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Breeding season food limitation drives population decline of the Little Owl *Athene noctua* in Denmark

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Many farmland bird species have declined markedly in Europe in recent decades because of changes in agricultural practice. The specific causes vary and are poorly known for many species. The Little Owl, which feeds extensively on large invertebrates and is strongly associated with the agricultural landscape, has declined over most of north-western Europe, including Denmark. We investigated the likely reasons for the population decline in Denmark by identifying patterns of local extinction (scale, 5×5 km^2) and estimating demographic parameters affecting local survival, focusing on changes over time and their relationship to habitat characteristics. The distribution of the Little Owl in Denmark contracted considerably between 1972–74 and 1993–96. The extent of contraction varied across the country, and the only habitat correlate was that local disappearance was associated with smaller amounts of agricultural land. Analyses of ring recovery data suggested a constant annual adult survival rate of 61% from 1920 to 2002, which is similar to estimates from countries with stable populations. First-year annual survival rates were much lower than values previously reported. From the 1970s into the 21st century, the mean number of fledglings declined from around 3 to < 2 young per territory, but the decline in clutch size was considerably less. Reproductive parameters were higher closer to habitat types known to be important foraging habitats for Little Owls, and were also positively correlated with the amount of seasonally changing land cover (mostly farmland) within a 1-km radius around nests as well as temperatures before and during the breeding season. Experimental food supplementation to breeding pairs increased the proportion of eggs that resulted in fledged young from 27 to 79%, supporting the hypothesis that the main proximate reason underlying the ongoing population decline is reduced productivity induced by energetic constraints after egg-laying. Conservation efforts should target enhancement of food availability during the breeding season. Other farmland species dependent on large invertebrates are likely to share the problems that Little Owls face in modern agricultural landscapes.

Keywords: agriculture, conservation, experiment, food supplementation, habitat association, invertebrates, reproductive output, survival.

Many bird species associated with farmland have suffered severe declines in Europe, often attributed to landscape changes following the development of modern agricultural techniques (Donald *et al.* 2001, Tucker & Heath 2004). These declines are not associated with any single factor, and a variety of causes have been described for different species,

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largely depending on differences in biology (Newton 2004). However, where documentation of direct effects of agricultural intensification in causing declines is lacking, this prevents effective management.

The Little Owl *Athene noctua* declined considerably in northwestern Europe in the latter half of the 20th century (Tucker & Heath 2004, Nieuwenhuyse *et al.* 2008). In this region, the species is closely tied to human-modified agricultural landscapes, both for breeding and for foraging. In Denmark, on the northwestern limit of the species' distribution, Little Owls have been declining at least since the 1970s, when the population probably numbered 1000 pairs at a minimum. Currently, one isolated population of around 100 pairs persists in Himmerland, in northwest Denmark, with only a few scattered pairs outside this area. This decline involves both contraction of the range and reduced density, even in the remaining core area (Jacobsen 2006).

The diet of the Little Owl is varied and consists mainly of small rodents, earthworms and insects (Nieuwenhuyse *et al.* 2008). The species is sedentary, with short dispersal distances and very little exchange between populations at a regional scale, although metapopulation dynamics are likely to be important at the local (< 25 km) population level (Schaub *et al.* 2006). Thus, recent changes in the Danish Little Owl population are likely to have been driven by changes in the production of young or in survival.

Here, our aim was to identify the causes of the decline of the Little Owl population in Denmark. We combined environmental and demographic information to: (1) investigate the overall habitat characteristics associated with changes in local populations; (2) examine the potential demographic drivers of population trends; and (3) evaluate the dependence of such demographic traits on environmental variation. First, we used two separate censuses of Danish birds (1972–74 and 1993–96) for analysis of disappearance of Little Owls at the scale of $5 \times 5\ \text{km}^2$ between the two census periods and related these findings to habitat factors, whilst taking into account spatial autocorrelation. Secondly, we estimated survival from ringing data and breeding output from surveyed nests, including temporal trends, and also tested the effects of a series of habitat and climate variables on breeding output. Finally, we tested the hypothesis of food limitation on production of young by means of a supplementary feeding experiment on breeding pairs.

METHODS

Spatial extinction pattern in Denmark, 1970s to 1990s

We used data from the two Danish breeding bird censuses in 1972–74 (Dybbro 1976) and 1993–96 (Grell 1998) to model changes in the breeding distribution of Little Owls in Denmark between these two periods. In both censuses, the occurrence of breeding (or presumed breeding) Little Owls was recorded in $5 \times 5\text{-km}^2$ squares. To assess which factors influenced the disappearance of the species, we categorized squares according to whether the species occurred in both censuses (61 squares) or only in the first (394). We did not investigate the smaller number of appearances of the species (96 squares in which the species was recorded only in the second census) because 'appearance' events are much more likely to arise simply from being overlooked in the first census rather than being real 'colonizations'. This is due in part to the slightly poorer coverage in the first census (Grell 1998) but more importantly to the fact that the species has become much rarer. Furthermore, we lacked the temporal resolution of the habitat data required to simultaneously link habitat and occupancy over time.

The spatial structure of the disappearance of Little Owls was investigated using a spatial autocorrelogram (based on Moran's I), which measures autocorrelation between squares as a function of the distance between them. We modelled the effects of habitat categories as the proportions of habitat types covering each square, using the habitat data from the Danish Area Information System (AIS) (Nielsen *et al.* 2000), in which Danish land cover is categorized into 12 standardized habitat categories based on satellite images of 25-m resolution, obtained during 1996–2000 (a much shorter period than that covered in our analysis). Annual habitat coverage maps were not available.

We modelled the effects on disappearance of the four habitat variables (seasonally changing land cover, grass, marsh and woodland) for which a separate univariate logistic regression model of disappearance from a square indicated a possible effect ($P < 0.10$). Spatial autocorrelation among squares was taken into account by estimating how much the disappearance in one square was reflected in the disappearance in surrounding squares. We used the commonly employed autocovariate model (Dormann *et al.* 2007; also called the lagged-response autoregressive model, Rangel *et al.* 2006) in which the autoregressive response occurs only in the response variable. Several other spatial models are available, but it is not clear in which cases one model should be preferred over another (e.g. Dormann *et al.* 2007, Bini *et al.* 2009). However, for our dataset the lagged-response autoregressive model had considerably lower Akaike's information criterion (AIC) values than other, more complex spatial models (lagged predictor, simultaneous and conditional autoregression models). All spatial analyses were performed using SAM (spatial analysis in macroecology) vers. 2.0 (Rangel *et al.* 2006).

Survival, 1920–2002

We used ringing data for 491 pulli and 87 adults ringed throughout the breeding area in Denmark during 1920–2002; of these, 34 pulli and 16 adults were found dead and reported before 2003. Reports of birds that were recaptured alive were not included in the analyses.

Annual survival rates were estimated in a capture–mark–recapture framework using the recovery data type in program MARK 4.1 (White & Burnham 1999). The capture–mark–recapture framework allows for separate estimation of survival rate S and recovery probability r and is well suited for evaluating different models based on, for example, age (Lebreton *et al.* 1992). Each individual was considered ringed on 15 June of the year of capture and the encounter history for this analysis included 83 yearly 'capture' occasions. We also included linear trends of survival rates and recovery probabilities. Furthermore, average temperature in the coldest period January–February from a Danish weather station in North Jutland (Cappelen *et al.* 2007) was included as an additional covariate to model a possible effect of winter severity on survival. Because the model with age-dependent survival and recovery probabilities $\{S(\text{age})\ r(\text{age})\}$ fitted the data well ($P = 0.62$, Goodness-of-fit bootstrap test; Cooch & White 2007) we did not adjust our AIC values for over-dispersion but only for small sample sizes, i.e. we used Akaike's information criterion corrected for small sample size (AICc), not the small sample version of the quasi-AIC (QAICc).

Reproductive success, 1975–2006

Survey of the area

Nests of 256 Little Owl territories throughout Jutland, but primarily from Himmerland, were surveyed during 1975–2006 by a small group of volunteer observers (Jacobsen 2006), for a total of 943 breeding attempts. In a 100-km^2 census area in Himmerland in northern Jutland that includes one of the few remaining strongholds for the Little Owl in Denmark, all suitable breeding localities were visited and playback was conducted in March–April. Other areas were not surveyed systematically for territories; instead, information was collected based on known pairs combined with playback in some suitable areas and advertising in local media. In many cases, clutch size or number of nestlings could not be confirmed. The number of nestlings was recorded as the number of young at age of ringing (12–25 days after hatching). Numbers of fledglings were recorded as the number of young seen or heard around the nest soon after fledging.

Clutch sizes were recorded for 71 breeding attempts, the number of nestlings for 126 and the number of fledglings for 350. Trends over time were investigated using linear regression analysis. The resulting error distributions were assessed visually and no obvious deviations from normal were found. Breeding attempts not resulting in fledged young occurred only in later years, necessitating control for a possible bias in later years towards increasing observer awareness of the importance of also recording zero fledglings. To address this potential bias, we tested for changes over time in the production of fledglings both with and without including counts of zero fledglings in the data.

Habitat and breeding performance analysis

To analyse the effects of habitat on breeding performance, we again used the AIS data (Nielsen *et al.* 2000). For each Little Owl nesting site, we measured the distance to each land-use class using the ANIMAL MOVEMENT extension (vers. 2.04, Hooge & Eichenlaub 1997) of ARCVIEW (vers. 3.2). We also calculated the areas of each land-use class within a 1-km radius from the nest, using in-built functions in ARCVIEW (vers. 3.2). Because Little Owls prefer to forage in open landscapes with short vegetation (Nieuwenhuyse *et al.* 2008; our unpubl. data) we merged in a single category called 'Little Owl habitat' the polygons classified in the AIS as grazed area, grassland and meadow. Seasonally changing land cover was not included in this category because in the AIS it is characterized by intensive arable agriculture with tall crops that are not suitable foraging habitat for nesting Little Owls. There was a strong correlation between some of the variables, especially between the distance to and the area of a particular habitat. None of the measures of Little Owl whether habitat had correlation coefficients larger than 0.5 with other habitat variables. Several studies have investigated occupancy as a function of habitat parameters in Little Owls (e.g. Nieuwenhuyse *et al.* 2001, Martínez & Zuberogoitia 2004, Cornulier & Bretagnolle 2006, Zabala *et al.* 2006). Overall, these reports show that habitat associations are scale-dependent. However, here we investigate whether habitat effects of production of young and effects at different scales may act in combination. We use a somewhat larger home-range scale compared with Martínez and Zuberogoitia (2004) (1 km vs. 309 m radius around nests), both to allow for different scales and because the Little Owls in Denmark have larger home-ranges (Sunde *et al.* 2009). Furthermore, the studies exhibit considerable regional variation. Thus, we included both the distance to each land use available in the AIS as well as the area of the habitat, as did Martínez and Zuberogoitia (2004). We could not include small-scale variables such as linear structures (Martínez & Zuberogoitia 2004), tree lines, edges (Nieuwenhuyse & Bekaert 2001, Nieuwenhuyse *et al.* 2001) or poles (Nieuwenhuyse *et al.* 2008) because the AIS data were too coarse.

Analysis of climate

To investigate the influence of climate on Little Owl breeding success, we used monthly weather data from the Vestervig meteorological station in northwest Denmark (Cappelen *et al.* 2007). The dataset included average monthly temperatures and precipitation as well as the number of days with local snow cover estimated to be above 50%. Most of the weather variables were significantly intercorrelated.

Statistical analysis

Production of young was modelled in SAS 9.1 (SAS Institute Inc., Cary, NC, USA), with Poisson-distributed errors. The numbers of eggs (71 Little Owl breeding attempts), nestlings (126 breeding attempts) and fledglings (350 breeding attempts) per pair were modelled as functions of the habitat (distance to and area around nest) and yearly climate data, considering habitat zones of a 1-km radius as well as distance to specific habitat types. Year (1975–2006) was included as a covariate in the models to investigate long-term trends in production. Models were identified using backward elimination of parameters from full models with the GENMOD (Poisson-distributed errors and log link) procedure. To control for possible pseudo-replication arising from use of data from more than 1 year from each nest-site being used, we tested the effect of adding the nest-site ID as a random factor (using the GLIMMIX procedure) to the models identified using backward elimination. The additional variance component for the mixed model with nest-site ID as a random variable was not significant in any of the models and was omitted from analyses. For the models identified, we calculated parameter estimates from normal linear regression to allow easy interpretation of the estimated effects.

In total, the following fixed, explanatory variables were entered into the models: Year, Distance to urban areas, Distance to road, Distance to Little Owl habitat, Seasonally changing land cover, Forest area, City area, Little Owl habitat area, December–February temperature, March–April temperature, May temperature, June temperature, March–April precipitation, May precipitation, June precipitation, and Days with snow cover the preceding winter.

Analysis of food as a limiting factor

To assess whether food was a limiting factor for offspring survival, we supplied two pairs during the breeding season 2005 and three different pairs during 2006 with supplemental food (one to three dead domestic mice or newly hatched chickens per day). Food was supplied daily from hatching until the young fledged. For the five food-supplemented nests and 23 control nests from the same 2 years, we assessed the success rate of raising young as the proportion of eggs that survived until fledging. Survival rates of eggs until fledging were estimated as binomial outcomes ($n_{\text{fledglings}}/n_{\text{eggs}}$ per nest) using a generalized linear model with a logit link and binomial error term (the GENMOD procedure in SAS 9.1). Estimates were adjusted for strong over-dispersion (Deviance/df ratio = 2.87 and 2.28, respectively with and without year effect included) arising from within-clutch variation using the DSCALE option in SAS. The effect of experimental treatment and year (2005 or 2006) was tested with a likelihood ratio test.

Parameterization of the population model

We parameterized a simple population model (Williams *et al.* 2002) with two age classes (first-year individuals and older, adult birds) corresponding to the estimated annual survival rates as the following Leslie matrix:

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \end{bmatrix} = \begin{bmatrix} S_0bX & S_1bX \\ S_0 & S_1 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \end{bmatrix}$$

where N_i is the total number of Owls in age class i, S_i is the annual survival of Owls in age class i, b is the number of fledglings produced per female, X is the proportion of females in the population times the proportion of adults breeding, and t is time.

Production of young was estimated as the average brood size at ringing (typically chicks about 20 days old; range 12–25) for 67 clutches ringed in 1982–2006 (L.B. Jacobsen unpubl. data). The few cases of pairs laying eggs but failing to raise young to this age were counted as non-breeders. The proportion of individuals breeding was estimated using data collected during 1994–2006 from an intensively surveyed area in Himmerland (Jacobsen 2006) by summing over all years the number of birds recorded breeding and dividing this value by the total number of birds recorded over the years (i.e. including unmated individuals or pairs that did not lay eggs). Little Owls are generally monogamous, breed once per season, start breeding in their first year, and rarely lay replacement clutches (Nieuwenhuyse *et al.* 2008). We set the proportion of females in the population at 0.5 and number of nesting attempts to one per year.

RESULTS

Spatial extinction pattern

The number of 25-km^2 squares with Little Owls recorded during the two Danish breeding bird censuses declined from 457 in 1972–74 (Dybbro 1976) to 157 in 1993–96 (Grell 1998). In 396 squares (87%), Little Owls disappeared between the first and the second censuses.

There was a strong spatial component in the pattern of disappearance, as relatively more squares lost Little Owls in the southeastern part of the range (Figs 1 and 2). After the spatial component in autoregressive models was accounted for, the seasonally changing land cover was the only

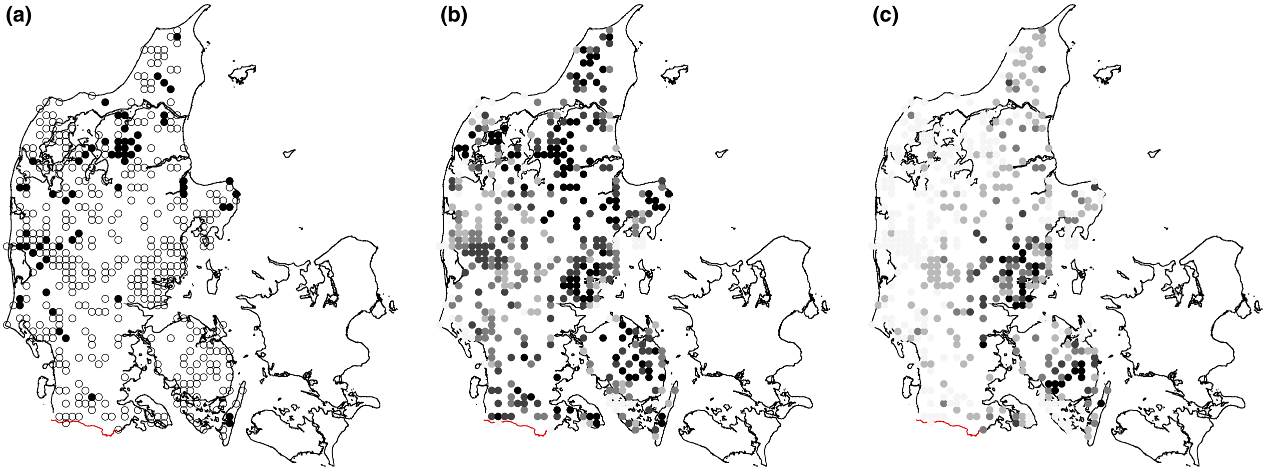

Figure 1. (a) Spatial structure of disappearance from 1972–1974 to 1993–1996 of Little Owls from 5 × 5-km^2 squares in Denmark. Squares in which Owls were observed in both periods are filled, whereas open symbols indicate squares in which Owls were recorded in the first period and not in the second. (b) Amount of seasonally changing land cover within each square indicated as shades of grey ranging from large (59–78%; black) to small (< 20%; lightest grey). (c) Amount of deciduous forest indicated as shades of grey ranging from large (10–19%; black) to small (0–2%; lightest grey).

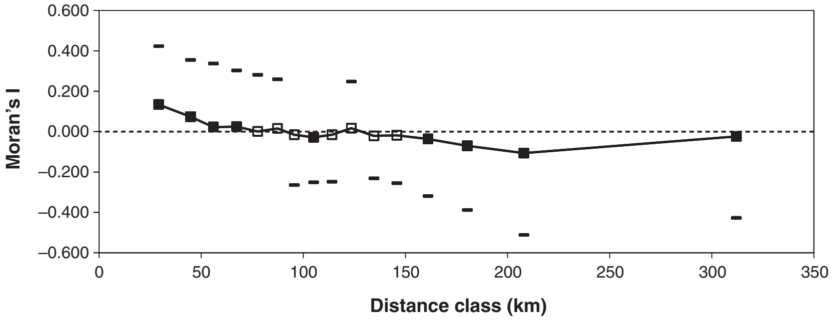

Figure 2. Spatial structure of disappearance of Little Owls from 5 × 5-km^2 squares in Denmark as indicated by the amount of autocorrelation (Moran's I) between squares that are close to each other compared with squares that are far apart. Squares = Moran's I, Filled = $P < 0.05$, Open = $P > 0.05$. Maximum Moran's I is indicated for each distance class. Squares that are closer to each other are positively correlated and distant squares are negatively correlated, as is typical of spatial autocorrelation.

landscape parameter that correlated with disappearance. Squares with high seasonally changing land cover were less likely to lose Little Owls between the censuses (Table 1). However, seasonally changing land cover explained only a small amount of variation (1%) compared with the 15% explained by spatial pattern alone (Table 1).

Survival

Annual survival rates and recovery probabilities differed between juveniles and adults in the best supported model (Table 2). The estimated annual survival rates of juveniles and adults were 0.15 (95% confidence interval 0.07–0.28) and 0.61 (CI

Table 1. Effect of the proportion of arable land, grass, marsh and woodland on the disappearance of Little Owls from 5 × 5-km^2 squares ($n = 455$) modelled as ordinary logistic regression and autoregressive models taking spatial autocorrelation among squares into account. All-subsets model selection. AICc for each model type for models with ΔAICc < 2 are shown. For best models, parameter estimates are given for the probability of disappearance (logit-transformed). Thus, a positive parameter estimate indicates that the parameter in question is associated with an increased likelihood of loss of occupancy. All models included an intercept.

Model	Variable	Parameter estimate	se	Wald χ^2	*P*	AICc	ΔAICc
Logistic regression model							
{Grass, marsh, woodland}						331.7	0
	Seasonally changing land cover	−0.027	0.008	8.55	0.0035		
	Marsh	0.24	0.16	2.23	0.14		
	Woodland	0.37	0.10	13.17	0.0003		
{Seasonally changing land cover, grass, marsh, woodland}						331.9	0.2
{Marsh, woodland}						332.4	1.3

Model	Variable	Coeff.	se	R^2	*t*	*P*	AICc	ΔAICc
Pure autoregressive model								
		0.386	0.721	0.151			−1048.0	0
Autoregressive lagged response model								
{Seasonally changing land cover}							−1049.3	0
	Seasonally changing land cover	−0.005	0.002	0.009	−2.093	0.037		
{Seasonally changing land cover, woodland}							−1048.1	1.2
{Marsh, woodland}							−1047.5	1.8
{Grass, woodland}							−1047.3	2.0

Table 2. Models of annual survival of ringed Little Owls. The survival rates *S* and recovery probabilities *r* estimated in each model are indicated in brackets. (age): separate estimates for first-year birds and older; (temp): winter temperature included as a covariate; (trend): linear trend included as covariate; and (.): constant over time. For the best model {*S*(age) *r*(age)}, this indicates separate first-year and adult annual survival rates and recovery probabilities. Model selection is based on AIC. #Par, number of parameters.

Model	AICc	ΔAICc	AICc weight	Model likelihood	#Par	Deviance
{*S*(age) *r*(age)}	478.8	0.00	0.508	1.00	4	198.87
{*S*(age temp) *r*(age)}	480.6	1.87	0.152	0.39	5	198.71
{*S*(age) *r*(age trend)}	480.7	1.92	0.195	0.38	5	198.75
{*S*(age trend) *r*(age)}	480.8	2.01	0.186	0.37	5	198.85
{*S*(age trend temp) *r*(age)}	482.7	3.88	0.056	0.14	6	198.68
{*S*(age trend) *r*(age trend)}	482.7	3.95	0.071	0.14	6	198.74
{*S*(age trend trend*age) *r*(age trend)}	484.6	5.87	0.027	0.05	7	198.61
{*S*(age) *r*(.)}	486.9	8.12	0.009	0.02	3	209.02
{*S*(.) *r*(.)}	489.2	10.42	0.003	0.01	2	213.34
{*S*(.) *r*(age)}	491.1	12.37	0.001	0.00	3	213.27

0.49–0.72), respectively. The associated recovery probabilities were 0.05 (CI 0.03–0.08) and 0.19 (CI 0.12–0.28), respectively. Models with a slight negative trend in juvenile survival estimate (from 0.18 to 0.13 over 83 years) or slight temporal trend in recovery probability were only weakly supported (ΔAICc = 1.87 and 1.92, respectively; Table 2). The best model did not include any effect of winter temperatures on survival (Table 2).

Reproductive success

All reproductive parameters declined from the 1970s to 2006 (Fig. 3). This was the case regardless of whether zero-counts nesting attempts were included in the analyses. Only the trend for fledged young was significant, either with (slope = −0.05, $P < 0.001$) or without (slope = −0.03, $P < 0.001$) inclusion of counts of zero fledglings. Each pair raised on average more than three young to

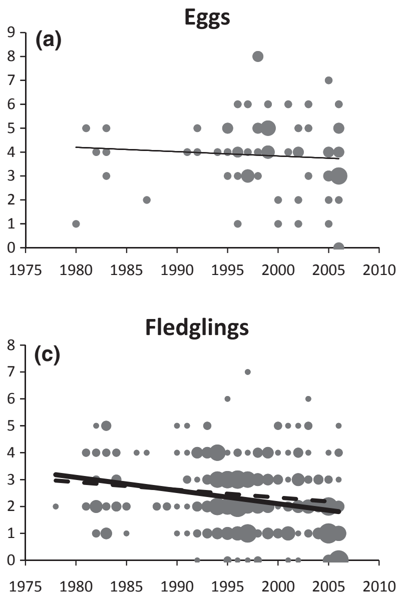

Figure 3. Production of eggs, nestlings and fledged young produced per breeding pair of Little Owls each year in the period 1975–2006. Thin lines indicate a non-significant trend over time. The thick lines for fledged young indicate a significant trend, either with (solid line) or without (dashed line) inclusion of counts of zero fledglings. Trend lines are not corrected for the influence of habitat and climate variables.

fledging age at the beginning of the period but this rate had decreased to < 2 in recent years (Fig. 3). After habitat and climate were taken into account using multiple regression, the trend (−0.05 young/year) was significant only for the number of fledged young per pair (Table 3).

Of the habitat variables correlating significantly with reproductive success (Table 3), a short distance to habitats categorized as Little Owl habitats had a positive effect on clutch size as well as on the number of young fledged (0.47 ± 0.20 fledglings/km; mean ± se in the general linear model), although the area of such habitats within 1 km of nests did not correlate with any reproductive parameter. Instead, more young fledged from nests in sites with a high coverage of seasonally changing land cover within 1 km (0.63 ± 0.23 fledglings/km^2).

Weather influenced reproductive output in several ways (Table 3). Clutch size and nestling brood size correlated negatively with the number of days of snow cover the preceding winter, whereas nestling brood size correlated negatively with high winter temperatures. In spring, clutch size correlated positively with the amount of precipitation, as did the number of young fledged with high temperatures (0.32 ± 0.08 fledglings/°C).

The proportion of eggs surviving to fledging was three times higher in food-supplemented nests than in control nests (0.79 vs. 0.27; $\chi^2_1 = 4.72$, $P = 0.03$). This difference was even more pronounced when yearly differences were taken into account (0.86 vs. 0.22; Type 3 analysis – year: $\chi^2_1 = 7.21$, $P = 0.0073$; feeding: $\chi^2_1 = 9.57$, $P = 0.002$; Fig. 4).

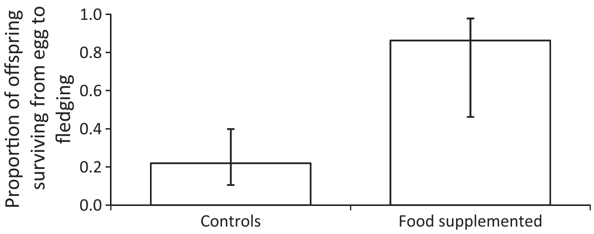

Figure 4. Effects of supplemental feeding on the proportion of offspring surviving from egg to fledging taking differences between years (2005 or 2006) into account. The difference between food-supplemented nests ($n = 5$) and control nests ($n = 24$) is significant. Bars show 95% confidence interval limits.

Population model

Using the average brood size at ringing during 1982–2006 (2.69 ± 1.28, mean ± sd, $n = 67$) and the proportion of recorded Little Owls breeding during 1994–2006 (85%), the population model with survival rates obtained from our 'best' model is

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \end{bmatrix} = \begin{bmatrix} 0.17 & 0.70 \\ 0.15 & 0.61 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \end{bmatrix}$$

Accordingly, the annual population growth rate of the Danish Little Owl population would be 0.78. Using the upper limit of the estimated 95% confidence interval for annual juvenile survival (0.28), the annual growth rate becomes 0.93.

DISCUSSION

After the early 1970s, Little Owls disappeared from large contiguous parts of their former Danish breeding distribution, with a tendency to disappear

Table 3. Factors influencing clutch size ($n = 71$), number of nestlings ($n = 126$ broods) and fledged young ($n = 350$ broods) per year per Little Owl breeding attempt. Models are backward-selected generalized linear models with Poisson errors (P_{Poiss}). Other variables were insignificant at the 0.05 level. Parameter estimates were obtained in models with normal errors and significance of the estimates is indicated by asterisks ($^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

	Clutch size		Brood size: Nestlings		Brood size: Fledglings	
Variable	Linear estimate	P_{Poiss}	Linear estimate	P_{Poiss}	Linear estimate	P_{Poiss}
Intercept	4.01		3.82		0.58	
Year (since 1975)					−0.049***	<.0001
Distance to Little Owl habitat (km)	−1.4**	0.005			−0.47*	0.026
Seasonally changing land cover (km^2)					0.63**	0.014
Temperature December–February (°C)			−0.25*	0.029	−0.083*	0.051
Temperature March–April (°C)					0.32***	<.0001
Precipitation March–April (mm)	0.03*	0.021				
Snow cover (days)	−0.02**	0.015	−0.025*	0.021		

from areas with less agriculture (seasonally changing land cover). Our estimates of survival did not indicate decreases over time, but the breeding output seemed to have decreased by more than one-third. Production of young was affected by distance to grassy habitats, proportion of seasonally changing land cover, and weather before and during the breeding season, and providing supplemental food during feeding had a positive effect. The sensitivity of reproductive parameters to landscape features and the positive response to experimental food supplementation after laying indicate that food access during the breeding season plays an important role for reproductive output and thus population dynamics.

Spatial components and habitat effects at different scales

There was a clear tendency for synchrony in local extinction patterns over a range of up to 50 km. Little Owls seem to depend on short-scale dispersal (Schaub *et al.* 2006), and dispersal distances are generally small (Bønløkke *et al.* 2006, Fuchs & Laar 2008). The strong spatial component with little dependence on environmental factors in the disappearance of Little Owls may result from a decrease in the pool of potential immigrants. Another factor resulting in spatial dependence of disappearance may be a second-order process, such as attraction or the social system. We cannot rule out that the spatial pattern observed here is the result of a lack of suitable habitat descriptors relevant for Little Owls in our study. On a smaller scale than the one considered here, Cornulier and Bretagnolle (2006) found no clustering of territories when they considered a habitat availability similar to the one used here. The difference may be attributable to the smaller scale in their study or to the evaluation of a population in steep decline in our case. Overall, the factors affecting reproductive output in the current work are quite similar to the variables generally found to affect Little Owl occurrence at the scale of the home range (e.g. Nieuwenhuyse *et al.* 2001, Martínez & Zuberogoitia 2004, Zabala *et al.* 2006).

Demographic rates and predicted population dynamics

We estimated annual survival rates of Danish Little Owls during 1920–2002 as 0.15 for juveniles and 0.61 for adults with no pronounced changes over time. Estimated recovery probabilities were lower for juvenile than for adult birds. This partly unexpected result is most likely caused by the fact that Danish ringing schemes generally discouraged recording of birds that had not moved away from the ringing site or that were recovered less than 30 days after ringing (Bønløkke *et al.* 2006).

Our estimated adult annual survival rate compares well with estimates reported in the literature (Exo & Hennes 1980, Schaub *et al.* 2006). Our juvenile annual survival rate of 0.15, however, is much lower than the 0.30 reported by Exo and Hennes (1980), although these authors did not take into account potential differences between adult and juvenile recovery/recapture probability. Other studies have reported estimates similar to ours but those studies did not include emigration (e.g. Letty *et al.* 2001, Schaub *et al.* 2006) and thus probably underestimated survival. Hence, it is likely that juvenile annual survival rate in Denmark is lower than that found in most of Central Europe.

The production of young declined considerably over time. The number of eggs and nestlings showed less decrease over time than the number of fledglings, indicating that the factors causing the decline act after the early nesting stages. Additionally, winter weather had a stronger effect on the number of eggs and nestlings than on fledgling numbers; temperature and precipitation had a greater effect in the nesting period on egg and nestling number, again emphasizing the sensitivity of post-laying losses.

To balance the estimated mortality alone in our 'best' model, each pair would have to produce 5.2 nestlings that reach the age of ringing, and all surviving birds would have to enter the breeding population (i.e. no floaters). Even though there were apparently very few floaters in the population after 2004, given that many widowed territories did not become re-occupied (Sunde *et al.* 2009), it does not seem realistic for production to balance mortality. However, the annual growth rate of 0.78 is probably unrealistically low. This low rate primarily results from our surprisingly low estimate of juvenile survival, which is, however, also quite uncertain. An annual growth rate of 0.93 (based on the upper 95% confidence interval limit of juvenile survival) is probably closer to a realistic population model for the Danish Little Owls. Assuming a growth rate of 0.93 results in an 89% decrease over 30 years, which roughly corresponds to the presumed decline from in the order of 1000 pairs in the 1970s to the current estimated 100 pairs, although early population size estimates are very uncertain.

Food limitation as the direct cause of the decline

Our results suggest that food limitation during the breeding period may be the main reason for the declining numbers of Little Owls in Denmark. Little Owl parents are very active and probably energetically stressed during the post-hatching period (Exo 1988, Holsegård-Rasmussen *et al.* 2009). The decrease in production of young with increasing distance to preferred habitat is probably a direct result of adults only being able to bring a smaller amount of food to the nest if they have to fly further to forage.

The results from the food supplementation experiment are based on a very small sample size and should be treated with caution, and other factors such as predation could also influence breeding output. Nevertheless, the direct, positive effect of supplemental feeding on the number of fledging young supports the limiting role of food supply. Positive effects of experimental food supplementation on reproductive success through improved nestling survival have been shown in a several raptor species (Amar & Redpath 2002, Brommer *et al.* 2004, Gonzalez *et al.* 2006, Byholm & Kekkonen 2008), although the mechanism appears to differ among species, including an indirect, delayed response in a large raptor, the Ural Owl *Strix uralensis* (Brommer *et al.* 2004).

Ultimate reasons for the population decline: habitat quality?

A decline in productivity may well have started long before our recording of productivity began. The correlation between production of young and grassy habitats indicates that the decline may be related to the large-scale landscape changes associated with changes in agricultural practices. Such a dependence on agricultural practices has also been found in another small raptor, the insectivorous Scops Owls *Otus scops*, in the Alps (Marchesi & Sergio 2005, Sergio & Marchesi 2009) and Spain (Martínez *et al.* 2007) and suggests that agricultural changes are a general cause for recent declines in small, European owls. The amount of grassy habitats on which the owls seem to depend for successful reproduction has decreased in the past and is likely to be further reduced in the near future (Ellemann *et al.* 2001), as for example when grazed areas are converted to cropland. Our study documents a link between breeding performance and habitat, and indicates that this link is most likely caused by food limitation when suitable habitat is not readily available. A similar situation was found in Hen Harriers *Circus cyaneus* (Amar *et al.* 2003, 2008) that fed primarily on small vertebrates. This pattern of the interaction between food limitation and suitable habitat causing reduced breeding performance in an intensified agricultural landscape is probably common among animals dependent on small vertebrates or larger invertebrates.

In correlation with agricultural intensification, including habitat loss and change, and the increased use of pesticides and fertilizers, there has been a dramatic decline in the abundance and biomass of larger insects (Benton *et al.* 2002). The Danish Little Owl population apparently feeds relatively more on earthworms than do other European populations (Ottesen & Svenné 2008). This could be due to reduced insect abundance, although the reduction in insect abundance is not as extreme in Denmark as in, for example, the UK (Fox 2004).

Conservation implications

With an estimated population size of about 100 pairs, and an estimated annual growth rate of 0.93, the Danish population is likely to fall to a critical size of fewer than 25 pairs within 20 years unless actions target improved reproductive success. Because the main reason for reproductive failure appears to be related to food limitation after egg-laying (which is the period in which offspring are most affected), the energetic situation of breeding birds should be the main target for conservation initiatives. Our results indicate that the availability of grazed or other areas with short vegetation is important for adults when providing food to the young. In the short term, provision of additional food to breeding pairs might be an efficient strategy for boosting the number of potential recruiters to the population by improving survival of initiated broods. The consequences of such management action should be monitored to confirm our small-scale results of food provision at the population level.

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