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BREEDING ECOLOGY OF MACKINDER'S EAGLE-OWLS (*BUBO CAPENSIS MACKINDERI*) IN FARMLANDS OF CENTRAL KENYA

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ABSTRACT.—African owls are relatively little known and studying them is difficult due to negative effects of cultural beliefs and consumptive uses of owls. Over a 5-yr period from 2004–08, we studied the breeding ecology of 13 pairs of Mackinder's Eagle-Owls (*Bubo capensis mackinderi*), a subspecies of the Cape Eagle-Owl (*B. capensis*), inhabiting a densely populated farming community in central Kenya. Mean owl density was 0.24 pairs/km² and mean nearest neighbor distance averaged over all years was 1.9 km. Most nests (65%) were located in a cave or on a covered ledge, and mean nest site elevation was 2191 m asl. Nests were located close to farms and grasslands, but far from forests. Initiation of breeding was associated with rainfall patterns. Mean breeding success was 51% and reproductive rate was 1.36 young fledged per successful pair. Increased reproductive success was associated with breeding after the long rainy season, nesting on cliffs or covered ledges, and nesting close to grasslands and human habitation. The majority (59%) of recorded owl deaths were caused by human activities and poisoning was the most common source of mortality. Compared to other populations of *Bubo* spp., the birds in our study area had a high breeding density but a low reproductive output. Human-induced mortality may be negatively affecting productivity in this population.

KEY WORDS: *Mackinder's Eagle-Owl; Cape Eagle-Owl; Bubo capensis mackinderi; Africa; breeding; density; human disturbance; raptor; reproductive rate.*

ECOLOGÍA REPRODUCTIVA DE *BUBO CAPENSIS MACKINDERI* EN TIERRAS DE CULTIVO DEL CENTRO DE KENIA

RESUMEN.—Se conoce poco acerca de los búhos africanos y es difícil estudiarlos debido a los efectos negativos de las creencias culturales y los usos que se hace de ellos. En un período de cinco años, entre el 2004 y el 2008, estudiamos la ecología reproductiva de 13 parejas de *Bubo capensis mackinderi*, una subespecie de *Bubo capensis*, que habitan en una comunidad agrícola del centro de Kenia. La densidad media de búhos fue de 0.24 parejas/km² y la distancia media al vecino más cercano fue de 1.9 km. La mayoría de los nidos (65%) se ubicaron en una cueva o en una cornisa cubierta y la altitud media de los sitios de nidada fue de 2191 m snm. Los nidos se ubicaron cerca de granjas y pastizales, pero lejos de los bosques. El inicio de la reproducción estuvo asociado con los patrones de precipitaciones. El éxito medio de reproducción fue 51% y la tasa de reproducción fue 1.36 volantones por pareja exitosa. El incremento en el éxito reproductivo se asoció con criar después de la larga época lluviosa, anidar en acantilados o cornisas cubiertas y anidar cerca de tierras de cultivo y poblados. La mayoría (59%) de las muertes de búhos registradas fueron causadas por actividades humanas y el envenenamiento fue la causa más común de

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mortalidad. Comparada con otras poblaciones de *Bubo* spp., las aves en nuestra área de estudio presentaron una densidad de reproducción elevada pero un rendimiento reproductivo bajo. La mortalidad inducida por humanos puede estar afectando negativamente la productividad en esta población.

[Traducción del equipo editorial]

Tropical ecosystems are among the most productive and diverse in the world (Bazilevich et al. 1971, Wilson 1988). They contain three-quarters of the world's 'endemic bird areas' or areas relatively rich in endemic bird species. (Bibby et al. 1992). Half of all tropical countries support at least 50 species of raptors (Bildstein et al. 1998). Yet avian species in tropical regions remain relatively understudied and this is particularly true for species that are notoriously difficult to study, such as those inhabiting forests and nocturnal species (e.g., *Strigiformes*; Bildstein et al. 1998). The study of owls in tropical regions and particularly in Africa is also confounded by strong cultural prejudices, the widespread use of owls for witchcraft, and by security concerns due to working at night (Enriquez and Mikkola 1997, Ogada and Kibuthu 2008). Collectively these have resulted in a paucity of knowledge about African owls and an almost complete lack of long-term studies, particularly from unprotected areas.

Mackinder's Eagle-Owl is one of two subspecies of the nominate Cape Eagle-Owl (*B. c. capensis*). Preliminary DNA evidence suggests that *B. c. mackinderi* is a subspecies of *B. c. capensis*, whereas *B. c. dilloni* may warrant separate species status (M. Wink pers. comm.). Currently, *B. capensis* is listed as a species of Least Concern (BirdLife International 2011), though *B. c. mackinderi* is a regionally vulnerable subspecies in Kenya (Bennun and Njoroge 1996).

Mackinder's Eagle Owl has a discontinuous distribution from Zimbabwe to Kenya (König et al. 1999). In Kenya, this raptor inhabits highland areas and is known mostly from protected areas such as Mt. Kenya, Aberdare, and Mt. Elgon National Parks, though small, fragmented populations of this subspecies also exist in unprotected areas. Mackinder's Eagle Owls have a diverse diet, though typically 1–2 mammalian species constitute >75% of the diet of each area studied (Sessions 1972, Gargett and Grobler 1976, Rodel et al. 2002, Ogada and Kibuthu 2009). Overall, the breeding ecology of this species is poorly known, with the exception of one long-term study in the Matopos, Zimbabwe (Gargett 1978, Tarr and Tarr 1991).

Here we report on a 5-yr study on the breeding ecology of Mackinder's Eagle Owls (*Bubo capensis mackinderi*) in a densely populated agricultural area

in central Kenya. In particular, we: (1) report breeding density, phenology, and reproductive rate, (2) characterize nest sites of these owls, and (3) describe known causes of mortality.

METHODS

Study Area. Our study area was 40-km² located in the foothills of the Aberdare Mountains in Nyeri District, central Kenya (00°11.37'S, 36°147.98'E, 1900–2600 m asl). Rainfall averaged 600–1000 mm per year, concentrated during March–May and November–December. The landscape consisted of steep valleys of bushy grassland dotted with small-scale farms (<1 ha) and interspersed with cliffs where the owls typically nested. The cliffs overlooked a cluster of small farms. Few trees above 5 m tall were present, because most have been cut for timber or charcoal. The area was densely populated by humans and levels of human disturbance were high. Farms supported both subsistence and commercial agriculture, and major crops included beans, maize, potato, tomato, onions, and cabbage.

Surveys, Nests, and Reproduction. We censused eagle-owl breeding sites monthly from June 2004 to December 2006 and from February to December 2008. In 2007 breeding sites were surveyed opportunistically during the months of January, July, August, and December. We initially found new sites primarily because of information from local farmers, although we surveyed appropriate habitat for potential nesting cliffs during June 2004–December 2006. A breeding site was defined as the area containing one or more nests within the range of one mated pair of owls (Postupalsky 1974). Confirmation of a breeding site was made by observing owl behaviour or by climbing the cliff. We did not use call-playback to detect new breeding sites because (1) pilot studies showed that this subspecies was not very responsive to call-playback (D. Ogada unpubl. data) and (2) security concerns at the study area precluded fieldwork at dusk, when such surveys would have been most effective. We did not mark individual owls for purposes of identification, but confirmed the establishment of new breeding sites, as opposed to relocation by a previously known pair, by confirming the simultaneous presence of neighboring pairs in the course of a single day. Because

Table 1. Density and nest spacing of Mackinder’s Eagle-Owls in central Kenya (2004–08).

YEAR	TERRITORIAL PAIRS PER km ² (<i>n</i> ^a)	MEAN NEAREST NEIGHBOR DISTANCE (km)	G-STATISTIC
2004	0.15 (6)	1.70	0.842
2005	0.22 (9)	1.74	0.787
2006	0.32 (13)	2.00	0.839
2007	0.22 (9)	2.00	0.605
2008	0.30 (12)	2.00	0.810
Mean	0.24	1.88	0.777

^a Number of territorial pairs in the study area each year.

this owl is primarily nocturnal, individuals were unlikely to move between breeding sites during daytime surveys and any pairs counted simultaneously in the course of a single day were considered distinct pairs. GPS locations of all breeding sites were recorded.

Observations of dead nestlings, unhatched eggs, or cessation of activity prior to the calculated date of first fledging indicated nest failure. Laying dates were calculated by subtracting the incubation period of 36 d from hatching dates, which were estimated by nestling size (Sessions 1972, Steyn and Tredgold 1977). At a few sites, nestlings were found at an advanced age and it was not possible to establish the month when breeding commenced. These nests were omitted from analyses of breeding phenology. To avoid disturbing the owls, we did not determine clutch size for most breeding attempts. Young were classified as fledged when they reached an approximate age of 70 d and their number was determined by the observation of young within the territory over subsequent visits. After a breeding failure, we returned to assess whether owls attempted reneesting. Reneesting attempts were included in calculations of reproductive rate, but not for breeding phenology.

A territorial pair was defined as a pair holding a territory, which was defined as an area containing one or more nests within the home range of a mated pair (Steenhof and Newton 2007). A breeding pair was one that laid eggs, and a successful pair was one that fledged at least one young (Steenhof 1987). Productivity was expressed as breeding success (the percentage of territorial pairs that were successful) and the mean number of young fledged per breeding pair, and per successful pair.

Environmental Variables. We measured 13 environmental variables (see Table 2 for definitions) at 12 breeding sites using GIS or a range finder. At one site we were unable to measure environmental variables. Nest location (cave, covered ledge, open ledge, or ground) was recorded for all breeding

attempts where the exact nest location was known. Rainfall was recorded daily at nearby Solio Ranch.

Mortality. We attempted to verify reports of owl mortality and injury, all of which came from the public. We included reports of dead owls where no carcass was found only if the individual reporting it was deemed credible and follow-up visits to the nest site confirmed the absence of an owl.

Statistical Analyses. Values reported represent mean $\pm$ SE. Regularity of nest spacing was calculated using the *G*-statistic; this index ranges from 0–1 with values >0.65 indicating a uniform distribution of nests (Brown 1975). Differences in mean nearest neighbor distance (NND) were analyzed using a one-way ANOVA.

We used a Generalized Linear Mixed Model (GLMM) to test the relationship between the success of breeding attempts (0 = unsuccessful, 1 = successful) and month of breeding onset. We included ‘year’ as a random effect to avoid pseudoreplication. We used a normal distribution for the GLMM and evaluated whether covariates fit this distribution by testing whether deviance residuals were normally distributed.

Reproductive outcomes (i.e., breeding success and number of fledged young) were related to environmental variables using Generalized Linear Models (GLM). We used only univariate GLMs due to small sample sizes. All GLMs were fitted assuming a normal distribution and this was evaluated by testing that the deviance residuals for each GLM were normally distributed. Breeding success was related to type of nest location using a Chi-square test.

RESULTS

Breeding Density and Distribution. We identified a maximum of 13 breeding sites within the study area, but not all sites were occupied every year. Density ranged from 0.15 to 0.32 pairs/ km² (Table 1). Mean NND did not vary among years ($F = 0.18$, $df = 4$, $P = 0.95$). Nests were uniformly distributed in

Table 2. Environmental variables at Mackinder’s Eagle-Owl nest sites ($n = 12$). Distance variables were measured by GIS. Length and width variables were measured with a range finder.

VARIABLE	DESCRIPTION	MEAN $\pm$ SE	RANGE
Elevation	Meters above sea level measured at cliff base	2191 $\pm$ 48	1993–2595
Height of cliff complex	Maximum height of the cliff complex (m)	29.5 $\pm$ 3.3	17.2–51
Length of cliff complex	Maximum width of the cliff complex (m)	120.0 $\pm$ 17.7	50–216
% vegetation on cliff	Visual assessment of scale of vegetation cover ^a	2.4 $\pm$ 0.2	1–4
Nearest neighbor distance	Distance to nearest neighboring nest site (km)	2.00 $\pm$ 0.34	1.0–5.6
Average canopy height	Average height of all trees measured within a 5-m radius located within 10 m in horizontal distance from the base of the cliff (m)	2.54 $\pm$ 0.63	0–6.3
Average canopy density	Total number of trees within a 5-m radius located within 10 m in horizontal distance from the base of the cliff	5.33 $\pm$ 1.86	0–22
Distance to water	Distance to the nearest river or dam (m)	45.3 $\pm$ 18.8	1–191
Distance to road	Distance to the nearest road (m)	568.9 $\pm$ 84.1	154–1143
Distance to agriculture	Distance to the nearest farm (m)	46.1 $\pm$ 16.9	7–190
Distance to human habitation	Distance to the nearest homestead (m)	292.9 $\pm$ 51.6	73–716
Distance to grassland	Distance to the nearest grassland (m)	94.3 $\pm$ 63.1	0–634
Distance to forest	Distance to the nearest protected forest (m)	961.8 $\pm$ 392.1	0–3140

^a 1 $\leq$ 25%, 2 = 26–50%, 3 = 51–75%, 4 = >75%.

all years except 2007 when they were nearly uniform (Table 1).

Nest Sites. We identified the precise location of 19 nests for 39 breeding attempts. At two breeding sites we were unable to identify the location of any nests and at four breeding sites one nest was used twice. Most nests (65%) were located in caves or on covered ledges ($n = 13$). Other nests were on open ledges or on the ground ($n = 6$). The same nest was used in 17% ($n = 5$) of breeding attempts in consecutive breeding seasons. There was an average of 2.5 ± 0.35 alternative nests per breeding site (range 1–5, $n = 13$). Mean breeding site elevation was 2191 ± 48 m (range 1993–2595, $n = 13$; Table 2). Breeding cliffs averaged 30 m high and 120 m long and <50% of the cliff face was covered with vegetation (Table 2). The tree canopy beneath the breeding cliff was sparse and consisted mainly of shrubs (Table 2). All breeding sites were located within 200 m of farms and the majority (67%) were <20 m from an active farm. Nests were located closer to grasslands (mean <100 m) than to forests (mean >1000 m; Table 2).

Phenology and Breeding Performance. Laying date was estimated by observation of incubation behavior or by back-calculating based on nestlings’ estimated age upon discovery. Laying date was concentrated in seven different months of the year and was bimodally distributed, usually commencing

approximately 2 mo after the short (October–November) and long rains (March–May; Fig. 1). Attempts to renest when initial nests failed were made in June ($n = 2$) and November ($n = 1$). Individual pairs did not conform to any regularly repeated breeding cycle (e.g., bred annually, biannually, etc). Pairs bred in successive years 36% of the time ($n = 39$ breeding attempts) and of these 57% were successful ($n = 14$ breeding attempts).

The 39 breeding attempts resulted in 34 fledged young. Most breeding attempts (67%) produced one nestling, 31% ($n = 10$) had two nestlings, and one had three. Overall, the percentage of territorial pairs that were successful was 50.9% ($n = 25$ successful nesting attempts; Table 3). The mean number of fledged young was 0.67 ± 0.09 per territorial pair (range 0–3, $n = 49$ nesting attempts), 0.95 ± 0.11 per breeding pair (range 0–3, $n = 36$ breeding attempts), and 1.36 ± 0.14 per successful pair (range 1–3, $n = 25$ successful nestings; Table 3). Of eleven breeding failures, one was due to poisoning of the female, one nest was raided by Pied Crows (*Corvus albus*), one nest was abandoned due to an influx of bees, one was washed away by a flood, and the remainder failed due to unknown causes.

Factors Affecting Breeding Performance. Timing of the onset of breeding was a significant predictor of breeding success. Breeding attempts that began during April–August after the long rains were 85%

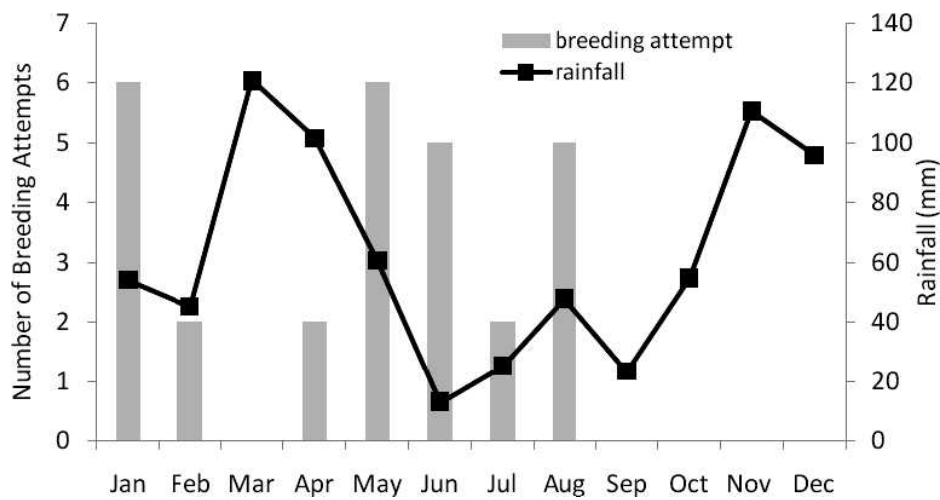


Figure 1. Number of breeding attempts ($n = 28$) by month in relation to the mean local monthly rainfall. Renesting attempts are not included.

successful compared to a 55% success rate for breeding attempts that began breeding during January–February (month: $X^2 = 19.41$, $P = 0.003$; year: $X^2 = 1.70$, $P = 0.791$).

Breeding success increased with nest-site elevation above sea level (Table 4). Nests located in caves or on covered ledges were more likely to be successful than those located on open ledges or on the ground ($X^2 = 11.43$, $P = 0.010$). Nests located in close proximity to human habitation and grasslands had higher breeding success. Nests closer to grasslands also fledged more young (Table 4). Proximity to agricultural fields had a negative effect on the number of fledged young

(Table 4). Other variables, including the height and length of the breeding cliff, NND, and the height and density of the canopy beneath the breeding cliff, had no effect on productivity (Table 4).

Mortality. Ten young and six adult owls were found dead during the study. Six died from unknown causes. Of those that died from known causes, the majority (59%) were induced by human activities. Five owls (50%) were poisoned (three intentionally and two incidentally), two (20%) collided with vehicles, one (10%) died as a result of being captured for sale, one (10%) collided with a wire fence, and one nestling (10%) was killed by a Pied Crow.

Table 3. Reproductive rates of Mackinder’s Eagle-Owls in Kenya 2004–08.

	2004	2005	2006	2007	2008	MEAN
Breeding sites	7	9	13	12	13	10.8
Territorial pairs	6	9	13	9	12	9.8
Breeding pairs	4	4	9	9	10	7.2
Successful pairs	3	3	6	6	7	5.0
% successful nests ^a	0.50	0.33	0.46	0.67	0.58	0.51
Brood size ^b	4	5	7	9	13	7.6
Young fledged ^c	3	5	7	7	12	6.8
Young fledged/territorial pair	0.50	0.56	0.54	0.78	0.10	0.67
Young fledged/breeding pair	0.75	1.25	0.78	0.78	1.20	0.95
Young fledged/successful pair	1.00	1.67	1.17	1.28	1.71	1.36

^a Number of territorial pairs that were successful.
^b Nest sites for which the number of fledged young was known were assumed to have the same number of young in the nest.
^c Newly discovered nest sites that indicated successful hatching of nestlings; i.e., many pellets and remains found at nest site, were assumed to have fledged one young if no nestling carcass was found at the nest site.

Table 4. Environmental variables affecting Mackinder’s Eagle-Owl productivity at 12 nest sites. Results are for GLMs. * indicates $P < 0.10$; ** indicates $P < 0.05$.

DEPENDENT VARIABLE	BREEDING SUCCESS ^a	NUMBER OF FLEDGED YOUNG
Elevation	$X^2 = 3.14, P = 0.076^*$	$X^2 = 0.44, P = 0.505$
Height of cliff complex	$X^2 = 0.03, P = 0.869$	$X^2 = 2.31, P = 0.129$
Length of cliff complex	$X^2 = 0.31, P = 0.579$	$X^2 = 0.00, P = 0.945$
% vegetation on cliff	$X^2 = 1.35, P = 0.717$	$X^2 = 3.21, P = 0.360$
NND	$X^2 = 0.20, P = 0.653$	$X^2 = 2.34, P = 0.126$
Average canopy height	$X^2 = 0.02, P = 0.879$	$X^2 = 0.16, P = 0.690$
Average canopy density	$X^2 = 1.07, P = 0.301$	$X^2 = 1.37, P = 0.242$
Distance to water	$X^2 = 0.54, P = 0.462$	$X^2 = 2.53, P = 0.112$
Distance to road	$X^2 = 2.63, P = 0.105$	$X^2 = 0.63, P = 0.428$
Distance to agriculture	$X^2 = 0.72, P = 0.397$	$X^2 = 4.24, P = 0.039^{**}$
Distance to human habitation	$X^2 = 2.78, P = 0.095^*$	$X^2 = 1.86, P = 0.173$
Distance to grassland	$X^2 = 2.98, P = 0.084^*$	$X^2 = 3.56, P = 0.059^*$
Distance to forest	$X^2 = 0.48, P = 0.486$	$X^2 = 0.60, P = 0.439$

^a Percentage of territorial pairs raising at least one nestling until fledging.

DISCUSSION

Studies of the density and productivity of African owls are rare, though increasingly important due to mounting threats from climate change, land conversion, use of owls in witchcraft, and human population growth. Ours is one of the few studies on the distribution and reproduction of Mackinder’s Eagle-Owls. Our study showed that these owls are capable of living at high population densities within suitable highland habitat. Although there are few comparable data for this species, our study population lived at a relatively high density and had high productivity compared to a population in southern Africa (Gargett 1978, Appendix). Compared to eagle-owl (*Bubo* spp.) populations in other regions, our study population lived at high density, but had relatively low breeding success and reproductive rates (Appendix).

In this population, attempts at ground-nesting were unsuccessful and nest sites that were easily reached by climbing were occasionally robbed of young or eggs by humans who intended to sell them (P. Kibuthu unpubl. data). Illegal collection of eggs for use in witchcraft has become a major threat to this population in recent years (P. Kibuthu unpubl. data). Although this subspecies has successfully nested on the ground in protected habitats (Sessions 1972, Steyn and Tredgold 1977, Gargett 1978), our observations suggest that human interference at nests may be a factor limiting productivity in this population.

Altitude was the major determinant of the breeding range of Mackinder’s Eagle-Owls in Kenya; on the

Mau escarpment in the Rift Valley, this species was never observed nesting below 2100 m (Sessions 1972).

Results of productivity for this population should be interpreted with caution because owls in our study were not individually marked. We could not assess the potential turnover of individual owls at territories among breeding seasons, which may influence reproductive rates. However, given that productivity remained fairly constant throughout the 5 yr of our study, we suspect this had little effect on our overall results.

Populations of the Eurasian Eagle-Owl (*B. bubo*) living in relatively low-elevation, highly human-altered landscapes had higher densities, lower mean nearest neighbor distances, and similar reproductive rates compared to populations in landscapes only slightly altered by humans (Marchesi et al. 2002). Similar results were also described for the Rock Eagle-Owl (*B. bengalensis*) in India (Pande et al. 2011). Results of this study and a previous study (Ogada and Kibuthu 2009) suggest there may be a link between farming activities and high density in this species. However, breeding success was low and this may be related to human interference at nests and related mortality. Human activities contributed to at least two of the breeding failures we documented and may have had a greater effect than our results indicated, given that the majority of owl injuries and mortalities were related directly or indirectly to human activities. Mortality related to anthropogenic causes is a likely consequence of the owls living in close proximity to humans and has been associated with increased risk of mortality

in other species of eagle-owls, notably the Eurasian Eagle-Owl (Marchesi et al. 2002, Martínez et al. 2006). Intentional and secondary poisoning of owls through the use of highly toxic agrochemicals was the biggest threat to this population and the farmers we interviewed indicated that crop pests (e.g., rodents, weaver birds [*Ploceus* spp.], mousebirds [*Colinus* spp.], and insects) were the greatest threat to their livelihoods (Ogada and Kibuthu 2008).

This study has provided important knowledge about the breeding ecology of Mackinder's Eagle-Owl, a little-known African subspecies of the Cape Eagle-Owl. We found that in Kenya this species breeds successfully in open highland habitat and can breed successfully in areas of high human activity, if nests are located on cliffs or other inaccessible areas. Rainfall patterns were associated with the onset of breeding and mortality is largely related to human causes.

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Appendix. Density, mean nearest neighbor distance (NND) and productivity for four species of eagle-owl (adapted from Marchesi et al. 2002).

SPECIES	COUNTRY	APPROXIMATE LATI- TUDE, LONGITUDE	DENSITY ^a (n)	NND (km) (n)	BREEDING SUCCESS ^b (n)	ANNUAL PRO- DUCTIVITY (X̄/P/PAIR/ Yr)		YOUNG PER TERRITORIAL PAIR (n)		YOUNG PER BREEDING PAIR (n)		YOUNG PER SUCCESSFUL PAIR (n)		REFERENCE
<i>B. bubo</i>	France	43°47'N, 004°51'E	16.00 (32)	1.4 (32)	74 (50)			1.44 (50)		1.63 (347)		1.95 (37)		Bergier and Badian 1979
<i>B. bubo</i>	France	43°48'N, 005°22'E	15.30 (59)	1.8 (59)	92 (347) ^c							1.83 (306)		Penteriani et al. 2002
<i>B. bubo</i>	France	44°00'N, 003°30'E	0.44 (22)									1.89 (9)		Cochet 1985
<i>B. bubo</i>	France	43°17'N, 003°26'E	1.47 (25)		87 (107)			1.73 (107)				1.99 (93)		Defontaine and Ceret 1990
<i>B. bubo</i>	Germany													
<i>B. bubo</i>			8.00 (8)	4.4 (36)						1.17 (98)		1.59 (37)		Mebs 1972
<i>B. bubo</i>	Spain	42°00'N, 002°30'E	5.71 (40)	2.4 (40)						2.04 (62)		2.30 (54)		Beneyto and Borau 1996
<i>B. bubo</i>	Spain	38°00'N, 001°30'W	2.00 (142)	4.6 (19)				1.70 (55)		2.90 (42)				Martínez et al. 1992
<i>B. bubo</i>	Austria	48°20'N, 015°45'E		2.4				0.99		1.30		2.00 (703)		Frey 1992
<i>B. bubo</i>	Switzerland	46°25'N, 010°00'E	0.92 (30)	6.5 (18)	92 (50)			1.32 (50)				1.80 (46)		Haller 1978
<i>B. bubo</i>	Sweden			8.5 (29)	40 (219)			0.60 (219)		0.90 (145)		1.60 (87)		Olsson 1979
<i>B. bubo</i>	Czech Rep.	49°30'N, 017°00'E	1.16 (50)	4.3 (81)	41 (231)			0.62 (231)		1.24 (115)		1.96 (73)		Kunstmüller 1996
<i>B. bubo</i>	Italy	46°04'N, 11°08'E	1.82 (24)	3.5 (169)	49 (160)			0.89 (160)		1.81 (21)		1.81 (79)		Marchesi et al. 2002
<i>B. virginianus</i>	USA		17.00 (12)		81 (28)					1.95 (28)		2.36 (24)		Frank and Lutz 1997
<i>B. virginianus</i>	USA		8.02 (13)							1.28 (60)				Adamcik et al. 1978
<i>B. bengalensis</i>	India		17.0 (34)	3.3 (34)	91 (88)			1.5 (88)						Pande et al. 2011
<i>B. c. mackinderi</i>	Zimbabwe		1.23 (8)	2.2 (8)										Gargett 1978
<i>B. c. mackinderi</i>	Kenya		50.00 (10)											Sessions 1972
<i>B. c. mackinderi</i>	Kenya	00°11'S, 04°48'E	24.5 (15)	1.9 (13)	51 (49)			0.67 (49)		0.95 (36)		1.36 (25)		This study

^a Number of pairs/100 km².

^b Percentage of territorial pairs raising at least one nestling until fledging.

^c Estimation of territory size based on approximation of distances between land features and between nest sites.