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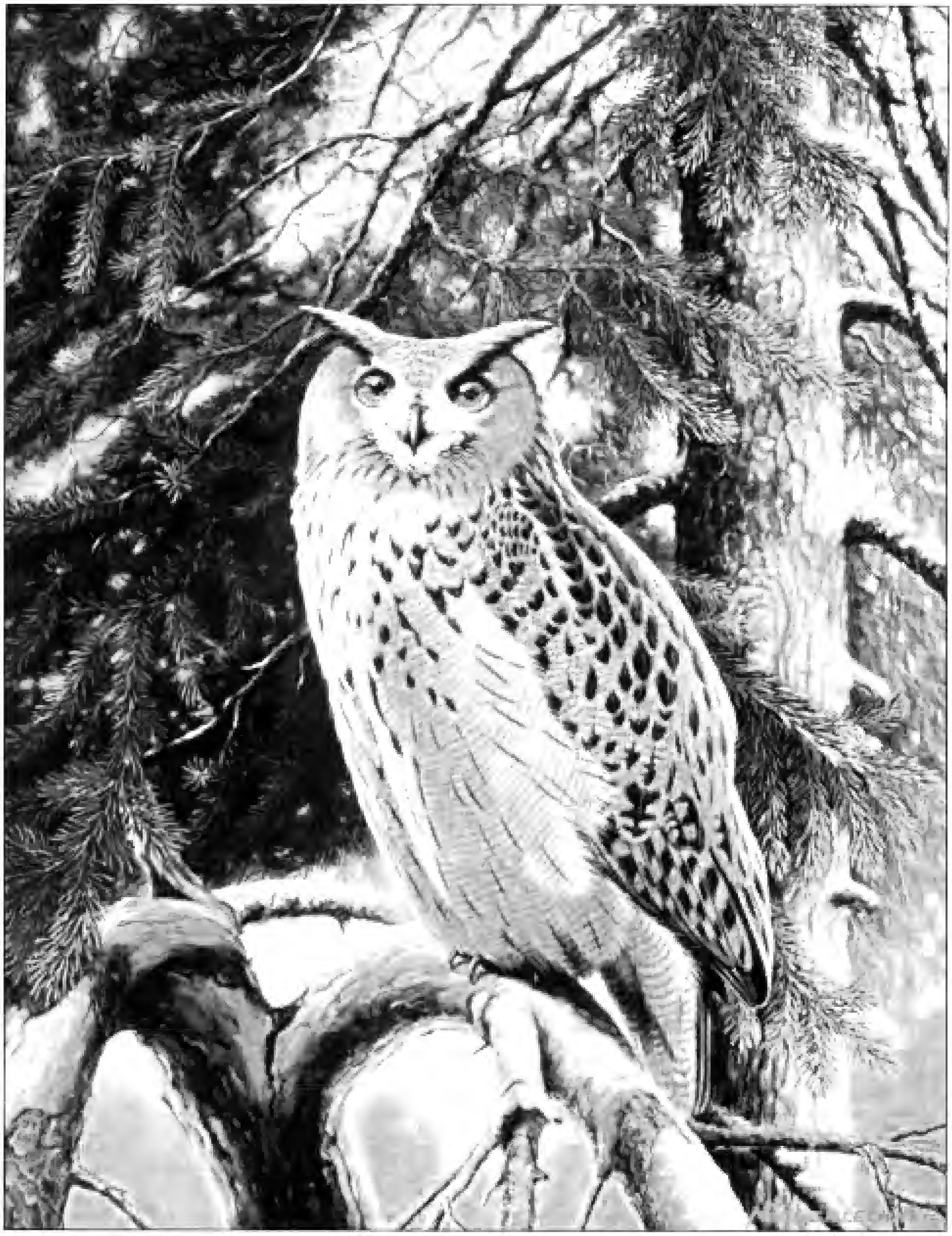

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The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, short communications, letters to the editor, and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 216 × 278 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (7th ed., 1998) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1999).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 35(4), and are available from the editor. Submit manuscripts to J. Bednarz at the address listed above.

COVER: Eurasian Eagle-Owl (*Bubo bubo*). Painting by Josef Niederlechner, Anton-Mangold-Weg 8, 82362 Weilheim, Germany.

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Short Communications

The Raptor Research Foundation, Inc. gratefully acknowledges funds and logistical support provided by Arkansas State University to assist in the publication of the journal.

THE JOURNAL OF RAPTOR RESEARCH

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J Raptor Res. 36(1):1–2

EDITOR'S PAGE

WORKING TOWARD EXCELLENCE

JAMES C. BEDNARZ, EDITOR

Perhaps you noticed that the *Journal of Raptor Research* has gone through a minor adjustment during the last year. Editor Marc Bechard, after a half decade of dedicated efforts to improve the *Journal,* stepped down and passed the awesome responsibility of managing our flagship research publication to me and a small, part-time editorial staff at Arkansas State University. During Marc's tenure as Editor, the *Journal of Raptor Research* (*JRR*) took on a new look and prospered. *JRR*'s impact factor, a measure of the scientific "impact" of peer-reviewed periodicals based on the number of citations compiled by the Institute of Scientific Information in *Journal Citation Reports,* has grown exponentially over the last few years. Although the value of "impact factors" in ranking the quality of scientific journals is debatable, it represents one measure of the exposure that articles published in a particular journal will receive and their potential influence on science. Currently, *JRR*'s impact factor is on par with several respected international journals in the disciplines of ornithology (e.g., *Wilson Bulletin*) and organismal biology (e.g., *Wildlife Society Bulletin*). As editor, I pledge to you that the current editorial staff will continue to strive toward publishing the best journal of raptor science in the world.

As I anticipated, the transition of editorial responsibilities from Marc's shop to my lab set us back a little bit. Our new Editorial Assistant, Rebecca Maul, and I received the official authorization from the Board of the Raptor Research Foundation, Inc. to begin processing manuscripts at the end of February 2001. Although we got right to work, we were faced with an instant backlog of manuscripts. In addition, Rebecca and I had lots to learn about the ins and outs of publishing a scientific journal. Thankfully, we received much help during the transition from Marc Bechard, Joan Clark (the long-time proofreader of *JRR*), the folks at Allen Press, and the Department of Biological Sciences at Arkansas State University. We greatly appreciated this assistance and support during the transition process, that enabled us to produce our first issue (Volume 35, Number 3) only slightly behind schedule.

The second issue of *JRR,* edited and produced by the new editorial office (Volume 35, Number 4), showcased the proceedings of the Second International Burrowing Owl Symposium. It presented a huge challenge for our meager resources. Even though we received outstanding cooperation from Special Editors of this issue, Troy Wellicome and Geoff Holroyd, and the many authors who contributed to this effort, this unique volume represents the largest single issue ever of the *JRR.* Throughout the production of these proceedings, all contributors, cooperators, and the entire editorial team endeavored to produce the best scholarly product possible. All contributions went through thorough reviews and multiple edits, and several submitted manuscripts that were not deemed suitable for publication in *JRR* were rejected to maintain a high standard of peer review. If you have not looked at this special issue of *JRR,* I encourage you treat yourself and review some excellent science on Burrowing Owls (*Athene cunicularia*).

As new editor-in-chief, I am currently very satisfied with the quality and format of our journal and have elected to maintain most of the specifications put in place by my recent successors. However, we will continue to tweak things in an effort to improve the presentation of raptor science and better accommodate both authors and readers. For example, we now publish e-mail addresses of the corresponding author for each article published. This contemporary contact information will, hopefully, further encourage constructive interactions between scientists and conservationists interested in raptor biology. We also have instituted an optional electronic submission procedure (*J. Raptor Res.* 35: 409) that should speed up the processing of manuscripts. Our current priority objective is to accelerate the turn-around time from manuscript receipt to publication. Let me emphasize, however, our current turn-around time in publishing papers is faster than most other ornithological and organismal biology journals: less than 8 months to a final decision on acceptability and most manuscripts are in print within 14 months after the date of submission. In 2002, we intend to reduce these turn-around intervals as much as feasible. You may also see other minor changes in future issues and we welcome suggestions and comments from both authors and readers concerning further improvements to the *JRR* (jrr@astate.edu).

As I have discovered over the past 10 months, publishing a quarterly, peer-reviewed journal in raptor biology is a monumental undertaking. I want to express special thanks for the contributions of our current staff of Associate Editors: Jim Belthoff, Clint Boal, Cole Crocker-Bedford, Joan Morrison, Juan José Negro, Marco Restani, Ian Warkentin, and Troy Wellicome. Our Book Review Editor, Jeff Marks, and Spanish Editor, César Márquez Reyes, continue to do outstanding work. We currently have two part-time Editorial Assistants, Rebecca Maul and Allie Fowler, who accomplish the tough, day-to-day legwork that gets the *JRR* out on time. Finally, I want to express my appreciation to all the referees, whose thoughtful evaluations make the quality of the *Journal*. Publication of the *JRR* is a cooperative effort involving the entire membership and raptor scientific community, who provide the original research and peer review that fuels the forward progress of science. When we request that you contribute to the quality of the *JRR* by refereeing a manuscript, I strongly encourage you to agree and to take part in this vital process. I look forward to working with all of you in the near future!

J. Raptor Res. 36(1):3–10

SURVIVAL OF FLORIDA BURROWING OWLS ALONG AN URBAN-DEVELOPMENT GRADIENT

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ABSTRACT.—I estimated survival rates of a Florida Burrowing Owl (*Athene cunicularia floridana*) population on a 35.9-km^2 study area in Lee County, Florida, 1987–91 to determine if there was a relationship between annual survival and development density. The study area spanned a residential development density gradient ranging from <2% to >74% of lots with houses. Survival rates were estimated from a sample of 119 banded adult male, 152 adult female, and 310 juvenile Burrowing Owls using Cormack-Jolly-Seber capture-recapture models and Fisher's maximum likelihood method of parameter estimation. Survival rates were estimated separately for sections of the study area where <20% of 0.2-ha lots were developed (i.e., homes built), 20–39% were developed, 40–60% were developed, and >60% were developed. The most parsimonious models indicated that adult male survival was 81% (SE = 0.04) where <20% or >60% of lots were developed, and 62% (SE = 0.05) elsewhere. Adult female survival was 52% (SE = 0.06) where 40–60% of lots were developed and 69% (SE = 0.04) elsewhere. Juvenile survival was 18% (SE = 0.08) where <20% of lots were developed, 43% (SE = 0.08) where 20–39% of lots were developed, 28% (SE = 0.04) where 40–60% of lots were developed, and 11% (SE = 0.03) where >60% of lots were developed. I speculate that the inverse relationship between adult and juvenile survival across development zones reflected the greater recruitment opportunities that existed for juveniles in development zones where adult mortality was high. Patterns of adult mortality more closely tracked trends in the rate of home construction than the density of homes, suggesting factors associated with home building and the attendant landscape changes might result in high Burrowing Owl mortality.

KEY WORDS: *Burrowing Owl*; *demography*; *development*; *Florida*; *mark-recapture*; Athene cunicularia floridana; *survival*; *urban wildlife management.*

Supervivencia de *Athene cunicularia floridana* en un gradiente de desarrolo urbano

RESUMEN.—Estimé las tazas de supervivencia de una población de búhos cavadores de la florida (*Athene cunicularia floridana*) en un área de estudio de 35.9-km^2 en el condado Lee, Florida, 1987–91 para determinar si habia una relación entre la supervivencia anual y la densidad del desarrollo. El área de estudio comprende un gradiente de densidad de desarrollo residencial que va desde <2% a >74% de lotes con casas. Las tasas de supervivencia fueron estimadas partir de una muestra de 119 machos adultos anillados. 152 hembras adultas, y 310 búhos cavadores juveniles usando los modelos de captura recaptura de Cormack-Jolly-Seber y el método de máxima probabilidad de la estimación de parámetros de Fisher. Las tasas de supervivencia fueron estimadas separadamente por secciones del área de estudio que estaban bajo desarrollo así: <20% de los lotes de 0.2 ha (V. Gr. construcciones familiares), 20–39%, 40–60%. Y >60 % en desarrollo. La mayoría de modelos de parsimonia indican que la supervivencia de los machos adultos fue 81% (SE = 0.04)en donde <20% o >60% de los lotes estaban desarrollados, y 62% (SE = 0.05) en cualquiera de los otros. La supervivencia de los juveniles fue 18% (SE = 0.08) en donde <20% de los lotes estaban desarrollados, 43% (SE = 0.08) donde 20–39% de los lotes se habían desarrollado, 28% (SE = 0.04) donde 40–60% de los lotes estaban desarrollados, y 11% (SE = 0.03) donde >60% de los lotes se habían desarrollado. Especulo que la relación inversa entre la supervivencia de adultos y juveniles a lo largo de las zonas desarrolladas reflejan las mayores oportunidades que tienen los juveniles para restablecerse en zonas desarrolladas en donde la mortalidad de los adultos fue elevada. Los patrones de mortalidad de adultos mostraron tendencias mas cercanamente asociadas a la tasa de construcción de hogares que a la densidad de los mismos, sugiriendo que los factores asociados a la construcción y a los consecuentes cambios del paisaje podrían dar como resultado una alta mortalidad de búhos cavadores.

[Traducción de César Márquez]

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The disjunct population of Burrowing Owls (*Athene cunicularia floridana*) in Florida was historically closely associated with native prairies in the central peninsula (Rhodes 1892, Nicholson 1954). The species began a rapid range expansion in the state in the 1950s as human settlement converted vast areas of former woodland to pasture and home development (Ligon 1963, Courser 1979, Millsap 1996). Today, many of Florida's Burrowing Owl populations occur in suburban neighborhoods, airports, and industrial parks (MacKenzie 1944, Neill 1954, Ligon 1963, Courser 1979). Several urban Florida Burrowing Owl populations have shown declines, and some urban populations have been extirpated (Courser 1976, Consiglio and Reynolds 1987). The collapse of a few highly visible urban populations prompted concern for the species' status in Florida, and it was listed as a Species of Special Concern by the Florida Fish and Wildlife Conservation Commission in 1979 (Millsap 1996).

Subsequent studies have shown that a complex relationship exists between Burrowing Owl population status and development in some urban areas. Wesemann and Rowe (1987) showed that Burrowing Owl nest density, as well as arthropod and anole (*Anolis* spp.) prey populations, were highest where houses occupied from 54–60% of the landscape in Cape Coral, Lee County, Florida. Millsap and Bear (2000) reported that productivity (number of young fledged per occupied breeding site) in this same population increased with increasing housing development until 45–60% of the landscape was developed. Productivity seemed to decline where development exceeded 70%.

The objective of this paper is to determine how Burrowing Owl survival rates varied along the development density gradient on this same Cape Coral study area. I also assess implications of variation in survival rates relative to trends in density and productivity described in the previous studies (Wesemann and Rowe 1987, Millsap and Bear 2000).

STUDY AREA AND METHODS

Study Area. I conducted this work from 1 January 1987–10 July 1991 on a 35.9-km^2 study area (of which 32.7 km^2 was suitable Burrowing Owl habitat) in Cape Coral, Lee County, Florida, latitude 81°99′N, longitude 26°57′W (Fig. 1). Climate in Cape Coral is subtropical, with an annual mean temperature of 23.1°C. Precipitation averages 125.7 cm annually, and 75% of rainfall occurs between May–September (climate data from NOAA climatological data summaries for Fort Myers, Florida, 20 km southeast of the study area). The area was historically unsuitable Burrowing Owl habitat, but it was rendered favorable when wetland filling and land clearing for development occurred in the early 1950s (Zeiss 1983).

The study area consisted of filled upland subdivided into 0.2-ha lots suitable for homes, and dissected by access roads and saltwater canals. With the exception of a golf course (that was excluded from the study area due to access restrictions), three school campuses, and four recreation fields, the entire upland portion of the study area was subdivided for development. Groups of undeveloped lots of various configurations are interspersed with single-family homes throughout the study area. Vacant lots were maintained as grasslands by regular mowing by city maintenance crews. Developed lots usually contained manicured lawns of fibrous mats of sod with landscaped beds of trees and shrubs. The ratio of homes to vacant lots varied across the study area, with highest development in the eastern sections (where up to 74% of lots had homes built on them) and lowest in western sections (where as few as 2% of lots had homes on them).

Definitions. Burrows attended by one or more adult owls or decorated with shredded paper and grass were considered occupied nest sites. A nest site was the area within 88 m (½ the mean inter-nest distance [Millsap and Bear 2000]) of a burrow where a nest attempt occurred, or where a single adult Burrowing Owl not known to be breeding elsewhere was seen on three or more occasions between 1 January–10 July. The term survival (Φ) does not distinguish between individuals that survived from one year to the next and those that permanently emigrated (e) from the study area, unless it is specifically noted that adjustments to account for e were made. Recapture probability (p) is the probability of encountering a previously banded individual known to be alive in year i.

Methods. I obtained measures of the percent of lots that were developed for each of 14 legal sections (2.59 km^2) on the study area in each year of the study from the city of Cape Coral. Nearly all upland throughout the study area was divided into 0.2-ha lots, so the percent of developed lots provided a reliable relative measure of the extent of home development in each section. Development was not necessarily uniform, and school campuses and clusters of undeveloped lots provided pockets of open space even in the most densely developed areas. Consequently, the percent of developed lots is best considered an index to the relative level of development around nest sites at a landscape scale.

I had insufficient data to assess survival of banded Burrowing Owls in each section, so I grouped owls into four development zones according to the percent of lots developed in the section where they were banded or last encountered. Development zones and area were: (1) zone 1, ≥60% development, 8.0 km^2; (2) zone 2, 40–60% development, 5.1 km^2; (3) zone 3, 20–39% development, 7.5 km^2; and (4) zone 4, <20% development, 12.1 km^2. I chose the break point at 60% based on changes in owl population density and productivity that occurred at this level of development (Wesemann 1986, Wesemann and Rowe 1987, Millsap and Bear 2000).

Surveys to locate occupied nest sites were conducted from 1987–91 as described in Millsap and Bear (2000) using a team of trained volunteers. From 1987–90 this team banded 20–25% of breeding adult and juvenile Burrowing Owls in each section on the study area. Nest sites

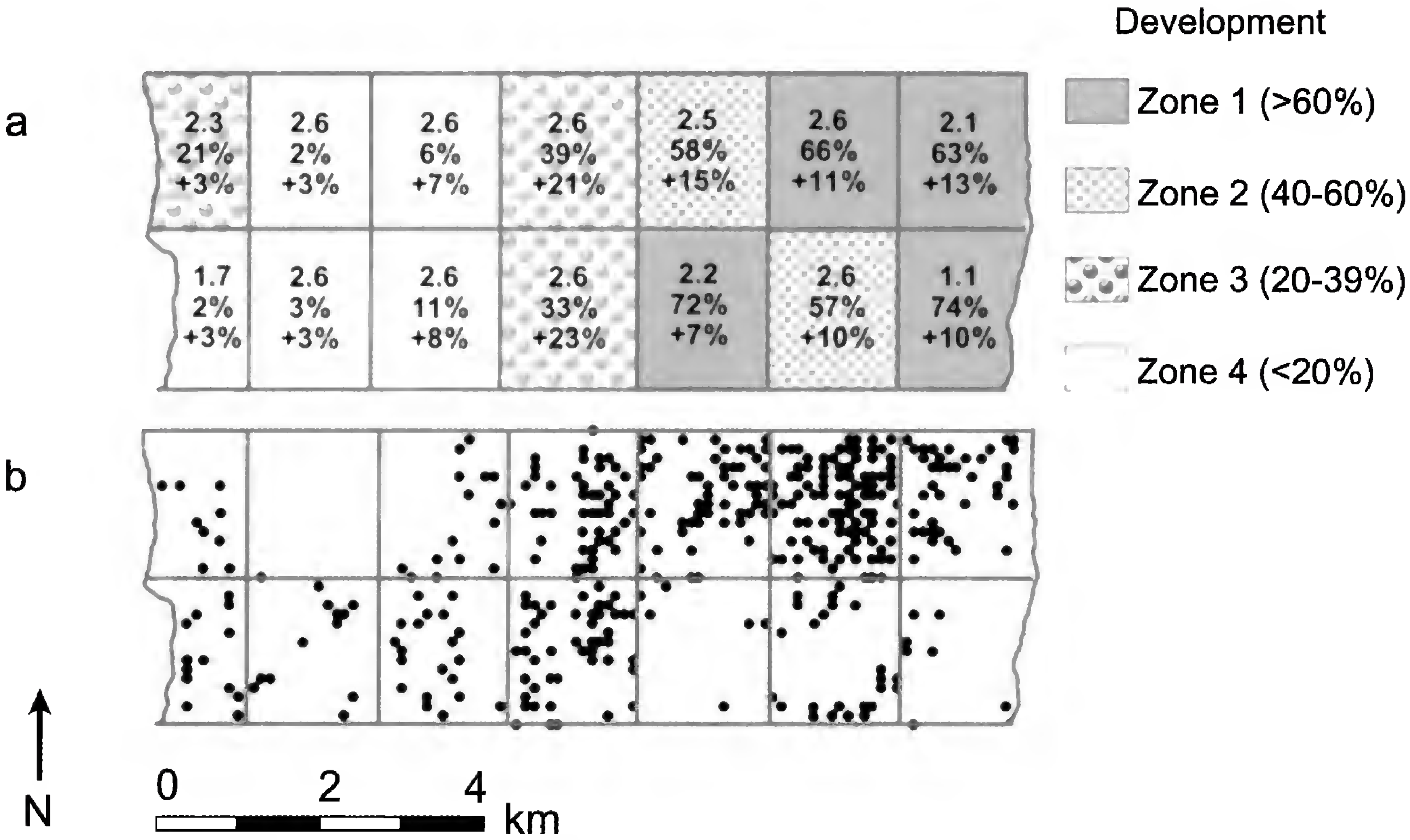

Figure 1. Map of the Burrowing Owl study area in Cape Coral, Lee County, Florida, showing (a) development zones and (b) distribution of nest sites for the period 1987–90. In a, numbers from top to bottom are: (top) number of km^2 of suitable Burrowing Owl habitat, (middle) mean percent of lots with homes for period 1987–90, and (bottom) percent increase in home density from 1987–90.

were randomly selected for banding from the pool of occupied sites each year, but some owls not selected *a priori* were also banded. Owls were captured with noose carpets placed at the burrow entrance and by hand at night with flashlights. Approximately 98% of adults attending known nests on the study area were checked for bands annually from 1988–91, allowing me to generate annual survival estimates for the periods 1987–88, 1988–89, 1989–90, and 1990–91. When banded owls were observed, we confirmed identification by reading band numbers with spotting scopes or binoculars or by retrapping. Members of the public who reported encounters with banded owls were queried to determine the details of the encounter. The sex of breeding adults could usually be determined at a distance by plumage (males were paler than females due to increased sun-bleaching) or behavior (Millsap and Bear 1997). Breeding females with eggs or small young could be distinguished in the hand by the presence of a large, vascularized incubation patch. We were unable to determine the sex of nestlings when they were initially banded, but sex was determined for those that were subsequently encountered as breeders.

Capture-recapture data were analyzed using the Cormack-Jolly-Seber (CJS) family of models, which produce estimates and estimated standard errors (SE) of Φ and p. Goodness-of-fit tests in Program RELEASE (Burnham et al. 1987) were used to assess the adequacy and utility of the basic CJS model for my data. Parameter estimates were calculated using Program SURGE (Pradel et al 1990). I calculated estimates of Φ and p separately for owls banded as adults (which were further separated by sex) and nestlings (which were not identified to sex upon initial banding). For both adults and young, I examined parameters over categorical time intervals (subscript *t*) and development zones (subscript *z*). For birds banded as juveniles, I also examined variation with age (subscript *a*).

My objective was to find the model with the simplest structure and fewest parameters that still accounted for significant variability in the data. Model notation follows Lebreton et al. (1992). I initiated model testing for adults with a global model of $\{\Phi_{t4*z4};\ p_{t4*z4}\}$, where t denotes a time effect over the four recapture years (1988–91), z denotes an effect over the four development zones, and * denotes interaction between time and development effects. Thus, my adult global model tested separate $\{\Phi_{t*z,}\ p_{t*z}\}$ for each sex over all four recapture occasions and all four development strata. The global model for owls banded as nestlings was $\{\Phi_{a2*t4*z4;}\ p_{a2*t4*z4}\}$, where a denotes an age effect over two age classes (juveniles and >1-yr-old) For the subscripts t, z, and a, I distinguished between nonspecific categorical groups with the additional subscript n, and specific categories with the subscript n'. For example, the notation $z4$ denotes a model where development zone effect is partitioned across all four zones, whereas the model subscripted $z1'$, $z2' = z3' = z4'$ denotes a model where development zone effect was partitioned between zone 1 and zones 2–4 pooled.

I tested reduced nested variations of these models against the global models using Akaike's Information Criterion (AIC) to distinguish the most parsimonious model from among those tested (Lebreton et al. 1992). The probability that each of the six highest-ranked nested models (based on AIC scores) was the best model was estimated by the AIC weight (ω) for each model (Burnham and Anderson 1998).

In 1988–89, my team and I searched for banded Burrowing Owls that had dispersed and settled at nest sites in a 3.2-km-wide band immediately north of study area, as well as south of study area to the southern terminus of the Cape Coral peninsula. I used these data to adjust my estimates of Φ to account for permanent emigration using the formula in Burnham et al. (1996).

I contacted persons who reported dead banded owls to determine the cause of death whenever possible. Many recoveries were reported by a local wildlife rehabilitation center (Care and Rehabilitation of Wildlife, Inc.), and center veterinarians routinely conducted necropsies on banded Burrowing Owls.

RESULTS

The percent of lots with homes ranged from <2% to 74% across the study area, as measured at the section level (Fig. 1). The extent of development changed over the course of the study in all sections, but the greatest increase in the percent of developed lots was in moderately-developed parts of the study area. In the 20–39% and 40–60% development zones, from 10–23% of lots that were undeveloped at the start of the study had homes on them when the study ended.

My team and I banded 581 Burrowing Owls involved in 785 breeding attempts on 264 discreet nest sites on the study area from 1987–90 (Table 1, Fig. 1). For the purposes of survival analyses, I assigned each banded owl to the development zone where the owl was located the preceding time it was encountered.

Recapture Probabilities and Survival. No model incorporating variation in p with year or development zone was a satisfactory fit (Table 2), so I pooled data. Overall estimates of p were relatively high: adult males = 91% (SE = 3%), adult females = 87% (SE = 4%), and juveniles = 86% (SE = 5%). No models that incorporated variation among years in Φ were a good fit, so I pooled data over years for survival analyses.

The best overall estimate of Φ was 71% (SE = 3%) for adult males, and 64% (SE = 3%) for adult females. The unadjusted overall estimate of Φ for juveniles from the 2 age-class model was 21% (SE = 3%), but this did not account for known emigration. Five of 35 Burrowing Owls banded as nestlings on the study area in 1987–88 were known to have survived to breed and settled at nest sites away from the study area, yielding an estimated *e* of 0.14 (SE = 0.06) for juveniles. Adjusting for *e,* Φ for age 0–1 yr = 24%. Survival increased among owls banded as nestlings at >1 yr of age to 62% (SE = 6%). No Burrowing Owls banded as adults on the study area were found nesting off the study area, so there was no basis for adjusting Φ to account for breeding dispersal.

Table 1. Capture-recapture data set used to estimate survival of Florida Burrowing Owls from Cape Coral, Lee County, Florida, 1987–91. See Fig. 1 for zone descriptions.

	NUMBER BANDED	NUMBER RECAPTURED			
	yr_i	yr_{i+1}	yr_{i+2}	yr_{i+3}	yr_{i+4}
Σ Adult male	119	83	44	22	2
Zone 1	36	26	19	12	1
Zone 2	35	27	11	4	0
Zone 3	35	22	8	4	1
Zone 4	13	8	6	2	0
Σ Adult female	152	80	49	22	4
Zone 1	46	25	18	9	3
Zone 2	48	21	12	4	1
Zone 3	38	22	12	5	0
Zone 4	20	12	7	4	0
Σ Juvenile	310	55	26	13	4
Zone 1	83	7	1	1	0
Zone 2	113	20	11	6	3
Zone 3	91	26	12	6	1
Zone 4	23	2	2	0	0

Patterns of Survival. The adult male survival model with the lowest AIC and fewest parameters pooled together the >60% and <20% development zones, and pooled together the 20–39% and 40–60% development zones (Table 3). The AIC weight for this model was low overall, but was over twice that of the next best model. The best adult female survival model pooled together the >60%, 20–39%, and <20% development zones, and had an AIC weight 2.5 times that of the next best model. There was little difference in AIC weights among four of the six best survival models for Burrowing Owls banded as nestlings, so there was no clear basis for pooling survival estimates for any development zones. The small sample size in the <20% development zone prevented calculation of

Table 2. Comparison of six best capture-recapture models based on Akaike's Information Criterion (AIC) for adult male, adult female, and juvenile Florida Burrowing Owls, Cape Coral, Lee County, Florida, 1987–91. Models are listed in order of decreasing fit, based on AIC weights (ω).

MODEL[a]	DEVIANCE	K[b]	AIC	ω[c]
Adult males				
$\{\Phi_{z1'=z4',z2'=z3'}; p\}$	327.170	3	333.2	0.57
$\{\Phi_{z1',z2'=z3',z4'}; p\}$	326.820	4	334.8	0.26
$\{\Phi_{z4'}; p\}$	326.617	5	336.6	0.11
$\{\Phi_{z1'=z2',z3',z4'}; p\}$	331.092	4	339.1	0.03
$\{\Phi_{z1'=z2'=z3',z4'}; p\}$	334.143	3	340.1	0.02
$\{\Phi; p\}$	336.978	2	341.0	0.01
Adult females				
$\{\Phi_{z2',z1'=z3'=z4'}; p\}$	410.502	3	416.5	0.54
$\{\Phi_{z1'=z4',z2'=z3'}; p\}$	412.349	3	418.3	0.22
$\{\Phi_{z4}; p\}$	409.447	5	419.5	0.12
$\{\Phi_{z4',z1'=z2'=z3'}; p\}$	415.049	3	421.0	0.06
$\{\Phi; p\}$	417.193	2	421.2	0.05
$\{\Phi_{t4*z4}; p\}$	404.259	17	438.3	<0.01
Juvenile				
$\{\Phi_{a2*z1'=z4',z2'=z3'}; p\}$	430.780	5	440.8	0.29
$\{\Phi_{a2*z1',z2'=z3'=z4'}; p\}$	431.317	5	441.3	0.23
$\{\Phi_{a2*z3',z1=z2'=z4'}; p\}$	431.715	5	441.8	0.18
$\{\Phi_{a2*z1',z2'=z3',z4'}; p\}$	428.033	7	442.0	0.16
$\{\Phi_{a2*z4}; p\}$	424.541	9	442.5	0.13
$\{\Phi_{a2}; p\}$	441.740	3	447.7	0.001

[a] Model notation is as follows: Φ = survival; p = recapture probability; a_n = categorical age, where n denotes the number of age classes (when n = 2 the model uses 2 age classes, one for owls ≤1 yr old and one for owls >1-yr-old); t_n or $t_{n'}$ = time, where n denotes the number of nonspecific time categories modeled, and n' denotes a specific time category (i.e., 1' = 1988, 2' = 1989, 3' = 1990, and 4' = 1991); z_n or $z_{n'}$ = development zone, where n denotes the number of nonspecific development zones modeled and n' denotes a specific development zone (i.e., 1' = ≥60% development, 2' = 40–60% development, 3' = 20–39% development, and 4' <20% development).

[b] K = number of parameters estimated in the model.

[c] ω = AIC weight, which is the estimated probability the particular model is the best of the suite of models evaluated (Burnham and Anderson 1998).

meaningful survival estimates for the >1 yr age class for this zone.

Overall, estimates of survival for adult males (from the adult model) and juveniles (from the 2 age-class model) were strongly inversely correlated across development zones (Spearman's rank r = −0.89). All five juvenile emigrants captured off the study area came from nest sites in the >60% (4 individuals) and 40–60% (1 individual) development zones.

Causes and Timing of Mortality. Cause of death was estimated for 27 of 41 (65.9%) banded owls. Nineteen (70.3%) were hit by cars, six (22.2%) were the victims of predation (three by domestic dogs or cats, three by other raptors), one (3.7%) was killed during home construction on the nest lot, and one (3.7%) died of an unknown illness.

The seasonal distribution of recoveries of owls >1 yr of age (N = 30) was not uniform (χ^2_3 = 17.2, P = 0.001) (Fig. 2). Significantly (P < 0.10) more recoveries of adults were reported during the breeding season than expected, and significantly (P < 0.10) fewer were recovered in the fall. No marked differences were evident between males and females. The seasonal distribution of recoveries of juveniles (N = 11) was also not uniform (χ^2_3 = 10.5, P = 0.02), with more recovered at and shortly after fledging in spring than expected (P < 0.10) and fewer recovered than expected in fall (P < 0.10).

DISCUSSION

Survival rates of Burrowing Owls have not been widely investigated. The only other similarly derived survival estimates in the literature are from a migratory population in central Colorado (Lutz and Plumpton 1997), where adult survival averaged 39% per yr over a 4-yr period, but varied among years (range = 18–71%), and nestling survival to 1 yr averaged 12%. Clayton and Schmutz (1997) estimated over-summer survival rates at 83% for adult female, 46% for adult male, and 48% for juvenile migratory Burrowing Owls in Alberta and Saskatchewan using radiotelemetry, but additional mortality would be expected in this population on migration and during winter. Estimates of annual survival from band resightings unadjusted for emigration range from 37–57% for adults in a migratory population in Saskatchewan (James et al. 1997), to 30% for juveniles and 81% for adults in a sedentary population in Oakland, California (Thomsen 1971). Estimates for Cape Coral fall within the upper limits of survival from these previous studies, and are most comparable to estimates for the Oakland, California population. The Cape Coral Burrowing Owl population shares several other traits with the Oakland, California population, among them relatively low productivity (Millsap and Bear 2000) and high nest site and mate fidelity (Millsap and Bear 1997). These simi-

Table 3. Estimates of annual survival of Florida Burrowing Owls in Cape Coral, Lee County, Florida, 1987–91 from best-fit models using Program SURGE (see Table 2 for models and model selection criteria).

MODEL CLASS[a]	ESTIMATED ANNUAL SURVIVAL (SE)			
	>60% DEVELOPMENT	40–60% DEVELOPMENT	20–39% DEVELOPMENT	<20% DEVELOPMENT
Adult models				
Adult male	0.81 (0.04)	0.62 (0.05)	0.62 (0.05)	0.81 (0.04)
Adult female	0.69 (0.04)	0.52 (0.06)	0.69 (0.04)	0.69 (0.04)
Age-class models				
Age 0–1 yr[b]	0.11 (0.03)	0.28 (0.04)	0.43 (0.08)	0.18 (0.08)
Age >1 yr	0.46 (0.02)	0.60 (0.09)	0.63 (0.09)	—

[a] Adult models are based on birds first captured as breeding adults. Age-class models use birds first banded as nestlings at their natal burrow.

[b] Age 0–1 yr survival was adjusted to account for measured emigration following the approach in Burnham et al. (1996).

larities might reflect the absence of seasonal migration and mild climate common to both study sites.

Vehicle collisions were an important source of mortality for both juvenile and adult Burrowing Owls in Cape Coral. Most road mortality I observed was on residential streets with reduced speed limits (i.e., ≤56 km/hr). Highway collision was also found to be a substantial mortality factor in North Dakota (Konrad and Gilmer 1984), Saskatchewan (Haug and Oliphant 1987, Clayton and Schmutz 1997), and Alberta (Clayton and Schmutz 1997), and it is identified as a principal mortality factor in the Canadian Burrowing Owl Recovery Plan (Hjertaas 1997). In radiotelemetry studies of survival, predation has also been shown to be an important source of mortality (Clayton and Schmutz 1997), and I suspect it was more important in Cape Coral than indicated by band recoveries. This was particularly true in heavily-developed areas where cover for predators was high. During the course of the study, I observed, in order of decreasing frequency, Cooper's Hawks (*Accipiter cooperii*), Fish Crows (*Corvus ossifragus*), house cats, Merlins (*Falco columbarius*), and Peregrine Falcons (*F. peregrinus*) capture Burrowing Owls.

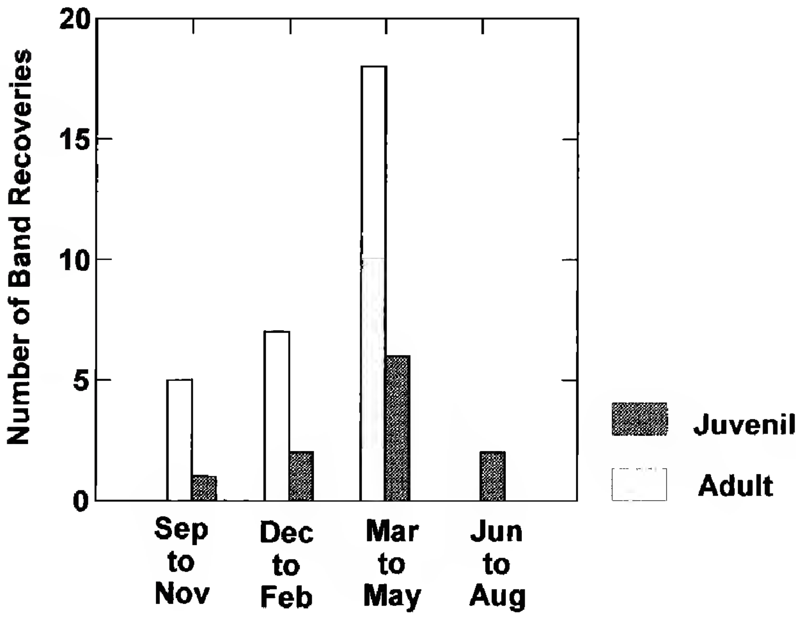

Figure 2. Histogram of recoveries of deceased banded Burrowing Owls reported by the public by season from Cape Coral, Lee County, Florida, 1987–91.

Although band recoveries by the public may provide a misleading picture of the timing and seasonality of Burrowing Owl mortality, my results suggest that adult Burrowing Owls are at higher risk of mortality in spring while breeding. This implies that there is a cost of reproduction to Burrowing Owls on the study area, although I have insufficient data to compare annual survival for breeders with nonbreeders. The high mortality of juveniles at about the time of fledging is not unexpected. The drop in mortality in both adults and young in fall is surprising, because it is at this time that mortality from predation by migrant raptors should probably increase. As noted earlier, however, this kind of mortality would not be detectible through band recoveries reported by the public.

The inverse relationship between survival rates for adult males, the group for which conclusions regarding survival were least apt to be confounded by emigration because of high nest site fidelity (Millsap and Bear 1997), and juveniles is curious. I suspect this occurred because high adult mortality in moderate-development zones created more opportunities for surviving banded juveniles to settle near their natal nest sites where they had a high probability of being encountered. This hypothesis is consistent with the high natal philopatry observed in this study population (Millsap and Bear 1997), and is further supported by the limited data on juvenile emigration, which showed higher rates of movement off the study area by juveniles from heavily-developed areas than from less-developed areas. Because emigration appeared to affect apparent juvenile survival greatly, actual survival might have been much different. The only conclusion, I believe, that can be drawn safely about juvenile survival is that it was as high as 43% in some parts of the study area.

It is not immediately apparent from the available data why adult male, and, to a lesser extent, adult female survival was lowest in moderately-developed parts of the study area. Both Burrowing Owl nest site density and productivity were positively associated with home development in the <20%, 20–39%, and 40–60% development zones (Millsap and Bear 2000); hence, adult survival was lowest in areas where both density and productivity were relatively high. Although it is conceivable that low adult survival was directly related to pressures associated with high adult population density in moderate development zones, this is not consistent with the high rate of juvenile recruitment in these areas. If there was strong competition among adults for nest sites, fewer rather than more 1-yr-olds would be expected to find breeding vacancies to fill (Newton 1991). A possible explanation that better fits the available data is that the comparatively rapid rate of home construction in the 20–39% and, in particular, the 40–60% development zones (Fig. 1a) caused, either directly or indirectly, higher adult mortality. More work is needed to ascertain whether or not this is the case, and to determine the mechanism of the effect. Such work could have significant implications for future conservation of urban Florida Burrowing Owl populations.

Acknowledgments

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BIASES ASSOCIATED WITH DIET STUDY METHODS IN THE EURASIAN EAGLE-OWL

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ABSTRACT.—The diet of the Eurasian Eagle-Owl (*Bubo bubo*) was assessed by collecting pellets and prey remains near the nesting cliffs of 21 pairs in the central-eastern Italian Alps between 1993–97. Taxonomic and prey mass composition of the diet was compared between two methods of analysis, pellets and prey remains, to assess biases associated with these techniques. When compared with pellets, remains overestimated avian occurrence, underestimated mammals, and completely failed to detect fish occurrence ($P < 0.0001$). Large prey were also over-represented in remains ($P < 0.002$). Overall, pellets gave a more realistic and diverse picture of Eurasian Eagle-Owl diet, but failed to detect 26 avian species and 12 avian families identified in remains. Biases associated with the two methods may be lowered by pooling items collected by both methods, assuming the minimum possible number of individuals per species per collection event. However, care must be taken to show the relative contribution of each method in the pooled sample. Further research is needed to quantify biases in diet study methods, by using controlled feeding of captive owls. Similar biases may apply to the study methods commonly employed to assess the diet composition of other owls and predatory birds.

KEY WORDS: *bias;* Bubo bubo; *diet; diet assessment methods; Eurasian Eagle-Owl; Italy.*

Sesgos asociados con los métodos de estudio de dieta de *Bubo bubo*

RESUMEN.—La dieta de *Bubo bubo* fue evaluada mediante colecta de egagropilas y restos de presas cerca de las cornisas de anidación de 21 parejas en el centro oriente de los alpes italianos entre 1993–97. La composición taxonómica y la masa de las presas de la dieta fueron comparadas entre dos métodos de análisis en las egagropilas y los restos de presas, para evaluar los sesgos asociados con estas tecnicas. Cuando fueron comparados con las egagropilas, los restos sobre estimaron la ocurrencia de las aves, subestimaron los mamíferos, y fallaron completamente en detectar la ocurrencia de peces ($P < 0.0001$). Las presas grandes además fueron sobre representadas en los restos($P < 0.002$). En conjunto, las egagropilas dieron una imagen mas real y diversa de la dieta del búho, pero fallaron en detectar 26 especies de aves y 12 familias de aves identificadas en los restos. Los sesgos asociados con los dos métodos pueden ser disminuidos utilizando mancomunadamente los ítems colectados por ambos métodos, asumiendo el minimo numero posible de individuos por especie por evento de colección. Sin embargo, debe tenerse cuidado para la contribución relativa de cada método en la muestra mancomunada. Es necesaria mayor investigación para cuantificar los sesgos en los métodos de estudio de dieta, usando alimentación controlada en búhos cautivos. Sesgos similares pueden aplicar al estudio de métodos comunmente empleados para evaluar la composición de dieta de otros búhos y otras aves de presa.

[Traducción de César Márquez]

The diet of raptors has been assessed by analysis of stomach contents, pellets, or prey remains and by observation/photography of prey captured or delivered to the nest (Marti 1987, Rosenberg and Cooper 1990). Biases associated with such methods have been examined in at least 11 species of diurnal raptors (Newton and Marquiss 1982, Collopy 1983, Goszczynski and Pilatowski 1986, Simmons et al. 1991, Bielefeldt et al. 1992, Mersmann et al. 1992, Mañosa 1994, Oro and Tella 1995, Real 1996, Sánchez-Zapata and Calvo 1998, Redpath et al.

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2001). Some common conclusions emerged from these studies: (1) remains usually overestimate the amount of large and conspicuous prey in the diet, such as large birds, large fish, or medium to large mammals; (2) pellets tend to overestimate the occurrence of medium to small prey, such as small mammals and passerine birds; and (3) when compared to direct-observation methods, remains seem to yield a more biased description of diet than pellets, but allow the detection of many unusual prey types not recorded in pellets, and the recognition of more items to the species level than pellets. Assessment of biases in diet study methods in nocturnal raptors presents additional problems, because of the difficulty of direct observation of prey capture or prey deliveries to the nest that usually occur at night.

The Eurasian Eagle-Owl (*Bubo bubo*) is a nocturnal top predator, with a generalist diet, locally specialized in medium-sized birds and mammals (Hiraldo et al. 1976, Donázar et al. 1989). Due to its frequent predation on other diurnal and nocturnal raptors, Eurasian Eagle-Owl populations can be a limiting factor for those of other birds of prey (Mikkola 1983, Sergio et al. 1999a, 1999b). The Eurasian Eagle-Owl diet has been extensively studied and recently reviewed (Mikkola 1983, Cramp 1985, Donázar et al. 1989, Penteriani 1996). Diet assessment has been carried out through analysis of pellets and/or remains, but no studies on biases associated with such methods have ever been published for this species. A correct evaluation of Eurasian Eagle-Owl diet is particularly important for two reasons: (1) to obtain a better understanding of its habitat use, diet composition, and conservation requirements; and (2) to obtain a more precise assessment of the impact of Eurasian Eagle-Owl predation on other raptors, or other conservation priority species. The aim of this work was to compare pellet contents with uneaten prey remains and to determine the most accurate method to assess the diet composition of this species. In particular we expected: (1) remains to overestimate large and conspicuous prey; (2) pellets to overestimate small items; and (3) the two methods to differ in their degree of taxonomic accuracy of prey identification.

STUDY AREA

Eurasian Eagle-Owls were surveyed in a 1330-km^2 study plot, located in the central-eastern Italian Alps (46°04′N, 11°08′E) (Marchesi et al. 1999). The area supported a population of 23–25 pairs. Elevation ranged from 70–2400 m. The landscape was characterized by mountain slopes covered by broad-leaved woodland interspersed with extensive cliffs. The valley floors were intensively cultivated or urbanized.

METHODS

Pellets and prey remains were collected near the nesting cliffs of 21 pairs between 1993–97, by carefully searching the area near and under the nest, and at traditional roosting places. Collections were carried out at regular intervals throughout the year, so as to avoid biases caused by seasonal variations in the diet (Oro and Tella 1995). Prey items were identified by comparison to a reference collection at the Trento Natural History Museum. For each method and when pooling prey items based on both methods, items were identified assuming the minimum possible number of individuals per collection event. For example, if two individuals of a prey type were identified in pellets but only one individual was detected in remains from the same collection event, we registered two items to the pooled sample.

Prey mass was calculated based on information provided by Perrins (1987) and Macdonald and Barrett (1993). Eurasian Eagle-Owls usually capture juvenile individuals of prey species larger than a lagomorph (Donázar et al 1989). Thus, half the mean adult mass of these species was employed, following Donázar et al. (1989). In addition, to avoid affecting the calculations of mean prey mass by few unusually heavy prey, no items were assigned a mass of more than 2500 g (ca. half the weight of an adult red fox, *Vulpes vulpes*, the heaviest local prey).

Statistical Analysis. Comparison of prey taxa between the two methods of diet assessment was performed by means of χ^2 analysis on contingency tables (Sokal and Rohlf 1981). To avoid cells with inadequate expected frequencies, prey items were grouped in the following categories: family Muridae, Gliridae, Erinaceidae, other mammals, Accipitridae, Strigidae, Phasianidae, Columbidae, Rallidae, Turdidae, Corvidae, other birds, unidentified birds, and fish. Hereafter, we refer to such groups as "main prey categories."

Mean prey mass was compared between methods by means of t-tests (Sokal and Rohlf 1981). Mean number of species identified per detected family was compared between methods with Matched Pairs t-tests (Sokal and Rohlf 1981). Dietary breadth within each diet analysis-method was estimated through the Simpson's index, calculated as $\Sigma\ p_i^2$, where p_i is the relative proportion of each prey category within the sample (Simpson 1949) The index ranges between 0–1, with higher values indicating lower diet diversity. Dietary overlap between different methods was estimated through the Pianka's index, ranging from zero (no overlap) to one (complete overlap; Pianka 1973). When comparing pellets and remains, different analyses were carried out for birds, mammals, and overall vertebrates composition to gain further insights into differences between the methods. When multiple comparisons were carried out on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989). Means are given with 1 SE, all tests are two-tailed, and statistical significance was set at $P < 0.05$.

Table 1. Percentage frequency of main prey categories of Eurasian Eagle-Owls in the Italian Alps (1993–97), as determined by two methods of diet analysis and by the combination of both methods (pooled).

	Pellets		Remains		Pooled[a]	
Prey Category	*N* (%)	% Mass	*N* (%)	% Mass	*N* (%)	% Mass
Mammals:	461 (76)	83.1	53 (28.2)	45.4	493 (65.6)	69.9
Muridae	203 (33.5)	29.3	0 (0.0)	0.0	203 (27.0)	21.2
Gliridae	173 (28.5)	11.9	4 (2.1)	0.5	175 (23.3)	8.7
Erinaceidae	63 (10.4)	25.8	45 (23.9)	35.2	92 (12.3)	27.3
Other mammals[b]	22 (3.6)	16.2	4 (2.1)	9.7	23 (3.1)	12.6
Birds:	130 (21.5)	13.4	135 (71.8)	54.6	243 (32.3)	28.4
Accipitridae	9 (1.5)	1.9	9 (4.8)	4.5	15 (2.0)	2.6
Strigidae	5 (0.8)	0.9	16 (8.5)	4.9	18 (2.4)	2.1
Phasianidae	5 (0.8)	4.2	9 (4.8)	11.3	12 (1.6)	6.2
Columbidae	0 (0.0)	0.0	24 (12.8)	8.7	24 (3.2)	3.4
Rallidae	0 (0.0)	0.0	7 (3.7)	2.0	7 (0.9)	0.8
Turdidae	85 (14.0)	4.4	23 (12.2)	2.2	96 (12.8)	3.6
Corvidae	5 (0.8)	2.0	26 (13.8)	13.6	29 (3.9)	6.1
Other birds[c]	3 (0.5)	1.1	18 (9.6)	7.4	21 (2.8)	3.7
Unidentified birds	18 (3.0)		3 (1.6)		21 (2.8)	
Fish	15 (2.5)	2.3	0 (0.0)	0.0	15 (2.0)	1.7
Total	606		188		751	
Simpson's index	0.23	0.22	0.13	0.18	0.16	0.16

[a] Calculated by pooling pellets and prey remains and assuming the smallest possible number of individuals per prey species per collection event.

[b] Includes families Talpidae, Canidae, Felidae, and Leporidae.

[c] Includes families Podicipedidae, Ardeidae, Anatidae, Falconidae, Tetraonidae, Laridae, Cuculidae, Apodidae, Picidae, Hirundinidae, Sturnidae, and Laniidae.

RESULTS

Comparison of Pellets and Prey Remains.

All vertebrates. Pellets and prey remains differed significantly in frequency of mammals, birds, and fish recorded (χ^2_2 = 194, $P < 0.0001$; Table 1). Frequency of main prey categories differed between the two methods (χ^2_{13} = 421, $P < 0.0001$; Table 1). Twelve species and six families recorded in pellets went undetected in remains. Twenty-six species and 12 families found in remains were not recorded in pellets. Of the main prey categories, two were undetected in pellets and two in remains (Table 1). Fewer items were identified at the species level in pellets than in remains (76% and 98%; χ^2_1 = 76, $P < 0.0001$). Mean number of identified species per detected family did not vary significantly between methods (0.97 ± 0.2 and 1.37 ± 0.3, $t_{30} = -1.44$, $P = 0.16$). Mean prey mass was significantly lower in pellets than in remains (332 ± 16 and 552 ± 37, respectively; $t_{588,185} = -5.3$, $P < 0.002$; Fig. 1). Diet diversity was higher in remains than in pellets (Table 1). Pianka's index of overlap was 0.30 by number and 0.59 by mass.

Mammals. Frequency occurrence of taxonomic groups significantly differed between pellets and remains (χ^2_3 = 134, $P < 0.0001$; Table 1). Nine species, four families and one main prey category recorded in pellets went completely undetected in remains, while all species, families, and main prey categories identified in remains were represented in pellets (Table 1). A lower frequency of items was identified at the species level in pellets than in remains (78% and 91%; χ^2_1 = 20, P = 0.0001). Mean number of identified species per detected family was higher in pellets than in remains (1.56 ± 0.3 and 0.56 ± 0.2, respectively; t_9 = 3.00, P = 0.034). Mean prey mass was significantly lower in pellets than in remains (333 ± 17 and 534 ± 34, respectively; $t_{573,200} = -5.3$, $P < 0.003$). Dietary breadth was higher in pellets than in remains: the Simpson index was 0.36 in pellets and 0.73 in remains. Pianka's index of overlap between the two methods was 0.29 by number and 0.68 by mass.

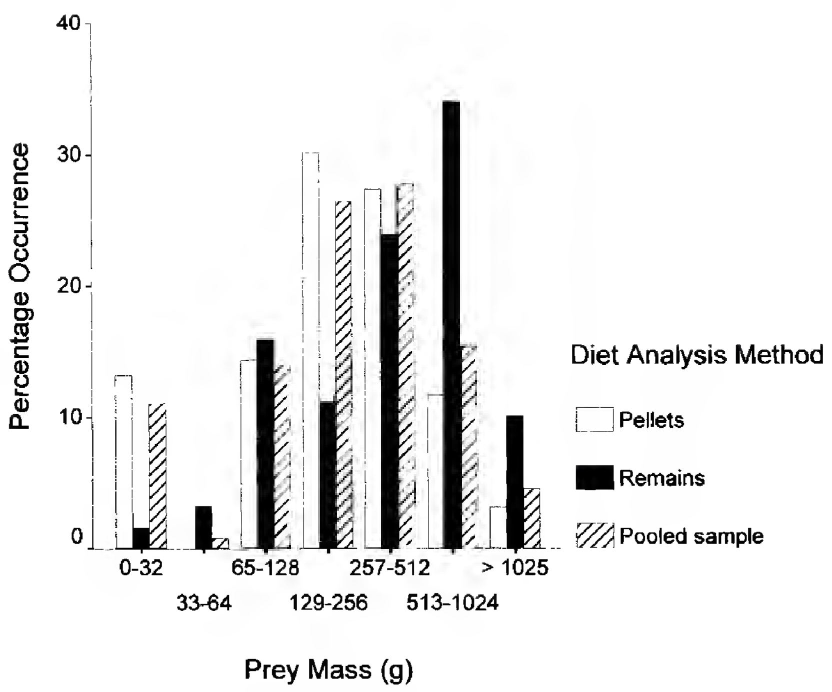

Figure 1. Mass distribution of prey captured by Eurasian Eagle-Owls in the central-eastern Italian Alps (1993–97), as estimated by pellet analysis, remains analysis, or by pooling pellets and remains. Prey items were grouped by mass categories using an exponential distribution in base two.

Birds. Taxonomic composition significantly differed between pellets and remains ($\chi^2_8 = 127$, $P < 0.0001$; Table 1). Twenty-six species and 12 families identified in remains went completely undetected in pellets, while only three species and one family identified through pellet analysis were not detected in remains. Two main prey categories went unrecorded in pellets, but were common in remains (Table 1). A higher percentage of items were identified at the species level in remains than in pellets (82% and 2%, respectively; $\chi^2_1 = 206$, $P < 0.0001$; Table 1). The mean number of identified species per detected family was significantly higher in remains than in pellets (1.89 ± 0.3 and 0.68 ± 0.3, respectively; $t_{19} = -4.46$, $P < 0.003$). Mean avian prey mass was significantly higher in remains than in pellets (423 ± 38 and 254 ± 37, respectively; $t_{132,112} = -3.1$, $P = 0.002$). The Simpson's index was 0.57 in pellets and 0.13 in remains, indicating a more diverse diet in the latter method. Pianka's index of overlap between the two methods was 0.56 by number and 0.69 by mass.

Comparison of the Pooled Sample with Pellets and Remains. All species, families, and main prey categories recorded in pellets or remains were obviously detected in the pooled sample. A higher percentage of items were identified at the species level in the pooled sample than in pellets (81% and 76%, respectively; $\chi^2_1 = 5$, $P = 0.019$) and in remains than in the pooled sample (98% and 81%, respectively; $\chi^2_1 = 49$, $P < 0.0001$). Mean number of identified species per detected family was higher in the pooled sample than in pellets (1.77 ± 0.2 and 0.97 ± 0.2, respectively; $t_{30} = -4.00$, $P < 0.001$) and remains (1.37 ± 0.2, $t_{30} = 3.29$, $P = 0.003$). Mean prey mass did not differ between the pooled sample and pellets (368 ± 15 and 332 ± 16, $t_{730,588} = -1.62$, $P = 0.12$; Fig. 1) and was significantly lower in the pooled sample than in remains (552 ± 37; $t_{730,185} = 5.21$, $P < 0.001$). Diet diversity in the pooled sample was intermediate between that in pellets and remains (Table 1). Overlap between the pooled sample and pellets was 0.99 by number and 0.94 by mass. Overlap between the pooled sample and remains was 0.46 by number and 0.79 by mass.

DISCUSSION

The direct observation of prey capture or delivery to the nest is considered the least biased method of diet analysis (Simmons et al. 1991, Bielefeldt et al. 1992). However, this method is very time-consuming, often unfeasible for many species, and particularly poorly suited to the study of Eurasian Eagle-Owl diet, because of this species' nocturnal habits and generally inaccessible cliff nest sites. Indirect methods, such as analysis of pellets and remains, are thus required. Due to the above difficulties, we were unable to compare pellet and remains analyses with direct observation of prey delivered to the nest. However, comparison of the two indirect methods suggested that both of them incorporated inherent biases.

Overlap in frequency of main prey categories between the two methods was extremely low. When compared to pellets, remains overestimated birds, underestimated mammals, and failed to detect the presence of fish in the diet. Large prey were also overrepresented in remains when compared to pellets. Biases in remains toward underestimation of fish occurrence and overestimation of bird occurrence and of large prey have been detected in other studies which compared remains with direct observations (Simmons et al. 1991, Bielefeldt et al. 1992, Mersmann et al. 1992, Real 1996). Such biases are probably caused by the different conspicuousness and rates of deterioration of the different body parts of different taxa (Goszczynski and Pilatowski 1986, Mersmann et al. 1992). For example, avian pluckings are generally more colorful and conspicuous than other vertebrates' remains

(Bielefeldt et al. 1992); in addition, pluckings of large birds are generally more conspicuous and characterized by lower decay rates than those of smaller birds (Goszczynski and Pilatowski 1986, Newton and Marquiss 1982). Overall, remains generally consisted of large, easily-identifiable body parts. As a result, they were more frequently identifiable to the species level than prey items in pellets.

Comparison of pellets and remains within different vertebrates' prey groups showed biases to be affected by an interaction between different methods of analysis and different prey taxa. Within mammals, remains failed to detect the presence of the whole family Muridae, which accounted for 33.5% of the items in pellets. Remains were strongly dominated by the conspicuous, large skins of hedgehogs (*Erinaceus europaeus*). Within birds, pellets failed to record the presence of 26 species and 12 families identified in remains. Thus, remains gave a more complete and diverse picture of avian diet, but still overestimated prey size. Finally, fish were recorded only in pellets. Thus, pellets seemed to yield a more balanced and realistic picture of Eurasian Eagle-Owl diet, but remains seemed to be a useful complementary tool to assess avian occurrence. As an additional advantage, pellets yielded a much higher number of prey items than remains, despite equal search effort by the researchers. Pellets were thus a more cost-effective method to collect large numbers of prey.

Research Implications. Because of the difficulty of direct-observation methods and the biases inherent in pellets and remains analyses, Eurasian Eagle-Owl diet should be assessed through multiple techniques, including the pooling of samples derived from different methods of analysis. In our study, all species and families identified in pellets and remains were represented in the pooled sample. When compared to pellets and remains, the pooled sample showed an intermediate mean prey mass, diet diversity, and frequency of items identified at the species level. Because of the different sample sizes of pellets and remains, the overlap was high between the pooled sample and pellets, and less so between the pooled sample and remains. By reflecting more the taxonomic and prey-mass composition of pellets and by adding to it the additional avian prey detected through remains, the pooled sample lowered biases associated with each method and provided additional insights in Eurasian Eagle-Owl diet composition. The use of pooled samples consisting of pellets and remains has been proposed for other raptors (Goszczynski and Pilatowski 1986, Simmons et al. 1991, Mañosa 1994, Oro and Tella 1995) and has been demonstrated to yield a relatively close fit to diet composition assessed by direct observation (Simmons et al. 1991, Mañosa 1994, but see Redpath et al. 2001).

Further research is needed to assess precise biases associated with different methods of diet analysis by means of controlled feeding of captive Eurasian Eagle-Owls, as carried out for other species (Mersmann et al. 1992, Real 1996). In the absence of such data, we suggest that future studies of Eurasian Eagle-Owl diet be carried out by using multiple techniques in a complementary way. Pooling samples obtained through pellet and remains can reduce biases, but care should be taken to show the relative contribution of each method to the pooled sample in terms of taxonomic and prey mass composition (Table 1). In the past, pooled samples have been presented without specifying the relative contribution of pellet items and remains to the overall sample (e.g., Olsson 1979, Hiraldo et al. 1975). Such inaccuracy can produce biases in different studies, making them difficult to compare and adding statistical noise to review analyses of diet composition (Donázar et al. 1989). Review studies on predation rate of Eurasian Eagle-Owls on raptors or other conservation sensitive species (e.g., Serrano 2000) should take into account biases inherent to different diet-analysis techniques: studies based exclusively on remains or pellets are likely to overestimate or underestimate, respectively, Eurasian Eagle-Owl impact on other large avian species. Such review analyses should be carried out ideally on pooled samples and rerun for each diet analysis technique separately, to compare their results. Finally, as similar biases are likely to apply to many other species, we suggest that similar approaches to diet assessment be used on other owls or other avian predators.

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DESCRIPTION OF A NEW SUBSPECIES OF THE EGYPTIAN VULTURE (ACCIPITRIDAE: *NEOPHRON PERCNOPTERUS*) FROM THE CANARY ISLANDS

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Abstract.—On the basis of four study skins from museum collections and 37 live birds from the island of Fuerteventura, we describe a new subspecies of the Egyptian Vulture *(Neophron percnopterus majorensis)* from the Canary archipelago. Canarian Egyptian Vultures are significantly larger than Western European and North African individuals. In addition, some genetic differentiation may exist; analyses of the mitochondrial DNA control region revealed that there are haplotypes exclusive to the Canary Islands. The current population of Egyptian Vultures in the Canary Islands is 25–30 breeding pairs restricted to the islands of Fuerteventura and Lanzarote, and this subspecies is therefore endangered.

Key Words: *Egyptian Vulture*; *Canary Islands*; *control region*; *mitochondrial DNA*; Neophron percnopterus majorensis; *subspecies.*

Descripción de una nueva subespecie de alimoche (*Neophron percnopterus majorensis)* nativa del archipiélago de Canarias

Resumen.—Describimos una nueva subespecie de alimoche (*Neophron percnopterus majorensis)* nativa del archipiélago de Canarias, sobre la base de 4 pieles de museo y 37 individuos capturados vivos. Los alimoches canarios son significativamente mayores que los del oeste de Europa y norte de África. Además, presentan diferenciación genética: un análisis de la Región Control del ADN mitocondrial mostró que existen haplotipos exclusivos de las Islas Canarias. La población actual de alimoches canarios es de 25–30 parejas restringidas a las islas de Fuerteventura y Lanzarote, y está, por tanto, gravemente amenazada.

[Traducción de los autores]

The genus *Neophron* has only a single species, the Egyptian Vulture (*Neophron percnopterus*), which lives in dry ecosystems of the Palearctic, Ethiopic, and Indo-Malayan biogeographic regions. Two subspecies have been recognized: *N. p. percnopterus* occurring in most of the range of the species: Europe, Africa, Middle East, central Asia, and northwest India, and *N. p. ginginianus* in most of the Indian subcontinent (Brown and Amadon 1968, del Hoyo et al. 1994). Following Brown and Amadon (1968) the latter is slightly smaller, having yellow as opposed to dark-brown bill and comparatively-weaker feet and claws.

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The Canary Islands are an archipelago of volcanic origin formed in the past 20 million years close to the western African coast (100 km for Fuerteventura, the nearest island). The islands have a subtropical climate; fauna and flora are related to other Macaronesian archipelagos (Madeira, Azores) and to the Mediterranean region. Twenty-seven percent of the vascular plants and 50% of the invertebrates are endemic (Juan et al. 2000). In addition, seven avian species are considered to be endemic of the archipelago (Blanco and González 1992). Endemic subspecies have already been described for three birds of prey living in the islands: Common Buzzard (*Buteo buteo insularum*, Foericke 1903), Eurasian Sparrowhawk (*Accipiter nisus granti*, Sharpe 1890), and Eurasian Kestrel (*Falco tinnunculus canariensis*, in the West islands, Koenig 1890; and *F. t. dacotiae* in the East islands, Hartert 1913). Three other raptor species exist in the archipelago without known distinct subspecific status: Egyptian Vulture, Osprey (*Pandion haliaetus*), and Barbary Falcon (*Falco pelegrinoides*) (del Hoyo et al. 1994).

In Macaronesia (Palearctic subregion including the Atlantic Islands), the Egyptian Vulture inhabits the Canary and Cape Verde archipelagos (Bannerman 1963, Bannerman and Bannerman 1965, 1968). In the Canary Islands this bird was common historically; the species formerly occurred in the islands of La Gomera, Tenerife, Gran Canaria, Fuerteventura and Lanzarote (Martín 1987). At present, the Egyptian Vulture persists only in the two easternmost islands (Fuerteventura and Lanzarote) with a total population estimated at 25–30 pairs in the year 2000 (pers. observ.).

We have observed strong differences in the morphology (see below) of this population in relation to that of Western Europe and North Africa. In addition, analyses of the mitochondrial DNA control region revealed that haplotypes exist exclusive to the Canary Islands. This result suggests that the population has been isolated from others for a very long time. Consequently, we propose the recognition of this population at the subspecific level. In this paper, we describe the Canarian Egyptian Vultures as *Neophron percnopterus majorensis* subsp. nov.

DESCRIPTION

Holotype. This specimen is an immature (second plumage) male collected on 22 October 1913 in Tostón (northwestern coast of Fuerteventura) by D. Bannerman. It is located in the British Museum of Natural History (BMNH) collection (Tring Catalogue No. 199).

Geographical Distribution. The subspecies is currently endemic to the islands of Fuerteventura and Lanzarote (eastern Canary Islands). It almost certainly occurred in the remaining islands of the archipelago until extirpated in the 20th century. There are three specimens in the British Museum of Natural History (Tring) which were collected at Gran Canaria (BMNH No. 121) and Tenerife (BMNH No. 231 and BMNH No. 232, respectively) at the beginning of the 20th century.

Description. Plumage patterns of color of *Neophron percnopterus majorensis* resembles the nominate subspecies *N. p. percnopterus* (Brown and Amadon 1968, Cramp and Simmons 1980). Adult individuals of the Canarian subspecies typically show white plumage impregnated by rufous coloration, especially in the crown, nape, median wing coverts, breast, and tail. This coloration is variable among individuals and seems to be acquired from iron oxides derived from the local soils, which are rich in iron compounds; evidently, this is an ecological attribute associated with this population and not a taxonomic characteristic. Canarian Egyptian Vultures are sedentary and thus differ behaviorally from Western European populations, which are long-distance migrants (Cramp and Simmons 1980).

Measurements. We captured and measured 37 wild individuals in 1999–2000 (all birds released after capture), and compared these data from individuals from continental Spain (Table 1). Measurements (mm) of the holotype (BMNH-Tring 199) are: flattened wing chord 516.3 mm; tarsus 88.2 mm; tail: 240.6 mm; bill length with cere 63.5 mm; bill length to the distal edge of cere: 31.8 mm.

Morphological Comparisons. *N. p. majorensis* differs from the nominate subspecies on the basis of larger body measurements. Comparisons with live Iberian individuals (Table 1) revealed significant differences for every trait when the effects of age and sex were controlled. Differences were particularly large for body mass, with the island birds being 18% heavier than Iberian vultures. Tail feathers and wing chord were about 4–8% longer in Canarian vultures. Smaller (ca. 2%), but still significant differences were detected in the length of the tarsus, primary-feather, bill, and bill with cere. Gigantism is well known to occur on islands (Petren and Case 1997, Grant 1998), which has been

Table 1. Biometry of live-trapped Canarian vs. European (Iberian) Egyptian Vultures. For each measurement (see methods) mean, range, standard deviation (SD), and sample size (*N*) are given; % = percent of increase in measurements of Canarian vs. Iberian individuals. Statistical comparisons were performed through three-way Analysis of Variance including effects of age (preadult, adult), sex, and locality. Significance of each factor is shown (*P*).

	CANARY ISLANDS				IBERIAN PENINSULA						
	MEAN	RANGE	SD	*N*	MEAN	RANGE	SD	*N*	%	LOCALITY (*P*)	OTHER EFFECTS (*P*)
Mass (g)	2413.8	1900–2850	232.5	34	1963.2	1550–2300	152.8	79	18.4	<0.0001	Age: 0.0167
Tarsus (mm)	85.9	73.5–93.0	3.6	37	83.9	76.9–98.5	3.8	81	2.3	0.0004	—
Wing chord (mm)	519.7	485–554	20.6	36	499.3	470–535	12.4	73	3.9	<0.0001	Age: 0.0041
Primary (mm)	385.0	346–410	15.9	32	378.2	342–412	13.8	64	1.7	0.0003	Age: 0.0015
Tail (mm)	264.8	240–285	32.0	32	242.7	212–274	13.8	43	8.4	<0.0001	Sex: 0.0055
Bill length (mm)	32.4	29.1–36.5	1.5	35	31.8	29.4–34.5	1.2	69	1.9	0.0153	Sex: 0.0003
Bill cere (mm)	62.8	57.1–68.5	3.0	35	61.7	55.0–70.3	2.9	70	2.5	0.0057	Sex: <0.0001

attributed to the absence of dominant species (Thaler 1973).

We lack measurements of birds from neighboring "Sahara," where the small resident population seems to have been extirpated (see below). We have examined one live bird from the former Spanish Sahara (now Morocco), captured in 1975, which is currently at the Zoo of Jerez (Spain). This bird's measurements (mm) were: wing chord = 505, tail = 256, tarsus = 75.9, primary = 376, bill length = 31.1, bill cere = 59.4, and mass = 1820 g. These measurements are similar to those of continental birds from the Iberian Peninsula (Table 1).

Measurements from existing museum specimens are not reliable for the description of the Canarian subspecies as there is only a single skin from Fuerteventura and the taxonomic status of the extirpated Egyptian Vultures from other Canary Islands is unknown. In addition, problems relative to the condition of skins, small sample size, and the existence of variability linked to age and sex precluded statistical analyses. Nonetheless, we took measures of flattened wing chord (the measure that can be taken with least error in our experience) from specimens deposited at the BMNH (Tring) (Table 2). The four Canarian Egyptian Vulture skins showed the highest values for wing-chord for the entire range. Their values were well above those of individuals from neighboring populations in the western Mediterranean, continental Africa, and Cape Verde Islands. This suggests that birds from the Canary Islands constituted a single subspecies, which is today restricted to Fuerteventura and Lanzarote. There are no additional skins deposited in other museums, which precludes further comparisons. It seems interesting that Cape Verde Egyptian Vultures are smaller than Canarian birds. Hazevoet (1995) reported that these birds are similar in plumage to individuals from African populations; he considered them as belonging to the nominal subspecies.

ETIMOLOGY

Scientific Name. The name of the proposed new subspecies is derived from "Majorata," the ancient name of Fuerteventura Island. It was so called by the Spanish conquerors, since the main native guanche tribe of the island was known as the "Majos." At present, the inhabitants of the island are still called "majoreros."

English Name. According to the species geo-

Table 2. Flattened wing chord measurements (mm) of Egyptian Vulture (*Neophron percnopterus*) skins kept in the British Museum of Natural History (Tring).

REGION	SUBSPECIES	MEDIAN	RANGE	*N*
Canary Islands	*N. p. majorensis*	505.7	490.0–516.3	4
Cape Verde Islands	*N. p. percnopterus*	489.6	456.0–515.6	6
Western Mediterranean[a]	*N. p. percnopterus*	490.0	472.0–510.0	14
East Africa[b]	*N. p. percnopterus*	480.4	450.0–518.0	13
Middle East[c]	*N. p. percnopterus*	501.3	485.5–505.0	4
South Arabia[d]	*N. p. percnopterus*	475.7	351.1–491.3	4
Indian subcontinent	*N. p. percnopterus*	493.5	471.0–510.0	14
Indian subcontinent	*N. p. ginginianus*	460.6	441.5–495.3	23

[a] Spain, France, Algeria, Morocco.
[b] Abyssinia, Somalia, Kenya.
[c] Egypt, Palestine, Turkey.
[d] Oman, Socotra, Arabia.

graphical distribution of this subspecies we propose the name Canarian Egyptian Vulture.

GENETIC DIFFERENTIATION

Methods. We used sequence data of the control region of mitochondrial DNA from 11 Egyptian Vultures of different provinces (two from Fuerteventura, two from the Balearics, four from continental Spain, one from western Sahara [Morocco] and two from India [*N. p. ginginianus*] (Table 3). Analyses of mtDNA have been particularly common for studies of subspecies and closely related species because of the relatively rapid rate of evolution and ease of analysis relative to nuclear (chromosomal) DNA (Wilson et al. 1985, Avise et al. 1987).

Total DNA was extracted from blood samples following Gemmell and Akiyama (1996) with some modifications. Preliminary work in our laboratory indicated that the order of genes in the mitochondrial molecule of Egyptian vultures is consistent with the new avian gene order recently described by Mindell et al. (1998). We thus targeted for amplification by PCR a potentially hypervariable fragment located between the conserved sequence block called Fbox and the flanking Thr-tRNA (for primer sequences and PCR conditions please contact authors). Sequencing reactions were run in an ABI-377 automatic sequencing system (Applied Biosystems) in an external laboratory. Sequences were manually edited and aligned. Genetic distance calculations and phylogenetic analyses were performed with the program PAUP–Version 4.Ob4a (Swofford 2000). Previous analysis of families of captive birds showed a strict maternal inheritance of the analyzed sequences, indicating that these were of mitochondrial origin and not from nuclear insertions.

Results. A fragment of 459 base pairs of control region was used in the sequence analyses. Sequences for the 11 individuals were all different, i.e., each individual presented a unique haplotype (Fig. 1). A total of 53 polymorphic sites were observed (11.5% of the 459 bp sequenced). Absolute numbers of pair-wise differences ranged from 2 (0.44%) between samples from Canary Island and 35 (7.63%) between Iberian and Indian samples. Net mean Kimura's 2 parameter distances between Indian and other groups ranged from 0.066 to 0.077, while the range of distances between non-Indian groups was 0.005 (Iberian and Balearic) to 0.020 (Canarian and Saharian). Consequently, phylogenetic analyses of these sequences with using different algorithms approaches (maximum parsimony, minimum evolution, and maximum likelihood) consistently grouped the two Indian sequences in a clade widely separated from the rest of Iberian, Balearic, Canarian or Saharian sequences, with bootstrap values close to 100% (Fig. 1). The two Canarian sequences also consistently grouped together as a subclade within non-Indian sequences, with bootstrap values up to 92%. A clade of Balearic sequences was obtained with some algorithms, with values of up to not higher than 62%. Finally, the only Saharian sequence included was more closely related to Iberian or Balearic than to Canarian sequences. The sequences are deposited at the EMBL databank under accession numbers AJ305147 to AJ305150 (*N. p. majorensis*), AJ305151

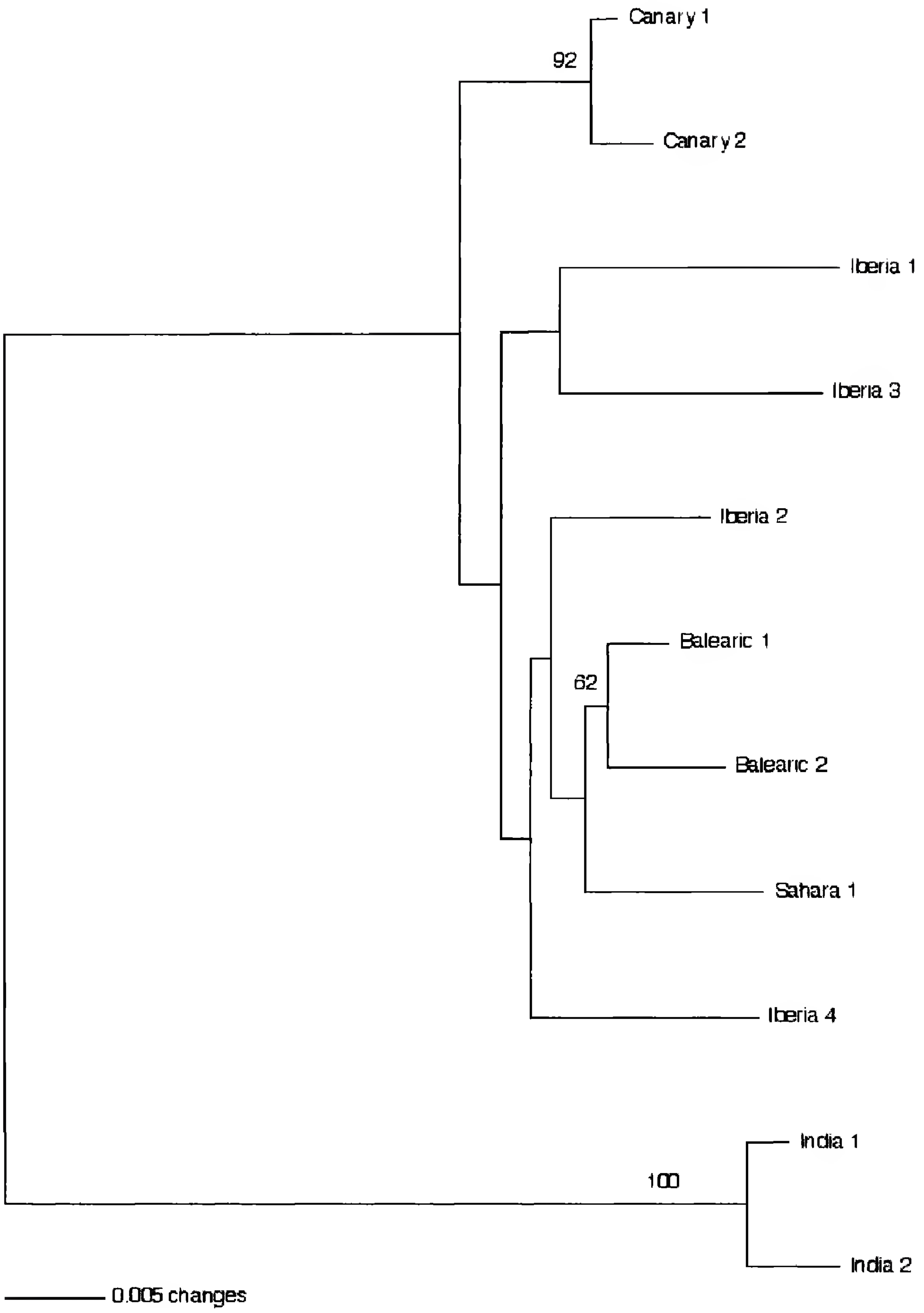

Figure 1. Phylogenetic relationships among the Egyptian Vulture Control Region sequences identified in this study Minimum evolution tree, constructed with the program PAUP using Kimura's 2 parameter distances and the neighbor-joining algorithm followed by a branch-swapping procedure. Values above branches represent support from 100 bootstrap replications (only values above 50% are shown).

to AJ305162 (*N. p. percnopterus*), and AJ305163 to AJ305166 (*N. p. ginginianus*).

DIAGNOSIS

The new subspecies can be distinguished from individuals belonging to the nominal subspecies *percnopterus* on the basis of its larger size (Table 1, 2); the difference is strong with respect to Iberian Egyptian Vultures, which constitute the main western Palearctic population. These latter birds migrate along the African coast (Cramp and Simmons 1980) and, thus, have some chance of straggling to the Canary Islands. Morphological differences between *majorensis* and *percnopterus* of western European and African populations (including Cape Verde Islands) are as marked as those existing between the subspecies *ginginianus* and *percnopterus* in central Asia (Table 2).

A wider population genetic screening of the species will be needed to assess levels of genetic variability and estimations of gene flow among subpopulations. Meanwhile, the analysis of Control Region sequences in a limited number of Egyptian Vultures shows limited low genetic diversity within the Canary Islands populations versus the larger Iberian populations. On the other hand, the Canarian population shows unique mitochondrial haplotypes that group monophyletically within *N. p. percnopterus* non-Indian sequences. Both results are consistent with colonization and further expansion in the islands by individuals from the mainland and suggest limited gene flow between Canarian and other populations. A differentiated evolution of the Canarian population of Egyptian Vultures would have been favored by the isolation resulting from the 100 km-wide sea corridor existing between the eastern coast of Fuerteventura and that of the African continent. Possibility of individual interchange with other breeding populations appears to be low. The current population in the western Sahara seems to be virtually extinct (J. Donázar unpubl. data), and therefore the main possibility of genetic exchange would seem to come from Iberian birds migrating along the African coast and straggling to the islands. We cannot rule out the possibility that some Iberian individuals reach the island and eventually interbreed with local individuals. However, there is strong evidence that Fuerteventura's Egyptian Vultures constitute an ecologically-isolated population with well-differentiated morphological and genetic characteristics.

Summarizing, we propose that the naming of this new subspecies is justified. Description of new subspecies, and even of avian species, has been recently done on the basis of only biometric approaches and taking in account only a few specimens (e.g., Smith et al. 1991, Forero and Tella 1997, Safford et al. 1995, Preleuthner and Gamauf 1998, Yosef et al. 2000). In some cases the distance between these new taxa and those closely related were lower than that found in our study. We cannot discard that further genetic analyses might permit the discovery of additional haplotypes which may show them closer to continental birds. This would not invalidate, however, the existence of a differentiated Canarian lineage as it is shown in this paper.

CONSERVATION

As was stated above, the entire Canarian Egyptian Vulture population is restricted to Fuerteventura and Lanzarote, where no more than 30 territories remain occupied. Total population has been estimated at around 130 birds (pers. observ.). Breeding success has been extremely low in recent years (ca. 0.5 fledglings/pair in 1998–2000). Current threats to this population include mortality from power lines due to collision and electrocution (12 cases during the study period; see also Lorenzo 1995), poisoning (4 cases), and lead intoxication by ingestion of lead bullets (pers. observ.). Theft of eggs and young at the nest, and other human activities may account for some cases of nest desertion during the breeding period (Palacios 2000). Conservation measures should be directed preferentially to prevent casualties related to power lines, lead intoxication, and illegal poisoning. Reinforcement with individuals from continental areas is not recommended, on the basis of the genetic differences showed by the Canarian birds with respect to those of neighboring populations.

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DENSITY, NEST SITES, DIET, AND PRODUCTIVITY OF COMMON BUZZARDS (*BUTEO BUTEO*) IN THE ITALIAN PRE-ALPS

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Abstract.—We studied a Common Buzzard (*Buteo buteo*) population of 32–35 territorial pairs between 1993 and 1999 in a 113-km^2 plot located in the central Italian pre-Alps. Density progressively increased from 28 to 31 pairs/100 km^2. Territorial pairs were regularly dispersed with a mean distance from the nearest occupied nest of 1108 m (N = 108). Eighty-one percent of 108 used nest sites were on cliffs, while the remaining 19% were placed on mature trees. Each year, 16–21% of the nests built by Common Buzzards were taken over by migratory Black Kites (*Milvus migrans*). Mean laying date was 9 April (earliest = 7 March, latest 30 April, N = 45). Mean clutch size was 2.32 (N = 19). Hatching success was 91% (N = 33 eggs from 14 clutches). Mean brood size at hatching was 2.14 (N = 14). Eighty-nine percent of the territorial pairs laid eggs (N = 37) and 72% raised at least one chick to fledging (N = 100). Mean number of fledged young was 1.07 per territorial pair (N = 100), 1.11 per reproductive pair (N = 33), and 1.49 per successful pair (N = 72), with no significant differences among years. Diet was dominated by medium to small passerines, small mammals, and snakes. Recorded density and productivity were comparable and often higher than those reported for other European populations. Human persecution was high until the 1970s, but is currently unimportant. Future conversion of young coppice stands to mature forest could further favor pre-Alpine populations of Common Buzzards.

Key Words: *breeding success*; Buteo buteo; *Common Buzzard*; *density*; *diet*; *forestry*; *Italy*; *pre-Alps.*

Densidad, sitios nido, dieta y productividad de los gavilanes comunes (*Buteo buteo*) en los Pre Alpes Italianos

Resumen.—Estudiamos una población de gavilanes comunes (*Buteo buteo*) de 32–35 parejas territoriales entre 1993 y 1999 en una parcela de 113 km^2 localizada en los pre Alpes del centro de Italia. La densidad incremento progresivamente de 28 a 31 parejas/100 km^2. Las parejas territoriales estuvieron dispersas regularmente con una distancia media al nido mas cercanamente ocupado de 1108 m (N = 108). Ochenta y uno por ciento de los 108 sitios nidos usados estaban en cornisas, mientras que el restante 19% estaban ubicados en árboles maduros. Cada año, 16–21% de los nidos construidos por gavilanes comunes tomados en posesión por milanos negros migratorios (*Milvus migrans*). La fecha media de postura fue 9 de abril (los primeros = 7 marzo, los mas tardíos 30 de abril, N = 45). El tamaño medio de la postura fue 2.32 (N = 19). El éxito en la postura fue 91% (N = 33 huevos de 14 nidadas). El tamaño medio de la nidada en la postura fue 2.14 (N = 14). Ochenta y nueve por ciento de las parejas territoriales pusieron huevos (N = 37) y 72% sacaron adelante al menos un polluelo hasta volantón (N = 100). El numero promedio de jóvenes volantones fue 1.07 por pareja territorial (N = 100), 1.11 por pareja reproductiva (N = 33), y 1.49 por pareja exitosa (N = 72), sin diferencias significativas entre años. La dieta fue dominada por passeriformes medianos a pequeños, pequeños mamíferos, y culebras. La densidad y productividad registradas fueron comparables y a menudo mas altas que aquellas reportadas para otras poblaciones europeas. La persecución humana fue alta hasta los 70's, actualmente no es importante. La futura conversión de los bosquecillos jóvenes a bosques maduros podría favorecer mayormente a las poblaciones pre-alpinas de gavilanes comunes.

[Traducción de César Márquez]

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The Common Buzzard (*Buteo buteo*) is one of the most abundant European raptors (Bijlsma 1997). Except for a possible decrease in Sweden (Ryttman 1994), its populations are generally stable or increasing, and in some areas still recovering from declines caused by pesticide poisoning and human persecution in the 1950s and 1960s (Taylor et al. 1988, Bijlsma 1997). Factors currently limiting density, productivity, and range expansion, include low availability of food and nest sites, direct persecution, and poisoning (Newton et al. 1982, Elliott and Avery 1991, Gibbons et al. 1994, Graham et al. 1995).

In Italy, the Common Buzzard occurs from sea level to an elevation of 1800 m in the Alps (Canova 1992). However, despite its abundance and wide distribution, the species' breeding ecology and population trends are virtually unknown. The few existing estimates refer mainly to the density of territorial pairs and are usually based on low sample sizes (Canova 1992). In this paper, we present data on density, nest spacing, diet, and productivity of a sedentary population of Common Buzzards studied for seven years in the Italian pre-Alps.

STUDY AREA

The study area is a 113-km^2 plot located along the Italian margin of Lake Lugano, within the central Italian pre-Alps (45°55'N, 8°50'E). Altitude ranges from 275–1125 masl. The landscape is characterized by forested mountain slopes interspersed with medium-sized cliffs and rare patches of herbaceous and scrub vegetation, caused by frequent burning. Overall, open areas were scarce, mainly due to human modifications, and concentrated on the valley floors. The area included 16 small villages, all located on the valley floors. Seventy-one percent of the area was covered by woodland, 13% by urban areas, 9% by water bodies, 6% by natural grassland, and 1% by farmland.

Dominant tree species in the forest included sweet chestnut (*Castanea sativa*), downy oak (*Quercus pubescens*), sessile oak (*Quercus petraea*), European hop-hornbeam (*Ostrya carpinifolia*), and locust tree (*Robinia pseudoacacia*). Forests were managed for timber production primarily by means of stool shoots regeneration (coppice system; Matthews 1989), with a rotation of 20–30 yr. Mature trees were often maintained as single individuals or in small clumps as seed bearers (coppice with standards; Matthews 1989). However, most of the woodland had been recently felled and consisted of a homogeneous cover of young second growth forest. Some young woodland patches were being converted to mature woodland, but at the time of study mature forest was still concentrated on a few steep slopes.

Except for forestry operations, human activities were mainly confined to lowlands and mostly absent from the mountain slopes. Climate is temperate continental with wet springs and dry summers (Pinna 1978). Further details on the area can be found in Sergio and Boto (1999)

METHODS

Common Buzzards were surveyed between 1993 and 1999. We censused territorial pairs during the pre-incubation period, between 1 February and 15 April, by observing territorial displays and transfers of nest material. Common Buzzards typically refurbish many alternate nests each year, before selecting the one which they eventually use (Cramp and Simmons 1980). We put effort into finding all the active alternate nests of each pair every year. An alternate nest was defined as active when it contained greenery or freshly broken branches during the preincubation period, and was defined as used when eggs were laid in it.

Whenever possible, nests were visited at least three times: (1) about a week after the mean local laying date to assess clutch size; (2) just after hatching to estimate hatching success, brood size, and hatching date; and (3) when the nestlings were older than 45 d to record the number of fledged young (nestlings usually fledge at 50–55 d; Cramp and Simmons 1980). Nests were checked by climbing the nest tree, descending cliffs with a rope, or watching the nest from a vantage point up the slope with a 20–60× telescope. To minimize the risk of disturbance, nest desertion, or egg/chick predation by Black Kites (*Milvus migrans*) or Ravens (*Corvus corax*), only nests that could be checked very rapidly were visited during incubation/early hatching. Thus, estimates of clutch size, hatching success, number of laying pairs and brood size represented a subsample of nests. Hatching date was estimated by backdating from the feather development of nestlings first observed when ≤15 d old, by observations at eight focal nests and reference to information contained in Tubbs (1974), Melde (1976), and Cramp and Simmons (1980). Laying date was estimated by subtracting 34 d, the median incubation period (Cramp and Simmons 1980), from hatching date. Prey remains found in the nest cup during each nest visit were identified assuming the minimum possible number of individuals per collection event, and by reference to a reference collection and information contained in Debrot (1982).

Terminology follows Steenhof (1987): a reproductive pair is one which laid ≥1 egg, a successful pair is one which raised ≥1 nestling until >45 d old, and breeding success is the percentage of successful territorial pairs. A nest area is an area where ≥1 alternate nest is found within any one year, but where only one pair nests each year (Sergio and Boto 1999, Sergio and Bogliani 1999).

Statistical Methods. The degree of regularity of nest dispersion was estimated by means of the G-statistic (Brown 1975), calculated as the ratio between the geometric and arithmetic mean of the squared nearest neighbor distances (NND) between used nests and varying between 0 and 1. Values close to 1 (>0.65) indicate a regular dispersion of nest sites (Brown 1975). Statistical significance of the deviation from randomness toward regularity of nest spacing was assessed by means of the test proposed by Clark and Evans (1954). To minimize the bias caused by the NNDs of pairs located along the border of the study area, we applied the correction suggested by Donnelly (1978). Details of mathematical pro-

Table 1. Density, nest spacing, and regularity of nest dispersion of a Common Buzzard population in the Italian pre-Alps (1993–99). Means are given ±SE.

YEAR	TERRITORIAL PAIRS/100 km^2 (N^a)	MEAN NEAREST NEIGHBOR DISTANCE (m) (N)	G-STATISTIC	z	P^b
1993	28 (32)	1041 ± 98 (16)	0.776	8.9	<0.001
1994	28 (32)	1057 ± 132 (15)	0.660	9.1	<0.001
1995	29 (33)	1074 ± 108 (17)	0.721	9.5	<0.001
1996	29 (33)	1028 ± 131 (16)	0.614	9.0	<0.001
1997	29 (33)	1381 ± 140 (13)	0.785	13.2	<0.001
1998	29 (33)	1082 ± 134 (13)	0.696	9.6	<0.001
1999	31 (35)	1134 ± 88 (18)	0.818	10.7	<0.001
Total	29 (7)^c	1108 ± 44 (108)	0.703	8.06	<0.001

[a] Number of territorial pairs censused in the study area each year.

[b] Statistical significance of the deviation of nest spacing pattern from randomness toward regularity (Krebs 1998).

[c] Grand mean for the 7 years of study.

cedures can be found in Krebs (1998). To meet the assumptions of normality, NNDs were $\log_e$ transformed, and laying dates were square root transformed prior to parametric tests. All means are given with SE, all tests are two-tailed, and statistical significance was set at $P < 0.05$.

RESULTS

Density and Nest Dispersion. The number of territorial pairs increased from 32 to 35 through the study period. Density correspondingly increased from 28 to 31 pairs/100 km^2 (Table 1). Mean NND did not vary significantly among years (ANOVA, $F_{6,101} = 1.06$, $P = 0.39$), and was on average 1108 ± 44 m (range = 400–2500 m, $N = 108$; Table 1). The G-statistic indicated a regular dispersion of nest sites in all years except 1996 (Table 1). The spacing pattern significantly deviated from randomness toward regularity in all the study period (Krebs 1998, Table 1).

Nest Sites. Mean altitude of used nests was 585 ± 16 m (range = 270–870 m, $N = 108$) and did not vary significantly among years ($F_{6,102} = 0.43$, $P = 0.86$). Mean altitude of cliff nests was higher than that of tree nests (608 ± 15 m and 483 ± 46 m, respectivly; $F_{1,106} = 10.53$, $P = 0.002$). Fourteen to 15 pairs were closely monitored every year until we were reasonably sure to have detected all their active alternate nests. On average, these pairs had three active alternate nests (range = 1–7; Table 2), with no year-to-year variation in their mean number ($F_{6,96} = 0.02$, $P = 1.0$). Overall, we censused 377 active alternate nest-years; 76% of them were positioned on cliffs and 24% on trees, with no significant among-year variation in the two proportions ($\chi^2 = 1.37$, df = 6, $P = 0.97$; Table 2). Cliff nests accounted for 81% of 108 used nest-years, with no year-to-year variation in their frequency of occurrence ($\chi^2 = 5.53$, df = 6, $P = 0.48$; Table 2). Of 52 nests which were used at least once during the seven years of study, 15 were placed on trees, 13 on bare rock ledges, and 24 at the base of trees growing from the cliff faces. Of 15 tree nests, seven were placed on sweet chestnut, two on Scotch pine (*Pinus silvestris*), two on oak (*Quercus* spp.), and one each on spruce fir (*Picea excelsa*), Weymouth pine (*Pinus strobus*), common lime (*Tilia europaea*), and European ash (*Fraxinus excelsior*). The mean height of these 15 nests on trees was 15 ± 1 m. Five pairs had alternate nests on both cliffs and trees, and laid eggs in both types of nests in different years. The mean number of years that a nest was consecutively occupied was 1.2 ± 0.1 for tree nests (range = 1–3, $N = 15$) and 2.1 ± 0.3 for cliff nests (range = 1–7, $N = 37$); the difference between the two was significant (Mann-Whitney U test, $z = -2.07$, $P = 0.038$).

Each year, 16–21% of the active alternate nests were taken over by migratory Black Kites on their arrival (18 March to beginning of April; Sergio and Boto 1999); this percentage did not vary significantly among years ($\chi^2 = 2.88$, df = 6, $P = 0.82$; Table 2). To assess whether Common Buzzards may have selected cliff or tree nests, we compared the frequency of cliff nesting between used nests and active alternate nests. We removed all nests taken over by Black Kites from the sample of active alternate nests, as these were actually not available to buzzards. There was no significant selection for

Table 2. Mean number of active alternative nests/pair, percentage of cliff nests, and percentage of nests taken over by Black Kites in a Common Buzzard population in the central Italian pre-Alps (1993–99). Means are given ±SE.

VARIABLE	YEAR							
	1993	1994	1995	1996	1997	1998	1999	TOTAL
Mean No. of active alternative nests/pair (*N*)	3.0 ± 0.4 (14)	3.1 ± 0.4 (15)	2.9 ± 0.4 (15)	3.0 ± 0.4 (14)	3.1 ± 0.5 (14)	3.1 ± 0.5 (15)	3.1 ± 0.5 (15)	3.0 ± 0.2 (103)
Percent cliff nests among active alternative nests (*N*)	74 (54)	74 (54)	73 (52)	76 (54)	79 (53)	80 (54)	73 (56)	76 (377)
Percent cliff nests among used nests (*N*)	81 (16)	91 (11)	73 (15)	75 (20)	92 (13)	93 (14)	74 (19)	81 (108)
Percent active alternative nests taken over by Black Kites	19	20	21	19	17	17	16	18

Table 3. Mean (±SE) estimates of reproductive success of a Common Buzzard population in the central Italian pre-Alps (1993–99).

VARIABLE	1993	1994	1995	1996	1997	1998	1999	1993–1999
Number of monitored pairs	13	13	11	18	12	14	19	100
Percent successful pairs	69	62	55	83	75	86	68	72
Mean No. of young fledged per territorial pair	1.23 ± 0.26	0.85 ± 0.22	0.63 ± 0.20	1.44 ± 0.22	1.08 ± 0.23	1.14 ± 0.18	0.95 ± 0.78	1.07 ± 0.08
Mean No. of young fledged per successful pair	1.77 ± 0.15	1.38 ± 0.18	1.17 ± 0.17	1.73 ± 0.18	1.44 ± 0.18	1.33 ± 0.14	1.38 ± 0.14	1.49 ± 0.07

cliff or tree nests within any of the seven study years ($\chi^2 \leq 1.71$, df = 6, $P \geq 0.19$).

Breeding Season. Birds were observed on their territories all year. Mean laying date did not vary significantly among years (Kruskal-Wallis $\chi^2 = 11.15$, df = 6, $P = 0.08$). First egg laying dates ranged from 7 March to 30 April, averaging 9 April (SE = 1.60 d, $N = 45$). No cases of replacement clutches were observed in any year, even after breeding failures occurred early in the breeding season. The mean date of the first flight of a nestling in a brood was 19 June (SE = 2.76 d, earliest = 4 June, latest = 5 July, $N = 14$ broods).

Productivity. Mean clutch size was 2.32 ± 0.13 ($N = 19$). Hatching success was 91% ($N = 33$ eggs from 14 clutches). Brood size at hatching was 2.14 ± 0.18 ($N = 14$). Thirty-three of 37 pairs that were monitored laid eggs, and raised a mean of 1.11 ± 0.15 young per pair. There was no year-to-year variation in the percentage of successful territorial pairs ($\chi^2 = 5.16$, df = 6, $P = 0.52$; Table 3). Overall breeding success was 72% (Table 3). The mean number of fledged young per territorial pair was 1.07 (Table 3), with no significant among-year differences ($F_{6,93} = 1.52$, $P = 0.18$). The mean number of fledged young per successful pair was 1.49 (Table 3), and did not vary significantly among years ($F_{6,65} = 1.60$, $P = 0.16$). Causes of failure were usually unknown, apart from two cases of partial brood predation by Black Kites, and one case in which a young was electrocuted just after fledging.

The number of fledged young declined with laying date, but not significantly ($r = -0.17$, $N = 44$, $P = 0.27$). There was no significant correlation between the number of fledged young and nest site elevation ($r = 0.04$, $N = 99$, $P = 0.67$) or NND ($r = 0.11$, $N = 88$, $P = 0.30$). The mean number of fledged young did not differ between cliff nests and tree nests ($F_{1,98} = 0.002$, $P = 0.97$).

Diet. Diet was dominated by birds, mammals, and reptiles which accounted for 46, 29, and 21% of 142 prey remains collected, respectively, in the nests of 20 pairs (Table 4). We were able to assess the age of 36 avian prey individuals: 19% were nestlings, 72% were recently fledged juveniles, and 8% were adult individuals.

Table 4. Diet of breeding Common Buzzards in the Italian pre-Alps (1993–99), as estimated by food remains ($N = 142$) collected from nests. Remains collected during 67 visits to 25 nests.

PREY CATEGORY	NUMBER OF ITEMS (%)
Birds	66 (46)
Blackbird (*Turdus merula*)	26 (18)
Eurasian Jay (*Garrulus glandarius*)	21 (15)
Others[a]	8 (6)
Unidentified Passeriformes	11 (8)
Mammal	41 (29)
Common Mole (*Talpa europaea*)	8 (6)
Muridae spp.[b]	12 (8)
Others[c]	21 (15)
Reptiles[d]	30 (21)
Amphibians[e]	4 (3)
Fish	1 (1)

[a] Includes: European Robin (*Erithacus rubecula*) ($N = 2$), Green Woodpecker (*Picus viridis*) ($N = 2$), Eurasian Sparrowhawk (*Accipiter nisus*) ($N = 1$), Great Spotted Woodpecker (*Dendrocopos major*) ($N = 1$), Chaffinch (*Fringilla coelebs*) ($N = 1$).

[b] Includes: *Pitymys* spp. ($N = 2$), bank vole (*Clethrionomys glareolus*) ($N = 1$), wood mouse (*Apodemus sylvaticus*) ($N = 1$), yellow necked mouse (*Apodemus flavicollis*) ($N = 1$), house mouse (*Mus musculus* ($N = 1$), unidentified Muridae ($N = 5$).

[c] Includes: red squirrel (*Sciurus vulgaris*) ($N = 4$), *Crocidura* spp. ($N = 1$), weasel (*Mustela nivalis*) ($N = 1$), dormouse (*Myoxus glis*) ($N = 1$), brown hare (*Lepus europaeus*) ($N = 1$), unidentified mammal ($N = 13$).

[d] Includes: western whip snake (*Coluber viridiflavus*) ($N = 6$), Aesculapian snake (*Elaphe longissima*) ($N = 7$), unidentified Colubridae ($N = 11$), common wall lizard (*Podarcis muralis*) ($N = 4$), slow worm (*Anguis fragilis*) ($N = 2$).

[e] Includes: common toad (*Bufo bufo*) ($N = 4$).

DISCUSSION

Eighty-one percent of the nests used for breeding in our area were placed on cliffs. In most of Europe, Common Buzzards are tree nesters, and the availability of woodland can be a key factor limiting population density (Dare and Barry 1990, Bijlsma 1993, Halley 1993). Cliff nesting does occur throughout their range, but generally at low frequency, and in areas with limited tree availability (Dare 1995). In our study area, buzzards tended to select nest trees within woodland patches that were more mature than those around random trees (F. Sergio and C. Scandolara unpubl. data). Among alternate nest sites, no preference was evident between cliff and tree nests, even though cliff nests were occupied for higher numbers of consecutive years than tree nests. High frequency of cliff nesting may have been caused by low availability of sufficiently mature woodland patches, even though single tall trees were relatively abundant and widespread in the study area. This is consistent with

Table 5. Density, nearest neighbor distance (NND), and productivity of selected Common Buzzard populations in Europe (1980s–90s).

						MEAN NO. OF FLEDGED YOUNG PER			
AREA	HABITAT	DENSITY (*N*)[a]	NND (km) (*N*)	CLUTCH SIZE (*N*)	BREEDING SUCCESS[b] (*N*)	TERRITORIAL PAIR (*N*)	BREEDING PAIR (*N*)	SUCCESSFUL PAIR (*N*)	SOURCE
Scotland, Highlands	Low mountains	23 (22)							Halley 1993
Scotland, Argyll	Low mountains			2.24 (73)			1.75 (73)	1.98 (66)	Austin & Houston 1997
Scotland, south	Low mountains	8 (19)	1.9 (16)						Graham et al. 1995
Scotland, Glen Urquhart	Low mountains		1.1 (17)	2.40 (162)			1.13 (171)	1.50 (129)	Swann & Etheridge 1995
Scotland, Moray	Low mountains		1.7 (12)	2.90 (64)			2.23 (140)	2.50 (123)	Swann & Etheridge 1995
Wales, Snowdonia	Low mountains	10 (96)[c]	2.0 (96)[c]	2.09 (46)	51 (91)	0.64 (91)	1.00 (58)	1.39 (42)	Dare 1995
Wales, Hiraethog	Low mountains	14 (62)[c]	1.5 (62)[c]	2.40 (39)	67 (57)	0.88 (57)	1.16 (43)	1.35 (37)	Dare 1995
England, Devon	Lowland	52 (17)	1.1 (17)	3.36 (11)	58 (66)	0.95 (66)	1.40 (45)	1.60 (38)	Dare 1998
Netherlands, Drenthe	Lowland	116[d]	0.8 (294)	2.73 (292)	40 (710)	0.87 (710)		2.24 (281)	Bijlsma 1993
Poland, central	Lowland	17 (19)			63 (200)	1.67 (200)	1.78 (186)	2.34 (126)	Goszczynski 1997
Germany, Rhine	Lowland	10[e]			67 (366)	1.15 (366)		1.73 (244)	Kostrzewa 1996
Germany, S. Holsteins	Lowland	45 (45)		2.56 (104)	63 (214)		1.23 (164)	2.04 (135)	Hohmann 1995
Switzerland, Lac Leman	Mountains	13 (17)							Henrioux & Henrioux 1995
Austria, pre-Alps	Mountains	9 (10)							Dvorak et al. 1993
Italy, Apennines	Mountains	8 (17)	2.5 (17)						Penteriani & Faivre 1997
Italy, central Alps	Mountains	29 (53)	1.1 (108)	2.32 (19)	72 (100)	1.07 (100)	1.11 (33)	1.49 (72)	This study

[a] Number of pairs/100 km^2.

[b] Percentage of territorial pairs raising at least one chick until fledging.

[c] Source: Dare and Barry (1990).

[d] Source: Bijlsma (1997); sample size not given.

[e] Source: Kostrzewa (1991); sample size not given.

buzzards responding more to the structural characteristics of breeding woodland patches than to the micro-characteristics of individual nesting trees. Alternatively, cliff nesting may be a response to the recent history of persecution and nest robbing suffered by the species in this area (Bianchi et al. 1969). From discussion with local villagers, we know of at least three territories where nestlings were regularly collected up until the 1970s, and we have indirect evidence of nest robbing at one easily accessible site during our study. In a high-persecution area of Sicily, only two tall and inaccessible tree nests out of seven were not robbed of chicks (Cairone 1982). Cliff nests are generally less accessible than tree nests to humans and cliffs allow buzzards to place their nests higher from the ground than trees. In our study area, cliff nests were also on average at a higher elevation than tree nests, affording additional advantages in terms of distance from sources of human disturbance, which are mostly located at low altitude in the valley floors. Thus, the interaction between the selective pressure associated with potential nest robbing and the low availability of mature woodland patches may cause the local high frequency of cliff nesting, a pattern also observed in the local Black Kite population (Sergio and Boto 1999). Each buzzard pair had on average three alternate nests, and up to seven, within its nest area. This is in agreement with data from other parts of Europe; Tubbs (1974) reported an average of 3.2 alternate nests per nest area (range 1–14) for the New Forest of England. In our study area, some nests, especially on cliffs, were used for a number of consecutive years. However, most nests were used for only one or two years. Such frequent nest switching was possibly enhanced by competition with Black Kites, but has also been reported in other Common Buzzard populations free of such competition (Tubbs 1974, Cramp and Simmons 1980).

Despite the sporadic persecution, the observed density and productivity were in the range of that reported for other European populations (Table 5). In Europe, Common Buzzard breeding densities peak in areas of lowland traditional farmland interspersed with abundant mature woodlots (Bijlsma 1997). Density in the Italian pre-Alps was only slightly lower to that found in such optimal agricultural habitats (Bijlsma 1993, Kostrzewa 1996, Dare 1998, Goszczynski 1997), and higher than any published estimate for mountainous areas (Dare and Barry 1990, Halley 1993, Graham et al. 1995, Penteriani and Faivre 1997; Table 5). Productivity was also comparable or higher than those reported for other mountainous environments (Dare 1995, Swann and Etheridge 1995) and for some lowland areas (Kostrzewa 1996, Dare 1998; Table 5).

The diet of the study population was diverse, as typical for this species (Cramp and Simmons 1980), and dominated by birds, small mammals, and snakes. We caution that diet analyses based on prey remains tend to overestimate large or conspicuous prey species compared to analysis of pellets or direct observations of prey delivered to the nest (e.g., Goszczynski and Pilatowski 1986, Redpath et al. 2001, Marchesi et al. 2002). However, preliminary results of the analysis of 366 pellets gave a picture of diet composition similar to that obtained by the analysis of remains in the nest (F. Sergio and C. Scandolara unpubl. data). Overall, the high frequency of reptiles confirms the importance of such prey for Common Buzzards in Mediterranean countries and at southern latitudes (Cramp and Simmons 1980, Haberl 1995). Finally, the frequent occurrence of typical woodland species in the diet agreed with our many qualitative observations of individuals hunting by sit-and-wait tactics within woodland habitats. On such occasions, buzzards usually perched on intermediate-height branches scanning the forest floor and canopy for periods of 2–5 min, before moving to another perch on a nearby tree (pause-travel tactic; Widén 1994).

The exploitation of a wide range of habitats, the selection of suitable nest sites inaccessible to humans, and the adoption of a diverse opportunistic diet allowed Common Buzzards to settle at a relatively good density and reproduce successfully within the heavily wooded landscape of the central Italian pre-Alps. The local breeding population was stable or slightly increasing in number. No strong threats were apparent: persecution was sporadic and the continued succession of coppice woodland to mature forest could further increase available nesting and foraging habitat. The role of habitat availability, weather, diet, and competition with Black Kites as potential factors limiting density and breeding performance of the local Common Buzzard population is currently under investigation.

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VITAMINS E AND A, CAROTENOIDS, AND FATTY ACIDS OF THE RAPTOR EGG YOLK

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ABSTRACT.—A captive population of falcons was fed a diet containing a known quantity of vitamin A (retinol) and vitamin E (α-tocopherol) for 6 wk prior to and during egg laying. Infertile eggs were analyzed for vitamin A, vitamin E, carotenoid, and fatty acid composition. Mean daily vitamin intake was 29 mg VitE (35IU) and 1157 μg VitA (3363IU). Adjusted mean egg yolk content for infertile, unincubated eggs was 314 μg/g α-tocopherol and 3.06 μg/g VitA. A distinctive feature of the raptor egg yolk is a very high proportion of arachidonic acid that is probably a reflection of their carnivorous diet. A small number of plasma samples were also available from egg-laying falcons. Mean plasma vitamin E was 32.2 μg/ml and plasma vitamin A 1.02 μg/ml.

KEY WORDS: *raptor nutrition; egg yolk; vitamins; fatty acids; plasma.*

Vitaminas E y A, carotenoides, y ácidos grasos de la yema de huevos de rapaces

RESUMEN.—Una población cautiva de halcones fue alimentada con una dieta que contenía una cantidad conocida de vitamina A (retinol) y vitamina E (α-tocoferol) por seis semanas antes y durante la postura de huevos. En los huevos infértiles fue analizada la composición de vitamina A, E carotenoides y ácidos grasos. La entrada media diaria de vitamina fue 29 mg VitE (35IU) y 1157 μg VitA (3363IU). La media ajustada para el contenido de yemas de huevos infértiles y no incubados fue 314 μg/g α-tocopherol y 3.06 μg/g VitA. Una característica distintiva de la yema de huevo de rapaces es una proporción muy alta de ácido araquidonico lo que probablemente es un reflejo de su dieta carnívora. Estuvieron disponibles tambien un pequeño numero de muestras de plasma de halcones durante la postura. El promedio de vitamina E en el plasma fue 32.2 μg/ml y 1.02 μg/ml de vitamina A.

[Traducción de César Márquez]

In recent years attention has focused on the breeding of certain raptor species in captivity as a means of conservation (Cade 1988, Fox and Fox 1993); one example is the Fiji Peregrine Falcon, *Falco peregrinus nesiotes* (D. Brimm pers. comm.). Productivity is dependent on good-quality eggs and without baseline data for raptor species it is difficult to assess egg quality in a breeding project. There are few data on the egg composition of wild or captive Falconiformes and virtually nothing is known about the fatty acid and the antioxidant profiles of the yolks of these species. Wild raptors have a predetermined clutch size and nutrients from the female, deposited in the egg prior to laying, provide all the necessary nutrition for the embryo to develop and for the chick to survive for a few days after hatching. Depending on the species, clutch size in Falconiformes is usually no more than five eggs. However in captivity, this number can be increased to as many as 14 eggs in one season by techniques of egg pulling and clutch pulling (Weaver and Cade 1991) and the requirement for nutrients is therefore much higher. Ideally, captive populations should be fed the same prey items that they would eat in the wild (Clum et al. 1997). Because this is often impractical, it is important to provide a varied, balanced diet with, if necessary, additional supplements of vitamins and minerals to ensure that the egg has sufficient nutrients needed to support successful development (Clum et al. 1997, Fox and Barton 2000).

In the yolk, vitamin E and carotenoids are lipid-soluble antioxidants which protect the developing embryo and chick against peroxidative damage,

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Table 1. Vitamin and water content of food items fed to captive raptors (Forbes and Flint 2000).

FOOD TYPE	SAMPLE SIZE	VITA IU/100 g DM	VITE IU/100 g DM	PERCENT WATER CONTENT
Whole day-old chick	200	497	40.7	76.1
De-yolked, day-old chick	200	363	21.4	78.5
VitE-enhanced quail	100	3633	10.1	66.6

regulate aspects of cell differentiation, and promote the function of the immune system (Surai and Speake 1998, Surai 1999). These are stored in the maternal liver and mobilized during the laying cycle. Studies on the Lesser Black-backed Gull (*Larus fuscus*) have shown that the concentrations of vitamin E and carotenoids in the yolk decrease with each egg laid as the maternal reserves become depleted (Royle et al. 1999). It is therefore possible that captive breeding programs which involve the extension of clutch sizes to increase productivity may result in eggs which are deficient in these antioxidants with potentially-harmful consequences for embryonic survival. There is also evidence that some captive-breeding projects for raptors and other birds may not be producing at maximum capability due to an inadequate dietary provision of vitamin E (Nichols and Montalli 1987, Dierenfeld et al. 1989). For example, captive Peregrine Falcons fed on whole quail (*Coturnix* spp.) achieved plasma vitamin E concentrations of only about 3 μg/ml compared with about 26 μg/ml in wild counterparts; injection or dietary supplementation of the quail with vitamin E was necessary for the captive peregrines to attain plasma vitamin E levels similar to those typical of the wild birds (Dierenfeld et al. 1989). Thus, supplementation of prey items with vitamin E may be needed to achieve optimal reproductive performance in captive raptors.

The polyunsaturated fatty acids of yolk lipids, especially the long-chain polyunsaturates arachidonic (20:4n-6) and docosahexaenoic (22:6n-3) acids, have vital roles in the functional development of certain embryonic tissues, particularly the brain and retina (Speake et al. 1998). For many avian and reptilian species, eggs produced in captivity often display markedly reduced levels of n-3 polyunsaturates, vitamin E, and carotenoids in comparison with eggs laid in the wild. Noble et al. (1996) and Speake et al. (1999a) suggested that these differences may be related to low hatchabilities in the captive situation.

The main aim of the present study was to evaluate the yolk concentrations of vitamins E and A and carotenoids in seven raptor species and one hybrid as part of a viable captive breeding program in which the female parents were fed on vitamin E-enriched quail and day-old chickens (*Gallus gallus*). Since there is currently very little information on the effects of a carnivorous diet on yolk lipids, the fatty acid composition of the yolk is also reported.

METHODS

Eggs were collected from captive raptors held at the Falcon Facility, U.K. Infertile, unincubated eggs were taken from imprint falcons that laid eggs prior to insemination. Other eggs analyzed were infertile, but had been incubated for 14 days, at which time infertility was confirmed. All the females were fed a diet of vitamin-E-supplemented quail, day-old cockerels, vitamin supplements (Nekton E and Nekton S—Günter Enderle, Pforzheim, Germany) and cod-liver oil. Nekton E (100 g) and Nekton S (100 g) mixed and dissolved in 1 litre water produces an injectable solution containing 5.66 mg/ml VitE (6.8 IU) and 229 μg/ml VitA (666 IU).

Vitamin content of food items (Table 1) was used to determine total daily vitamin E and vitamin A intake. Wet weights for quail, whole chick, and de-yolked chick were 200 g, 40 g, and 30 g, respectively. Over the winter from 1 August–1 February, female peregrines, Sakers (*F. cherrug*), Gyrfalcons (*F. rusticolus*), Gyrfalcon × Saker hybrids (*F. rusticolus* × *F. cherrug*), a Common Buzzard (*Buteo buteo*) and a Harris's Hawk (*Parabuteo unicinctus*) were fed 6 d of the week with up to eight de-yolked, day-old cockerels and 1 d with rabbit (*Oryctolagus cuniculus*). The estimated content of the daily food intake was 7 mg or 8 4 IU vitamin E and 45 μg or 131 IU vitamin A. New Zealand Falcons (*F. novaezeelandiae*) and a Barbary Falcon (*F. pelegrinoides*) were fed a smaller amount of the same diet, but the same concentration of supplements on a body mass basis.

The diet was changed on 1 February to three whole day-old chicks and half a quail enhanced with vitamin E, slightly less for the smaller Barbary and New Zealand falcons. Each chick was supplemented daily with an injectable solution of Nekton E and Nekton S containing 5.66 mg VitE/ml. Each chick was injected with 1 ml of the solution. Daily vitamin E intake from 1 February over 6 wk to the start of egg-laying and during egg-laying was calculated as 29 mg or 35 IU/day. Daily vitamin A intake was 1157 μg or 3363 IU, although from 1 March this was increased to ca. 1650 μg or 4800 IU vitamin A three

Table 2. Mean vitamin levels (μg/g) in raptor egg yolk from infertile, unincubated eggs and selected captive raptor species (SD in parentheses). *N* is the number of eggs.

SPECIES	*N*	α-TOCOPHEROL	γ-TOCOPHEROL	RETINOL	CAROTENOIDS
Saker	4	310 (53.8)	10.63 (4.7)	3.1 (1.0)	46.1 (25.8)
Peregrine	7	326 (72.0)	9.1 (1.3)	3.8 (0.5)	32.1 (14.3)
New Zealand Falcon	5	212 (67.3)	5.94 (0.8)	2.4 (0.4)	48.3
Barbary Falcon	1	247	10.78	3.3	—
Common Buzzard	4	443 (75.0)	16.84 (1.6)	2.49 (0.5)	53.8 (4.0)

times/wk when a cod-liver oil supplement was added. Weekly vitamin A intake was therefore about 27 000 IU.

Eggs were delivered to the Scottish Agricultural College, Department of Biochemistry and Nutrition where the yolk was separated from albumin. Vitamin A, vitamin E, carotenoid, and fatty acid levels were determined. Eggs were analyzed from eight peregrines, four Sakers, two Gyrfalcons, four New Zealand Falcons, one Harris's Hawk, one Common Buzzard, one Barbary Falcon and five Gyrfalcon × Saker hybrids. Vitamins A and E were determined by the method of McMurray et al. (1980). To determine carotenoid levels, 2 ml of tissue or yolk homogenate (20% in 0.01 M phosphate buffer, pH 7.4) were mixed with 2 ml ethanol. Hexane (5 ml) was then added and the mixture was shaken vigorously for 5 min. The hexane phase containing the carotenoids was separated by centrifugation and collected. The extraction was repeated twice more with 5 ml hexane. Hexane extracts were combined and carotenoids were determined from absorption at 446 nm. For lipid extraction, yolk samples were homogenized in an excess of chloroform:methanol (2·1, v/v) and extracts of total lipid were prepared. The extracts were subjected to thin layer chromatography on silica gel G using a solvent system of hexane:diethyl ether: formic acid (80:20:1, v/v) and the band corresponding to phospholipid was eluted from the silica with methanol. The total lipid extract as well as the isolated phospholipid fraction was transmethylated and the fatty acid composition was determined by gas-liquid chromatography (Speake et al. 1999a). The phospholipids are the major lipids found in cell membranes that are transferred from the yolk to the chick during embryogenesis.

During the course of routine veterinary investigations, plasma vitamin E and vitamin A levels were also measured in two Saker Falcons and one peregrine during the laying cycle.

RESULTS

For unincubated eggs from the falcons (Saker, peregrine, Gyrfalcon), mean α-tocopherol level was 320 μg/g (N = 11, SD = 60.6); mean α-tocopherol 11.24 μg/g (N = 11, SD = 3.2); mean retinol 3.55 μg/g (N = 11, SD = 0.77); mean carotenoids 36.7 μg/g (N = 9; SD = 17.5; Table 2). Using the peregrine data of seven incubated (Table 3) and seven non-incubated eggs (Table 2), incubating eggs significantly reduces the levels of α-tocopherol (t_{12} = 3.25, $P < 0.01$) and retinol (t_{12} = 5.71, $P < 0.01$).

Fatty acid composition of the raptor egg yolk included saturates (16:0 and 18:0), monounsaturates (16:1n-7, 18:1n-9, and 18:1n-7) and polyunsaturates (18:2n-6, 20:4n-6, and 22:6n-3). The fatty acid profiles of eggs from different raptors were similar (Table 4, 5) and only buzzard egg yolk composition had distinctive features, including the highest proportion of linoleic acid (18:2n-6) and lowest proportions of 16:1n-7 and 18:1n-7 acids compared to other raptor eggs. As with the total lipid, the phospholipid fraction of buzzard eggs was characterized by the highest proportion of 18:2n-6 and the lowest proportions of monounsaturated fatty acids compared to the other raptor species studied. A notable feature of the fatty acid profiles of total lipid and phospholipid was the very high proportion of arachidonic acid.

Table 3. Mean vitamin levels (μg/g) in raptor egg yolk from infertile eggs artificially incubated for 14 days (SD in parentheses). *N* is the number of eggs.

SPECIES	*N*	α-TOCOPHEROL	γ-TOCOPHEROL	RETINOL	CAROTENOIDS
Saker	17	290 (61.3)	7.9 (1.9)	2.24 (0.7)	40.0 (8.18)
Peregrine	7	261 (56.4)	8.84 (2.2)	2.15 (0.5)	37.0 (9.7)
Gyrfalcon	2	291	6.4	3.8	38.8
New Zealand Falcon	2	174	5.07	1.85	38.1
Gyr/Saker	5	234 (81)	6.2 (3.0)	2.7 (1.1)	37.1 (16.3)
Harris's Hawk	3	193 (25.1)	4.9 (0.2)	3.14 (0.9)	23.8 (7.1)

Table 4. Mean fatty acid composition of the total lipids extracted from egg yolk as a percentage of total extracted fatty acids (mean ± SD; *N* is number of eggs).

FATTY ACIDS	SAKER	PEREGRINE	BUZZARD	NEW ZEALAND FALCON	HYBRIDS	HARRIS'S HAWK
16:0	26.54 ± 0.25	27.14 ± 0.16	26.53 ± 0.16	26.58 ± 0.14	28.25 ± 0.49	26.2
16:1n-7	3.60 ± 0.14	3.36 ± 0.13	1.86 ± 0.12	3.03 ± 0.21	3.73 ± 0.45	2.71
18:0	6.61 ± 0.07	7.07 ± 0.13	7.37 ± 0.17	7.16 ± 0.11	6.45 ± 0.61	14.8
18:1n-9	40.28 ± 0.16	38.95 ± 0.27	37.24 ± 0.62	38.15 ± 0.73	39.42 ± 0.81	9.21
18:1n-7	3.27 ± 0.06	3.07 ± 0.10	2.32 ± 0.03	3.23 ± 0.05	3.16 ± 0.24	2.6
18:2n-6	9.22 ± 0.16	9.40 ± 0.34	13.95 ± 0.62	9.46 ± 0.83	9.32 ± 0.74	10.41
20:4n-6	5.72 ± 0.08	4.79 ± 0.65	6.23 ± 0.08	7.31 ± 0.13	5.39 ± 0.30	5.79
22:6n-3	1.65 ± 0.05	1.40 ± 0.17	1.82 ± 0.10	2.22 ± 0.07	—	2.73
N	20	14	4	4	5	2

From the three falcons where plasma vitamin levels were measured, mean α-tocopherol was 32.2 μg/ml and mean vitamin A was 1.02 μg/ml.

DISCUSSION

Sufficient eggs were available to provide summary statistics, but the number of individuals of each species limited interspecific comparisons. Incubation of infertile eggs decreases fat-soluble vitamin concentrations with vitamin A being the most sensitive to this process. Thus, for future analyses it is recommended to use fresh, unincubated eggs. In birds, the level of vitamin E in the egg yolk and embryonic tissues reflects its level in the food (Surai 1999). There are some species-specific differences in vitamin E accumulation and transfer to the egg yolk with chicken (*Gallus gallus domesticus*) being more effective compared to turkey (*Meleagris gallopavo*), duck (*Anas platyrhynchos*), or goose (*Anser anser*) (Surai et al. 1998). Raptor eggs contain a very high α-tocopherol concentration compared to other avian species (Dierenfeld et al. 1989), probably reflecting dietary vitamin E supplementation. It has been suggested that increased vitamin E supplementation may have a positive effect on falcon reproductive performances (Dierenfeld et al. 1989). In chickens, recent studies also show a positive effect of vitamin E on immune system development and a protective effect in stress conditions (Surai 1999). For certain species such as the Gyrfalcon which often show poor immune responses particularly in captivity or under stressful situations, adequate dietary vitamin E levels would be essential for good health.

Information is available on the concentration of vitamin E in the yolks of a range of avian species in the wild. These currently include the Lesser Black-backed Gull (*L. fuscus*) (Royle et al. 1999), the Canada Goose (*Branta canadensis*) (Speake et al. 1999a) and the Emperor Penguin (*Aptenodytes forsteri*) (Speake et al. 1999b) which all have vitamin E concentrations of about 80 μg/g fresh yolk.

Table 5. Mean fatty acid composition of the phospholipid fraction extracted from egg yolk as a percentage of total fatty acids (mean ± SD; *N* is number of eggs).

FATTY ACIDS	SAKER	PEREGRINE	BUZZARD	NEW ZEALAND FALCON	HYBRIDS	HARRIS'S HAWK
16:0	24.47 ± 0.21	23.39 ± 0.24	26.28 ± 0.11	24.99 ± 0.25	24.24 ± 0.73	25.91
16:1n-7	1.08 ± 0.05	0.91 ± 0.05	0.47 ± 0.03	0.74 ± 0.06	1.14 ± 0.14	0.78
18:0	18.88 ± 0.23	20.28 ± 0.18	19.39 ± 0.10	19.93 ± 0.16	18.51 ± 1.05	19.89
18:1n-9	19.20 ± 0.21	17.62 ± 0.48	10.99 ± 0.50	14.11 ± 0.59	18.97 ± 1.00	12.58
18:1n-7	2.50 ± 0.04	2.24 ± 0.05	1.86 ± 0.01	2.34 ± 0.04	2.39 ± 0.17	2.10
18:2n-6	6.98 ± 0.14	6.96 ± 0.45	12.51 ± 0.29	6.76 ± 0.34	7.54 ± 0.54	10.59
20:4n-6	19.10 ± 0.24	20.49 ± 0.26	21.30 ± 0.13	22.78 ± 0.15	19.16 ± 0.91	19.02
22:6n-3	4.31 ± 0.14	4.51 ± 0.18	4.13 ± 0.29	4.77 ± 0.10	4.63 ± 0.27	6.28
N	20	14	4	4	5	2

The raptor eggs of the present study contained vitamin E at concentrations averaging 330 μg/g and would therefore seem to be very well provisioned with this vitamin. Thus, feeding the female parent with quail and chickens enriched with vitamin E is a successful strategy for achieving high levels of this vitamin in the egg.

Despite the small sample size, the mean plasma vitamin E levels of 32.2 μg/ml are similar to the levels which the Peregrine Fund, Boise, ID U.S.A. measured in their captive peregrine population. They achieved these levels either by feeding quail that had been injected with vitamin E (220 IU/kg quail) or quail which had been raised on a diet containing 220 IU/kg feed. Wild peregrines on migration had plasma vitamin E levels of 26.3 μg/ml compared to captive peregrines at the Peregrine Fund with 3.4 μg/ml (Dierenfeld et al. 1989). Because migratory individuals probably have levels lower than breeding individuals, the levels measured in migratory falcons were taken as a minimum requirement for a healthy, captive-breeding population (Dierenfeld et al. 1989). From the three falcons in this study that plasma was taken, egg composition was also analyzed and the fertile eggs from these individuals were all viable and produced healthy offspring. There is no reason to assume that the infertile egg composition was any different.

The concentration of the carotenoids in the raptor yolks was similar to that in the first-laid eggs of *L. fuscus* (Royle et al. 1999) and higher than the values reported for *B. canadensis* (Speake et al. 1999a) and *A. forsteri* (Speake et al. 1999b). The vitamin A content of the raptor yolks was slightly less than the value reported for *L. fuscus* (Royle et al. 1999).

The salient feature of the fatty acid profiles of the raptor yolks is the very high proportion of arachidonic acid in the phospholipid fraction which is about five times higher than the values reported for the domestic chicken and for various wild granivorous and herbivorous birds (Speake and Thompson 1999). This may be a consequence of carnivory because the edible parts of many animals are a rich source of arachidonic acid (Phetteplace and Watkins 1989, Li et al. 1998). The proportion of docosahexaenoic acid in the phospholipid of the raptor yolks was similar to the values for eggs of the chicken and many wild birds, but less than the level reported for the piscivorous *A. forsteri* (Speake and Thompson 1999).

In conclusion, the prey items supplemented with vitamin E were a very effective means of fortifying the yolks of raptors with this antioxidant. Vitamin E deficiency reduces hatchability in the quail (Kling and Soares 1980) and has been identified as a cause of late embryo mortality in an established raptor breeding program (Dierenfeld et al. 1989). Achieving adequate levels of vitamin E, carotenoids, and polyunsaturated fatty acids in the yolk may be essential for the efficient reproduction of birds in captivity. Further studies should focus on analyzing egg composition of wild falcons because such a comparison would give important information for improvement of the falcon diets in captivity.

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PRELIMINARY GROUND AND AERIAL SURVEYS FOR ORANGE-BREASTED FALCONS IN CENTRAL AMERICA

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Abstract.—Ground and aerial surveys for Orange-breasted Falcons (*Falco deiroleucus*) were conducted during March–June 1999 in Honduras, and March–May 2000 in El Salvador, Honduras, Nicaragua, Costa Rica, and Panama, all within the likely range of this species. Sixty-six cliffs were checked by ground surveys. No Orange-breasted Falcon was found in Central America. We examined 55 cliffs by fixed-wing aircraft during 24 hr of flying. No Orange-breasted Falcon was seen in El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. In Honduras and Panama, we checked 262 limestone cliffs by helicopter during 47 hr of flying and one Orange-breasted Falcon was seen in a limestone canyon in the Darién Province of Panama, and one sighting of two birds, possibly Orange-breasted Falcons, 11 km south in the same region. The apparent absence of cliff-nesting Orange-breasted Falcons in seemingly suitable habitat in much of Central America is inexplicable and warrants further surveys but indicates that the population in Guatemala and Belize is geographically and genetically isolated from the South American birds.

Key Words: Falco deiroleucus; *Orange-breasted Falcon*; *Central America*; *survey*; *cliffs*.

Estudios preliminares terrestres y aereos para los Halicones de Pecho Naranja en Centro America

Resumen.—Estudios terrestres y aéreos para el halcón de pecho naranja (*Falco deiroleucus*) fueron conducidos durante marzo–junio de 1999 en Honduras, y marzo–mayo 2000 en El Salvador, Honduras, Nicaragua, Costa Rica, y Panamá, todos dentro del rango probable de la especie. Sesenta y seis cornisas fueron revisadas en los estudios terrestres. No se encontró ningún halcón de pecho naranja en Centro América. Examinamos 55 precipios con aeronaves de ala fija durante 24 horas de vuelo. Ningún halcón de pecho naranja fue visto en El Salvador, Honduras, Nicaragua, Costa Rica, y Panamá. En Honduras y Panamá, revisamos 262 cornisas de piedra caliza en helicóptero durante 47 horas de vuelo y un halcón de pecho naranja fue visto en una cañón de piedra caliza en la provincia del Darien en Panamá, y un avistamiento de dos aves, posiblemente halcones de pecho naranja, 11 km al sur en la misma región. La aparente ausencia de halcones de pecho naranja anidando en cornisas en un hábitat hipotéticamente adecuado en la mayoría de Centro América es inexplicable y requiere mayores estudios para indicar que la población en Guatemala y Belice esta aislada geográfica y genéticamente de las aves de Sur América.

[Traducción de César Márquez]

The Orange-breasted Falcon (*Falco deiroleucus*) is a little known and, perhaps, rare falcon (Baker 1998). Although distributed in Central and South America, the species is local (del Hoyo et al. 1994), sparsely distributed and difficult to detect (Cade 1982), and probably threatened by habitat alteration (Jenny 1989, Baker 1998, Baker et al. 2000). The historical distribution of Orange-breasted Falcons in Central America is summarized in Baker et al. (2000). Apart from 19 nest sites documented recently in Guatemala and Belize (Jenny 1989, Baker 1998, Baker at al. 2000) most reliable records for Central America are more than 20 years old, and none of them involve breeding. Possibly, the species has been extirpated from parts of its former breeding range (Cade 1982). This species may warrant special status due to the isolation of the known population in Central America from larger populations in South America (Collar and Andrew 1988, Baker et al. 1992, Collar et al. 1994, Baker 1998, Baker et al. 2000).

Substantial areas of seemingly suitable habitat for Orange-breasted Falcons exist in Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama among limestone mountains, yet recent ob-

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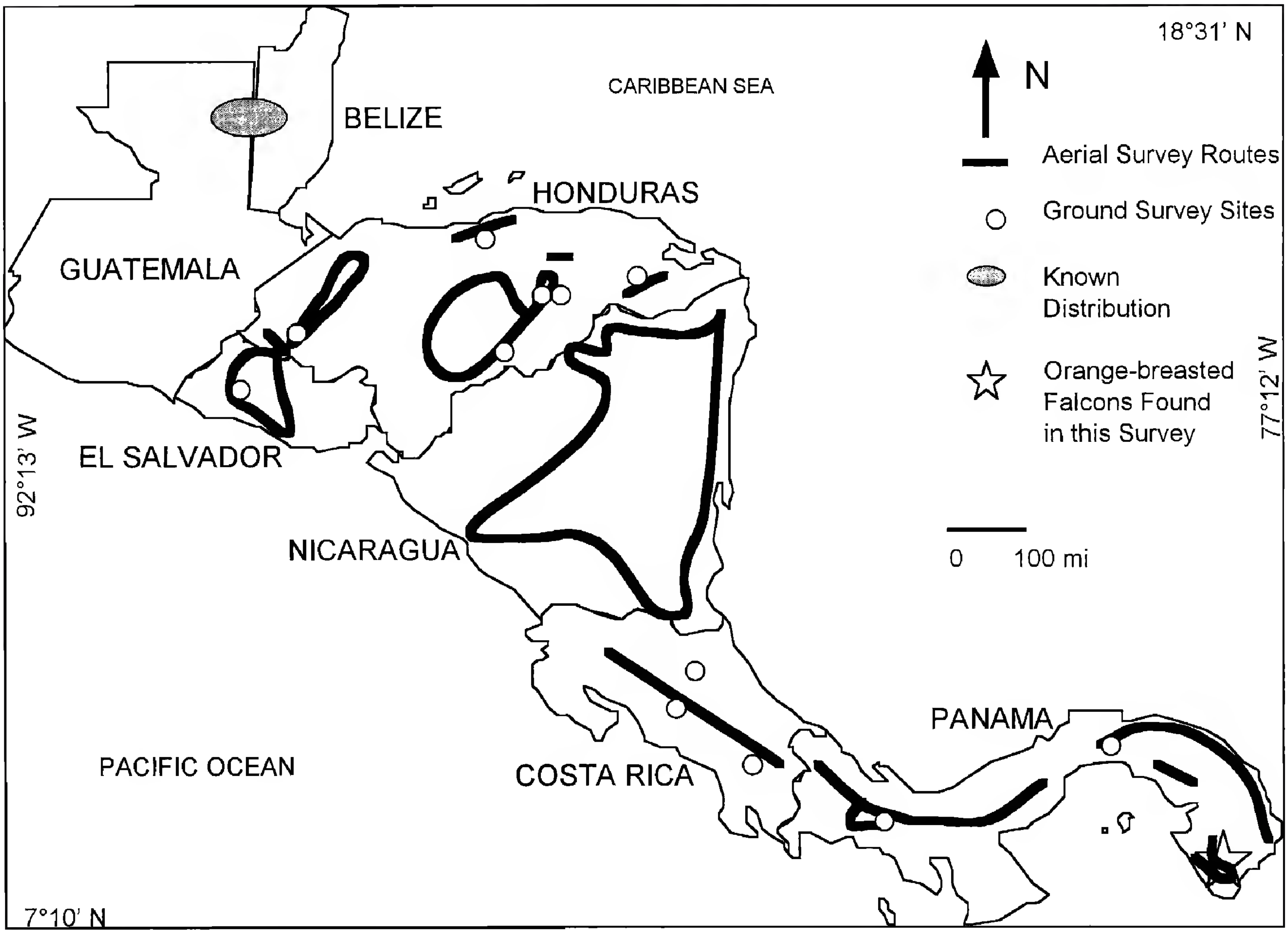

Figure 1. Ground and aerial surveys for Orange-breasted Falcons in Central America from April 1999–May 2000.

servations of this species are almost nonexistent throughout this region. We conducted ground and aerial surveys for Orange-breasted Falcons from El Salvador to Panama to improve knowledge of its present breeding range in Central America.

STUDY AREA AND METHODS

The breeding season for Orange-breasted Falcons in Guatemala and Belize begins with courtship in January and February. Eggs are laid in late March and early April, and young fledge mainly in June and July at the beginning of the wet season (Baker 1998). Nesting pairs are particularly aggressive toward congeners and other raptors during the courtship period and the post-fledging dependence period in June and July. We chose March–June for the aerial surveys to take advantage of the conspicuousness of breeding pairs tending their nest and young. Ground surveys were conducted from March–May in 1999–2000. Because most of the Pacific slope from El Salvador through Costa Rica is deforested, significantly drier, and has yielded few, if any, Orange-breasted Falcon records historically, we concentrated our survey effort on the Atlantic slope (Fig. 1).

Honduras. Ground surveys were conducted in April–May 1999 within a 15-km radius of the Tawahka Indian village of Krausirpe (15°02′N, 84°52′W) in the Sierra del Warunta (Anderson 1999). The small area of ground coverage was limited by walking distance and the lack of a trail system in this region.

Ground surveys were conducted by D. Anderson accompanied by 2–3 Tawahka guides to locally-known, limestone cliffs (Fig. 1). We searched for falcons using 7 × 42 binoculars and a 16–24 zoom spotting scope from 0700–1230 H and 1530–1730 H. Eighteen cliffs and one large limestone mountain were searched during 17 days Cliff surveys consisted of looking for whitewash on cliff faces, falcons perched on cliffs and on trees atop cliffs, flying birds, prey remains at the bases of cliffs, and listening for vocalizing falcons.

Aerial surveys were conducted by R. Watson and R Thorstrom in a larger area of the Sierra del Warunta and adjacent Montañas de Colón (ca. 14°50′—15°05′N, 84°45–85°05′W) (Fig. 1). Three survey flights totaling 8.83 hr were made on 25–26 June 1999 in a Robinson 44 helicopter equipped with a Global Positioning System (GPS) navigational system. Survey routes were chosen at first by visiting the same cliffs surveyed from the ground by D. Anderson, as located by GPS and marked on 1. 50 000 maps of the region. These cliffs were visited dur-

Table 1. Summary by country of suitable cliffs surveyed for Orange-breasted Falcons (*Falco deiroleucus*) from the ground, by fixed-wing aircraft and helicopters in 1999–2000.

COUNTRY	NUMBER OF SUITABLE CLIFFS SURVEYED FROM THE GROUND	NUMBER OF SUITABLE CLIFFS OBSERVED DURING FIXED-WING AIRCRAFT SURVEYS (hr)	NUMBER OF SUITABLE CLIFFS OBSERVED DURING HELICOPTER SURVEYS (hr)
El Salvador	12	15 (3)	0
Honduras	41	25 (5.75)	62 (8.5)
Nicaragua	0	0 (4)	0
Costa Rica	9	15 (6)	0
Panama	4	0 (5)	200 (38.5)
Total	66	55 (23.75)	262 (47)

ing the first part of the first flight, after which survey routes were chosen by sight, keying on potentially suitable nesting habitat (e.g., exposed cliffs with forest below) and major topographic features such as valleys and rivers. Our survey route was tracked by GPS and mapped between flights to ensure the entire mountain range was surveyed.

Surveys were conducted by flying the helicopter within 20–50 m of the cliff face, at about its highest point so two observers could look down on the cliff face and look into ledges and potholes. We were also able to see the top of the cliff and potential perches, such as snags and overhanging trees. Some cliffs were too tall for an adequate view of the entire cliff, so a second, third or even more passes were made at lower elevations in such cases. The helicopter flew slowly past the cliff face while observers scanned the face and all potential perch sites. The helicopter made a second pass or hovered in front of cliffs that needed more time to survey thoroughly. The helicopter provided ample time in front of cliffs, and maneuverability to complete visual surveys in narrow valleys and canyons.

El Salvador to Costa Rica. Fixed-wing aerial surveys to locate cliffs were conducted by A. Baker and S. Ayers from March–May 2000 (Fig. 1). Areas of potential habitat for aerial surveys were identified from topographic maps where relief might indicate cliffs. We communicated with individuals (both locally and abroad) known to have experience and information in and about the region. In addition, surveys were limited to below 2000 masl (meters above sea level) because this species is not known to occur above ca. 1000 masl. Surveys were conducted from a variety of small single-engine planes and, in one case, a twin-engine, fixed-wing plane chartered locally in each country. All flights were conducted at between 200–500 m above the ground at speeds of between 160–250 kmph, suitable altitudes and speeds for surveying the area for cliffs. When cliffs were spotted we circled for a closer look, recorded the locality with a GPS receiver, and noted cliff size, surrounding habitat, and accessibility from the ground.

Ground surveys were conducted by A. Baker and S. Ayers after cliffs were located from the air and consisted of spending several hours on the ground in view of and within hearing distance of any falcons on the cliff. Cliffs were selected for ground survey based on accessibility and quality in terms of cliff size, height of cliff above surrounding forest, and extent of surrounding forest.

Panama. Between 12–26 April 2000, R. Thorstrom searched from a Robinson 44 helicopter for Orange-breasted Falcons on cliffs, rocks, and escarpments, using 10 × 42 binoculars and a Garmin 12 XL GPS receiver. We visited five major areas in Panama: Pacific side of the Darién region, the Majé range in central-eastern Panama, the Chagrés area of the Atlantic Colón region, Bocas del Toro, Veraguas, Coclé in the Atlantic western region, and the central range at Volcano Barú on the Chiriquí (Pacific side) (Fig. 1).

A. Baker and S. Ayers spent 9.25 hr in a helicopter on 22–23 May revisiting the three sites where R. Thorstrom had recorded an Orange-breasted Falcon on 26 April and other unidentified falcon activity. Fixed-wing aircraft flights were made by A. Baker and S. Ayers to survey Chagrés National Park and surrounding areas and all of San Blas from Nujagandi to the Colombia border on both sides of the coastal range totaling 5 hr (3 flights including 1 uncompleted flight due to weather). Ground surveys were made to Madden Dam by R. Thorstrom, and three cliffs were checked near Fortuna Reservoir north of Davíd by A. Baker and S. Ayers (Fig. 1).

RESULTS

Honduras. Eighteen cliffs and one large limestone mountain (Cerro Wampú) were searched from the ground during 17 days between 12 April–8 May 1999 (Table 1), dates corresponding to the incubation/nestling period in Guatemala and Belize (Baker 1998). One additional cliff was searched earlier on 15 March. Cliff size ($N = 18$) ranged from 30–250 m tall ($\bar{x} = 102$ m) and 35–500 m wide ($\bar{x} = 153$ m). Cliff surfaces were broken by crevices, ledges, caves, and epiphytic bromeliads, providing many potential nest surfaces as well as abundant shade. Cliffs were oriented predominately northward, with eight cliffs facing north, five northwest, one northeast, and four east.

We checked an additional 22 cliffs by ground survey in El Boquerón National Park, El Chile National Park, Sierra de Agalta National Park, Rio Cangrejal, and Celaque National Park.

Sixty-two distinct cliff faces were surveyed by helicopter in the Sierra del Warunta and Montañas de Colón ranges, as well as one isolated mountain in the Río Plátano Biosphere Reserve (en route to the main survey site) called Cerro Chachahuate (Table 1). We observed four Bat Falcons (*Falco rufigularis*), but no Orange-breasted Falcons.

El Salvador to Costa Rica. We detected 55 apparently-suitable cliff faces during 23.75 hr of fixed-wing aerial surveys (Table 1). Of these, we surveyed 41 cliffs from the ground (Table 1). Cliffs that were not surveyed from the ground were unreachable on foot due to their remote nature, extreme topography, and flooded rivers. All cliffs were of igneous origin and ranged from 50–700 m high and 50–1000 m wide (mode = ca. 100 m high × 200 m wide). Although all of these cliffs were located in forested areas, the surrounding forest was patchy, and the patches were mostly small. No suitable cliffs were found in Nicaragua where we conducted fixed-wing surveys (Table 1). No Orange-breasted Falcons were found in El Salvador, Honduras, Nicaragua, or Costa Rica. We are confident both that no Orange-breasted Falcons occurred on cliffs in the areas that we surveyed and that we surveyed thoroughly almost all suitable cliffs in these countries.

Panama. During 38.5 hr of helicopter survey, we visited over 200 cliffs, rock slopes, and escarpments (Table 1). No suitable cliffs were found in the Chagrés National Park or San Blas province of Panama where we conducted fixed-wing surveys (Table 1). In the Darién province, we observed one Orange-breasted Falcon on 26 April at 1304 H (07°44′N, 078°05′W) when a large dark-backed, heavy-winged falcon flew five times around the helicopter inside a box-like canyon at 610 masl (Fig. 1). This falcon had slightly larger and thicker wings with slower wing beat than a typical female Bat Falcon. On 13 April at 1030 H, two large dark-backed falcons were flushed off a cliff face by the helicopter (07°39′N, 078°05′W) and descended and disappeared into a ravine, allowing a 2 s observation of the darting falcons. We believe these two disappearing falcons were Orange-breasted Falcons. This site was at 770 m elevation, and the cliff contained one slightly overhung large pothole with a potential scrape and whitewash. We returned to the same site on 26 April at 1100 H but failed to detect the falcons at the site or on the cliff extension to the north (07°40′N, 078°05′W).

In the Coclé province, on 22 April 2000 at 1700 H an unidentified falcon nest was located (08°41′N, 080°40′W). This nest site was a pothole with two cavities at the base of an overhung rock. It contained two nestlings with dark rufous on the sides of neck, blue ceres, and no down on the head. On the first helicopter pass by this site a small dark-backed falcon was flushed from the face and disappeared. On the second pass a larger dark-silhouetted falcon flew above the helicopter and disappeared. On 23 April, we visited this site at 1300 H and found no young present in the pothole. One silhouetted heavy-billed falcon was observed flying from the helicopter. At 1500 H, we returned to this site after investigating other cliffs in the area; here we located a Bat Falcon on a nest with two eggs on the opposite side of the cliff face formerly containing the unidentified nestlings and at a distance of ca. 200–300 m.

During a follow-up helicopter survey in Panama we confirmed the presence of an adult female Orange-breasted Falcon at one site in the Darién. At another Darién cliff, we flushed either a female Bat Falcon or male Orange-breasted Falcon from a ridge-top perch. At the Coclé site, we observed either a female Bat or male Orange-breasted Falcon flying away from the helicopter. During 38.5 hr of helicopter time, we recorded eight observations of Bat Falcons perched in trees or evading the helicopter near cliffs and two nests; one in the Majé mountains and the other in the Coclé region.

DISCUSSION

Orange-breasted Falcons formerly occurred in a broad range from southern Mexico south through Central America and into South America, where the species was found east of the Andes as far south as northern Argentina (del Hoyo et al. 1994). Records of the species, however, are sparse throughout its range. The most concentrated records, including the only breeding records from Central America, come from Guatemala and Belize (Baker 1998). Baker (1998) studied 13 breeding pairs in Belize and six pairs in Guatemala from 1991–97, of which the closest neighboring pairs were 1.7 km apart. If our survey in Central America was in similarly suitable habitat, we estimate there would be sufficient cliffs, spaced far enough apart, to support numerous breeding pairs. In Nicaragua, no cliffs were found in forested habitat and in El Salvador, no cliffs were associated with primary forests. The fact that we found no Orange-breasted Falcons in El Salvador, Honduras, Nicaragua, or Costa Rica suggests that either the habitat is not suitable, they are not using cliffs as nest sites, or we overlooked this species' presence. The only Orange-breasted Falcons detected during these surveys were in the Darién province of Panama. This area contains the northernmost foothills of the Andes of South America. The presence of these falcons in the Darién suggests that these birds are at the northern limit of the South American population.

Panama appears to have many cliffs in the Coclé and Darién regions surrounded by intact primary forest, perhaps as many as the Belize and Petén, Guatemala region. It seems very likely that Panama contains a breeding population of Orange-breasted Falcons. The presence of this species in Belize, Guatemala, and the Darién province of Panama, where an abundance of cliffs in conjunction with large tracts of forest remains, lends support to this hypothesis.

One pair of palm-nesting Orange-breasted Falcons was recorded in Petén, Guatemala (Baker 1998) and equally suitable palm trees and other canopy emergent trees potentially suitable as nesting sites occur throughout Central America. Due to the rarity of this behavior we suspect that it may result from the size of the population in the Guatemala and Belize region relative to a limited number of suitable nesting cliffs, leading to the occasional use of trees for nesting sites.

The seeming absence of cliff-nesting Orange-breasted Falcons from El Salvador, Nicaragua, and Costa Rica is not surprising because of the low museum records of the species from the region. A very low abundance of suitable cliffs in Costa Rica and El Salvador, and no cliffs in Nicaragua compounded by extensive deforestation and dry areas, especially in El Salvador and most of Honduras, is a likely explanation. The lack of nesting Orange-breasted Falcons in parts of Honduras is surprising, because there are many limestone cliffs with an extensive tract of primary forest. Detection of four Bat Falcons during 8.5 hr of helicopter surveys provides evidence that our observation methods should have revealed the Orange-breasted Falcons if they were present.

We offer the following speculative explanations for the apparent absence of Orange-breasted Falcons from most of Central America, with the understanding that they might influence further study. Populations of this falcon may have been negatively affected in the period before DDT was banned in the United States (prior to 1972) as a result of feeding on contaminated migratory and resident birds, but this is not consistent with the presence of the Belize/Guatemala population. DDT and other organochlorines were used for years in developing countries after being banned in the U.S., particularly for pest control on cotton crops. Cotton was grown extensively along the Pacific seaboard of Central America from southern Mexico through Guatemala, El Salvador, Honduras, Nicaragua, and into Costa Rica, expanding rapidly in the 1950s and 1960s, and reaching peak production in 1978 (Murray 1994). Because pesticide contamination has never been associated with a decline of Orange-breasted Falcons and DDT has been used primarily on the Pacific coastal side, however, we suggest it is unlikely that this was the main cause for extirpating this species from most of Central America.

Alternatively, the lack of detection of nesting falcons may be a result of our focusing only on cliffs in areas where Orange-breasted Falcons may be nesting in trees. However, while Orange-breasted Falcons are sometimes difficult to locate when nesting in trees, when nesting they are usually near their nests and quite vocal making detection a bit easier. In 7 yr, staff of The Peregrine Fund's Maya Project located 1 tree nest in Guatemala and Belize (Baker 1998). In Ecuador, searches by boat, air, and truck during five months resulted in observations of 15 Orange-breasted Falcons and four nests in emergent trees (Cade 1982). Furthermore, Orange-breasted Falcons may have been more difficult to detect from the ground in Central America if April and May correspond to the incubation period, as in Guatemala (Baker 1998), which could have contributed to our lack of detections.

Orange-breasted Falcons are regarded as threatened in Central America because of their small population size and the probability that breeding populations in Guatemala and Belize are genetically isolated from the South American population (Collar and Andrew 1988, Collar et al. 1994, Baker 1998). The lack of detection of Orange-breasted Falcons in apparently all suitable habitat in Honduras and Costa Rica is an important observation that should stimulate further study. If the species is sensitive to habitat alteration, as suggested by some authors (Jenny and Cade 1986, Jenny 1989, Baker 1998), it could be a useful indicator of native-plant community alteration in the remaining lowland tropical rain forests of Central America. We recommend additional studies to understand nest site selection in areas where this bird may nest in emergent trees as in Ecuador and possibly Brazil (Whittaker 1996) or in palms as in Guatemala. Results would be useful in implementing surveys for tree-nesting Orange-breasted Falcons in the Sierra del Warunta range of Honduras, La Mosquitia region of Honduras and Nicaragua, and the Coclé, Bocas del Toro, Veraguas, and Chagrés regions of Panama.

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DISPERSING VULTURE ROOSTS ON COMMUNICATION TOWERS

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ABSTRACT.—Communication towers provide attractive roost sites for Black (*Coragyps atratus*) and Turkey vultures (*Cathartes aura*). The birds' roosting activity creates problems, however, for tower operators, nearby businesses, and adjacent homeowners. To alleviate these problems, at six sites in northern Florida we evaluated the effectiveness of suspending vulture carcasses or taxidermic effigies from towers to disperse vulture roosts. In each case, vulture numbers decreased immediately after installation of the stimulus, and roosts declined 93–100% within nine days. The effect was independent of the composition of the roost and occurred regardless of which vulture species was used as the carcass or effigy. At one site, the roost was substantially reduced using a commercial plastic goose decoy painted to resemble a Turkey Vulture. At three sites, the deterrent effect persisted up to 5 mo even after the carcass or effigy was removed from the tower. Hanging a vulture carcass, taxidermic effigy, or even an artificial decoy, from a tower creates an unfavorable roosting environment for vultures and offers a simple, effective means to manage problem-roost situations.

KEY WORDS: Cathartes aura; *communication tower*, Coragyps atratus; *effigy*; *roost dispersal*; *vultures.*

Dispersión de perchas para gallinazos en torres de comunicación

RESUMEN.—Las torres de comunicación proveen unos sitios de percha atractivos para los gallinazos comunes (*Coragyps atratus*) y los de cabeza roja (*Cathartes aura*). El uso de perchas de las aves crea problemas para los operadores de las torres, negocios cercanos y casas familiares adyacentes. Para aliviar estos problemas, en seis sitios del norte de la Florida evaluamos la efectividad de suspender esqueletos de gallinazos o figuras disecadas e las torres para dispersar las perchas de los gallinazos. En cada caso, el numero de gallinazos disminuyó inmediatamente después de la instalación del estimulo, y las perchas declinaron 93–100% en nueve días. El efecto fue independiente de la composición de la percha y ocurrió sin importar cual especie de gallinazo fuera usada como el esqueleto de la figura. En un sitio, la percha fue sustancialmente reducida usando un señuelo comercial plástico de ganso pintado para simular un gallinazo negro. En tres sitios, el efecto disuasivo persistió por mas de cinco meses aun después de que los esqueletos o las figuras fueran removidas de la torre. Colocar un esqueleto de gallinazo, una figura disecada, o aun un señuelo artificial en una torre, crea un efecto desfavorable para que los gallinazos puedan perchar y ofrece un medio simple y efectivo para manejar situaciones problemáticas con las perchas.

[Traducción de César Márquez]

Recent estimates suggest that in the United States there are nearly 45 000 communication and broadcast towers taller than 61 m, and industry projections suggest that 10 000 more are likely to be built in the next decade (Evans and Mannville 2000, Tollefson 2001). Vulture populations also are increasing. Analyses of Breeding Bird Survey data (1980–99) indicate that Black Vultures (*Coragyps atratus*) are increasing at an annual rate of 2.9% in Florida and 2.4% nationwide, and Turkey Vultures (*Cathartes aura*) are increasing annually by 1.2% in Florida and 1.8% throughout the country (Sauer et al. 2000).

Vultures sometimes roost on communication and broadcast towers and similar structures. Stolen (1996) recorded as many as 130 vultures roosting on a microwave tower in east-central Florida. In

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Table 1. Various types of stimuli were evaluated as means to disperse vulture roosts on towers at six sites in northern Florida.

TOWER SITE	HEIGHT (m)	VULTURES AT SITE: INITIAL NO.	VULTURES AT SITE: % BLVU	STIMULUS[a]	DATE INSTALLED
Macclenny A (F)[b]	105	100–200	80	BLVU carcass	25 Sep 2000
Macclenny B[c] (G)	85	25–40	65	TUVU carcass	28 Nov 2000
(F)	31	15–25	65	BLVU effigy	28 Nov 2000
Waldo (F)	83	140–170	90	BLVU effigy	30 Oct 2000
Durbin (F)	78	40–60	85	BLVU effigy	27 Nov 2000
Jacksonville (F)	45	100–150	40	BLVU effigy	29 Jan 2001
Niceville (G)	92	50–150	25	Goose decoy	27 Feb 2001
				TUVU effigy	15 Mar 2001

[a] BLVU—Black Vulture; TUVU—Turkey Vulture.

[b] (F)—free-standing; (G)—guyed.

[c] Two towers, ca. 45 m apart.

Texas, Buckley (1998) observed 4–136 Black and Turkey vultures roosting on power transmission line support structures. Kirk and Mossman (1998) state that Turkey Vultures may roost on communication towers "especially on warm, still nights" but provide no documentation of this activity.

Defecations by roosting vultures interfere with the operation of expensive equipment and create unsafe and unpleasant conditions for workers who climb towers to service and install equipment. In addition, businesses and homeowners adjacent to a vulture roost site are adversely affected by vulture droppings and the unpleasant odor that results.

Given current trends in vulture populations and tower construction, it is probable that roosting on towers by vultures will become more widespread, and the need for effective, nonlethal solutions to this problem will increase as well. Pyrotechnics and other noisemakers are disruptive to neighboring businesses and homeowners and provide short-term relief at best. Physical and chemical deterrents applied to perching substrates would be impractical because of the expansive perching area available on a tower. Furthermore, they would interfere with operation and maintenance activities on the tower. Visual deterrents such as reflecting tape and scare-eye balloons seemed impractical and probably ineffective based on previous evaluations with other species (Tobin et al. 1988, Tipton et al. 1989).

One method that appears to have some promise is hanging a vulture carcass or effigy in the roost. This technique was suggested on a fact sheet on vulture management in Virginia, but no supporting data were presented (M. Lowney pers. comm.). Trials in Ohio demonstrated that Turkey Vultures in a tree roost and on an abandoned tower, dispersed when freeze-dried Turkey Vulture effigies were suspended at each site (T. Seamans pers. comm.). These promising results with Turkey Vultures have not been duplicated for Black Vultures, however. The only Black Vulture effigy trial that we are aware of comes from a newspaper article (Tampa Tribune-Times, 20 February 1994). On a Virginia farm where Black Vultures reportedly attacked and killed several ducks, a Black Vulture carcass suspended near a farm pond deterred the vultures for "about two hours."

Our principal objective in this study was to determine whether whole carcasses or taxidermic effigies would disperse Black Vultures from roosts on towers. Secondarily, we examined responses of Black Vultures to Turkey Vulture effigies, and vice versa. In addition we conducted a limited trial to evaluate a plastic goose decoy as a vulture dispersal agent.

METHODS

In northern Florida, we conducted trials at six sites (Table 1). The towers were not selected at random but were determined by requests for assistance from the tower owners. There was considerable variability among the structures (Fig. 1). Black Vultures were predominant roosting species at most sites (Table 1).

We monitored vulture numbers at each site 3 d before and 9 d after installation of the vulture carcass, taxidermic effigy, or goose decoy. At a given site, we counted roosting birds at the same time each day, either early in the morning (0630–0830 H) or late in the afternoon (1630–1830 H). At four sites, we counted all of the birds

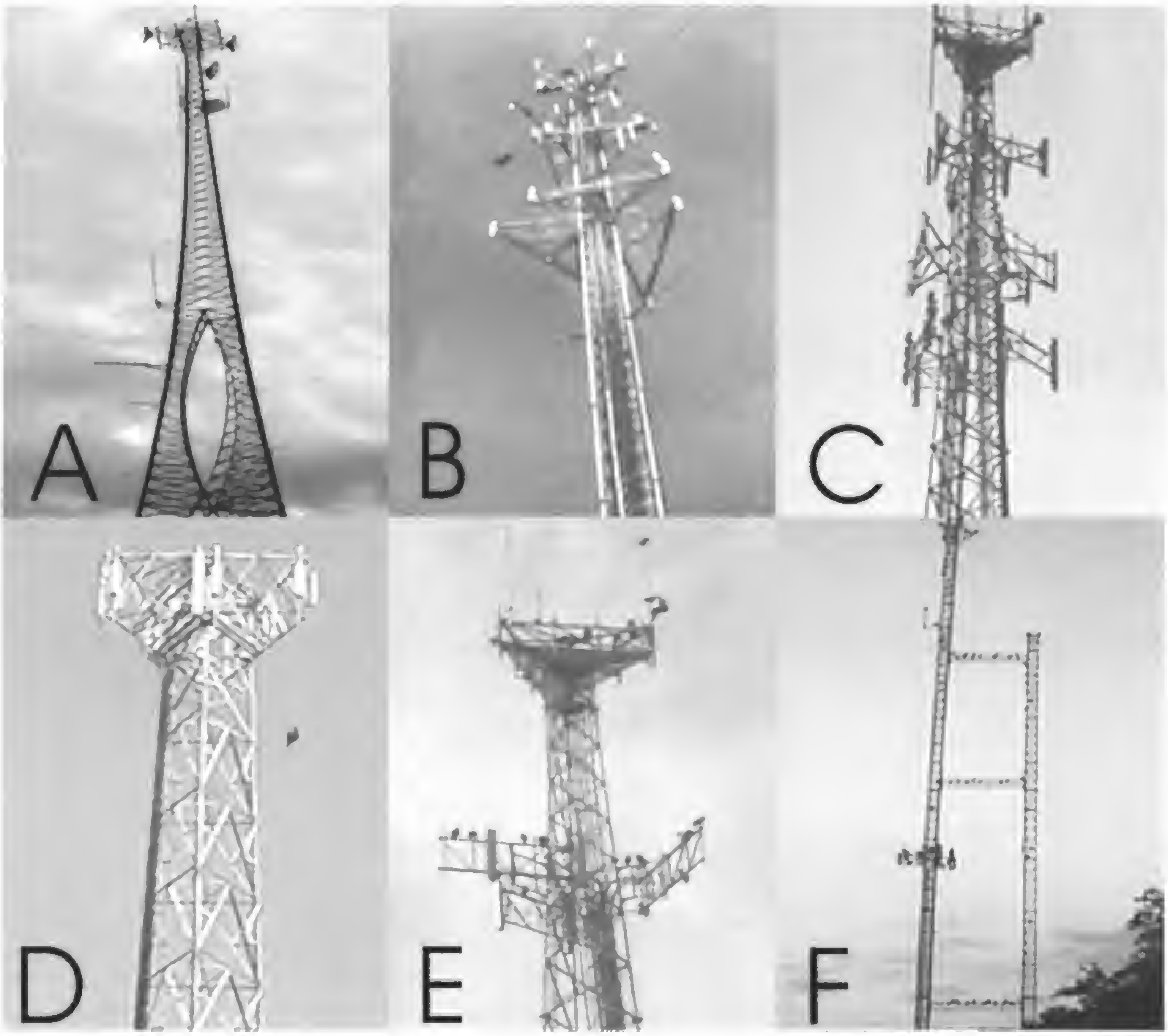

Figure 1. Towers used as roost sites by vultures in northern Florida: A—Macclenny A; B—Macclenny B; C—Waldo; D—Jacksonville; E—Durbin; F—Niceville.

on the tower at the start of the daily observation period and then recorded all vultures that arrived or departed during the next 2 hr. We then derived a maximum daily vulture count for each of the four sites. At the Macclenny B site, we counted vultures once in the morning (0800–0830 H), and at Durbin, cooperators counted all the vultures they could see on the tower each day at 1700 H. Cooperators were asked to be consistent and to count all vultures roosting on the tower at the same time each day. Total numbers of vultures are reported without regard to species.

Professional climbers installed the carcass, effigy, or decoy so that it hung freely and was able to swing and twist in the wind without becoming entangled in the structure. Installation always occurred at midday to avoid any contact with vultures using the site. We secured the ends of a short leather strap to the legs of the carcass, effigy, or decoy and clipped a fishing tackle swivel to the strap. The other end of the swivel was tied to a length of coated twine 1.5 m–3.5 m long, and then secured to the tower at the specified location by whatever means the climber felt appropriate. At two sites, the climbers installed pulley systems so the stimulus could be recovered and replaced or redeployed if necessary. The taxidermist prepared the vulture effigies so that one wing extended beyond the head and the other wing was folded. The plastic goose decoy was painted to resemble a Turkey Vulture and had the wings outstretched perpendicular to the body.

For analysis, we grouped data into one 3-d pretreatment period and three 3-d posttreatment periods. For each study site, we calculated a mean vulture count for each of the four periods. We analyzed these data using Friedman's test (Steel and Torrie 1980) to compare the number of vultures recorded during pretreatment with those present after the stimulus was installed. The four time periods were treatments and the six study sites were blocks.

At some sites, we deviated from the general procedures to collect additional information not included in the data analysis. At Macclenny B, 3 km north of Macclenny A, there is a guyed 85-m communications tower (Fig. 1B) as well as a free-standing 31-m Doppler radar tower 45 m away. On 28 November, a Turkey Vulture carcass was installed on the guyed tower, ca. 75 m above the ground, and a taxidermic Black Vulture was installed ca. 25 m up on the Doppler tower. We used different stimuli on each tower because we did not know which would be more effective or if just one would suffice for both structures. Through March 2001, both Macclenny sites were checked for vultures at 0800–0830 H, an average of 3 d weekly.

On 13 November 2000, to see if vultures would reoccupy the structure, we removed the effigy on the Waldo tower and counted birds there on 14–17 and 20–23 November. Thereafter, irregular visits to the tower were made for 2 mo to document any additional vulture activity.

The guyed structure at Niceville consists of two vertical masts, 92 m and 73 m, connected by three horizontal crosspieces. On the morning of 27 February 2001, a climber installed a plastic Canada Goose (*Branta canadensis*) decoy that we painted to resemble a Turkey Vulture. The decoy was suspended from the uppermost horizontal crosspiece, ca. 70 m above the ground. Because there were still vultures on the tower, on 15 March 2001 we replaced the decoy with a taxidermic Turkey Vulture effigy.

RESULTS

Vulture Dispersal. During pretreatment, the mean daily number of vultures at the six sites varied from 29–157 ($\bar{x}$ = 89, SE = 21). After installation of the vulture carcass, taxidermic effigy, or goose decoy, vulture numbers declined markedly (P = 0.002, Friedman's test, S = 15.10, 3 df). Excluding the Niceville site, numbers of roosting vultures were reduced 93–100% by day 12 (Fig. 2). At Niceville, the presence of a goose decoy caused vulture numbers to decline, although not as dramatically as with a vulture carcass or effigy. Replacement of the goose decoy with a Turkey Vulture effigy (15 March 2001) then dispersed the residual roosting population.

Nine days into the treatment period at Macclenny A, there were no vultures on the tower. The carcass deteriorated over time, and by mid-November 2000 all that remained attached to the tower were the legs and back. Nevertheless, through March 2001, vultures did not reoccupy the tower. We obtained the same long-term response at Macclenny B, despite the fact that the Turkey Vulture carcass installed on the guyed tower fell off on day 7. The Black Vulture taxidermic effigy on the nearby Doppler unit remained in place throughout the study.

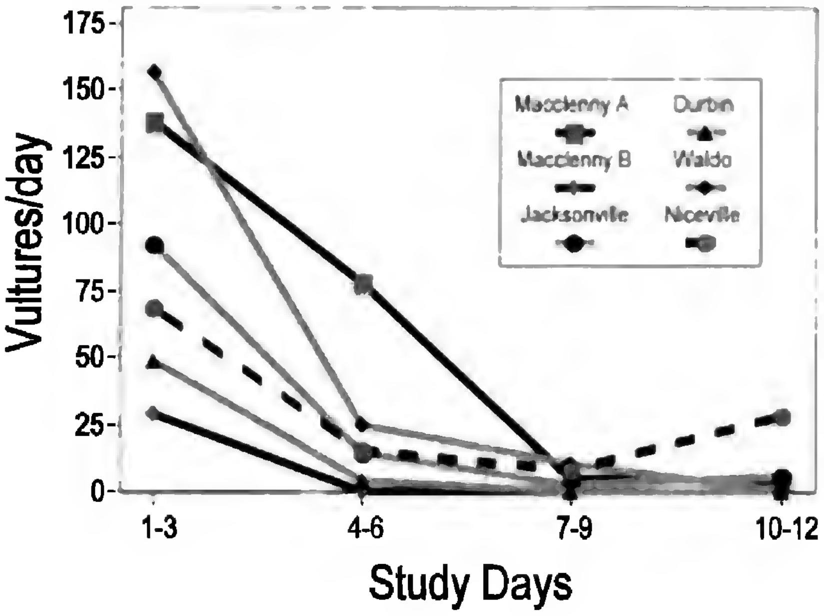

Figure 2. Roosting vultures were counted at six tower sites during 12-day study periods. Following the count on day 3, a vulture carcass was installed on the Macclenny A and Macclenny B towers, a plastic goose decoy painted to resemble a vulture was installed at Niceville, and a taxidermic vulture effigy was installed at the other sites.

At Waldo, the average maximum daily count on the tower prior to installation of the vulture effigy was 157 (SE = 9, N = 3), compared to 12 vultures (SE = 7, N = 9) with the effigy in place, and 9 (SE = 5, N = 8) after it was taken down. Even with the effigy no longer in place, regular checks of the tower in the morning and afternoon revealed no vultures through March 2001.

Behavioral Observations. Vultures that encountered an effigy or carcass hanging from a tower typically circled the structure and flew close to the effigy or carcass. Most birds did not land on the tower. Among vultures that did, there was no obvious trend or preference to be above, below, or at the same level as the stimulus. Many that landed on a tower peered at the carcass or effigy for up to several minutes and then departed. Those that stayed on the tower preened and interacted with other vultures in what appeared to us to be a normal manner. Vultures that perched on the tower did not demonstrate overt avoidance of the effigy or carcass. Many perched very close with no obvious concern. Several times we noted that all the vultures on the tower flew up and departed the area en masse. On at least one occasion this was due to the arrival of a Red-tailed Hawk (*Buteo ja-*

maicensis), but usually the reason for a mass departure was not apparent.

DISCUSSION

Not every available tower is occupied by vultures. It is not known what features of a tower attract roosting vultures. We noted many unoccupied towers of seemingly identical design as those in this study. Site microclimate is likely an important factor in vultures' choice of a roost site (Thompson et al. 1990). Birds roosting on a tower are not protected by branches and surrounding vegetation like they would be in a tree roost. Exposure to the ambient conditions is possibly offset by birds' ability to roost closer together on a tower than they could in a tree roost with consequent thermoregulatory benefits (Buckley 1998). Because towers are higher than surrounding trees, vultures probably can enter and depart the roost more easily. Furthermore, wind striking the structure might create updrafts, called obstruction currents, that facilitate the birds' flight near the tower (Thompson et al. 1990). The towers we studied are near heavily-traveled roads or highways. Roosting close to roads could be advantageous for vultures because of thermals generated from the pavement and the availability of road kills (Thompson et al. 1990).

Vulture roosts can form in response to temporary availability of local food resources (Sweeney and Fraser 1986, Coleman and Fraser 1989). Among these study sites, the Waldo tower is within 2 km of a small pig farm frequented by Black Vultures that sometimes preyed upon newborn piglets. The owner of the farm informed us that the number of vultures at his farm declined substantially after we installed the effigy and dispersed birds at the Waldo tower. This observation supports the notion that local food availability can be a determining factor in the formation of vulture roosts on towers.

From the consistent responses that we recorded, it is obvious that the presence of a dead vulture hanging by its feet makes a tower less suitable as a vulture roost site. In every trial, there was immediate reduction in numbers of roosting birds, followed soon by abandonment of the roost site, regardless of the species composition of the roost and regardless of the species of vulture carcass or effigy. Even the installation of a Canada Goose decoy caused substantial reduction, although not abandonment, at one site.

It is not clear what features of the effigies are offensive to the vultures. Taste, tactile, and aural cues can be ruled out because vultures never contacted the effigies and the effigies produced no sounds. Conceivably, the odor of a decaying vulture carcass could be perceived by other vultures as a signal to stay away from the area. However, we observed similar responses with intact carcasses, taxidermic effigies, and a plastic decoy. The odors produced by these stimuli are, no doubt, sufficiently distinct for vultures to discriminate them. Thus, at this time, we think it unlikely that odor cues are important. Rather, we feel that visual cues are predominant. This is supported by observations of many perched vultures peering at the effigy hanging from the tower and by vultures circling the tower, flying close to the effigy, and then departing. The more challenging task is determining what visual attributes are most salient to the vultures. Possibilities include size, shape, color, orientation, movement, and height on tower. In this study, we did not experiment or manipulate these variables because our goal was to solve the problems of our cooperators, not to isolate the factors that might be essential to the effectiveness of this roost dispersal technique.

Particularly noteworthy was the degree to which the repellent effect of the effigy or carcass persisted after the stimulus was removed. Months after the carcass at the Macclenny A tower had rotted away, no vultures occupied the tower. Similarly, the carcass installed on the Macclenny B tower fell off after 4 days yet vultures continued to avoid the structure. At this site, the presence of a Black Vulture effigy on the 31-m Doppler tower might have contributed to the absence of vultures on the taller tower 45 m away. Finally, at Waldo, we intentionally removed the Black Vulture effigy, and regular monitoring disclosed no reoccupation of the tower through March 2001, over 4 mo later. We did not intentionally remove effigies at other sites because of commitments to our cooperators, but it is certainly of interest to determine the relationship between length of vultures' exposure to the stimulus and the duration of their avoidance responses.

Our findings would have been strengthened by the inclusion of unmanipulated vulture roosts as controls. However, we feel that pretreatment observations at each site provide sufficient evidence that the roosts would have persisted had we not intervened. Vulture roosts can be ephemeral (Sweeney and Fraser 1986, Coleman and Fraser

1989), but it is unlikely that each of the roosts we studied happened to disperse coincidentally with the installation of the carcass, effigy, or decoy.

Management Implications. Suspending a vulture effigy or carcass in a tower appears to be a quick, effective means to rid the structure of roosting vultures. Once the stimulus is properly installed, the only problem likely to be encountered is possible entanglement of the support line with the structure. This can be avoided by keeping the support line to an appropriately short length. The extent to which the effigy/carcass approach to management of nuisance vulture roosts can be extended to other types of roosts remains to be determined. Initial trials that we have conducted in vulture tree roosts affecting residential neighborhoods have been promising. In each case the roost has dispersed, although the response by the vultures was not as rapid as we observed in the tower roosts (M. Avery unpubl. data).

There are constraints to the general use of a vulture carcass or taxidermic effigy. Both species of vultures are protected by Federal laws and it is unlawful to possess them without a permit from the U.S. Fish and Wildlife Service. Therefore, this technique can only be used under supervision of the appropriate authorities. Also, the hanging of a vulture carcass or taxidermic effigy could be distasteful to the public. If this technique is used in areas of high visibility, then it might be prudent to contact local conservation or birding groups so that the carcass or effigy is not mistaken for a bird that accidentally became entangled in the tower. Finally, prolonged exposure to the weather deteriorates the carcass or effigy.

We feel the development of an effective, durable, readily available alternative is essential to the widespread use of this vulture management method. The trial we conducted at Niceville with the Canada Goose decoy was an encouraging step in this direction. The decoy cost about $25.00 (U.S.), and we made only minor changes in its appearance, yet vulture use of the tower was reduced 60% after the decoy was installed. This suggests that successful roost dispersal can be accomplished without the use of actual carcasses or taxidermic effigies. The focus of future field trials will be the evaluation of various commercial decoy alternatives.

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RAPTOR ABUNDANCE AND HABITAT USE IN A HIGHLY-DISTURBED-FOREST LANDSCAPE IN WESTERN UGANDA

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Abstract.—We conducted roadside raptor surveys in an area of western Uganda that included undisturbed forest, agricultural mosaics, and tea plantations. Between September 1997–April 1998, we surveyed three transects (51 km of roadway) twice each month, once during the morning and again in the afternoon. During these surveys, we detected 14 falconiform species and 77 individuals. We detected significantly more raptors during morning than afternoon surveys. Wahlberg's Eagles (*Aquila wahlbergi*) and Long-crested Eagles (*Lophaetus occipitalis*) were observed most frequently and were sighted consistently throughout the study. Most raptors observed were resident species, whereas Palearctic migrants comprised less than 25% of all raptors, noteworthy considering their abundance in other African regions. We did not detect an equal number of raptors in all habitat types. Agriculture mosaics accounted for 61% of the habitat we surveyed and 75% of all raptor detections were in these habitats. In contrast, tea plantations were 14% of the area surveyed, but only 3% of all raptors were detected there. Based on these results, we suggest that tea plantations may be suboptimal habitat for larger, open-habitat raptors. We did not detect large, forest-dwelling eagles outside of large areas of undisturbed forest, which are probably critical to their persistence in these landscapes.

Key Words: *Uganda; roadside survey; conservation; habitat use; deforestation; tea plantation;* Aquila wahlbergi; *Wahlberg's Eagle;* Lophaetus occipitalis; *Long-crested Eagle.*

Abundancia de repaces y uso de habitat en un paisaje de bosque altamente disturbado en el oeste de Uganda

Resumen.—Hicimos estudios de rapaces alrededor de las carreteras en un área del oeste de Uganda que incluía bosque sin intervención, mosaicos agrícolas, plantaciones de te. Entre septiembre de 1997–abril de 1998, estudiamos tres transeptos (51 km de carreteras) dos veces cada mes, una vez en la mañana y otra en la tarde. Durante estos estudios detectamos 14 especies falconiformes y 77 individuos. Detectamos significativamente más especies durante los estudios de la mañana que en los de la tarde. Las águilas de Wahlberg (*Aquila wahlbergi*) y las águilas de cresta alargada (*Lophaetus occipitalis*) fueron observadas más frecuentemente y fueron avistadas consistentemente a lo largo del estudio. La mayoría de rapaces observadas fueron especies residentes, mientras que las migratorias palearticas comprendieron menos del 25% de todas las rapaces, esto es digno de mencionarlo considerando su abundancia en otras regiones africanas. No detectamos un número igual de rapaces en todos los tipos de hábitats. Los mosaicos agrícolas dieron cuenta de 61% del hábitat que estudiamos y 75% de todas las detecciones de rapaces estuvieron en esos hábitats. En contraste, las plantaciones de te fueron 14% del área estudiada, pero únicamente 3% de todas las rapaces fueron detectadas allí. Basados en estos resultados, sugerimos que las plantaciones de te pueden ser hábitats sub óptimos para las rapaces más grandes y de hábitats abiertos. No detectamos grandes águilas residentes de bosque fuera de grandes áreas de bosque no perturbado, los cuales probablemente son críticos para su supervivencia en estos paisajes.

[Traducción de César Márquez]

When compared to Nearctic and Palearctic species, Afrotropical raptors are relatively unstudied. This deficiency was recently illustrated by Virani and Watson (1998); describing the state of knowledge of 79 raptors breeding in East Africa, they considered only 6.3% of these species "well-known," while rating 60.8% "unknown." For many of these unknown species, little or no information exists on distribution, abundance, breeding biology, or feeding ecology—basic information for iden-

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tifying populations that are threatened by habitat alteration. Determination of populations that are threatened is an important aspect of conservation, especially in areas where forests are being cleared to support growing human populations.

With ca. 104 people per km^2, Uganda has one of the densest populations in sub-Saharan Africa and it continues to grow at a yearly rate of 2.6% (FAO 1999). This population has driven widespread deforestation. A hundred years ago, ca. 13% of Uganda was covered by moist, broadleaf forest, but only 3% of this forest remains (Sayer et al. 1992). The remaining forested areas, many in reserves and national parks, are under increasing pressure from growing rural populations. Thus, information on raptor abundance and habitat use both inside and outside of these protected areas is important for management and conservation decisions.

Roadside raptor surveys have been widely used to study relative abundance, community composition, and habitat use of raptors (e.g., Woffinden and Murphy 1977, Ellis et al. 1990). Although limitations of roadside surveys are well-recognized (Millsap and LeFranc 1988, Bunn et al. 1995), the method offers an efficient means of describing raptor communities. Roadside raptor surveys have been conducted in East Africa (Brown 1971, Thiollay 1978, Sorley and Andersen 1994), but these efforts have occurred mostly in savanna habitats that are characterized by high densities of large mammals, vultures, and eagles. Here we present results from eight months of roadside raptor surveys in the Kabarole District of western Uganda. We describe the abundance and diversity of raptors in mature forest, agriculture/forest mosaic, agriculture/grassland mosaic, tea plantation, secondary vegetation, villages, papyrus swamp, and lakeshore habitats.

STUDY AREA AND METHODS

The study area (0°13′–0°41′N, 30°19′–30°32′E) lies just north of the equator at the foot of the Ruwenzori Mountains in western Uganda (Fig. 1). This area is volcanic in origin and characterized by rolling hills. Elevation ranges from 1100 m in the south to 1590 masl in the north. Although historically forested, much of the land has been cleared for subsistence farming and banana (*Musa* spp.) and tea (*Thea sivensis*) plantations to support the growing human population. Within this agricultural landscape, forest fragments remain, especially on steep slopes around crater lakes (Onderdonk and Chapman 2000), but the only extensive forested area is within the 766 km^2 Kibale National Park (KNP). Yearly rainfall, measured at the Makerere University Biological Field Station in KNP, averaged 1778 mm between 1990–98 (L. Chapman and C. Chapman unpubl. data) and peak periods of rainfall occur in April and October (Struhsaker 1997).

We conducted roadside raptor surveys along three transects (19, 15, and 17 km in length; Fig. 1) between September 1997–April 1998. We surveyed transects twice each month, once in the morning (between 0800–1000 H) and again in the afternoon (between 1500–1700 H), usually on the same day. Driving at speeds of 20–40 km/hr with five observers in the vehicle, we stopped briefly to identify raptors on both sides of the transect and recorded the time, distance from the transect, habitat type, and activity (perched or flying) for each bird. During heavy rain we did not conduct surveys.

To quantify habitat availability, we visually estimated habitat composition (10% increments) within 100 m of either side of the road of each km traveled. For this analysis, we recognized eight habitat types: mature forest, agriculture/forest mosaic, agriculture/grassland mosaic, tea plantation, secondary vegetation, villages, papyrus swamp, and lakeshore. *Mature forest* was primarily encountered when transects passed through portions of Kibale National Park. This forest is considered moist, evergreen forest, transitional between lowland rainforest and montane forest (Struhsaker 1997). Canopy height ranges from 25–30 m, with a few trees as tall as 55 m, and common tree species include *Diospyros abyssinica*, *Markhamia platycalyx*, *Celtis durandii*, *Uvariopsis congensis*, and *Bosqueia phoberos* (Chapman et al. 1997). *Agriculture/forest mosaic* was characterized by a patchwork of remnant forest fragments surrounded by subsistence agriculture (primarily bananas, millet, cassava, and corn), fallow fields dominated by elephant grass (*Pennisetum purpureum*, 3–5 m tall), cattle pasture, pine and eucalyptus plantations, and scattered houses. Similar to this habitat, *agriculture/grassland mosaic* was also a patchwork of farmland, cattle pasture, and forest plantations, but uncultivated land was covered by large areas of elephant grass, and there were no remaining natural forest fragments. *Agriculture/grassland mosaic* occurred in the southern portion of the study area. *Tea plantations* are large fields of tea shrubs grown in rows and trimmed regularly to maintain a uniform height of about 1 m. This crop is one of the few intensive, large-scale agricultural industries in western Uganda. Four other habitat types—*secondary vegetation, villages, papyrus swamp, and shores of crater lakes*—together comprised <10% of the area surveyed.

Because the number of raptors detected per transect was low, we pooled survey results from the three transects and considered them a single transect, though surveyed on different days. We considered monthly surveys independent samples and used a Wilcoxon signed-ranks test to compare distributions of raptor count data from morning and afternoon surveys. We investigated the relationship between monthly rainfall and raptor detections (morning and afternoon surveys pooled) using Spearman rank correlation. We used Chi-square goodness-of-fit tests to compare observed and expected numbers of raptors among months and habitat types (all months pooled). We recognize that pooling survey results violates conditions of statistical independence, but

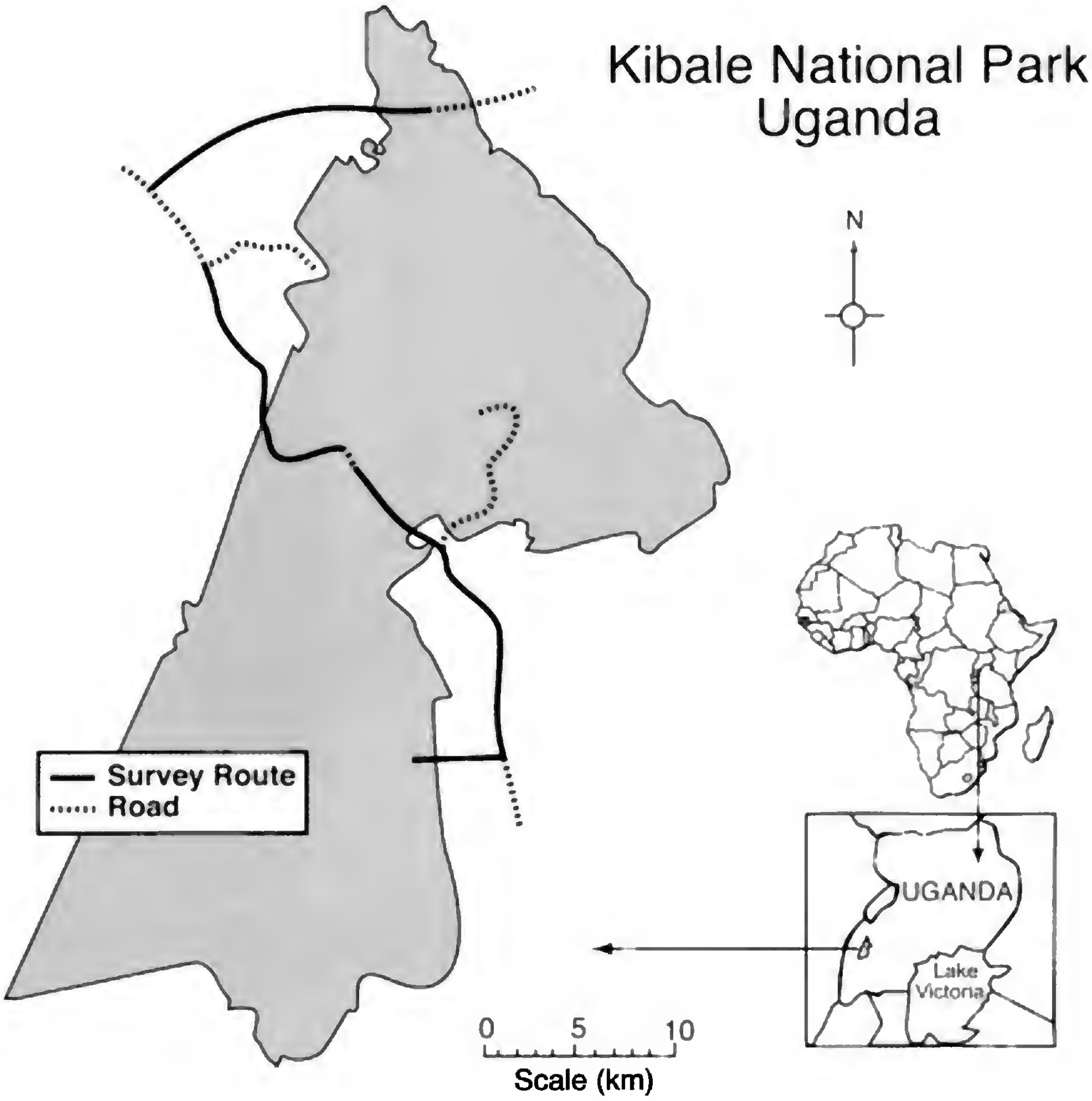

Figure 1. Map of study area and roadside survey transects in Kabarole district, Uganda.

our limited sample size prevented us from using other techniques to compare data.

To meet the assumptions of the Chi-square goodness-of-fit test for the habitat analysis, we combined habitat types that made up less than 5% of the transect length (secondary vegetation, villages, papyrus swamp, and lakeshore) into one category, so all categories had >5 expected detections. Differences between observed use and availability may occur if raptor detectability varies systematically among habitat types. To evaluate whether detectability varied among habitats, we compared detection distances (Kruskal-Wallis test) for mature forest, agriculture/forest mosaic, and agriculture/grassland mosaic. Significance level for all tests was $P = 0.05$.

Finally, based on eight months of pooled data, we present three measures of relative abundance to facilitate comparison to other roadside raptor literature: (1) individuals detected per km traveled, (2) km traveled per individual detected, and (3) Woffinden and Murphy's (1977) Index of Relative Abundance (IRA), calculated as:

$$\text{IRA} = \frac{\text{No. ind. of each species observed}}{\text{No. km traveled}} \times 1000$$

RESULTS AND DISCUSSION

We observed 14 falconiform species and 77 individuals during our study (Table 1). During morning surveys we detected more raptors (median = 5.5, $\bar{x} = 6.5$ raptors/survey) than during afternoon surveys (median = 2.5, $\bar{x} = 3.1$, Wilcoxon signed-ranks test, $z = -2.54$, $N = 8$, $P < 0.05$). This difference is consistent with temperate zone studies demonstrating that roadside raptor surveys are affected by raptor activity patterns (Bunn et al. 1995). The mean number of detections per month was 8.0 raptors, ranging from 5 (December) to 20 (October). The number of detections in October was inflated when we observed 13 Common Buzzards (*Buteo buteo vulpinus*) migrating southward. When these sightings were omitted there was no significant difference between the number of raptors detected each month ($\chi^2_7 = 4.25$, $P > 0.05$). There was no relationship between monthly rain-

Table 1. Numbers of raptors detected, detection frequencies, and relative abundance indices of raptors during roadside surveys in Kabarole district, Uganda.

SPECIES	NO. OBSERVED	INDIV. PER km	Km TRAV. PER INDIV.	INDEX OF REL. ABUND.[a]
Black-shouldered Kite(*Elanus caeruleus*)	3	0.004	272.0	3.7
Black Kite (*Milvus migrans*)	5	0.006	163.2	6.1
African Fish-Eagle (*Haliaeetus vocifer*)	1	0.001	816.0	1.2
Palm-nut Vulture (*Gypohierax angolensis*)	3	0.004	272.0	3.7
African Harrier-Hawk (*Polyboroides typus*)	4	0.005	204.0	4.9
Unidentified harrier (*Circus* spp.)	1	0.001	816.0	1.2
African Goshawk (*Accipiter tachiro*)	2	0.002	408.0	2.5
Lizard Buzzard (*Kaupifalco monogrammicus*)	2	0.002	408.0	2.5
Common (Steppe) Buzzard (*Buteo buteo vulpinus*)	14	0.017	58.3	17.2
Wahlberg's Eagle (*Aquila wahlbergi*)	18	0.022	45.3	22.1
Long-crested Eagle (*Lophaetus occipitalis*)	16	0.020	51.0	19.6
Crowned Hawk-eagle (*Stephanoaetus coronatus*)	2	0.002	408.0	2.5
Gray Kestrel (*Falco ardosiaceus*)	2	0.002	408.0	2.5
Northern Hobby (*Falco subbuteo*)	1	0.001	816.0	1.2
Unidentified hobby (*F. subbuteo* or *cuvieri*)	3	0.004	272.0	3.7

[a] Analysis of relative abundance after Woffinden and Murphy (1977).

fall and the number of raptors detected (r_s = 0.13, N = 8, P = 0.76). Omitting the October flight of Common Buzzards did not change the significance of this relationship (r_s = −0.12, N = 8, P = 0.77).

Raptors were not equally abundant in all habitats (χ^2_4 = 19.0, $P < 0.05$). However, the detection distances for mature forest (median = 0, $\bar{x}$ = 0.9 m, N = 9), agriculture/forest mosaic (median = 40, $\bar{x}$ = 44.7 m, N = 31) and agriculture/grassland mosaics (median = 40, $\bar{x}$ = 64.2 m, N = 27) were significantly different (Kruskal-Wallis, H_2 = 20.26, $P < 0.05$). As a result, raptor detectability was undoubtedly reduced in forest habitats, but when forest habitat was excluded from the analysis, raptor detections were still not equally abundant in all habitats (χ^2_3 = 15.57, $P < 0.05$). Therefore, we do not believe that this result simply reflects differential detectability.

Agricultural/forest mosaic was the most common habitat along the route and accordingly had the greatest species richness (N = 8) and total detections (N = 31; Table 2). Agriculture/grassland mosaic had the second highest species richness (N = 6) and total number of detections (N = 27; Table 2). However, detections per km were higher in agriculture/grassland mosaic (0.17 raptors/km) than in agriculture/forest mosaic (0.09 raptors/km).

Tea plantations accounted for 14% of the area surveyed, but only 3% of all raptor detections. In this habitat, we detected 0.02 raptors/km and only a single species, the small, insectivorous Gray Kestrel (*Falco ardosiaceus*; Table 2). Larger, vertebrate-eating raptors were conspicuously absent from tea plantation habitats, despite the fact that these fields were often bordered by forest fragments or crossed by rows of utility poles, providing suitable perches.

In mature forest we detected only Crowned Hawk-Eagles (*Stephanoaetus coronatus*) and Common Buzzards. All observations (N = 7) of Common Buzzards in this habitat occurred during a single survey in October while this species was passing through on migration. Common Buzzards normally winter in open savanna habitats throughout Africa, and their occurrence in this forested area was probably an unusual event associated with migration. In contrast, Crowned Hawk-Eagles are breeding residents in KNP, where they prey primarily upon arboreal monkeys (Skorupa 1989, Mitani et al. 2001). The absence of Crowned Hawk-Eagles outside of mature forest suggests that they may be sensitive to deforestation in this region of Africa, perhaps because many primates are absent from forest fragments outside of the park (Onderdonk and Chapman 2000).

The least common habitat, lakeshore, occurred only where one transect passed a small crater lake

Table 2. Number of raptors observed in eight habitat types during roadside surveys in Kabarole district, Uganda.

	HABITAT TYPE[a]							
SPECIES	AFM	AGM	TP	MF	VI	SV	PS	LS
Black-shouldered Kite		3						
Black Kite	3				2			
African Fish-Eagle								1
Palm-nut Vulture								3
African Harrier-Hawk	3	1						
Unidentified harrier		1						
African Goshawk	2							
Lizard Buzzard	2							
Common Buzzard	2	3		7	1	1		
Wahlberg's Eagle	2	16						
Long-crested Eagle	13	3						
Crowned Hawk-Eagle				2				
Gray Kestrel			2					
Northern Hobby	1							
Unidentified hobby	3							
Total species	8	6	1	2	2	1		2
Total individuals	31	27	2	9	3	1		4
Raptors per km	0.09	0.17	0.02	0.06	0.10	0.05	0.0	1.25
Km habitat surveyed	337.6	160.0	110.4	148.8	28.8	22.4	4.8	3.2
Percent of total survey length	41.4	19.6	13.5	18.2	3.5	2.8	0.6	0.4

[a] Habitat types: AFM = Agriculture/forest mosaic, AGM = Agriculture/grassland mosaic, TP = Tea plantation, MF = Mature forest, VI = Village, SV = Secondary vegetation, PS = Papyrus swamp, and LS = Lakeshore.

and accounted for <1% of the habitat surveyed. However, this habitat was the only area where we observed an African Fish-Eagle (*Haliaeetus vocifer*) and Palm-nut Vultures (*Gypohierax angolensis*; Table 2).

Long-crested Eagles (*Lophaetus occipitalis*) and Wahlberg's Eagles (*Aquila wahlbergi*) were the most abundant raptors, accounting for 34 of 77 (44%) raptors detected (Table 2). We observed no true vultures during our surveys, despite the fact that Brown (1971) recorded four vulture species during roadside surveys in Queen Elizabeth National Park, less than 50 km south of our study area. Most (75%) of the raptors we observed were either residents or intra-African migrants. The other 25% of detections were Palearctic migrants, but this percentage is inflated by migrating Common Buzzards that did not have a sustained presence in the area. Thus, the proportion of migrant species wintering in the area was much less than 25%, even though our surveys took place during the Palearctic winter when northern migrants would be present. Determining the exact proportion of wintering migrants is difficult, because some or all of the unidentified raptors (e.g., *Circus* spp. and *Falco* spp.) may have been migratory and some species, such as Black Kites (*Milvus migrans*), may have been represented by both migrant (*M. m. migrans*) and resident (*M. m. parasitus*) subspecies. However, even if we assume that all unidentified species were wintering Palearctic migrants, these individuals account for only 8% of all raptor detections when Common Buzzards are omitted.

Based on raptor surveys in Mexico, Guiana, and Ivory Coast, Thiollay (1985) demonstrated that when tropical forests are fragmented and converted to open agricultural habitats, resident species tolerant of open habitats and northern migrants replace resident forest species. Similarly, in a review of roadside raptor surveys in South Africa, Cade (1969) recognized that Palearctic migrants were abundant in the disturbed agricultural habitats of Transvaal and Orange Free State, where they accounted for 33–95% of all raptor detections, but were relatively rare in Kruger National Park and Kalahari Gemsbok Park, where they accounted for only 2–4% of all detections. In savanna habitats of Uganda, Palearctic migrants comprised only 11% of the raptors detected by Brown (1971) and 31–43% of raptors detected by Thiollay (1978). Most of our study area was deforested and highly-disturbed, and although the commonly-detected residents were associated with open, agricultural mosaic habitats, we did not observe a large proportion of wintering migrants.

Roadside raptor surveys generally work well in open habitats; however, they are less effective in forested habitats (Millsap and LeFranc 1988). This may be especially problematic in tropical forests where raptor communities are notoriously difficult to sample and complete surveys often involve special techniques (Thiollay 1989, Whitacre et al. 1992). Thus, the low number of raptors we detected in mature forest is probably not indicative of overall raptor abundance and species richness in this habitat. For instance, we did not detect Cassin's Hawk-Eagles (*Spizaetus africanus*) nor Ayres' Hawk-Eagles (*Hieraaetus ayresii*). Both are large, uncommon, forest-dwelling eagles that breed in Kibale National Park (Skorupa et al. 1985, Seavy 2000). Similarly, smaller raptors that use easily overlooked perch sites are often difficult to detect (Millsap and LeFranc 1988) and these biases should be considered when interpreting our survey results. Species that were observed in the study area, but not detected on our transects, were Osprey (*Pandion haliaetus*), Banded Snake-Eagle (*Circaetus cinerascens*), Black-chested Snake-Eagle (*Circaetus pectoralis*), African Marsh-Harrier (*Circus ranivorus*), Black Goshawk (*Accipiter melanoleucus*), Little Sparrowhawk (*Accipiter minullus*), Martial Eagle (*Polemaetus bellicosus*), and African Hobby (*Falco cuvieri*).

The results of our surveys provide two conclusions with implications for raptor conservation in East African forest landscapes. First, in the dominant agricultural habitat we detected species associated with agricultural habitats, but very few forest-associated species. Thus, although some raptors may be numerous in these cleared habitats, forest-associated species appear to be uncommon, restricted to large tracts of forest, and sensitive to deforestation. If the large, forest-dwelling raptors are entirely absent from open habitats surrounding KNP, then these species may be confined to the forest inside the park. Second, our results suggest that tea plantations may provide unique foraging opportunities for small insectivorous raptors, but unsuitable habitat for many larger, open-habitat raptors. In short, not all open habitats are of equal value to all open-habitat raptors. These results should be considered by managers and researchers concerned with raptor conservation and protected area design in forested landscapes of East Africa.

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TROPHIC NICHE OF NORTH AMERICAN GREAT HORNED OWLS

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Abstract.—The trophic niche of Great Horned Owls (*Bubo virginianus*) was summarized using 22 North American studies reporting >100 prey items each. Twenty-one of these studies were reviewed from the published literature, and one, our Montana data, is presented here for the first time. More than 92 species from four taxonomic classes have been recorded from 19 278 prey items. Mammals constituted >93.3% of prey from all studies, with six studies reporting 100% mammalian prey. Food-niche breadth ranged from 2.09–19.15 ($\bar{x}$ = 5.17) for combined studies, 2.12–19.15 ($\bar{x}$ = 6.29) for breeding seasons, and 2.09–4.72 ($\bar{x}$ = 3.50) for non-breeding seasons. Evenness values ranged from 0.408–0.840 ($\bar{x}$ = 0.620) for combined studies, 0.420–0.703 ($\bar{x}$ = 0.596) for breeding seasons, and 0.408–0.724 ($\bar{x}$ = 0.609) for non-breeding seasons. Estimated masses of individual prey species ranged between 2 and 6300 g. Birds were only a minor part of the owl diet, although a variety of species were eaten.

Key Words: *diet; food-niche breadth; Great Horned Owl;* Bubo virginianus; *North America.*

Nicho trofico del Gran Buho Cornado Americano

Resumen.—El nicho trófico de (*Bubo virginianus*) fue compendiado usando 22 estudios norte americanos reportando >100 ítems presa cada uno. Veintiuno de esos estudios fueron revisados en la literatura publicada, y uno, nuestros datos de Montana, se presentan aquí por primera vez. Más de 92 especies de cuatro clases taxonómicas han sido registradas a partir de 19 278 ítems presa. Los mamíferos constituyeron >93.3% de presas en todos los estudios, con seis estudios reportando 100% de presas mamíferas. La amplitud del nicho alimenticio estuvieron en el rango de 2.09–19.15 ($\bar{x}$ = 5.17) para estudios combinados, 2.12–19.15 ($\bar{x}$ = 6.29) para estaciones reproductivas, y 2.09–4.72 ($\bar{x}$ = 3.50) para temporadas no reproductivas. La masa estimada de especies presa individualmente estuvo entre 2 y 6300 gr. Las aves fueron tan solo una parte menor de la dieta del búho, aunque una variedad de especies fueron consumidas.

[Traducción de César Márquez]

The Great Horned Owl (*Bubo virginianus*) is perhaps the most widely-distributed owl in North America (Houston et al. 1998, Holt et al. 1999). Numerous studies of the food habits of Great Horned Owls have been conducted in North America and it has been considered to be an opportunistic feeder. Indeed, the Great Horned Owl has been reported to have the broadest diet of any North American owl species (Marti and Kochert 1996, Houston et al. 1998). However, the owl's trophic niche has not been reviewed continent-wide. Earhart and Johnson (1970) summarized principal food habits of Great Horned Owls from published literature, but did not identify prey to the species level, provide prey numbers, or discuss their conclusions. Jaksic and Marti (1984) made comparisons between a few Neotropical and Nearctic localities, but compared owl diets from only two regions in North America. Our paper summarizes the trophic niche of Great Horned Owls from 22 North American studies; 21 from published literature, and one, our original Montana data.

Our objectives were to: (1) determine Great Horned Owl trophic niche from west-central Montana and (2) compare trophic niche among North American studies.

Methods

In Montana, we collected pellets and prey remains annually from 10 territories in the Missoula and Mission valleys during the breeding and non-breeding seasons from 1987–95. Prey was identified using local dichotomous keys for mammals (Hoffmann and Pattie 1968) and by comparing feather and body parts of prey with museum specimens at the Philip L. Wright Zoological Museum (University of Montana). Numbers and proportions

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of prey types were then compared between breeding and non-breeding seasons for Montana. Comparisons of trophic niche were then made among other available North American data sets.

We defined trophic niche as the relationship between owls and their prey. We followed Marti's (1987) definitions for trophic diversity in which a broad food-niche breadth (FNB) has a high number of prey species, which are nearly equally distributed, and a narrow food-niche breadth has a low number of prey species unequally distributed. However, we found no method to determine the statistical significance between narrow and wide food-niche breadth. We compared owl trophic niche from 22 North American studies with >100 prey items each (Tables 1–3). We then divided these studies into breeding season and non-breeding season diets. To compare trophic niche among studies, we primarily used prey identified to the species. Prey identified to genus were included if they occurred frequently or exhibited an unusual body mass. Insects, arachnids, and unidentified reptiles, birds, and mammals were eliminated from trophic niche comparisons because they were either not identified to genus or occurred only rarely (<1%) in the diet.

Food-niche breadth (H') was calculated for each study using the antilog of the Shannon-Weiner diversity index (Marti 1987). We used this equation because it is linearly related to the number of prey categories in the sample. Evenness was calculated using Alatalo's (1981) modification of Hill's (1973) equation: Evenness = $(N_2 - 1)/(N_1 - 1)$, where $N_1 = \exp H'$ and $N_2 = 1/p_i^2$. Evenness values range from zero to one. An evenness value of one indicates prey proportions in the diet are equal. We compared food-niche breadth and evenness values from all studies as well as those from breeding and non-breeding seasons using the Mann-Whitney U-test (Fowler and Cohen 1990).

Spearman rank correlation (Fowler and Cohen 1990) was used to examine the relationship between the number of mammalian species and number of prey items with food-niche breadth values among studies. We did so to determine if wider food-niche breadth values were associated with increased numbers of prey or species in the diet. The Spearman rank correlation was also used to examine the relationship between number of prey items and food-niche breadth because food-niche breadth values can fluctuate with sample size, thus influencing the results.

A relative-size category of the main prey classes eaten by the owls was derived using body mass estimates of mammals (Whitaker 1992) and birds (Dunning 1984). Standard mean prey biomass estimates were not calculated based on species because of unfounding factors. For example, standard prey biomass estimates are usually derived from the adult age class and do not consider other age classes in the population. Further, mean prey biomass estimates generally give whole carcass masses and do not consider that only specific portions of some medium to large prey are eaten (Holt 1993, 1994).

RESULTS

The Montana study yielded 4350 prey items: 2696 from the breeding season and 1654 from the non-breeding season. Although collectively the owls ate a wide variety of prey (N = 28), they ate predominately small mammals, particularly voles (Table 1).

Table 1. The number of individual prey consumed by Great Horned Owls during breeding and non-breeding seasons in Montana from 1987–95.

	NO. OF PREY	
SPECIES	BREEDING SEASON	NON-BREEDING SEASON
Mammals		
Microtus pennsylvanicus	1264	902
Microtus montanus	1158	470
Microtus spp.	72	159
Peromyscus maniculatus	37	52
Thomomys talpoides	54	39
Ondatra zibethicus	13	14
Mustela frenata	1	1
Sylvilagus nuttallii	2	—
Tamias amoenus	—	1
Tamiasciurus hudsonicus	2	—
Glaucomys sabrinus	—	1
Birds		
Sturnus vulgaris	30	4
Phasianus colchicus	12	4
Fulica americana	6	1
Pica pica	7	1
Turdus migratorius	3	—
Colaptes auratus	2	1
Xanthocephalus xanthocephalus	12	—
Anas platyrhynchos	2	2
Anas spp.	1	—
Bombycilla spp.	1	—
Sturnella neglecta	1	—
Asio otus	1	—
Porzana carolina	1	—
Rallus limicola	1	—
Bonasa umbellus	1	—
Agelaius phoeniceus	—	1
Other		
Catostomus spp.	4	—
crayfish	6	1
squawfish	2	—
Total	2696	1654 = 4350

During the breeding season, the owls consumed 28 species of prey. Of these however, they ate predominately small mammals, especially *Microtus* voles (92.5%, N = 2494). During the non-breeding season, the owls ate only 16 species of prey, again consuming predominately *Microtus* voles (92.5%, N

Table 2. Landscape diets of Great Horned Owls in North America. Percent of prey in taxonomic classes calculated from 22 studies, representing 19 278 prey items.

	PERCENT					
NO. OF PREY	OSTEICHTHYES	CRUSTACEA	AVES	MAMMALIA	LOCATION	SOURCE
Breeding season						
2696	0.2	0.2	3.09	6.6	MT	This study
1896	—	—	—	100.0	OR	Maser & Brodie 1966
1300	—	—	1.4	98.6	ID	Marti & Kochert 1996
398	—	1.5	2.8	95.7	UT	Smith & Murphy 1973
356	0.8	—	2.2	96.9	WY	Craighead & Craighead 1969
276	3.3	—	31.5	65.2	NY, NJ, CT	Bosakowski & Smith 1992
209	—	—	—	100.0	MB	Bird 1929
142	—	9.2	20.4	70.3	MI	Craighead & Craighead 1969
119	—	—	30.3	69.7	OH	Springer & Kirkley 1978
Non-breeding season						
1845	—	—	1.4	98.6	MI	Craighead & Craighead 1969
1654	—	0.1	1.0	98.9	MT	This study
756	2.5	—	1.9	95.6	MT	Seidensticker 1968
584	—	—	0.3	99.7	CA	Rudolph 1978
210	—	—	2.4	97.6	IN	Kirkpatrick & Conway 1947
161	—	—	—	100.0	NE	Rickart 1972
122	—	—	—	100.0	YT	Weir & Hanson 1989
Breeding and non-breeding seasons						
2571	—	0.1	4.4	95.2	WI	Errington 1932
2152	—	—	1.7	98.1	CO	Marti 1974
809	0.1	—	1.7	98.1	WA	Knight & Jackman 1984
568	—	—	—	100.0	CA	Barrows 1989
273	—	0.7	21.2	78.0	WI	Orians & Kuhlman 1956
178	—	—	—	100.0	OK	Tyler & Jensen 1981

= 1531). The decreased prey species diversity during the non-breeding season reflected the fewer species of prey available during the fall and winter months in Montana.

The 22 studies combined yielded 19 278 prey items (Table 2) from eight western, six central, and three eastern states, and two Canadian provinces. Studies from New York and Pennsylvania (Latham 1950), and Alberta (Rusch et al. 1972, McInvaille and Keith 1974, Adamcik et al. 1978) were also reviewed but omitted from trophic calculations because dominant prey species were not always identified to genus or species.

The owls consumed ≥92 prey species from four taxonomic classes: Osteichthyes, Crustacea, Aves, and Mammalia (Table 2). Mammals composed ≥65.2% of the prey from each study, constituting 93.3% of the total prey from all studies. Six studies reported 100% mammalian prey (Table 2).

Although the owls preyed on a broad number of species overall, *Microtus* (N = 10 studies), *Peromyscus* (N = 6), *Perognathus* (N = 2), *Sigmodon* (N = 1), and *Lepus* (N = 1) species represented the highest percentage of prey in all studies. Overall, food-niche breadth values ranged from 2.09–19.15 ($\bar{x}$ = 5.17, SD ± 3.61) (Table 3). Food-niche breadth values for the breeding season (range = 2.12–19.15, $\bar{x}$ = 6.29, SD ± 5.39, N = 9) and non-breeding season (range = 2.09–4.72, $\bar{x}$ = 3.50, SD ± 0.82, N = 7) were similar. Food-niche breadths were not significantly different (Mann-Whitney U = 24.5, $P > 0.05$) between seasons.

The broadest food-niche breadth (FNB = 19.15) was from New York, New Jersey, and Connecticut, where 15 mammal species constituted 65.2% of the diet, with *Peromyscus* representing 14.3% (Bosakowski and Smith 1992) (Table 3). Fourteen other mammal, 20 bird, and two fish species comprised the remainder. The broad FNB in this study, compared to other studies, may be explained by the

Table 3. Trophic parameters calculated from twenty-two studies representing 19 278 prey items.

NO. OF PREY	FOOD-NICHE BREADTH	EVENNESS	LOCATION	SOURCE
Breeding season				
2696	3.27	0.644	MT	This study
1896	2.12	0.465	OR	Maser & Brodie 1966
1300	8.12	0.686	ID	Marti & Kochert 1996
398	4.47	0.420	UT	Smith & Murphy 1973
356	2.85	0.566	WY	Craighead & Craighead 1969
276	19.15	0.670	NY, NJ, CT	Bosakowski & Smith 1992
209	2.94	0.687	MB	Bird 1929
142	4.55	0.527	MI	Craighead & Craighead 1969
119	9.10	0.703	OH	Springer & Kirkley 1978
Non-breeding season				
1845	2.94	0.669	MI	Craighead & Craighead 1969
1654	3.43	0.649	MT	This study
756	3.91	0.622	MT	Seidensticker 1968
584	2.09	0.724	CA	Rudolph 1978
210	4.72	0.631	IN	Kirkpatrick & Conway 1947
161	3.84	0.558	NE	Rickart 1972
122	3.56	0.408	YT	Weir & Hanson 1989
Breeding and non-breeding season				
2571	4.89	0.629	WI	Errington 1932
2152	6.36	0.605	CO	Marti 1974
809	5.27	0.602	WA	Knight & Jackman 1984
568	3.89	0.840	CA	Barrows 1989
273	6.98	0.604	WI	Orians & Kuhlman 1956
178	5.87	0.720	OK	Tyler & Jensen 1981

large number of bird, as well as mammal, species included in the diet, or the relatively small sample size ($N = 276$).

Food-niche breadth calculated from Ohio (Springer and Kirkley 1978) was also broad (9.10) compared to other studies (Table 3). In this study, six mammal species constituted 69.7% of the owl's diet with *Microtus* representing 26.1%. Six mammal and 12 bird species represented the remainder of the diet. The narrowest FNBs came from California (2.09), Oregon (2.12), Wyoming (2.85) and Manitoba (2.94), respectively (Table 3). In all these cases, small mammals dominated the diet (Bird 1929, Maser and Brodie 1966, Craighead and Craighead 1969, Rudolph 1978).

Evenness values overall ranged from 0.408–0.840 ($\bar{x} = 0.620$, SD ± 0.101). Evenness values for the breeding (range = 0.420–0.703, $\bar{x} = 0.596$, SD ± 0.105, $N = 9$) and non-breeding season (range = 0.408–0.724, $\bar{x} = 0.609$, SD ± 0.102, $N = 7$) were also similar (Table 3). Evenness was not significantly different (Mann-Whitney $U = 30$, $P > 0.05$) between seasons.

A weak positive correlation existed between the number of mammalian species in the diet and food-niche breadth values ($r_s = 0.299$, $P < 0.01$). A weak negative relationship occurred between the number of prey items and food-niche breadth values ($r_s = -0.207$, $P > 0.01$), suggesting that sample sizes were not influencing the results.

Mammal prey biomass ranged from 2 g, (masked shrew [*Sorex cinereus*]) to 6300 g, (striped skunk [*Mephitis mephitis*]) (Whitaker 1992). The majority of prey ranged from 2–1800 g and included shrews, voles, mice, rats, pocket gophers, squirrels, and rabbits. The dominant prey from each study, *Microtus*, *Peromyscus*, *Perognathus*, *Sigmodon*, and *Lepus* ranged in body mass from 16–85 g, 10–43 g, 16–47 g, 80–120 g, and 1800–3600 g, respectively (Whitaker 1992). Other medium-sized mammals, including yellow-bellied marmot (*Marmota flaviventris*) and white-tailed jackrabbit (*Le-*

pus townsendii) rarely occurred in the diet and ranged from 2200–4500 g.

Birds were not a major part of the owl's diet, but a wide variety of species were eaten. Waterfowl, shorebirds, pheasants and allies, and passerines represented the majority of bird prey. Several owl species were also reported as prey in nine studies: Northern Saw-whet Owl (*Aegolius acadicus*) (Bosakowski and Smith 1992), Long-eared Owl (*Asio otus*) (Marti 1976, Holt this study), Barn Owl (*Tyto alba*) (Knight and Jackman 1984), and Eastern Screech-Owl (*Otus asio*) (Errington 1932, Orians and Kuhlman 1956, Craighead and Craighead 1969, Bosakowski and Smith 1992). Body masses of avian prey ranged from: 318–1100 g, waterfowl; 74–415 g, shorebirds; 178–1317 g, pheasants and allies; 88–580 g, owls; and 29–458 g, passerines (Dunning 1984). Passerines constituted most of the avian prey.

DISCUSSION

Great Horned Owls are generally considered to be opportunistic feeders, preying on a broader range of species than any other North American owl (Craighead and Craighead 1969, Voous 1988, Marti and Kochert 1996, Houston et al. 1998). Bosakowski and Smith (1992) reported such unusual species as a raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), and a Red-shouldered Hawk (*Buteo lineatus*); Marti (1974) reported a yellow-bellied marmot and black-tailed prairie dog (*Cynomys ludovicianus*); Errington (1932) reported a striped skunk; and Rudolph (1978) reported a Brazilian free-tailed bat (*Tadarida brasiliensis*). Llinas-Gutierrez et al. (1991) reported a wide variety of arachnids, insects, and reptiles in the owl diet, and Rohner and Doyle (1992) reported a Great Horned Owl feeding on an adult Northern Goshawk (*Accipiter gentilis*).

The moderate trophic niche (high number of prey species unequally distributed [see Methods section]) of the Great Horned Owl reported herein somewhat contrasts with previous studies (see text). Excluding predominately insectivorous owl species, the Great Horned Owl's moderate food-niche breadth (opportunistic feeding) aligns it with species such as the Burrowing Owl (*Speotyto cunicularia*) (Haug et al. 1993), Spotted Owl (*Strix occidentalis*) (Gutierrez et al. 1995), and Eastern Screech-Owl (Gehlbach 1995), for example. Species apparently more opportunistic than Great Horned Owls include the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) (Proudfoot 1997) and Northern Pygmy-Owl (*Glaucidium gnoma*) (Holt and Leroux 1996, Holt and Petersen 2000). More specialized species include the Snowy Owl (*Nyctea scandiaca*) (Watson 1957, Parmelee 1992), Short-eared Owl (*Asio flammeaus*) (Holt 1993, Holt and Leasure 1993), Northern Saw-whet Owl (Holt et al. 1991, Cannings 1993), and Barn Owl (Marti 1989, 1992).

Other *Bubo* species have a trophic niche similar to the Great Horned Owl. Herrera and Hiraldo (1976) reported FNB values ranging from 2.40–6.68 ($\bar{x}$ = 4.13, SD ± 0.01) for the Eurasian Eagle-Owl (*Bubo bubo*) in Europe. Jaksic and Marti (1984) found that Great Horned Owls and Eurasian Eagle-Owls followed a similar trophic pattern in North American and European shrubland. Donázar et al. (1989), however, reported limited dietary convergence between these two species. They attributed discrepancies in trophic diversity to the differences between similar North American and European biomes, variations in the composition and abundance of prey types, and differences in the body masses of Great Horned Owls and Eurasian Eagle-Owls.

The moderate trophic niche of Great Horned Owls could be the result of several factors, including prey species size, diversity, density, availability, and distribution. Marti (1974) suggested that although owls can capture a broad range of prey sizes, an optimum size exists in terms of how efficiently a particular individual prey item can be found and caught. He argued that very small prey is only efficient for Great Horned Owls if it can be caught quickly and easily. Marti felt that prey density, ease of killing, overlap of time of activity between predator and prey, and learning by individual owls all determine what proportions of the diet a particular prey species will comprise.

The Great Horned Owl's moderate food-niche breadth may also reflect the habitat or time of day in which they forage. Open areas the Great Horned Owl inhabits are frequented by mice, voles, lagomorphs, and gophers, which may emerge during the owl's optimal feeding periods of evening, night, and early morning (Maser et al. 1970). The community structure of predators within a particular habitat may also affect food-niche breadth. Marti et al. (1993) found that although predators in an area may utilize prey resources in different fashions, patterns of resource use do emerge, particularly in terms of predator size.

The diet of Great Horned Owls may vary depending upon the particular region the owls inhabit (Marti et al. 1993). Hayward et al. (1993) found that coastal Great Horned Owls in Washington fed exclusively on birds during the summer months. Bosakowski et al. (1989) reported owls living in the deciduous forests of New Jersey, New York, and Connecticut preyed more heavily upon birds than those living in open coniferous forests of the western United States. Desert owls fed on a variety of arachnids, insects, and reptiles because of their availability and abundance in that biome (Jaksic and Marti 1984, Barrows 1989, Llinas-Gutierrez et al. 1991).

Jaksic and Marti (1984) found that the diversity of Great Horned Owl prey at the class level was very low in the temperate regions and very high in the desert regions of North America. They believed this difference reflected the greater representation of mammals in the diet of temperate owls, thus resulting in a moderate trophic niche.

Great Horned Owls may respond opportunistically to the local profile of prey sizes and densities (Jaksic and Delibes 1987, Jaksic 1988). Llina-Gutierrez et al. (1991) suggested that lagomorphs and rodents were the dominant prey species in their study compared with other desert studies in the region because of their high abundance. Rusch et al. (1972) reported that the diet of Great Horned Owls was strongly affected by changes in the numbers of snowshoe hare (*Lepus americanus*). They found that in years with high snowshoe hare populations, owls exhibited higher predation rates on snowshoe hare and lower predation rates on mice and voles.

The data herein support the general conclusion that Great Horned Owls prey on a wide range of species. However, the data also show convincingly that Great Horned Owls feed primarily on only three to four species of voles and mice under most conditions, indicating a moderate food-niche breadth.

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SOCIAL ORGANIZATION OF A TRIO OF BEARDED VULTURES (*GYPAETUS BARBATUS*): SEXUAL AND PARENTAL ROLES

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KEY WORDS: *Bearded vulture;* Gypaetus barbatus; *cooperative polyandry; parental roles; homosexual matings; copulation behavior; Spain.*

In birds, cooperative polyandry (Oring 1986) is an unusual mating strategy. In raptors it only happens extensively in the Galápagos Hawk (*Buteo galapagoensis*) (Faaborg and Bednarz 1990), but polyandry has been described as occasionally occurring in some other species, that are usually considered monogamous (e.g., Tella 1993, Arroyo 1996).

The Bearded Vulture (*Gypaetus barbatus*) is a large, territorial vulture which nests on rocky cliffs in certain mountain areas of the southern Palearctic and of the Afrotropical regions (Hiraldo et al. 1979), and that feeds mainly on bones. The species is generally considered monogamous, but in the Pyrenees, polyandrous trios are relatively common (Heredia and Donázar 1990). The Pyrenees (Spanish and French sides) hold a small isolated population of Bearded Vultures which constitutes the bulk of the breeding population in the western Palearctic. In this population, the percentage of territories occupied by trios has increased gradually since 1979, when the first case was reported; 11.5% of 56 territories were recorded in 1988 (Heredia and Donázar 1990); and 15.2% of 92 were observed in 2000 (Heredia and Margalida 2001, M. Razin pers. comm.). These trios generally remain stable from one year to the next, but occasionally they may break up (pers. observ.). Trios tend to be observed in traditional breeding areas with the highest food availability, but their productivity is similar to that of monogamous pairs (Heredia and Donázar 1990). The factor explaining the existence of trios remains obscure, although it seems probable that the formation of such groups might be favored by a reduced availability of suitable sites for reproduction (Heredia and Donázar 1990).

Observing the Bearded Vulture is a difficult task, and this, coupled with its low reproductive success (Heredia and Margalida 2001), accounts for the little information available on the structure in such formations. In addition, trios were not known until recently. The first observations carried out by Heredia and Donázar (1990) indicated that the two male members of a trio copulate with the female and that both males provide food for chicks. However, no detailed data are available to quantify the behavior and parental contribution of each individual in these groups.

In this paper, the copulatory behavior and sexual relationships in a Pyrenean Bearded Vulture trio are described in detail for the first time, and the individual investment of the three birds in parental activities are examined.

STUDY AREA AND METHODS

We conducted the present study in the Catalonian Pre-Pyrenees (northeastern Spain), between 1991 and 1992. This is an area with isolated calcareous massifs (maximum altitude of 2070 masl) and Mediterranean vegetation.

The trio studied was formed in 1986 after an adult bird joined the territory already occupied by a reproductive pair. No successful breeding occurred between 1986–89, after which this group first bred as a trio in 1990. The study site was visited in bouts of two consecutive days at 5-d intervals resulting in a total of 699 hr of observation distributed as follows: pre-laying period (October–December 1991) 212 hr; incubation (December 1991–February 1992) 101 hr; and nestling period (April–July 1991 and February–May 1992) with 253 and 133 hr, respectively. We made observations with spotting scopes from vantage points at a distance of about 300 m from the nests.

Birds were sexed using size criteria and based on differences noted in their parental activities. Females are slightly larger than males (Hiraldo et al. 1979) and tend to be more intensely colored (Negro et al. 1999). In this respect, the male that appeared to be subordinate (male B) was smaller and showed a paler ventral coloring compared to the other individuals (the female and male A). Males are more active than females in supplying material to the nest and in territorial defense behavior (Margalida and Bertran 2000a, Margalida and Bertran 2000b). The identification of the birds was based on comparison of the molt patterns and the individual markings and patterns on pectoral bands and crowns. The long molting

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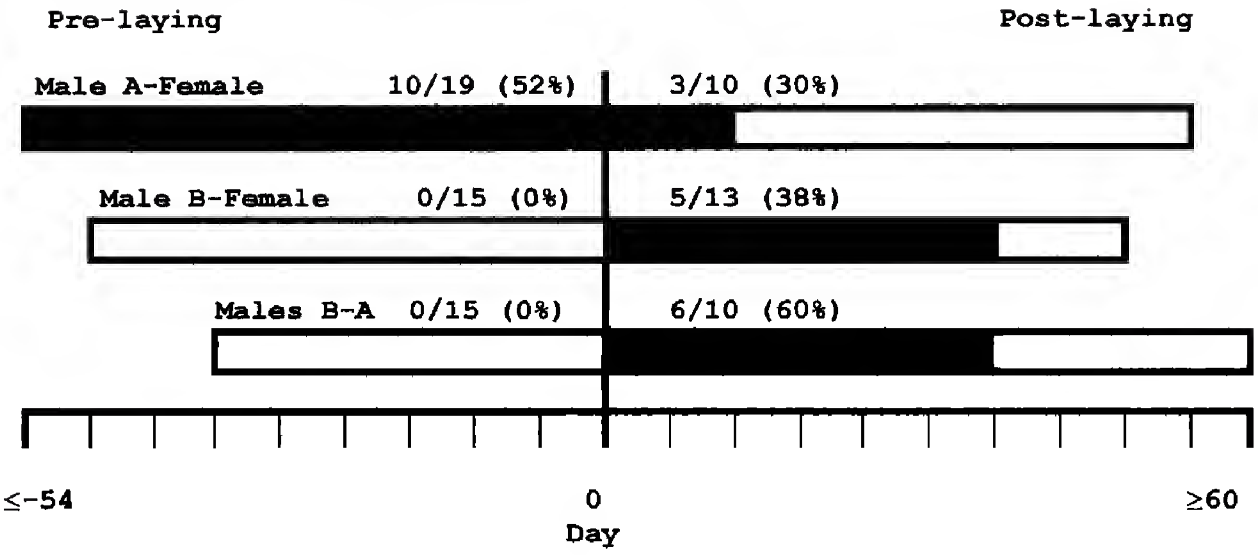

Figure 1. Temporal distribution of individual copulation behavior and success in a trio of Bearded Vultures in relation to the day on which incubation began (day 0). Shading indicates the time period during which behaviors were observed with probable contact of the cloaca; the proportions and percentage (in parentheses) of successful copulations are indicated.

process facilitated identification of the birds during much of the study period.

Bearded Vultures usually copulate on an exposed area of the cliff where they are nesting (Bertran and Margalida 1999). During the sexual activity period, all copulation attempts and related behavior were recorded. We noted the individuals involved in each copulation attempt and whether this was successful or not. A copulation was recorded as being successful behaviorally if cloacal contact was observed. We noted whether the female accepted or refused a copulation attempt. The relative frequency of copulations was estimated daily as the number of attempts hr^{-1}. The temporal distribution of copulations was examined in relation to the day on which incubation began (day 0). Laying was estimated with a maximum error of 5 d. Clutch size in this species is habitually two eggs, which are laid at intervals of 3–7 d, and incubation starts as soon as the first egg is laid (Hiraldo et al. 1979, Brown 1990, pers. observ.). We quantified the individual contribution to the following parental tasks: nest building, territorial defense, incubation, brooding, and feeding of the chick. We recorded prey deliveries, chases against conspecifics or birds from other species (principally Griffon Vultures [*Gyps fulvus*] and Common Ravens [*Corvus corax*], see Margalida and Bertran 2000a), and deliveries of nest material. Data were analyzed with nonparametric tests because data were not normally distributed (Sokal and Rohlf 1981). Values are presented as means ±SD.

RESULTS

The trio showed an extended copulation period (114 d). Similar to monogamous pairs (Bertran and Margalida 1999), the first copulation attempts were noted in November and continued until the early stages of chick rearing in March. We observed a total of 123 copulation attempts (including both successful and aborted ones). Of these, the female copulated with one of the males in 74% of cases, whereas in the remaining 26%, the two males copulated with one another (homosexual copulations).

During the pre-laying period, male A's copulation attempts with the female were more frequent than those of male B (male A: 0.33 ± 0.26, $N = 40$ copulation attempts h^{-1} vs. male B: 0.18 ± 0.21 copulation attempts h^{-1}, $N = 21$; Mann-Whitney U-test, $P = 0.047$). Most copulation attempts by male A (90%, $N = 40$) took place in the presence of male B, while male A witnessed male B's copulation attempts in 48% of the cases ($N = 21$; Fisher exact test, $P = 0.003$). During 25% of 16 cases in which male A tried to copulate with the female while sharing the same perch with male B, the latter interfered aggressively in the copulation attempt; although on only one occasion did he succeed in interfering with the attempt. In contrast, male A did not demonstrate any aggressiveness when he witnessed copulation attempts by male B The response of the female to the sexual advances of the two males differed substantially. Male A obtained successful copulations from the early attempts (54 d before laying) and these continued until 12 d after egg-laying took place. Successful copulations by this male made up 52.6% and 30% during pre-laying and after egg-laying periods, respectively (Fig. 1). In contrast, the female did not accept most copulations initiated by male B during the pre-laying stage: the male was rejected in 15 of 21 copulation attempts. However, successful copulations by male B were observed around the onset of incubation, and these continued for 24 d longer than those of male A. Copulations between male B and the female were performed when male A was at the nest.

Both males displayed bisexual behavior, although the proportion of homosexual mounts attempted by male B was significantly greater (male B: 45.4% of 66 copulation attempts vs. male A: 3.5% of 57 copulation attempts; $\chi^2 = 25.82$, df = 1, $P < 0.001$). None of the observed attempts of homosexual mounts were forced or refused and 97% of these occurred in the presence of the female. On four occasions, male A was mounted immediately af-

Table 1. Frequency and percentage of territorial defense attacks by individual group members observed during pre-laying and post-laying periods.

INDIVIDUALS	PRE-LAYING (N = 49)	POST-LAYING (N = 131)
Male A	32 (63.3%)	43 (32.8%)*
Male B	3 (6.1%)	61 (46.6%)*
Female	14 (28.6%)	27 (20%)

* Significantly different ($P < 0.05$) in relation to preceding period based on Chi-square test.

ter male B tried to interrupt the former's mating attempt with the female. We observed only apparent cloacal contact (60% of cases, $N = 10$) when male B took the initiative for mating. Male B's behaviorally successful copulations obtained from male A and from the female occurred over the same chronological period (Fig. 1).

Significant differences were found in the material supplied to the nest in relation to the number of individual visits: male A and the female were mostly responsible for this task, delivering material during 67.6% and 58.5% of their 71 and 51 visits, respectively, as Male B only delivered nesting material during 21.4% of 17 visits (χ^2 = 14.09, df = 2, $P < 0.001$).

We registered a total of 180 instances of territorial defense that took place between October 1991 and April 1992. The majority of the attacks (66.1%) were directed at Griffon Vultures (*Gyps fulvus*) and at Common Ravens (*Corvus corax*) (24.4%). The remainder (9.5%) were directed to other raptors and corvids. By periods, we detected significant differences related to contrasting territorial behavior shown by both males. In male A a higher than expected frequency of attacks was observed during the pre-laying period, contrary to that seen during post-laying. In contrast, male B increased his territorial behavior after laying took place ($P < 0.05$, for both cases; Table 1).

The daily investment of the three adults in relation to incubation of the clutch did not differ significantly (male A. 38.5 ± 22.7%; male B: 34.4 ± 22.3%; female: 27.1 ± 20.6%, Kruskal-Wallis $H = 1.85$, df = 2, $P = 0.397$). However, the amount of time invested by male B at the nest during brooding was significantly less, both in 1991 (male A: 37.08 ± 18.14%; male B: 13.23 ± 14.36%; female 49.69 ± 20.68%; Kruskal-Wallis $H = 35.919$, df = 2, $P < 0.001$) and in 1992 (male A: 46.55 ± 14.25%; male B 19.73 ± 12.38%; female: 33.72 ± 14.96%; Kruskal-Wallis $H = 25.238$, df = 2, $P < 0.001$). The distribution of prey deliveries to the nest by the three individuals did not differ significantly from a theoretical distribution in which all individuals delivered the same number of items ($\chi^2 = 1.30$, df = 2, $P > 0.05$; Table 2). However, significant differences were obtained when comparing the frequency of feedings with that expected from the individual contributions ($\chi^2 = 14.97$, df = 2, $P < 0.001$; Table 2) with male B feeding the chick less than the other two individuals ($\chi^2 = 14.12$, df = 2, $P < 0.001$).

DISCUSSION

This first detailed record of behavior of a reproductive trio of Bearded Vultures suggests a social structure consisting of an alpha pair and a subordinate male. Levels of aggressiveness were not high between the two males in the trio. However, some conflicts associated with sexual activity were observed, and these were always initiated by the presumed subordinate male. Conflicts between the male birds were only recorded during heterosexual copulation attempts, and these were always initiated by the subordinate male. A remarkable aspect of our results is the tolerance shown by the alpha male, and the fact that he accepted a number of mountings by the subordinate male. A similar behavior has been noted in two other Pyrenean groups (Margalida et al. 1997, unpubl. data) In other cooperative breeders, homosexual behavior is seen as a means of appeasement that would increase cohesion within the group (Heg and van Treuren 1998).

Cooperative polyandry in the Bearded Vulture may not provide reproductive compensations in the short term, but may in the long term when overall survival is considered (Heredia and Donázar 1990). In a long-living species such as the Bearded Vulture, being in good condition would permit a greater number of breeding attempts. This species has a long breeding cycle, during which the adult birds are committed to providing food and to chick-rearing, while they also have to obtain food for themselves (Margalida and Bertran 2000a). Therefore, some direct benefit for breeding pairs should be

Table 2. Frequency and percentage of contributions of prey items delivered to the nest and feedings to the chick by individual group members.

INDIVIDUALS	PREY DELIVERIES (N = 60)	EXPECTED	FEEDINGS (N = 108)	EXPECTED
Male A	24 (40.0%)	20	49 (45.4%)	36
Male B	17 (28.3%)	20	13 (12.0%)	36
Female	19 (31.7%)	20	46 (42.6%)	36

expected from the collaboration of helpers, because searching for food, which is spatially and temporarily unpredictable, remains a difficult task. By remaining in a territory, subordinate males might have a possibility of acquiring an alpha breeding position within the group. By using a helper strategy, B males would be in a position to inherit the territory and the female. This would be particularly important for birds in pre-adult plumage at breeding age, if suitable breeding territories are not available (Heredia and Donázar 1990). Young birds might be capable of evaluating the individual quality of the different territories in the course of their dispersive movements (Bertran and Margalida 1996). Short-term direct benefits of the sexual relationship with the male birds seem more obvious for the females. This hypothesis is based on the fact that during the pre-laying stage, the female only permitted successful copulations by male A, whose total contribution to the breeding effort was larger. Yet, at the time of egg-laying, the female apparently accepted the secondary male furtively, and this coincided chronologically with the latter's increased help contribution (principally territorial defense and provisioning of prey to the nest). In the Bearded Vulture, both sexes share parental duties, but females tend to participate more actively in the direct care of the offspring (Margalida and Bertran 2000a). Thus, polyandrous females may benefit from the males' investment: both males provide parental care and, consequently, the female has more time to fly around (see Birkhead 1998).

Female Bearded Vultures may, because of their larger size, actively refuse males in unwanted copulation attempts (pers. observ.). There may be a relationship between size, coloration, and dominance in this species. For instance, it has been suggested that coloring of the ventral area might act as a status signal (Negro et al. 1999). The coloring is acquired deliberately (Negro and Margalida 2000) and its intensity is directly related to the birds' age and probably to their status as well. Females, which are slightly larger than males and may be behaviorally dominant, show more intense coloring (Negro et al. 1999). In this trio, coloring intensity increased progressively from the secondary male (markedly paler) to the female. A probable relationship between social rank and coloring intensity was also observed among other vulture groups as well (Negro et al. 1999).

Our results suggest a defined hierarchical social rank within groups. In that context, females, due to their larger size and behavioral characteristics, would be able to exert social control within such groups. This would open new and interesting perspectives in the study of these social groups, which should be examined in larger samples.

Resumen.—El Quebrantahuesos (*Gypaetus barbatus*) ocasionalmente forma grupos cooperativos (tríos). Durante 1991 y 1992 examinamos la conducta reproductora de un trío Pirenaico (NE España). Nuestras observaciones indican que el grupo estuvo formado por una pareja alfa y un macho secundario. El trio exhibió un periodo inusualmente extenso de cópulas donde la hembra copuló preferentemente con el macho alfa, pero también aceptó aparentemente de forma furtiva al macho secundario, en concreto tras la puesta. Fueron observadas algunas cópulas macho-macho comportamentalmente exitosas, si bien el significado de éstas es desconocido. Nuestros resultados sugieren que la hembra pudo beneficiarse a través de las cópulas de la inversión parental suministrada por ambos machos. En este contexto, les hembras, debido a sus características físicas y comportamentales podrían ejercer un control social dentro de estos grupos.

[Traducción de los autores]

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GENETIC EVIDENCE OF ALLOPARENTAL CARE OF A FEMALE LESSER KESTREL IN AN ALIEN NEST

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KEY WORDS: *Lesser Kestrel;* Falco naumanni; *alloparental care; DNA multilocus fingerprinting.*

Care of nondescendant young (alloparental care) is relatively common in many bird species (Reidman 1982, Skutch 1987). In most cases, alloparental behavior occurs either when nonbreeding birds care for offspring that are not their own or when reproductive adults adopt or feed young that are not their own. Provisioning of food by birds other than the parents is expected more frequently in communal species because of the increased chance of exposure of nonbreeding individuals to hungry nestlings (Jamieson 1989) and also because of the chance of amalgamation of nestlings among contiguous nests (Cooper and Miller 1992). In any case, alloparental care poses a nonresolved question on its possible adaptive significance (Jamieson 1989, 1991, White et al. 1991, Ligon and Stacey 1991, Emlen et al. 1991).

The Lesser Kestrel (*Falco naumanni*) is a colonial falconiform in which adoption has been reported (Donázar et al. 1991). This behavior may occur at high frequencies in certain populations when nest-site densities are manipulated, and when nestlings are able to move to alien nests, where they may benefit from alloparental feeding (but see Tella et al. 1997). Adoptions like this could be actively sought by nestlings in species in which adults show no apparent ability to discriminate between their own and alien young (Tella et al. 1997). In this colonial species there has also been one case reported in which two females mated polygynously with the same male and laid eggs in one nest, though only one female attended the mixed brood and provided alloparental care to the unrelated young (Tella et al. 1996). In this paper, how-

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Table 1. Independent band-sharing coefficients of two neighboring families of Lesser Kestrels. F1 was the adult female breeding at nest 1; M1 was the adult male breeding at nest 1; F2 was the first-year female of nest 2 that also provisioned at nest 1; O11–O14 were offspring from nest 1; O21–O22 were offspring from nest 2. Mean number of bands scored = 17.8 ± 1.7 (SD; N = 9).

	F1	M1	O11	O12	O13	O14	F2	O21	O22
F1	—	0.2	0.4	0.4	0.5	0.4	0.2	0.1	0.1
M1		—	0.7	0.6	0.7	0.6	0.2	0.1	0.2
F2			0.2	0.2	0.2	0.2	—	0.4	0.5

ever, we describe and analyze through DNA multilocus fingerprinting, a different kind of alloparental care in which a breeding female provisioned food in two different nests: her own and an alien nest in the colony.

Study Area and Methods

Lesser Kestrels form breeding colonies in abandoned field houses and nests are usually under tiled roofs or inside holes in the walls. The colony under study consisted of 27 breeding pairs and was located in the tiled roofs of an abandoned farm of La Mancha (Ciudad Real, Spain). Aparicio (1997) provides more details about the study area.

Nest sites were located before the onset of laying by watching mated pairs. Each potential nest was monitored every 4 d from 20 April to find the first eggs and then every 2 d until the clutch was finished. Eggs were labeled with a water-proof, felt-tip pen. Adult kestrels were caught and marked with a unique combination of colored and metal rings. At hatching, each chick was marked with a felt-tip pen or with nail varnish on the nape, back or wings, and they were also banded with metallic rings at the age of 6–7 d. Parental feeding rate was routinely recorded either by direct observation or with a video camera for 30 min at each nest every 5 d. Two nests were involved in this study: nest 1 (N1) that contained the chicks of adult pair 1 (P1) and nest 2 (N2), 3.5 m apart that was attended by a 1-yr-old pair (P2), a male in first-year plumage and a female (F2) ringed the previous season as fledging. The female (F1) from N1 had bred for several years in the colony, whereas the male (M1) was in full-adult plumage and was unringed. No other occupied nest was located between the mentioned nests, although two more pairs nested in that particular roof of the farm. The 1-yr-old female (F2) also provisioned food to offspring of N1. Intraspecific brood parasitism has been recorded in the Lesser Kestrel (Negro et al. 1996). To detect possible cases of brood parasitism which could explain the behavior of F2 provisioning N1 offspring, both adults from N1 and the female from N2 were trapped with a noose carpet trap and blood samples were collected; we could not capture the first-year male from N2. We extracted DNA from blood samples of the three adults and their respective attended nestlings and analyzed for parentage using Jeffreys' derivate pSPT 18.15, following a standard protocol for DNA-multilocus fingerprinting (Wetton et al. 1987). All results given are mean ±SD.

Results and Discussion

During the recording of parental feeding rates in 1997, alloparental care was detected three times during 30 min of observation at N1, located in an area of the roof with only two occupied nests. However, no instance of feeding by F2 at her own nest (N2) was detected during this time When the observations occurred, the offspring of the receiver nest (N1) consisted of four chicks, 20-d-old, attended by P1 and F2 of N2. N2 contained two 17-d-old chicks, fed by both parents. N1 later produced four fledglings with a mean mass of 145 g and N2 two fledglings with a mean mass of 129.5 g (mean fledgling mass in the colony = 133.4 ± 11.6, N = 21 nests measured at 30–35 d). Feeding rates per hr and per nestling were similar at N1 (5 ± 2.6 deliveries by the male and 3.7 ± 2.1 by the female) and at N2 (4.9 ± 5.9 by the male and 2.4 ± 4 5 by the female), (males: t = 0.04, df = 12, P = 0.97; females: t = 0.7, df = 12, P = 0.5; males and females: t = 0.65, df = 12, P = 0.52).

Adults attending N1 were the genetic parents of the complete brood, although band sharing was not the same for the father (0.68 ± 0.02) and the mother (0.46 ± 0.04, paired t = 13.5, df = 3, $P < 0.001$; Table 1). Also, F2 attending N2 was the genetic mother of her attended offspring. The mean proportion of band sharing of presumptive first-degree relatives was 0.55 ± 0.12 (N = 10) and the mean for the presumed unrelated individuals was 0.21 ± 0.04 (N = 11); this latter value was consistent with the background band-sharing coefficient for a distinct population of the same species using a different probe (Negro et al. 1996). Young from N2 were unrelated to the adults of N1 (band-sharing coefficients of 0.13–0.27 and 8–9 novel bands were absent in F1 and M1) and F2 had no apparent genetic relationship with P1 or the young of N1 (Table 1). Based on total number of bands and number of bands shared, and assuming a band sharing of 50% for first-degree relatives, we calculated the binomial probability for two individuals to be first-degree relatives. We estimated that the probability of F2 being a first-degree relative with F1 was 0.018 and the probability that F2 was a first-degree relative with M1 was 0.005. The combined probability of F2 being a first-degree relative with either F1 or M1 was 0.02. These estimates do not discard a second-degree relationship between F2 and either F1 or M1 although, in such a case, kin recognition among breeding individuals should not be expected in a species in which parents do not seem to recognize their own offspring (Tella et al. 1997, J. Aparicio unpubl. data). For this reason we discard that kin relationships were responsible for the behavior described here.

The analysis of DNA multilocus fingerprinting also precluded the possibility of intraspecific brood parasitism and potential switching of the chicks in the nests. This was also supported by field observations as the female from N1 started laying eggs two days before the female at N2. Further, the laying intervals were uniform and clutch size in both nests was five eggs, a large value in a population in which clutches of six are very rare (0.9%). Also, nestlings were ringed at a very early age (6–7 d) and it was unlikely that they moved to the other nest before ringing because this behavior occurs, on average, at 25 d (Tella et al. 1997).

Other possible explanations for the alloparental care observed were mistaken identity, reciprocal altruism, or manipulation of the adults by the chicks (e.g., Birkhead and Nettleship 1984). Mistaken identity may be a source of nonadaptive provisioning to nonrelated broods. However, because of the distance of the two nests (3.5 m) and their different positions (N1 was by the edge of the roof whereas N2 was central, and there was a garret exit of 1 5 × 0.8 m and a chimney separating them), a location mistake seems unlikely even though we do not know the precise cues used by adult Lesser Kestrels to locate their nests. Also, we did not detect reciprocal altruism during the observations; however, this possibility could not be discarded altogether. Adults from N1 provisioning N2 chicks could have gone unnoticed during our observations.

We do not know how rare this behavior might be. In fact, during more than 10 yr of study of several breeding colonies (e.g., Aparicio and Cordero 2001, Aparicio and Bonal 2002), this behavior was detected only when systematic observations were made at a few nests for another purpose. In a species, in which adoption may be relatively frequent and adults do not recognize alien offspring as in the Lesser Kestrel (Tella et al. 1997, J. Aparicio unpubl. data), begging may be a strong stimulus promoting alloparental care, particularly if the cost of infrequent provisioning is negligible (Pierotti and Murphy 1987). Nestlings from N1 were larger than those of N2 and begged for food more frequently and more vigorously, displaying their beggings by putting their heads out of the nest whereas chicks from N2 did not when the alloparental behavior occurred. Nevertheless, the differences in mass, feeding rates, and incubation length obtained for N1 and N2 may be more attributable to individual differences of the parents (i.e., because of age) rather than to observed alloparental behavior. This may be particularly so in the exceptionally good year of 1997 in which prey were extraordinarily abundant, which diminishes the cost of foraging (J. Aparicio unpubl. data) Our results suggest that in the absence of kin selection, a more parsimonious mechanism for the alloparental care described here may be an irresistible response to food begging and gaping (Jamieson 1989). Thus, under certain circumstances, nestlings may manipulate alloparental care by begging, especially care from inexperienced females, even from their own nests.

RESUMEN.—El cernícalo primilla es una especie que nidifica en densas colonias en construcciones humanas. En esta especie es conocida la conducta aloparental cuando los pollos de cierta edad pueden moverse hasta otros nidos donde se camuflan entre los pollos del mismo y son alimentados por adultos no emparentados genéticamente con ellos. Aquí describimos una conducta diferente de cuidado aloparental, de una hembra de primer año alimentando pollos en dos nidos, uno propio y otro ajeno. Los análisis de DNA multilocus fingerprinting revelan que no existe parentesco genético entre dicha hembra y los pollos o los adultos del nido ajeno. Se revisan las distintas hipótesis que pueden explicar este caso de cuidado aloparental. Se sugire que bajo ciertas circunstancias, los pollos pueden manipular el cuidado aloparental incluso desde sus propios nidos.

[Traducción de los autores]

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NESTING OF LONG-EARED OWLS ALONG THE LOWER BIG LOST RIVER, IDAHO: A COMPARISON OF 1975–76 AND 1996–97

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KEY WORDS: *Long-eared Owl;* Asio otus; *nesting; riparian; Idaho.*

Long-eared Owls (*Asio otus*) are found throughout much of North America and Eurasia, typically inhabiting open forests or dense vegetation adjacent to open grasslands or shrublands (Marks et al. 1994). These owls generally nest in abandoned stick nests of other birds. Research from 1975–76 (Craig 1977, 1979, Craig and Trost 1979) provided information on Long-eared Owls that nested along a 25-km stretch of the Big Lost River on the Idaho National Engineering and Environmental Laboratory (INEEL) in southeastern Idaho (Fig. 1). These nesting Long-eared Owls used abandoned Black-billed Magpie (*Pica pica*) nests built in narrow-leaved cottonwood (*Populus angustifolia*) trees.

Diversion of water for irrigation, the INEEL flood control diversion dam, and recent droughts have dewatered the Big Lost River during much of the summer, contributing to the decline of narrow-leaved cottonwood trees growing on its banks. The INEEL diversion dam was constructed in 1958, and the dam and containment dikes were enlarged in 1984 to reduce the threat of floods to research facilities on the INEEL (Stone et al. 1993). Annual flow records from 1965–98 for the Big Lost River on the INEEL (at Lincoln Boulevard Bridge) vary greatly but demonstrate a general decline in stream flow and two multi-year periods of zero or nearly zero stream flow (Fig 2). The periods from 1977–80 and 1987–94 were partic-

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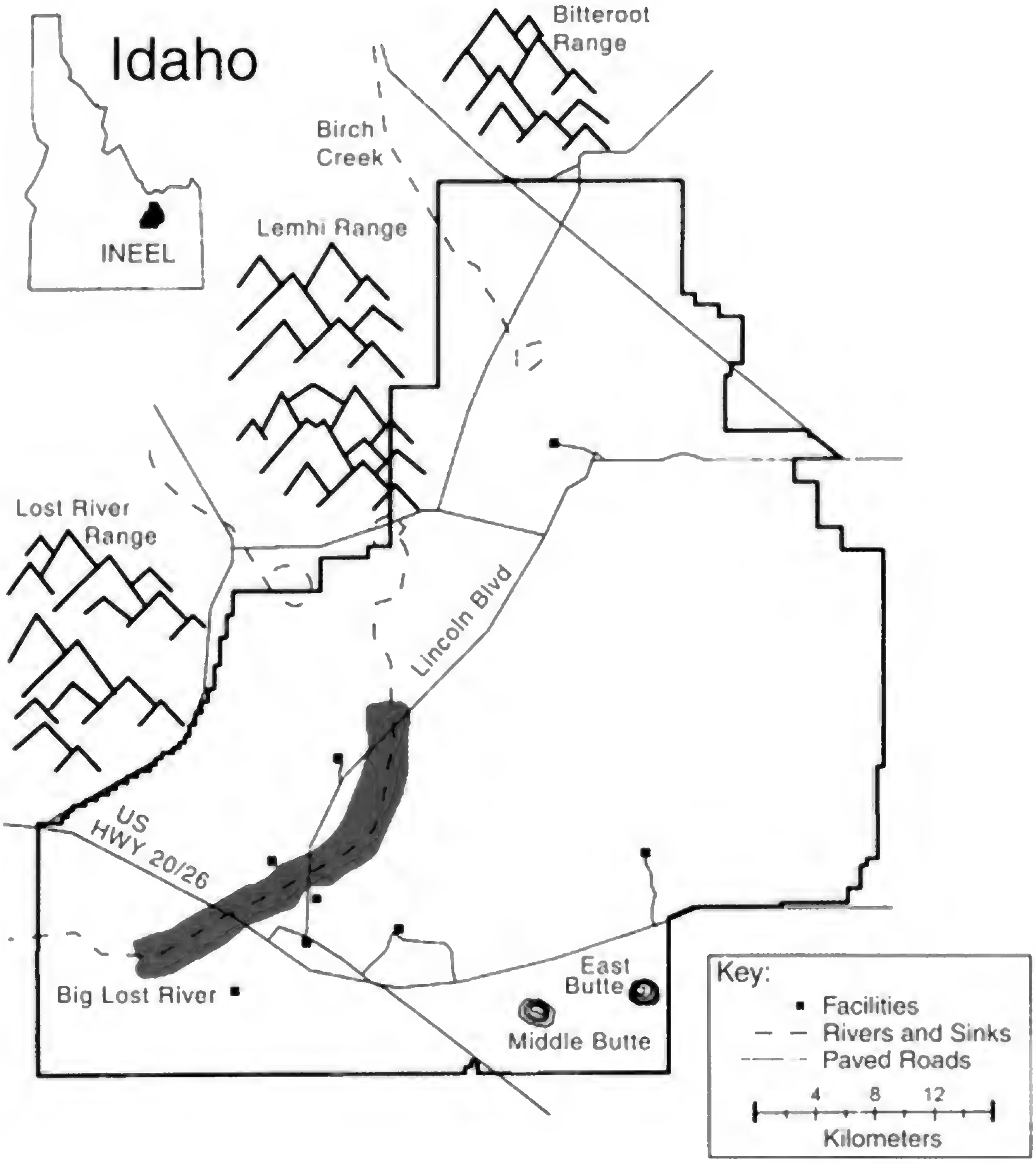

Figure 1. Study area along the Big Lost River (darkened; width not to scale) on the Idaho National Engineering and Environmental Laboratory (INEEL), was set up to duplicate area studied by Craig (1977).

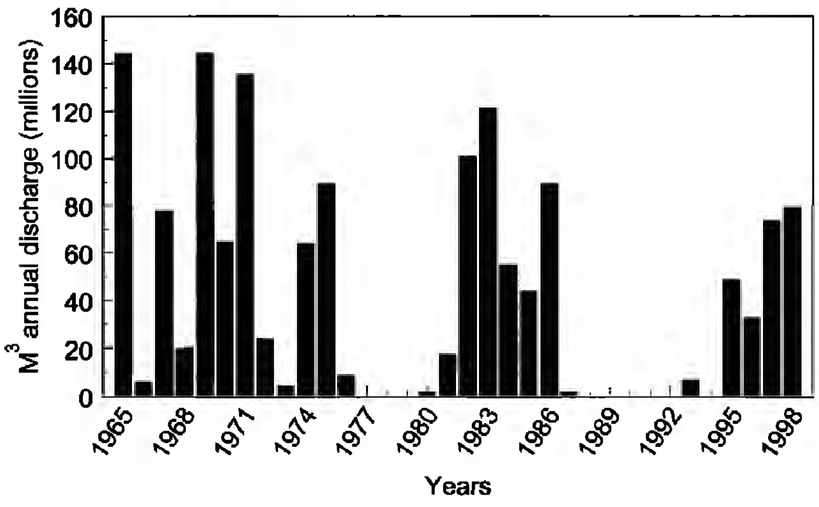

Figure 2. Stream flow on the study area as indicated by annual discharge (m^3) of the Big Lost River at Lincoln Boulevard Bridge, approximately in the middle of the study area.

ularly devastating for narrow-leaved cottonwood survival (Bennett 1990, U.S. Geological Survey, Idaho District unpubl. data). Aerial photographs from 1976 and 1991 indicate a reduction of live narrow-leaved cottonwoods from 124 to 23 trees (81.5%) within the lower two-thirds of Craig's (1977) study area (S. Majors unpubl. data).

Our objectives were to determine whether changes in numbers of nesting Long-eared Owls and potential nest sites (e.g., Black-billed Magpie or other concealed stick nests) have occurred along the lower Big Lost River on the INEEL, given the increasing decadence of narrow-leaved cottonwood trees.

STUDY AREA AND METHODS

The INEEL is a 2315 km^2 U.S. Department of Energy research and development facility located in the shrub-steppe habitat of southeastern Idaho. The study area was a 25-km stretch of the Big Lost River that extended from ca. 8 km south of Highway 20/26 on the southern end of the INEEL, north across Highway 20/26, to just downstream of where the Big Lost River crosses Lincoln Boulevard on the INEEL for the second time. We attempted to sample the same area studied by Craig (1977) (Fig. 1). The majority of this stretch of the Big Lost River was accessible by vehicle, though some less accessible sites required hiking. We followed Craig (1977) by checking stick nests on both sides of the river by climbing trees and looking directly into the nest bowl, or by viewing them from a site on the ground if the nest bowl was visible. Most trees were narrow-leaved cottonwood, but Utah juniper (*Juniperus osteosperma*) trees within 100 m of the Big Lost River channel were also searched. The area searched along the river in 1975–76 was at least as wide as we searched during this study and probably extended out further at locations where junipers were near the river and not occluded from view by the terrain (T. Craig pers. comm.). Utah junipers were lacking or sparse in most of the study area particularly north of Highway 20/26. Searches for Long-eared Owl nests were conducted 9–18 July 1996, relatively late in the fledging period, and 28 May–5 June 1997. Nesting attempts included occupied nests and evidence of recent nesting. Occupied nests contained eggs or young, or we found young nearby (i.e., branching stage); the adults were normally observed. Recent nesting attempts included those sites where we found a combination of feathers, fecal droppings and pellets, or evidence of abandoned or destroyed eggs or young, indicating nesting earlier within the same year.

Results and Discussion

Comparison of 1996–97 to 1975–76. In spite of the late survey in 1996, three Long-eared Owl nests were found containing young that varied in age from recently hatched to branching age (21 d, Marks et al. 1994). Two of the occupied nests were in dead narrow-leaved cottonwood trees in the cavity of Black-billed Magpie nests while the third was in a hawk nest in a live Utah juniper. Recent whitewash (feces), pellets, and feathers matching that observed at occupied Long-eared Owl nests were also discovered at seven Black-billed Magpie nests in partially live or dead, narrow-leaved cottonwoods as well as one old hawk nest in a live juniper. Long-eared Owl feathers at these recent nest attempts were primarily smaller feathers from the breast or abdominal region. With the addition of these eight nest attempts, we concluded that Long-eared Owls used at least 11 nests in 1996.

Eleven occupied nests were found in 1997 with some adults still incubating during the survey. In addition, one recent attempt was found that contained preyed-upon eggs of Long-eared Owls. Thus, a total of 12 nest attempts were located in 1997. Seven of these nest attempts were located in partially live or dead, narrow-leaved cottonwood trees, while five were in live Utah junipers.

In both 1996 and 1997, all Long-eared Owl nests within narrow-leaved cottonwood trees were in the nest chamber of abandoned Black-billed Magpie nests. Black-billed Magpie nests have the outside appearance of a large hollow ball of sticks or twigs. The stick or twig matrices on the sides and top (canopy) are sparser than the base and include an opening (sometimes two openings) for entrance to the nest bowl. All of the Long-eared Owls using magpie nests in this study used nests with the stick canopy intact. The Long-eared Owl nests in Utah junipers were in old nests of buteos (*Buteo* spp.), and the tree foliage provided substantial concealment around and over the nest. During this study, almost all of the narrow-leaved cottonwoods available and used as nest trees had only a few live branches, or were completely dead, while all junipers with nests were live with full foliage.

Craig (1979) counted three Long-eared Owl nesting attempts in 1975 and 16 nesting attempts in 1976 on the Big Lost River study area. All of the nesting Long-eared Owls found in that study used Black-billed Magpie nests, and all but one was inside the nest cavity (Craig 1979, Craig and Trost 1979). Furthermore, all Long-eared Owl nests in 1975–76 were in narrow-leaved cottonwoods, though Utah junipers near the river were also searched (T. Craig pers. comm.). In contrast, in 1996–97 we found 70.6% of Long-eared Owl nests in old magpie nests in cottonwoods, while the rest were in former hawk nests concealed in Utah juniper. Similarly, in Idaho's Snake River Birds of Prey area, ca. 70% of the Long-eared Owl nests were in former magpie nests (Marks 1986) and the rest in old American Crow (*Corvus brachyrhynchos*) nests. We found no evidence of nesting American Crows along the Big Lost River or elsewhere on the INEEL, but we did observe occupied and old nests of buteos in both Utah junipers and narrow-leaved cottonwoods (Hansen and Flake 1995).

Eighty-eight old Black-billed Magpie nests that appeared to be suitable for Long-eared Owls were located on the study area during 1975–76 (Craig 1977, Craig and Trost 1979), almost all of which were in cottonwood trees (T. Craig pers. comm.). Assuming all 88 sites were available during both years of that study, 3.4% were used by Long-eared Owls in 1975 and 18.2% in 1976. In 1997, we found 61 old Black-billed Magpie and hawk nests that appeared suitable for Long-eared Owl occupancy. We did not record suitable nests by hawk or magpie category, but we recollect that 10 or fewer of the nests suitable for Long-eared Owls were hawk nests in Utah junipers, while at least 51 were magpie nests, primarily in narrow-leaved cottonwoods.

In comparison, Long-eared Owls at the Snake River Birds of Prey Area used both platform type nests (American Crows) and Magpie nests in deciduous trees and large shrubs (Marks 1986). Long-eared Owls did not use the platform stick nests of hawks within the narrow-leaved cottonwoods in our study area, perhaps due to inadequate foliage for concealment (i.e., the cottonwoods were dead or only partially foliated), or possibly due to interference by other raptors. In any event, we did not count these as potential nests. Therefore, assuming all 61 suitable nests existed during both years of our study, 18.0% of available nests were used by Long-eared

Owls in 1996 and 19.7% in 1997. These rates are almost identical to the rate of 1976 but exceed the occupancy rate for 1975 (Craig 1977, 1979).

Ecological Implications. Densities of nesting Long-eared Owls can vary directly with small mammal prey abundance (Korpimäki and Norrdahl 1991, Korpimäki 1992). Thus, variation among years as observed by Craig (1979) from 1975–76 is not unusual and could be directly related to prey availability. Unfortunately, data on small mammal abundance in the study area was not collected during our study or in 1975–76. Differences and similarities among numbers of nesting Long-eared Owls from the mid-1970s (Craig and Trost 1979, Craig 1979) and this study could primarily reflect variation in prey availability; thus, nesting population comparisons between these two studies should be made with caution.

The ability of trees along the Big Lost River to support nesting Long-eared Owls has apparently not declined appreciably since the 1975–76 study of Craig (1977, 1979) and Craig and Trost (1979), despite the increased decadence and decrease in numbers of cottonwoods. However, in this study 33% of the Long-eared Owl nests were in old hawk nests in Utah juniper, while all the nests in 1975–76 were associated with Black-billed Magpie nests in narrow-leaved cottonwoods. Concurrent with the death and increased decadence of most cottonwoods has been a coincidental increase in the apparent numbers of Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks (*Buteo swainsoni*) nesting on the INEEL (Hansen and Flake 1995) compared to the mid 1970s (Craig 1979). Long-eared Owls may be increasing their use of old hawk nests in junipers due to increased availability of these nests and the reduction in available Black-billed Magpie nests in narrow-leaved cottonwoods. Black-billed Magpie populations have remained relatively stable in Idaho since 1966 (Sauer et al. 2000). We could not clearly decipher Utah junipers from dark lava flows, dark soils, and shrubs on 1976, 1978, and 1991 aerial photos. Thus, we cannot comment on possible changes in the availability of Utah junipers.

Regulation of stream flow in the Big Lost River was initiated as early as 1918 when the Mackay Dam and reservoir were completed (Big Lost River Irrigation District, Mackay, Idaho). Stream flow in the lower portion of the Big Lost River has been impacted by upstream irrigation, as well as by the INEEL diversion dam, during all but the highest runoff periods. Because of these restrictions on water flow into the lower Big Lost River, narrow-leaved cottonwoods along the river channel are either dead or retain a few live branches. Furthermore, little cottonwood regeneration exists, and no regeneration lives beyond the sapling stage. Intact Black-billed Magpie nests, and therefore potential nesting sites for Long-eared Owls, have been reduced in the study area (81 in 1975–76 vs. ca. 51 in 1996–97). Utah juniper trees and associated *Buteo* nests appear to be buffering the effects of narrow-leaved cottonwood losses on nesting Long-eared Owls. Unless adequate stream flows are restored, narrow-leaved cottonwoods will likely continue to decline in abundance and vigor, and the ability of this riparian area to support nesting Long-eared Owls (as well as other nesting raptors) will likely be reduced.

Dewatering and loss of cottonwoods has also occurred on considerable portions of the lower Big Lost River above our study area. Thus, the potential effects on Long-eared Owls, other raptors, and the riparian community in general are more extensive than our limited study area might suggest. Management for at least some water at all times within the lower Big Lost River, both above and within the INEEL, could restore narrow-leaved cottonwoods and reverse the damaging effects of past dewatering. We encourage periodic monitoring of the cottonwoods and nesting raptors in this important, but currently degraded, ecosystem.

RESUMEN.—Dos registros desde 1965 indican que la regulación del flujo de la corriente y la desviación para irrigación ha reducido progresivamente el flujo del agua en el canal mas bajo del Gran Río Perdido en el sureste de Idaho, esto ha causado la decadencia y la perdida de regeneración en algodones silvestres de hoja angosta (*Populus angustifolia*) a lo largo de su hábitat ripario. Estudiamos la anidación de búhos de orejas largas (*Asio otus*) en el bajo Gran Río Perdido en 1996–97 y comparamos los conteos con aquellos de 1975–76 en la misma área (Craig 1977, 1979, Craig and Trost 1979). Encontramos números similares de nidos a aquellos encontrados a mediados de los 70's, a pesar de la perdida, decadencia y carencia de regeneración del algodón silvestre. A mediados de los 70's, 100% de los nidos de los búhos orejilargos estaban en los nidos de urracas de pico negro (*Pica pica*) en los algodonales; sin embargo, en este estudio, 70.6% de los nidos estaban en nidos de Urraca en algodonales mientras que los nidos restantes ocurrieron en nidos de Buteo en juníperos de UTA (*Juniperus osteosperma*) cerca al canal del río. Nuestros conteos de nidos viejos de chamizos indican que este cambio puede estar relacionado al decline en la disponibilidad de nidos de urraca en los algodonales que aun permanecen y a un incremento en los nidos de gavilanes en los juníperos cerca al río. Nosotros recomendamos un monitoreo periódico de los algodonales de hoja angosta, de los búhos de orejas largas que están anidando, de otras rapaces y de las urracas de pico negro asociadas con este hábitat ripario degradado.

[Traducción de César Márquez]

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BEHAVIORAL AND PHYSICAL DEVELOPMENT OF A NESTLING CRESTED EAGLE (*MORPHNUS GUIANENSIS*)

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KEY WORDS: *Crested Eagle;* Morphnus guianensis; *nestling; behavior; development; nesting biology; tropical.*

Rates of physical and behavioral development in nestling birds are key aspects of avian life histories (Starck and Ricklefs 1998). Details of the growth and development of many falconiforms are lacking. One such poorly known species is the Crested Eagle (*Morphnus guianensis*). Although this is the second largest of widespread Neotropical forest eagles, virtually all that is known concerning the species' nesting biology and behavior is based on a single nest (Bierregaard 1984).

We studied nesting biology, behavior, and diet at two nests of Crested Eagles in Guatemala's Petén lowlands Most results are presented elsewhere (Whitacre et al. in press a, D. Whitacre unpubl. data). Here we describe the progression of behavioral and physical development in a single wild nestling, and present a growth curve and behavioral notes from a captive-reared nestling.

STUDY AREA AND METHODS

We studied two Crested Eagle nests. Nest No. 1 (1994) was 7 km south of Tikal National Park, and nest No. 2

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Table 1. Behavioral and physical development of a Crested Eagle nestling at Tikal, Guatemala.

NESTLING AGE (DAYS)	DEVELOPMENTAL FEATURE FIRST NOTED ON THIS DAY
0	Chick mostly immobile; holds head up for brief moments; ate only three bites during all-day watch.
7	Chick moves around more.
9	Chick attempts to shuffle on horizontal tarsi toward female.
16	Chick moves more easily across the nest, shuffling on its tarsi, falling at times; moves into shade provided by female and tree limbs; makes preening motions.
17	Makes preening motions several times; raises hind end to defecate, with most of mutes falling outside nest.
18	Chick attempts to stand, with the aid of its wings.
23	Stands briefly on nearly straightened legs rather than over horizontal tarsi; takes faltering steps, though still without legs fully extended; noticeably more active than during prior week, but still spends much time sprawled out, sleeping.
24	Wing-stretching behavior, repeatedly.
25	Chick responds to distant Keel-billed Toucan (*Ramphastos sulfuratus*) vocalizations by looking in that direction. When male arrives at nest, chick walks toward male, flapping wings, bites at prey, and drags prey around nest. Chick attempts, unsuccessfully, to eat in the female's absence; becomes motionless when several Brown Jays (*Cyanocorax morio*) approach the nest.
26	When male arrives with prey, chick vocalizes and attempts to seize prey; feather shafts emerging on chick's head and wings.
37	Chick stands firmly on straightened legs and flaps wings as in flight exercise.
38	Chick stands solidly several seconds at a time; stands up to defecate.
39	When a Black Vulture (*Coragyps atratus*) flies over the nest, both chick and adult female extend wings and vocalize.
40	Chick jumps as it flaps in place—increasingly common thereafter.
44	Feathers appearing on nestling's wings.
45	First time chick wet from rain, the female absent.
46	Chick is so large that the female cannot completely cover it.
51	Nestling stands for up to 2 min, but spends most of time lying in the nest; fed in small bites by the female; female still broods and shelters the chick from sun and rain.
52	Chick remains standing for 6 min; walks away from female, remains in the sun for several min.
53	Chick remains standing for 17 min. When female arrives at nest, chick spreads its wings and erects its feathers in apparent threat display. Chick first seen to mantle with wings spread over prey brought by male; moves nest material around with its beak.
54	Chick again manifests a defensive display, looking upward with wings spread and beak open, although we cannot see what elicits this response. Hereafter, chick often responds to vultures in this fashion. Chick stands for 38 min, is unsuccessful at feeding itself.
58	Chick extends its wings and calls loudly when a pair of White Hawks (*Leucopternis albicollis*) soars over.
59	Chick lowers head and spreads its wings when two helicopters pass overhead; in subsequent days, airplanes repeatedly elicit this response, sometimes accompanied by gaping of the beak and erected plumage. Chick stands for >2 hr; is wet from rain, as the female spends a good portion of the day away; afterwards, chick spreads its wings in the sun. Chick first seen to tear off and eat a few bites on its own, though with difficulty.
65	Chick jumps and flaps frequently; pounces on and seizes a stick (nest material) with its talons.
72	Chick weighs 1630 g (ca. adult female mass); wing chord is 245 mm, total length 450 mm, and wingspan 870 mm; eyes are dark gray, feet buffy yellowish, and cere, facial skin, and beak black.
80	Chick often feeds on its own.

Table 1. Continued.

Nestling Age (days)	Developmental Feature First Noted on This Day
81	Adult female begins remaining away from nest most of time and periodically brings prey to the nest. Chick adept at plucking prey and feeding itself. Chick now weathers frequent heavy rains on its own.
92	On 28 August, chick equipped with a backpack radiotransmitter. Chick weighs 1697 g, wing chord is 400 mm, total length 590 mm, and wingspan 1140 mm.
93	Chick pouncing, seizing and pecking at nest material and prey remains and exercising wings more frequently and vigorously; commonly jumps, flapping, from rim to rim of the nest, and periodically tugs at the antenna of its radiotransmitter. When wet from rain, the nestling often spreads its wings in the sun.
100	Chick frequently moves nest material around with its bill; practice hunting and flapping have reached a fever pitch.
114	On 19 September, nestling flies around within nest tree and to other trees; fledged at 109–114 d of age (in nest at age 108 d).

(1995) was near the center of the park. Tikal National Park is a tropical lowland site at 17°N latitude in Guatemala's Petén Department. Tikal's environment is described by Schulze and Whitacre (1999). Because nest No. 1 failed prior to hatching, we report here on observations at nest No. 2, which produced one fledgling. We discovered nest No. 2 on 8 May 1995, while the adults were incubating. The nest was 16.4 m high in a live Jobillo tree (*Astronium graveolens*). At a similar height in a tree 74 m from the nest, we built a wooden observation platform, using poles cut from the forest, a 1.2 × 0.6 m piece of plywood, and baling wire. Construction of the platform took several hours during three days, from 8–10 May. The Crested Eagles gave no indication of being disturbed by the construction process.

On 11 May we began dawn-to-dusk observations, usually 13–14 hr in duration, using a spotting scope. We logged 979.3 hr of observation on 83 d; observation periods averaged 11.8 hr in duration. We observed this nest during the last three weeks of the incubation period and until the chick fledged at 109–114 days of age. Using a backpack arrangement and 6 mm teflon ribbon, we placed an 18 g radiotransmitter (216 KHz; Holohil Systems Ltd., Carp, Ontario) on the juvenile once it neared fledging age. We monitored the radio-tagged fledgling until 16 mo of age, when we ended fieldwork.

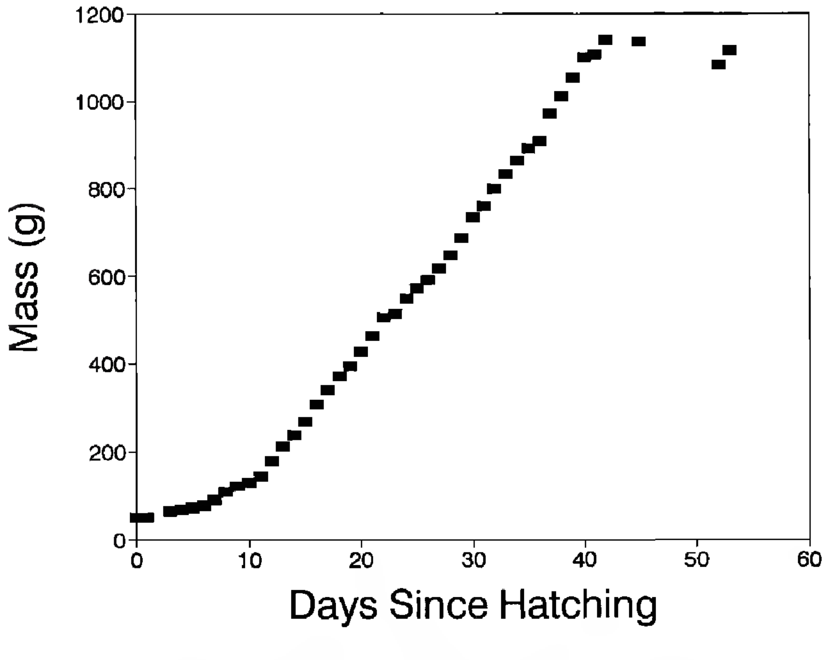

Figure 1. Mass gain of hatchling male Crested Eagle (band number = 220107) in the Oklahoma City Zoological Park. Data from zoo records, courtesy of Barbara Howard.

Results

The nestling, later judged by size to be a female, was not hatched as of 26 May and was very tiny and weak the morning of 29 May; we estimated she hatched 28 May, which was designated as day 0. The chick's physical and behavioral development during the 114 d brood-rearing period are described in Table 1.

Post-Fledging Period. At first, the fledgling returned to the nest to sleep and receive prey, but within a few days it spent little time in the nest, flying frequently between various trees up to 100 m from the nest, and returned to the nest mainly to receive prey from the adults At this time, the female often fed the chick, bill to bill. With radiotelemetry, we followed the fledgling to the age of nearly 16 mo, when she still remained dependent on the adults. Unlike some other raptor species at Tikal, the fledgling did not indulge in protracted food-begging while adults were away from the nest area, but rather, it called mainly when they approached. At least as late as day 141 (16 October), the female still occasionally fed the chick bit-by-bit when she delivered prey.

Data on a Captive-reared Nestling. Because no growth curves are available for wild birds, here we report data for a male (surgically sexed) hatched at the Oklahoma City Zoo (Fig. 1). This male weighed 51 g on hatching day, showed essentially linear mass gain after two weeks, and stabilized at ca. 1117 g at age 42–53 d (Fig. 1). Allowing 5–10% additional mass gain thereafter (Newton

1979:120, T. Cade pers. comm.), its predicted adult weight is ca. 1170–1230 g. At 21 days, this chick's talons were beginning to turn from white to gray, and covert feathers were emerging from quills. At four weeks, primary feathers were emerging from sheaths and at six weeks the chick was very alert and interested in his surroundings. On day 51 he stood in the nest, on day 72 he sat on the nest rim, and on day 76 he was found on the floor and returned to the nest. On day 94 the primaries were hard-penned, though the tail was still growing. On day 103, the chick flew across the room to another perch, and two days later was flying about the room (B. Howard pers. comm.).

DISCUSSION

Developmental mileposts accord closely between the captive-reared and wild chicks. Both were able to stand for some time during their seventh week, and both made their first significant flights at 103–114 days. The Crested Eagle nestling at Tikal developed at a slower rate than did Ornate Hawk-Eagle (*Spizaetus ornatus*) nestlings (Whitacre et al. in press b), which in turn developed more slowly than did Black Hawk-Eagle nestlings (*S. tyrannus*; Whitacre et al. in press c). We observed chicks first standing up for prolonged periods at 5 wk in the Black Hawk-Eagle, during the seventh week in the Ornate Hawk-Eagle, and at 8 wk in the Crested Eagle. Chicks first flapped in place vigorously at 4 wk in the Black Hawk-Eagle, 5 wk in the Ornate Hawk-Eagle, and during the seventh week in the Crested Eagle. The age at which we noted chicks first able to feed themselves was less variable; this occurred at 8 wk in the Black Hawk-Eagle and during the ninth week for both the Ornate Hawk-Eagle and Crested Eagle. A Black Hawk-Eagle chick first walked out onto limbs near the nest early in the fourth week and did so commonly by the end of the fourth week. We observed this behavior at 9 wk in the Ornate Hawk-Eagle and 16 wk in the Crested Eagle. First flights within the nest tree were observed during the eighth week for the Black Hawk-Eagle, the tenth week in the Ornate Hawk-Eagle, and at 16 wk in the Crested Eagle. Fledging from the nest tree took place during the tenth week in the two hawk-eagles and at 16 wk in the Crested Eagle.

The relative speed of development of the above three species accords with their relative body sizes. Black Hawk-Eagles (most rapid to develop) are also smallest, with mean adult female mass of 1115 g (Whitacre et al. in press c). Ornate Hawk-Eagles, with intermediate rate of development, are intermediate in size, with females averaging 1450 g (Whitacre et al. in press b). Crested Eagles, slowest to develop, have a mean adult female mass of about 1850 g (Whitacre et al. in press a).

The nestling periods of these two Crested Eagles (103–105 d for the captive bird and 109–114 d for the wild bird) are notably long for a raptor of this size. The Crested Eagle falls well above the curve relating nestling period to female mass in a wide range of falconiforms (Newton 1979:119). Indeed, the nestling period we documented is equivalent to that of the Philippine Eagle (*Pithecophaga jefferyi*), Crowned Hawk-Eagle (*Stephanoaetus coronatus*), and Martial Eagle (*Polemaetus bellicosus*), all substantially larger birds than the Crested Eagle (Newton 1979:344). It is unclear why the Crested Eagle should have a nestling development period as long as these larger tropical eagles. Further data are needed in order to more confidently estimate the duration of the nestling period in *Morphnus*.

RESUMEN.—Se observó dos nidos de Aguila Monera *Morphnus guianensis* en Petén, Guatemala. Reportamos sobre el desarrollo comportamiento de un polluelo. También presentamos datos sobre el crecimiento y comportamiento de un juvenil en cautiverio. La juvenil silvestre, una hembra, eclosionó aproximadamente 28 Mayo, designado día 0. La primera vez que observamos el polluelo arreglarse las plumas fue en día 16; en día 17 defecó hacia la orilla del nido, y siempre lo hizo así después. Día 18 intentó pararse por primera vez, y en día 23 pudo pararse brevamente. En día 24 estiró las alas de manera estereotípica. A partir del día 25, respondió agresivamente cuando el macho trajo presa, y a especies tal como buitres. A partir del día 37 el polluelo logró pararse por un buen rato, y batió las alas en ejercicio. En día 59, logró alimentarse ella mismo por primera vez, y quedó parada por dos horas. Cuando el polluelo tenía 81 días, la hembra adulta empezó a ausentarse la mayor parte del día, supuestamente cazando, y trajo presas al nido periodicamente. A partir del día 93, el polluelo frecuentemente saltó, aleteando, de una orilla del nido a la otra, manejaba palitos del nido en su pico, y las atacaba con las garras como que fueran presa. Entre días 109 y 114, voló fuera del árbol del nido por primera vez, pero siguió regresando al árbol del nido para recibir presas. Usando radio-telemetría, seguimos la juvenil hasta 16 meses de edad, cuando terminamos el estudio. En aquella fecha, la juvenil quedaba todavía dependiente en los adultos. Hacemos comparaciones entre la rapidez de desarrollo del Aguila Monera, el Aguilucho de Penacho (*Spizaetus ornatus*), y el Aguilucho Negro (*S. tyrannus*). El desarrollo del juvenil de *Morphnus* fue lento en comparación con otros rapaces de igual tamaño.

[Traducción de los autores]

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SPRING WEATHER AND BREEDING SUCCESS OF THE EURASIAN KESTREL (*FALCO TINNUNCULUS*) IN URBAN ROME, ITALY

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KEY WORDS: *Eurasian Kestrel;* Falco tinnunculus; *breeding success; weather conditions; urban habitats; Mediterranean areas.*

The breeding biology of the Eurasian Kestrel (*Falco tinnunculus*) has been well-studied in northern and central Europe mainly focusing on the influence of prey fluctuations on clutch size and productivity (e.g., Village 1990, Plesnik and Dusík 1994, Valkama et al. 1995) as well as on the influence of weather conditions on timing of breeding (Kostrzewa and Kostrzewa 1990, 1991). In Mediterranean Europe, few studies addressed these aspects (Gil-Delgado et al. 1995) and relevant accounts on kestrel breeding success are by Rizzo et al. (1993), Gil-Delgado et al. (1995), Fargallo et al. (1996), and Avilés et al. (2000). Here, I provide data on the breeding success of kestrels in two different habitats of Rome, central Italy, through 5 yr. I studied between-year differences in breeding success in relation to spring weather and I compare my results with data collected 15 yr earlier from the same population (Sommani 1986).

STUDY AREA AND METHODS

I conducted fieldwork from March 1996–July 2000 in Rome, Latium, central Italy (41°53′N, 12°28′E). The area is characterized by developed areas, urban parks, open-lands (mainly dry pastures and cereal crops), and small oak woods (mainly *Quercus ilex*). The two census plots included one strictly urban area (inner city) and one suburban, built-up area (Appia Antica park). Breeding density was 1.9 pairs/km^2 (N = 86 pairs) in the urban area and 0.6 pairs/km^2 (N = 34 pairs) in the suburban area (Salvati et al. 1999). For census procedure to locate breeding pairs see Salvati et al. (1999, 2000).

Nests were monitored weekly from the pre-incubation period. Visits were increased to 2–3 d intervals during the nesting period. Laying date for each nest was determined by subtracting the mean incubation period of the species (28 d; Avilés et al. 2000) from the hatching date Hatching date was determined taking into account that all eggs hatch in 4 d (Avilés et al. 2000). Fledging date was defined as the first day when all fledglings leave the nest. Young generally stay for 5–10 d in the vicinity of the nest using perches previously frequented by the parents, but rarely come back to the nest during daylight (Komen and Myer 1989, Bustamante 1994). As the interval of nest visits was 2–3 d, an error of ±1 d should be assigned to fledging date. Clutch size and laying date were recorded for a subsample of breeding pairs, because many nests were inaccessible for an exact count of eggs or chicks during the early stages of breeding (Salvati et al. 1999). I measured percent egg productivity as the number of fledglings in a nest divided by the total number of eggs laid in that nest. Breeding parameters for the years 1979–85 were obtained through the same technique from Sommani (1986).

As weather variables, I used mean monthly rainfall and

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Table 1. Breeding success and fledgling dates of Eurasian Kestrels in Rome (1979–85, 1996–2000).

Year	Fledglings per Breeding Pair	N	Mean Fledging Date (1 = 1 June)	N	Seasonal Decline in No. of Fledgings/Pair with Date[a,b]
1979–85[c]	2.98 ± 1.10	40	16.53 ± 6.41	38	—
1996	3.08 ± 0.57	25	13.28 ± 4.54	11	$r = -0.61$, df = 9*
1997	3.07 ± 0.83	27	15.43 ± 6.93	23	$r = -0.44$, df = 21*
1998	3.06 ± 1.01	36	23.97 ± 8.33	33	$r = -0.38$, df = 31*
1999	3.06 ± 1.00	46	27.11 ± 11.92	45	$r = -0.69$, df = 43**
2000	2.98 ± 0.84	54	28.28 ± 10.43	54	$r = -0.63$, df = 52**
1996–2000	3.04 ± 0.88	188	24.43 ± 10.84	166	$r = -0.56$, df = 154**

[a] Pearson correlation between fledging date and number of fledglings per pair (probability levels: * $P < 0.05$, ** $P < 0.001$).

[b] Fledging dates were log-transformed to obtain a normal distribution.

[c] Data recalculated from Sommani (1986).

mean minimum temperatures in March–June from 1979–85 and from 1996–2000. There were no correlations between monthly rainfall and minimum temperatures (Spearman's rank correlation test, $P > 0.1$). All meteorological data were obtained from the station of Collegio Romano, which is located within the study area.

All breeding parameters were compared by means of t-tests and analysis of variance (ANOVA) in order to investigate differences among years. Logarithmic transformation was performed on fledging date to correct for deviations from normality. Relationships between each weather variable and breeding parameters were examined using Spearman's rank correlation analysis. In all tests (two-tailed), a minimum probability level of $P < 0.05$ was accepted. Statistical analyses were performed using STATISTICA software. Results are presented as mean ±SD.

RESULTS

Mean clutch size was 4.43 ± 0.94 eggs (range = 3–6 eggs, $N = 14$), and mean laying date was 22.15 April ± 13.13 d ($N = 13$). Mean number of fledglings per successful pair was 3.08 ± 0.82 (range = 2–6 young, $N = 186$), and mean fledging date was 24.43 June ± 10.84 d ($N = 166$). Percent egg productivity was 80.6% ($N = 14$). As two pairs failed breeding (percentage of successful pairs = 98.9%, $N = 188$), mean number of fledglings per breeding pair was 3.04 ± 0.88 ($N = 188$). Seasonal decline in number of fledglings per pair was observed in all years of study (Table 1). I did not detect between-year differences in mean number of fledglings per breeding pair ($F_{4,183} = 0.09$, $P = 0.985$), whereas mean fledging date showed significant differences among years ($F_{4,161} = 6.78$, $P < 0.0001$). Pooling all data collected in urban Rome from 1979–85 and from 1996–2000, the difference in mean number of fledglings per breeding pair was not significant ($t_{226} = -0.37$, $P = 0.709$). Pairwise correlations between mean fledging date and all weather variables were not significant ($P > 0.1$), with only April rainfall bordering the significance level ($r_s = 0.56$, $P = 0.058$, $N = 12$).

DISCUSSION

Breeding parameters of kestrels in Rome are similar to those observed in other Mediterranean areas (Rizzo et al. 1993, Gil-Delgado et al. 1995, Avilés et al. 2000). Since my study was restricted to pairs breeding in cavities other than nest-boxes, the overall reproductive success may be lower compared with that of populations breeding in nest-boxes, likely due to the potentially high predation rates (Avilés et al. 2000). However, the number of kestrel predators is generally low in cities, thus reducing the probability of nest predation.

Many authors have reported that large annual variations in kestrel productivity are linked to fluctuations in rodent density and to unfavorable weather conditions during breeding in northern and central Europe (Kostrzewa and Kostrzewa 1990, 1991, Village 1990, Valkama et al. 1995). In southern Europe, some studies have shown slight between-year differences in laying date (Avilés et al. 2000) and number of fledglings per pair (Gil-Delgado et al. 1995). Interestingly, voles generally show small fluctuations in density in the Mediterranean basin (Paradis and Guédon 1993, Rizzo et al. 1993). In these areas kestrels usually feed on alternative prey (Rizzo et al. 1993, Gil-Delgado et al. 1995, Piattella et al. 1999), thus reducing the influence of rodent fluctuations on productivity. Therefore, in southern Europe weather conditions may assume a role in determining annual variations in kestrel breeding success.

Mild climate (i.e., high temperatures and low rainfall) during spring triggers laying and favors chick rearing (Gil-Delgado et al. 1995). In Rome, the between-year stability of kestrel nesting success may confirm the importance of mild and stable weather conditions during breeding, as already observed for the Tawny Owl (*Strix aluco*) in the same area (Ranazzi et al. 2000), although it seems plausible that in the Mediterranean basin, high rainfall during spring may force kestrels to delay laying, as suggested by the weak relationship between mean fledging date and April rainfall. I suggest that the annual variation in mean fledging date is probably not affected by weather conditions. Factors linked to high population levels in Rome (Salvati et al. 1999) more likely could affect variations in laying date.

Following Avilés (2000) hypothesis, in dry and semi-arid landscapes of southern Europe, high rainfall in the spring may result in higher prey availability (e.g., insects; Rizzo et al. 1993, Avilés et al. 2000), contributing to annual fluctuations in breeding success. Although data from this study area do not support Avilés and co-workers' hypothesis, I suggest that the improved reproductive output related to rainfall also depends on the feeding habits of kestrels in each area. In those Mediterranean areas, like Rome, where kestrels prey mainly on birds (Piattella et al. 1999), the effect of spring rainfall could be negligible. Whereas in most arid European areas, where kestrels feed mainly on insects (Gil-Delgado et al. 1995), the Avilés and co-workers' hypothesis seems to be plausible to explain the between-year differences in breeding performance of this raptor.

Resumen.—Estudie las diferencias entre años en el éxito reproductivo del cernícalo euroasiático (*Falco tinnunculus*) en relación con el clima primaveral en un periodo de cinco años, y comparé mis resultados con datos colectados 15 años atrás en la mi misma población. El tamaño medio de la postura fue 4.43 ± 0.94 huevos, y la fecha media de la postura fue 22.15 Abril ± 13.13 d. El promedio de volantones por pareja exitosa fue 3.08 ± 0.82 y la fecha promedio del primer vuelo fue 24.43 Junio ± 10.84 d. La productividad de huevos fue 80.6%. La diferencia entre años en el promedio de volantones por pareja reproductora no fue significante, en tanto que la fecha promedio del primer vuelo mostró variaciones significativas entre años. No hubo correlación entre la fecha promedio del primer vuelo y las variables climáticas. El éxito reproductivo de los cernícalos en Roma es comparable a los observados en otras áreas del mediterráneo. El clima moderado durante la primavera puede ser el detonador de las posturas y favorecer la cría de los pichones. Por otro lado, en paisajes semi áridos, donde los cernícalos se alimentan principalmente de insectos, la alta precipitación en primavera puede dar como resultado la alta disponibilidad de presas, contribuyendo a las fluctuaciones anuales en el éxito reproductivo. Los datos de esta área de estudio, donde los cernícalos comen primordialmente aves, no dan soporte a esta hipótesis. Sin embargo esta hipótesis puede explicar las variaciones anuales en el éxito reproductivo de las rapaces insectívoras en algunas áreas del mediterráneo.

[Traducción de César Márquez]

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FATAL *CARYOSPORA* INFECTION IN A FREE-LIVING JUVENILE EURASIAN KESTREL (*FALCO TINNUNCULUS*)

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KEY WORDS: *coccidiosis;* Caryospora kutzeri; *Protozoa; Eurasian Kestrel;* Falco tinnunculus.

Infections in birds of prey by *Caryospora* spp. are a common and often serious problem in captive breeding stations (Heidenreich 1996). In British breeding centers, nestlings of Merlins (*Falco columbarius*) fall ill due to infections with *C. neofalconis* (Forbes and Simpson 1997). Typically, symptoms are displayed at an age of 28 to 55 d and may include regurgitation, hemorrhagic feces, depression, and reduced appetite. Peracute or acute death with or without clinical signs may occur also. The possible explanation for this disease in young birds at this particular age is waned maternal immunity and incomplete development of their own active immunity. In experimentally-infected adult Eurasian Kestrels (*F. tinnunculus*) the prepatency of *C. neofalconis* was 8–10 d and the patency 10–93 d, and for *C. kutzeri* 8–13 d and 4–34 d, respectively (Böer 1982). The developmental cycle can be either direct or indirect. In captivity caryosporans apparently utilize the direct life cycle, possibly also using paratenic hosts, such as earthworms (Heidenreich 1996); free-living birds of prey acquire infection by feeding on infected prey (Cawthorn and Stockdale 1982).

Previously, 16 species of *Caryospora* have been described in raptors, 10 from birds in Europe and six from North America, including one which also occurs in Venezuela (Upton et al. 1990, Klüh 1994). Because most publications on *Caryospora* (Yamikoff and Matschoulsky 1936, Wetzel and Enigk 1937, Schellner and Rodler 1971, Böer 1982) consider only captive birds of prey, the distribution and significance of *Caryospora* in free-living birds of prey remains unclear. No *Caryospora* oocyst could be found in 72 free-living Merlins examined in Great Britain (Forbes and Fox 2000), nor in 247 birds of prey (including 35 Eurasian Kestrels, four Hobbys [*F. subbuteo*] and 22 Peregrine Falcons [*F. peregrinus*] from Germany [Krone 1998]). However, *C. boeri* was found in seven of 15 free-living Eurasian Kestrels from Germany in another study (Klüh 1994). Furthermore, in free-living Eurasian Kestrels from Austria, oocysts of *C. falconis* and oocysts of *Caryospora* spp. were diagnosed (Kutzer et al. 1980).

CASE REPORT

A juvenile Eurasian Kestrel observed in Berlin on 29 August 2000 showed distinct signs of a general weakness. The bird was conspicuous, it demonstrated a reduced-flight distance, and when chased away, the bird flew only short distances. On 30 August 2000 the kestrel was captured and a hemorrhagic diarrhea was reported. On the morning of 31 August 2000 the kestrel died. Post-mortem findings indicated a heavy protozoan infection which lead to death from associated severe dehydration and cachexia.

As the bird was banded its history was known. The bird and its clutch mates had been banded on 11 July 2000 at an age of 18–19 d in a nesting box. The bird was found less than 500 m away from the nesting box. The necropsy of the 69-d-old male Eurasian Kestrel revealed a poor condition and a mass of 101 g. A heavy *Caryospora* spp infection (Fig. 1) resulting in a severe hemorrhagic enteritis was documented during the examination of the digestive tract. The highest level of oocysts (ca. 100/visual field at magnification of 200×) were detected in the first third of the jejuno-ileum.

Oocysts were mixed with potassium dichromate solu-

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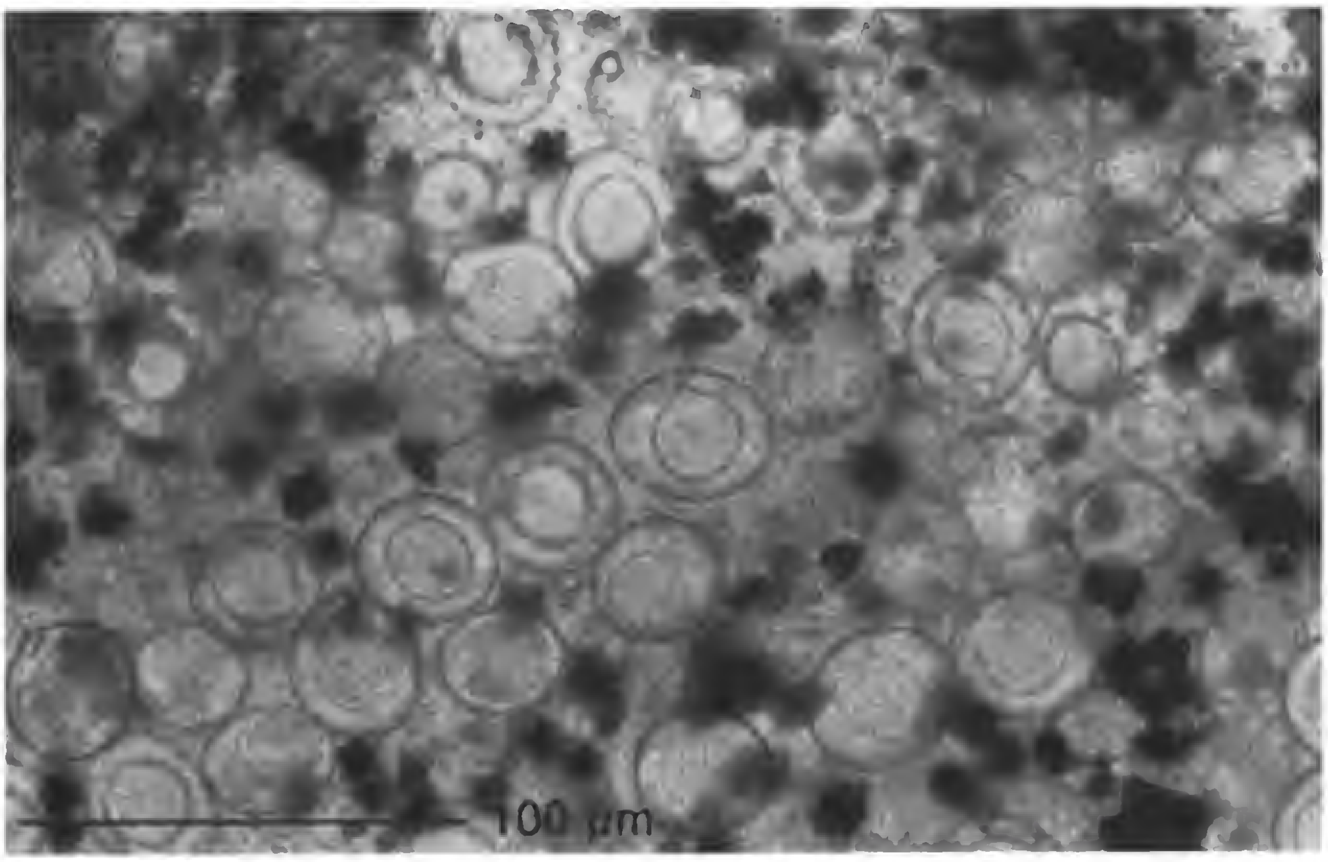

Figure 1. Unsporulated oocysts of *C. kutzeri* from the Eurasian Kestrel (*F. tinnunculus*) found in Berlin, Germany.

tion and sporulated in Petri dishes at room temperature (22–24°C) within three days.

DISCUSSION

The clinical signs including the cachexia are similar to those described in captive-bred birds, in which the disease is well-known. This is the first record of a fatal caryosporan infection in a free-living bird of prey species in Europe. In his survey, Cawthorn (1993) did not identify any cases of a fatal coccidiosis in a raptor, but stated that clinical coccidiosis is uncommon in free-living birds of prey. Measurements of oocysts and sporocysts (Table 1) were within the range for *C. kutzeri* given by Böer (1982). Due to their round oocysts, *C. falconis* and *C. boeri* were excluded as potential candidates. *C. megafalconis* is too large and *C. neofalconis* too small to be considered as candidates in this case. *C. henryae* were described with a triple oocyst wall. *C. kutzeri* is a specific parasite of the genus *Falco* as determined by cross infection experiments with the genera *Buteo*, *Accipiter*, *Milvus*, *Bubo* and *Asio* where transmission was unsuccessful (Böer 1982). Species identification solely based on measurements of oocysts and sporocysts is difficult and uncertain. Five of 10 *Caryospora* species from Europe are still described inadequately or have only been found on one occasion. More reliable identification would be derived from cross-transmission experiments and a comparison using molecular genetics

Table 1. Measurements of *Caryospora kutzeri*.

	LENGTH (µm)	WIDTH (µm)
Oocysts (N = 15) ×	37.58	32.54
SD	3.07	1.77
Range	32.5–43.13	30.0–35.0
Length-width-ratio	1.15	
Sporocysts (N = 15) ×	24.17	21.96
SD	2.45	2.66
Range	18.75–28.75	18.75–28.75
Length-width-ratio	1.1	
Residual body (N = 3) ×	10.8	10.8

The extremely low prevalence of species of *Caryospora* in free-living birds of prey from central Europe contrasts with the high prevalence found in captive birds of prey. Böer (1982) diagnosed a prevalence of 9% of caryosporan oocysts in fecal samples of captive Falconiformes (N = 628) from Germany. In contrast to *Caryospora*, oocysts of *Sarcocystis/Frenkelia* spp. occur at much higher prevalence (31.4%, N = 194) in free-living birds of prey from Germany (Krone 1998). One reason could be that *Caryospora* spp. are found predominantly in young birds at an age of 28–55 d and these birds are examined less frequently than older ones in the wild. Another explanation could be the geographic distribution of the protozoa The parasite may not occur naturally in central Europe, but may have been introduced with birds used for falconry (mainly Saker Falcons [*F. cherrug*]). This would imply that the parasite has its natural nidus in the distribution range of the Saker Falcon and its appropriate intermediate host. If an infected bird is imported into a breeding station, the parasite can infect many other falcons either due to its direct developmental cycle or possibly via an intermediate host. Cawthorn and Stockdale (1982) have demonstrated that mice (*Mus musculus*) can act as experimental intermediate hosts for *C. bubonis* from the Great Horned Owl (*Bubo virginianus*) in North America. Nothing is known about possible intermediate hosts of *Caryospora* spp. in Europe.

Currently, we do not know whether endemic areas exist around captive breeding facilities where falcons are frequently exchanged, with a high possibility for caryosporan infections to be introduced to wild birds. In captive-breeding programs in which birds of prey, especially of the genus *Falco*, are planned to be reintroduced into the wild, birds should be checked for *Caryospora* spp. before release.

RESUMEN.—Una infección cariospórica fatal fue diagnosticada en un macho inmaduro de cernícalo euroasiático (*Falco tinnunculus*) encontrado moribundo en Berlín, Alemania. Las señales clínicas de esta enfermedad coccidial incluyen diarrea hemorrágica, depresión, y una distancia de vuelo reducida. El ave murió debido a la alta infección de *Caryospora kutzeri* dando como resultado deshidratación y caquexia. En aves de presa silvestres en Europa *Caryospora* spp. no ha sido registrada, mientras que las infecciones en aves cautivas son comunes.

[Traducción de César Márquez]

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BOOK REVIEW

J. Raptor Res. 36(1):87–88

The Raptor Almanac. By Scott Weidensaul. 2000. The Lyons Press, New York, NY. ix + 382 pp., numerous color photographs, figures, and tables. ISBN 1-58574-170-1. Cloth, $40.00.—Scott Weidensaul has assembled an impressive compendium of facts about raptors in this attractive and comprehensive volume. Designed "for the birder or naturalist who wants to go beyond the fundamentals," the almanac includes information about evolution, behavior, migration, conservation, and just about every other topic related to raptors. The book is packed with amusing anecdotes and interesting trivia that one would be hard-pressed to find anywhere else in a single volume. The well-written text is accompanied by numerous charts, graphs, and an excellent collection of stunning photographs taken by several well-known wildlife photographers. I found that the book had answers to almost all the questions that nonbiologists typically ask about diurnal raptors: How big is a Bald Eagle? How long does an Osprey live? How fast does a Peregrine Falcon fly? How can I build a kestrel nest box?

The title, "Raptor Almanac," is somewhat misleading, however, because Weidensaul does not discuss owls (raptors by anyone's definition), but he does discuss New World vultures (now classed as ciconiiforms). The subtitle on the cover more accurately describes the book as "A Comprehensive Guide to Eagles, Hawks, Falcons, and Vultures." I am puzzled as to why the author chose to include New World vultures as "raptors" now that they have been reclassified. Weidensaul actually presents the latest DNA evidence that they are not raptors, but he then proceeds to treat them as if they were. The book seems to devote a disproportionate amount of space to the New World vultures; a high percentage of text and figures is about them, often because they are exceptions to so many "rules" about "true raptors." Although worldwide in scope, the book had a decided emphasis on taxa from North America and Europe. Raptors from Africa, Asia, and Australia were mentioned throughout the text but were noticeably underrepresented in the charts and tables. The North American bias was reflected by the fact that some (not all) measurements were given in English rather than metric units.

The book is divided into four main sections. The introductory section basically defines raptors and describes anatomical and physiological features that make them unique. The section on ecology and natural history comprises the heart of the volume (>120 pages) and covers behavior, social structure, courtship, nesting, diet, migration, longevity, and mortality. A chapter on conservation includes case histories of several endangered raptors and a review of effective management techniques. A final chapter on raptor-human relationships presents a unique collection of information about how human religious and economic perceptions about raptors have changed over time; this last section has an interesting list of biblical references to raptors as well as a number of suggestions on how people can help raptors. Appendix I has nine tables with interesting etymological information about raptors, and Appendix II provides a comprehensive reference for English and scientific names as well as general breeding distribution of all 310 species of diurnal "raptors."

The layout of the book is pleasing, with attractive headings. Many handy (but unnumbered) charts, maps, and tables break up the text. It would have been helpful to have a list of tables and figures for easy reference. Several of the illustrations were prepared by the multitalented author, himself; others were adapted from other sources. Some of these "adaptations" did not go smoothly, as seen by the unfortunate whiteout smudge in the drawing on page 66. An error like this stands out against the highly professional quality of the other figures and the outstanding quality of the color photographs. I spotted only one typographical error (in the chart on p. 109) and one grammatical error (bottom of p. 153).

It is usually easy to find fault with an account designed for a popular audience, but I found almost no exaggerations or erroneous statements in *The Raptor Almanac.* Weidensaul avoids restating popular myths. For example, his section on mate fidelity is accurate and balanced and makes it clear that raptors do not always "mate for life." In fact, most of what Weidensaul says is on target.

As a scientist, my biggest disappointment with *The Raptor Almanac* was that Weidensaul did not provide references for the statements he makes. I realize that this practice makes it easier for a nonscientist to read the text, but it is very frustrating for the serious biologist who wants to verify statements or to get more information about a specific topic. Weidensaul provides only a very incomplete "Selected Bibliography" at the end of the book. A more effective compromise would have been to include a list of references after each chapter. Some of the material in the charts and tables is referenced; these references suggest that Weidensaul relied heavily on the secondary literature (e.g., Brown and Amadon 1968, Palmer 1988, Johnsgard 1990) for facts. This practice works well 95% of the time, but doing so exclusively means missing out on some of the more recent and important studies. Unfortunately, it also can perpetuate unsubstantiated information. For example, Weidensaul mentions the notion that the sex of Golden Eagles can be determined by tail bands, even though more recent work has shown this technique to be invalid.

Readers may be disappointed to learn that the almanac, with a publication date of 2000, does not include the most up-to-date information on many topics. Data on California Condor chick production, number of occupied Bald Eagle territories, and number of Peregrine Falcon nesting pairs have not been updated since the early to mid-1990s. Information on the legal status of some species, like the Bald Eagle and the Peregrine Falcon, is no longer accurate. When Weidensaul stated (p. 242) that experimental reintroductions of Golden Eagles had been unsuccessful, he apparently was unaware of recent successful nesting by released birds in Georgia and Tennessee. Weidensaul relies on very old sources for several important topics. For example, he features Craighead and Craighead 1956 in his discussions of diet and home range, and uses Bent 1937 for his data on chronology.

Despite these shortcomings, Weidensaul's book will serve as a useful reference for anyone who wants or needs to know about raptors. Weidensaul deserves credit for taking on and successfully completing an enormous job. I would recommend *The Raptor Almanac* as a textbook for introductory courses about raptor biology. The beautiful photographs, by themselves, would make this book welcome on any coffee table.—**Karen Steenhof, USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street, Boise, ID 83706 U.S.A.**

J Raptor Res. 36(1):89

MANUSCRIPT REFEREES

The following people reviewed manuscripts for the *Journal of Raptor Research* in 2001. Peer review plays a vital role in the publishing process and in improving the quality of the Journal. The editorial staff would like to thank the following for reviewing manuscripts this past year. The names of those who reviewed two or more manuscripts are indicated with an asterisk.

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The Raptor Research Foundation, Inc. 2002 annual meeting will be held in conjunction with the Third North American Ornithological Conference on 24–28 September in New Orleans, Louisiana. For information about the meeting see the following website: http://www.tulane.edu/~naoc-02/ or contact Dr. Tom Sherry (tsherry@tulane.edu).

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