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Authors: Pande, Satish, Pawashe, Amit, Mahajan, Murlidhar N., Joglekar, Charu, and Mahabal, Anil

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EFFECT OF FOOD AND HABITAT ON BREEDING SUCCESS IN SPOTTED OWLETS (*ATHENE BRAMA*) NESTING IN VILLAGES AND RURAL LANDSCAPES IN INDIA

Satish Pande,[1] Amit Pawashe, Murlidhar N. Mahajan, and Charu Joglekar
ELA Foundation, C-9, Bhosale Park, Sahakarnagar-2, Pune 411009, Maharashtra, India

Anil Mahabal
Zoological Survey of India, WRS, Akurdi, Pune, 411044, Maharashtra, India

Abstract.—We measured breeding success of Spotted Owlets (*Athene brama*) in two habitats, villages (human habitations) and rural areas (open country) in India. We quantified habitat types in 500-m-radius circles surrounding 53 nest sites and examined owlet pellets collected at nest sites in both areas, to describe owlet diet. Breeding success was higher in the human habitations than in open country (3.3 young per successful nest vs. 2.2, respectively, $P < 0.001$). Diet at nests in human habitations contained more rodents and other noninsectivorous non-arachnid prey (by biomass and species richness) than those in open country ($P < 0.01$ for rodents and $P < 0.001$ for other prey). We used multivariate linear regression to examine which factors of habitat and diet most influenced breeding success and found that only the percentage of rodents, and the percentage of other prey were included as statistically significant variables in our final model. Thus, the most significant determinant of breeding success of Spotted Owlets was high-value prey items, which were more abundant in the areas of human habitations.

Key Words: *Spotted Owlet*; Athene brama; *breeding success*; *food*; *nesting habitat*; *reproductive success*.

EFECTO DEL ALIMENTO Y EL HÁBITAT SOBRE EL ÉXITO DE NIDIFICACIÓN DE *ATHENE BRAMA* EN PUEBLOS PEQUEÑOS Y PAISAJES RURALES EN INDIA

Resumen.—Medimos el éxito reproductivo de *Athene brama* en dos ambientes, pueblos pequeños (habitaciones humanas) y áreas rurales (campos abiertos) en India. Cuantificamos los tipos de hábitat en círculos de 500 m de radio ubicados alrededor de 53 sitios de nidificación, y examinamos egagrópilas colectadas cerca de los nidos en ambas áreas para describir la dieta de la especie. El éxito reproductivo fue mayor en las habitaciones humanas que en los campos abiertos (3.3 crías por nido exitoso vs. 2.2 crias por nido, respectivamente, $P < 0.001$). La dieta de las aves que anidaron en las habitaciones humanas incluyó más roedores y otras presas no insectívoras distintas a arácnidos en términos de biomasa y riqueza de especies que la dieta de las aves de los campos abiertos ($P < 0.01$ para roedores y $P < 0.001$ para otras presas). Empleamos análisis de regresión lineal multivariada para examinar cuáles factores del hábitat y la dieta influenciaron más la dieta y el éxito reproductivo. Sólo el porcentaje de roedores y el porcentaje de otras presas se incluyeron como variables estadísticamente significativas en nuestro modelo final. Por lo tanto, el factor determinante del éxito reproductivo de *A. brama* más importante fueron los ítems presa de alto valor, los cuales fueron más abundantes en áreas con habitaciones humanas.

[Traducción del equipo editorial]

Other than large cities and metropolises, villages account for most of the human habitations of rural India. The residential areas in villages consist of traditional mud and stone houses, temples, ruins, schools, and public buildings. These structures offer numerous nesting sites to Spotted Owlets (*Athene brama*; Jerdon 1862, Baker 1927, Dewar 1929, Ali and Ripley 1969, Kumar 1985). On the fringes of villages, and along riparian areas within villages, are dilapidated buildings that also offer a number of holes, suitable for nesting for Spotted Owlets and mynas (*Acridotheres tristis* and *A. fuscus*), House Sparrows (*Passer domesticus*), Rose-ringed Parakeets (*Psittacula krameri*), Indian Robins (*Saxicoloides fulicata*), and Barn Owls (*Tyto alba*). In rural open country

[1] Email addresses: pande.satish@gmail.com and satishpande@hotmail.com

outside the villages, the nests of owlets are predominantly in existing tree cavities, and also under bridges in wall holes. In India, owls are generally threatened due to superstition (Pande et al. 2005). Also, in recent years, tree-felling in rural areas has become intense, and as a result, Spotted Owlets have lost many tree-cavity nests. Spotted Owlets are a common resident species in villages as well as in rural areas, and they are territorial throughout the year (Ali and Ripley 1969). These birds are mostly crepuscular and nocturnal, but occasionally hunt during the daytime. At night, they often hawk insects in flight and hunt rodents and other creeping prey close to a source of illumination (Ali and Ripley 1969, Pande et al. 2004). Owlet diet includes small rodents and birds, geckos and other lizards, arachnids, insects, molluscs, and other prey (Baker 1927, Ali and Ripley 1969, Jain and Advani 1984, Kumar 1985, Duncan 2003, Jadhav and Parasharya 2003, Pande et al. 2004). The object of this study was to determine the effect of habitat and food on breeding success of Spotted Owlets in villages and rural areas in India. The analyses of the main determinants of breeding performance are crucial to understanding the effect of human disturbance on this species. Such factors are complex, with possible intrinsic variances in reproductive parameters within the same population, and represent one of the most challenging problems for ecologists (Krebs 1991, Penteriani et al. 2002).

Methods

Study Area. The study area consisted of 32.8 km^2 in and around Saswad and Kodit villages (18°19′N to 18°20′N and 73°57′E to 74°01′E) in Pune district, Maharashtra, India. This area is semiarid, with an annual rainfall of $<$500 mm. Elevation ranges from 764–846 m above sea level. The approximate human population of these villages is 31 000 and 5400 respectively. The adjacent Pune city has an approximate human population of 3.5 million.

Census of Nesting Pairs. In 2003 and 2004, occupied nest sites of Spotted Owlets were located by (1) information from local residents, or (2) search of probable nests sites, following passive auditory surveys at dawn and dusk during the breeding season (December–April), when owlet vocal displays are highest (Ali and Ripley 1969). Nest locations were recorded using a GPS, and distances between nearest neighbors (NND) were calculated from the coordinates (Newton et al. 1977). Regularity of nest spacing was computed for both the HH and OC groups by means of *G*-statistic (Brown and Rothery 1978; the index in this method ranges from 0 to 1 and values $>$0.65 indicate a uniform nest distribution).

Nesting Habitat Categorization. Following Penteriani et al. (2002), a simple model was adopted to categorize the nest sites into two groups, human habitations (HH) or open country (OC), by identifying the relative percentage of each of five landscape cover types found within a circle of 500 m radius centered at the nest site. The five landscape cover types were (1) residential habitat (including residences, temples, ruins, fortifications, and other anthropogenic structures); (2) agricultural habitat; (3) water body (river, stream, irrigation bund, tank or well); (4) open land (noncultivable or fallow area with scrub and interspersed huts or small temples) and (5) low undulating hills and ravines. The relative percentages were estimated by look-down visual surveys conducted from high vantage points (Bibby et al. 1998). The distance from each nest to the nearest source of light was also estimated, and the source of illumination was categorized as one of the following: light from a house, streetlight, public area or hut. The radius of 500 m was chosen because the Spotted Owlets usually forage near the nest sites within this range (Pande et al. 2004).

Diet. At least three visits were made each year to each of the nest sites during the breeding seasons of 2003 and 2004. Owlet pellets were collected from all the nest sites and were pooled separately for the two groups, HH and OC. Prey in pellets were identified to orders, families, genera or species by using published literature (Gude 1914, Ellerman 1961, Tikader and Bastawade 1983, Tikader and Sharma 1992, Corbet and Hill 1992, Agrawal 2000, Daniel 2002, Ramanujam 2004) or by comparing with specimens in the collection of the Zoological Survey of India, Pune. Pellet contents were categorized as rodents, arachnids, insects, or other prey species (Table 1). The fresh masses of species were estimated by weighing specimens in the field using Pesola scales (nearest 0.1 g) or by using published masses (Spillet 1966, Khajuria 1968, Ranade 1989, 1992, Kanakasabai et al. 1998, Pande et al. 2004; Table 1). Relative contribution of each prey item to the overall biomass of each of the four prey categories was calculated by multiplying the proportion of each prey item (for each of the four prey categories) and the mean body weight of an individual item. Species richness of food items was determined for each nest in the two groups. Richness was defined as number of identified prey species in the diet (Magurran 1988).

Breeding Outcome. Of the occupied nests found, seven randomly chosen but accessible nests were intensively studied for one year (2003) during the breeding season for the documentation of clutch size, egg size and weight, laying interval, incubating period, hatching interval, loss of egg weight during incubation, and eggshell thickness. Eggs were weighed with Pesola scales to the nearest 0.1 g. Eggshell thickness was measured with a plastic vernier caliper to the nearest 0.01 cm. We also recorded the age at which nestlings first opened their eyes, stood, preened, flapped their wings, and fledged, as well as the nestling masses (from 0–4.5 wk). For these seven nests, we determined hatching success rate (the percentage of eggs laid that hatched), fledging success (the percentage of nestlings hatched that fledged), nesting success (the percentage of nests that fledged at least one chick), and nestling survival [calculated using the Mayfield Exposure Day method (Mayfield 1961, Sutherland 2000)].

For all occupied nests in 2003 and 2004, we measured post-fledging dependence period, number of young fledged per active nest, number of young fledged per oc-

Table 1. Diet of Spotted Owlets as determined from pellets at two sites in Pune district, Maharashtra, India, human habitations (villages) and rural open country.

Species	Human Habitations[1] N (%)	Open Country[2] N (%)	Approximate Mass (g)[3]
RODENTS	1025 (27.6)	1049 (5.2)	
Mus musculus	719	736	15 (10–28)
Mus saxicola	4	4	22 (15–30)
Mus booduga	4	5	12.5 (10–15)
*Suncus stoliczkanus**	154	157	17.5 (15–20)
Suncus etruscus	14	15	2 (1.4–3)
Suncus murinus	8	8	43.5 (23.2–147.3)
Other unid. Muridae	48	50	8–20
*Golunda ellioti**	39	37	75 (50–100)
Bandicota sp. (Juvenile)	2	17	273
Tatera indica (Juvenile)	14	8	162
Rattus sp. (Juvenile)	15	7	160
Vandeleuria oleracea	4	5	15 (10–20)
ARACHNIDS	192 (5.2)	780 (3.9)	
Mesobuthus tammulus	115	467	1–3
Mesobuthus pachyurus	5	22	1–2.5
Orthochirus bicolor	17	71	1.0–1.5
Heterometrus xanthopus	46	181	2.5–3.5
Galeodes indicus	5	23	1.2
Galeodes orientalis	2	9	2
Galeodes sp. (unid.)	3	7	2
OTHER PREY SPECIES	640 (17.4)	268 (1.3)	
Gastropoda: snails*			
Thiara scabra	23	16	1.5–2
Lamellaxis gracile	9	5	1.5–2
Myriapoda: Millipedes*	46	27	Up to 4
Reptilia*			
Gekkonidae: Geckos	361	86	8–18
Agamidae: *Calotes* and	15	7	24–35
Sitana spp.	4	4	5–15
Scincidae: Skinks (*Mabuya* sp.)	12	6	8–18
Aves*			
Warblers (*Prinia* spp.)	130	24	6–10
Finch Larks (*Eremopterix* and *Ammomanes* spp.)	31	89	5–8
Mammalia			
Chiroptera: *Pipistrellus* sp.*	9	4	Up to 15
INSECTS (Orders)	1844 (49.8)	18048 (89.6)	
Coleoptera	996	10084	Up to 1
Orthoptera	415	3248	Up to 4
Mantodea	147	2165	Up to 4
Hymenoptera	131	812	Less than 0.5
Odonata	41	631	Up to 2
Lepidoptera	68	1082	Up to 3
Dictyoptera (Blattodea)	46	26	Up to 1
TOTAL	3701 (100)	20145 (100)	

[1] Total N = 3701 prey items in 1430 pellets from human habitations.
[2] Total N = 20145 prey items in 2015 pellets from open country.
[3] Masses of species marked by * are from our field data and all other masses are cited from literature.

Table 2. Reproductive rates of Spotted Owlets in Pune district, Maharashtra, India, 2003–2004 (years combined).

REPRODUCTIVE PARAMETER	HUMAN HABITATION STUDY AREA (*N*)	OPEN COUNTRY STUDY AREA (*N*)	ALL (*N*)
Young fledged per occupied nest	3.2 (22)	1.35 (31)	2.15 (53)
Young fledged per active nest	3.2 (22)	1.82 (23)	2.53 (45)
Breeding success[1]	3.2 (22)	2.2 (19)	2.78 (41)

[1] Defined as number of fledged chicks per successful nest.

cupied nest, and breeding success. Post-fledging dependence period was measured by repeated visits to each nest area to relocate the parents and young until the young were not seen with parents. An occupied nest was one where one pair of Spotted Owlets was present during breeding season even if there was no evidence that eggs were laid. An active nest was defined as one where at least one egg was laid or an adult was seen incubating, and a breeding pair was defined as one that laid at least one egg. A successful nest was one that fledged at least one young (Postupalsky 1974, Steenhof 1987). Breeding success was defined as the number of fledged young per successful nest.

Statistical Methods. Data are given as means for continuous variables (habitat, species richness, percent biomass, breeding success) and percent for categorical variables (distance from light source). Distance from light source was categorized into three groups (<100 m, 100–500 m and >500 m). Breeding success data for 2003 and 2004 were pooled in the analysis because there was no difference in breeding success between years. Offspring survival between two nest site groups (HH and OC) was tested by chi-square test. Correctness of our classification of nest sites in two nest site groups was tested by discriminate function analysis (DFA; Sokal and Rohlf 1995). Habitat and percent biomass variables were tested for normality. All the habitat variables except percent agriculture were skewed; thus, the following variables were normalized using log-transformations: percent residential, percent open land, percent water body, percent insects in diet, and percent arachnids. Hilly area was normalized using (1-1/square root). Differences between two nest site groups for various habitats, species richness, percent biomass, and breeding success were tested by Student's *t*-test and distance from light source by chi-square test. Associations between habitats and diet, breeding success and habitat, and diet and distance from a light source were tested by Pearson correlation. We used stepwise forward multivariate regression analysis as a global test for estimating determinants of breeding success. Statistical analysis was done with SPSS 11.0 software.

RESULTS

Breeding Chronology and Reproductive Rates. We located a total of 53 occupied Spotted Owlet nests in 2003 and 2004. Spotted Owlets laid eggs and began incubating during December–February; chicks fledged in February–March and the post-fledging dependence period was from April–November. Fledglings dispersed during November–December and began courtship and pairing behaviors in December–January.

For the seven intensively studied nests, clutch size $\bar{x}$ = 2.2 (range = 1–4), egg size $\bar{x}$ = 32.1 mm × 26.7 mm (range = 34 × 25 mm to 33 × 28 mm), egg mass $\bar{x}$ = 10.5 g (range = 9–12 g), and eggshell thickness $\bar{x}$ = 0.13 mm (range 0.11–0.15 mm). Laying interval was 24 hr for 2–4 eggs, incubation period was 31–32 d, and hatching asynchronous at intervals of 24 hr. At these nests, nestlings first opened their eyes at 5–6 d, stood, preened and flapped their wings at 7–10 d, and fledged at 31–32 d at a mass of 90–115 g. Hatching success was 37.5%, fledging success was 72.7%, and nesting success 53.1%. The daily nestling survival over 31 d was 33.5% (N = 7 nests, all from the OC habitat). The post-fledging dependence period was 8 mo.

Of the 53 occupied nests studied, 45 (84.9%) were active and 41 (77.4%) were successful. All the occupied nests in HH were active as well as successful, while 74% and 61.2% nests in OC were so (Table 2). Breeding success (number of young fledged per successful nest) was greater in HH than in OC ($P < 0.001$, Table 2). Similarly, the number of nestlings per occupied nest, as well as per active nest, was greater in HH than in OC ($P < 0.001$, Table 2). Fourteen nests in HH fledged large broods of 3–7 chicks each, but only six nests in OC did so; eight nests in HH produced 0–2 chicks each, but 25 nests in OC did so ($P = 0.001$).

Habitat Analysis. DFA significantly discriminated between the two groups (HH and OC), based on four variables (residential, water body, agriculture and hilly area). The discriminate equation was D = −2.250 + 0.062 (% residential) + 0.015 (% water body) + 0.004 (% agriculture) – 0.012 (% hilly area). Correct classification was obtained for 91% of nest sites in HH and 100% in OC. The percentage of residential habitat percentage was higher in HH ($P < 0.001$), whereas percentages of agricultural,

Table 3. Comparison of Spotted Owlet nest-site habitat and diet and two sites in Pune district, Maharashtra, India, human habitations (villages) and rural open country.

	HUMAN HABITATIONS (N = 22)	OPEN COUNTRY (N = 31)	P[1]
Habitat around nest site (%)			
Residential	74	3	<0.001
Agriculture	14	56	<0.001
Water body	6	14	ns
Open land	5	22	<0.001
Hilly area	1	5	<0.001
Distance to light source (%)			<0.001
<100 m	86	23	
100–500 m	14	45	
>500 m	0	32	
Owlet diet			
Species richness			
Rodents	2.6	1.8	<0.05
Insects	4.9	4.9	ns
Arachnids	0.5	0.9	ns
Other prey	1.8	0.6	<0.001
Percent biomass			
Rodents	72	53	<0.05
Insects	5	35	<0.05
Arachnids	2	6	ns
Other prey	21	6	<0.001

[1] P is by t-test except for distance from light source, which was determined by chi-square test.

open land, and hilly areas were higher in OC ($P <$ 0.001; Table 3). The nearest neighbor distance (NND) in HH was 0.73 km and 1.04 km in OC, and the nests were uniformly distributed (G-statistic >0.65).

Diet Analysis. A total of 3445 pellets were collected in two years, 1430 from HH and 2015 from OC. Owlet diet differed between HH nest sites and OC nest sites (Table 1, 3). Average species richness of prey items at HH sites was significantly higher for rodents and other prey, compared to the OC sites. Similarly, for relative percent biomass of prey items, HH nest sites had greater percentages of rodents and other prey in the pellets and correspondingly fewer insects in the pellets, compared to OC (Table 3).

Univariate Associations of Breeding Success with Habitat and Diet. Breeding success of Spotted Owlets was positively associated with the percentage of residential habitat within nest circles, inversely associated with the percentages of agriculture and open land habitats (Table 4), and negatively correlated to the distance to the nearest light source (Table 4). Breeding success was also positively correlated with species richness in the diet for all four prey categories (rodents, insects, arachnids, and other prey, Table 4) and the percentage biomass for rodents and other prey, but inversely associated with the percentage of insects (Table 4).

Multivariate Determinants of Breeding Success. We first performed a collinearity diagnostic, and as a result, we excluded percent insect biomass from the analysis. We used forward stepwise multiple linear regression analysis with breeding success as dependent variable and all five habitats variables, the four diet variables for species richness, three diet variables for percent biomass, and distance of light from nest site as independent variables. The percent biomass for rodents and other prey (P < 0.01) were the most significant determinants of breeding success with total r^2 = 0.50 (Table 5).

DISCUSSION

Residential habitat was predominant in the human habitation study area in spite of the fact that some of the nests were located along fringe areas near open country. Agriculture, open land, and hilly habitat were more common in the open country study area. Residential habitat was not entirely absent in open country because some huts, small

Table 4. Univariate correlations of breeding success with habitat and diet.

Variable	Correlation with Breeding Success (Pearson correlation coefficent)[1]
Percent habitat	
Residential	0.52*
Agriculture	−0.34*
Water body	−0.13
Open land	−0.36*
Hilly area	−0.18
Distance to light source	−0.58*
Diet	
Species richness	
Rodents	0.55*
Insects	0.33*
Arachnids	0.33*
Other prey	0.64*
Percent biomass	
Rodents	0.41*
Insects	−0.60*
Arachnids	−0.10
Other prey	0.62*

[1] * denotes $P < 0.05$.

temples, and other minor anthropogenic structures were present. In the human habitation study area, Spotted Owlets traditionally nest in holes or crevices in human-made structures, while in open country they nest in existing cavities in trees. The traditional nest sites such as natural tree holes are diminishing in the OC due to an increase in tree-felling. The response of Spotted Owlets to this habitat destruction is their increasing occupation of newer and alternative nest sites such as holes in earth cuttings and earthen walls of wells (Pande et al. 2006). In the past, these alternative nest sites were not considered traditional nest sites (Baker 1927) and were referred to as unusual (Jerdon 1862). Spotted Owlets also readily accept and occupy nest boxes (Naik 2004). We believe that the occupation of alternative nest sites in the rural areas is an expression of their ability to adapt. Paucity of natural nest sites such as tree cavities in OC is likely to increase in the future, because habitat disturbance continues unabated.

In HH, the nearest neighbor distance (NND) was 0.7 km as compared to 1.0 km in OC. Proximity of nests is likely to produce aggressive encounters between the pairs in adjacent nest sites as well as with other cavity-nesting birds, because Spotted Owlets are territorial birds which occupy and defend their nest sites and home ranges throughout the year. Hole-nesting birds like Common Myna (*Acridotheres tristis*), Jungle Myna (*Acridotheres fuscus*), Oriental Magpie Robin (*Copsychus saularis*), Indian Robin (*Saxicoloides fulicata*), Rose-ringed Parakeet (*Psittacula krameri*) and Barn Owl (*Tyto alba*) also compete with Spotted Owlets for the existing nest holes (S. Pande pers. observ.). It is possible that more energy is expended in the defense of the territory against conspecifics by each pair in HH, compared to those in OC, because of the shorter NND in HH. Such interactions are intensified during the breeding season and fights between territorial birds can adversely affect fecundity through various mechanisms (Hickey 1942, Lack 1954, Cade 1960, Ratcliffe 1962). However, this did not occur in our study, as reproductive rates were significantly higher in HH, in spite of closer nest spacing. It is also possible that the NND we reported do not actually reflect higher density or closer neighbors in HH; we did not find nests in an unbiased way, and it is probable that landowners were more likely to find and report nests in the villages than in the sparsely populated rural areas. Future study of the relationship between breeding success and density in this population of Spotted Owlets may yield interesting results.

Spotted Owlets are likely dietary generalists. In HH, open sewers and drains were abundant; thus, rodents were plentiful. Other prey species like geckos and other lizards were also found in HH in significant numbers. It is expected that the Spotted Owlets in HH would consume the more profitable high-energy foods such as rodents and lizards, as

Table 5. Multivariate determinants of breeding success, based on forward stepwise multivariate regression analysis with breeding success as the outcome and habitat and diet factors as independent variables. (Only the final model is shown.)

Variable	Standardized Beta	t	r^2	P
Percent biomass (rodents)	0.37	3.75	0.129	<0.001
Percent biomass (other prey)	0.59	6.03	0.369	<0.001
TOTAL			0.498	

per the law of optimal diet (Kamil and Sargent 1981, Donázar 1987, Kamil et al. 1987, Penteriani et al. 2002), because they are available. The negative correlation between breeding success and percent insect biomass in OC also may be significant. There are important conservation implications, because if habitat destruction and tree-felling leading to nest-site destruction in OC continues unabated, there may be a further negative effect on the already-lower breeding success in OC in the future, because alternative nest sites for the cavity-nesting birds are limited in rural areas.

Our observations on breeding chronology conformed to previous reports (Ali and Ripley 1969, Kumar 1985). However, the data on eggshell thickness, daily survival of nestlings, hatching success, nesting success, and post-fledging dependence period were reported here for the first time for this species.

Spotted Owlets are crepuscular and at night they prefer to hunt near a source of light (Ali and Ripley 1969). Sources of light were closer to the nest sites in HH and we found significant negative correlation between distance of light from the nest site and breeding success. This could affect breeding success by causing the owlets to expend more energy when the source of light is further from the nest site. Higher energy expenditure in moving to and from distant hunting areas to nests is known to adversely affect fecundity in Eurasian Eagle-Owls (*Bubo bubo*; Valverde 1967, Schoener 1971, Penteriani et al. 2002). However, we note that the distance to the nearest light source was also correlated to the percentage of residential habitat, and the relationship between breeding success and light may simply reflect the differences between HH and OC, which were primarily related to prey availability.

The most significant factor influencing breeding success of Spotted Owlets was food, particularly rodents and other prey, including lizards. These constitute high-value foods and high-value food items may improve the chance of offspring survival (Penteriani et al. 2002). Thus, our findings are consistent with results reported earlier for other owl species (Purroy 1974, Martínez et al. 1992).

Conclusions. Breeding success of Spotted Owlets in human habitations was significantly higher than that of birds in rural open country. The most important determinant of breeding success of Spotted Owlets was a diet including a relatively high percentage of rodents and other prey, which were classified as high-value foods.

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