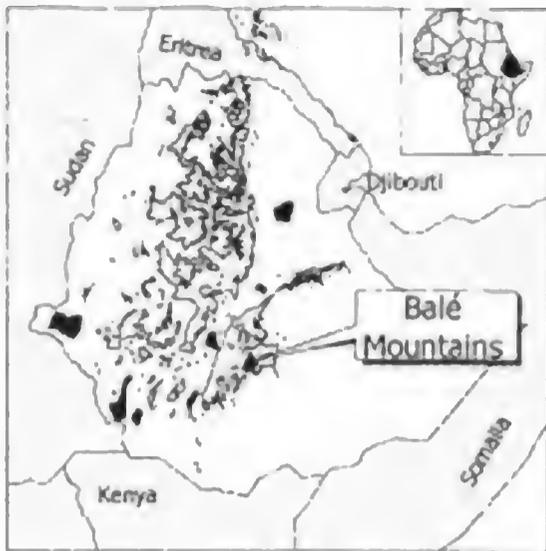


Figure 1. Location of the Balé Mountain study area in Ethiopia.

Verreaux's Eagle (*Aquila verreauxii*). To our knowledge, this assemblage that includes the southernmost extent of the Golden Eagle has never before been studied.

STUDY AREA AND METHODS

The study area was in Balé Mountains National Park in the upper Web River Valley and a portion of its tributaries above tree line (3500–4000 m) (Fig. 1). The area consists of a continuous network of cliffs stretching from the north bank of the Web River to the top of the Massif (Sanetti plateau). The afro-alpine habitat has a tropical climate tempered by the altitude and characterized by an alternating wet season that lasts from March–October and a dry season that lasts from November–February.

We searched for breeding raptors in a 200 km² area of potential nesting and hunting habitat over the course of seven expeditions covering five successive breeding seasons: August 1993, May 1994, March–November 1995, March 1996, and February–August 1997. One to three observers walked transects through Golden Eagle territories. Observations were made continuously for periods of 2–11 hr, recording the activities of the eagles and any interspecific behavior involving other raptors species. All eagle flights were plotted on a map to calculate their distances and areas covered. The total observation time for the seven expeditions was 210 h.

We estimated diet by observing kills and collecting prey items in nests during the fledging period. Diet diversity was calculated using a Shannon Index (Delibes et al. 1975, Clouet 1981, Fernández 1991). Productivity (number of young per occupied territory) was calculated by observing young in nests that were older than 51 d of age (Steenhof 1987) (except in one case when a nestling was only about 35-d old) or in flight with adults during the postfledging stage (August 1993, May 1994, and August 1997).

RESULTS

We identified seven territories occupied by Golden Eagles. We assumed that territories were centered on the occupied nest or, when the pair was

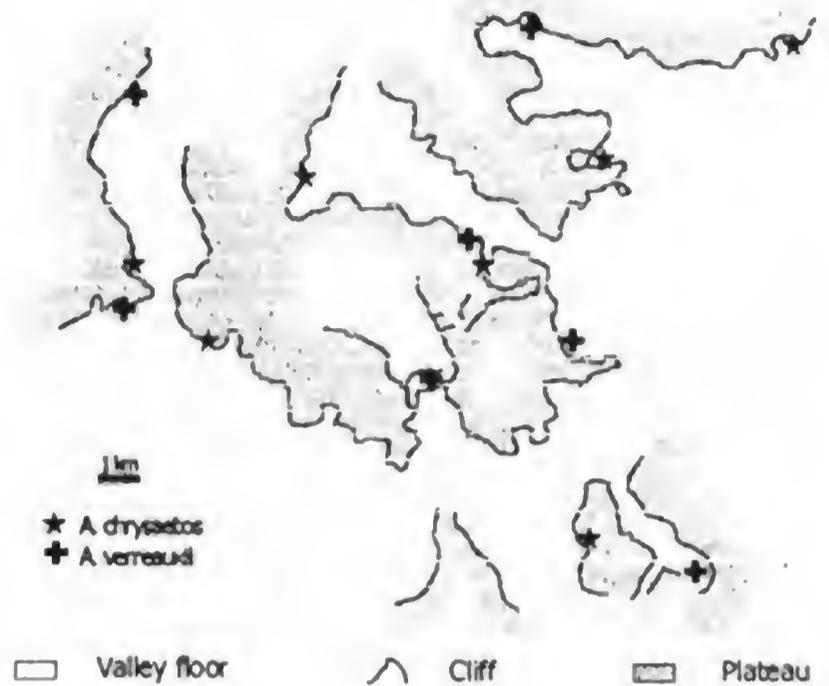


Figure 2. Distribution of Golden and Verreaux's Eagles in the 200-km² study area in the Balé Mountains National Park, Ethiopia, 1993–97.

not breeding or when it was occupied by an unpaired bird, we used the arithmetic center of the known unoccupied nests in the territory. The average distance between centers was 4.7 km (range = 2.5–7 km) (Fig. 2). Individual territories were monitored for 1–5 yr totaling 26 territory-years (Table 1). Single adults were observed in three out of the seven monitored territories and during 4 of the 5 yr of the study (i.e., seven (27%) of the 26 territory-years). Nonterritorial single birds were recorded only twice (1 adult and 1 immature eagle).

Topographically, the territories included a section of cliff where perches and nests were located and a part of the neighboring plateau. The slope located at the foot of the cliff was comprised of scree, grassland, and bushes, and it provided a variety of potential prey including hyraxes (*Procapra capensis*), hares (*Lepus strarki*), and francolins (*Francolinus* spp.). In the valley bottom, there were also colonies of mole rats (*Tachyoryctes macrocephalus*) and grass rats (*Arvicanthis* spp. and *Lophuromys* spp.).

We observed nine successful kills by Golden Eagles. All were made either on low altitude flights by eagles close to the slopes at the foot of cliffs (once) or within 200–2000 m of perches (eight times). Golden Eagles were also seen robbing prey from an Augur Buzzard (*Buteo augur*), Pallid Har-

Table 1. Territory occupancy and productivity of Golden Eagles in the Balé Mountains National Park, 1993–97.

YEAR	TERRITORY			
	1	2	3	4
1993 (6–13 August)	Single adult	Adult pair 1 young flying	Single adult	—
1994 (5–17 May)	Adult pair	Adult pair	Adult pair	Single adult
1995 (21 March–5 April)	Single adult	1 young flying Adult pair	Adult pair	Single adult
1996 (4–15 March)	Single adult	Adult pair	Adult pair	Single adult
1997 (3–12 February) (9–18 August)	Adult pair	Adult pair	Adult pair 1 5-wk-old young	Adult pair

rier (*Circus macrourus*), Lanner Falcon (*Falco biarmicus*), and Steppe Eagle (*Aquila nipalensis*).

Undulating display flights and attacks on intruders of other raptor species were performed by both paired or unpaired Golden Eagles, both near and ≤ 1 km from perches, cliffs and nests. In the case of one unpaired territorial adult, undulating flights accounted for up to 51% of the total flying time (115 min) in November at the beginning of the breeding season suggesting that the function of this flight was to display its territory.

The mean area of the home ranges, estimated from observations of hunting forays and territorial flights, such as undulating displays and attacks on intruders, was 3.6 km² (range = 1.5–9 km², $N = 7$). Home ranges were smaller for single adults (1–1.5 km², $N = 2$) and appeared to be larger where there was no rodent colony or where scrub (*Erica* spp.) was extensive (estimated to be about 9 km²).

Observations of kills ($N = 9$) and identification of prey items brought to nests ($N = 41$) showed a predominance of mammals which accounted for 86% of the prey: 25 hares (50%), 3 hyraxes (6%), 2 giant mole rats (4%), 13 grass rats (26%), 5 *Arvicanthis blicki* (10%), 1 *Lophuromys melanonyx* (2%), and 7 unidentified prey (14%). Small species were probably underestimated because they were often entirely consumed by eagles. Birds accounted for a smaller part of the diet (14%): 4 Moorland Francolins (*Francolinus psilolaemus*, 8%), 2 Blue-winged Geese (*Cyanochen cyanopterus*, 4%), and 1 unidentified bird. Mammals accounted for 90% of the total prey biomass and hares alone made up 78% of the biomass.

Other breeding raptors were observed in every Golden Eagle territory we observed, including one or two pairs of Augur Buzzards, one pair of Lanner Falcons and one pair of Common Kestrels (*F. tinnunculus*). Frequent mobbing behavior of these raptors triggered attacks by eagles. We observed Tawny Eagles (*A. rapax*) which were residents throughout the year and Greater Spotted Eagles (*A. clanga*), Lesser Spotted Eagles (*A. pomarina*), and Steppe Eagles which were either migrating through or spent the winter in the area flying over Golden Eagle hunting areas. The latter were very numerous and on several occasions approximately 30 were recorded simultaneously in flight in February. Steppe Eagles were observed attacking Golden Eagles on their prey (3 cases). Golden Eagles were also seen chasing off intruding Tawny and Steppe Eagles (3 cases).

The survey area contained seven territories of Verreaux's Eagles, all occupied by pairs. All pairs raised at least one young during the study period. The average distance between occupied nests was 5.2 km (range = 3–7 km). Observations at six territories showed that Verreaux's Eagles traveled from 12–13 km² on hunting forays and territorial flights and they established common boundaries between their territories. The mean distance between the nearest occupied nest or territory center of a Golden Eagle and a Verreaux's Eagle was 3.4 km ($N = 12$, range = 0.65–6.0 km). Territories of the two species were mutually exclusive. Interactions we recorded most often were attacks by Golden Eagles on Verreaux's Eagles ($N = 21$). Only one attack by a Verreaux's Eagle on a Golden Eagle was

Table 1. Continued.

TERRITORY		
5	6	7
—	—	—
Adult pair	—	—
1 10-wk-old young	—	—
Adult pair	—	—
1 7-wk-old young	—	—
Adult pair	—	—
1 7-wk-old young	Adult pair	—
Adult pair	1 9-wk-old young	—
incubating	Adult pair	Adult pair
1 young flying with adults	—	—

observed and it involved an attempted piracy at the boundary of two territories.

We recorded three types of behavior by the Golden Eagle toward Verreaux's Eagles ($N = 26$). One behavior we classified as tolerance. It occurred when one or a pair of Verreaux's Eagles flew at high altitudes (>500 m) ($N = 5$) above Golden Eagles. However, we observed birds of each species perched out of sight of each other on the same cliff at distances of <400 m. Flight and undulating display flight behaviors were triggered by a Verreaux's Eagle approaching within 500–1000 m of a Golden Eagle nest or perch ($N = 7$). Aggressive flight behavior toward an intruding Verreaux's Eagle occurred when the intruding eagle came within 500 m of an occupied nest or perch used by a Golden Eagle ($N = 14$). Aggressive flights usually ended when the intruder withdrew. In two cases, the interaction resulted in grappling of talons.

The most frequent and most intense interspecific

encounters observed occurred when two Golden Eagle territories were located between two Verreaux's Eagle territories and where inter-nest distances were short. In this situation, the number of Golden Eagle flights per hour of observation (38 hr) was 1.74. Territory defense flights and undulating flights made up 32% and 24% of all flights ($N = 66$), respectively. When the species were farther apart ($N = 4$ territories), the number of flights per hour of observation (44 hr) was 1.98 and the number of undulating flights accounted for only 6% of the total number of flights observed ($N = 87$).

Golden Eagles began building nests in November and unsuccessful breeding pairs often continued building until February. We observed five nests containing a single eaglet between March and May and immatures were seen flying together with adults in May and August (Table 1). Judging from the age of the young we observed, we estimated that laying occurred from mid-November to mid-January, and that fledgling occurred from mid-March through the end of May. The beginning of the breeding season corresponded with the beginning of the dry season and the young left the nest at the beginning of the rainy season. This phenology corresponded to the breeding seasons of most other nesting raptors in the Balé Mountains. The nesting season for Verreaux's Eagles started a few weeks earlier than that of Golden Eagles and the first females began incubation in November. Young Verreaux's Eagles left their nests from March–June. Productivity of Golden Eagles was 0.42 young per territorial pair per year ($N = 19$, Table 2).

DISCUSSION

Our observations of Ethiopian Golden Eagles showed similarities with holarctic populations but

Table 2. Golden Eagle productivity in the Balé Mountains National Park and locations of neighboring Verreaux's Eagles.

TERRITORY	YEARS OF STUDY	PRODUCTIVITY (YOUNG/YEAR)	DISTANCE FROM NEIGHBORING VERREAUX'S EAGLE PAIR(S) (km)	LOCATIONS OF NEIGHBORING VERREAUX'S EAGLE PAIR(S)
2	5	0.40	2.7	different valley
3	4	0.25	0.65	same cliff
			3.0	same valley
5	3	1.0	1.2	different valley
			4.0	same valley

differed in terms of their use of space, population regulation, and the type of predator community into which they integrated. Even though our prey sample was limited, Ethiopian Golden Eagles appeared to select terrestrial prey of similar size to that taken by Golden Eagles in European and North American populations (Brown and Watson 1964, Murphy 1975, Delibes et al. 1975, Clouet and Goar 1980, Haller 1982, Steenhof and Kochert 1988, Fernández and Purroy 1990). The number of small-sized prey (<2 kg) such as grass rats, which was likely underestimated by our sampling method, showed that these Golden Eagles were opportunistic predators taking small prey items when they became available in sufficient quantities (Delibes et al. 1975, Fernández 1991, Watson et al. 1993). Because hares were predominant prey, diet diversity was low ($H' = 1.44$) in comparison with Golden Eagles in the Pyrénées ($H' = 2.77$) (Clouet 1981).

The density of Golden Eagles in the Balé Mountains matched the highest figures recorded in the western highlands of Scotland (one pair per 38 km², Watson et al. 1992) and in North America (one pair per 29–36 km², Phillips et al. 1990). The home range size we recorded was the smallest reported for the species.

In Europe, territory size can range from 40–160 km² (Clouet 1988). In the Swiss Alps, the home range of four breeding pairs ranged from 22–48 km², and core areas used for hunting that ranged from 6–16 km² (Haller 1982) were larger than the areas used in Ethiopia. Variation in density between different areas in Europe was associated with food availability (Tjernberg 1985, Watson et al. 1992). The home range size documented in North America was influenced by the amount of favorable prey habitat and became smaller where high quality prey habitat was abundant (Dixon 1937, Collopy and Edwards 1989, Marzluff et al. 1997). The abundance of prey and its availability throughout the year in the Balé Mountains was probably an important factor in explaining the high density and the small home ranges we observed. Both hares and rodents occurred in high numbers in the afro-alpine moorland and grassland of the Balé Mountains. Their abundance was estimated by Gottelli and Sillero-Zubiri (1990) during their study of the Ethiopian wolf (*Canis simiense*). Hare density was 32 individuals/km² for a biomass of 120 kg/km². The biomass of mole and grass rats was estimated at 3000–4000 kg/km² (Gottelli and Sillero-

Zubiri 1990). These values are more than 20 times the available biomass of rodents above the tree-line on the northern slopes of the Pyrénées where the size of Golden Eagle territories is roughly 20 times larger than in Ethiopia (Clouet 1991).

Prey abundance influences breeding performance both in Europe and in North America (Murphy 1975, Smith and Murphy 1979, Clouet 1981, Haller 1982, Thompson et al. 1982, Tjernberg 1983, Jenny 1992, Watson et al. 1992, Steenhof et al. 1997). Productivity of Golden Eagles ranging from 0.79–0.82 young per territorial pair per year have been reported in long-term studies in North America (Phillips et al. 1990, Bats and Moretti 1994, Steenhof et al. 1997). Productivity has been lower in most European studies ranging from 0.48–0.53 young per territorial pair per year in the Alps (Haller 1996) and Pyrénées (Clouet 1988). Watson (1997) found a significant negative correlation between breeding success and diet diversity. Where Golden Eagles had a narrow feeding niche they tended to breed more successfully than where the niche was broad. In Ethiopia, despite high prey abundance and low diet diversity, productivity was low. This was probably due to the fact that territorial pairs did not breed successfully every year and only raised a single eaglet per brood and, in some years, certain territories were occupied by only single adults (27% of the total 26 territory-years studied). The latter may have resulted from a lack of surplus birds in the population. Surplus birds have often been noted in Golden Eagle populations (Haller 1982, 1996, Marzluff et al. 1997) and can compose up to 30% of the population in the Alps (Clouet and Couloumy 1994). The lack of surplus birds in the Balé Mountains could have been due to human persecution, but we have no data to support this. It may also have been due to the absence of recruitment of individuals from outside the Balé Mountain range. Because the population is sedentary, there is little opportunity for interaction with populations located 2000 km further to the north (Thiollay and Dhautois 1976). No Golden Eagles have been observed on the banks of the Red Sea during migratory movements (Bruun 1985, Welch and Welch 1989). Finally, insufficient productivity could explain the absence of surplus birds. Our estimated 0.42 young fledged per territorial pair per year is very low for a Golden Eagle population. In other African eagle populations, breeding success is not related to food availability but is highly density de-

pendent (Thiollay and Meyer 1978, Gargett 1977, 1990, Simmons 1993). The effect of density has also been documented in Golden Eagle populations in Europe (Haller 1982, 1996, Jenny 1992). The reduced productivity (0.48 young per pair per year) recorded in the Swiss Alps has been interpreted as the consequence of a density-dependent regulation process. The major limiting factor in breeding success in the Alps is the frequency of interactions with unpaired nonterritorial surplus birds causing a negative feedback effect. Regular interactions with settled birds increases the proportion of nonbreeding pairs and depresses successful incubation (Haller 1982, 1996, Jenny 1992). Perhaps, in the Balé Mountains, interactions between Verreaux's and Golden Eagles have the same negative effect on reproduction as surplus Golden Eagles in the Alps. Productivity of Golden Eagle pairs appeared to be influenced by the proximity of neighboring Verreaux's Eagle pairs. For the closest nests (650 m apart on the same cliff), neither species succeeded in breeding simultaneously. Such interactions with other species of eagles are exceptional, making the situation in Ethiopia rather unique.

Golden Eagle coexistence with other eagle species such as with Bonelli's Eagles (*Hieraaetus fasciatus*) has been reported in the Mediterranean region. Apparently, the two species become ecologically isolated through their territoriality and diets (Brosset 1961, Cheylan 1977, Jordano 1981, Clouet and Goar 1984, Parellada et al. 1984, Fernández and Insausti 1986, Bahat 1989). In Israel, apparently competition between the two species results in a lower density of Golden Eagles in areas where Bonelli's Eagles are abundant and where both species maintain exclusive home ranges (Bahat 1989).

In Ethiopia, the Golden Eagle is integrated into the largest eagle assemblage known which includes five other *Aquila* species. Here, ecological isolation between Tawny Eagles (resident) and Steppe, Lesser, and Greater Spotted Eagles (winter only) develops through specialized use of habitat (less rocky than that of the Golden Eagle), temporal separation of breeding periods and partly through diet. The Verreaux's Eagle is morphologically and ecologically very similar to the Golden Eagle and it is generally regarded to be its African equivalent. Both species are of similar size, have a similar predation potential (Voous 1970, Brooke et al. 1972), feed on terrestrial prey, use similar nesting habitat

and breed at the same time of the year. Evidently, the two species escape from interspecific competition by establishing mutually exclusive ranges and they use undulating display flights to advertise their territory boundaries (Harmata 1982, Collopy and Edwards 1989). The only niche parameter which actually distinguishes the two species is diet. Dietary studies in Africa show that Verreaux's Eagles prey almost exclusively on rock hyraxes which represent up to 98% of their food intake (Brown et al. 1982, Gargett 1990). The prey remains that we collected under Verreaux's Eagle nests confirmed that hyraxes also predominate in the diet of Verreaux's Eagles in the Balé Mountains. On the other hand, hyraxes represented only a very small part of the diet of Golden Eagles.

We believe that the unusual coexistence of Golden and Verreaux's Eagles is possible because the Ethiopian afro-alpine region supports a rich and dense rodent community (Yalden 1988) that makes possible the assemblage of the most diverse guild of raptors ever found at such a high altitude.

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SELECTION OF NEST CLIFFS BY BONELLI'S EAGLE (*HIERAAETUS FASCIATUS*) IN SOUTHEASTERN SPAIN

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ABSTRACT.—A total of 119 nests and 52 cliffs occupied by 32 Bonelli's Eagle (*Hieraaetus fasciatus*) pairs was studied during 1995–97 in southeastern Spain. Mean number of nests built by pairs exceeded that reported in previous studies ($\bar{x} = 3.7$; $N = 32$) and there was a trend among eagles to build their nests with a southeastern orientation. Breeding density was directly related to the availability of cliffs. Eagles occupied higher cliffs ($\bar{x} = 52.9$ m; $N = 32$), located on steeper slopes ($\bar{x} = 34.7^\circ$; $N = 31$) than was available. Occupied cliffs were highly heterogeneous due to the fact that use of different areas by Bonelli's Eagles was dependent on human disturbance. Thus, occupied cliffs with the shortest linear distance to paved roads were higher than occupied cliffs far from paved roads. Selection of high cliffs located on steep slopes with southern orientations may have been associated with the additional lift provided eagles, since these types of nest sites enhanced the possibility of thermal and slope soaring. Preservation of nest cliffs free from disturbances should be undertaken to ensure the survival of Bonelli's Eagle in this area of Spain.

KEY WORDS: *Bonelli's Eagle*, *Hieraaetus fasciatus*; *southeastern Spain*; *cliff selection*; *breeding density*.

Selección de los roquedos de nidificación del Águila Perdicera (*Hieraaetus fasciatus*) en el Sureste de España

RESUMEN.—119 nidos y 52 roquedos ocupados por 32 parejas de Águila Perdicera (*Hieraaetus fasciatus*), fueron analizados en el periodo 1995–97 en el sureste de España. El número medio de nidos construidos por pareja fue mayor que el descrito por otros autores ($\bar{x} = 3,7$; $N = 32$). Los resultados revelan una tendencia de las águilas de construir sus nidos hacia la orientación sureste. La densidad de parejas reproductoras estuvo directamente relacionada con la disponibilidad de roquedos. Los roquedos seleccionados para nidificar fueron de mayor altura ($\bar{x} = 52,9$ m; $N = 32$), y ubicados sobre laderas de mayor pendiente ($\bar{x} = 34,7^\circ$; $N = 31$), que la media disponible. Existió una gran versatilidad entre parejas en cuanto al tipo de roquedo ocupado, debido a que el Águila Perdicera nidificó en áreas muy diferentes en función de la presión humana. De esta forma, los roquedos ocupados más próximos a carreteras tuvieron una altura mayor que los que se encontraban lejos de las mismas. La selección de roquedos de gran altura, situados sobre pendientes elevadas, y con orientación sur, podría estar relacionado con la falta de sustentación en vuelo del Águila Perdicera, al favorecer este tipo de roquedos la formación de térmicas y el vuelo de ladera. La preservación de los roquedos de nidificación libres de la influencia antrópica, podría ser la medida más esencial requerida para la conservación del Águila Perdicera en el área de estudio.

[Traducción de Autores]

Among Mediterranean raptors, the Bonelli's Eagle (*Hieraaetus fasciatus*) has suffered one of the most severe population declines in Spain (Fernández and Insausti 1990, Real et al. 1991), Portugal (Palma et al. 1984), France (Cugnase 1984, Cheylan and Simeon 1985) and Greece (Hallmann 1985) that have resulted in its being listed as an Endangered European Raptor (Rocamora 1994). Recent data indicate that the principal European breeding population (80%) is located in Spain (Real et al. 1997), where the nesting population

has decreased 25% from 1980–90 (Arroyo et al. 1995). Consequently, this species has been catalogued as Vulnerable in Spain (Blanco and González 1992), and high-priority conservation has been urged (De Juana 1992).

Information concerning habitat is fundamental for the management of raptor populations (Moshier et al. 1987). Raptors are among the few groups of birds whose numbers can be limited by the availability of appropriate nesting places (Newton 1979). In Spain, Bonelli's Eagles most frequently

Table 1. Variables used to characterize Bonelli's Eagle nest-sites.

CLIFFNEST—number of cliffs with nests built by a pair
NESTBUIL—number of nests built by a pair
DISTNEST—greatest distance between nests belonging to the same pair (m)
HEIGBAS—height from the base of the cliff to the nest (m)
NEIGDIST—nearest-neighbor distance between adjacent pairs of Bonelli's Eagles (km)
AVACLIFF—availability of cliffs (percentage of 1 km ² squares with suitable cliffs for nesting in each territory)

nest in cliffs and rarely in trees (Arroyo et al. 1995). While some aspects of the biology of this raptor are well-studied, nest-site selection has received only limited study. The two main studies in Spain (Gil-Sánchez et al. 1996, Sánchez-Zapata et al. 1996) refer to the selection and characteristics of used and unused territories. No detailed information is available concerning the choice of nest sites within territories or characteristics of nesting cliffs (Donázar et al. 1989).

The aim of my study was to determine which cliffs in each territory were used for nesting of Bonelli's Eagles, to describe characteristics of cliff nesting sites, and to determine how human activity affects this selection in southeastern Spain.

STUDY AREA AND METHODS

The study was conducted in the province of Granada, southeastern Spain (36°45'–37°49'N, 2°40'–4°13'W) from 1995–97. The area is largely mountainous with altitudes ranging from 0–3482 m, and highly variable temperatures and rainfall. The vegetation includes different species of pines (*Pinus* spp.) and evergreen oaks (*Quercus ilex*) mixed with cultivated areas, mainly with olive trees (*Olea europaea*) and cereals (Rivas-Martínez 1985).

A total of 119 nests located on 52 cliffs that were used by 32 different pairs of Bonelli's Eagle was studied. Raptors frequently build more than one nest and use them alternately in different years (Newton 1979). Thus, all nests (regardless of whether they were occupied or not during the present study) were considered equally for the analysis if they were in occupied territories.

The variables used in the analysis of nest-site characteristics are defined in Table 1. The nearest-neighbor distance method from the last nest used was used to estimate breeding density of the pairs (Newton et al. 1977).

For the analysis of cliff selection, 32 occupied cliffs (last cliff used for nesting by each pair) were compared with 32 unoccupied cliffs within the territories (one cliff per territory). The comparative analysis was performed with variables to characterize the cliffs and human disturbance in surrounding cliffs (Table 2). Because most pairs built nests in the highest cliff of each territory, the comparison was made with the highest unoccupied cliff suitable for nesting within each territory. I considered a cliff suitable for nesting when there were suitable cavities and ledges for nesting, when it was located at <1500 m elevation (the distributional limit of the Spanish population, Arroyo et al. 1995), when it was higher than 10 m, and farther than 500 m from an urban center (minimal distances found for the population studied). I chose the unoccupied cliffs within each territory to eliminate the possibility that limited prey availability was the reason

Table 2. Variables used to characterize occupied and unoccupied cliffs in territories used by Bonelli's Eagles.

ALTITUDE—height above sea level measured in the middle of the cliff (m)
HEIGCLIFF—cliff height (m)
HEIGVAL—height from the bottom of the valley to the base of the cliff (m)
HEIGHILEV—height from the upper edge of the cliff to the summit of a hill located on the cliff (m)
WIDTHVAL—width of the valley at the base of the cliff (m)
SLOPE—inclination of the slope located at the base of the cliff (°)
TOPIND—topographic irregularity index (total number of 20 m contour lines, cut by two lines equivalent to 2 km designed on topographic 1:50 000 maps, in directions N–S and E–W, and crossed at the location of the cliff)
DISVIL—distance from cliff to nearest urban center (m)
DISPAVROAD—distance from cliff to the nearest paved road (m)
DISUNPAVROAD—distance from cliff to the nearest unpaved road passable by vehicle (m)
DISINHABUIL—distance from cliff to the nearest inhabited building (m)
DISCULTIV—distance from cliff to the nearest cultivated field (m)
KMPAVROAD—km of paved roads in the circular sampling area to the nearest 2 km
KMUNPAVROAD—km of unpaved roads in the circular sampling area to the nearest 2 km

Table 3. Means, standard deviations (SD) and ranges of variables characterizing nest sites.

VARIABLE	MEAN	SD	RANGE
CLIFFNEST	1.6	0.9	1-5
NESTBUIL	3.7	3.6	1-18
DISTNEST	774.1	897.7	1-2800
HEIGBAS	29.8	18.3	5-90
NEIGDIST	10.0	3.2	5.8-16
AVACLIF	10.0	4.3	4.7-22

the cliff was unoccupied given that food availability directly limits the distribution of some raptors (Newton 1979).

The territory of each pair was considered to be a radius equal to half the average distance between nests of neighboring pairs, based on the last nest occupied during the study (Howell et al. 1978, Bednarz and Dinsmore 1981, Gilmer and Stewart 1984, Rich 1986, González et al. 1992).

The orientation of nest cliffs was compared with the distribution of all available cliffs within territories ($N = 172$). Cliff orientation was determined using a compass to the nearest 5° . To determine a mean angle of a circular distribution, a simple calculation of an arithmetic mean of the observed angles is inadequate. Thus, specific methods for circular statistics were used for analyses of preference in nest placement orientation (Fisher 1995). Other variables were measured with an altimeter (VZ Performance; precision ± 1 m), theodolite (Pentax PTH 20; precision $\pm 10''$), clinometer, compass and 1:50 000 topographic maps prepared by the Spanish Army Cartographic Service.

A Pearson coefficient was used to determine the rela-

tionship between variables. For occupied and unoccupied cliffs, the mean values of the variables were compared using paired t -tests. As is usual in this type of analysis (González et al. 1992, Penteriani and Faivre 1997), a stepwise discriminant function analysis was conducted (STATISTICA statsoft Inc. 1993). The 0.05% level of significance was used for including variables in each step of the analysis. Because the sample size could not be increased to three times the number of variables measured (Willians and Titus 1988), a jackknifed classification was obtained for the analysis.

RESULTS

Most of the cliffs occupied by Bonelli's Eagles (96%, $N = 50$) were in river valleys and the nests were either in cavities (46.2%) or on ledges (53.8%). The remaining 4% of cliffs were surrounded by plains.

The number of nests built by a pair (Table 3) appeared to be dependent on nest-site availability since nests were built on the majority of suitable ledges and cavities. One pair had a surprising 18 nests with a maximum distance of only 350 m between them. The pairs with the highest availability of cliffs were closer to the nearest-neighbor pair (Table 1; $r = -0.46$, $P = 0.009$, $N = 32$). Therefore, breeding density was directly related to the availability of cliffs.

Occupied and unoccupied cliffs differed significantly in height and slope at the base of the cliff (Table 4). Nests were built on the highest cliffs with the steepest slopes. In fact, most of the pairs (84%) built nests on the highest suitable cliff in

Table 4. Features of the cliffs analyzed. Mean, standard deviation (SD), and results of the Student's t -tests. An asterisk indicates those tests that remained significant ($P < 0.05$) after Bonferroni sequential correction (Rice 1989).

VARIABLE	OCCUPIED CLIFFS	UNOCCUPIED CLIFFS	t	P
	($N = 32$) MEAN \pm SD	($N = 32$) MEAN \pm SD		
ALTITUDE	937.9 \pm 324.2	969.4 \pm 332.3	-1.37	0.18
HEIGCLIFF	52.9 \pm 27.8	37.6 \pm 19.2	4.85	0.00003*
HEIGVAL	135.9 \pm 63.6	130.1 \pm 65.9	0.48	0.63
HEIGHILEV	147.5 \pm 255.1	165.9 \pm 190.9	-0.78	0.44
WIDTHVAL	573.2 \pm 410.0	698.3 \pm 582.1	-1.01	0.32
SLOPE	34.7 \pm 8.2	30.3 \pm 5.9	3.63	0.001*
TOPIND	56.9 \pm 15.9	54.4 \pm 15.0	1.35	0.18
DISVIL	3362.5 \pm 2047.6	3654.7 \pm 2304.3	-1.46	0.15
DISPAVROAD	1640.6 \pm 1273.1	1856.2 \pm 1473.7	-1.24	0.22
DISUNPAVROAD	493.7 \pm 342.9	554.7 \pm 1017.2	-0.35	0.73
DISINHABUIL	917.2 \pm 669.8	1092.2 \pm 822.3	-1.22	0.23
DISCULTIV	1040.3 \pm 1198.4	1219.1 \pm 1138.8	-0.72	0.47
KMPAVROAD	3.7 \pm 3.6	3.4 \pm 3.5	0.53	0.59
KMUNPAVROAD	5.2 \pm 2.5	6.0 \pm 2.4	-1.80	0.08

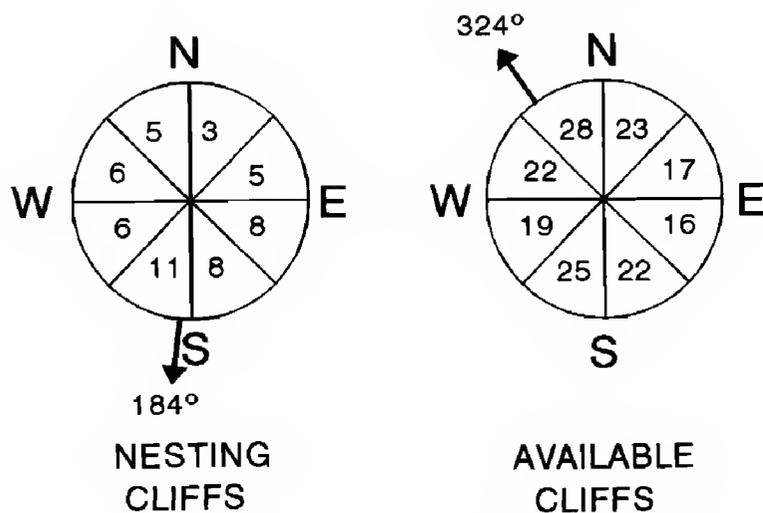


Figure 1. Orientation for Bonelli's Eagle nesting cliffs ($N = 52$) and available cliffs within territories ($N = 172$). Sample sizes are indicated in each direction and the mean orientation is indicated by arrows.

their territory. In the stepwise discriminant analysis, occupied and unoccupied cliffs were best distinguished by the following relationship:

Occupied cliffs

$$= -15.0262 + 0.6842\text{SLOPE} \\ + 0.0934\text{HEIGCLIFF}$$

Unoccupied cliffs

$$= -10.8732 + 0.5938\text{SLOPE} \\ + 0.0663\text{HEIGCLIFF}$$

Using these equations, 65.6% of occupied cliffs and 75.0% of unoccupied cliffs were correctly classified. A jackknife classification reduced the correct classification of occupied cliffs to 65.1% and unoccupied cliffs to 74.1%.

The mean orientations and angular deviations (equivalent to SD) obtained with the trigonometric method (Fisher 1995) were $184^\circ \pm 74^\circ$ and $324^\circ \pm 81^\circ$ for nesting cliffs ($N = 52$) and available cliffs ($N = 172$), respectively (Fig. 1). There were significant differences between study samples (Watson test: $Y_2 = 4.96$, $P = 0.02$). The analysis of 119 nests revealed a trend toward a southeastward orientation (Rayleigh test: $r = 0.178$, $P = 0.02$; mean orientation = $121^\circ \pm 70^\circ$).

Due to the height of nest cliffs near paved roads, I compared these with the other nest sites. Nest cliffs closer to paved roads than 1859 m (mean value for the 52 cliffs with nests) were higher than nest cliffs located farther from paved roads ($\bar{x} = 59.4 \pm 32.4$ m, $N = 30$; $\bar{x} = 33.3 \pm 20.8$ m, $N = 22$, respectively; $t = 3.31$, $P = 0.001$).

DISCUSSION

The results obtained for the elevational distribution of the pairs coincided with those of the overall Spanish population (Arroyo et al. 1995), but the number of nests built by pairs and their orientation differed from those observed in the Sierra Morena region (Jordano 1981). This was probably due to smaller sample size ($N = 10$ pairs) and lower availability of cliffs in the Sierra Morena area. In the Sierra Morena, a trend toward a north northwest orientation and an average of 1.8 nests per pair were observed. As in other raptor species, changes in nest orientation may be correlated with changes in latitude and elevation, which are both indicators of local temperature and insolation regimens (Mosher and White 1976). Nevertheless, a difference in the number of nests built was still found when the two pairs in this population with more than 10 nests were removed from the analysis ($\bar{x} = 2.9 \pm 2.1$).

Some pairs occupied irregular cliffs with many cavities and ledges and built a large number of nests. In raptors, maintaining more than one nest is an obvious advantage, since pairs can shift nests if they are disturbed, if the nest has been taken over by another species, or if their first breeding attempt failed early (Newton 1979). Moreover, use of many nests may help in avoiding parasites which remain in nests (Winberger 1984) and kill young already weakened by starvation (Seidensticker and Reynolds 1971, Beecham and Kochert 1975).

My results indicated that breeding density should be highest in uneven terrain. A similar trend was found by Ceballos and Donazar (1989) in a population of Egyptian Vultures (*Neophron percnopterus*) and by Donazar et al. (1993) for the Bearded Vulture (*Gypaetus barbatus*), both cliff-nesting raptors. They found breeding density to be directly related to the availability of cliffs.

Overheating and sunstroke are two factors that directly can limit the distribution of Bonelli's Eagles due to their morphology which makes them agile and swift but limits the amount of lift they can generate (Parellada et al. 1984). This would explain why Bonelli's Eagles were not found at >1500 m and why higher cliffs and steeper slopes were selected. Such nest-site selection improves the possibilities for thermal bubbles frequently used by Bonelli's Eagle (Cheylan 1979, Parellada et al. 1984) and favors slope soaring, a common technique in raptors with low aspect ratio wings such

as the Bonelli's Eagle (Janes 1984, Parellada et al. 1984). Because the southeastern area of Spain is rather cold during the Bonelli's Eagle breeding season, use of cliffs oriented toward the south, where the thermal bubbles are frequent, may be important for the reproductive success of Bonelli's Eagles. Selection of higher than average cliffs has also been demonstrated in the Bearded Vulture (Donázar et al. 1993), which inhabits cold mountain climates where lift problems are similar to those of the Bonelli's Eagle (Hiraldo et al. 1979, Brown 1988).

The discriminant function correctly classified 65.6% of the occupied cliffs. Lack of a higher discrimination was apparently due to the heterogeneity of the cliffs selected by Bonelli's Eagles and their potential for human disturbance. Paved roads were frequently located in river valleys inhabited by Bonelli's Eagle pairs. Human activity has been shown to influence the selection of nest sites in several species of raptors (Fyfe 1969, Hickey and Anderson 1969, Kumari 1974, Newton 1976, Sherrod et al. 1977), and for some, the minimum acceptable height of a cliff varies inversely with the degree of wilderness available (Newton 1979). Therefore, eagles can occupy lower cliffs far from paved roads, while in zones of heavy human use, higher cliffs must be used. The abandonment of some nests ($N = 5$) located on low cliffs in areas with high levels of human disturbance corroborated this finding (Ontiveros 1997).

A previous study of this same population analyzed the habitat selection of Bonelli's Eagle with and without competition from Golden Eagles (*Aquila chrysaetos*) (Gil-Sánchez et al. 1996). Several authors have doubted that Bonelli's Eagles compete with Golden Eagles (Brosset 1961; Cheylan 1979; Jordano 1981; Clouet and Goar 1984). Rejecting such competition, Gil-Sánchez et al. (1996) found differences between occupied and unoccupied territories that only occurred in habitats undergoing cereal crop cultivation. This pattern of habitat selection and the results of my study on cliff selection within territories show that nest cliffs are the most important resource for habitat selection in Bonelli's Eagle, regardless of food supply.

The availability of adequate nesting areas directly influences habitat selection in raptors (Newton 1979, Janes 1985). My data indicate that, for Bonelli's Eagles, suitable nest sites may be a more limiting resource than in other raptors, causing territories of this eagle to overlap frequently with

human-populated areas (Brown 1976, Cheylan 1981, Parellada et al. 1984). Human activity in territories can negatively affect Bonelli's Eagles and might account for the decline in the Mediterranean population in recent years when other raptors have recovered in Spain (Arroyo et al. 1990, 1995). The preservation of nest cliffs and protection from surrounding disturbances (Cade 1974), is essential to ensure the survival of the Bonelli's Eagle.

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EFFECTIVENESS OF CONSERVATION MEASURES ON MONTAGU'S HARRIERS IN AGRICULTURAL AREAS OF SPAIN

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ABSTRACT.—The breeding success of Montagu's Harrier (*Circus pygargus*) in farming areas of southwestern Spain was studied in a managed population vs. a controlled one. Conservation measures resulted in a decrease in nestling mortality rate, which in turn resulted in a higher breeding success in managed than in unmanaged pairs. However, the effectiveness of intervention at nest sites was constrained by laying date, brood age, clutch size, and type of crop where nesting took place. In very delayed clutches (with unhatched eggs or with broods younger than 10-d old at harvest time) total breeding failure was recorded. The impact of farming operations, mainly harvesting, depends largely on the degree of mismatch between the timing of fledging and harvesting. The type of crop selected as nesting habitat was also important, mainly because of variations in the timing of harvest of the respective crops. Southern populations of harriers appeared to be more influenced by farming operations than did northern ones because harvesting occurred earlier in southern locations. Therefore, conservation measures are of fundamental importance for the future of Montagu's Harrier populations, because Mediterranean areas provide nesting habitat to a large number of breeding pairs in the western Palearctic.

KEY WORDS: *Montagu's Harrier; Circus pygargus; Iberian Peninsula; agricultural environments; breeding success; conservation measures.*

Efectividad de las medidas de conservación de aguilucho cenizo en áreas agrícolas de España

RESUMEN.—Se estudió el éxito reproductivo del aguilucho cenizo (*Circus pygargus*) en áreas agrícolas del sur-oeste de la Península Ibérica, comparando una población manejada respecto a una controlada. Las medidas de conservación ocasionaron un descenso en la mortalidad de los pollos, lo que determinó un mayor éxito reproductivo en las parejas manejadas. Sin embargo, su efectividad estuvo limitada por la fenología reproductiva, la edad de las polladas, el tamaño de puesta, y el tipo de cultivo donde nidificaron. En puestas muy tardías (en estado de incubación, o con polladas menores de 10 días de edad en el momento de la cosecha) el fracaso reproductivo fue completo. Cuanto más temprana fue la cosecha en relación al ciclo reproductivo menor resultó el éxito reproductivo de las parejas. El tipo de cultivo seleccionado como hábitat de nidificación fue también un factor determinante, debido a las variaciones en las fechas de cosecha entre los mismos. Las poblaciones meridionales se hallan más influenciadas por el ciclo agrícola que las norteñas, ya que en las primeras la cosecha tiene lugar antes. Las medidas de conservación son por ello de vital importancia para el futuro de los aguiluchos cenizos, debido a que las regiones mediterráneas acogen buena parte de la población reproductiva de la especie en el Paleártico occidental.

[Traducción de César Márquez]

Montagu's Harriers (*Circus pygargus*) have a widespread but scattered distribution in the Palearctic. The species has suffered a decline in recent decades due to the loss of native habitats to agriculture and forest developments (Cramp and Simmons 1980, Tucker and Heath 1994). As a result, Montagu's Harriers have increasingly begun to use

farming areas where cereal crops are raised as their nesting habitat. Because the breeding season of harriers and the harvest season coincide, the increased use of mechanized farming practices has greatly decreased the breeding success of harriers in these areas (Pérez-Chiscano and Fernández-Cruz 1971, Berthemy et al. 1983, Castaño 1995,

Corbacho et al. 1997). Mediterranean populations of Montagu's Harrier seem to be highly dependent on conservation measures because of the high breeding failure rates that occur when these measures are absent (Corbacho et al. 1997). However, there have been no studies to analyze the factors constraining the effectiveness of management actions. The aim of this study was to evaluate the effectiveness of management actions on the breeding success of Montagu's Harriers.

STUDY AREA AND METHODS

The study was carried out from 1987–91 in Extremadura (southwestern Spain; see Corbacho et al. 1997), a region that provides refuge to one of the main populations of Montagu's Harriers in the western Palaearctic (Tucker and Heath 1994, Ferrero 1996). We monitored five breeding areas: two in La Serena and one each in Llanos de Cáceres, Cornalvo and Llanos de Badajoz-La Albuera. In all of these areas, nests were in cereal fields, with several pairs (2–10) nesting in the same plot (pseudocolonies, *sensu* Cramp and Simmons 1980). The study areas were in arable landscapes where land use was based on dry agricultural practices, with wheat, oats, and barley predominating along with vine, olive, sunflower, and small patches of holm-oak dehesas. Shrubsteppe habitats were also represented in both Llanos de Cáceres and La Serena. The study areas had a typical Mediterranean climate with mean annual precipitation ranging from 400–600 mm, distributed primarily from November–April, and mean annual temperature ranging from 14–17°C. During the breeding period, mean temperature and rainfall ranged from 13.5–15.0°C and 10–96 mm in April to 24–29°C and 0–50 mm in July. No statistical differences in any of the climatic variables (Kruskal-Wallis test, $P > 0.05$ in all cases).

A total of 108 nests was studied (26 in 1987, 12 in 1988, 18 in 1989, 39 in 1990, and 13 in 1991). The Cornalvo area had 69 nests, with the remainder located in La Serena (18), Llanos de Badajoz-La Albuera (17), and Llanos de Cáceres (4), respectively. All nests were in cereal crops: 67 (63%) in barley, 23 (21%) in wheat, 9 (8%) in oats, and 9 (8%) in mixed barley-oat crops. Harrier colonies were monitored regularly (once a week) from the beginning of the breeding cycle (early April); visits increased (every 3–4 d) during the nestling period (15 May–10 July). During the first visit, 88% of nests ($N = 95$) were in the incubation period, with the remainder ($N = 13$) in the nestling stage. Each breeding season, all the nests in some colonies were treated as controls ($N = 36$) and no conservation measures were applied to these nests. At the other nests ($N = 72$), management measures included the removal of young (or eggs) from nests prior to harvesting and baling, and their subsequent return to the nest after harvesting. It took <1 hr to remove eggs and young and return them to nests in all cases so artificial incubation and nursing of young were not necessary. There were no differences in laying date or clutch size between managed and unmanaged clutches (Mann-Whitney U test, $P = 0.64$ and $P = 0.26$).

In order to assess seasonal patterns in breeding performance, laying dates were classified in 10-d periods starting from 11 April (all years pooled), resulting in five phenological classes in relation to the onset of egg laying (Class 1: 11–20 April, 6 clutches; Class 2: 21–30 April, 20, Class 3: 1–10 May, 26; Class 4: 11–20 May, 10; and Class 5: >20 May, 10). For Montagu's Harrier, harvesting appears to be the main determinant of breeding success in arable farmland such as that in the study area (Corbacho et al. 1997). Hence, we classified clutches according to their breeding stage at harvesting time; this resulted in pairs at incubation stage ($N = 13$), pairs at nestling stage (rearing young, $N = 65$), and pairs with fledglings ($N = 12$). At the same time, we separated nestling pairs according to the age of broods at harvest time: early age (1–10 d, $N = 11$), middle age (11–20 d, $N = 26$) and late age (>20 d, $N = 16$). Analysis of reproductive output were performed using: hatching success as the number of eggs that hatched versus the number of eggs laid, including clutches deserted or preyed upon; nestling mortality rate (% of young that died versus the number hatched); proportion of successful pairs (the number of pairs with at least one nestling fledged versus total number of pairs that laid eggs); and breeding success (the mean number of fledglings per laying pair). Results are shown as arithmetic mean \pm standard deviation or %, with sample size indicated in each case. Nonparametric methods and two-way analysis of variance with interaction was used to test for differences (Zar 1996), with the exact method used in each case indicated.

RESULTS

We found the reproductive success of Montagu's Harriers to be strongly dependent on management measures undertaken at harvest time. They resulted in an important decrease in nestling mortality rate (28% in managed pairs vs. 67% in control ones; G -test, $P < 0.001$; $N_1 = 55$, $N_2 = 18$) which in turn resulted in a higher proportion of successful pairs (75% vs. 29%; G -test, $P < 0.001$) as well as breeding success (2.04 ± 1.53 vs. 0.77 ± 1.28 ; Mann-Whitney U test, $P = 0.001$) in managed ($N = 68$) than in unmanaged ($N = 34$) pairs.

A two-way Anova showed that breeding success was highly dependent on both laying date ($F_{4,56} = 4.45$, $P = 0.003$) and management performed ($F_{1,56} = 8.51$, $P = 0.005$) (Fig. 1). Hatching success, which was unaffected by management actions, showed a large seasonal decline (Spearman rank correlation test, $r_s = -0.57$, $P < 0.001$, $N = 59$, all data pooled). Nestling mortality rate increased as the laying date was increased in unmanaged broods ($r_s = 0.69$, $P = 0.009$, $N = 14$), and high mortality was recorded in late broods (80% in Class 3, 100% in Classes 4 and 5). However, this attribute showed no significant seasonal increase in managed clutches (17% in Class 1, 58% in Class 2,

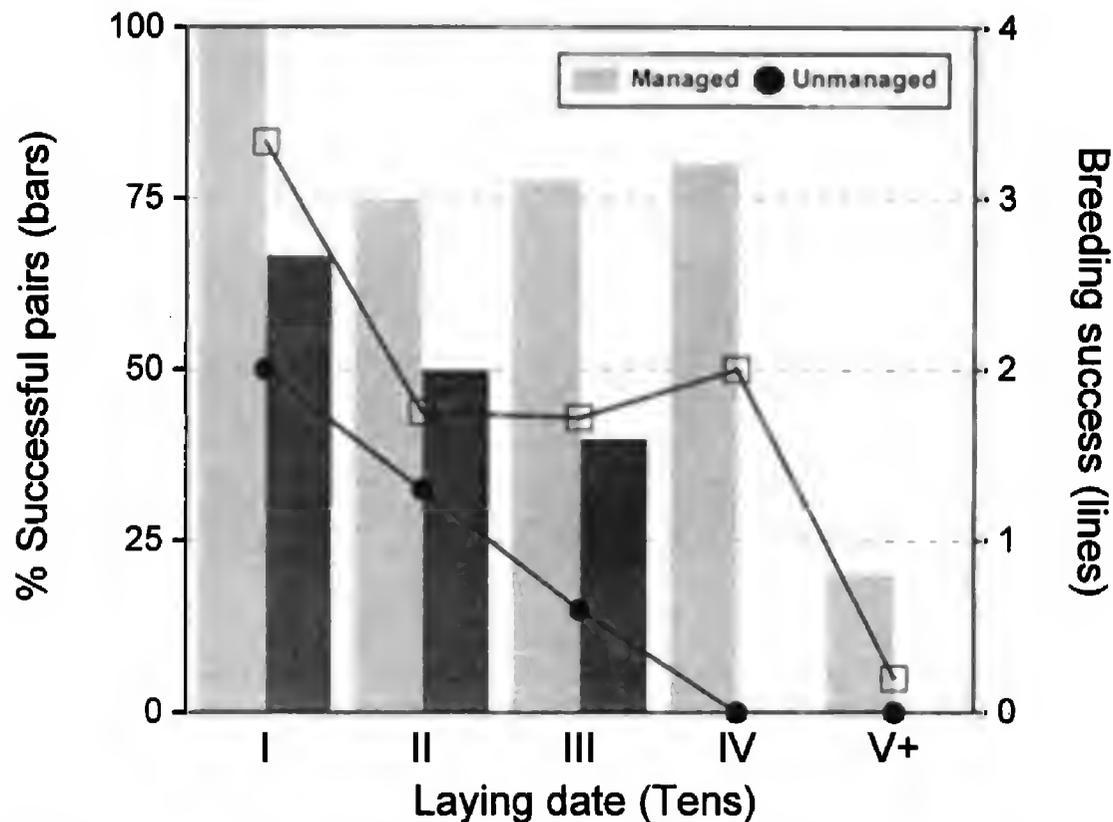


Figure 1. Variation in the percent successful pairs and breeding success of Montagu's Harriers in agricultural areas of southwestern Spain according to laying date and management measures undertaken. Laying date categories were determined as follows: day 1 = 10 April; I = 1-10; II = 11-20; III = 21-30; IV = 31-40; V = >40 days after 10 April.

41% in Class 3, 33% in Class 4, and 50% in Class 5; $r_s = 0.16$, $P = 0.40$, $N = 30$). As a result, managed clutches had a high proportion of successful pairs as well as breeding success; these values were maintained until well into the breeding season (Fig. 1). In contrast, unmanaged pairs showed high breeding failure, because only early clutches (Classes 1 and 2) had good reproductive output (Fig. 1). However, the effect of laying date was not linear, even in the absence of management. This was due to the variations in timing of farming activities (especially the harvest) either between localities or from one year to another. The different crops selected as nesting habitats in any one year or locality were also involved for the same reason.

It was better to relate reproductive output to the breeding stage of each pair at harvest time than to relate it to laying date. In our study, all pairs at incubation stage during harvesting ($N = 13$) failed because of total hatching failure. In contrast, all pairs that raised young before harvest (pairs that fledged young) showed a high breeding success both in managed (3.14 ± 0.69 , $N = 7$) and unmanaged clutches (3.00 ± 0.00 , $N = 5$). Two-way Anova (breeding stage-management) showed that the stage at harvest time was the only factor determining significant differences in breeding success ($F_{2,71} = 20.62$, $P < 0.001$). Therefore, breeding

stage at this critical moment appeared to be the main factor affecting reproductive output. In this sense, conservation measures were clearly effective at the nestling stage. First, management actions greatly increased survival of young (30 to 63%; G -test, $P < 0.001$, $N_1 = 11$, $N_2 = 37$), which in turn resulted in a higher proportion of successful pairs (82% vs. 47%; G -test, $P < 0.004$, $N_1 = 39$, $N_2 = 13$) and breeding success (2.08 ± 1.40 , $N = 39$ vs. 1.16 ± 1.34 , $N = 19$; Mann-Whitney U test, $P = 0.007$) in managed versus unmanaged pairs. Second, managed pairs at nestling stage had a reproductive success for both attributes that was similar to that of pairs at fledging stage (G -test, $P = 0.09$, and Mann-Whitney U test, $P = 0.30$, respectively).

The older the broods were, the greater the breeding success for both managed (Spearman rank correlation test; $r_s = 0.84$, $P = 0.001$, $N = 14$) and unmanaged broods ($r_s = 0.68$; $P = 0.002$; $N = 19$). Pairs with broods in the early-age group failed completely, while all pairs in the late-age group were successful, with high breeding success for both managed (2.60 ± 0.55 , $N = 8$) and unmanaged (2.14 ± 0.93 , $N = 8$) broods (Mann-Whitney U test, $P = 0.18$). Conservation measures appeared to be effective only for middle-age broods, which had higher scores in managed than in unmanaged pairs for both proportion of successful pairs (75%

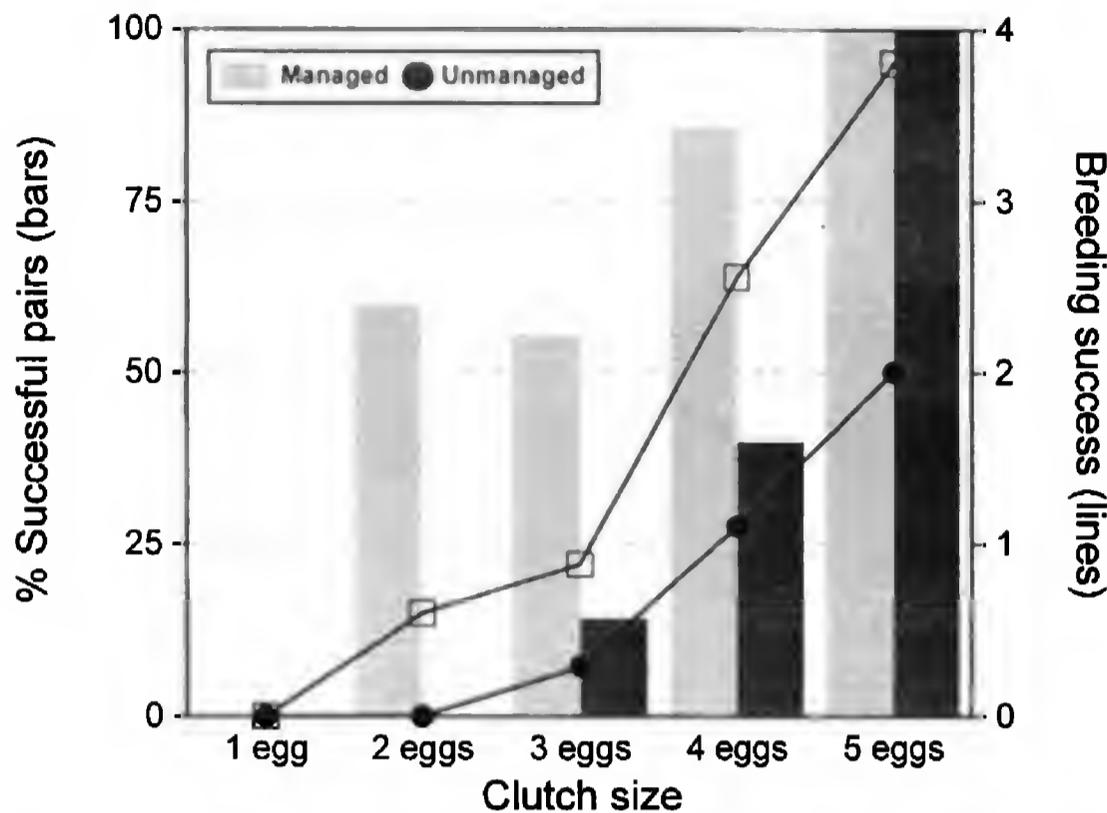


Figure 2. Variation in percent of successful pairs and breeding success of Montagu's Harrier in agricultural areas of southwestern Spain according to clutch size and management measures undertaken.

vs. 14%; G -test, $P < 0.001$) and breeding success (1.25 ± 0.96 vs. 0.29 ± 0.76 , $N_1 = 16$ and $N_2 = 8$; Mann-Whitney U test, $P = 0.045$), respectively.

Nesting habitat selection affected the success of pairs, because of variations in timing of harvest among the different crops. No differences in mean harvesting date were found among wheat (14 June), oats (14 June), or mixed wheat-oats (12 June) (Kruskal-Wallis test, $P = 0.82$), and thus these data were pooled. However, the timing of harvest for barley (26 June) was significantly later than for the rest of the cereal crops (Mann-Whitney U test, $P < 0.001$), and this in turn affected the age of young at harvest time. The later the harvest occurred, the older were the broods (Spearman rank correlation, $r_s = -0.60$, $P < 0.001$, $N = 57$). Thus, in barley crops at harvest age of broods (24.31 ± 10.83 , $N = 13$) was older than in both wheat and/or oat crops (15.16 ± 8.48 , $N = 44$) (Mann-Whitney U test, $P = 0.008$). Similarly, the number of pairs with fledglings at harvest time in barley crops (35.4%) was higher than in the other crops (9.30%) (G -test, $P = 0.04$, $df = 2$). However, with respect to breeding success, the few data available (only two clutches) for unmanaged pairs nesting in barley crops made it impossible to test the influence of nesting habitat selection. In managed clutches, no differences in reproductive output were observed between pairs nesting in wheat-oats and barley crops with regard to breeding success

(1.53 ± 1.46 vs. 1.88 ± 1.58 ; Mann-Whitney U test, $P = 0.48$) and proportion of successful pairs (66.67% vs. 70.59%; G -test, $P = 0.33$; $N_1 = 30$ and $N_2 = 17$ in both cases). This pointed out the effectiveness of conservation measures on the breeding of Montagu's Harriers in farmlands.

Breeding performance showed clear trends that depended on clutch size but these differences were independent of management measures performed. No seasonal decrease in clutch size was associated (Spearman rank correlation test, $P > 0.05$; Corbacho et al. 1997). The greater the number of eggs laid, the greater the hatching success (Spearman rank correlation; $r_s = 0.32$; $P = 0.002$; $N = 92$) that was realized. Clutches of 1, 2, and 3 eggs yielded a lower reproductive output for all variables in comparison to 4- and 5-egg clutches in both managed and unmanaged clutches (Fig. 2). Nevertheless, for a given clutch size, managed clutches resulted in a higher proportion of successful pairs and greater breeding success than unmanaged clutches (Fig. 2). Thus, both clutch size ($F_{4,82} = 9.31$, $P < 0.001$) and management actions ($F_{1,82} = 5.68$, $P = 0.019$) had decisive influences on breeding success.

DISCUSSION

Breeding success of Montagu's Harrier in Mediterranean areas, where breeding occurs chiefly in cereal crops, appears to be highly dependent on

conservation measures (Corbacho et al. 1997). We showed that the effectiveness of management actions had some constraints. Laying date was the main factor affecting it, by its influence on breeding stage and brood-age at harvest time. Thus, neither hatching success nor mortality rate of young increased with the use of conservation measures in very delayed clutches. This happened because of the helpless situation of clutches (eggs in unhatched clutches) or broods (young <10-d old) during and after harvesting as they became more vulnerable to predation and/or theft, or desertion by females. The longer the eggs and broods remained in a defenseless situation, the lower the reproductive success. On average, all pairs that delayed laying until after 15 May were unsuccessful, regardless of any management applied. However, breeding failure occurred in unmanaged clutches even when laying occurred in the beginning of May. Although this 15-d period may not be important, it occurs at a time when a considerable number of pairs start their clutches (33%, Corbacho et al. 1997).

A comparative analysis in the western Palearctic showed that although breeding season starts earlier in the Mediterranean area than in northern Europe (Schipper 1979, Corbacho et al. 1997), the timing of harvest in cereal crops in southern latitudes also occurs earlier. Consequently, the overlap of the breeding cycle with the postharvest period is greater in southern populations, with the result that the number of pairs that finish breeding before harvesting decreases southwards (10–40%, Berthemy et al. 1983; 70%, Pandolfi and Giacchini 1991; 40%, Arcà 1989; over 50%, Arroyo 1995; 18%, Castaño 1997; 16%, this study). In our study, the number of pairs affected by farming practices (either at incubation or brooding stages) varied from high (>80%) to complete (100%). The increasing use of early varieties of cereal crops may constitute a further threat to breeding harriers in arable lands.

Breeding condition of the pair may also play a role in determining reproductive output (Schipper 1979, Newton 1979), but in agricultural environments this factor is overshadowed by farming practices. If clutch size is an indicator of pair quality (Drent and Daan 1980), low quality breeders achieved a low reproductive output despite management (Corbacho et al. 1997, this study).

In conclusion, conservation measures offset the negative influence of intensified mechanization of

farming practices on Montagu's Harrier nesting in cereal fields, with the result that breeding success of managed populations in agricultural environments of Mediterranean areas was similar to that of northern European breeders in natural habitats (Corbacho et al. 1997). However, predation and theft of young was more pronounced in managed (50%) than in unmanaged nests (30%), suggesting that management activities attract attention from predators and humans (Arcà 1989). Therefore, although cultivated areas in southern Europe seem to provide suitable habitat for the species, integral conservation measures are urgently needed, especially because that region provides refuge to one of the largest populations of Montagu's Harrier in the western Palearctic (Berthemy et al. 1983, Tucker and Heath 1994, Ferrero 1996). In addition to conventional conservation schemes (removal of young to increase survival), other actions such as delayed harvesting or setting sheltering areas around main colonies should be considered. Such actions could be accompanied by subsidies for farmers in order to compensate for any economic losses incurred. Environmental education programs should be carried out in the areas near the sites of the main colonies, because of the large number of nests that are unsuccessful because of theft and destruction at harvest time.

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COOPERATIVE HUNTING OF JACKDAWS BY THE LANNER FALCON (*FALCO BIARMICUS*)

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ABSTRACT.—Cooperative hunting has been recorded for several subspecies of Lanner Falcon (*Falco biarmicus*). On average, the success rate for pairs is higher than for single birds. During 1988–90, I collected data on the success of five Lanner Falcon pairs that cooperatively hunted Jackdaws (*Corvus monedula*) in western Sicily. Fifty-three percent of attacks were aimed at larger groups of Jackdaws. Males made most of the initial attacks (74%) but prey captures were mainly made by females (87%). Pairs tended not to share prey and used visual contact to coordinate chases. Most attacks were by partial surprise (60.8%), followed by nonsurprise (21.6%), and surprise attacks (17.6%). Surprise attacks tended to involve small flocks of Jackdaws, whereas partial surprise tended to involve large flocks.

KEY WORDS: *Lanner Falcon*; *Falco biarmicus*; *cooperative hunting*; *Sicily*; *Jackdaw*; *prey group size*.

Caza cooperativa de *Corvus monedula* por *Falco biarmicus*

RESUMEN.—La caza cooperativa de *Falco biarmicus* ha sido registrada para varias subespecies a lo largo de su distribución. En promedio la tasa de éxito por pareja es mas alta que la individual. Durante 1988–90 recolecté datos sobre el éxito de la caza cooperativa de *Corvus monedula* de cinco parejas en el oeste de Sicilia. Cincuenta y tres por ciento de los ataques fueron dirigidos a grandes grupos de *Corvus monedula*. Los machos efectuaron los ataques iniciales (74%) pero la captura de presas fue efectuada por las hembras (87%). Las parejas tendían a no compartir la presa y utilizaron contactos visuales para coordinar las persecuciones (60.8%), seguidas de ataques sin sorpresa (21.6%), y ataques sorprendidos (17.6%). Los ataques por sorpresa involucraron pequeñas parvadas de *Corvus monedula*, mientras que los parcialmente sorprendidos involucraron parvadas mas grandes.

[Traducción de César Márquez]

Cooperative hunting is a social foraging behavior where predators coordinate their movements to increase efficiency of capture (Ellis et al. 1993). Prey may be shared among members according to social organization, prey size and individual functional role (Bednarz 1988, Ellis et al. 1993). Pair hunting is cooperative when participants perform separate roles. In certain species and under certain circumstances, cooperative hunting is more successful than solitary foraging (Hector 1986, Thiollay 1988, Yosef 1991, Ellis et al. 1993).

Cooperative hunting in the genus *Falco* seems to be restricted to bird-eating species, such as Lanner Falcons (*Falco biarmicus*), Aplomado Falcons (*F. femoralis*), and Red-headed Falcons (*F. chicquera*), which inhabit semi-open savannas and desert and Mediterranean scrub (Mebs 1959, Osborne 1981,

Hector 1986). Southern Mediterranean Peregrine Falcons (*F. peregrinus brookei*) hunt cooperatively in areas where prey density is low (Thiollay 1988).

Cooperative hunting in Lanner Falcons has been recorded for several subspecies throughout the species' geographic range (Cramp and Simmons 1980, Tarboton and Allan 1984, Leonardi et al. 1992). Lanner Falcon pairs pursue swift flying prey (e.g., swifts [*Apus* spp.]) along parallel paths (Mirabelli 1982, Bijlsma 1990). They hunt flocks of gregarious small birds (e.g., swallows [*Hirundo* spp.]) working together with repeated stoops upon the same individual (Mirabelli 1982). In contrast, for larger perched prey (e.g., shorebirds and pigeons [*Columba* sp.]), one falcon flushes the quarry while it is taken by the mate (Mebs 1959, Massa et al. 1991, Yosef 1988). Partners have distinct roles. Males usually attack and direct prey toward females (Yosef 1991) and females tend to pursue large prey (Brossett 1961, Tree 1963, Kemp 1993). Success

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rates when hunting in pairs (20–25%) are higher than that of single birds hunting alone (15–40%) (Bijlsma 1990, Yosef 1991, Kemp 1993).

This paper describes my observations of cooperative hunting in Lanner Falcons nesting in western Sicily. In this region, pairs frequently attack colonial nesting Jackdaws (*Corvus monedula*). This provided an opportunity to compare success rates among attacks on different sized flocks, as it related to sex of pursuers and attack strategies utilized.

STUDY AREA

I studied Lanner Falcons on the island of Sicily in the central Mediterranean. I observed five pairs during the breeding season: two breeding pairs near the northern periphery of the Sicilian distribution and three pairs in a southern area where the species was studied previously by Mascara (1986).

The climate of the northern study area is temperate-wet with 600–800 mm of rainfall and an average annual temperature of 12–14°C. The southern study area has a subarid climate (<600 mm of rainfall and temperature >16°C) (Istituto Geografico De Agostini 1987).

Land use in the study areas was predominately farming and pasture. Cereal farming and pasturelands covered by olive (*Olea europaea*) and prickly pear (*Opuntia ficus-indica*) cultivation dominated northern open spaces. The southern study area was largely in a wheat monoculture with interposing spots of xeric Mediterranean vegetation and small *Eucalyptus* plantations. Within both study areas, lanners nested on clay-sand and calcareous cliffs with heights of 50–1150 m (Massa et al. 1991).

METHODS

I visited breeding sites 21 times during two prereproductive periods (November–January 1988–90). Each breeding site was visited 10 times for 55 total H. I watched Lanner Falcons hunting in pairs from 200–600 m with 8 × 40 and 10 × 40 binoculars. Age and sex of observed falcons was recorded for each sighting according to criteria in Cramp and Simmons (1980) and Porter et al. (1981).

Attacks were defined as very rapid flights or stoops toward one or more clearly observed prey (an individual or group of specific prey species) (Cresswell 1994, 1996). First attacks were defined as the first, fast approach by falcons toward potential prey. During each attack, I recorded the following data: position and sex of each falcon at the start of the attack, size of the prey flock, and type of attack strategy. I placed attack strategies into three categories: surprise attacks, partial surprise attacks, and nonsurprise attacks. In surprise attacks, Lanner Falcons first approached close to Jackdaws from behind rock cliffs. In partial surprise attacks, one of the two attacking falcons was visible to prey while the other falcon attacked by surprise. In partial surprise attacks, two perched falcons would depart at different times (Yosef 1991, Kemp 1993). In nonsurprise attacks, both falcons were visible at the onset of attacks, then they tried to encircle Jackdaw flocks (Cresswell 1994, 1996). In nonsurprise attacks, one falcon stooped on prey after soaring while the other at-

tempted to flush prey (Mebs 1959, Massa et al. 1991, Kemp 1993, Jenkins 1995).

I observed Lanner Falcons cooperatively hunting both Rock Pigeons (*Columba livia*) and Jackdaw flocks near their nests. Both prey species nest on cliffs 100–300 m from Lanner Falcon nests (Sodhi et al. 1990, Suhonen et al. 1994). For evaluating the importance of cooperative hunting, I only investigated hunts of Jackdaws. Preliminary observations indicated that single female Lanner Falcons initiated nearly all pursuits of pigeons. Also, <5% of the total attempts on pigeons ($N = 32$) were performed by males. Cooperative hunting, and necessarily, participation by males, was more common in hunts of Jackdaws. In addition, Jackdaws consistently comprised a large percentage of dietary biomass for lanners in Sicily (Massa et al. 1991, Leonardi et al. 1992, Leonardi 1994). Finally, Jackdaws responded to attacking falcons with intricate forms of mobbing behavior. This provided an opportunity to investigate interactions between cooperative hunting and antipredator defense behavior (Kenward 1978, Caraco et al. 1980, Turner and Pitcher 1986, Cresswell 1994).

The number of Jackdaws present was estimated daily by counting the maximum number of birds seen simultaneously. Jackdaw colonies typically contained 20–70 individuals. During an attack, I estimated the size of each flock attacked by assuming the members to be all birds within 25 m of each other (Cresswell 1994, 1996). At times entire colonies behaved as a single flock. Under these circumstances, I counted the number of individuals in the group first attacked (Kenward 1978). For statistical comparisons, I placed Jackdaw flocks into three size categories according to previous studies of predation on prey groups (Kenward 1978, Cresswell 1994, 1996): 2–10, 11–30 and 31–50 individuals. I assessed the validity of the above flock size classes for this study through preliminary observations of flocking reactions measured for single and paired Lanner Falcons (Leonardi 1991, Leonardi unpubl. data).

I compared F -frequencies of hunting strategies and success rates among different flock sizes and strategies using chi-squared tests and G -tests (Zar 1984). I used Cochran's corrected chi-square test for differences between males and females using a 2 × 2 contingency table (Zar 1984).

RESULTS

In 52 cooperative hunts, I detected no vocalizations which might have functioned to coordinate pursuits. Females alone ate 70% of prey captured in cooperative hunts (captures $N = 10$). In only 2 of 16 cases (12%), males fed on prey captured in cooperative hunts after the departure of females. Although Lanner Falcons preferred to attack larger flocks (Table 1; $\chi^2 = 12.33$, $df = 2$; $P < 0.001$), hunting success was inversely proportional to flock size ($G = 10.7$, $df = 2$; $P < 0.005$).

Female Lanner Falcons initiated attacks less often than did males (26% vs. 74%). Although males preferred to pursue larger prey (87% of 52 pur-

Table 1. Distribution of Lanner Falcon attacks on flocks of Jackdaw by cooperative hunting in Sicily.

	JACKDAW FLOCK SIZE CLASS		
	2-10	11-30	31-50
Attempts	10	14	27
Kills	2	5	9
Total	12	19	36
Captures (%)	20	35.7	33.3

suits) and larger flocks more often than did females (Table 2; $G = 13.9$; $df = 2$; $P < 0.001$), male hunting success rates tended to be lower than those of females (Table 2; $\chi^2 = 2.86$, $df = 2$; $P < 0.10$).

Lanners attacked Jackdaws by partial surprise (60.8%) much more frequently than they did by nonsurprise (21.6%) and surprise attacks (17.6%) ($N = 52$). Although degree of surprise is one of the most important factors in improving the success of raptor attacks, lanners used this technique in only nine of 52 attempts. Also, open attacks give time for antipredatory behavior by prey. Nevertheless, partial surprise was used significantly more often ($\chi^2 = 17.40$, $df = 2$; $P < 0.001$). In addition, lanner pairs captured more prey using nonsurprise attacks (Table 3; $\chi^2 = 11.90$, $df = 2$; $P < 0.01$).

Cooperative hunting techniques were not uniformly distributed among prey flock classes. Hunting success in relation to prey flock size was significant for partial surprise on larger groups (22%; Table 3; $P < 0.01$) and nonsurprise attacks on medium flocks (27%; $\chi^2 = 14.40$, $df = 2$; $P < 0.01$).

DISCUSSION

Evidence of coordinative signaling among hunting predators is indicative that hunts are cooperative (Hector 1986, Ellis et al. 1993). Male Aplomado Falcons initiate attacks and then vocalize a "chip" call (Keddy-Hector pers. comm.). Although I detected no vocalizations among hunting lanners, Thomsett (1987) reported that pairs of lanners hunting bats gave chipping calls. Mebs (1959), however, failed to mention any calls given by cooperative hunting lanners in Sicily. Participants in hunts, however, can coordinate pursuits without vocal signals. Massa et al. (1991) suggested that partners monitor their movements by visual contact. Predators should avoid vocalizations during surprise attacks, which would reveal their pres-

Table 2. Capture success (%) from first attacks of Lanner Falcons cooperatively hunting flocks of Jackdaws in Sicily.

	JACKDAW FLOCK SIZE CLASS			
	2-10	11-30	31-50	Total
Males				
First attack	2	12	24	38
Kills	0	1	1	2
Captures (%)	0	0.08	0.04	
Females				
First attack	8	2	3	13
Kills	2	5	7	14
Captures (%)	0.25	2.5	2.3	

ence. In partial surprise attacks, flying Lanner Falcon males from outside the colony area would suddenly stoop on Jackdaws.

Prey capture percentage of this study was lower (31%) than that observed for other lanner subspecies (50%; Yosef 1991, Kemp 1993) and Aplomado Falcons (45%; Hector 1986). Sicilian lanners pursued small- and medium-sized prey with solitary hunting strategies and used cooperative hunting for large-size prey like Jackdaws. Nevertheless, this low percentage may have been due to Jackdaw antipredator behavior. Large Jackdaw flocks frequently used mobbing (43%, $N = 58$) against lanners. This active defense, combined with the dilution effect of individuals in a flock, can improve predator avoidance by prey. The dilution effect is an advantage because individuals are less likely to be taken by predators when in a flock (Turner and Pitcher 1986). Morgan and Godin (1985) reported that the rate of predator attack per individual prey is inversely proportional to group size.

Although examples of role reversal are known (Mebs 1959, Mirabelli 1982, Massa et al. 1991), the

Table 3. Percent hunting successes (kills/attempts; total of 52 attempts, 16 kills) by Lanner Falcons hunting cooperatively on flocks of Jackdaws in Sicily.

ATTACK TYPE	JACKDAW FLOCK SIZE CLASS		
	2-10	11-30	31-50
Partial surprise	0	6	22
Surprise	11	11	0
Nonsurprise	9	27	9

male success rate of <1% was irrelevant in comparison to the 50% reported. This was probably because of the strong reversed sexual dimorphism (RSD) of this species and its tendency not to share prey. In other words, females physically dominated males during hunts and feedings. RSD may also account for divergences in hunting and prey choice. Males of *F. b. feldeggii* weigh 69% that of females and capture prey which average 45% the size of the female's prey (Leonardi et al. 1992). It is likely that RSD favors cooperative hunting, since it allows the hunting of a wide range of prey and also the use of different hunting strategies.

Data on flock size choice showed that lanners prefer to attack larger groups. In previous studies of flocking behavior and hunting, hunting success has been shown to be inversely proportional to flock size (Kenward 1978, Turner and Pitcher 1986, Cresswell 1994, Krause and Godin 1995). Krause and Godin (1995) suggested that flock conspicuousness, rather than flock size per se, influenced predator choice. Flock conspicuousness lends to repeated attacks in a single chase, thereby increasing success (Krause and Godin 1995). In Jackdaws, antipredator defense is based on the group's conspicuousness (which determines the encounter rate) and on the total number of individuals in the group (dilution effect; Turner and Pitcher 1986). In my study, the effect of group conspicuousness on rates of encounter with falcons may have been immaterial because Jackdaws lived so close to nesting lanners (Pitcher 1986, Krause and Godin 1995).

As in my study, partial surprise was the strategy most commonly used by cooperative hunting Lanner Falcons in South Africa (Kemp 1993, Jenkins 1995). Sicilian lanners frequently use this strategy (60.8%) in capturing Jackdaws only. In South Africa, nonsurprise attacks were aimed at small prey (Kemp 1993, Jenkins 1995). Previous Sicilian studies described nonsurprise attacks as frequent cooperative techniques used against larger prey (Mebs 1959, Massa et al. 1991). My data indicated a subordinate use of this strategy in comparison with the partial surprise attack. Inversely, lanners using nonsurprise attacks had good hunting success rates. This technique was probably used because it involved energetically inexpensive soaring and resulted in relatively high hunting success (Jenkins 1995).

The surprise attack was reported as the most important factor in Peregrine Falcon and Merlin (*Fal-*

co columbarius) hunting success when pursuing small flocks of birds (Cresswell 1996). In this study, surprise attacks were less successful than were other strategies (17.6%) and were employed mostly for attacks of pigeons. In South Africa, surprise attacks from fast, low coursing flight were principally aimed at small birds and doves (*Streptopelia* spp.; Kemp 1993). In my study in Sicily, surprise attacks on Jackdaws caused intense confusion inside flocks. This confusion, and the dilution effect, produced an abatement effect; Lanner Falcons had difficulty attacking the group repeatedly, decreasing capture chances (Leonardi 1991, Turner and Pitcher 1986, Krause and Godin 1995).

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METHODS FOR GENDER DETERMINATION OF CRESTED CARACARAS

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ABSTRACT.—We report details of a method that is reliable for gender determination of Crested Caracaras (*Caracara plancus*). Using the microsatellite probe Poly(dA-dG)·(dC-dT), we detected sex-specific (female only) high-molecular weight restriction fragments in DNA from blood samples collected in the field. This method correctly identified the gender of 14 known-sex captive caracaras and was subsequently used to identify gender for 28 wild adults. We also evaluated morphometric measurements for these 42 individuals to determine whether any single characteristic or combination could be used in the field to make reliable gender determinations. No morphometric measurements were found that were reliable for gender determination in adult caracaras. Bill depth and wing length tended to be larger for females, but there was considerable overlap among the sexes for all measurements. Bill depth and wing length were retained in a model developed using multiple logistic regression analysis, but the model's overall predictive capability for indicating gender was poor. Because young caracaras are only 80% of adult size at fledging, their morphometric measurements are not usable for gender determination. Genetic methods are likely the only reliable methods suitable for determining gender in Crested Caracaras.

KEY WORDS: *Crested Caracara; Caracara plancus; DNA; blood sampling; gender determination.*

Metodos para la determinacion de genero de *Caracara plancus*

RESÚMEN.—Reportamos detalles de un método confiable para la determinación de género de *Caracara plancus*. Mediante la utilización de la exploración de microsatélite Poli (dA-dG)·(dC-dT) detectamos altos fragmentos moleculares de peso restringidos (en hembras solamente) en el ADN proveniente de muestras tomadas en campo. Este método identificó en forma correcta el género de 14 caracaras cautivos de los cuales se conocía el sexo. Subsecuentemente fué utilizado para la identificación de 28 adultos silvestres. También evaluamos las medidas morfométricas de estos 42 individuos para determinar si alguna característica o combinación puede ser usada en campo para la determinación de género. Ninguna medición morfométrica fué confiable para la identificación de género en caracaras adultos. La profundidad del pico y la longitud del ala tendían a ser mayores en las hembras, hubo coincidencias en las medidas de ambos sexos. La profundidad del pico y la longitud del ala fueron utilizados para la aplicación de un análisis de regresión múltiple, pero en general la capacidad predictiva del modelo para la identificación del género fué pobre. Debido a que los caracaras jóvenes son un 80% del tamaño adulto cuando son pichones, sus medidas morfométricas no son utilizables para la determinacion de género. Los métodos genéticos parecen ser los únicos confiables para determinar el género de los caracaras crestados.

[Traducción de César Márquez]

The ability to identify the gender of birds is critical to ecological studies for addressing a variety of topics including population and brood sex ratios,

sex-ratio manipulation and gender-related differences in dispersal, habitat use, site fidelity, and survival. However, gender determination can be difficult for young birds and sexually monomorphic species. Discriminant function and logistic regression analyses have been used along with morphometric data to determine gender for breeding adults in a variety of avian species (Edwards and

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Kochert 1987, Clark et al. 1991, Smith and Wiemeyer 1992), but rates of misclassification can exceed 20%, particularly for species with considerable overlap in measurements, and these methods cannot be used on young individuals. Hormone immunoassays and genetic methods such as karyotyping and flow cytometry have been used for sexing birds but with varying success (Tiersch et al. 1991) and only to a limited extent for raptors (Ivins 1975). The usefulness and reliability of micro- and minisatellite probes for gender identification in birds, including members of Falconiformes, has been well-documented (Longmire et al. 1991, 1993, Epplen et al. 1991, Delehanty et al. 1995, Fleming et al. 1996).

The Crested Caracara (*Caracara plancus*) is a little-known tropical raptor with a limited distribution in North America. Although distinct plumage differences can be recognized among age groups (Wheeler and Clark 1995, Morrison 1996), there are no distinguishable gender-related plumage differences. Snyder and Wiley (1976) reported a low index of dimorphism (2.2) for this species, and considerable overlap in measurements exists between males and females for all subspecies (Morrison 1996). Both males and females incubate, so both have a brood patch (Morrison 1996).

In Florida, the Crested Caracara occurs as an isolated population in the southcentral peninsula (Stevenson and Anderson 1994). Because of its small size, restricted range, and apparent vulnerability to habitat changes, this population is listed as Threatened by the U.S. Fish and Wildlife Service and by the state of Florida. Recent studies on the ecology and dynamics of this population have been limited by the inability to determine the gender of individuals.

The objective of this study was to identify techniques suitable for gender determination in Crested Caracaras. We investigated the feasibility of using genomic DNA obtained from blood samples to look for the presence of high-molecular weight, female-specific, microsatellite fragments, following Longmire et al. (1993). We also examined external morphological characteristics for known-sex individuals. Reliable gender determination using genetic methods would facilitate our ability to evaluate the use of morphometric measurements for gender determination in the field. Although surgical examination also provides gender information, this was not a viable option for this study because of the cost, difficulties of use in the field,

lack of usefulness for sexing juveniles and concern regarding use of an invasive technique on a Threatened Species.

STUDY AREA AND METHODS

We studied Crested Caracaras in southcentral Florida (27°10'N, 81°12'W). Nesting territories were located in eight counties: Highlands, Glades, Okeechobee, Osceola, DeSoto, Polk, Hendry, and Indian River. This region constitutes most of the species' current breeding range in Florida.

During 1994–96, we took blood samples and morphometric measurements from 42 Crested Caracaras, including 14 captives and 28 wild, breeding adults that were captured throughout the study area (Morrison and McGehee 1996). Using laparoscopy, we determined gender of the 14 captive individuals, which were subsequently used for genetic gender determination.

We used blood samples obtained from the 14 known-sex captive caracaras (5 M, 9 F) to identify a suitable probe for gender identification. Approximately 0.2 µl of blood was collected from a brachial vein of the wing and transferred immediately into 5 ml of lysis buffer (Arctander 1988). Samples were sent to the laboratory for processing without information on the known gender of the captive individuals.

Genomic DNA was isolated using a modified procedure from Longmire et al. (1991). The concentration of each DNA sample was estimated using a UV spectrophotometer. Approximately 10 µg of DNA from each sample was digested with the enzymes *Hae* III and *Hinf* I in two separate reactions using reaction conditions recommended by the supplier (New England Biolabs, Beverly, MA U.S.A.). Digested samples were electrophoresed in a 0.8% agarose gel at 40 volts for 36 hr. Restriction fragments were transferred to positively charged nylon membranes (Amersham, Arlington Heights, IL U.S.A.) using a modification of Southern (1975). Membranes were then baked for 2 hr at 65°C. Hybridization procedures followed the protocol of Longmire et al. (1993) except that prehybridization and hybridization solutions were 6 × SSC, 0.01 M EDTA pH 8.0, 10 × Denhardt's solution and 1% (w/v) SDS. The probe used to identify gender was Poly(dA-dG)·(dC-dT) (supplied by Pharmacia, Piscataway, NJ U.S.A.). Post hybridizations, membranes were washed twice for 5 min each in 2 × SSC, 0.1% SDS at 22°C and twice for 5 min each in 0.05 M NaCl, 0.1% SDS at 42°C. Membranes were then exposed to film (Amersham Hyperfilm MP) overnight in cassettes with two intensifying screens. Radiographs were examined for presence of gender-specific high-molecular-weight bands (Longmire et al. 1993).

Blood samples from wild caracaras were collected and processed for gender determination, as above. We determined gender of the 28 wild caracaras by applying the genetic method after it was validated using the 14 captives.

We took five external morphometric measurements on all 42 Crested Caracaras. The captive individuals had originally come from the wild as either immatures or adults, so we assumed that their measurements were not different (due to being in captivity) from those of other

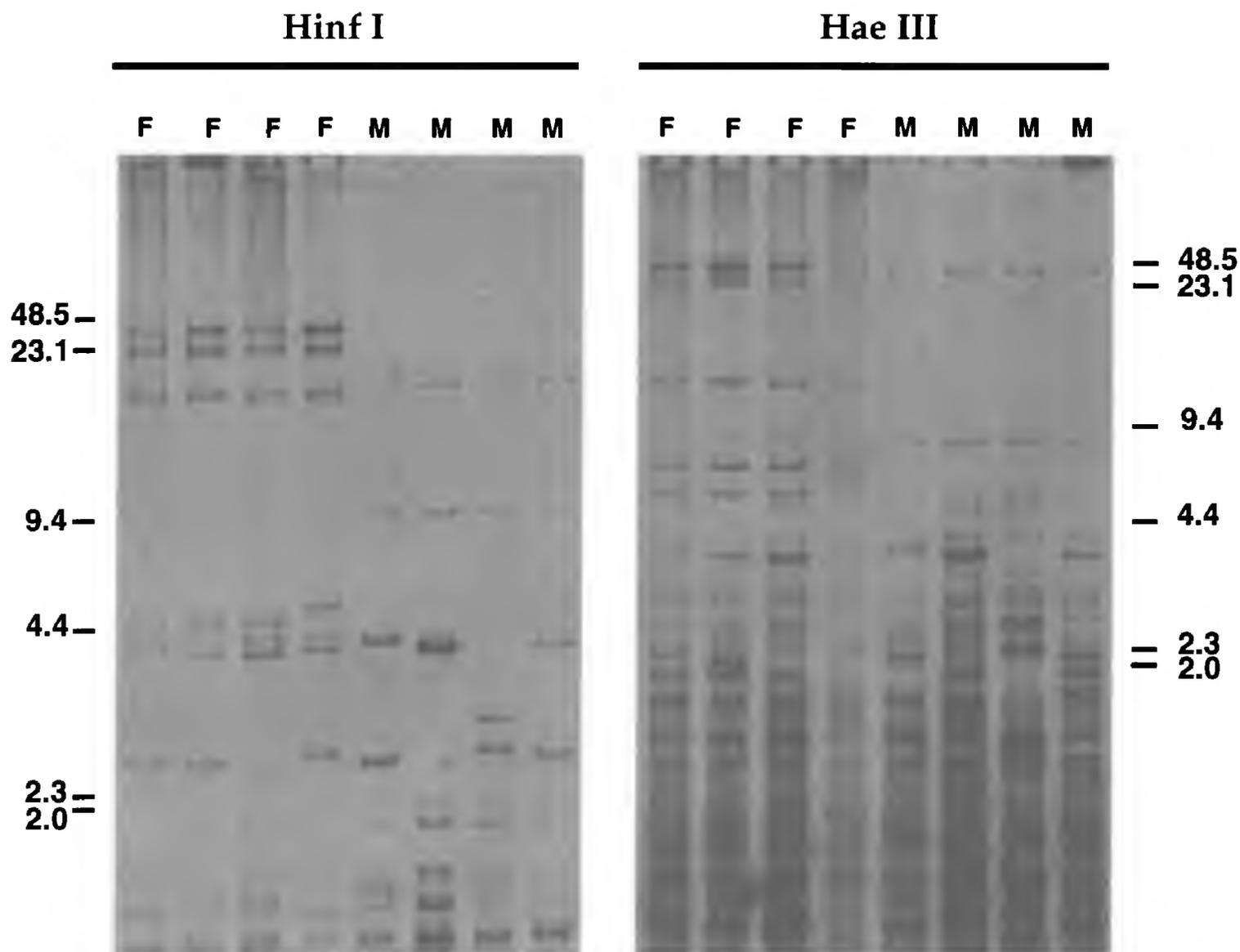


Figure 1. Representative autoradiograms of four female (F) and four male (M) Crested Caracaras. Genomic DNA was digested with the enzymes *Hinf* I (left panel) and *Hae* III (right panel). Both sets of digestions are hybridized with the probe Poly(dA-dG)·(dC-dT). To the side of each autoradiogram are the molecular weight markers in kilobases.

wild individuals. Four of the 14 (1 M, 3 F) were in Basic I plumage (Wheeler and Clark 1995) so were at least one year old. We assumed their measurements were not different from those of adults (Morrison unpubl. data).

Measurements followed the North American Bird Banding Techniques Manual (1984). All the following were taken in mm: wing length (length of the unflattened wing from the bend to the tip of the longest primary), culmen (from the cere edge to the tip of the bill), tarsus length (back of the intertarsal joint to the lower edge of the last complete scale before the toes), bill depth (cere edge to the bottom of the lower mandible at the deepest point), and bill width (maximum measurement at the posterior part of the bill). We did not measure tails because we considered this measurement unreliable. Caracaras regularly walk on the ground while foraging, and their tails incur considerable wear and breakage distally. Mass was not considered reliable because many captured wild individuals had engorged crops.

We compared measurements ($\bar{x} \pm 1$ SE) between males and females for all 42 caracaras using unpaired, 2-tailed *t*-tests. We also used multiple logistic regression (MLR) on the entire set of measurements. MLR relates several explanatory variables, in this case morphological measurements, to a dichotomous dependent variable, in

this case, gender. MLR is more appropriate than discriminant function analysis for these comparisons, particularly when assumptions of multivariate normality are violated (Press and Wilson 1978). The multiple logistic function is the probability of an individual belonging to one particular group, in this case, the probability of any individual being female. Probabilities below a threshold value (assigned as 0.50) indicate male and higher probabilities indicate female. MLR was conducted using SigmaStat ver. 2.0 (Jandel Scientific, Inc. 1995).

RESULTS

Genetic Method. We correctly identified the gender of all 14 captive caracaras using the microsatellite probe. All females ($N = 9$) exhibited 2 fragments larger than 23 kb. All males exhibited only a single band in this same size range (Fig. 1). Thus, female caracaras were distinguishable by the presence of another band at or in excess of 23 kb, in comparison to males, which did not show this second band. In the *Hae* III digested samples, the

Table 1. Comparison of five external morphological characteristics of 42 (14 captive and 28 wild) Crested Caracaras in southcentral Florida, 1994–96. All measurements in mm.

CHARACTERISTIC	MALE (N = 23)			FEMALE (N = 19)			t	P
	MEAN	SE	RANGE	MEAN	SE	RANGE		
Wing length	392.41	2.99	345.0–408.0	404.68	2.64	384.0–430.0	3.07	0.004
Tarsus	103.77	0.45	98.6–107.8	103.89	0.98	94.6–113.0	0.18	0.91
Culmen	33.12	0.20	31.5–35.0	33.56	0.55	24.6–35.6	0.74	0.46
Bill depth	23.56	0.13	22.5–24.9	24.2	0.17	22.9–25.6	2.97	0.005
Bill width	13.86	0.13	12.2–15.0	14.04	0.12	13.0–15.0	0.98	0.35

marker was above 23 kb. The marker in the *HinfI* digested samples started at about 23 kb (Fig. 1).

Morphometric Analyses. Only bill depth and wing length differed between males and females (Table 1), though considerable overlap was noted even for these two characteristics (Table 2). Only bill depth and wing length were retained in the logistic regression model: probability of being female = $-55.79 + (0.064 \times \text{wing length}) + (1.263 \times \text{bill depth})$ ($\chi^2 = 40.81$, $P < 0.001$). Predictive capability of the model was poor, however, resulting in a mean misclassification rate of 59%.

Table 2. Percentage of male and female Crested Caracaras in each measurement group for wing length and bill depth. All measurements in mm.

WING LENGTH	NO. OF MALES	%	NO. OF FEMALES	%
345–350	2	0.09	0	0.00
386–390	6	0.26	2	0.10
391–395	4	0.17	2	0.10
396–400	7	0.30	3	0.16
401–405	1	0.04	2	0.10
406–410	3	0.13	4	0.21
411–415	0	0.00	3	0.16
416–420	0	0.00	3	0.16
Total	23		19	
BILL DEPTH	NO. OF MALES	%	NO. OF FEMALES	%
22.5–23.0	5	0.22	1	0.05
23.1–23.5	6	0.26	3	0.16
23.6–24.0	8	0.35	5	0.26
24.1–24.5	2	0.09	4	0.21
24.6–25.0	2	0.09	2	0.11
25.1–25.5	0	0.00	3	0.16
25.6–26.0	0	0.00	1	0.05
Total	23		19	

Most females were correctly identified but 86% of males were incorrectly classified as females.

DISCUSSION

Genetic analyses correctly identified the gender of all known-sex Crested Caracaras. This technique can also be used for gender determination in hatch-year (HY) and after hatch-year (AHY) caracaras. Even at fledging, young caracaras cannot be sexed reliably using morphometric measurements because they are only approximately 80% of overall adult size (Morrison 1996).

A variety of techniques have been used for gender identification in birds, reviewed by Ellegren and Sheldon (1997). Recently, a set of universal primers were published that will identify gender in all groups of birds except for ratites (Griffiths et al. 1996). Use of these universal primers would have been the technique of choice if we had sought only gender information for individual caracaras. An advantage of using microsatellite fingerprint analysis for gender identification is that these fingerprint patterns can also be used to examine population-level parameters such as genetic diversity within the study group. Membranes obtained from our analyses can be rehybridized with other mini- and microsatellite probes to obtain information on the frequency of polymorphic fragments. Hypervariable DNA fragment patterns have been successfully used in other population studies of birds (Longmire et al. 1991, 1992).

We did not detect any adverse effects of blood sampling and handling procedures on sampled individuals. Because adults were year-round residents within their territories, all individuals sampled were resighted numerous times following handling and blood sampling. We also sampled over 100 HY caracaras that were fitted with radiotransmitters. The resighting rate at independence (2 months

postfledging) for these individuals was 100%. Even nestlings that were sampled at 4–6 wk of age did not appear to incur any adverse effects of the sampling procedures.

Although the caracara does exhibit some slight sexual dimorphism in external characteristics, morphometric measurements proved to be unreliable indicators of gender even for adults. Larger overall size, particularly larger wing length and bill depth, was generally indicative of females. Considerable variation and overlap existed among all characters measured, however, so reliable gender identification of birds in the field from observation alone is not possible. Because of the multivariate nature of these differences, no single combination of characters was found that could reliably predict gender in breeding adults.

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WHY DO GRASS OWLS (*TYTO CAPENSIS*) PRODUCE CLICKING CALLS?

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ABSTRACT.—Flying Grass Owls (*Tyto capensis*) continuously produce double clicks and trains of single clicks with an emphasized frequency of 1.9 kHz. Double clicks have a click rate of seven per second while click trains have a rate of 32 single clicks per second. We examined the possible role that clicking could play in echolocation or in prey capture. The owls did not increase clicking when no moonlight was available. In most cases the birds landed at the roost without clicking. Spectral analysis using a dead Grass Owl showed that the facial mask was directionally insensitive to sounds at 2 kHz. An echolocative function was thus unlikely. Neither of the prey rodents (*Otomys angoniensis* and *Mastomys natalensis*) reacted to recorded Grass Owl clicks. The clicks, therefore, probably did not play a role in prey capture. We present evidence that clicks are involved in social communication between Grass Owls.

KEY WORDS: *Grass Owl*; *Tyto capensis*; *echolocation*; *prey location*; *communication*; *territoriality*.

Porque *Tyto capensis* emite vocalizaciones “click?”

RESÚMEN.—*Tyto capensis* continuamente produce “clicks” dobles y seriados de un solo “click” con una frecuencia de 1.9 kHz. Los “clicks” dobles tienen una tasa de siete por segundo mientras que los seriados tienen una tasa de 32 “clicks” individuales por segundo. Examinamos el posible papel de las vocalizaciones “click” con la ecolocalización o en la captura de presas. Las lechuzas no aumentaron estas vocalizaciones sin luz de luna. En la mayoría de los casos las aves llegaron a las perchas sin producir sonido. El análisis del espectro utilizando un *Tyto capensis* muerto demostró que el disco facial fué direccionalmente insensible a sonidos de 2 kHz. Por lo tanto la función de ecolocalización fué descartada. Tampoco los roedores presa (*Otomys angoniensis* y *Mastomys natalensis*) reaccionaron a las grabaciones de vocalizaciones “click” de *Tyto capensis*. Por lo tanto las vocalizaciones “click” probablemente no juegan un papel en la captura de presas. Presentamos evidencias que las vocalizaciones “click” están involucradas en la comunicación social de las lechuzas.

[Traducción de César Márquez]

The Grass Owl (*Tyto capensis*) is a Red Data Book Species which inhabits grasslands, usually in long grass and often in the vicinity of water (Steyn 1982). Although it is mainly nocturnal, it occasionally hunts during daylight (Steyn 1982). Tytonid owls produce loud bill snapping or clicking sounds under conditions of fear or aggression (Campbell and Lack 1985). Walker (1974) and Bunn et al. (1982) found breeding Barn Owls (*Tyto alba*) using a peculiar rapid vocal clicking call and suggested that this may be connected with courtship, excitement, or intimidation. Little is known of Grass Owl vocalizations but they emit sharp clicking calls during flight, presumably by repeatedly flicking the tongue against the palate (Steyn 1982, Kemp and

Calburn 1987, Erasmus 1992). Grass Owls are exceptional among the owls in that these calls, which have never been described quantitatively, are emitted almost continuously in flight. This requires explanation. There are three hypotheses explaining these clicking sounds. The first is that the clicks are used for echolocation. Since the owls cannot see in absolute darkness and have to rely on a detailed knowledge of local topography during dark nights (Campbell and Lack 1985, Martin 1986), clicking sounds enable them to echolocate obstacles (Kemp and Calburn 1987). Curtis (1952) (cited in Payne 1971) found the performance of Barn Owls in avoiding obstacles to be dependent on available light and concluded that Barn Owls do

not echolocate. Both Oilbirds (*Steatornis caripensis*) and Cave Swiftlets (*Aerodromus* spp.) perform echolocation by means of clicking sounds (Schnitzler and Henson 1980) associated with obstacle avoidance (Medway 1967, Fenton 1975, Schnitzler and Henson 1980). There are two types of echolocative sounds: broadband clicks and more complex calls (broadband or narrowband, Fenton 1980). Broadband clicks are used by Oilbirds comprising a rapid burst of sound impulses lasting up to 25 ms. Some swiftlets and megachiropteran fruit bats emit double clicks with an internal interval of 15–40 ms. The mask and external ear of tytonid owls have several adaptations which increase auditory acuity (Bunn et al. 1982) and which could potentially aid in echolocation. Payne (1971) investigated the acoustic abilities of Barn Owls, and concluded that asymmetrically-placed ear flaps, feathers that are modified to reflect sound and held in a tightly packed and almost parabolic wall, and even the characteristic position in which the head itself is held (downward tilting) are all adaptations involved in hearing. Grass Owls share these characteristics. Payne (1971) conducted playback experiments to dead Barn Owls and found a positive relationship between directional sensitivity and increasing frequency. However, these experiments only took into account the external structure of the facial mask and not the neural basis of hearing which may, in itself, strongly affect owl hearing and which may assist echolocation.

The second hypothesis for clicking calls is that they are used for prey stimulation. The clicking calls of Grass Owls could be a means of stimulating rodents into activity, causing them to reveal their whereabouts (Kemp and Calburn 1987). Given the well-developed auditory power of owls (Campbell and Lack 1985), this would facilitate the capture of prey. The majority of studies on the influence of owl activity on rodents concern owl foraging behavior and rodent use of microhabitat (Abramsky et al. 1996, Thompson 1982, Brown et al. 1988, Longland and Price 1991). However, none of these studies measured the initial reaction of rodents to owl-generated cues but rather at the longer-term activity patterns of the rodents in response to predation.

A third hypothesis suggests that clicking calls are used for intraspecific communication. Erasmus (1992) noted that Grass Owls often click when in the vicinity of their breeding site. This gives rise to

the hypothesis that the clicks are used as signals between Grass Owls.

The aims of this study were, firstly, to give a quantitative description of the clicking call of Grass Owls and, secondly, to test the three hypotheses.

METHODS

During March and April 1997, recordings were made on 22 occasions (1800–2300 H) at Rietvlei Dam Nature Reserve, Pretoria (25°54'S, 28°18'E) using a Sony TC-D5M cassette recorder with a Sony ECM-1035 directional microphone. The frequency response of the recording system was 30 Hz–18 kHz within 4 dB. Most of the recordings were made at two Grass Owl roosts. The first was located in a temporary marshland and inhabited by a Grass Owl pair. The second roost, from which only a single Grass Owl was flushed, was located in a permanent marsh at least 1 km from the first roost. During recording sessions the observer sat approximately 15 m from the roost. Visual observations of the owls were made when possible. Three different light classes were identified using the phase of the moon: (1) full moon, waxing and waning gibbous, (2) waxing and waning crescent, first and last quarter, and (3) no moon. The number of click sequences heard per observation hour was calculated for each of the three light classes.

We characterized the spectral and temporal properties of each recording using Canary 1.2 (Cornell Laboratory of Ornithology) on a Power Macintosh 7100/66 computer. Except for some click trains which were too short in duration, we performed 30 measurements of each of the six parameters (Fig. 1 and Table 1) for a particular recording. The means of these values were used for describing the clicks and for comparing clicks emanating from owls at the two main roosts. Recorded calls were usually in the form of click pairs or as trains of single clicks. Since the amplitude of the recorded clicking calls varied depending on the distance between the microphone and the owl, detail of spectral range also varied. For this reason the emphasized (peak) frequency was the only spectral characteristic measured (Table 1).

To measure the directional hearing characteristics of Grass Owls, we played sounds to a dead Grass Owl; an undamaged road casualty. Due to the protected nature and rarity of this species, other carcasses could not be obtained. Measurements were conducted in an anechoic chamber provided by the South African Bureau of Standards (SABS). We connected a Bruel and Kjaer (B & K) 1405 noise generator to a B & K 1617 filter; the latter was, in turn, connected to a B & K 2706 amplifier which drove a Philips AD11400 tweeter loudspeaker (LS) through which pink noise of $\frac{1}{3}$ octave was played to the carcass (2.0, 10.0, and 12.5 kHz, respectively). We mounted the LS on a flat metal baffle on a tripod. We used a B & K 4165 calibration microphone, calibrated by means of a B & K 4230 calibrator, to measure the frequency response of the LS. We then determined the frequency response of a G-196 miniature electret microphone (Matsushita Corporation). The weakest response was at 12.5 kHz where the signal-to-noise ratio was better than 11 dB. This microphone and an OP07 buffer amplifier were imbedded in resin and placed in the dead owl's head from

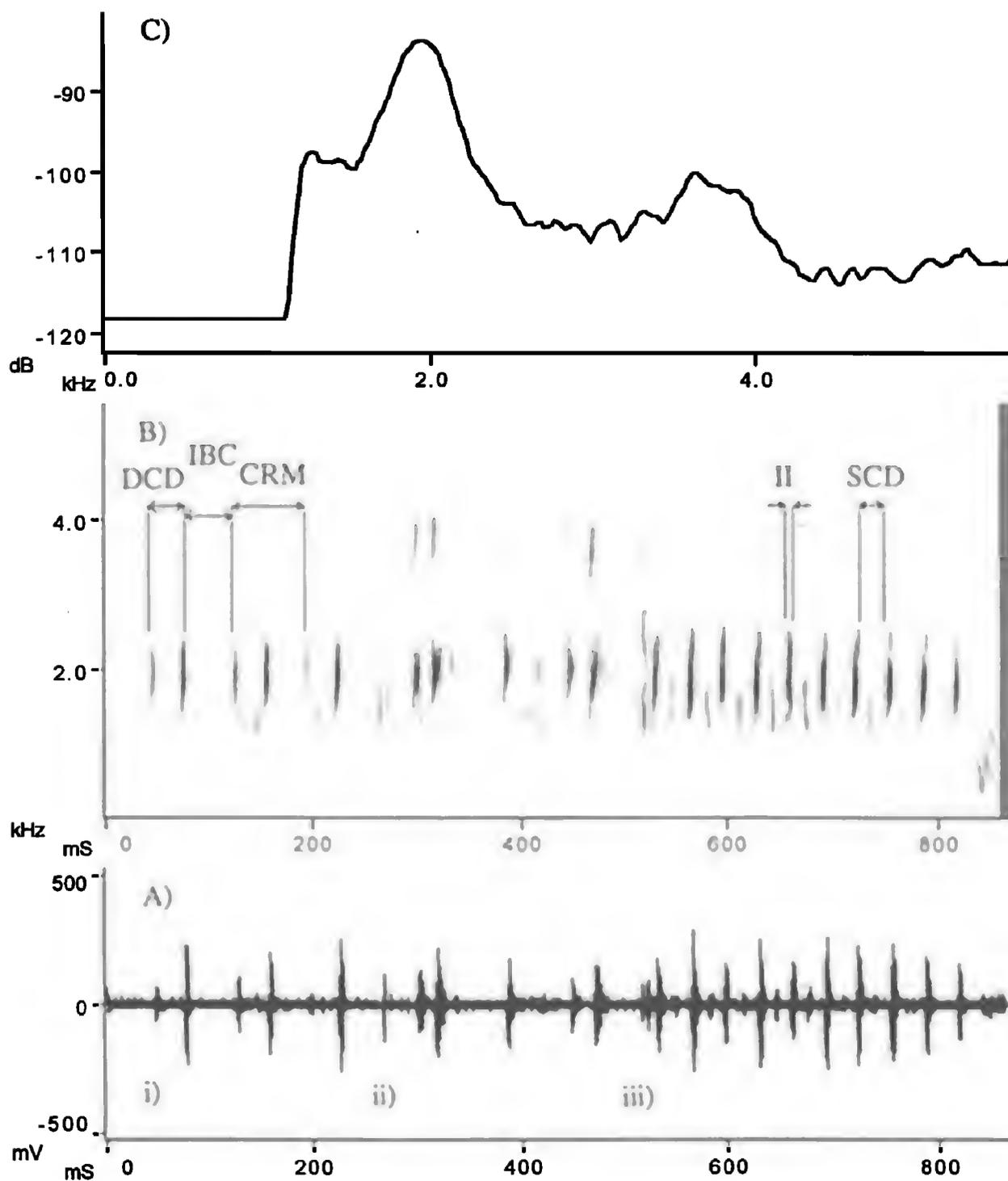


Figure 1. Graphical representations of Grass Owl clicking calls. (A) Oscillogram depicting (i) double clicks recorded at roost 1, (ii) double clicks recorded at roost 2 and (iii) a click train recorded at roost 2 indicating call durations and the temporal characteristics of sound amplitude. (B) Spectrogram of the same sounds. (C) Frequency spectrum of clicks in parts (i) and (ii), above, indicating a single emphasized frequency just below 2 kHz with no significant energy between 2 kHz and 10 kHz. Energy below 1 kHz, resulting from background noise, has been filtered out. Analysis of Fig. 1a, b: FFT size 1024 points; frequency grid size 21.53 Hz. Analysis for Fig. 1c: FFT size = 2048 points, frequency grid size = 10 Hz. The important parameters measured for these calls are indicated on this figure. Double clicks from roost 1 and from roost 2 differ in the durations of single clicks (SCD), the presence of clear harmonics and many other characteristics (Table 1).

above so that the diaphragm of the microphone occupied the position formerly taken by the tympanum of the right ear. The owl was strapped to a mount on a tripod in such a position that the microphone was 1 m from the LS. The microphone was connected to a B & K 2610 measuring amplifier from which the output was measured in microvolts and transformed to relative sound pressure values in dB. Readings of the microphone output were taken through angular increments of 5° in the

horizontal plane of the owl head, starting from 90° with respect to the forward orientation.

Rodent trapping was performed close to the owl roost sites used for sound recordings, enabling us to decide on suitable rodent species for playback experiments. During May 1997, 100 Sherman live traps were set for 1000 trap nights in the vicinity of roost 1, where owls were regularly observed flying parallel to the marsh. Four trap lines, each with 25 traps 10 m apart, were arranged into two

Table 1. Properties of clicks recorded near roost 1 (single bird), roost 2 (a pair) and three other roosts. Rightmost column gives results of a Mann-Whitney *U*-test, comparing the values for roost 1 and roost 2. The data for other roosts are not analyzed since these comprise observations at a collection of other sites in the study area. Number of observations varies between 20–30 per roost.

PROPERTY DESCRIPTION	SYMBOL & UNITS	ROOST 1		ROOST 2		OTHER ROOSTS		U-TEST ROOSTS 1 & 2
		MEAN	SD	MEAN	SD	MEAN	SD	<i>P</i>
Emphasized frequency: audio frequency with the highest amplitude	EF (Hz)	1916	68	1865	95	1945	110	<0.001
Duration of double click, from start of 1st click to end of 2nd click	DCD (ms)	48	27	43	6	42	10	<0.03
Duration of an individual click	SCD (ms)	14	4	10	3	14	5	<0.001
Time duration from end of a click to the start of subsequent click	II (ms)	17	5	25	3	18	5	<0.001
Time duration from end of 2nd click of a double click to start of 1st click of subsequent double click	IBC (ms)	114	35	93	13	104	19	<0.001
Time duration from start of 1st click of a double click to start of 1st click of following double click	CRM (ms)	155	35	123	42	147	19	<0.001

grids of two trap lines per grid. Grids were 500 m apart and the lines within each grid were 50 m apart. Peanut butter with oats was used as bait and alternated with a mixture of raisins and oats in consecutive traps along a trap line. Traps were cleared twice daily at 0700 H and 1700 H. Trapped rodents were sexed, marked using toe clipping and released. Density, by species, was estimated using the Petersen density estimate (Caughley 1977) of the resulting mark-recapture data for the two grids combined. Animals were found to move between trap lines within a grid (50 m). The area covered by a grid was thus calculated as the length of the transect line 250 m and 150 m wide, thereby assuming the animals moved into the grid from at least 50 m distant. This translated to a capture area of 7.5 ha for both grids combined.

In the laboratory, rodents were subjected to recorded owl clicks. Recorded owl clicks were played to five vlei rats (*Otomys angoniensis*) and four multimammate mice (*Mastomys natalensis*) removed from the trapping site at the end of the survey. These species were used because they were the two most common nocturnal rodents with vlei rats also being a favored food item of Grass Owls (Kemp and Calburn 1987). Calls of Crowned Plover (*Stephanibyx coronatus*) and a recording of traffic in a busy street were used as control sounds, respectively, representing sounds to which the rodents were accustomed to in the field and sounds which were foreign to them. These three sounds alternated during consecutive play-

back events and each of the sounds was 25 sec in duration, separated by a silent interval of 15 sec. This sequence was recorded twice onto a four-min endless loop tape. Two glass tanks (surface 150 cm × 70 cm) were used to hold test animals. The floor of each tank was covered with white sand. In one corner was an artificial burrow, while food, water and a passive infrared detector were positioned on the other side of the tank. This area was kept clear. A rodent was placed in each tank. While one animal was tested the other was given time to settle down (>24 hr). Two time switches regulated a 12L:12D cycle, while a pair of red light bulbs remained switched on for the entire duration of the experiment. At night these provided light to record data on a Panasonic AG-455 ME video recorder. When the mouse triggered the infrared detector, a computer switched on the video camera which recorded for 90 sec. After the video camera had been recording for 10 sec, the computer activated a Panasonic RQ-L305 tape player positioned above the tank. The tape played for 40 sec (7.5 sec silence, 25 sec sound, 7.5 sec silence), after which it stopped. The video camera recorded for a further minute before it was deactivated. Each rodent's response to the three test sounds was recorded at least 10 times. Six reaction categories were identified from observation of the video recordings: (1) no movement, (2) rodent moved less than half of length of tank, (3) moved at least half of length of tank, (4) moved to opening of burrow but didn't enter, (5)

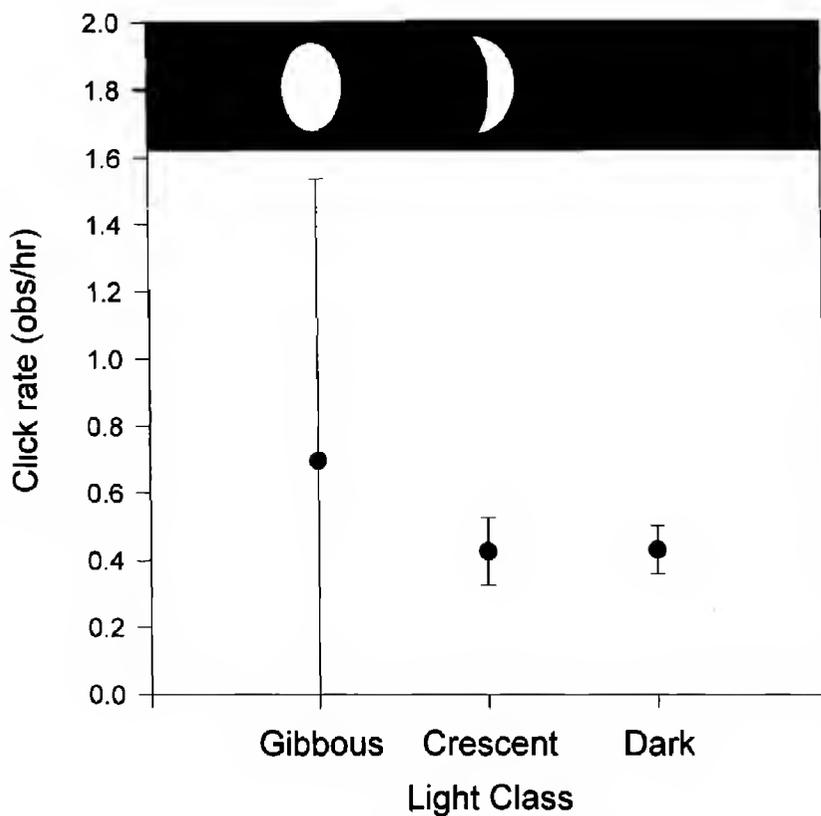


Figure 2. The frequency of Grass Owl clicking (number of owls heard per observation hour) at Rietvlei Dam as a function of the amount of moonlight. There is no trend towards an increase of clicking when no moonlight is available. Bars indicate standard deviations of observations.

ran into burrow but emerged within 10 sec or while sound still played, and (6) ran into burrow and remained there for the duration of the 10 sec or playing time. A reaction was noted for the first 10 sec of the playback (i.e., initial reaction) and also for the entire playing duration (ED) of the sound (i.e., overall reaction).

RESULTS

Field Observations. During 28 nights, we made 64 observations on Grass Owls. When landing at the roost (four observations), the owls did not click at all. On two of these occasions, the owls clicked while approaching the roost but not when landing. When taking off from the roost, the owls produced the clicking call once. While perched on the roost, they clicked on four occasions. On two occasions, owls were seen flying, then stopped clicking and landed, before almost immediately taking off again and resuming clicking. On two other occasions, two owls appearing to chase each other produced click trains. Grass Owls also answered clicks produced by other individuals. This was observed on five occasions though only one bird was visible. The owls tended to increase their clicking activity when ample light was available (Fig. 2). However, the difference in clicking activity between the three

light classes is not statistically significant (Kruskal-Wallis ANOVA, $P = 0.654$).

Spectrographic Analysis. Double clicks, comprising pairs of single clicks, were recorded during 30 observation periods. Click trains, comprising more than two single clicks following in close succession, were recorded seven times (Fig. 1, Table 1). Double clicks had an emphasized frequency of around 2 kHz (Table 1). The mean value for click trains was 1891 ± 144 Hz ($N = 7$), similar to that of double clicks. The single clicks within double clicks exhibited an internal interval (II) of some 20 ms (Table 1), compared to 20.4 ± 6.6 ms ($N = 7$) for the internal interval within click trains. The click rate measurements (CRM) for the double clicks and click trains were 123–155 ms (Table 1) and 31.6 ± 5.0 ms ($N = 7$), respectively. This corresponded to approximately seven double clicks per sec and 31.5 click train clicks per sec. The click trains, however, had a mean duration of only 275 ms ($N = 7$). Double clicks had a duration (DCD) of 42–48 ms (Table 1) and an interval between double clicks (IBC) of 93–114 ms. Single clicks within double clicks and within click trains had similar durations, respectively 10–14 ms (Table 1) and 11.9 ± 4.5 ms ($N = 7$). A Mann-Whitney U -test indicated significant differences in all the click properties produced at roost one (a single bird) compared with those emanating from roost two (a pair, Table 1).

Playback to Dead Owl. At all three playbacks to dead owls, the experimental frequencies (2.0, 10.0, and 12.5 kHz) showed a decline in amplitude of the incoming sound toward 90° (i.e., as the right ear, in which the microphone had been placed was turned away from the loudspeaker; Fig. 3). The microphone was thus shielded from the loudspeaker by the owl's head. Playbacks at 2.0 kHz indicated no clear amplitude peaks or nulls at various orientations (Fig. 3). Three such peaks were measured at 10.0 kHz. The highest was at -15° with two smaller peaks at -60° and 75° , respectively and a distinct null at -45° . Readings taken at 12.5 kHz had a distinct peak at 20° and nulls at -60° and 85° . A 7-dB difference in amplitude existed between the highest peak and the clearest null at 10 and 12.5 kHz.

Rodent Trapping. Six mammal species were trapped. Their densities (animals per ha \pm S.E.M., based on the Peterson estimators for the two grids) were 28 ± 2.9 for the diurnal striped mouse (*Rhabdomys pumilio*), 13.3 ± 2.6 for the multimammate mouse (*Mastomys natalensis*), 2.7 ± 2.5 for the an-

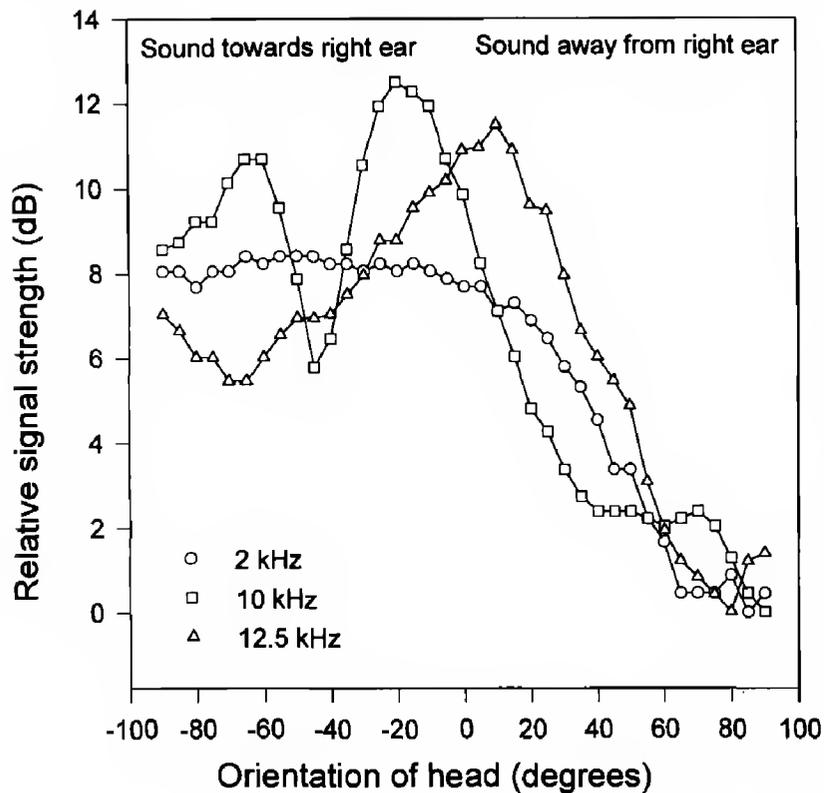


Figure 3. The directional sensitivity of the facial mask of a dead Grass Owl towards pink noise of $\frac{1}{3}$ octave at 2 kHz, 10 kHz and 12.5 kHz. No clear peaks and nulls were evident at 2 kHz, indicating no directional sensitivity at 2 kHz, but which was evident at the higher audio-frequencies.

goni vlei rat (*Otomys angoniensis*), 2.4 ± 2.1 for swamp musk shrew (*Crocidura mariquensis*), 1.3 ± 0.6 for the forest shrew (*Myosorex varius*), and 0.27 ± 0.1 for the grey climbing mouse (*Dendromus melanotis*). The striped mouse was diurnal, the other species nocturnal or crepuscular.

Rodents Subjected to Owl Clicks. For both the 10 sec and entire duration categories, the reactions of the rodents did not differ significantly between the three different treatments (Fig. 4, $\chi^2 < 11.36$; $df = 10$ for each of the nine individuals tested, $P > 0.35$). Most of the rodents either did not move (reaction category one), or they reacted by moving only a short distance (reaction category two). On a few occasions the animals reacted to plover and traffic recordings by running into their burrows (reaction category six, Fig. 4). This reaction was never exhibited in response to the Grass Owl clicks.

DISCUSSION

The repetitive broadband clicks of Grass Owls have a structure which is potentially useful for echolocation. Buchler and Mitz (1980) argued that the signal-to-noise ratio of a signal can be increased by the integration of successive pulses into

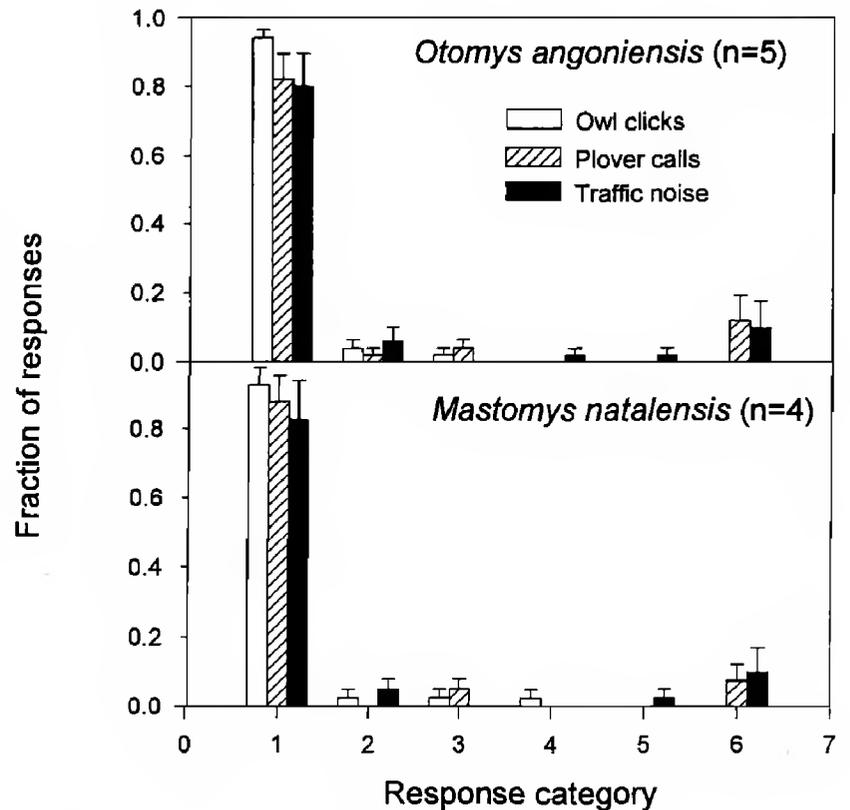


Figure 4. The response of two species of rodents (captured at Rietvlei Dam) towards recordings of Grass Owl clicks and to two other control sounds. Responses during a period of 85 sec following the initiation of a playback are summarized here (see methods). There are no differences in the responses towards the three types of sounds heard by the rodents. Top: *Otomys angoniensis*, Bottom: *Mastomys natalensis*. Bars indicate standard errors of means.

double clicks, allowing for the derivation of relative velocity information. Alternatively, Suthers and Hector (1985) provided a physiological explanation for the use of paired pulses by vocal tract vocalization. Double clicking may also allow individuals to discriminate their echolocation calls from those of others during crowded flights (Fullard et al. 1993); however, Grass Owls defend territories and occur in low numbers. Even though the emphasized frequency of the Grass Owl clicks (1.9 kHz) is lower than that of swiftlets (3–8 kHz; Fenton 1975, Coles et al. 1987, Fullard et al. 1993) and megachiropteran fruit bats (10–17 kHz; Schnitzler and Henson 1980), the temporal characteristics of Grass Owl calls fall within the ranges of other clicking birds. The interval between clicks within double clicks (20 ms) is similar to that of the swiftlets (18 ms; Coles et al. 1987) and megachiropteran fruit bats (18–20 ms; Schnitzler and Henson 1980). The single click duration (12 ms) is much longer than those of swifts (1–3 ms; Fullard et al. 1993), but shorter than the single pulse bursts of Oilbirds (15–20 ms; Konishi and Knudsen 1979). The click

rate for double clicks (7 s^{-1}) appeared to fall within the range used by Cave Swifts ($6\text{--}25 \text{ s}^{-1}$; Medway 1959, Coles et al. 1987), while the click rate for a Grass Owl click train (32 s^{-1}) exceeded this range.

Even though there was structural similarity between Grass Owl clicks and those of other echolocating bird species and bats, several arguments indicated that Grass Owls do not echolocate. First, Grass Owls click while sitting at ground level on their roosts and it is unlikely that such clicks could have an echolocative function. Second, swiftlets and Oilbirds increase their click rates when landing on the nest or when approaching obstacles (Fullard et al. 1993) and when approaching obstacles (Fenton 1975, Konishi and Knudsen 1979). This also occurs in microchiropteran bats (feeding buzz, Jones and Rayner 1990, Miller and Treat 1993) which allows increased resolution of location as the animal approaches the object. No similar increase in click rate has been observed for Grass Owls. In fact, the click rate had a high degree of constancy (Table 1). The owls frequently landed without clicking at all. This contrasts with Erasmus' (1992) finding that the steady pulse rate of flying Grass Owls sometimes increased rapidly when bringing prey to the nest and which probably was related to the presence of chicks, not observed during the present study. Third, there was no correlation between the amount of ambient nocturnal light and the incidence of Grass Owl clicking (Fig. 2). This indicated that clicking is not used to complement visual acuity. In fact, there was a slight trend for increased use of clicking when enough light was available for vision. Fourth, assuming that sound travels at the speed of 350 ms^{-1} in Grass Owl habitat, echos could only travel 4.2 m in 12 ms, the duration of clicks. This would render flying Grass Owls deaf to obstacles within 2.1 m. Assuming that the neural system of the owl can respond within 20 ms, as do some response systems in bats (Suga 1988), Grass Owls should be oblivious of objects closer than about 5 m. This ruled out the echolocation of small, close by objects. Apart from this, open grassland presents few large obstacles which need to be negotiated while hunting. Fifth, the facial mask of the Grass Owl measured in the laboratory was directionally insensitive at 2 kHz (Fig. 3); therefore, it was insensitive to Grass Owl clicks. This can be understood by considering the wavelengths of the frequencies used: 17.2 cm at 2 kHz, 3.4 cm at 10 kHz, and 2.7 cm at 12.5 kHz. It follows that the mask, which has a width of approximately

7 cm, is more directionally sensitive to higher frequencies and implies that echolocation for Grass Owls is not possible at such low audio-frequencies. Although this argument ignores the auditory neural structures and the structure of the internal ear, Payne (1971) showed that Barn Owl auditory acuity during hunting can be explained by the characteristics of the facial mask alone. We conclude that Grass Owls do not use clicking as a means of echolocation.

The fact that Grass Owls were observed flying low and clicking, then stopped clicking, landed, and shortly afterwards resumed the clicking flight could be seen as being supportive of the hypothesis that the clicks aid in hunting. However, it was not certain whether these birds were indeed hunting. Trapping was performed to aid in the choice of rodent prey species used in the experiments. We believe that the use of multimammate mice and vlei rats as experimental subjects is justified by the fact that they were the most abundant nocturnal rodents in the study area and since vlei rats are known preferred prey items of Grass Owls (Kemp and Calburn 1987, Steyn 1982). In other areas, Barn Owls prey on nocturnal species (voles) in relation to their abundance (Campbell et al. 1987).

There was no significant difference in reaction between the three different sound treatments for any of the nine experimental rodents. In fact, the animals in general reacted to none of the sounds (Fig. 4). On a few occasions, they ran into burrows in response to traffic and plover sounds, but not after hearing owl clicks (Fig. 4). The rodents probably reacted to plover and traffic recordings in this way because the latter sounds had a larger dynamic range (becoming louder, then softer) than did the Grass Owl recordings which had more constant characteristics. One might argue that the rodents did not react to recorded clicking calls, but may have reacted to the clicking calls of live Grass Owls. Indeed, Abramsky et al. (1996) found that the strongest response of gerbils (reduction of activity) was to visual stimuli of flying Barn Owls, with weaker responses to recorded hunger calls. However, they were still able to recognize a clear response to recorded owl calls. However, the clicking call of Grass Owls did not stimulate the rodents into activity and it was therefore unlikely to be important in prey capture.

Lack of behavioral reaction by rodents may actually be a response to owl clicks. Even though no evidence of freezing was observed when the ro-

dents heard any of the sound stimuli, this facet of the rodent behavior needs more study within the Grass Owl context. Even though freezing may be adaptive, it does not affect our hypothesis test about prey stimulation.

Our data suggested that Grass Owl clicks have a communicative function toward other Grass Owls. First, we heard owls that double clicked, apparently in response to clicking by another owl, on five occasions. Erasmus (1992) stated that a Grass Owl pair appeared to use their clicking calls to maintain contact with each other while hunting. Second, we observed Grass Owls which emitted click trains while chasing each other on two occasions. Kemp and Calburn (1987) also mentioned bursts of clicking by pairs of flying Grass Owls at the onset of the breeding season, while Erasmus (1992) observed click trains when owls brought prey to their young in the nest. In our study, however, a single bird inhabiting roost 1 was frequently heard clicking while flying within its territory. We speculated that this clicking was a means of making the signaler's presence known to other owls nearby, similar to the behavior of some microchiropteran bats (Leonard and Fenton 1984). Third, the statistically significant differences in clicks of owls at roosts 1 and 2 indicated that significant individual variation existed in call characteristics. While acknowledging that the data for roost 2 are confounded between the two owls roosting there, all the parameters measured at that roost were unimodal and the Mann-Whitney test indicated significant differences in call structure from the two roosts and, by implication, between individual owls. Such individual variation might be audible to Grass Owls, enabling individual recognition by owls. This is consistent with the fact that with microchiropteran bats, echolocating calls are significantly less variable than social calls (Fenton 1994).

Obrist (1995) argued that echolocation has probably evolved from acoustic communication, still serves such functions and could be as flexible. Echolocation signals and some vocalizations following them have a communication function in swifts (Fullard et al. 1993) and Oilbirds (Suthers and Hector 1982, 1985). Fenton (1994) also believed that signals as reliable as those used in echolocation sometimes have a communicative function. Some microchiropteran bats use these signals to eavesdrop in locating vulnerable prey (Balcombe and Fenton 1988), to monitor conspecific intrusions into an area (Leonard and Fenton 1984) and

as a long-range signal advertising its presence in a foraging area (Leonard and Fenton 1984). We believe that, in the case of Grass Owls, clicking is a preadaptation that might potentially constitute raw material from which echolocation in these owls could evolve. However, if the hypothesis of the conspecific communicative function of Grass Owl clicks is robust, the transition from communicative clicks to echolocative sounds has not occurred in the Grass Owl.

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Appendix 1. Parameters used for the analysis of spectral and temporal characteristics of Grass Owl vocalizations.

PROPERTY	MEASUREMENT	
	SPECTRAL	TEMPORAL
Filter bandwidth (Hz)	170.97	638.89
Frame length (ms)	23.22	5.805
Time (ms)	5.805	2.902
Overlap (%)	75	50
Frequency (Hz)	21.53	21.53
FFT size (points)	1024	1024
Windowing function	Hamming	Hamming
Clipping level (dB)	-115	-115

DIET COMPOSITION AND REPRODUCTIVE SUCCESS OF MEXICAN SPOTTED OWLS

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ABSTRACT.—We identified 3793 prey remains from 44 and 41 Mexican Spotted Owl (*Strix occidentalis lucida*) territories in Arizona and New Mexico, respectively, from 1991–95. We found no relationship between Mexican Spotted Owl reproductive success and the proportion of dietary biomass comprised of white-footed mice (*Peromyscus* spp.) or woodrats (*Neotoma* spp.). This was contrary to previously observed diet patterns in Northern (*S. o. caurina*) and California Spotted Owls (*S. o. occidentalis*) showing that mammals can comprise 88.2% of the dietary biomass in Arizona and 94.0% in New Mexico. We found that the most important prey based on relative biomass for Mexican Spotted Owls were woodrats (47.8%) and white-footed mice (17.0%). Gophers (*Thomomys bottae*) and birds occurred more frequently in owl diets in Arizona, while rabbits (*Sylvilagus* spp.), insects, and woodrats occurred more frequently in diets of New Mexico owls.

KEY WORDS: Mexican Spotted Owl; *Strix occidentalis lucida*; *Neotoma* spp.; diet; *Peromyscus* spp.; reproductive success.

Composicion de la dieta y exito reproductivo de *Strix occidentalis lucida*

RESUMEN.—Identificamos los restos de 3793 presas de 44 y 41 territorios de *Strix occidentalis lucida* en Arizona y Nuevo México respectivamente entre 1991–95. No encontramos ninguna relación en el éxito reproductivo de este buho y la proporción de biomasa en la dieta comprendida para *Peromyscus* spp. o *Neotoma* spp. Al contrario de *S. o. caurina* y *S. o. occidentalis* en los cuales los mamíferos pueden comprender 88.2% de la biomasa en la dieta en Arizona y 94.0% en Nuevo México. Encontramos que la presa mas importante con base en la biomasa relativa para *Strix occidentalis lucida* fue *Neotoma* spp. (47.8%) y *Peromyscus* spp. (17.0%). *Thomomys bottae* y aves ocurrieron mas frecuentemente en las dietas de los buhos de Arizona, mientras que *Sylvilagus* spp., insectos y ratas de bosque ocurrieron mas frecuentemente en las dietas de los buhos de Nuevo México.

[Traducción de César Márquez]

The Spotted Owl (*Strix occidentalis*) is a medium-sized forest owl of western North America that eats a variety of prey but primarily small and medium-sized rodents (Forsman et al. 1984, Ganey 1992, Verner et al. 1992, Gutiérrez et al. 1995). Previous dietary studies have suggested that, when breeding, Northern (*S. o. caurina*) and California Spotted Owls (*S. o. occidentalis*) take larger prey items than when they are not breeding (Barrows 1987, Thrailkill and Bias 1989, White 1996). Northern Spotted Owls also appear to concentrate their foraging based on the distribution of large prey (Carey and Peeler 1995, Ward et al. 1998). Finally, when older forests that contain large prey are widely distributed, home-range size increases (Carey et al. 1992).

Since none of this has been adequately studied and documented in the Mexican Spotted Owl (*S. o. lucida*), we have been studying the demography of two Mexican Spotted Owl populations in the south-

western U.S. Because most of the owls in these populations were color marked, we were able to collect representative prey remains from egested pellets in most of the owl territories over several years. Therefore, we could address the population's breeding response to variation of important prey species. Additionally, we were able to assess individual territory breeding response in relation to variation in the diet. An ancillary result of our analysis was an enumeration of the diet from these two populations. Collectively, our results will be important to the conservation of this endangered subspecies because the relationship between demography and prey is an essential element of any conservation strategy.

STUDY AREAS

Our studies are located in Arizona and New Mexico. The U.S. Forest Service chose the study areas based on previous occupancy by owls and their access. The study areas are at opposite ends of the Upper Gila Mountains

Forest Province (Bailey 1980). This province has the highest known number of Mexican Spotted Owls and is considered key to the subspecies conservation (USDI 1995).

The Arizona study area (AZ) encompassed 635 km² and was located in central Arizona on the Coconino Plateau. Elevations ranged from 1800–2660 m. The New Mexico study area (NM) encompassed 323 km² and was located in westcentral New Mexico in the Tularosa Mountains. Elevations ranged from 1900–2900 m. Based on random vegetation points ($N = 141$ for AZ and $N = 130$ for NM), dominant forest cover types were pine-oak (82.2% of AZ and 30.8% of NM), mixed-conifer (14.4% of AZ and 28.5% of NM) and piñon-juniper woodland/grassland (3.4% of AZ and 40.7% of NM). Both areas were characterized by warm summers and cold winters with two distinct periods of precipitation with winter snow and summer monsoon thundershowers.

METHODS

We surveyed owls by imitating their calls and listening for a response at established calling points and along transects ≤ 0.8 -km apart throughout both study areas (Forsman 1983, Franklin et al. 1996). We located owls during daytime visits to check for reproductive activity by feeding live mice (*Mus musculus*) to individuals (Franklin et al. 1996). One or two visits were conducted at a territory to estimate its nesting status and, if found nesting, two or more visits were conducted to estimate the number of young fledged. Nonreproduction (no young fledged) was inferred for a territory if during a single daytime survey, one owl ate four mice or took ≥ 2 mice and cached the last mouse (Franklin et al. 1996).

Regurgitated pellets were collected from 1 April–20 August 1991–95, which encompassed the breeding period from incubation to the fledging of young (Gutiérrez et al. 1995). Pellets were collected opportunistically below owl roosts and nests. Although no random or systematic survey design was used to collect pellets, we assumed the prey remains we identified reflected the true diet composition of the owls. We combined pellets collected on the same day from the same site into one sample unless some pellets were markedly older; in which case older pellets were separated from more recent pellets.

We used skull, appendicular skeletons, beaks, and feathers to identify mammalian and avian remains. Remains were identified using keys in Findley et al. (1975), Hoffmeister (1986) and Dalquest and Stangl (1983), and by comparison with collections at the Humboldt State University Vertebrate Museum and the Museum of Southwestern Biology (MSB) at the University of New Mexico. We estimated the number of prey items in a sample by counting pairs of mandibles, skulls, or appendicular remains, whichever gave the highest count (Forsman et al. 1984). We used mandibles, legs, and exoskeletons to identify and enumerate insects.

We estimated diet composition for each owl site by multiplying counts of each prey species by species-specific body mass. Mean body mass of individual species was estimated from known weights of specimens at the MSB. Most MSB specimens we used were collected within the counties of the study areas or adjacent counties. We attempted to use at least 50 museum specimens for each

prey species to estimate mean weight. Comparison with reference collections indicated rabbit (*Sylvilagus* spp.) remains were probably all small individuals or juveniles. Thus, we used an average weight of juvenile rabbits from the MSB. We did not attempt to age other prey items. We used an estimate of 1.0 g for each insect.

Diet of individual owls probably varies owing to differences in territory composition (vegetation and prey), competition, sex, breeding status, and possibly learned or inherent individual preference. Biases in dietary patterns likely are introduced by lumping prey remains across individuals or territories which have unequal sample sizes. To avoid such bias, we estimated owl diet composition by considering diet composition on a territory by territory base, or by using the aggregate percentage of individual prey remains. The aggregate percentage equaled the proportion of an individual prey species from an individual territory averaged over all territories (Swanson et al. 1974). We compared the frequency of occurrence of the most important prey groups in the diet (arbitrarily defined as groups that comprised $>10\%$ of the diet by number or weight) between the study areas using *t*-tests (Zar 1984), using each territory in each year as the sample. For inclusion into the analysis, we only considered territories with >20 prey remains in a year.

We examined the relationship between owl reproductive success and diet following two approaches. The two null hypotheses we tested were: (1) H_0 : There was no population response in reproductive output to composition of the diet, and (2) H_0 : There was no individual (territory) response in reproductive success to composition of the diet. We used the aggregate percentages of white-footed mice (all *Peromyscus* species) and woodrats (all *Neotoma* species) by year and study area as the samples for the population approach. We used the percentages of white-footed mice and woodrats for individual territories by year as the samples for the individual approach. We only considered white-footed mice and woodrats because they were the only two prey items that comprised $>10\%$ of the dietary biomass on both study areas. We arbitrarily used 20 prey remains within a year as the cutoff point for a territory to enter the analyses.

We used analysis of covariance (ANCOVA; Zar 1984) to test for a population response, with the mean number of young fledged by pairs as the dependent variable, study area as a categorical factor and the aggregate percentages of white-footed mice, and woodrats as the covariates. We used logistic regression (Hosmer and Lemeshow 1989) to test for an individual response in reproductive success to diet. The response variable was divided into unsuccessful territories (zero young fledged) and successful territories (≥ 1 young fledged). The predictor variables were year, study area, the proportion of the diet comprised of white-footed mice, and the proportion of the diet comprised of woodrats. We tested the significance of predictor variables using the Wald statistic (Hosmer and Lemeshow 1989). We excluded territories occupied by single (unpaired) owls for both analyses.

RESULTS

We identified 16 species of mammals, 13 species of birds, and 3 families of insects among 3793 prey

remains from 44 and 41 Spotted Owl territories in AZ and NM, respectively (Table 1). Mammals comprised 69.2% of owl diet by number and 91.9% by mass. The most important mammalian prey groups were woodrats (16.1% by frequency and 47.8% by mass), white-footed mice (38.6% and 17.0%), northern pocket gopher (*Thomomys bottae*, 3.6% and 11.5%), and rabbits (1.8% and 10.1%). Birds comprised 5.4% of the diet by frequency and 7.5% by mass (Table 1). No single bird species accounted for >2.0% of the diet. Insects accounted for 25.4% of the diet by frequency and 0.6% by mass. Mean prey mass for both study areas combined was 42.5 g.

Woodrats ($t = 2.60$, $df = 76$, $P = 0.01$), rabbits ($t = 2.10$, $df = 76$, $P = 0.04$) and insects ($t = 2.10$, $df = 76$, $P = 0.04$) occurred more frequently in NM owl diets while gophers ($t = 2.17$, $df = 76$, $P = 0.03$) and birds ($t = 2.05$, $df = 76$, $P = 0.04$) occurred more frequently in AZ owl diets. The frequency of occurrence of white-footed mice was not different ($t = 1.59$, $df = 76$, $P = 0.12$) between study areas. Mean prey mass was 36.3 g for AZ and 47.3 g for NM.

We collected 20 or more prey remains in a year from 32 territories in AZ and 46 territories in NM. There was no population response in reproductive output to composition of the diet (ANCOVA model $F = 0.85$, $df = 3,6$, $P = 0.52$). There was no indication of a pattern among the individual terms in the model (study area $F = 0.06$, $df = 1,6$, $P = 0.82$; white-footed mice $F = 1.72$, $df = 1,6$, $P = 0.24$; woodrats $F = 0.50$, $df = 1,6$, $P = 0.51$).

To test for an individual response in reproductive success to composition of the diet, the basis for calculating log odds for the logistic model were AZ for the study area effect and 1991 for the year effect. The logistic model adequately fit the data based on a goodness-of-fit test ($\chi^2 = 76.59$, $df = 70$, $P = 0.28$). There were differences in individual territory reproductive success among years, but not between study areas or in relation to the proportion of the diet composed of white-footed mice or woodrats (Table 2).

DISCUSSION

Mexican Spotted Owls in our study took a wide variety of prey, but concentrated on small mammals, especially woodrats, similar to the Northern and California Spotted Owl subspecies (Forsman et al. 1984, Verner et al. 1992). However, except in the canyonlands of southern Utah, the Mexican

Spotted Owl appeared to depend more on small rodents such as white-footed mice and voles (*Microtus* spp.; Ganey 1992, Young et al. 1997) than the other Spotted Owl subspecies (Gutiérrez et al. 1995).

Regional differences in diet have been noted within the ranges of all three subspecies (Forsman et al. 1984, Ganey 1992, Verner et al. 1992), and dietary differences between our study areas may reflect differences in prey abundance, prey availability, or prey selection. We could not address the latter two possibilities given the nature of our study. However, the habitat preferred by gophers (gentle topographic relief with deeper soils) was more abundant in AZ while habitat preferred by rabbits (piñon-juniper woodland) was more abundant in NM (Findley 1975, Hoffmeister 1986). The Mexican woodrat (*N. mexicana*) has been associated with montane coniferous forest and rock outcrops (Cornely and Baker 1986, Hoffmeister 1986), and in New Mexico reaches its highest abundance in montane mixed-coniferous forests (Findley et al. 1975). There appeared to be an abundance of montane coniferous forest on both study areas.

In contrast to previous studies of California and Northern Spotted Owls (Barrows 1987, Thrailkill and Bias 1989, White 1996), breeding owls in our study did not consume larger prey than nonbreeding owls. There were three possible reasons for this difference. First, the Mexican Spotted Owl may be different ecologically from the two coastal subspecies. The Mexican subspecies may depend on the overall abundance of prey within the landscape to successfully reproduce, or may respond to other environmental cues such as predator abundance, or intra- or interspecific competition.

A second possible explanation is that the prey remains we collected did not accurately reflect the true diet of the owls. This should not have contributed to the differences in findings because our protocol for pellet collection was similar to those for studies of the two coastal subspecies. A further concern was that reproducing males may have taken larger prey back to the nest and consumed smaller prey at the point of capture. Under such a scenario, prey remains in pellets might not represent the general diet. Bull et al. (1989) found such a pattern for Great Gray Owls (*S. nebulosa*). However, based on pellet egestion rates, we believe that pellets collected below Spotted Owl roosts and nests accurately depicted overall diet. In an exper-

Table 1. Mexican Spotted Owl diet composition in central Arizona and westcentral New Mexico, 1991–95.

PREY SPECIES OR GROUP	MASS (g) ^a	ARIZONA			NEW MEXICO		
		N	NUMBER %	MASS %	N	NUMBER %	MASS %
<i>Sylvilagus</i> spp.	232.4	7	0.4	2.8	63	2.9	14.3
<i>Spermophilus lateralis</i>	173.9	1	0.1	0.3	0	0.0	0.0
<i>Tamiasciurus hudsonicus</i>	218.5	5	0.3	1.8	3	0.1	0.6
<i>Neotoma mexicana</i>	121.3	143	8.8	29.3	288	13.3	34.2
<i>N. albigula</i>	146.9	21	1.3	5.2	22	1.0	3.2
<i>Neotoma</i> spp.	134.1	38	2.3	8.6	100	4.6	13.1
<i>Neotoma</i> total		202	12.4	43.2	410	19.0	50.5
<i>Thomomys bottae</i>	114.4	89	5.5	17.2	49	2.3	5.5
<i>Eutamias</i> spp.	63.2	4	0.2	0.4	7	0.3	0.4
<i>Microtus mogollonensis</i>	30.8	47	2.9	2.4	82	3.8	2.5
<i>M. longicaudus</i>	34.9	4	0.2	0.2	43	2.0	1.5
<i>Microtus</i> spp.	32.9	3	0.2	0.2	87	4.0	2.8
<i>Peromyscus maniculatus</i>	16.9	403	24.7	11.5	409	18.9	6.8
<i>P. boylii</i>	21.4	141	8.6	5.1	148	6.8	3.1
<i>P. difficilis</i>	22.0	0	0.0	0.0	96	4.4	2.1
<i>Peromyscus</i> spp.	20.1	82	5.0	2.8	186	8.6	3.7
<i>Peromyscus</i> total		626	38.4	19.4	839	38.8	15.6
<i>Zapus princeps</i>	25.3	0	0.0	0.0	1	0.0	0.0
<i>Sorex</i> spp.	5.3	7	0.4	0.1	14	0.6	0.1
<i>Eptesicus fuscus</i>	16.4	1	0.1	0.0	8	0.4	0.1
<i>Lasionycteris noctivagans</i>	9.0	0	0.0	0.0	4	0.2	0.0
<i>Myotis</i> spp.	6.7	6	0.4	0.1	5	0.2	0.0
Unidentified bats	10.7	5	0.3	0.1	2	0.1	0.0
Mammal total		1007	61.7	88.2	1617	74.8	94.0
<i>Cyanocitta stelleri</i>	107.7	8	0.5	1.5	10	0.5	1.1
<i>Colaptes auratus</i>	132.9	5	0.3	1.1	4	0.2	0.5
<i>Accipiter striatus</i>	128.8	1	0.1	0.2	0	0.0	0.0
Unidentified large avian	123.1	15	0.9	3.1	16	0.7	1.9
<i>Myadestes townsendi</i>	31.6	0	0.0	0.0	1	0.0	0.0
<i>Otus flammeolus</i>	50.0	3	0.2	0.3	2	0.1	0.1
<i>Glaucidium gnoma</i>	62.5	3	0.2	0.3	4	0.2	0.2
Unidentified medium avian	48.1	43	2.6	3.5	23	1.1	1.1
<i>Parus gambeli</i>	11.0	0	0.0	0.0	8	0.4	0.1
<i>Dendroica coronata</i>	12.3	0	0.0	0.0	1	0.0	0.0
<i>Junco hyemalis</i>	19.2	0	0.0	0.0	3	0.1	0.1
<i>Sialia mexicana</i>	24.5	2	0.1	0.1	2	0.1	0.0
<i>Sitta carolinensis</i>	17.5	0	0.0	0.0	4	0.2	0.1
<i>Tachycineta</i> spp.	16.7	0	0.0	0.0	1	0.0	0.0
<i>Catharus guttatus</i>	25.4	1	0.1	0.0	0	0.0	0.0
Unidentified small avian	17.9	26	1.6	0.8	20	0.9	0.4
Aves total		107	6.6	10.9	99	4.6	5.6
Cerambycidae	1.0	263	16.1	0.4	275	12.7	0.3
Gryllacridae	1.0	47	2.9	0.1	77	3.6	0.1
Scarabacidae	1.0	4	0.2	0.0	16	0.7	0.0
Unidentified insect	1.0	203	12.4	0.3	78	3.6	0.1
Insect total		517	31.7	0.9	446	20.6	0.4
No. prey items		1631			2162		

^a Prey weights were estimated from specimens at the Museum of Southwestern Biology, Albuquerque, New Mexico.

Table 2. Results of logistic regression for test of individual Mexican Spotted Owl territory response in reproductive success to diet. Data from central Arizona and westcentral New Mexico, 1991–95.

PREDICTOR VARIABLE	PARAMETER ESTIMATE	SE OF PARAMETER	WALD χ^2	
			VALUE	P
Study Area	-0.508	0.565	4.58	0.03
Year				
1992	1.677	1.722	2.05	0.15
1993	2.254	1.163	3.75	0.05
1994	3.019	1.215	6.18	0.01
1995	3.125	1.352	5.34	0.02
White-footed mice	1.693	2.292	0.55	0.46
Woodrats	1.298	1.579	0.67	0.41

imental study of Barred Owls (*S. varia*), Duke et al. (1980) estimated that pellet egestion occurred on average 16.24 hr (SD = 3.48) after meal consumption. Thus, pellets collected below Spotted Owl roosts probably represented food consumed from the previous night, regardless of where it was consumed. In addition, we observed nesting females egesting pellets away from nests, often in the vicinity of male roosts, making pellets collected at roosts of nesting owls a reflection of the pair's diet.

A third possible reason is the different statistical methods used to compare owl diets. We used an aggregate percentage method to estimate population level responses to diet and territories to estimate individual pair response to diet. Previous studies have lumped all prey remains across territories before estimating diet. Thus, there was little information on the contribution of individual territories to the total number of prey remains. Consequently, the observed patterns may have been the result of one or a few territories consuming unique prey items and contributing most of the prey remains to the final tally (Swanson et al. 1974).

A difficult question in estimating diet following our methods is what should be the required minimum number of prey items for including a territory in the analysis. We arbitrarily chose 20 prey remains for the cutoff, but more prey remains would have led to a higher precision in diet estimates. For example, if white-footed mice comprise 20% of the diet ($\hat{p} = 0.20$), the estimated coefficient of variation (CV) given a sample size of 20 is 45%, and given a sample size of 200 the CV is 14%. Although the latter CV estimate is obviously preferred, collecting 200 prey remains from a territory

during the breeding season would be nearly impossible due to logistical constraints. Our choice of 20 prey remains was a tradeoff between precision of diet estimates and sample size considerations. However, simulations using different cutoff points revealed our results were somewhat unstable. An increase or decrease of 10 prey remains from our cutoff point (10 or 30 prey remains to be included in the analysis) resulted in significant associations between reproductive success and white-footed mice in the diet. Because of this instability, we chose to infer no patterns of associations, recognizing that future studies with larger samples or more sophisticated analyses might detect such patterns. Thus, future studies should first consider the sampling effort required to obtain sufficient samples to adequately describe variation among individuals.

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PHILOPATRY AND NEST SITE REUSE BY BURROWING OWLS: IMPLICATIONS FOR PRODUCTIVITY

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ABSTRACT.—We examined demographics of an annually migratory population of western Burrowing Owls (*Athene cunicularia hypugaea*) in Colorado from 1990–94. We banded 555 Burrowing Owls (60% of the known population on the study area) as adults or as nestlings. Five hundred thirteen banded owls (92%) were never reencountered after the year in which they were banded. Forty-two banded owls (8%) returned to the area in ≥ 1 year following banding, and used the area for 2–4 years. Males and females banded as adults returned at similar ($P = 0.45$) rates (19% and 14%, respectively); 5% of banded nestlings returned. Adult males and females nested in formerly used sites at similar rates (75% and 63%, respectively; $P = 0.71$). We found no difference in productivity between philopatric adults (those returning to any portion of the study area) and presumed new adults. However, past brood size was greater for females that returned to former nest sites ($\bar{x} = 4.9 \pm 0.69$) than for females that changed nest sites in subsequent years ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$). Females banded as nestlings that returned as adults always did so after a 1-yr absence from the study area. Conversely, males banded as nestlings that did return, with one exception, returned first in the year following hatch. Fledge rate from 167 nests ranged from 0–9 young per nest ($\bar{x} = 3.62 \pm 0.19$). Nest density increased with the number of years sites were used by breeding owls, but density did not affect mean fledge rate.

KEY WORDS: *Burrowing Owl*; *Athene cunicularia*; *demography*; *migration*; *nest-site reuse*; *philopatry*; *reproduction*.

Filopatría y reutilización de sitios de anidación por *Athene cunicularia hypugaea*: implicaciones para su productividad

RESUMEN.—Examinamos la demografía de una población migratoria anual de *Athene cunicularia hypugaea* del oeste en Colorado entre 1990–94. Anillamos 555 lechuzas (60% de la población conocida en el área de estudio) adultos y pichones. Quinientos trece lechuzas anilladas (92%) nunca fueron encontradas después del año en que fueron anilladas. Cuarenta y dos lechuzas anilladas (8%) regresaron al área después del año en que fueron anilladas y utilizaron el área por 2–4 años. Los machos y hembras anilladas como adultos retornaron en tasas similares (19% y 14% respectivamente; $P = 0.45$); 5% de los pichones anillados regresaron. Los machos y hembras adultos anidaron en sitios previamente utilizados, con tasas similares (75% y 63% respectivamente; $P = 0.71$). No encontramos diferencias en la productividad entre adultos filopátricos (aquellos que regresaron a alguna porción del área de estudio) y los presumibles nuevos adultos. Sin embargo, los pasados tamaños de la nidada fueron mayores para las hembras que retornaron a los sitios de anidación anteriores ($\bar{x} = 4.9 \pm 0.69$) que para las hembras que cambiaron de sitio en los años subsecuentes ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$). Las hembras anilladas como pichonas regresaron después de un año de ausencia al área de estudio. Opuestamente, los machos anillados como pichones que regresaron al área de estudio lo hicieron al año de haber eclosionado con una sola excepción. La tasa de pichones de 167 nidos osciló entre 0–9 por nido ($\bar{x} = 3.62 \pm 0.19$). La densidad de nidos se incrementó con el número de sitios/año utilizados por las lechuzas en reproducción, pero esta densidad no afectó la tasa de pichones.

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The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a species of concern throughout much of its range in the U.S. (Rich 1984) and Canada (Ratcliff 1986, Johnsgard 1988). Campaigns against burrowing mammals that provide nest sites for Burrowing Owls (Butts 1973, Zarn 1974) and habitat loss to development by humans (Zarn 1974, Millsap and Bear 1997) are principal factors suspected in population declines. In Colorado, Burrowing Owls depend chiefly on black-tailed prairie dogs (*Cynomys ludovicianus*) for nesting burrows, and often return to nesting areas used previously (Plumpton and Lutz 1993a). Philopatry and nest burrow reuse by Burrowing Owls have been well-documented (Martin 1973, Gleason 1978, Rich 1984). However, little is known about demographic parameters and the effects of prior reproductive success on site fidelity.

STUDY AREA

We conducted fieldwork on the Rocky Mountain Arsenal National Wildlife Refuge (RMANWR), located 16 km from Denver, CO in southwestern Adams County. This 6900 ha area is vegetated primarily by weedy forbs, cheatgrass (*Bromus tectorum*), perennial grasses and crested wheatgrass (*Agropyron cristatum*). Shrubs include yuccas (*Yucca* spp.), sand sagebrush (*Artemisia filifolia*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) that occur in patches throughout the area.

METHODS

We captured and banded Burrowing Owls during the breeding seasons (1 April–31 July) from 1990–94. We used primarily Sherman and Tomahawk traps to capture nesting Burrowing Owls and their young (Plumpton and Lutz 1992, 1993b). We banded owls with color-anodized aluminum leg bands engraved with unique alpha/numeric combinations (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta Canada) and classified owls as either young of the year or adult (≥ 1 yr). We surveyed the study site daily during the breeding season to locate nest burrows, count young and trap owls. Our surveys consisted of driving roads and using spotting scopes to identify nesting and previously banded Burrowing Owls. We also walked prairie dog towns inspecting burrows for signs of occupancy by Burrowing Owls (whitewash, castings and prey remains). We defined mated pairs as those that used a single burrow and attempted to nest. We defined successful nesting attempts as those in which ≥ 1 young fledged (Steenhof 1987). We estimated minimum brood size as the maximum number of young seen at each burrow prior to fledging.

We classified Burrowing Owls that returned to RMANWR after residency in any prior year as philopatric. We calculated the rate of philopatry by dividing the number of owls banded in any year by the number that returned in one, two, three, or four subsequent years. To explore the relationship between reproductive performance and philopatry, we tested the null hypothesis that

brood sizes of philopatric Burrowing Owls and broods from those owls nesting for only a single season were equal.

Because we did not measure individual territory sizes, we defined nest-site fidelity subjectively to include those owls that nested within the same or an adjacent $\frac{1}{16}$ section (0.162 km²) site used in any previous year. We included adjacent sites because roads surround all sections at RMANWR, often bisecting contiguous prairie dog towns, and Burrowing Owls commonly nest along roadsides (Plumpton and Lutz 1993a, 1993b). Therefore, consecutive nest attempts in adjacent sites were often in close proximity and within the same prairie dog town. The rate at which adults returned to previous nest sites was the proportion of banded Burrowing Owls that returned to previous nest sites, or those banded as nestlings that returned as adults to nest within the same or adjacent sites. To determine whether nest outcome influenced future returns to nest sites, we tested the hypothesis that brood sizes from the prior year for returning Burrowing Owls and broods from owls that changed nest sites in successive years were similar.

We banded owls as nestlings and as adults. Banded nestlings encountered in subsequent years could be aged to a specific year class. Owls banded as unknown-aged adults and encountered in subsequent years were assigned an age class by adding the number of years since initial capture to ≥ 1 . We excluded owls initially captured in the last two years of study to minimize bias in estimating returns.

We tested whether $\frac{1}{16}$ section sites that were used in more years supported more nests, and whether the density of breeding pairs influenced the average productivity of nests.

For all paired analyses, we used *t*-tests when data were normally distributed and Wilcoxon 2-sample tests (*z*) to make comparisons when data were nonnormally distributed. For comparisons involving > 2 samples, we used Kruskal-Wallis *H* tests (SAS Inst. Inc. 1988). For small sample size tests for differences in proportion (e.g., return rates between sexes), we used pooled *t*-tests. All statistical tests were conducted at a significance level of $\alpha = 0.05$. Means are expressed \pm SE.

RESULTS

We banded 555 Burrowing Owls from 1990–94, providing 4 consecutive years of potential return to RMANWR involving 514 individuals (those banded before 1994). During all nesting years, 201 of 334 nesting adults (60%) were known individuals (banded or band-resighted; Table 1). We estimated that this population fledged 533 owlets prior to 1994, of which we banded 369 (69%).

Of the 514 Burrowing Owls banded prior to 1994, 42 (8%) returned in ≥ 1 year after the year of banding. The return rate of banded owls was highest in the year immediately following banding for both sexes and age classes (Table 2). Males and females banded as adults returned at similar rates (19% and 14%, respectively; $P = 0.45$).

Table 1. Burrowing Owls banded or band-resighted (percentage of breeding population^a) at Rocky Mountain Arsenal Wildlife National Wildlife Refuge, Colorado, 1990–94.

AGE/SEX	YEAR					TOTAL
	1990	1991	1992	1993	1994	
Adult/F	15 (56)	26 (68)	22 (56)	32 (76)	14 (67)	109
Adult/M	19 (70)	21 (55)	21 (54)	22 (52)	9 (43)	92
Nestling/Unk.	61 (56)	114 (69)	57 (37)	137 (85)	36 (51)	405
Total	95	161	100	191	59	606

^a # banded or identified from banding in a previous year/# breeding.

Of the 369 Burrowing Owls banded as nestlings prior to 1994, 18 (5%) returned in one or more years after hatch. Of these, 13 (72%) were male and 5 (28%) were female. None of the females returned in the year following their hatch; all returned after a 1-yr absence from RMANWR. Conversely, all but one of the males banded as nestlings that returned in any year, returned first in the year following hatch. Brood sizes of philopatric owls were not different from those of single-season nesters for males (philopatric males: $N = 16$, $\bar{x} = 4.2 \pm 0.66$; single season males: $N = 43$, $\bar{x} = 3.7 \pm 0.43$; $z = 0.47$, $P = 0.64$) or females (philopatric females: $N = 15$, $\bar{x} = 3.7 \pm 0.63$; single season females: $N = 69$, $\bar{x} = 3.8 \pm 0.28$; $z = -0.22$, $P = 0.83$).

Of the owls that returned to RMANWR, 75% of the males banded as adults returned to previously used nest sites, while 63% of females returned to former nest sites ($P = 0.71$). Adult males that returned to nest sites supported broods in the previous year ($\bar{x} = 3.9 \pm 0.81$) no different in size from returning males that changed nest sites ($\bar{x} = 5.0 \pm 1.08$, $t_{14} = 0.69$, $P = 0.49$). However, productivity in the preceding year was greater for fe-

males that returned to former nest sites ($\bar{x} = 4.9 \pm 0.69$) than for females that changed nest sites in subsequent years ($\bar{x} = 2.2 \pm 0.79$; $t_{14} = -2.52$, $P = 0.02$).

Five hundred thirteen owls (92%) banded at the RMANWR were encountered in only the year of banding. Excluding the last two years of study, of those encountered during at least one year after banding, males ($N = 17$) occupied RMANWR for 2 or 3 yr, and females ($N = 13$) for 2–4 yr. The longest-lived owls we encountered were females; one was banded as a nestling and encountered during its fourth year, and one was at least one year old when banded, and encountered three years thereafter, in at least its fourth year (Fig. 1). The

Table 2. Philopatry rate (%) of Burrowing Owls banded at Rocky Mountain Arsenal National Wildlife Refuge, Colorado, 1991–94.

YEARS POST-BANDING	AGE AT BANDING			
	NESTLING <i>N</i> (%)	ADULT		BOTH <i>N</i> (%)
		MALE <i>N</i> (%)	FEMALE <i>N</i> (%)	
1	12 (3)	11 (19)	12 (14)	23 (16)
2	7 (3)	2 (5)	2 (4)	4 (4)
3	3 (1)	0 (0)	1 (3)	1 (2)
4	1 (1)	0 (0)	0 (0)	0 (0)

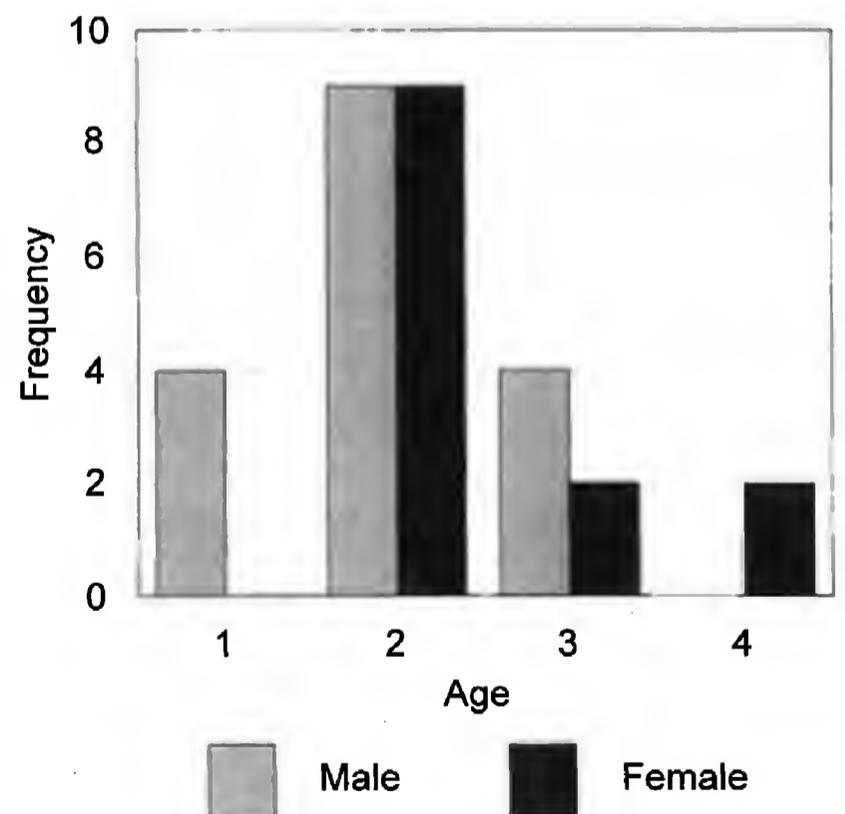


Figure 1. Age classes of banded Burrowing Owls reencountered (including multiple reencounters for some individuals) at Rocky Mountain Arsenal National Wildlife Refuge.

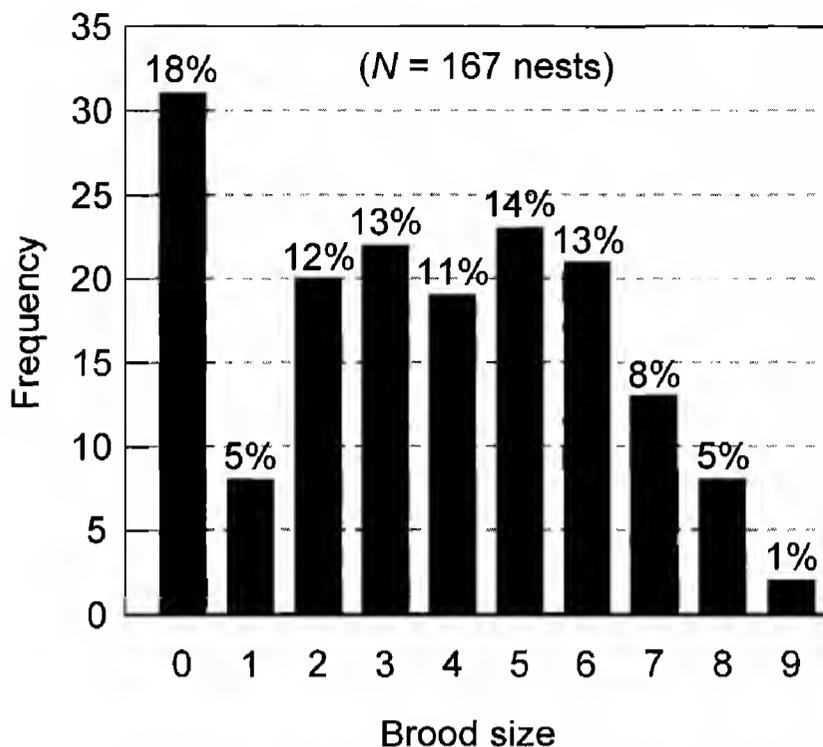


Figure 2. Productivity of 167 Burrowing Owl nests at the Rocky Mountain Arsenal National Wildlife Refuge.

median number of years that owls of both sexes were reencountered at the RMANWR was two.

From 1990–94, 167 nests were observed. At least 31 nests (18%) failed to produce a single chick. Nest success ranged from 0–9 young fledged ($\bar{x} = 3.62 \pm 0.19$; Fig. 2).

The $\frac{1}{16}$ section sites were occupied from 0 to all 5 yr of this study (0/5: $N = 361$, 1/5: $N = 19$, 2/5: $N = 18$, 3/5: $N = 4$, 4/5: $N = 6$, 5/5: $N = 4$). The study area was not homogeneous, and not all sites were suited for occupancy by owls. The mean number of nests/site increased with the number of years of five that the site was occupied (1/5: $\bar{x} = 1.2 \pm 0.12$, 2/5: $\bar{x} = 2.5 \pm 0.12$, 3/5: $\bar{x} = 4.25 \pm 0.75$, 4/5: $\bar{x} = 7.33 \pm 0.61$, 5/5: $\bar{x} = 8.5 \pm 0.87$; $h_4 = 42.48$, $P < 0.0001$; Fig. 3). However, the mean fledging rate did not differ among the 5 levels of annual reuse (1/5: $\bar{x} = 3.8 \pm 0.61$, 2/5: $\bar{x} = 4.1 \pm 0.37$, 3/5: $\bar{x} = 3.4 \pm 0.69$, 4/5: $\bar{x} = 3.4 \pm 0.28$, 5/5: $\bar{x} = 3.7 \pm 0.24$; $h_4 = 1.58$, $P = 0.8$; Fig. 3).

DISCUSSION

Traditionally, differences in philopatry between sexes have been explained as mechanisms to enhance reproductive success (Greenwood 1980). In our study, males and females were equally philopatric and returned to nest sites at an equal rate, but females obtained a reproductive advantage in this behavior by increasing their productivity. However, the relationships we observed between philopatry and reproductive success suggested that, for

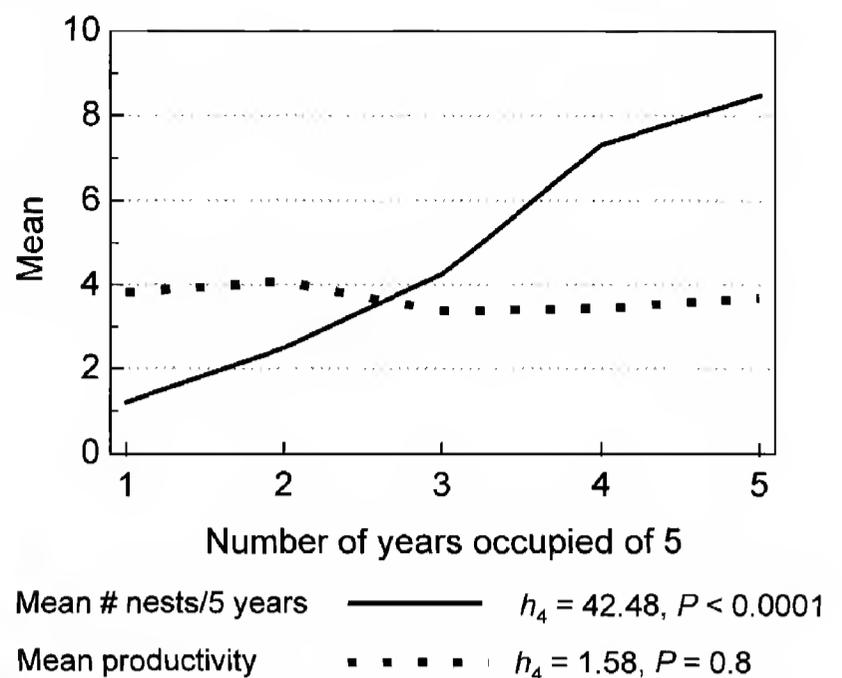


Figure 3. The effects of increasing annual site reuse on mean Burrowing Owl nest-site density and productivity at the Rocky Mountain Arsenal National Wildlife Refuge, 1990–94.

females, a former mate is not as important to reproductive success as is the former nest site. The actual criteria used by females to choose mates are not known for most species (Wittenberger 1983). In our earlier work, we found only weak relationships between morphological characteristics in mated owl pairs (Plumpton and Lutz 1994) and only moderate differences between nesting burrows used and those available, but unused by nesting Burrowing Owls (Plumpton and Lutz 1993a). Assuming female selection, male Burrowing Owls may be chosen for the nesting territories they hold preferentially over other criteria.

For Florida Burrowing Owls (*A. c. floridana*), Millsap and Bear (1997) observed much higher reencounter rates for both sexes of adults, and for owls banded as nestlings. They also observed that male adults reused former nest territories most frequently. As Millsap and Bear (1997) observed for the Florida subspecies, we observed two pairings between a female and her offspring from the previous year. We concur that migration would tend to separate breeding pairs, and that returns to natal sites by yearling males, combined with nest-site fidelity by their mothers, could contribute to such mother-son pairings. Millsap and Bear (1997) also reported adult male Burrowing Owls excavated burrows for themselves on their prior territories, while allowing their sons to occupy their own natal burrow for nesting. They attributed this behavior to reproductive advantages gained by the male in instances where female

selection favors a mate with previous site familiarity, in this instance her son. We offer as an alternative (though not mutually exclusive), hypothesis that the father of the yearling male may increase his inclusive fitness by guaranteeing his son a nest territory and mate, while assuring a territory for himself, and presumably not reducing his own direct fitness. Density of breeding pairs appeared to be unrelated to brood size in our study, so a male sharing a territory with his son may not suffer decreased direct fitness as a result.

Millsap and Bear (1997) also indicated the possibility that there may be little advantage, in terms of retained site familiarity, conferred upon migratory owls. Our population consisted of complete annual migrants, and yet we did observe nest-site reuse in successive years. Therefore, migration may lessen the advantages gained by previous experience on a nest site, but may not eliminate them entirely. Because we lack band returns from elsewhere in the migratory cycle, we do not know whether owls that failed to return to the study area were killed or migrated elsewhere.

Unlike results from Millsap and Bear (1997) our study found that nest-site reuse by females was more often preceded by above-average brood sizes. In our work, broods from previous years were significantly larger for females that reused a site than for those that selected a new nest site.

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USE OF RAPTOR MODELS TO REDUCE AVIAN COLLISIONS WITH POWERLINES

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ABSTRACT.—We evaluated the use of raptor models to decrease bird mortalities caused by collisions with powerlines. One realistic statue of a Golden Eagle (*Aquila chrysaetos*) and two *Accipiter* silhouettes were placed on top of utility towers. Flight behavior of both resident and migrating birds near these power structures was compared to flight behavior we observed at towers where models were not installed. Overall, the number of flocks, number of crossings, and flight altitudes were not affected by the models. Our results indicated that the models did not in any way reduce the risk of collisions. Potential collision victims such as waterfowl, storks, and lapwings were generally indifferent to the models. Most reactions were shown by raptors primarily because the eagle model provoked abundant attacks. We felt that, due to the intensity of attacks on the eagle model, it may have actually increased the possibility of collisions by raptors with powerlines.

KEY WORDS: *avian collisions; mortality; avoidance models; powerlines.*

El uso de modelos de rapaces para reducir la colisión de aves con tendidos electricos

RESUMEN.—La eficacia de modelos de rapaces para disminuir la colisión de aves contra tendidos eléctricos fue comprobada. Un modelo realista de un águila real (*Aquila chrysaetos*) (estatua) y dos siluetas de halcones (*Accipiter* sp.) fueron colocados en lo alto de torres eléctricos. El comportamiento de las aves cerca del tendido fue comparado entre un tramo tratado y un tramo control y entre aves migratorias y residentes de dos áreas de estudio. En conjunto, el número de bandos, el número de cruces y la altura de vuelo fueron independientes de los tramos. Estos resultados indicaron que los modelos no cambiaron el comportamiento de las aves en la manera que pudiera reducir el riesgo de colisión. La composición de especies mostraba dependencia de tramos. Las potenciales víctimas de colisión en las áreas (aves acuáticas, cigüeñas, avefrías) parecían, en general, indiferentes ante los modelos. La mayoría de las reacciones fueron registradas en rapaces, porque el modelo de águila real provocó ataques de otras rapaces. Por ello, un mayor uso de los tramos tratados fue registrado. En consecuencia la probabilidad de una colisión podría incluso aumentar.

[Traducción de Autores]

Collisions with powerlines can be an important cause of death for some species of birds, especially those in unstable populations (Crivelli et al. 1988, Morkill and Anderson 1991). Species that fly in flocks (e.g., waterfowl) and species with high wing loading (e.g., storks [*Ciconia* spp.] and cranes [*Grus* sp.]) (Bevanger 1994, 1998) most frequently collide with and die at power structures. Measures tested to decrease collision mortality have mainly

focused on the use of wire markers to increase the visibility of powerlines. Wire markers have been shown to reduce mortality by 50–80% (Alonso et al. 1994, Brown and Drewien 1995, Jansse and Ferrer 1998).

In some areas where bird collisions are a problem, the use of models of raptors has been suggested as a useful mitigation measure. However, the effectiveness of these models in decreasing col-

lisions has not been tested (Heijnis 1980, Brown 1993, APLIC 1996). If effective, they might have other applications such as at airports and along highway corridors where they might frighten birds away before collision accidents can become a problem (Solman 1973, Burger 1985, Hernandez 1988, Dolbeer et al. 1993, Work and Hale 1996). Habituation of birds to raptor models is a potential problem since it would make them only effective (Brown 1993) along migratory pathways where exposure to the models would only occur once or twice a year (Brown 1993, APLIC 1996).

We assessed the effectiveness of three different raptor models in reducing bird flights near power structures in two study areas. We discuss the effectiveness of these models in reducing collision mortality on powerlines for both migratory and resident birds.

METHODS

We used three models of raptors. Model A was a realistic statue of an "oversized" Golden Eagle (*Aquila chrysaetos*; height 70 cm, length 120 cm, about 130% of normal size) on a perch made of fiberglass. Models B and C were flat, brown and white silhouettes of *Accipiters* made of wood. Model B simulated an *Accipiter* (height 30 cm, length 40 cm) on a perch and model C an *Accipiter* in flight (wingspan 105 cm, length 50 cm) (Heijnis 1980). The models were placed on top of powerpoles or other utility structures.

The first study area was in the south of Cádiz (southern Spain), near the Straits of Gibraltar, where large numbers of birds from Europe pass through when migrating to Africa (Bernis 1980, Finlayson 1992). The high-voltage powerline (400 kV) used was under construction and was without conductors or static wires (Fig. 1a, b). Towers were about 40-m high and about 400 m apart. We tested all three models in this migration area.

The second study area was in the Doñana National Park (southwest Spain). Two powerpoles were erected in marshland and scrub ecotone, where both wintering and breeding birds concentrated at the end of winter. The poles were not connected with any wire or conductor. The poles were about 10 m high and were 150 m apart, as in a distribution powerline (Fig. 1c). In this resident area only model A was tested.

Species we expected to be most susceptible to collisions in the study areas were waterfowl, pigeons (*Columba* spp.), White Storks (*Ciconia ciconia*) and Lapwings (*Vanellus vanellus*) (Fiedler and Wissner 1980, Bevanger 1994, Janss and Ferrer 1998).

Our observation periods were designed to coincide with periods when birds would be most abundant in each of the study areas. In the migration area, observations were made during the postnuptial migration period from 10 July–20 August 1996. In the resident area, observations were made from 12 February–13 March 1997. This period coincided with the end of the winter period and the start of the breeding period. All observations started

immediately after the models were installed. Observations were made almost daily in sessions which lasted at least 2 hr (60 sessions on model A, 62 on models B and C in the migration area, and 24 sessions on model A in the resident area). Observation sessions covered all daylight hours and several sessions were conducted on the same day.

We analyzed the total number of flocks (i.e., bird groups) we observed because individuals in the same flock could not be considered as independent observations. Numbers of flocks were compared between utility towers with raptor models and adjacent towers where raptor models were not installed. Sections were further divided into subsections with one central tower and two lateral subsections which ended at the center of the spans (left and right from the tower subsection) (Fig. 1).

Using a telescope and binoculars, birds were recorded simultaneously at both types of sections from a fixed observation point centered between the two types of sections (approximately 200 m away). All birds and flocks that flew within 100 m of the structures were recorded. For each observation of a bird or flock, we recorded the subsection where the bird came closest to the powerline, the flight altitude at this minimum distance, if the bird (flock) crossed the powerline, and any reactions to the raptor models (e.g., changes in flight direction or altitude either toward or away from the model, any aggressive behavior and vocal reactions). Three levels of flight altitude were recorded in the migration area: 0–20 m (under powerlines), 20–60 m (powerline level) and >60 m (above powerlines). Because utility towers differed in height in the resident area, flight altitude was assigned to two levels: 0–20 m (near poles) and >20 m (above poles).

In the resident area, observations recorded at the central subsections were omitted because of the small distance between the poles (Fig. 1). Observations in the treated sections where models B and C were placed, were compared with the same control section, which was situated in between both treated sections (Fig. 1b).

The number of flocks per subsection and per flight altitude category, and the number of flocks crossing vs. those not crossing over powerlines were compared using either chi-square or $R \times C$ tests of independence (Sokal and Rohlf 1995). This way we tested the homogeneity of the distribution of numbers (i.e., if proportions of birds near the towers were independent of treated and control sections). We used Yates's correction when necessary (Sokal and Rohlf 1995). Based on the experimental design (which had fixed control and treatment sections), we chose a significance level of $P < 0.01$. This way we lowered the probability of drawing wrong conclusions due to random effects. Although we planned to evaluate the use of the models to reduce collisions, we used two-tailed tests because we suspected that models could be both able to attract and scare off birds. Distributions of the number of flocks in tower subsections vs. lateral subsections (the sum of left and right) per taxonomic group, per flight altitude category and birds crossing sections vs. not crossing sections were compared between treatments and controls. We analyzed the number of flocks independent of species as well as pooled by taxonomic groups (Appendix 1).

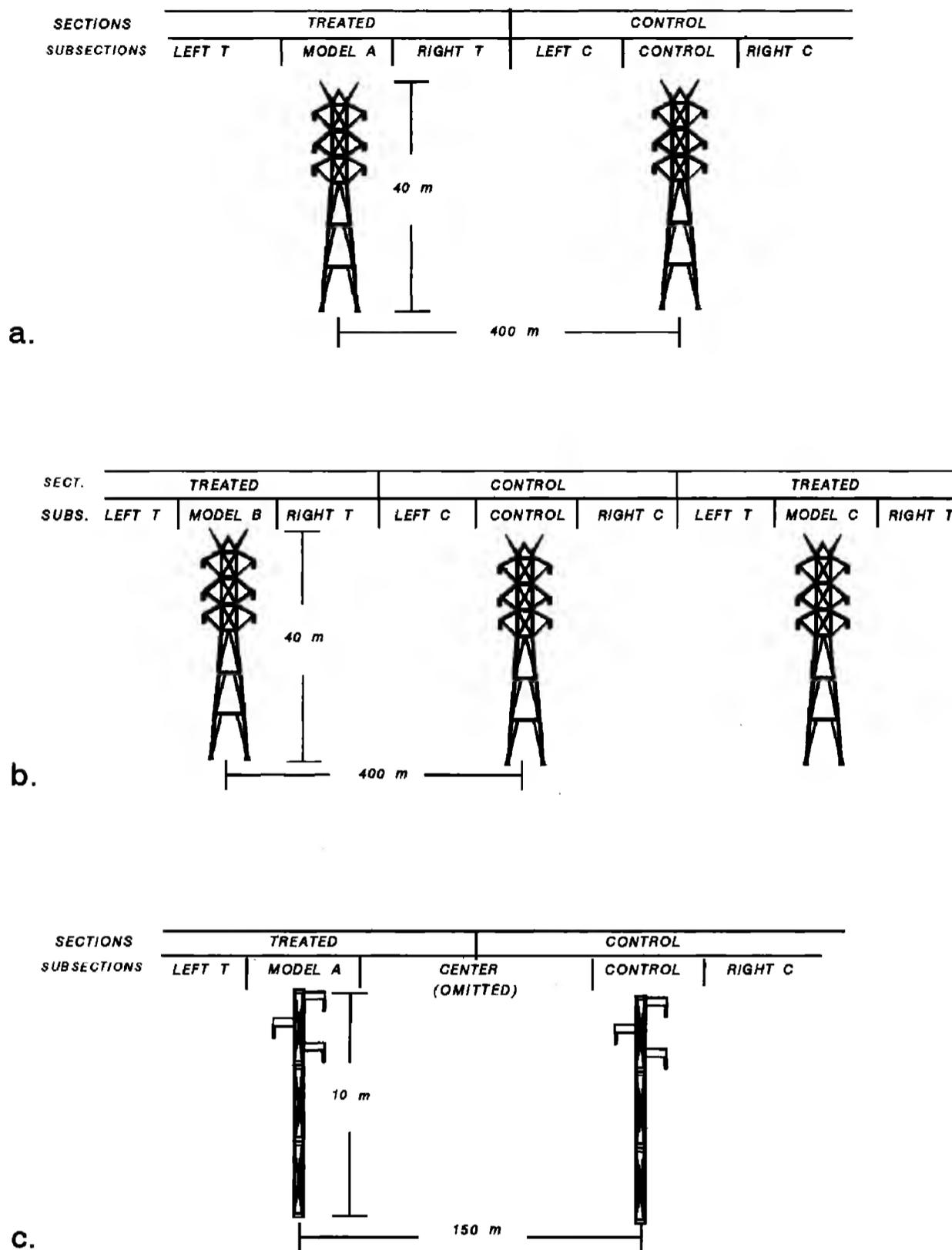


Figure 1. Experimental setting where raptor models were tested in reducing avian collisions with powerlines, (a) utility towers and study sections for model A in the migration area, (b) utility towers and study sections for models B and C in the migration area, and (c) powerpoles and study sections for model A in the resident area.

RESULTS

Model A in Migration Area. During 120 hr of observations, we recorded 466 flocks (2738 individuals) of 30 bird species that came within 100 m of the powerline sections (Table 1, Appendix 1). Number of flocks observed did not differ by subsections ($\chi^2 = 0.98$, $df = 1$, $P = 0.322$); however, species composition did differ by section ($\chi^2 = 119.00$, $df = 4$, $P < 0.001$). At sections where models were installed 41.9% of the birds observed were

raptors (119 records) while, at sections without models, raptors represented only 20.9% of the birds observed (43 records). Flocks also used the second and third flight altitude categories (20–60 and >60 m) more frequently ($\chi^2 = 11.66$, $df = 2$, $P = 0.003$) at sections that were equipped with raptor models. All taxonomic groups tended to be more frequent in higher altitude levels, but this was not significant. Only Griffon Vultures (*Gyps fulvus*) were observed more frequently at flight level

Table 1. Number of flocks per taxonomic groups within 100 m of subsection of powerline tested. Flocks in lateral subsections (left and right) were summed (Lat A, B, C indicate the numbers in lateral subsections of models A, B and C, respectively; Lat X indicates the numbers in the lateral subsections of corresponding control sections). Species per group are indicated in Appendix 1.

MIGRATION AREA	MODEL A	LAT A	CONTROL	LAT X
Ciconiiformes	20	34	15	14
Vultures	10	14	19	24
Raptors	79	40	19	19
Gulls	3	5	1	0
Other birds	31	36	20	34
Passerines	3	9	10	4
Corvids	0	0	1	2
Total	146	138	85	97

MIGRATION AREA	MODEL B	LAT B	CONTROL	LAT X	MODEL C	LAT C
Ciconiiformes	24	47	25	32	22	18
Vultures	9	6	8	20	13	15
Raptors	17	17	23	22	49	27
Other birds	10	4	22	24	48	33
Passerines	7	2	4	8	0	3
Corvids	0	0	1	1	0	1
Total	67	76	83	107	132	97

RESIDENT AREA	MODEL A	LAT A	CONTROL	LAT X
Ciconiiformes	45	60	17	81
Waterfowl	22	16	6	8
Raptors	51	13	15	10
Lapwings	21	19	31	23
Other birds	4	1	4	0
Corvids	20	4	5	5
Total	163	113	78	127

>60 m at sections with raptor models (83.3%) compared to sections without raptor models (53.5%, $\chi^2 = 4.74$, $df = 1$, $P = 0.030$). The number of flocks crossing vs. those not crossing was independent of section ($\chi^2 = 1.70$, $df = 1$, $P = 0.161$).

In 32 cases (6.9%), birds reacted to the models. Nearly all of the reactions were by raptors (90.6%). Fifteen of these we identified as "curiosity," 10 were "attacks," six were "vocal" reactions and one was "scared off." Black Kites (*Milvus migrans*) showed the highest reaction rate (33.8% of the records), followed by the Common Buzzard (*Buteo buteo*, 16.7%). There was no relationship between the number of days since the model was installed and the number of reactions per observation session (Spearman's $r_s = -0.18$, $P = 0.463$; $N = 18$). A Common Kestrel (*Falco tinnunculus*) actually

perched twice in the tower with model A installed at a lower level and it was apparently not bothered by the model.

Models B and C in Migration Area. In 124 hr of observations, we recorded 562 flocks (4062 individuals) of 24 bird species within 100 m of the sections (Table 1, Appendix 1). As in the former case, number of flocks observed did not differ by subsection (model B, $\chi^2 = 0.33$, $df = 1$, $P = 0.565$; model C, $\chi^2 = 0.10$, $df = 1$, $P = 0.756$). Flocks per taxonomic group did differ by section for both models, but no clear pattern was shown (model B, $\chi^2 = 12.01$, $df = 3$, $P = 0.007$; model C, $\chi^2 = 13.17$, $df = 3$, $P = 0.004$). The number of flocks per flight altitude category also did not differ by section (model B, $\chi^2 = 2.15$, $df = 2$, $P = 0.341$; model C, $\chi^2 = 5.54$, $df = 2$, $P = 0.063$), nor did the propor-

tions of flocks crossing vs. not crossing powerlines (model B, $\chi^2 = 4.34$, $df = 1$, $P = 0.037$; model C, $\chi^2 = 3.59$, $df = 1$, $P = 0.058$).

We felt that birds reacted to these models in only four cases (0.7%; three toward model C and one toward model B). These reactions were recorded for two raptors and two vultures and were classified either as "changes in flight direction" (three records) or "curiosity" (one record, model C). Three of these reactions were recorded on the first 2 d after the models were installed. The fourth reaction was recorded 7 d after installation.

Birds also perched on the utility towers with the models 10 times (five times near model B and five times near model C). These were kestrels (*Falco tinnunculus* and *F. naumanni*), Short-toed Eagles (*Circaetus gallicus*) and a Spanish Starling (*Sturnus unicolor*).

Model A in Resident Area. In 98 hr of observations, we recorded 481 flocks comprising 1288 individuals of 31 bird species (Table 1). The number of flocks observed varied between subsections ($\chi^2 = 22.14$, $df = 1$, $P = 0.001$). Over 33% of the observations were made at subsections with raptor models, while only 16.2% were recorded near control subsections. The number of flocks per taxonomic group also varied by section ($\chi^2 = 25.93$, $df = 5$, $P < 0.001$). Waterfowl, raptors and corvids were more often recorded near treated sections (13.8%, 23.2% and 8.7%, respectively) than near control sections (6.8%, 12.2% and 4.9%, respectively). Number of flocks was independent of altitude category ($\chi^2 = 5.34$, $df = 1$, $P = 0.021$). Flocks crossing vs. not crossing over powerlines was also independent of section ($\chi^2 = 1.74$, $df = 1$, $P = 0.187$).

In 59 cases (8.6%), we felt that a bird reacted to models. These reactions were mainly out of "curiosity" (21 records) but 19 birds were "scared off," 13 birds "attacked," and six showed "vocal reactions." Raptors seemed most curious or aggressive while waterfowl and storks were scared off by the model. Black Kites were recorded only four times near the structures equipped with models and in all of the cases the kite attacked model A. Marsh Harriers (*Circus aeruginosus*) approached model A 71.1% ($N = 31$) of the time it was observed. Both kites and harriers breed in the area. The Grey Heron (*Ardea cinerea*) was most frequently "scared off" (9.8%). Again, no correlation was found between the number of reactions and the days passed after the model was installed (Spearman's $r_s = -0.43$, $P = 0.086$, $N = 17$).

DISCUSSION

We found that the installation of raptor models on utility structures in Spain had no effect on decreasing the number of flocks or the types of birds that came near powerlines. Neither did we find that the number of birds in the highest flight altitude category increased over sections equipped with raptor models nor that there were fewer flocks that crossed over treated sections.

In general, raptors were responsible for the differences that we found. The eagle model (model A) had more effect on bird behavior (although not the intended effects) than the *Accipiter* silhouettes. This suggested that models designed to deter birds from approaching powerlines need to be as real as possible. Visible reactions toward the models such as attacks, curiosity or being scared off occurred only 10% of the time. Resident raptor species were more persistent in attacking models. Black Kites and Marsh Harriers had high reaction rates and we did not observe an accommodation toward the models. Although raptors are seldom recorded as collision casualties (Olendorff et al. 1981, Olendorff and Lehman 1986, Bevanger 1994), their reactions to the models suggested that models should not be used to deter raptors near powerlines because the possibility of collisions could actually increase. Based on our results, we concluded that the raptor models we tested would not reduce avian collisions with powerlines. None of the models had a significant effect in scaring off birds and, in the case of raptors, models even attracted birds toward the power structures.

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Appendix 1. Species observed in each taxonomic group for all experiments.

TAXONOMIC GROUPS	SPECIES
Ciconiiformes	<i>Ardea cinerea</i> ; <i>Bubulcus ibis</i> ; <i>Ciconia ciconia</i> ; <i>Egretta garzetta</i> ; <i>Platalea leucorodia</i>
Waterfowl	<i>Anas clypeata</i> ; <i>Anas platyrhynchos</i> ; <i>Anser anser</i> ; <i>Himantopus himantopus</i> ; <i>Limosa limosa</i> ; <i>Numenius arquata</i> ; <i>Tringa totanus</i>
Vultures	<i>Gyps fulvus</i>
Raptors	<i>Accipiter nisus</i> ; <i>Athene noctua</i> ; <i>Buteo buteo</i> ; <i>Circus aeruginosus</i> ; <i>Circus cyaneus</i> ; <i>Circus pygargus</i> ; <i>Circus caetus gallicus</i> ; <i>Falco naumanni</i> ; <i>Falco peregrinus</i> ; <i>Falco tinnunculus</i> ; <i>Hieraaetus pennatus</i> ; <i>Milvus migrans</i> ; <i>Milvus milvus</i> ; <i>Neophron percnopterus</i>
Lapwings	<i>Vanellus vanellus</i>
Gulls	<i>Larus cachinnans</i>
Other birds	<i>Apus apus</i> ; <i>Apus caffer</i> ; <i>Coccothraustes coccothraustes</i> ; <i>Columba livia</i> ; <i>Columba palumbus</i> ; <i>Delichon urbica</i> ; <i>Hirundo rustica</i> ; <i>Lanius senator</i> ; <i>Merops apiaster</i> ; <i>Streptopelia turtur</i> ; <i>Upupa epops</i>
Passerines	<i>Alauda arvensis</i> ; <i>Carduelis cannabina</i> ; <i>Carduelis carduelis</i> ; <i>Galerida cristata</i> ; <i>Miliaria calandra</i> ; <i>Saxicola torquata</i> ; <i>Sturnus unicolor</i> ; <i>Sylvia melanocephala</i> ; <i>Turdus merula</i>
Corvids	<i>Corvus corax</i> ; <i>Corvus corone corone</i>

SHORT COMMUNICATIONS

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WINTER DIET OF THE BARN OWL (*TYTO ALBA*) AND LONG-EARED OWL (*ASIO OTUS*) IN NORTHEASTERN GREECE: A COMPARISON

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KEY WORDS: *Barn Owl*; *Tyto alba*; *Long-eared Owl*; *Asio otus*; diet; Greece.

There have been several comparative studies of the diets of Barn (*Tyto alba*) and Long-eared (*Asio otus*) Owls (Marti 1974, Amat and Soriguer 1981, Mikkola 1983, Delibes et al. 1983, Marks and Marti 1984, Cramp 1985, Capizzi and Luiselli 1996). Dietary information has been useful in documenting the trophic relationships in the areas where the two species are sympatric (Herrera and Hiraldo 1976, Marks and Marti 1984). Greece is within the breeding and wintering areas of these species. Information on the diet of Barn Owl in Greece has come mainly from islands and parts of central and western Greece (Böhr 1962, Cheylan 1976, Pieper 1977, Niethammer 1989, Tsounis and Dimitropoulos 1992). Only a single study has provided information on the diet of these two species on Euboea Island (Akriotis 1981). This study compares the winter diet of the Barn Owl and the Long-eared Owl in a Greek wetland area.

STUDY AREA AND METHODS

Our study was conducted in northeastern Greece near Porto Lagos (40°99'N, 25°32'E) in an area with an extensive coastal wetland complex including lagoons, salt-marshes, mudflats, reedbeds, open cultivated and uncultivated land, small villages, and pinewood plantations. Pellets of Long-eared Owls were collected at a large communal, winter roost in a pinewood and those of Barn Owls were collected in neighboring ruined buildings in February and early March of 1987. Prey were identified according to Brown et al. (1987), Chaline (1974), and MacDonald and Barrett (1993). Mean prey weights were taken mainly from Perrins (1987) for birds, MacDonald and Barrett (1993) for mammals and from our own data for insects.

We estimated the trophic diversity of birds and mammals in the owl diets at the generic level and that of insects at a class level using the antilog of the Shannon Index ($NB = \exp H'$, where $H' = -\sum p_i \ln p_i$, where p_i represents the proportion of prey items of each genus in the sample. To standardize diversity for comparison between

species, we calculated evenness (E) ($N_{2,1} = (N_2 - 1)/(N_1 - 1)$, where $N_1 = \exp H'$ and $N_2 = 1/\sum p_i^2$) (Alatalo 1981, Marks 1984). In order to compare the dietary overlap between species in each wetland, we used Pianka's Index (1973), multiplied by 100 to express it as a percentage.

RESULTS

The diets of both owls contained small mammals, birds, and insects, in descending order of importance (Table 1). Small mammals made up 92% of the Barn Owl diet by number and 85% by biomass. At least 10 mammal species were eaten. The most important of them were *Mus* spp. (40% by number and 32% by biomass), *Microtus epiroticus* (20% and 28%), *Apodemus* spp. (7% and 10%), and *Crocidura suaveolens* (19% and 8%). Birds of at least five species formed 6% of the diet by number and 15% by biomass. Insects (orthopterans) were a minor diet constituent (2% by number and less than 1% by biomass). The average prey weight was 14.7 g (range 0.5–70 g) Prey diversity was 5.19 and evenness 0.67.

Mammals made up 89% of the diet by number and 85% by biomass of Long-eared Owls. We identified at least 12 mammalian species in the diet but the main mammalian prey were *Mus* spp. (48% by number and 35% by biomass), *Apodemus* spp. (23% and 28%), and *M. epiroticus* (13% and 15%). Birds (at least 16 species) formed 11% of the diet by number and 15% by biomass, while insects (orthopteran, Tettigoniidae) were less than 1% by both number and biomass. The average prey weight was 16.5 g (range 2–80 g). Prey diversity and evenness values were 4.29 and 0.56, respectively, both being lower than these of the Barn Owl.

The proportions of all mammalian prey, in terms of number and biomass, were very similar in both owl species. Nevertheless, the proportions of the four most important genera (*Mus*, *Apodemus*, *Microtus*, and *Crocidura*) differed significantly ($\chi^2 = 208.83$, $df = 3$, $P < 0.0001$) *Crocidura* were much more abundant in the Barn Owl's diet while *Apodemus* was more common in the Long-eared Owl's diet. Although fewer birds were taken by the Barn

Table 1. Diet of Barn and Long-eared Owls in Porto Lagos.

PREY	BARN OWL			LONG-EARED OWL		
	NUMBER	% NUMBER	% BIOMASS	NUMBER	% NUMBER	% BIOMASS
Insects	7	2.3	0.2	2	0.2	0.1
Tettigoniidae	1	0.3	0.1	2	0.2	0.1
Gryllidae	6	1.9	0.1	—	—	—
Birds	18	5.8	14.7	102	10.6	15.5
<i>Alcedo atthis</i>	—	—	—	1	0.1	0.3
<i>Lullula arborea</i>	—	—	—	2	0.2	0.4
<i>Alauda arvensis</i>	—	—	—	1	0.1	0.2
<i>Galerida cristata</i>	—	—	—	9	0.9	1.8
<i>Phylloscopus</i> spp.	—	—	—	3	0.3	0.2
<i>Erithacus rubecula</i>	—	—	—	4	0.4	0.5
<i>Turdus</i> spp.	—	—	—	3	0.3	1.5
<i>Aegithalos caudatus</i>	—	—	—	6	0.6	0.3
<i>Parus caeruleus</i>	1	0.3	0.2	2	0.2	0.1
<i>Parus</i> spp.	—	—	—	4	0.4	0.3
<i>Sturnus vulgaris</i>	3	1.0	4.6	2	0.2	0.9
<i>Emberiza</i> spp.	1	0.3	0.5	2	0.2	0.3
<i>Miliaria calandra</i>	5	1.6	4.4	—	—	—
<i>Fringilla coelebs</i>	—	—	—	11	1.1	1.4
<i>Carduelis chloris</i>	—	—	—	3	0.3	0.6
<i>Carduelis</i> spp.	—	—	—	2	0.2	0.2
<i>Serinus serinus</i>	—	—	—	3	0.3	0.2
<i>Passer</i> spp.	3	1.0	1.6	10	1	1.6
Unident.	5	1.6	3.3	34	3.5	4.3
Mammals	286	92.0	85.1	857	89.2	84.5
<i>Crocidura leucodon</i>	6	1.9	1.1	3	0.3	0.2
<i>Crocidura suaveolens</i>	60	19.3	7.9	3	0.3	0.1
<i>Suncus etruscus</i>	2	0.6	0.1	1	0.1	<0.1
<i>Talpa europaea</i>	—	—	—	2	0.2	0.9
<i>Rhinolophus ferrumequinum</i>	—	—	—	1	0.1	0.1
<i>Myotis</i> sp.	—	—	—	1	0.1	0.1
<i>Pipistrellus</i> sp.	1	0.3	0.1	—	—	—
<i>Tadarida teniotis</i>	—	—	—	1	0.1	0.2
<i>Microtus epiroticus</i>	63	20.3	27.6	121	12.6	15.2
<i>Arvicola terrestris</i>	1	0.3	1.3	—	—	—
<i>Micromys minutus</i>	2	0.6	0.2	—	—	—
<i>Apodemus</i> spp.	23	7.4	10.1	219	22.8	27.6
<i>Rattus rattus</i>	3	1.0	3.9	—	—	—
<i>Rattus norvegicus</i>	—	—	—	1	0.1	0.4
<i>Rattus</i> spp.	—	—	—	1	0.1	0.4
<i>Mus</i> spp.	125	40.2	31.6	464	48.3	35.1
Unident. Muridae	—	—	—	33	3.4	3.1
Unident. Rodentia	—	—	—	6	0.6	1.1
Total	311	100	100	961	100	100

Owl, some larger-sized species (*Sturnus*, *Miliaria*) were proportionally more common, so bird biomass was similar in the diet of both owls. Average prey weights were similar. Both the total prey overlap and mammalian prey overlap of the two owl species were 86%.

DISCUSSION

We found small mammals to be the most important prey of both Barn and Long-eared Owls in northeastern Greece. In other Greek areas, Barn Owls have also been reported to prey mainly on small mammals (4–15 spe-

cies), mice (*Mus* or *Apodemus*) being the most important prey by number and usually also by biomass (Akriotis 1981, Böhr 1962, Cheylan 1976, Tsounis and Dimitropoulos 1992). On some islands such as Crete and Corfu, a diverse spectrum of bat species was taken but in low overall proportions (Böhr 1962, Pieper 1977). In comparison to the Barn Owl's diet in Euboea (Akriotis 1981), we found higher biomass proportions of birds (15% vs. 3%) and *C. suaveolens* (8% vs. 1%) but similar proportions of *Apodemus* (10% vs. 11%). In contrast, the diet of the Long-eared Owls we studied had higher proportions of birds (32% vs. 15% by biomass) and *Apodemus* (34% vs. 28%) but those of *C. suaveolens* were low (both <1%). In Euboea, Long-eared Owls preyed upon some mammal species not found in our study. While owls probably differ in terms of the species of mammals they eat in various habitats (Akriotis 1981, MEHPW 1986), they seem to consistently use mammals as their most common prey source.

In Europe and the Canary Islands, both owl species are also mainly mammal predators. As in Greece, in some areas the Long-eared Owl's diet can become heavily reliant on birds (Mikkola 1983, Amat and Soriguer 1981, Delgado et al. 1986). Mice and voles, where abundant, are often the main prey of both species, but their relative proportions in diets vary greatly among areas (Cramp 1985, Taylor 1994). In the U.S., both owl species are primarily mammalian predators but the Long-eared Owl tends to prey on *Microtus* spp. in lower proportions than the Barn Owl, taking fewer birds than in Europe (2% vs. 14% by biomass) (Marti 1976, Marks and Marti 1984).

Bunn et al. (1982) have described the Barn Owl as an unspecialized predator of small mammals while Taylor (1994) suggested that it shows a definite preference for *Microtus* because they are of small size and easy to capture. Long-eared Owls seem to concentrate on relatively few mammal species regardless of habitat type or location they are found (Marti 1974). There is controversy whether *Microtus* are selected or simply taken according to their availability (Mikkola 1983, Cramp 1985). As far as the availability of small mammals in our area is concerned, among 93 individuals snap-trapped at Porto Lagos area between June 1984–October 1986, 48% were *Mus* spp. (41% *M. abboti*), 38% *Crocidura suaveolens*, 11% *Apodemus sylvaticus*, and 3% *Microtus epiroticus* (Vohralik and Sofianidou 1992). Trapping results may not reflect the true proportions of small mammals in their habitats (Yom-Tov 1991, Blem et al. 1993), but we felt they were a good indicator of the relative abundance of small mammals in our study area. They indicated that mice *Mus* were mostly taken by both owls probably because they were plentiful. *M. epiroticus* was somewhat preferred by both and *Crocidura suaveolens* was generally avoided, especially by the Long-eared Owl that seemed to prefer *Apodemus*. Although shrews are in general distasteful to many predators, including the Long-eared Owl, Barn Owls have been found to take them in large numbers, a fact frequently

related to this prey's local availability (Bunn et al. 1982, Mikkola 1983).

The average prey weight of the Barn Owl in Porto Lagos was within the limits of the European populations (range = 12.8–25 g, Taylor 1994). That of the Long-eared Owl was much lower than that of the rest of Europe (37.4 g, Marti 1976), where *Microtus* spp. (average weight range = 30–35 g) make up a larger percentage of the diet (41.5% vs. 12.6% in our study). The lighter prey weight in our study was primarily due to the preponderance of *Mus* spp. in the diet which weighed only 12 g. Average prey weight in the U.S. is even higher than that in Europe for both species reflecting the availability of larger-sized prey species (Taylor 1994). The higher average prey weight of Barn Owls in the U.S. may also simply be due to its larger size than its European relative (Marti 1974, Marks and Marti 1984, Mikkola 1983).

Dietary overlap of the two species varied greatly in six studies in the U.S. ranging from 56–90% (Marks and Marti 1984). In Spain, overlap was much higher in winter (89%, Delibes et al. 1983) than in summer (69%, Delibes et al. 1983; 78%, Amat and Soriguer 1981). The trophic diversity (H') of Barn Owls in our area was 0.32 and evenness (E) was 0.29 (calculated according to Herrera, on a prey class level). Both values were much lower than those reported in Spanish studies (Herrera 1974) suggesting that Barn Owl in northeastern Greece have a more stenophagic diet and that, unlike the Mediterranean region, prey in Greece, especially some small mammals, are probably not in short supply for owls. The high dietary overlap we found between the two owl species, coupled with the similarity in average prey weights, suggested that the two species are grouped along their food dimension and belong to the same trophic guild of owls wintering in this area.

Also in other areas, where the Barn and Long-eared Owl are syntopic, Barn Owls have been shown to have a broader diet (Marti 1976, Amat and Soriguer 1981, Veiga 1981, Capizzi and Luiselli 1996). This probably results from the high dietary overlap between them and it may facilitate their coexistence in areas of syntopy (Marks and Marti 1984). The noticeable difference in the bird species composition in the diets of the two owl species in our area may simply have been related to differences in their hunting habits. Although both forage in the open, Long-eared Owls also hunt under tree canopy (Cramp 1985) (which may also account for the higher proportion of *Apodemus* taken) and they also raid bird roosts in bushes and trees to a much greater extent than Barn Owls.

RESUMEN.—En Porto Lagos (noreste de Grecia), las dietas de invierno de *Tyto alba* y *Asio otus* consistieron básicamente de pequeños roedores (en ambos 85% de la biomasa). Ratones (*Mus* y *Apodemus*) y ratas (*Microtus epiroticus*) fueron las presas más importantes para ambos buhos. Las musarañas (*Crocidura*) fueron importantes solamente para *Tyto alba* (8% de la biomasa). Las

proporciones de las presas de los cuatro mamíferos más abundantes fueron significativamente diferentes entre los buhos. Mas especies de aves fueron capturadas por *Asio otus* (16 vs. 5) pero la contribución a la biomasa fue similar para los dos (15%). El promedio del peso de las presas fue similar (*Tyto alba*: 14.7 g; *Asio otus*: 16.5 g), la diversidad de presas fue mayor en *Tyto alba* (5.19 vs. 4.29). Las dietas coincidieron en un 86%.

[Traducción de César Márquez]

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SIBLICIDE, SPLAYED-TOES-FLIGHT DISPLAY, AND GRAPPLING IN THE SAKER FALCON

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KEY WORDS: *Saker Falcon*; *Falco cherrug*; *social display*; *Grappling*; *siblicide*; *cannibalism*.

Here we report three types of novel aggressive behavior for the Saker Falcon (*Falco cherrug*). The first concerns siblicide, never before directly witnessed for the genus *Falco* (see Newton 1979:117). The remainder concern aggressive behavior of adults, including a new social display we call Splayed-toes-flight and observations of Grappling (wherein two birds lock feet) and Whirling.

On 16 June 1997, we visited a Saker Falcon nest in an elm tree (*Ulmus* spp.) containing three nestlings in Sookhbaatar Aimag (Axe Hero Province), eastern Mongolia. When we went back the next day, we saw one young tearing at prey. Upon climbing to the nest, we discovered that the healthy-looking nestling (age ca. 14 d; compared with photographs of known-aged Prairie Falcons [*F. mexicanus*]: Moritsch 1983) had both feet locked onto its still alive but bloodied and emaciated sibling (Fig. 1). The aggressor repeatedly tore at the wing of its sibling and the whole lateral surface of the right wing was tattered and sodden with blood. After the larger sibling delivered a long series of blows and tugs, it rested, but its feet remained clutching its nestmate. Its lack of responsiveness to our nearness was a surprise and likely reflected that it was starving.

After a few moments, the victim gave a series of hoarse, quiet peeps, then lay silent. It seemed very near death and the tattered condition of its wing evidenced that the larger sibling had already consumed a small portion of it.

We were unable to find remains from the third sibling observed on the previous evening. Holthuijzen et al. (1987) and Court et al. (1988) concluded for their study areas, that missing falcon chicks had likely been consumed. Based on the difficulty the older sibling was having tearing at its nestmate, we concluded that, if the third

nestling was consumed since the previous night, it must have been with the assistance of an adult. After about 15 min, we left the nest with the older sibling still locked onto its victim.

Although siblicide is common in the family Accipitridae (Ingram 1959), Newton (1979) concluded that it was unknown for the genus *Falco*. The best substantiation (but no eye witness account) of siblicide for a falcon is by Ristow et al. (1983), Ristow and Wink (1985), and Wink et al. (1993) for Eleonora's Falcon (*F. eleonora*). They reported many cases of the youngest nestling (in broods of three) being wounded or killed and partly eaten. They clearly documented cannibalism, but they never saw the actual killing. They were confident that the wounds they observed were due to sibling attacks rather than rat (*Rattus rattus*) predation or adult attacks (i.e., infanticide). Cade (1960:208) recorded a probable case of siblicide and cannibalism in the Gyrfalcon (*F. rusticolus*), and Tordoff and Redig (1998) reported a possible case of Peregrine Falcon (*F. peregrinus*) siblicide. We hasten to state that the behavior we observed, and what we believe these authors inferred in other falcons, is probably not the Cainism common in Accipitridae, but rather the concerted attempt of hungry young to eat their nestmates.

Cannibalism is also apparently rare (or seldom reported) for species in the genus *Falco*, except for the Eleonora's Falcon and the American Kestrel (*F. sparverius*) (Bortolotti et al. 1991). A small number of clear records of cannibalism exist for the Peregrine Falcon and Prairie Falcon (Ratcliffe 1980:142, Holthuijzen et al. 1987, Court et al. 1988).

Another novel observation of aggressive behavior occurred on 23 June 1997, also in Sookhbaatar Aimag. Our observations began when a lone adult male Saker Falcon performed a ledge-display bout, including the saker homolog of the Eechup-call (Herbert and Herbert 1965),



Figure 1. Two-week-old Saker Falcon in process of killing and eating its sibling.

at a nest that had failed earlier that year. Later, this bird performed various courtship displays at a larger cliff about 1.5 km away from the failed nest and within the crater of a dormant volcano. There followed a 23-min aggressive encounter between this bird and a pair of adults within the crater.

Deciphering the interactions that follow was possible because all three sakers were physically very different. The two males were conspicuously smaller than the female. The lone male was extremely light and was also readily distinguished from the paired male by its different molt pattern. The female exhibited spot-belly plum-

age, very unlike the males. Our first observations were made unconcealed about 60 m from the 1997 nest. The later observations were made from about 400 m away.

The social encounter began at about 1335 H when the lone male saker flew to an old eagle nest on the crater wall and Eechup-called (the saker version is a monosyllabic Chup; T.J. Cade pers. comm.) while watching the adult female flying away. As the female continued flying away, the lone male began Cliff-racing (Nelson 1977), flying very fast back and forth in front of the cliff and periodically landing on the cliff. After about 3 min, the lone male perched, watched westward, and then flew rapidly up and west as the second male stooped from the west and dove three times at it.

At 1340 H, the two males Grappled (i.e., locked feet) about 10 m from the ground, Whirled two revolutions, then separated just before or just as they hit the ground. They then immediately flew off in different directions. About 500 m from the eagle nest, the lone male settled on a grassy hillside, still within the crater. Next began a 4-min attack wherein the paired sakers stooped many times at the lone male on the hillside. The frequency and high velocity of the stoops effectively kept it grounded. In response to many of the stoops, the lone male would leap into the air, flip upside down, and thrust its feet upwards to ward off the attacks. No exact count was made of the number of stoops during this flurry of activity, but we estimate that the lone male flipped up about 20 times to fend off about 30 stoops. About half of the stoops were by the female, but it appeared that each time contact was made, it was the paired male that had stooped. Contact between the two males probably occurred about five times and definitely occurred twice (i.e., once when they Grappled and Whirled and once when feathers were dislodged).

At 1344 H, the lone male flew rapidly toward the eagle cliff, but was immediately attacked by the pair. In response, the lone male sought refuge amidst boulders at the mouth of a small cave about 50 m below the lower eagle nest. At this juncture, the pair circled many times about 50–100 m above the cave. During this low-level soaring bout, both members of the pair performed an obvious social display which we called Splayed-toes-flight. This display differed from normal soaring flight in that the feet were held about 3 cm below the ventral contour feathers and the toes were spread apart and held slightly below horizontal. From careful, but distant, scrutiny, we estimated that the angle between the outer and inner toes was about 45°.

At 1350 H, the male of the pair flew into the upper eagle nest and Chup-called several times. At 1353 H, the lone male flew up the slope a short distance to some large caves below the lower eagle nest. This action prompted more stoops by the pair, but at 1356 H, the male of the pair circled higher and drifted over the rim of the crater. At 1357:30 H, the lone male flew from the big cave. At 1358 H, the pair stooped very fast and pur-

sued the lone male over the crater rim and east out of sight. At 1406 H, the female returned and circled in the crater. Then at 1408 H, the female landed high on the cliff, then flew west out of sight. At 1420:30 H, the male of the pair returned, circled, landed on the upper cliff, Chup-called and then circled with the female. Both performed Splayed-toes-flight but for neither bird were the legs so conspicuously down as at 1344 H.

By 1426 H, all birds were gone from the crater. At 1427 H, both members of the pair returned, circled in the crater and again performed the less intense form of Splayed-toes-flight. After a few moments, we left the crater.

Talon Grappling has previously been observed in at least six species of falcons (Herbert and Herbert 1965, Simms 1975, Balgooyen 1976:12, Nelson 1977:35–36, 121–122, Newton 1979:153, Ellis 1992). We know of no previous record of talon Grappling for the saker.

Splayed-toes-flight has been observed for two other sakers, both in central Mongolia. On 2 July 1998, an adult female performed two bouts of this display, each about 10 sec in duration, while circling about 200 m from us as we approached a nest containing four nestlings. The display was initiated when a fifth, and already fledged, young flew from the vicinity of the nest to the female's position. The first observation of Splayed-toes-flight was made 22 May 1997 when an adult female saker dangled one leg and repeatedly circled our team during our climb to the nest that contained four young about 12 d of age.

To our knowledge, Splayed-toes-flight has never been previously reported as a social display for any raptor. Lowered flight may serve a thermoregulatory (cooling) function in some raptors (T. Fleming and an anonymous reviewer pers. comm.), but cooling fits the context of only one of our saker bouts. Splayed-toes-flight is very different from the leg-dangle displays found in the Common Buzzard (*Buteo buteo*; Weir and Picozzi 1975) and others of Accipitridae. The only published falcon display involving lowered legs is the Mutual-floating-display described by Platt (1989), wherein mated Gyrfalcons, with wings partly furled and tails spread, perform a slow, parallel descent. Nothing like Splayed-toes-flight was mentioned by either Monneret (1974), Weick (1989), or Nelson (1970, 1977) in their ethograms for the Peregrine Falcon.

RESUMEN.—Proveemos información sobre un pichón de dos semanas de *Falco cherrug* matando a su compañero de nido, siendo este el primer reporte de fratricidio en el género *Falco*. También reportamos combates aéreos entre tres adultos de *Falco cherrug*. Se incluyen observaciones de aferramientos, volteretas y talones extendidos, un comportamiento social previamente no descrito.

[Traducción de César Márquez]

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IMPROVING THE SUCCESS OF A MOUNTED GREAT HORNED OWL LURE FOR TRAPPING NORTHERN GOSHAWKS

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KEY WORDS: *Great Horned Owl*; *Bubo virginianus*; *Northern Goshawk*; *Accipiter gentilis*; *trapping*.

Dho-gaza nets with live Great Horned Owl (*Bubo virginianus*) lures are one of the most effective ways of capturing raptors during the breeding season (Bloom et al. 1992, Steenhof et al. 1994). However, the rigors of field conditions, stress on the owl during handling and transport and risk of injury or death to both the owl and intended capture bird should be considered and may preclude use of a live owl. Mounted Great Horned Owls have been used to capture raptors but they are typically not as effective as live owls (Bloom 1987). Using a mounted owl, Gard et al. (1989) reported that the lack of movement resulted in a less aggressive response by breeding American Kestrels (*Falco sparverius*). Jacobs (1996) constructed a mechanical owl using a remote control unit to capture three species of hawks. Although his method was relatively successful, he did not provide detailed assembly instructions or mention factors (e.g., cost or mechanical failure) that may limit the use of this technique. Here, we describe a simple technique to improve the success of mounted Great Horned Owl lures and report the success of this method for trapping breeding Northern Goshawks (*Accipiter gentilis*).

METHODS

Trapping was conducted at 14 goshawk nest sites within Ashley National Forest located in northeast Utah. We used a modified dho-gaza (as described by Clark 1981) with a taxidermic mount of a Great Horned Owl as a lure to capture breeding goshawks during the nestling period. We placed the dho-gaza (net size 139.5 cm high × 256.5 cm long with 4.5 cm mesh) within 30 m of nests, selecting areas where natural vegetation provided flyways that would funnel goshawks into the net. Subsequently, one person laid face up on the ground <1 m in front of and toward the center of the net (between the net and the nest) covered by camouflaged netting. This individual held the owl upright on their chest and after the crew was out of sight, voiced the 5-note territorial hoot of the

Great Horned Owl while moving the owl with their hands. Once an adult goshawk was captured, we reset the dho-gaza and attempted to capture the mate.

During the nestling period, male goshawks frequently forage away from the nest for extended periods. In contrast, females remain relatively close to nests and will aggressively defend against potential predators (Palmer 1988). For these reasons and because we did not always attempt to capture mates, we separated success rates into two categories: (1) birds caught first at each nest site and (2) capture of the mate. Trapping success was determined by calculating captures per attempt and we considered multiple trapping attempts at the same nest site as one attempt (see Bloom et al. 1992, Jacobs 1996). When attempting to capture mates, the individual with the owl was not placed under the net until we heard or observed the bird, thus minimizing discomfort to the individual. Because we were evaluating the effectiveness of the lure (not the net) to incite the bird to stoop at the net, we considered it a success even if a goshawk hit the net and escaped (i.e., this was our failure, not that of the lures).

RESULTS

Between 24 June–4 July 1995, we captured a total of 15 adult goshawks. We had an 86% (12/14) success rate for capturing goshawks during our initial attempts (category 1) and a 60% (3/5) success rate for subsequent attempts to capture mates (category 2). All but one (11/12) of the initially captured birds were females and all (3/3) subsequently captured birds were males. The remaining birds that were not captured during initial attempts vocalized but never stooped at the lure. Of the five attempts to capture mates, two were actually caught, one bounced out of the net, one vocalized but never stooped and one never appeared. Overall, there was a 79% (15/19) success rate using our technique to capture nesting goshawks.

DISCUSSION

Using a mechanical owl to capture breeding Red-shouldered Hawks (*Buteo lineatus*), Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipiter striatus*), Jacobs (1996) reported a 54% (15/28), 60% (3/5), and 77% (48/62) success rate, respectively. Gard et al. (1989) reported 21 of 24 (87%) American Kestrels either vocal-

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ized or dove at a live Great Horned Owl placed 10 m and 50 m from nests. The same study reported that only 8 of 24 (33%) kestrels responded aggressively to a mounted owl placed at the same distance from the nest. Our technique enables trappers to simulate the natural movement of the owl while hooting from the same location. These factors improved our success compared to techniques that used a mechanical or mounted owl alone.

Bloom et al. (1992), using three independent trapping studies of breeding goshawks, reported a 76% (41/54), 54% (27/50), and 67% (68/102) success rate using a live Great Horned Owl as a lure. These results are territory trapping success (TTS) rates (see Bloom et al. 1992 for definition) and are not directly comparable to our definition of success. Using their definition of raptor trapping success (RTS), our success increases to 93% (14/15) or 100% (if we include the one male that escaped). Thus, our definition is more conservative than RTS and more comparable to TTS. We feel our definition is appropriate, considering we targeted both sexes at only 5 of 14 territories. Perhaps a more precise method of evaluating trapping success would be to include time spent for each capture (Steenhof et al. 1994).

Bloom (1987) reported two incidents where female goshawks locked talons with bait owls. With other hawk species he suggests that injury to the live owl lure or attacking hawk is rare. In any case, we agree with Schulz (1990) who suggests that we not forget our moral and ethical responsibility, which includes respect, sensitivity, and compassion for the animal being manipulated. Because our trapping success equals or exceeds those reported by Bloom et al. (1992) and considering the ease of maintaining and transporting a mounted owl compared to a live owl, we suggest that a live owl be used only when absolutely necessary.

The mechanical owl built by Jacobs provides a safe and effective alternative to a live owl. Using our method of placing an individual covered with camouflaged netting (and hooting) at the location where the owl is placed, or using taped vocalizations placed near the owl, may further improve the success of the mechanical owl. However, weather conditions, condensation, wet vegetation, and other logistical considerations (i.e., cost, maintenance, and difficulty of construction) may prevent proper functioning or practical use of a mechanized decoy. Our technique is an easy, safe, and effective method for capturing breeding goshawks. This method should be effective for capturing other raptors that aggressively defend their nest, but it has not been evaluated. We recommend this method or Jacob's mechanical owl, in lieu of a live owl, for capturing breeding Northern Goshawks.

RESUMEN.—Buhos (*Bubo virginianus*) vivos, disecados o mecánicos han sido utilizados como señuelos para mejorar la captura de las redes dho-gaza y atrapar aves ra-

paces. Los buhos vivos han sido los más efectivos, pero existen ciertos riesgos para el buho como para la rapaz. Los buhos disecados son menos efectivos debido a la falta de movimiento y vocalizaciones. Los buhos mecánicos son efectivos pero carecen de vocalizaciones, no funcionan adecuadamente bajo ciertas condiciones de campo y son difíciles de construir y mantener. En este artículo, describimos una técnica simple y segura que permite vocalización y movimiento de un buho disecado. Documentamos el éxito de este método para atrapar a *Accipiter gentilis*. Nuestra técnica fue tan exitosa como la de un buho vivo pero sin riesgos y mejor que un simple buho disecado o uno mecánico.

[Traducción de César Márquez]

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PREY SIZE MATTERS AT THE UPPER TAIL OF THE DISTRIBUTION:
A CASE STUDY IN NORTHCENTRAL CHILE

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KEY WORDS: *prey selection; Barn Owl; Tyto alba; Great Horned Owl; Bubo virginianus; Chile; semiarid ecosystem.*

Sympatric raptors are known to consume different prey species, often cueing on the abundance, size, morphology, or behavior of the prey (Kotler 1985, Kotler et al. 1988, Jaksic 1989). Less known is how raptor predation applies on different size or age classes of a given prey species (Fulk 1976, Marti and Hogue 1979, Zamorano et al. 1986, Vargas et al. 1988, Longland and Jenkins 1987, Dickman et al. 1991), but abundance, size, and behavior of age classes have also been postulated as the cues used for hunting them.

Castro and Jaksic (1995) showed that sympatric Barn Owls (*Tyto alba*) and Great Horned Owls (*Bubo virginianus*) at a study site in northcentral Chile (Aucó) did not take different sizes of their most frequently shared prey, the leaf-eared mouse (*Phyllotis darwini*). The larger Great Horned Owl (1200 g) preyed on average on 50-g mice, while the Barn Owl (300 g) consumed 54-g mice. The lack of statistical difference resulted from both owls preying across all size/age classes of their shared prey.

Because leaf-eared mice in Aucó average 47 g, which is close to the mean prey size for the Barn Owl in Chile (45.1 g, Marti et al. 1993), we decided to investigate predation on a prey species shared by both Great Horned and Barn Owls that exceeds the mean prey size for the Great Horned Owl in Chile (72.8 g, Marti et al. 1993). The species studied was the 182-g chinchilla rat (*Abrocoma bennetti*), the second largest rodent species at our study site in northcentral Chile (Jaksic et al. 1992, Jaksic 1997).

MATERIAL AND METHODS

Las Chinchillas National Reserve (31°31'S, 71°06'W) at Aucó is located approximately 300 km north of Santiago, Chile. This site has a semiarid climate, mean annual precipitation of 157 mm, elevations ranging from 400–1700 m and slopes with vegetation dependent on solar exposure. On equator-facing slopes, vegetation is dominated by cacti, bromeliads and a few evergreen shrubs; on polar-facing slopes, evergreen shrubs are the dominant species. More details about this site may be found in Castro and Jaksic (1995).

From March 1993–February 1996, we collected pellets of Great Horned and Barn Owls under perches, roosts, and nests in Aucó. At least one pair of Great Horned and four pairs of Barn Owls inhabited the study area. Prey

remains in pellets (mostly small mammals) were determined to species level. More details about procedures may be found in Castro and Jaksic (1995).

Whole cranial remains of chinchilla rats found in owl pellets were set apart and measured. According to the morphometric characters of each cranium, we estimated the body mass by regression analysis. The relationship between cranial measurements and body mass was calculated from specimens of known mass in the Museo Nacional de Historia Natural (Santiago, Chile). Three cranial dimensions were measured with calipers at 0.5 mm precision: width of the zygomatic arch (cf. Green and Jameson 1975), minimum distance between upper incisor and first molar (upper diastema, cf. Blem et al. 1993) and length of the upper tooth row.

We used bilateral Kolmogorov-Smirnov tests (Sokal and Rohlf 1981) to compare the size distribution of chinchilla rats preyed upon by each species of owl. Although estimates of body mass derived from cranial measurements were computed to 1 g, we preferred to group individuals into 20-g increment classes because of the inherent statistical error contained in making extrapolations based on regressions. We pooled data obtained during the entire study period of 36 mo. (March 1993–February 1996).

RESULTS AND DISCUSSION

The three cranial measurements were good estimators of chinchilla rat body mass ($r > 0.949$), but tooth row length was chosen because of its better fit ($r = 0.978$, $P < 0.05$), and because it could be measured in 97% of the cranial remains (256 out of 264). The equation was: body mass (g) = antilog ($2.341953 + 3.386149 \log$ tooth row length in mm).

On average, Barn Owls consumed chinchilla rats weighing 145 ± 73 g (\pm SD, $N = 182$), whereas those in the diet of Great Horned Owls weighed 178 ± 70 g ($N = 73$). This difference in prey weight consumed was significant at $P = 0.00119$ (Kolmogorov-Smirnov $D = 0.28005$). Nevertheless, the prey weight ranges consumed overlapped considerably: 31–332 g for Barn Owl and 47–348 g for Great Horned Owl (Fig. 1). How a 300-g Barn Owl can take such large-sized chinchilla rats eludes us, unless our equation overestimates prey weights based on cranial measurements. We would like to emphasize that chinchilla rats >290 g were preyed upon only sporadically by Barn Owls (Fig. 1). On the other hand, it is not surprising that 1200-g Great Horned Owls preyed on

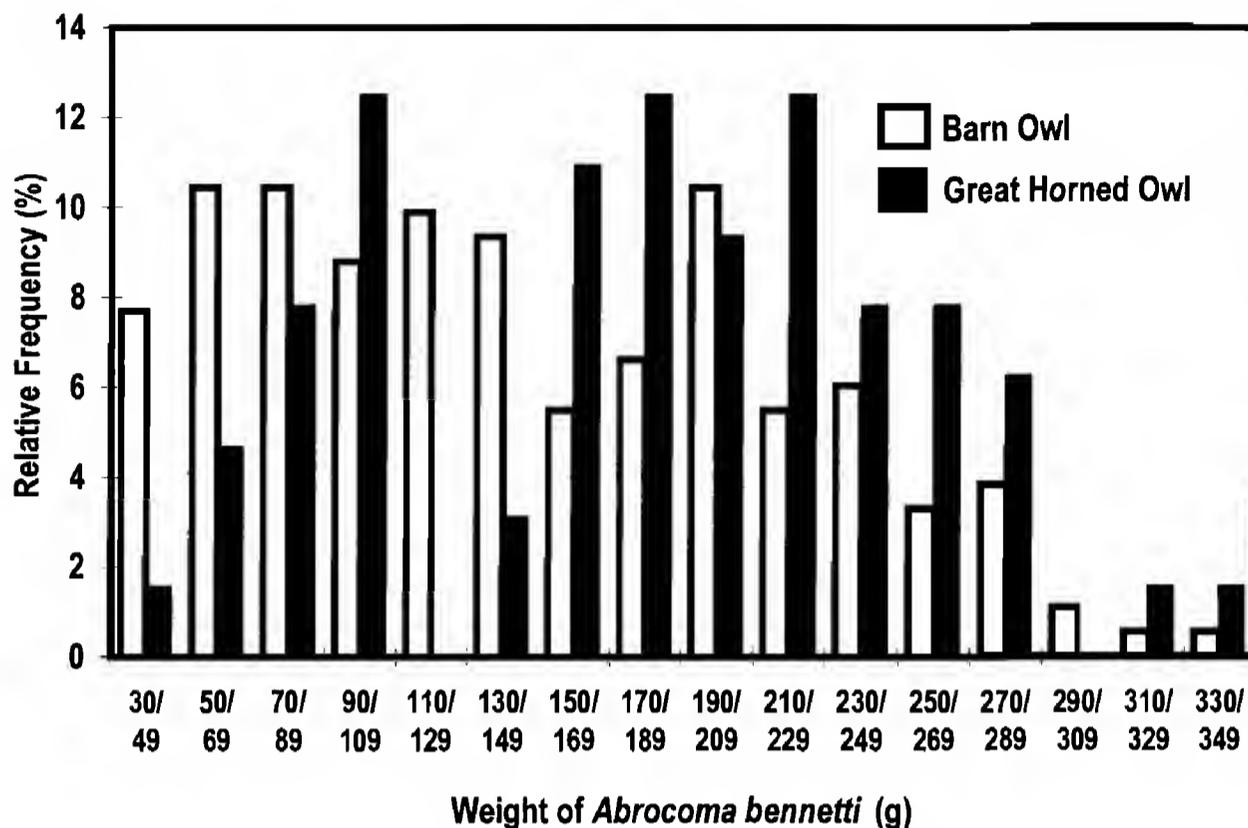


Figure 1. Body mass frequency distribution of chinchilla rats (*Abrocoma bennetti*) consumed by Great Horned Owls (*Bubo virginianus*; $N = 73$ rats) and Barn Owls (*Tyto alba*; $N = 182$ rats) in Aucó, northcentral Chile, March 1993–February 1996.

<49-g chinchilla rats because this owl is known to consume even smaller rodents at the study site (Castro and Jaksic 1995). It should also be noted that chinchilla rats comprise only a minor part of the diet of Barn Owls at the study site ($\bar{x} = 2.2\%$ by prey numbers throughout 1988–90; see Jaksic et al. 1992), whereas they are the second most common mammal consumed by Great Horned Owls ($\bar{x} = 22.7\%$ throughout 1988–90; Jaksic et al. 1992).

Tyto (300 g) and *Bubo* (1200 g), which differ in body weight by a factor of 4, and by 23% in mean prey size (145 vs. 178 g, respectively), were able to exploit a single prey species ranging over one order of magnitude in mass (31–348 g). This suggested that the Barn Owl was able to handle, even if infrequently, prey of 50% its own body weight which is remarkable. The equivalent figure for the Great Horned Owl would be 15%, well within its handling power (Marti et al. 1993).

Our results indicated that small prey such as the 47-g leaf-eared mouse does not allow segregation by size between these two owls, likely because of its limited size range (Castro and Jaksic 1995). However, the two owls did show segregation by size when preying on larger prey such as the 182-g chinchilla rat, likely because of the greater opportunity afforded by its ample size range. These observations support Wilson's (1975) assertion that prey size matters to predators chiefly at the upper tail of the frequency distribution.

RESUMEN.—En un estudio previo en Chile central (Aucó), se detectó que las lechuzas *Tyto alba* (300 g) y *Bubo virginianus* (1200 g) consumían individuos del roe-

dor *Phyllotis darwini* de peso promedio 50 y 54 g, respectivamente. Esta diferencia no era significativa. Debido a que este roedor está cerca del tamaño promedio de presa calculado en Chile para *Tyto* (45 g) y lejos del calculado para *Bubo* (73 g), decidimos investigar qué ocurría con la depredación de estas lechuzas sobre un roedor mucho más grande, *Abrocoma bennetti* (182 g). Encontramos que *Tyto* consumía individuos de peso promedio 145 g y que *Bubo* consumía aquellos de peso promedio 178 g, una diferencia significativa de 28%. Nuestra conclusión es que cuando la presa es pequeña (*Phyllotis*) las dos lechuzas no alcanzan a segregarse en cuanto a los tamaños consumidos, y que sólo ocurre cuando la presa es grande (*Abrocoma*).

[Traducción de Autores]

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SPATIAL AND TEMPORAL VARIATIONS IN THE DIET OF THE COMMON KESTREL (*FALCO TINNUNCULUS*) IN URBAN ROME, ITALY

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KEY WORDS: *Common Kestrel; Falco tinnunculus; diet; avian prey; urban area; Rome, Italy.*

Several studies have described the ecology of raptors in urban areas (e.g., Galeotti 1994). Common Kestrels (*Falco tinnunculus*) breed in many European towns, fre-

quently occurring in urban areas in higher densities than in farmland areas (Village 1990, Shrubbs 1993). Nevertheless, few studies have described details of the feeding ecology of kestrels in these urban areas (Quere 1990, Romanowski 1996). Therefore, the aim of our study was to describe the composition of the kestrel diet and any sea-

Table 1. Common Kestrel (*Falco tinnunculus*) diet in urban Rome, Italy.

	SUMMER				WINTER			
	PREY NUMBER (%)		PREY BIOMASS (%)		PREY NUMBER (%)		PREY BIOMASS (%)	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Stylommatophora	0.6	1.3	0.1	0.3	0.1	0.2	0	0.1
Scorpiones	0.2	0.6	0	0	0	0	0	0
Mantodea	0	0	0	0	0.5	1.1	0.1	0.4
Orthoptera	5.2	4.4	0.4	0.4	22.1	12.8	3.1	3.2
Dermaptera	0.4	1.0	0	0	1.2	2.6	0	0
Coleoptera	29.3	11.9	1.4	0.8	30.9	14.7	1.9	0.8
Hymenoptera	0.1	0.2	0	0	2.7	4.6	0	0
Unidentified insects	0.3	0.5	0	0	0.1	0.2	0	0
Sauria	15.1	6.1	7.2	4.7	9.6	7.9	5.8	4.5
Columbiformes	0.9	1.4	10.8	15.8	0.1	0.2	3.2	5.6
Apodiformes	4.8	5.4	9.4	10.6	0.3	0.9	1.1	2.9
Passeriformes	21.7	9.6	41.6	15.4	4.4	2.8	16.4	10.0
Unidentified birds	2.4	4.1	5.3	10.4	0.1	0.2	0.3	0.8
Insectivora	0	0	0	0	0.5	0.5	0.2	0.3
Chiroptera	7.0	9.7	4.1	6.5	0.6	0.8	0.4	0.6
Rodentia	12.1	6.6	19.6	12.6	26.8	8.7	67.3	15.5
Total prey	1123		16 504 g		1238		11 574 g	

sonal variation in a Mediterranean urban area like Rome, Italy.

METHODS

We conducted our study in urban Rome where Common Kestrels occur at higher breeding densities (0.1–2.3 pairs/km²) than anywhere else in Italy. The kestrels nest in scaffolding holes in Roman ruins and monumental buildings (Salvati and Manganaro 1997). We assessed the diet by analyzing pellets and prey remains collected from 16 sites during the years 1996 and 1997. A total of 13 and 7 pellet samples were analyzed for the spring to summer (breeding period) and winter, respectively. In the city center, pellets were collected every month from April 1996–March 1997.

Pellets and prey remains were dissected in water. Prey remains were identified using diagnostic keys (Manganaro et al. 1990) and by comparison with museum specimens in the Zoology Museum, "La Sapienza" University, Rome, Italy. Mean weights for each prey taxon were estimated using data from Mediterranean areas (Manganaro et al. 1990). The number of individuals (scored as minimum value) was calculated taking into account all different kinds of prey items found. Paired anatomical parts were counted as belonging to the same individual. This method allowed us to estimate the frequency of occurrence of prey numbers (PN) and biomass (PB) for each prey category and to relate PN and PB to the habitat composition of hunting areas.

A Spearman Rank Correlation was used to assess relations among prey numbers for the most important prey categories and between the habitats of hunting areas and prey categories found in the diet during the breeding

period, when kestrels generally feed close to nests (Village 1990).

Using the mean size of hunting ranges given in Village (1990) and Shrub (1993), habitat composition within a 1-km radius of nests (3.14 km²) was characterized as farmland, wooded, modern urban, and ancient urban. A sequential Bonferroni test (1989) was used to adjust the significance level to the number of comparisons using the same data set. A minimum probability level of $P < 0.05$ was accepted (all tests were two-tailed). Statistical analyses were performed using STATISTICA software (version 4.5, 1993). Results are presented as mean \pm SD.

RESULTS

We identified 1123 prey items at breeding diets (86.4 \pm 85.9 prey per nest) and 1238 prey items in the winter diets (176.9 \pm 120.3 prey per roosting site), for a total biomass of 28 078 g. The number of prey items per pellet varied from 1.6–3.7 in summer (\bar{x} = 2.8 \pm 0.5), and from 2.7–4.9 in winter (\bar{x} = 3.2 \pm 0.7) (t = -1.45, df = 18, P = 0.165).

Kestrels preyed on species ranging in size from ants (*Messor* sp., 0.01 g) to adult Feral Pigeons (*Columba livia*, 300 g). Throughout the year, the main prey groups were insects, reptiles, birds, and mammals. Beetles (especially families widely distributed in Mediterranean areas like scarabs and tenebrionids) and birds were most commonly consumed in summer and grasshoppers and small mammals were most common in winter (Table 1). Birds and mammals were the main prey groups by biomass. Other prey included molluscs, scorpions, and ants. The

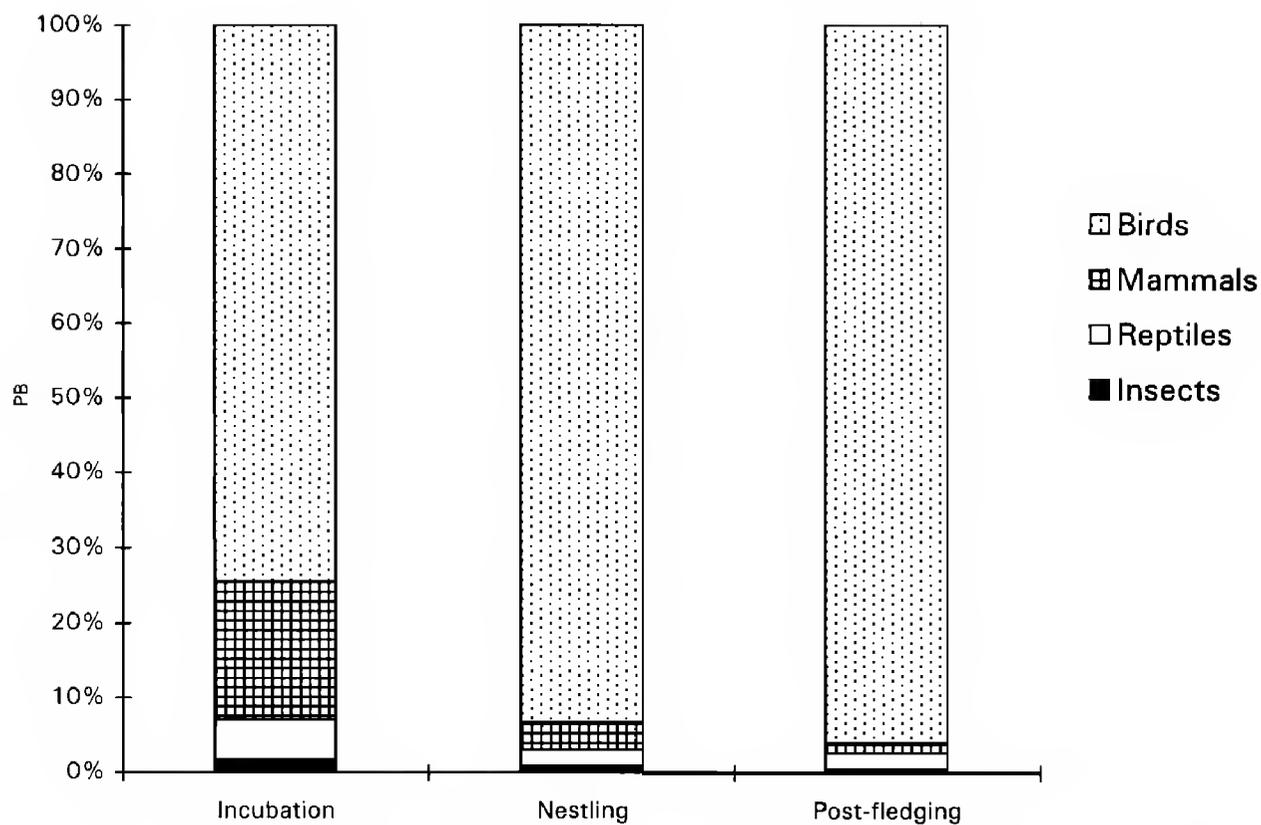


Figure 1. Diet of the Common Kestrel (*Falco tinnunculus*) in an urban area of Rome, Italy during the breeding season.

number of Feral Pigeons taken was positively correlated with the the number of Swifts (*Apus apus*) taken ($r_s = 0.63$, $P < 0.005$, $N = 20$). The number of passerines taken was negatively correlated with the number of rodents ($r_s = -0.70$, $P < 0.001$, $N = 20$) while the number of shrews (*Suncus etruscus* and *Crocidura* sp.) taken was positively correlated to numbers of rodents taken ($r_s = 0.60$, $P < 0.01$, $N = 20$). The number of Swifts taken was positively correlated with ancient urban areas ($r_s = 0.76$, $P < 0.005$, $N = 13$) and negatively with farmland areas ($r_s = -0.77$, $P < 0.005$, $N = 13$). By contrast, the number of rodents taken was positively correlated with farmland areas ($r_s = 0.93$, $P < 0.001$, $N = 13$) and negatively with ancient urban areas ($r_s = -0.77$, $P < 0.005$, $N = 13$). Monthly analysis of diets from pellets of a city-center nest showed a wide variation for some prey groups: insects were regularly taken throughout the year, but their biomass was always very low. Birds and reptiles were mainly taken in summer and small mammals in winter. The proportion in biomass of different prey groups varied significantly ($\chi^2 = 180.3$, $df = 6$, $P < 0.00001$) during the breeding season with rodents and lizards taken mostly during incubation, while birds predominated in the diet during the nestling and postfledging periods (Fig. 1).

DISCUSSION

The diet of the Common Kestrel in its typical habitat that consists of farmland areas with small woodland patches is generally composed of small mammals such as voles (*Microtus* spp.; Village 1990, Shrubbs 1993). The increase in predation on reptiles and insects observed in Rome was probably due to the large availability of these

prey in Mediterranean areas (Village 1990). An increase in birds in the diet of Tawny Owls (*Strix aluco*) has also been observed in European towns (Galeotti et al. 1991), probably because of the greater availability of birds and the decreased abundance of rodents in these areas (Galeotti 1994).

In some European cities, kestrels take prey far from their nest sites (Quere 1990, Romanowski 1996). In Rome, however, kestrels hunt near their nests during the nesting period most likely because a wide variety of prey is available both in the city center (birds, bats, and reptiles) and in the suburban open areas (small mammals, reptiles, and insects).

Predation on birds and small mammals, the two most important prey groups, varied in relation to the distance between open areas and the city center, and prey groups with similar ecological habits were correlated to each other and to the habitat types in hunting territories. Thus, both Swifts and Feral Pigeons were caught in archeological and ancient urban areas, where they were a readily available and conspicuous food source for city-center kestrels. By contrast, rodents and shrews were less common in these areas.

RESUMEN.—Estudiamos la dieta del cernícalo euroasiático (*Falco tinnunculus*) por dos años en la Roma urbana, Italia. Identificamos un total de 2361 items de presas en egagrópilas y restos de presas recolectados en 13 sitios de anidación y 7 perchas de invierno. Los cernícalos capturaron una gran variedad de presas, desde pequeños insectos incluyendo hormigas hasta aves grandes como palomas. Las aves y los murciélagos predominaron dur-

ante la estación reproductiva mientras que los pequeños mamíferos y las lagartijas fueron más comunes en invierno. Los insectos estuvieron presentes en la dieta a lo largo del año, pero su biomasa fue muy baja. Las aves fueron capturadas predominantemente en áreas urbanas y los roedores en áreas agrícolas.

[Traducción de César Márquez]

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LETTERS

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OSPREYS INCUBATE GOOSE EGG TO HATCHING

Serial use of the same nest by Canada Geese (*Branta canadensis*) and Ospreys (*Pandion haliaetus*) has increased in recent decades. Campbell et al. (1990, *The Birds of British Columbia*, Royal British Columbia Museum, Victoria BC Canada) reported that 13% of the nesting Canada Geese utilized nests of Ospreys and Bald Eagles (*Haliaeetus leucocephalus*) in British Columbia. Because geese begin nesting earlier, Ospreys sometimes return to find their favored nesting site occupied by a pair of geese. Attempts to drive them from these nests vary in success (e.g., Flath 1972, *Auk* 89:446–447).

On 1 June 1995, while trapping adult Ospreys near the mouth of the Coeur d'Alene River in northern Idaho, I found a pair of Ospreys attending a nest containing an Osprey egg and a goose egg. I intended to leave the eggs undisturbed until I heard soft vocalizations and discovered that the goose egg was already pipped. Because there was no chance of its survival at the nest, I removed the gosling from the shell in the hope of releasing it into a brood on the Coeur d'Alene River Wildlife Management Area nearby. However, John Nigh, the area manager, informed me that most local broods hatched from 15 April–15 May which limited the opportunity to foster the bird. I was advised to euthanize it, a step I carried out with much regret. I am uncertain if the Osprey egg hatched; no birds were present when I returned in mid-July to band nestlings in the area.

I assume that a dispute over use of the nest occurred soon after Ospreys arrived from the south in late March or early April, before the geese had completed egg laying. A 1 June hatching date lagged behind that of most local clutches by 2–6 weeks, suggesting that the nest contained a single goose egg at the time Ospreys drove the geese off. The goose egg was not incubated until an Osprey egg was laid several weeks later when the incubation of both began. Alternate scenarios such as a delay in the initiation of egg laying or the reduction of a completed clutch to a single egg seem less likely.

Alteration of clutch size or differences in egg size or color apparently have little influence on incubation effort by Ospreys. Fannin (1894, *Auk* 11:322) found a pair of Ospreys incubating a mixed clutch of goose and Osprey eggs which they continued to incubate after he reduced the clutch to a single goose egg. Reese (1977, *Auk* 94:202–221) found Mallard (*Anas platyrhynchos*) eggs in several clutches of Ospreys nesting in Maryland. In a cross-fostering experiment involving extensive replication, nesting Ospreys closely incubated 1–2 dummy Bald Eagle eggs for several weeks. All pairs later completed incubation of their clutches, which were maintained in an incubator during the experiment (E. Bizeau pers. comm.).

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SWAINSON'S HAWKS IN NUEVO LEÓN, MEXICO

In Mexico, the Swainson's Hawk (*Buteo swainsoni*) is considered mostly a migratory species that nests mainly in the U.S. and Canada. Here, we report our observations of two Swainson's Hawk nests in the state of Nuevo León, Mexico.

Previously, Urban (1959, *Birds from Coahuila, Mexico*. Univ. Kansas Publ., Mus. Nat. Hist. 11(8):443–516) reported two Swainson's Hawks in western Coahuila, Mexico. The first specimen was collected on 20 June 1952, two miles west of Jimenez. Measuring the gonads to be 6 × 4 mm, Urban concluded the bird must have been breeding. The second individual was collected at Iglesias, 24 km southwest of Sabinas on 22 August 1949. Swainson's Hawks have also been

recorded breeding in the following states of Mexico: Baja California, Sonora, Durango and Chihuahua (Oberholser 1974, *The bird life of Texas*. Vol. I. Univ. Texas Press, Austin, TX U.S.A.; AOU 1998, *Check List of North American Birds*. 7th edition. Washington, DC U.S.A.); Coahuila and Baja California (Urbina-Torres and Morales-Gonzalez 1996, *Aves rapaces de Mexico*, Centro de Investigaciones Biologicas, U.A.E.M., Mexico); Nuevo León, Sonora through Chihuahua, Durango and Coahuila, and extreme northern Tamaulipas (Howell and Webb 1995, *A guide to the birds of Mexico and northern Central America*, Oxford Univ. Press, London, U.K.; England et al. 1997, Swainson's Hawk (*Buteo swainsoni*). In *The Birds of North America*, A. Poole and F. Gill [Eds.]. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.). We have previously reported the Swainson's Hawk primarily to be a migrant in our area that is vulnerable to deforestation for ranching (Contreras-Balderas et al. 1995, *Lista preliminar de las aves del estado de Nuevo León*. Capítulo 3:41–54; Contreras-Balderas 1997, pages 35–44 in R.W. Dickerman [Ed.], *Resumen avifaunístico de Nuevo León*. The era of Allan R. Phillips. A Festschrift. Horizon Communications, Albuquerque, NM U.S.A.)

We surveyed select trails in two areas in the northcentral part of Nuevo León, Mexico from January–September 1996. One area was near the municipality of Pesqueria (22.5 km northeast of Monterrey; 25°47'N, 100°06'W). Vegetation in the area included *Bumelia spiniflora*, *Prosopis glandulosa*, *Acacia farnesiana*, and various species of sedges (*Bouteloua* spp.). The second area was near China (93.7 km southeast of Monterrey; 25°39'30"N, 99°20'15"W). Vegetation in this area included *Bumelia spiniflora*, *Prosopis glandulosa*, *Acacia farnesiana*, *Acacia wrightii*, *Leucophyllum texanum*, *Jatropha dioica*, *Opuntia* spp., and various species of sedges (*Bouteloua* spp.), both in the Coastal Plain Gulf region among predominately high thorn brush. Both areas have a warm climate with an annual precipitation of 60–100 cm and median annual temperatures in Pesqueria and China of 22 and 18°C, respectively (Instituto Nacional de Estadística, Geografía e Informática 1981, *Síntesis geográfica de Nuevo León*. Secretaría de Programación y Presupuesto, Nuevo León, Mexico).

We found two Swainson's Hawk nests in Nuevo León. The first, just east of Monterrey in Pesqueria, had the following chronology: on 10 January 1996, five adults arrived at the site; on 8 April, a pair remained in the area; on 21 April, the pair established its territory; on 14 May, nest construction was observed; on 23 May, two eggs were being incubated; on 13 June, two young were observed in nest; and on 1 July, the young fledged. The nest was in a *Prosopis glandulosa*, 6.90 m from the ground.

We found the second nest in the municipality of China on 27 July 1996. It contained one young. The nest was in a *Pithecellobium flexicaule*, 8.0 m above the ground. At both nests, the adults had typical light morph plumage.

Our findings confirm that Swainson's Hawks breed in Nuevo León, although they are probably not common. This increases the number of species that nest in the state while extending the southeasternmost boundary of the breeding range of the Swainson's Hawk 360 km.

We appreciate the English editorial skills of Laura Cholodenko, Association of Field Ornithologists' program of editorial assistance, and Arturo Peñaflor for his help on fieldwork. We thank reviewers Stuart Houston, Peter H. Bloom, and A. Sidney England for improvements they made in the manuscript.—**Armando J. Contreras-Balderas and Fernando Montiel-de la Garza, Laboratorio de Ornitología, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Apartado Postal 425, San Nicolás de los Garza, Nuevo León, México 66450.**

BOOK REVIEW

EDITED BY JEFFREY S. MARKS

J Raptor Res. 33(2):178–179

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The Raptors of Europe and The Middle East: A Handbook of Field Identification. By Dick Forsman. 1999. T. & A.D. Poyser, London. xviii + 589 pp., 71 line drawings, 737 color photographs. ISBN 0-85661-098-4. Cloth, \$45.—As stated in the subtitle, this book is a compilation of information about the field identification of diurnal raptors. It covers the 43 species that occur regularly in Europe and the Middle East but not the vagrants to that area. *The Handbook* goes well beyond any of the available field guides in describing how to identify raptors as to species, age class, and in many cases, sex. New are the use of color photographs in place of color illustrations (although a photographic guide exists for North American raptors) and the thorough description of molt, especially of flight feathers, and its use in aging raptors.

Dick Forsman has published several books (in Swedish) and numerous articles on field identification of raptors. He has traveled throughout much of Europe and the Middle East taking photos of and studying raptors in the field. After 25 years of experience, Forsman is well qualified to write this book. The book begins with a preface and acknowledgments, as well as an extensive glossary entitled "Abbreviations and Terminology." This is followed by "How to Use the Book," which provides a brief description of each heading in the species accounts.

The first chapter, "Introduction to the Field Identification of Raptors," begins with a detailed discussion of molt in falconiforms. Differences in molt sequences of flight feathers among members of the Accipitridae, Pandionidae, and Falconidae are covered, as is the use molt to determine age, especially for species that take more than one year to reach definitive basic plumage. Other topics covered in this chapter are identification based on plumage characters, size, shape, structure, and characters of flight and movement. The chapter concludes with short discussions of variable light

conditions, hybrids, and points to remember, all relating to field identification. Anyone with an interest in identification or molt, especially for diurnal raptors, should study this chapter.

The 43 species accounts constitute the meat of *The Handbook*. Each begins with short paragraphs summarizing subspecies, distribution, habitat, population (estimates and trends), movements, and hunting and prey. This is followed by a more extensive section, "Species Identification." Measurements of length and wingspan are given first (most are taken from live birds), followed by a sentence or two about the degree of difficulty of identifying the species in the field. Next is a blue-background box entitled "Identification Summary," which is a particularly helpful feature because some discussions are lengthy and detailed.

Then follow sections entitled "In Flight, Distant," "In Flight, Closer," "Perched," "Bare Parts," and "Confusion Species," and a section on molt by age class. The final section of each species account, "Ageing and Sexing," includes another helpful blue-background summary. References to the photographs of each species are given for age and sex classes. The text concludes with a list of references; full citations are given in the bibliography at the end of the book. Many species accounts also include illustrations showing wing attitudes and plumage characters; some of these are in color, others in black-and-white.

The heart of the book is a set of color photographs that depict both perched and flying individuals, and for some species, birds in hand (covering all of the different plumages). Photographs of captive birds were used for at least one species. The caption for each photo gives information on age, sex (if possible), field marks, date, location, and photographer.

I, too, have studied raptor identification in Europe and the Middle East and have a raptor field guide in press for that area that uses color plates and a few color photos. Although it may appear that I would be somewhat biased in reviewing a book that could be considered a competitor for

mine, please read on and reserve judgment on that issue until you have read the entire review.

Somewhat at random, I have chosen four species accounts for detailed scrutiny: White-tailed Eagle (*Haliaeetus albicilla*), Pallid Harrier (*Circus macrourus*), Eastern Imperial Eagle (*Aquila heliaca*), and Sooty Falcon (*Falco concolor*). While reading through the book, I had to keep in mind that English is Forsman's third language; he lives in a Swedish-speaking area of Finland. Although at times the wording is somewhat cumbersome, he still manages to describe plumages and behaviors clearly. The sets of photographs and the descriptions of the various age and sex classes and identification points for these four species were all accurate and thorough, with the exception of some points mentioned below.

The description of the first prebasic molt in the White-tailed Eagle is biased toward northern European eagles, because it is stated that they replace only "some inner secondaries," when clearly the second-plumage eagle in plate 77 taken in Israel shows a minimum of seven new inner, outer, and middle secondaries. The field mark of uniformly dark leg feathers (called "trousers") is mentioned but not stressed as a character of second- and third-plumage eagles not found on juveniles, whose trousers have tawny-buff spotting.

In the Pallid Harrier account, the relative position of the wingtip to tail tip on perched birds, and the facial ring extending across the throat, both of which are useful field marks for distinguishing adult females from the very similar Montagu's Harrier (*C. pygargus*), are not mentioned under Confusion Species. However, my article in *Birding World* (July 1997) describing these field marks was published after *The Handbook* was already in press. Also not mentioned is the absence of streaking on the flanks of juvenile Pallid Harriers, which is useful for distinguishing them from juvenile Montagu's Harriers, which always show such streaking. The adult males in plates 229 and 231, labeled "First plumage adult," show dusky bands on the tips of the secondaries and a dark breast. I believe that these are just variants of the second-plumage male.

The only item that I question in the Eastern Imperial Eagle account is the number of immature plumages. Based on detailed examination of specimens and birds in the field, John Schmitt and I found that adult plumage is attained in four or five

years, the same time required for all of the other large eagles, such as Golden (*Aquila chrysaetos*), Steppe (*A. nipalensis*), and White-tailed eagles. Forsman gives this as six or seven years. I think that his second and third plumages are the same, just variations in the amount of molt, and correspond with our second plumage. Likewise, his fourth and fifth plumages are the same; we consider this to be the third plumage. And his sixth plumage, the first adult plumage, is the same as our fourth plumage. Further fieldwork, particularly with marked individuals, would be helpful in determining which of us is correct.

I question that there are 200 pairs of Sooty Falcons breeding in Israel. I wonder if this is a misprint, because I had thought that there are no more than 20 pairs there, based on my fieldwork in the mid-1980s. I have never seen any Sooty Falcon, alive or as a specimen, with "nearly black" feathers as described by Forsman for some second-year birds, nor does any photograph in the book show this. Adult Barbary Falcons (*F. pelegrinoides*) were not mentioned in the Confusion Species section; they are also blue-gray above, only slightly larger than Sooty Falcons, and breed in the same areas.

Almost all of the accounts have a complete set of photographs showing all plumages described; however, only four photos are shown for the Spanish Imperial Eagle (*A. adalberti*), three of which are of birds in captivity. Also, no photos of dark-morph Marsh Harriers (*Circus aeruginosus*) were included.

In spite of the nit-picking comments above, *The Handbook* provides an excellent and nearly complete compilation of color photographs and information on raptor identification in Europe and the Middle East. This reflects the time and effort expended by the author over many years to understand how to identify raptors in the field, including age and sex determination. It certainly lives up to the subtitle, *A Handbook of Field Identification*. I highly recommend *The Handbook* for anyone interested in raptor field identification or working on raptors in Europe and the Middle East. It is worth acquiring solely for the wonderful collection of photographs, which is all the more remarkable given that the original photographs were misplaced, and the author had to spend more than a year assembling a new set.—**William S. Clark, 7800 Dasset Court, Apt. 101, Annandale, VA 22003 U.S.A.**

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