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EFFICIENT PLACEMENT OF NEST BOXES FOR THE LITTLE OWL (*ATHENE NOCTUA*)

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ABSTRACT.—The use of artificial nest boxes to bolster populations of endangered cavity-nesting birds has increased significantly, but spatial variation of nest-box occupancy rates and breeding success within a nest-box population has been little studied. In a case study with 798 Little Owl (*Athene noctua*) nest boxes established in central Germany, we analyzed the dependence of occupancy rate and breeding success on the characteristics of the surrounding habitat. The analysis focused on two aspects of general concern for nest-box management: (1) whether nest boxes were occupied for breeding or were left unoccupied, and (2) whether Little Owls had different reproductive rates, depending on the location of nest boxes. A high resolution (1 × 1 m) land-use map was used to analyze species-habitat relationships, and Generalized Linear Mixed Models were used to predict suitable nest-box locations. During the period from 2004 to 2006, 544 (68%) of the nest boxes were never occupied, 144 (18%) housed birds with low breeding success and only 108 (14%) housed pairs that produced more than 2.35 nestlings annually, a reproductive rate thought necessary for population stability. Nest boxes were more likely to be occupied if they were located near orchards, at lower altitude, and in areas of higher densities of fields and less forest. Higher breeding success was associated with fallow fields and field margins, and with greater distance to roads and forests. Our results suggested that the efficiency of this nest-box program could be substantially increased if unoccupied nest boxes were relocated to sites where occupancy is more likely, and if unproductive nest boxes were relocated to locations that would enhance breeding success.

KEY WORDS: *Little Owl*; Athene noctua; *breeding success*; *nest boxes*; *population management*; *spatial modeling*.

EMPLAZAMIENTO EFICIENTE DE CAJAS NIDO PARA *ATHENE NOCTUA*

RESUMEN.—El uso de cajas nido artificiales para reforzar las poblaciones de aves amenazadas que nidifican en cavidades ha aumentado significativamente, pero la variación espacial de las tasas de ocupación de las cajas nido y el éxito reproductivo dentro de una población que utiliza cajas nido han sido poco estudiados. En un caso de estudio con 798 cajas nido de *Athene noctua* establecidas en el centro de Alemania, analizamos la dependencia de la tasa de ocupación y el éxito reproductivo con las características del hábitat de los alrededores. El análisis se enfocó en dos aspectos de interés general para el manejo de poblaciones con cajas nido: (1) si las cajas nido estaban ocupadas para reproducción o no fueron ocupadas, y (2) si *A. noctua* tuvo tasas reproductivas diferentes, dependiendo de la ubicación de las cajas nido. Un mapa de uso del territorio de alta resolución (1 × 1 m) fue usado para analizar las relaciones especie-hábitat y se usaron Modelos Mixtos Lineales Generalizados para predecir la ubicación apropiada de las cajas nido. Durante el período desde 2004 a 2006, 544 (68%) cajas nido nunca fueron ocupadas, 144 (18%) albergaron aves con bajo éxito reproductivo y sólo 108 (14%) albergaron parejas que produjeron más de 2.35 pichones por año, una tasa reproductiva que se estima necesaria para la estabilidad de la población. Las cajas nido tuvieron una mayor probabilidad de ser ocupadas si estaban ubicadas cerca de huertas de frutales, a baja altitud y en áreas de mayor densidad de campos y con menos bosque. Un éxito reproductivo

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mayor fue asociado con campos de cultivo en reposo y márgenes de campos, y con mayores distancias a caminos y bosques. Nuestros resultados sugirieron que la eficiencia de este programa de cajas nido puede ser substancialmente mejorada si las cajas nido no ocupadas fueran relocalizadas a sitios con mayor probabilidad de ocupación, y si las cajas nido improductivas fueran relocalizadas a sitios que realzaran el éxito reproductivo.

[Traducción del equipo editorial]

Nest boxes have been widely used in species conservation of cavity-nesting birds (Newton 1994, Lalas et al. 1999, Stamp et al. 2002, Avilés and Parejo 2004, Katzner et al. 2005) and have substantially contributed to increasing the populations of endangered species (Wiley et al. 1991, Cade and Jones 1993, Bolton et al. 2004, Priddel et al. 2006). Although many nest-box projects proved successful, nest boxes have also been identified as ecological traps (Gehlbach 1994, Avilés and Parejo 2004, Mänd et al. 2005), where in an ''attractive sink'' the mortality exceeds the reproduction rate (Delibes et al. 2001, Battin 2004, Mänd et al. 2005). Considering the risk that nest boxes may fail to increase population viability, there is a need to evaluate the efficacy of nest-box programs. It is essential that nest boxes are installed at locations where the surrounding habitat is suitable, and where it is likely that breeding pairs can successfully raise young. Efficient placement of nest boxes can spare labor and cost, and may reduce the critical time span until a threatened population reaches sustainable size. This study is to our knowledge the first one to investigate the spatial variation of breeding success within a nest-box program.

The ecology of the Little Owl (*Athene noctua*) has been well studied (Schönn et al. 1991, Exo 1992, Hölzinger et al. 2001, Hardouin et al. 2006, Van Nieuwehuyse et al. 2008), including nest-site selection (Tomé et al. 2004) and modeling of populations (Schaub et al. 2006) and habitat (Van Nieuwehuyse et al. 2001, Zabala et al. 2006). In Hesse, central Germany, nest boxes were installed for Little Owls to compensate for the shortage of natural nesting sites formerly present in old fruit trees. In the course of this campaign, the Little Owl population in Hesse increased from 234 pairs in 1987 to 938 pairs in 2005 (Burbach 1997, HGON AG Eulen 2005). This trend is in contrast to that observed in other states in Germany (Jöbges 2004) and Europe (BirdLife International 2004) where the Little Owl is generally decreasing, mainly as a result of reduced nesting habitat and decreased food availability, due to the intensification of agriculture. Although there was an obvious increase in the number of Little Owls breeding in nest boxes within our study area, it was unclear what habitat features were associated with differences in occupancy and productivity within the study area.

As a complement to the ecological studies mentioned above, we addressed the conservation of the Little Owl through provision of artificial nest boxes. The primary goal of our study was to analyze nest-box occupancy for breeding and breeding success of Little Owls included in the nest-box program, and to identify unfavorable nest-box locations. Nest boxes were installed without a prescribed minimum distance in this campaign, and we analyzed whether relocation of some of the nest boxes might increase owl reproduction. Specifically, we investigated the relationships between habitat and both, nest-box occupancy for breeding and owl reproductive rates in nest boxes.

METHODS

Study Area. The study area covered the catchment area of the Nidda River in the middle of Hesse, Germany. The southern boundary was located 10 km northeast of Frankfurt. The study area comprised 1620 km^2 at an elevation increasing from 106 m in the south to 765 m in the northeast. Although the central lower part of the study area was intensively exploited for agriculture, the higher western and eastern highlands of the Taunus and the Vogelsberg encompassed wider areas of forests and meadows. Depending on altitude, mean annual temperature and mean annual rainfall ranged from 5°C to 10°C and 500 mm to 1300 mm, respectively (Deutscher Wetterdienst 2005).

Nest Boxes. It is widely acknowledged that Little Owls are only found in orchards if old fruit trees are present or nest boxes are provided (Van Nieuwehuyse et al. 2008). Orchards are a traditional land-use form in Europe, where rows or groups of fruit trees, mainly apple, pear, cherry, and plum are loosely dispersed on managed grassland. Standard apple trees whose branches start from 1.5 m above the ground (as opposed to half-standard trees, which have a shorter growth form) were used by members of the nature conservation society ''Hessische Gesellschaft für Ornithologie und Naturschutz'' to install 798 nest boxes for the Little Owl within the Nidda catchment area. Installation of nest boxes began in the early 1990s. Nest boxes included in our analysis were placed ≥1 yr prior to this investigation. The nest-box design followed Hölzinger (1987); box size and entrance hole were identical in all nest boxes. The two nearest boxes were 19 m apart, and the average distance to the nearest nest box was 148 m.

We compiled breeding records of Little Owls in the nest boxes between 2004 and 2006. All nest boxes were inspected to determine whether they were occupied, as well as to count and to ring nestlings, once each year during May and June, when the young were not yet able to fly. In this study, we considered a nest box occupied for breeding if eggs or nestlings were present or if there were signs of nest failure, such as eggs, shell fragments, or dead young. Double nest checks (Mayfield 1961, Steenhof and Newton 2007) were not conducted to minimize disturbance during the nestling period. Nest boxes were not visited before 15 May to reduce the risk of nest failure caused by disturbing incubating birds. The reproductive rates in our study were compared to the mean reproductive rate necessary for population stability, 2.35 fledglings per breeding pair per year, based on long-term ring recovery records of the Little Owl in Germany and the Netherlands (Exo and Hennes 1980).

The number of years in which a nest box was occupied by a breeding pair (occupancy rate), and the number of nestlings produced in those years (reproductive rate) was recorded for each nest box. We assumed that Little Owls were able to identify appropriate nest-box locations within the landscape. We classified all nest-boxes into three categories according to occupancy and reproductive rates: (1) nest-boxes that were not occupied by breeding pairs of Little Owls in 2004–2006, (2) nest-boxes that were occupied by a breeding pair at least once, but produced fewer than 2.35 nestlings in the years they were occupied, and (3) nest-boxes where breeding pairs produced ≥2.35 nestlings per year.

Environmental Variables. From digital maps, we extracted environmental variables considered important for the persistence of Little Owls (Hölzinger et al. 2001, Van Nieuwehuyse et al. 2008). Environmental information included a high resolution (pixel size: 1 × 1 m) habitat map derived from color infrared (CIR) aerial photographs from 2005 (EFTAS 2007) and a digital elevation model (pixel size: 20 × 20 m, HLBG 2005). These maps covered the complete area of 1620 km² of the Nidda catchment (Table 1). The habitat map was constructed from an unsupervised and a supervised classification. Information on the European Union integrated administrative and control system (IACS) was incorporated to classify the habitat map. User accuracy of correctly categorized map pixels reached 85% (EFTAS 2007). The habitat map originally contained 24 habitat classes, which we merged into 11 classes (coniferous forests, deciduous forests, mixed forests, arable land, grassland, fallow, garden, orchard, water, urban area, other areas) relevant for Little Owls. From these maps we derived two types of environmental variables, which were used in combination: (a) local variables, which relied on the map pixel under consideration, and (b) matrix variables, which were derived from the surrounding of the pixel, within a radius of 400 m. This radius corresponds to the year-round average home-range size of Little Owls, which was estimated to be 50 ha near our study area (Orf 2001). To avoid multicollinear-

Table 1. Predictor variables used to model the occupancy and the productivity of Little Owls in artificial nest boxes in Hesse, Germany.

	PREDICTOR VARIABLE
	Local variables
A	X coordinate (1000 km)
B	Y coordinate (1000 km)
C	Elevation (m asl)
D	Distance to roads (m)
E	Distance to orchards (m)
F	Distance to forests (m)
G	**Local land-use class**
	Grassland
	Fallow
	Forest
	Orchards
	Water
	Urban
	Variables of the surrounding matrix within a 400-m radius
H	Land-use diversity (Shannon)
I	Habitat fragmentation (IJI)
J	Density of fields (n/km²)
K	Nest-box density (n/km²)
L	Cover of forest (%)
M	Cover of hedges (%)
N	Cover of fallow and field margins (%)
O	Cover of winter grain (%)

m asl = meters above sea level.

ity, only variables that were not correlated (i.e., $r^2 < 0.7$) were used (Fielding and Haworth 1995). From groups of correlated variables, only the variable with the most straightforward ecological interpretation was included.

Local variables comprised geographic coordinates, elevation, and the local land-use class, as well as the distances to fruit trees, forest patches, and roads derived from the habitat map. The Little Owl is known to breed in orchards and to avoid forests, possibly in order to avoid predation by species such as the Tawny Owl (*Strix aluco*; Zuberogoitia et al. 2005). As both habitat types influence the species' occurrence, the Euclidian distance of each map pixel to the closest orchard and forest was calculated. The distance to roads was also calculated as an index to anthropogenic disturbance and potential car collision mortality.

Matrix variables comprised the diversity of land-use types (Shannon index), habitat fragmentation (Interspersion and Juxtaposition Index, IJI, McGarigal and Marks 1995), field density and nest-box density, as well as the percent cover of selected habitat elements such as forest, hedges, fallow/field margins, and winter grain. Field density was calculated because we assumed that a higher number of fields per area would lead to higher land-use heterogeneity and to more field edges, both of which may affect prey availability. Field density was quantified by generating the center of each field and calculating the number of centers per area. Nest-box density was quantified to analyze the effects of varying nest-site availability. The amounts of forest, hedges, fallow/field margins, and winter grain were calculated to obtain proximate measures of resource availability within a Little Owl home range.

Statistical Analysis. We calculated resource-selection functions for occupancy and breeding success. Although we adopted a similar modeling technique in both cases, the two analyses differed in rationale and scope. Analysis of occupancy rate was based on all nest-boxes as the primary units, and was aimed at identifying the influence of habitat characteristics and nest-box density on whether boxes were used for breeding or not. Analysis of breeding success was based on nest boxes occupied by breeding pairs only, i.e., on breeding sites as primary units, and was aimed at identifying the influence of habitat characteristics and nest-box density on the reproductive success of Little Owls at particular breeding sites. We used generalized linear mixed-effect models (GLMMs), with a logit link function and a binomial error distribution (logistic regression) for presence–absence data, and with a logarithmic link function and Poisson error distribution for the number of nestlings of each nest box. The explanatory variables were coded as fixed effects and the year was coded as a random effect. A second order polynomial of all continuous predictor variables was included to account for possible nonlinear relationships between predictor variables and dependent variables. To select the set of variables with the most relevant contribution to model fit we used Akaike's Information Criterion (AIC; Akaike 1973), AIC differences (Δ_i) and Akaike weights (ω_i). Akaike weights, which provide a relative weight of evidence for each model, were derived from differences in AIC between the best model and other models (Burnham and Anderson 2002). We show results for the three models with the greatest support, based on Akaike weights ($\geq$70% sum of Akaike weights).

We used a ''presence/available design'' (Boyce et al. 2002) to model nest-box occupancy for breeding. We chose this design because unbiased absence data could not be obtained in this kind of investigation, as all nest boxes were placed in orchard trees, which are known to be selected by Little Owls (Génot and van Nieuwehuyse 2002). Specifically, unoccupied nest boxes could not serve as absence data because the locations of these nest boxes were spatially autocorrelated and not selected at random. Therefore, the 246 analyzed breeding sites (presence data) were complemented by 246 ''pseudo-absence'' points (Osborne et al. 2001, Engler et al. 2004, Poirazidis et al. 2004). To maintain spatial independence, the minimum distance between pseudo-absence points and observed presence points was set at 800 m to ensure that no overlap occurred between 400-m-radius sampling units. The number of breeding sites used for the GLMMs slightly differed from the total number of breeding sites known for the study area. This was caused by breeding sites located <400 m from the border of the study area, for which the matrix variables in the surrounding area could not be calculated.

The quality of the analysis models was checked with the area under the receiver operating characteristic (ROC) curve (AUC). The AUC can range between 0.5 (no discrimination between presence and absence) and 1.0 (perfect discrimination; Fielding and Bell 1997, Pearce and Ferrier 2000). We used a 5-fold cross validation and ran 100 permutations to quantify prediction accuracy in unknown plots (Verbyla and Litvaitis 1989).

Table 2. Occupation of and reproduction in 798 nest boxes provided for Little Owls in Hesse, Germany, 2004–2006.

	Occupied[1] Nest Boxes		Occupied Nest Boxes with No Nestlings		Occupied Nest Boxes with <2.35 Nestlings		Occupied Nest Boxes with ≥2.35 Nestlings		Total Nestlings
	n	%	*n*	%	*n*	%	*n*	%	*n*
2004	142	17.8	23	16.2	60	7.5	82	10.3	357
2005	173	21.7	23	13.3	74	9.3	99	12.4	467
2006	184	23.1	71	38.4	135	16.9	49	6.1	268
Overall 2004–2006	254	31.8	51	20.1	144	18.0	108	13.5	1092

[1] We considered a nest box occupied for breeding if eggs or nestlings were present, or if there were signs of nest failure, such as eggs, shell fragments, or dead young.

The occupancy model was used to create a map of potential breeding area. A threshold of 0.5 was set as the cut-off, taking the prevalence rate of the presence/absence data as the threshold (Liu et al. 2005). This was done by post-processing the occupancy map. Only habitat patches larger than 500 m^2 were considered suitable. This area corresponds approximately to the area typically occupied by five standard fruit trees. To assess new potential areas for nest boxes, we excluded areas closer than 400 m to an existing nest box, thereby maintaining spatial independence.

To characterize the locations preferred for breeding by Little Owls, we compared habitat characteristics between presence points (occupied nest sites) and absence points (random points in the landscape). For this analysis we used Mann-Whitney *U*-tests, where *P*-levels were adjusted by sequential Bonferroni correction to account for multiple testing (Rice 1989). To analyze the constancy of nest-box occupation across years, we quantified the proportion of nest boxes that were reoccupied in the following year. To analyze the constancy of relative reproductive success in occupied nest boxes across years, we compared the average number of nestlings and the coefficient of variation of the number of nestlings across years. Spearman rank correlation was used to test whether averages and coefficients of variation were correlated. Spearman rank correlation was also used to test the correlation between the number of years in which a nest was occupied and the number of nestlings produced in these years, in order to analyze whether Little Owls preferred successful nesting sites for breeding.

The Statistica 8 software package (StatSoft Inc., Tulsa, OK, U.S.A.) and R 2.10 (R Development Core Team 2009) were used for the statistical analyses. GIS work was conducted using the ArcGIS 9.3.1 package (ESRI Inc., Redlands, CA, U.S.A.).

Results

Occupation of Nest Boxes. Of 798 nest boxes analyzed in this investigation, 544 nest boxes (68%) were not occupied for breeding by Little Owls, whereas 254 nest boxes (32%) were used for breeding at least once from 2004 to 2006 (Table 2). Of the 142 nest boxes occupied in 2004, 109 (77%) were again occupied in 2005, and of the 173 nest boxes occupied in 2005, 121 (70%) were again occupied in 2006.

Quality of Breeding Sites. Of the 254 occupied nest boxes, 51 yielded no nestlings. Among the 51 unsuccessful nest boxes, 11 were occupied in 2 yr and three were occupied in 3 yr. Production of <2.35 nestlings per breeding pair per year occurred in 144 nest boxes, and production of >2.35 nestlings per breeding pair per year occurred in 108 nest boxes. Thirty-two nest boxes contributed >2.35 nestlings in the years they were occupied, whereas production of ≥2.35 nestlings occurred in nine boxes in all three years. Reproductive success at the same nest box varied between years (Fig. 1) and relative variation (coefficient of variation) was higher at boxes with a lower mean number of nestlings (Spearman $R = -0.78$, $p < 0.001$).

Reproduction Rates. The number of breeding pairs increased during the study: 142 pairs in 2004, 173 in 2005 and 184 in 2006. The total number of nestlings also varied: 357 nestlings in 2004, 467 in 2005, and 268 in 2006. Although the sustainable rate of 2.35 nestlings per breeding pair was exceeded in 2004 and 2005 (average rates of 2.53 and 2.67 nestlings per breeding pair, respectively), the rate dropped to 1.44 nestlings per breeding pair in

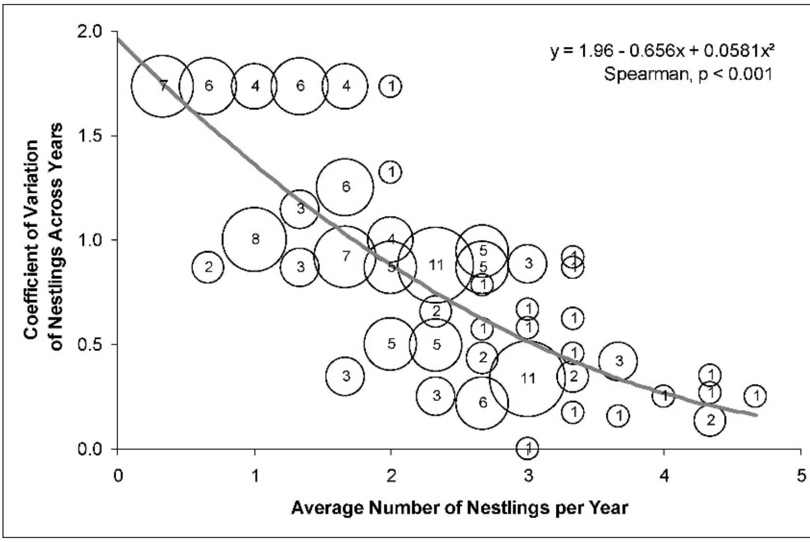

Figure 1. Temporal variation of reproductive success. The areas of the circles are proportional to the numbers in the centers, which indicate the numbers of nest boxes with the same combination of average count of nestlings (x-axis) and relative temporal variation of nestlings (y-axis) across years. The trend line is an ordinary least squares fit of a second order polynomial. High numbers of nestlings were negatively correlated with temporal variation of nestlings, i.e., nest boxes where birds had high breeding success tended to show higher constancy of breeding success across years.

2006. The overall reproductive rate for the three years averaged 2.21 nestlings per breeding pair per year.

Nest-site Characteristics. The locations of occupied nest boxes differed significantly from the pseudo-absence points generated for modeling (Table 3). On average, Little Owls bred at 761 m away from forests and 53 m from orchards. Compared to average landscape conditions, the birds nested far-

Table 3. Habitat characteristics associated with occupied nest boxes provided for Little Owls in Hesse, Germany, 2004–2006, and of randomly selected sites within the study area. Comparisons were made using Mann-Whitney *U*-test with Bonferroni correction ($P < 0.05$).

Predictor Variable	Breeding Sites (n = 242)		Random Sites (n = 242)		Relative Difference	
	Mean	SD	Mean	SD		
Local variables						
Elevation (m asl)	164	29	224	107	−27%	*
Distance to roads (m)	269	227	421	356	−36%	*
Distance to orchards (m)	53	151	683	623	−92%	*
Distance to forests (m)	761	485	500	733	+52%	*
Variables of the surrounding matrix within 400 m radius						
Land-use diversity (Shannon)	1.1	0.3	1.0	0.4	+30%	*
Habitat fragmentation (IJI)	71.4	4.7	62.5	16.1	+14%	*
Density of fields (n/km^2)	22.8	5.8	14.4	8.4	+59%	*
Nest-box density (n/km^2)	0.30	0.14	0.02	0.06	+1707%	*
Cover of forest (%)	3.1	6.7	32.5	36.6	−91%	*
Cover of hedges (%)	1.54	1.37	1.57	1.61	−2%	
Cover of fallow and field margins (%)	2.23	0.68	1.68	0.95	+33%	*
Cover of winter grain (%)	32.0	14.4	21.0	19.3	+53%	*

* $P < 0.05$, m asl = meters above sea level.

Table 4. Results for the three models with the highest Akaike weights predicting the breeding probability of Little Owls.

Number	Model[a]	K[b]	AIC	Δ_i[c]	ω_i[d]
1	B^2, C, C^2, E, E^2, F, F^2,G, J, J^2	10	1193.9	0.0	0.353
2	B, B^2, C, C^2, E, E^2, F, F^2, G, J, J^2, M, M^2	13	1195.3	1.4	0.175
3	B, B^2, C, C^2, E, E^2, F, F^2, G, J, J^2	11	1195.4	1.5	0.167

[a] Abbreviations of model variables are given in Table 1.
[b] Number of predictor variables.
[c] AIC differences of all models in comparison to the best one.
[d] Akaike weights.

ther from forest, closer to orchards, at lower elevations (164 m asl) and in areas with higher cover of fallow and field margins (2.2%). The number of nest boxes and the proportion of winter grain was significantly higher (32%) and the percent cover of forest (3.1%) was lower in the area around breeding sites than around the random sites (*U*-test, $P < 0.05$). Little Owls used breeding sites in locations with higher land-use diversity and habitat fragmentation. Slope and density of hedges did not show significant differences between breeding and random sites. Generally, Little Owls used nest boxes that ensured higher breeding success, as is indicated by the positive correlation between the number of years in which a nest was occupied and the number of nestlings produced in these years (Spearman $R = 0.29$, $P < 0.001$). However, the weak correlation may be explained in part by low productivity in some consistently used boxes and high productivity in some boxes that were occupied infrequently.

Habitat Models. The occupancy model performed well, with an AUC of 0.85, indicating that the model often discriminated correctly between presence and absence of Little Owls. In contrast, the reproductive-rate model exhibited relatively weak performance with a prediction error of ±42% (5-fold cross validation), indicating that breeding success was only partially related to the habitat variables analyzed. Ten and 13 of 29 variables were finally selected in the occupancy and the reproductive-rate model with the highest Akaike weights, respectively (Table 4 and 5). The model-selection procedure revealed that several of the differences found by univariate analysis were redundant with geographic and topographic parameters and were therefore eliminated from the multivariate model equations (Table 6). The highest density of breeding owls coincided with a field density of 26 fields/km² (Fig. 2a). Increasing distance from orchards (Fig. 2b), more northern areas and high elevations were negatively correlated with occupancy of nest boxes by Little Owls. Furthermore, local presence of orchards and greater distance to forests had a significant positive influence on nest-box occupancy rate. Reproductive rate of Little Owl breeding pairs was significantly correlated with increasingly northern location, higher elevation, greater distance to roads and forests and greater percent cover of forest, fallow and field margins. Further, Little Owl reproductive rate was positively correlated with habitat fragmentation and negatively correlated with land-use diversity.

Estimation of Available Suitable Habitat. After post-processing the raw results of the occupancy model according to incidence threshold, minimum

Table 5. Results of the three models with the highest Akaike weights predicting the productivity of Little Owls.

Number	Model[a]	K[b]	AIC	Δ_i[c]	ω_i[d]
1	A, B^2, C, C^2, D, D^2, F^2, G, H^2, I, J^2, L, N	13	1525.2	0.0	0.291
2	A, B^2, C, C^2, D, E, F^2, G, H^2, I, J^2, L, N	13	1525.5	0.3	0.250
3	A, B^2, C, C^2, D, D^2, E, F, F^2, G, H^2, I, J^2, L, N	15	1525.6	0.4	0.238

[a] Abbreviations of model variables are given in Table 1.
[b] Number of predictor variables.
[c] AIC differences of all models in comparison to the best one.
[d] Akaike weights.

Table 6: Generalized linear mixed models with the highest Akaike weights predicting the occupancy and the productivity of Little Owls in artificial nest boxes in Hesse (n = 484), Germany, 2004–2006.

Occupancy Model				Productivity Model			
	Predictor Variable	Coefficient			Predictor Variable	Coefficient	
	Intercept	−1.35586	***		Intercept	0.12767	
	Local variables				**Local variables**		
A	X coordinate (1000 km)	rejected		A	X coordinate (1000 km)	−0.0639	
B^2	Y coordinate^2 (1000 km)	0.33644	**	B^2	Y coordinate^2 (1000 km)	0.10081	***
C	Elevation (m asl)	−0.50013	*	C	Elevation (m asl)	0.15858	***
C^2	Elevation^2 (m asl)	−0.31907		C^2	Elevation^2 (m asl)	−0.02353	
H	Distance to orchards (m)	−1.51283	***	G	Distance to roads (m)	0.10519	*
H^2	Distance to orchards^2 (m)	−0.9807	***	G^2	Distance to roads^2 (m)	0.02262	
I	Distance to forests (m)	1.27072	*	I^2	Distance to forests^2 (m)	0.11201	***
I^2	Distance to forests^2 (m)	−1.3422					
J	**Local land-use class**			J	**Local land-use class**		
	Grassland	−0.09193			Grassland	−0.08993	
	Forest	−13.59155			Orchards	0.06024	
	Orchards	1.26136	***				
	Variables of the surrounding matrix				**Variables of the surrounding matrix**		
D	Density of fields (n/km^2)	0.78409	**	M^2	Land-use diversity^2 (Shannon)	−0.06518	*
D^2	Density of fields^2 (n/km^2)	−0.42738	**	N	Habitat fragmentation (IJI)	0.13401	***
				D^2	Density of fields^2 (n/km^2)	−0.04016	
				L	Cover of forest (%)	0.10283	*
				F	Cover of fallow and field margins (%)	0.08305	*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. m asl = meters above sea level.

patch size, and home-range overlap, we predicted that 8.3% (135 km^2) of the entire study area (1620 km^2) provided habitat where nest boxes are likely to be used for breeding by Little Owls. Predicted breeding habitat was mainly located in the southern part of the study area, separated into several patches near villages and smaller towns, which were surrounded by orchards (Fig. 3). At present, 30% (40 km^2) of this apparently suitable habitat contains nest boxes. Thus, 3.4 times the present area could be supplied with additional nest boxes, according to the model's predictions.

DISCUSSION

Our analysis of an exceptionally large nest-box program conducted to promote the conservation of Lit-

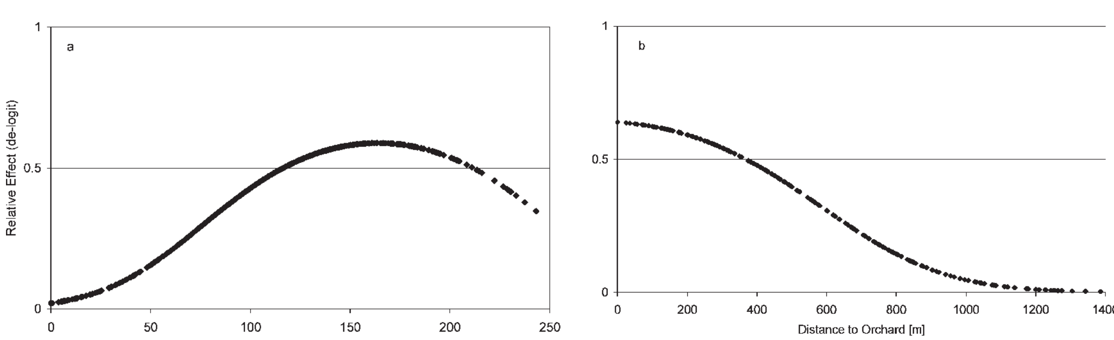

Figure 2. Effects of (a) field density ($P < 0.01$) and (b) distance to orchards ($P < 0.001$) on nest-box occupancy by the Little Owl.

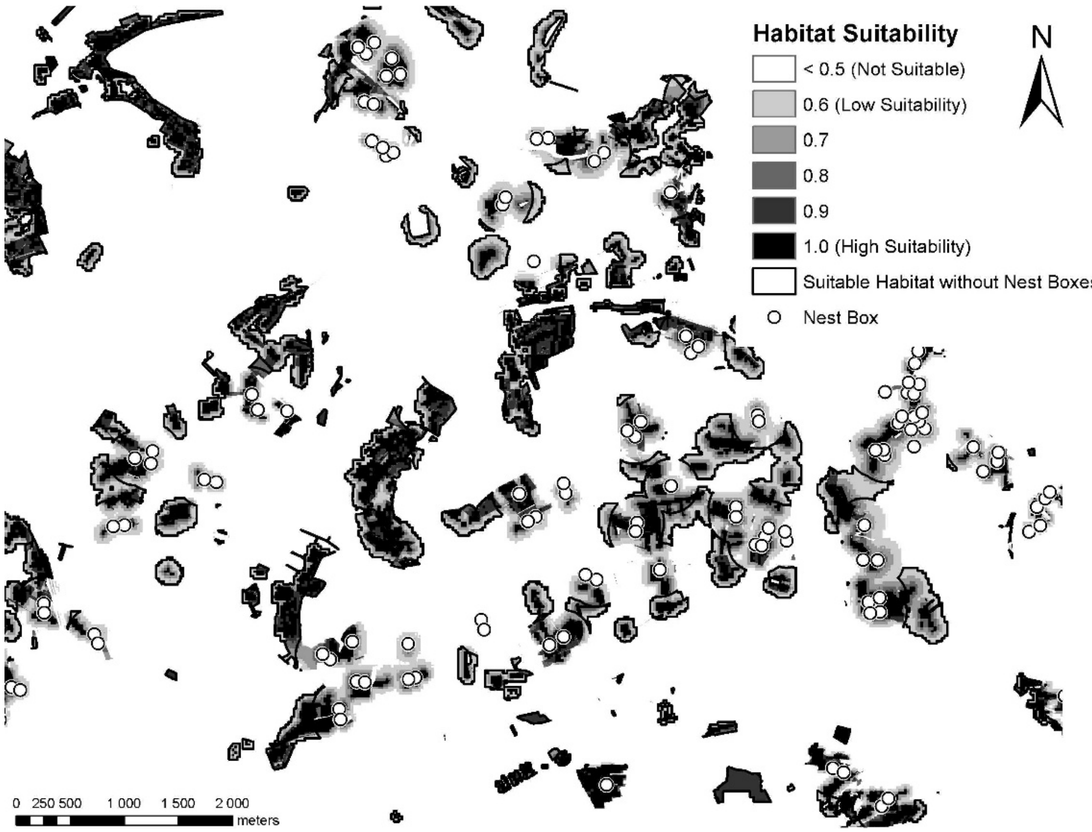

Figure 3. Detail of the modeled habitat suitability map of the Nidda catchment area, Hesse, Germany. Predicted probability of breeding for the Little Owl, derived from the occupancy model, is considered a proxy of habitat suitability. Predicted suitable habitat was often spread around villages and included narrow habitat strips, e.g., along rows of apple trees. Several nest boxes were placed in unsuitable habitat and several areas of suitable habitat were not equipped with nest boxes.

tle Owls suggests that its efficiency might be augmented by improving the placement of nest boxes. Such improvement requires monitoring of occupancy and breeding success of the owls using the nest boxes, and can be facilitated by spatial modeling.

Generally, the species-habitat relationships observed in our study were similar to those reported in the literature. Essential ecological conditions for Little Owls include year-round accessibility of prey, vertical landscape structures with cavities for hiding and breeding, and limited predation pressure (Van Nieuwehuyse et al. 2008). Tomé et al. (2004) found that the presence of predators was the main factor influencing nest-site selection and breeding success of Little Owls. Forests are often inhabited by Tawny Owls, a predator of the Little Owl, and Schönn et al. (1991) reported a strict separation of Little Owl and Tawny Owl territories. In our investigation, presence and proximity of orchards, as well as the absence of forests and greater distance from forests were among the strongest predictor variables of nest-box occupancy. Additionally, the negative response to altitude in the occupancy model reflects the known avoidance of higher altitudes by the Little Owl (Schönn et al. 1991). We are therefore confident that our results are relevant for nest-box management of Little Owls outside our study area. Because rodents and other Little Owl prey are attracted to field edges, the positive correlation of occupancy with field density and therefore with a higher number of edges most likely reflects the species' preference for areas of higher prey availability.

In contrast to nest-box occupancy, breeding success of Little Owl pairs was significantly higher at higher elevations. This might relate to the less intensive agriculture and reduced anthropogenic disturbance generally found at higher elevation in our study area. The correlation between higher reproductive rates and distance to roads corresponds well with previous findings that large numbers of Little Owls can be killed by road traffic (Génot 1991, Frias 1999). Nonetheless, the species does not consistently select breeding sites away from roads (Zabala et al. 2006), suggesting that some otherwise appropriate areas near roads may act as ecological traps (Battin 2004, Robertson and Hutto 2006). In our study, the rate of occupancy and breeding of the Little Owl was not correlated with the presence of roads, and in fact, breeding pairs with offspring were found within 250 m of highways with traffic densities of more than 85 000 cars per day. However, the identification of nest boxes acting as ecological traps would require further research on survival rates, especially of inexperienced one-year-old birds. Other than the contrasting responses to altitude and to the distance to roads, the occupancy model and the reproductive-rate model were fairly congruent with each other. The positive correlation between reproductive rate and increasing forest cover was unexpected, because it contradicts the positive correlation with distance to forests. The correlation with forest cover seems most likely to result from indirect habitat effects. Increasing cover of forest is mainly found in areas of less intensive agriculture and less anthropogenic disturbance, and therefore these areas are better suited for higher productivity (Génot and van Nieuwehuyse 2002, Tomé et al. 2004). Additionally, forest cover might not be a relevant factor if the Tawny Owl is not present in a forest. For more detailed analyses, data on Tawny Owl occurrence, or at least, information about the habitat suitability for this species would be required.

Our results indicated that the effectiveness of the investigated nest-box program could be improved. We found that 68% of 798 surveyed nest boxes were not occupied by Little Owls for breeding and were most likely either unattractive for the birds or in excess of the local breeding density. Although a few of these boxes might possibly be occupied within the coming years, a majority of them may be expected to remain ineffective in the foreseeable future. Generally, a surplus of nest boxes may enhance a territory, as a breeding pair often uses different daytime roosts and switches between alternative cavities around the nest site (Schönn et al. 1991). Furthermore, extra cavities may be important for post-fledging dispersal (King and Belthoff 2001). Conversely, a surplus of nest boxes may result in an increased density of breeding birds, accompanied by food shortage, intraspecific competition, increased brood parasitism, and low reproductive success (Newton 1994, Mänd et al. 2005). Studies in southwestern Germany showed that adding more nest boxes did not increase the local population of Little Owls when the carrying capacity of the habitat was reached (Hölzinger 1987, Exo 1992). In the investigated nest box program, the average distance to the nearest nest box was 148 m, and on average 4.1 nest boxes were placed within the Little Owl home range of 50 ha observed in the region. Given the high percentage (68%) of nest boxes left unoccupied during the three years of our investigation, we suspect that in some parts of our study area the nest-box density was too high to ensure optimal breeding conditions.

Furthermore, between 42% and 73% of the nest boxes that were occupied by Little Owls produced fewer than 2.35 nestlings, the minimum rate thought to be associated with a stable population (Exo and Hennes 1980). Low reproduction success may, of course, be in part attributable to young and inexperienced birds, or to the lack of fitness in some of the breeding pairs. Theoretically, a nest box housing a pair with low reproduction in one year might provide a valuable contribution under different conditions in another year. However in our study, nest boxes where high numbers of nestlings were produced also had more consistent reproductive success over time. In total, as many as 20% of the 254 nest boxes occupied for breeding housed pairs producing no nestlings in any of the years they were occupied. We consider this an indication that box placement may be enhanced by using areas where Little Owls can be more successful.

A moderate proportion of nest-box locations where Little Owls produce fewer than 2.35 nestlings may appear tolerable if conditions are otherwise favorable. In fact, during our investigation, the Little Owl population exhibited good overall reproduction and growth in two years, with 357 nestlings in 2004 and 467 nestlings in 2005. However, reproduction sharply declined by 43% in 2006. In that year, pairs in 38% of 185 nest boxes occupied for breeding produced no nestlings. The reproductive decline in 2006 was most likely caused by a drop in prey availability due to unfavorable weather (Gaßmann et al. 1994, G. Herbert pers. comm.).

Suboptimal nest-box placement may additionally constrain the population under such critical conditions. This is particularly true if habitat quality decreases during the course of the breeding season. For example, if agricultural practices include retaining tall and dense vegetation during the breeding season, this may reduce prey accessibility. Similarly, weather conditions may influence food resources and breeding phenology (Visser et al. 1998, Both and Visser 2001). Finally, nest boxes may be inferior to natural nesting sites, and this may be exacerbated during years of poor environmental conditions. Little Owls make less frequent use of nest boxes in areas where tree cavities are abundant (Tomé et al. 2004), and nest boxes in the same area have been used by stone martens (*Martes foina*) and common genet (*Genetta genetta*), predators of Little Owls (Tomé et al. 2008). Stone martens are known to examine Little Owl nest boxes for prey as they learn to exploit nest boxes as a food resource (Luder and Stange 2001). Relocating (Sonerud 1993) or modifying the construction of nest boxes (Yamaguchi et al. 2005) may reduce predation by martens.

Estimating both reproductive rate and mortality rate is essential to predict future population changes. About 60% of Little Owl eggs can fail to produce fledglings (Exo and Hennes 1980). To minimize disturbance of the breeding birds, we did not conduct double nest checks, and therefore we were not able to analyze potential changes of breeding conditions during the breeding period (Steenhof and Newton 2007). Furthermore, we counted nestlings (i.e., hatched young) and not fledglings. Although we have no evidence for a high mortality rate of Little Owls at the end of the breeding season, the reproductive rates reported here might be slightly overestimated compared to those reported by Exo and Hennes (1980). Our assessment of nest boxes that were occupied for breeding but did not contribute to net growth of the population was based on the published rate of 2.35 young per breeding pair per year thought necessary for population stability (Exo and Hennes 1980). However, the population may also remain stable with a lower reproductive rate if the mortality rate is also lower. We did not estimate mortality of Little Owls in our study area, so we do not know whether the threshold value of 2.35 young is altogether accurate for our population. Nonetheless, we assert that our assessment may be relevant to other areas if annual mortality rates of adult birds do not differ substantially from the rate of 35% reported by Exo and Hennes (1980).

The reproductive-rate model was characterized by a ±42% prediction error. We were unable to incorporate information on predation pressure, food availability, weather events, and other factors relevant to breeding success, across our large study area. Because these factors are likely influential, we recommend that future investigations of nest-box programs address these factors in smaller-scale projects, possibly using experimental designs.

Ultimately, nest boxes cannot be viewed as a remedy for the chronic problem of habitat loss and degradation that results from intensified land-use. In Hesse, traditional orchards with standard apple trees, which usually harbored a significant number of natural cavities, were reduced by about 83% from 1965 to 1987 (Pauritsch and Harbodt 1988). Nest boxes should be viewed as a critical but interim measure until natural nesting sites are no longer a limiting factor (Harley and Spring 2003). Apple trees need 50 yr or more to develop cavities. To ensure the future availability of cavity-bearing trees and to guarantee the viability of Little Owl populations, new orchards should be established and present orchards should be preserved.

Our habitat suitability model predicted that substantial parts of the study area provided potential breeding habitat, but currently lack nest boxes. Based on our assessment of available habitat, the Little Owl population could theoretically increase by a factor of 3.4 if all suitable areas were supplied with nest boxes. To achieve such a population increase, however, would require ten years of continuous population growth, based on a growth rate of ten percent per year. Increasing the efficiency of a nest-box program will involve continuous management of nest boxes. Overall reproductive success can be enhanced by avoiding high nest-box density and removing nest boxes from locations where Little Owls produce fewer than 2.35 nestlings. Monitoring and assessment should be conducted to assess the effectiveness of the nest-box program.

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