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ORIGINAL ARTICLE

Seasonal survival rates and causes of mortality of Little Owls in Denmark

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Abstract Survival rate is an essential component of population dynamics; therefore, identification of variation in mortality rates and the factors that influence them might be of key importance in understanding why populations increase or decrease. In Denmark, the Little Owl *Athene noctua*, a species strongly associated with anthropogenically modified landscapes, is declining fast and may soon face extinction. The population decline is ultimately associated with reduced survival of independent offspring, but reduced survival rates of adults may possibly contribute to the observed decline. To explore the causes of current survival rates, we estimated age- and season-specific survival rates and causes of mortality in Danish Little Owls on the basis of ringed birds 1920–2002, radio tagged adult and juveniles 2005–2008 and nest surveys 2006–2008. We estimate that 32 % of all eggs fledge and survive to 2 weeks post hatching (age of ringing) and 47 % of the nestlings from ringing to fledging. Fifty-five percentage of the radio-tracked fledged young survived to dispersal, i.e. a total survival rate from egg to dispersal of 8 %. Analyses of combined ringing and radio tracking data showed a lower survival rate in the 1st year of life and a much lower rate in the first 3 months of life. Furthermore, the analyses indicated that survival was lower in the winter months for ringing data during 1920–2002 but not for radio-tagged owls during 2005–2008 that experienced the highest mortality rates during the breeding season. In radio-tagged adults and fledged juveniles, accidents in buildings and other human infrastructures were responsible for two-thirds of all fatalities. Anthropogenic habitats currently comprise the nesting and roosting habitats for the last Danish Little Owls. The accidental deaths associated with these might to some extent be considered as a contributing factor to the present negative population growth rate of this population.

Keywords Little Owl · Population dynamics · Mortality · Conservation

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Zusammenfassung

Saisonale Überlebensraten und Ursachen für Sterblichkeit beim Steinkauz (*Athena noctua*) in Dänemark

Überlebensraten sind ein grundlegender Bestandteil der Populationsdynamik. Deshalb ist die Untersuchung der Schwankungen von Überlebensraten sowie der diese Raten beeinflussenden Faktoren für das Verständnis von Schwankungen der Populationsgrößen von besonderer Bedeutung. In Dänemark hängt der Steinkauz (*Athena noctua*) sehr von den vom Menschen veränderten Landschaften ab, sein Vorkommen geht rasch zurück, und er könnte schon bald vor dem Aussterben stehen. Letztendlich hängt das Überleben der Population davon ab, wie viele unabhängige Jungtiere

überleben; aber auch eine geringere Überlebensrate der Adulten könnte möglicherweise zum beobachteten Rückgang dieser Art führen. Für die Untersuchung der Ursachen der derzeitigen Überlebensraten schätzten wir die alters- und saisonspezifischen Überlebensraten sowie die Sterblichkeit dänischer Steinkäuze anhand von beringten Vögeln (1920–2002), von mit Sendern versehenen Adulten und Jungvögeln (2005–2008) und anhand von Nestuntersuchungen zwischen 2006 und 2008. Wir schätzen, dass aus 32 % aller Eier Junge schlüpfen und jedenfalls zwei Wochen (das Alter der Beringung) überleben, wie auch 47 % aller geschlüpften Vögel von der Beringung bis zum Flüggewerden. Von den mit Sendern versehenen Jungvögeln überlebten 55 % bis zum Ausfliegen. Das heißt, die Überlebensrate insgesamt betrug vom Ei bis zum Ausfliegen der Jungvögel 8 %. Die Kombination der Ringfunddaten mit denen des radio-tracking zeigte für das erste Lebensjahr eine nur etwas, für die ersten drei Lebensmonate aber eine wesentlich niedrigere Überlebensrate. Außerdem wiesen die Analysen darauf hin, daß für die Ringfunde 1920–2002 die Überlebensrate in den Wintermonaten geringer war, aber nicht für die von 2005 bis 2008 mit Sendern versehenen Tiere; diese zeigten während der Brutzeiten die höchsten Sterblichkeitsraten. Bei den Adulten und ausgeflogenen Jungtieren mit Sendern waren Unfälle an Gebäuden und anderen von Menschen gemachten Strukturen für zwei Drittel aller Todesfälle verantwortlich. Anthropogene Habitate beinhalten derzeit Nist- und Ruheplätze für die letzten dänischen Steinkäuze, und die damit zusammenhängenden Unfalltode tragen vermutlich in gewissem Grad zur derzeitigen negativen Wachstumsrate dieser Population bei.

Introduction

Survival rates are essential components of population dynamics; therefore, identification of variation in mortality rates and the factors that influence them might be of key importance in understanding why populations increase or decrease (Caughley and Gunn 1996). In particular, this might apply to decreasing populations of relatively long-lived species where an anthropogenically induced increase in adult or juvenile mortality might turn an increasing population growth rate into a negative trend (Ortega et al. 2009). In order to facilitate recoveries of threatened populations, identification of proximate as well as ultimate reasons for mortality is thus essential.

The population of the small Little Owl *Athene noctua* in Denmark is on the north-western edge of the species' range. However, like in most of West and Central Europe there has been a considerable decline in Denmark, both in number of pairs, which now may number as few as 50 pairs, and in the extent of its distribution (Grell 1998). If the current negative population trend continues, the species will become extinct in the near future in Denmark (Thorup et al. 2010). The widespread western and central European decline has been associated largely with changes in the agricultural landscape and practices (Tucker and Heath 1994) with which the species is connected strongly. Its decline is shared with many other species in the agricultural landscape (Donald et al. 2001). However, the exact factors driving declines and to what extent these are related to suboptimal conditions on the edge of the distribution (Brown 1984) or to general landscape changes (Newton 2004) have not been studied in detail.

The northern limit of the species' range is apparently associated with winter severity (Van Nieuwenhuyse et al. 2008). Potential factors causing the decline could be, among others, increases in predator populations, lack of nesting sites or insufficient food resources (Newton 2004). The Little Owl is a relatively small owl and, compared to most other Northwest European raptors, its diet has a relatively high non-mammalian proportion (i.e. earth worms and invertebrates; Van Nieuwenhuyse et al. 2008).

Survival can generally be estimated using capture-mark-recapture techniques based on recaptures and/or recoveries of birds ringed with metal or colour rings (Lebreton et al. 1992), or radio tracking, where the fate of each individual is (or can be considered) known (Kenward 2001; Schaub et al. 2010). Using these methods, general population parameters of European Little Owl populations have been estimated in several studies (e.g. Schaub et al. 2006; Thorup et al. 2010; Le Gouar et al. 2011).

With the large decline in the Danish Little Owl, acquiring information on what affects the basal population parameters is of high priority (Thorup et al. 2010). Here, we combine data from 3 years of radio tracking of adult birds and 2 years of tracking young birds with 83 years of ring recoveries to investigate patterns of survival in Danish Little Owls based on quarter-yearly estimates. Furthermore, we estimate daily survival rates and causes of death based on the more intensive radio tracking data.

In general, it is difficult to study causes of mortality based on birds found dead because the cause of death is likely to influence the likelihood of being found. For radio tracking data, we generally assume that the cause of death can be determined irrespective of the cause. Thus, we use these unbiased data on causes of mortality to quantify causes of death and discuss potential ways to avoid such mortality.

Materials and methods

We analysed data on ringed birds, nest monitoring and radio-tracked birds. Combined data on ringed and radio-

tracked birds were used to estimate seasonal and age-specific differences in quarter-yearly survival rates, analysed in a traditional capture-mark-recapture framework based on AIC using MARK 4.1 (White and Burnham 1999). Daily survival rates of birds with an assumed recovery probability of one (nestlings, radio-tagged adults and fledglings) were estimated by means of the Mayfield regression principle, i.e. as the conditional number of death events per exposure day (Hazler 2004) using SAS 9.1.

Data

Ringing data and breeding success

We used ringing data for 578 (491 pull. and 87 ad.) Little Owls ringed throughout the breeding area in Denmark 1920–2002 (83 years) for which ringing year and age at ringing was known. Of these, 50 individuals (34 pull. and 16 ad.) were recovered before 2003, i.e. were later found dead and reported by the public to Copenhagen Bird Ringing Centre. To avoid potential bias from uneven reporting efforts (i.e. "trap happiness"), reports of birds found again alive and birds reported by the ringer were not included in the analyses

From 2006 to 2008, we monitored breeding success of 37 pairs of Little Owls until fledging. Both eggs that failed to hatch and dead nestlings were included. 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 (see Thorup et al. 2010). In total, 119 eggs were recorded for 36 pairs, resulting in 38 nestlings and 18 fledglings.

Radio tagging

Analysis of radio-tagged individuals was based on 29 individual adults during 3 years 2005–2007 and 18 juveniles 2007–2008 in Himmerland, northern Jutland, Denmark (ESM Table 1; see Sunde et al. 2009 for more details of the study area and telemetric survey). Adult owls were trapped in mistnets near breeding sites or by hand in nestboxes and tagged with 5-g radio transmitters from Biotrack (Biotrack, Wareham, UK), which were fitted as backpacks using Teflon ribbons (7-g in total including harness). Transmitters had an expected life-time of 11–12 months but a few transmitters apparently failed after a few months (Sunde et al. 2009). The transmitters were in general detectable 1–1.5 km away from the ground, though often more or less depending on the landscape. Owls were surveyed intensively from the ground throughout the breeding season, less intensively in the non-breeding season (see ESM Table 1 for details). As a minimum, each individual was checked every month. After transmitter failure, owls were retrapped and the transmitter removed. No effects on behaviour or breeding performance of the tagged owls were detected (our unpublished data).

Six juveniles in 2007 and 12 juveniles in 2008 from eight nests had a VHF radio transmitter (type Ag393 leg mount tag; BioTrack) weighing 3–4 g (a maximum of 4 % of the juvenile weight at ringing) attached to their leg on the day of ringing. This was on average 20 (range 10–35; median 21) days after hatching and 13 (range 1–31; median 9) days before fledging. The radio transmitters had an expected battery life of 4–5 months and a maximum tracking range of ca. 600 m.

In 2007, tracking of young birds was performed during day time on a daily basis from mid-June to the end of July, and once a week in August. Night time positions were collected in late June and 4 times during July and August. From mid-June 2008 until mid-September each study site was visited on a regular basis 1–6 times a week during both day and night. Three daytime follow-up radio trackings were conducted in late September, mid-October and late October.

Each individual was radio tracked until it was found dead or the signal was no longer to be found within a 1 km radius from the nest. When signals of young were lost, sounds of fledglings begging for food were extensively listened for to check if the transmitter had collapsed and the owl was still alive.

Of the 18 young and 29 adult, radio-tagged birds, six young and seven adult were found dead or lost under circumstances that indicated death. The first two presumed deaths of juvenile birds were both early lost signals, and we expect these individuals to have died because their flying skills were not fully developed at the time of signal loss, and it is therefore highly unlikely that they have flown out of tracking range. Five young that disappeared from the natal area later than 50 days after fledging and after having stopped begging for food were considered to have dispersed and were excluded from the survival analysis.

Statistics

Seasonal quarter-yearly survival rates analyses in MARK

Quarter-yearly survival rates of birds ringed 1920–2002 and surveyed with telemetry 2005–2007 were estimated in a capture-mark-recapture framework using the program MARK 4.1 (White and Burnham 1999). The capture-mark-recapture framework allows for separate estimation of survival rate S and recovery probability r and is well suited to evaluating different models based on e.g. age (Lebreton et al. 1992). Separate analyses were conducted to estimate differences in monthly survival rates between juvenile

Table 1 Support given as ΔAICc for models of survival of ringed and radio tagged Little Owls

Model	Model numbers[a]	ΔAICc
First year survival differs from later years	22/25	10.614
First 3 months survival lower than next nine	7/22	7.182
Lower winter survival in radio tagged	2/3	0.375
First winter survival compared to later winters	2/5	−1.507
Survival of breeding radio tracked compared to ringed birds	1/2	0.020
Ringed adults compared with radio tracked	12/18	−1.511

[a] Model numbers refer to the model numbers in ESM Table 2

Table 2 Estimated monthly survival of ringed and radio-tracked Little Owls in best candidate model with age-specific survival rates for 1st year birds, first summer in radio tracked birds, winter in ringed birds and summer/breeding in adult radio tracked birds; and separate reporting rate for ringed birds in their first summer (Table 1)

Parameter	Period	Estimate	Lower 95 % CI	Upper 95 % CI
$S_{juvenile[radio]}$	Jun–Aug	0.65	0.45	0.84
$S_{1\ year[ring]}$		0.94	0.88	0.97
S_{adult}		0.98	0.96	0.99
$S_{summer[radio]}$	Jun–Aug	0.94	0.88	0.97
$S_{winter[ring]}$	Dec–Feb	0.94	0.83	0.98
S_{year}	Jun–May			

stages (ringing data) and between seasons and methods (ringing and radio tagging data). Because of the restricted data set we did not estimate rates for each year separately. For the long ringing series this was justified by the lack of such trends in earlier analyses (Thorup et al. 2010).

In MARK, survival was modelled with the recovery data type. To investigate the timing of potential major juvenile mortality during the first few months of life, we modelled a separate, juvenile survival rate during June to August. Trapping occasions were grouped in monthly intervals lasting from the 16th in 1 month to the 15th of the following month. Accordingly, each individual was considered ringed on the 1st day each month and survival was then considered on a monthly basis.

Ringing and radio tagging data were compared using the recaptures and recoveries data type in MARK (Cooch and White 2007). In these models, we also looked at differences between stages in the annual cycle: winter (December–February) and summer/breeding (June–August). Data from the two methods were included as different groups. Fidelity of both groups was fixed to one, probability of recapture of a ringed bird to zero and of a radio tagged to one, and the probability of recovery of a radio tagged bird also to one. Overall, we failed to find strong support that radio-tagging lowered survival rates compared to ringed birds (ΔAICc = −1.5) combining information from both ringing and radio-tagging (Table 1).

For each analysis, a number of potential models was considered (Tables 1, 2). Selection among these models was based on AIC_c (Burnham and Anderson 2002). Because bootstrap goodness-of-fit (GOF) simulation in MARK omits censored individuals from radio tracking data, we ran a bootstrap simulation on a general model where censoring was modelled indirectly as a decrease in fidelity, i.e. birds leaving the area. This general model with age- and time-dependent survival and age-dependent reporting rate fitted the data well ($P = 0.76$; bootstrap GOF).

Daily mortality rates analyses in SAS

We used logistic regression to estimate daily mortality rates and the effects of sex and reproductive status (divided into breeding vs non-breeding, or brooding, feeding and non-breeding). The daily mortality rates were analysed separately based on (1) verified deaths only; (2) verified and suspected deaths and (3) accidental deaths associated with buildings; (4) deaths from predation; and (5) deaths with reason unknown (including suspected deaths).

Survival from egg laying to fledging, egg laying to ringing, and ringing to fledging, was estimated by performing logistic regression Proc GENMOD (Logit-link and binomial distribution) on surviving offspring within each brood, entering brood size as trials and surviving individuals as events, and correcting for overdispersion. This procedure accounts for the heterogeneity in individual survival among broods. Daily mortality was calculated from GENMOD survival estimates, the time used being the average duration of the different periods. Variation in daily survival rates as a function of days after fledging year, and absence or presence of experimental feeding were tested by means of type 3 analyses.

For post-fledging survival, we tested for significant effects of hatching date, fledging date, days after fledging, with Proc GENMOD Likelihood ratio test, type 3 analyses.

Results

Age-dependence of, and seasonal variation in, survival rates

Our candidate CMR models combining ringing and tracking data (ESM Table 2) supported (ΔAICc = 10.6; Table 1) a lower monthly survival in the first year of life (0.94) compared to later years (0.98; Table 2; Fig. 1). Monthly survival was even considerably lower (0.65) in the

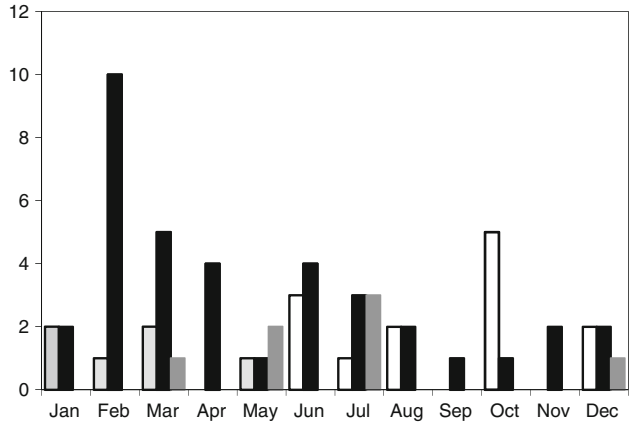

Fig. 1 Monthly distribution of Danish Little Owls found dead. Ring recoveries 1920–2002 of adult (*black*) and juveniles (*open bars*, first year: *white*; second year: *pale grey*), and mortality incidents of radio-tagged adults (*grey*)

first 3 months of life for the radio-tracked juveniles (ΔAICc = 7.2). Some support (ΔAICc = 0.37) was found for a lower winter survival (0.94) for ringed birds than adult monthly survival the rest of the year (0.98). Survival during first winter was apparently not lower than winter survival in later years (ΔAICc = −1.5). In addition, the number of radio-tagged birds dying during the breeding season indicated a slightly decreased survival (0.94) during this period (ΔAICc = −0.02). There appeared to be no differences in overall adult survival between ringed and radio-tracked birds (ΔAICc = −1.5).

Calculated from survival estimates in Table 2, 27 % [95 % confidence interval: (9; 57 %)] of the young survived through August, accounting for 86 % of the annual 1st-year mortality. Of the ringed birds, 83 % [68, 91 %] survived through the winter, while 94 % [87, 97 %] of radio-tagged birds survived the winter period. In total, an estimated 15 % [3, 44 %] survived their 1st year and, of the adult birds, 68 % [45, 83 %] ringed and 67 % [38, 85 %] radio-tagged individuals survived per year.

Stage-dependent estimates of survival from egg to dispersal

Of 139 eggs laid 2005–2008, 32 % hatched and survived until age of ringing, and 47 % hatchlings survived from ringing to fledging (Fig. 2), with corresponding average daily mortalities of 2.3 and 6.0 %, respectively.

From the 18 radio-tagged fledglings surveyed 2007–2008, we estimated post-fledging survival of young, radio-tagged owls as 55 % [95 % confidence interval: (16, 82 %)], and thus a total survival rate from egg to dispersal of 8 % (1, 23 %). Post-fledging survival rates were independent of hatch date (χ_1^2= 0.30, P = 0.59) and fledging date (χ_1^2= 0.28, P = 0.59), but daily mortality rates tended to decrease with the number of days passed since fledging (χ_1^2 = 3.48, P = 0.06; predicted relation: logit daily mortality = 3.0–1.5*days after fledging). Accidents and unknown reasons were each responsible for one-third of the deaths that occurred from fledging until dispersal. Based on the rather low number of birds, estimated mortality from this period was 15 % [4, 49 %] of young owls dying in accidents and 32 % [12, 69 %] presumably dying from unknown reasons.

Of 29 radio-tagged adults, 8 were recorded dead and 2 suspected to have died without being recovered, equalling an overall annual survival rate of 66 % [verified deaths only; 95 % (44, 81 %) or 60 % including suspected deaths; (38,76 %)], which differed only slightly from the estimated annual survival rate of 69 % for radio-tagged adults in the combined analyses. Daily survival rates of adult, radio-tagged birds were lower in the breeding season compared to the rest of the year (Fig. 3; Table 3). At least one-half of the annual adult mortality of 38 % (including suspected deaths) was caused by accidents, i.e. birds not deliberately being killed. All these were associated with man (Fig. 4). Only 10 % were predated (by raptors).

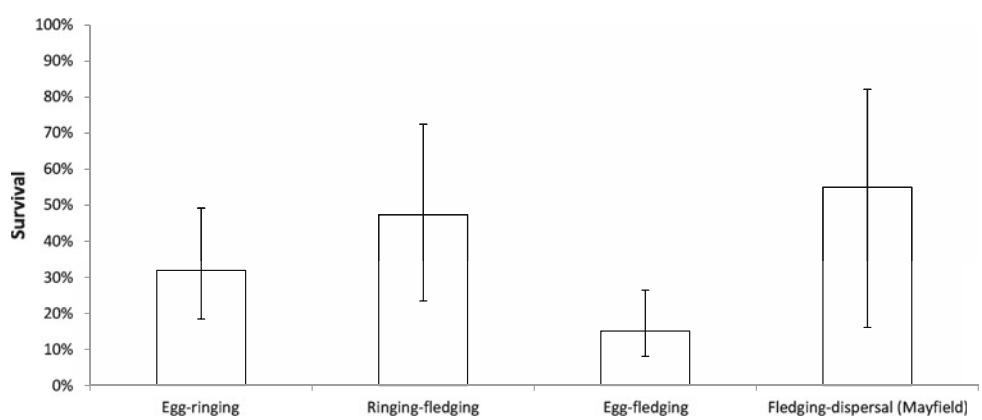

Fig. 2 Survival (with 95 % confidence limits) of young Little Owls during 2006–2008 based on nest surveys and radio-tagging data. Survival estimates are from models accounting for the heterogeneity in individual survival among broods. Mayfield logistic regression was used to estimate survival for Fledging-dispersal

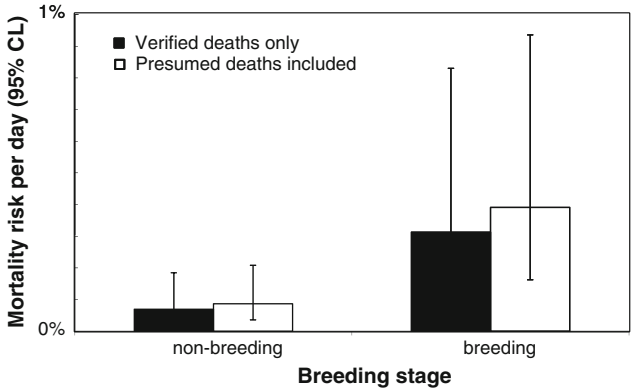

Fig. 3 Mortality rates of adult, radio-tagged Little Owls of different reproductive status

Table 3 Effects of sex and two divisions of reproductive status on mortality risks of radio-tagged Little Owls, analyzed with Mayfield logistic regression (7,036 survey days)

		K	AICc	ΔAICc
Verified deaths (8 events)	Base model	1	46.511	2.036
	Sex	2	47.716	3.241
	Non-breeding, eggs or young	3	45.489	1.014
	Breeding or non-breeding	2	44.476	0.000
Verified + presumed deaths (10 events)	Base model	1	55.131	3.078
	Sex	2	56.423	4.370
	Non-breeding, eggs or young	3	52.120	0.068
	Breeding or non-breeding	2	52.052	0.000

Discussion

Mortality in Little Owls was by far the highest during the first 3 months of life as suggested by the radio-tracked young and overall much higher in the 1st year of life than later. Furthermore, our results suggest that the daily mortality after fledging is highest just after fledging. Juveniles that fledge early in the summer were at no higher risk of dying than juveniles that fledge later. Adult monthly survival rate during winter was lower in the period 1920–2002 than in the period 2005–2007, where the winter mortality did not differ from mortality during the rest of the year. Instead, there was some evidence of a higher mortality rate during the breeding season. Most of the annual mortality was caused by accidents, which generally occurred in the breeding season.

From fledging to dispersal, there was a tendency for the daily mortality rate to peak after fledging and to decrease thereafter with age. This pattern of high mortality just after fledging is common in birds, including owls (e.g. Rohner and Hunter 1996; Overskaug et al. 1999; Todd et al. 2003; Sunde 2005 and references therein). In Little Owls, the chicks fledge before they are able to fly and hunt for themselves. Poor flying skills; loud begging increasing detectability; as well as inexperience with predators, resulting in high predation rates, are all factors contributing to the high mortality rate (Haskel 1994; McFadzen and Marzluff 1996; Anders et al. 1997).

The very low early survival was not apparent for the ringing data. It cannot be ruled out that there was some effect of the transmitters, but it is more likely it was caused by a recent decrease in survival or because little attention has been given to data collection from birds in, or soon after leaving, the nest. The estimated nestling survival of 15 % in this study during 2006–2008 is surprisingly low compared to estimates obtained in the same population before 2000, where 60 % of the nestlings survived to fledging (Jacobsen 2006), and other European populations where 48–60 % survive (Schönn et al. 1991). Pre-fledging survival in the remaining Danish Little Owls appear to have dipped since 2000 and might therefore be a strong component of the reason for the apparent, accelerating population decline in recent years (see Thorup et al. 2010). Our estimate of 55 % post-fledging pre-dispersal survival is similar to that found for other species of owls: Burrowing Owls 55 % (Todd et al. 2003) and 57 % (Davies and Restani 2006), Tawny Owls *Strix aluco* 61 % (Overskaug et al. 1999) and 50–73 % (Sunde 2005), Great Horned Owls *Bubo virginianus* 23–80 % (Rohner and Hunter 1996).

We found little support for an effect of radio tagging on adult birds. Our results indicate that the differences in monthly survival rates between radio tracking and ringing models could be caused by the short year span for collection for radio tracking data, which did not include very strong winters. Earlier studies have shown two peaks of adult mortality occurring during the winter and breeding season, respectively, and with a tendency for the winter peak to be larger in populations with colder winter climate (Exo and Hennes 1980), which fits well with the pattern observed here. Furthermore, Le Gouar et al. (2011) found that dry and cold years led to low adult survival and that adult survival was lower in severe winters.

The low number of deaths observed during the post-fledging period makes it difficult to draw any firm conclusions on important causes of post-fledging mortality. One-third of observed deaths (2 of 6) were caused by drowning in a slurry tank, indicating that accidents associated with human-made constructions could indeed be an important cause of juvenile mortality. Another category of human-associated accidents is road and railway casualties. Although not found in this study, such accidents have been

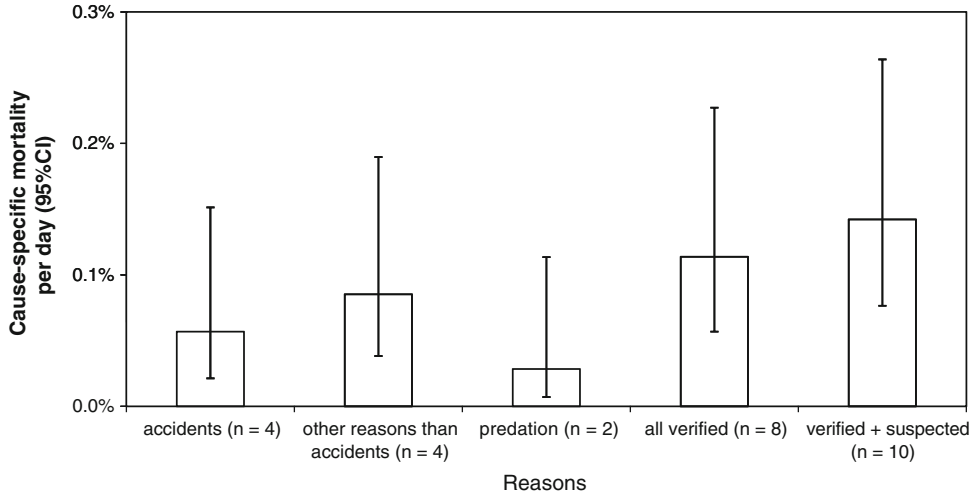

Fig. 4 Baseline mortality rates specific to reason of 29 adult, radio-tagged Little Owls, based on 7,036 exposure days during radio tracking

documented in Denmark (Jacobsen 2006) and in other European Little Owl populations (Exo and Hennes 1980; Ullrich 1980), and Le Gouar et al. (2011) found a negative trend of juvenile survival rate with road traffic. Although we did not document any deaths due to predation, it is very likely that the two early lost signals was a result of predation, since a high level of post-fledging predation has been documented in the similar Burrowing Owl (Todd et al. 2003; Davies and Restani 2006).

Although we observed only a limited number of deaths, a relatively large part of the observed deaths of adult birds could be attributed to human-related "accidents". This is attributable largely to the species being strongly dependent on human structures (e.g. birds easily become stuck in buildings) and anthropogenically modified landscapes (e.g. birds are killed by cars). Apart from road kills, which were not documented in this study for adults either, most of this mortality is likely to have been rather constant over time arising from the use of sheltered breeding sites in the vicinity of humans. This situation might reflect that simple fact that, in Denmark, virtually no pairs breed any more in "classical" outdoor habitats such as natural tree cavities in orchards and hedgerows, possibly because these microhabitats are no longer present in the modern Danish rural landscape.

Reducing mortality related to accidents will probably be important to stop the continued decline of the Danish Little Owl population. The mortality of young soon after fledging can probably be reduced to some extent by simple modifications of the buildings where Little Owls nest and their immediate surroundings. Thus, it will be essential to disseminate information to local land owners about how to best avoid this mortality. Given that mortality rates are lower in outdoor microhabitat, re-establishment of suitable breeding habitats outside buildings (hedges and tree lots with natural tree holes or nest boxes in vegetation) might be considered as a long-term initiative to improve survival of adults and fledged young.

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References

Anders AD, Dearborn DC, Faaborg J, Thompson FR (1997) Juvenile survival in a population of neotropical migrant birds. Conserv Biol 11:698–707

Brown JH (1984) On the relationship between abundance and distribution of species. Am Nat 124:255–279

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, Berlin

Caughley G, Gunn A (1996) Conservation biology in theory and practice. Blackwell, Cambridge

Cooch E, White G (2007) Using MARK–a gentle introduction. http://www.phidot.org/software/mark/docs/book/markbook.exe. Retrieved 23 November 2008

Davies JM, Restani M (2006) Survival and movements of juvenile burrowing owls during the postfledging period. Condor 108:282–291

Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc B 268:25–29

Exo KM, Hennes R (1980) Beitrag zur Populationsökolige des Steinkauzes (*Athene noctua*)–eine Analyse deutscher und niederländischer Ringfunde. Vogelwarte 30:162–179

Grell MB (1998) Fuglenes Danmark. Gad, Copenhagen

Haskel D (1994) Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proc R Soc B 257(1349):161–164

Hazler KR (2004) Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707–716

Jacobsen LB (2006) Ynglebestanden af Kirkeugle Athene noctua i Vendsyssel og Himmerland 1981–2000. Dansk Orn Foren Tidsskr 100:35–43

Kenward RE (2001) A manual for wildlife radio tagging. Academic Press, New York

Le Gouar PJ, Schekkermnan H, van der Jeugd HP, Boele A, van Harxen R, Fuchs P, Stroeken P, van Noordwijk A (2011) Long-term trends in survival of a declining population the case of the Little Owl (*Athene noctua*) in the Netherlands. Oecologia 166:369–379

Lebreton JD, Burnham KP, Clobert J et al (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

McFadzen ME, Marzluff JM (1996) Mortality of prairie falcons during the fledging-dependence period. Condor 98:791–800

Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579–600

Ortega E, Mañosa S, Margalida A, Sánchez RS, Oria J, González LM (2009) A demographic description of the recovery of the vulnerable Spanish imperial eagle *Aquila adalberti*. Oryx 43:113–121

Overskaug K, Bolstad JP, Sunde P, Øien IJ (1999) Fledgling behaviour and survival in northern tawny owls. Condor 101:169–174

Rohner C, Hunter DB (1996) First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. Can J Zool 74:1092–1097

Schaub M, Ullrich B, Knötzsch G, Albrecht P, Meisser C (2006) Local population dynamics and the impact of scale and isolation: a study on different Little Owl populations. Oikos 115:389–400

Schaub M, Aebischer A, Gimenez O, Berger S, Arlettaz R (2010) Massive immigration balances high anthropogenic induced mortality in a stable eagle owl population: lessons for conservation. Biol Conserv 143:1911–1918

Schönn S, Scherzinger W, Exo KM, Ille R (1991) Der Steinkauz. Ziemsen, Wittenberg Lutherstadt

Sunde P (2005) Predators control post-fledging mortality in tawny owls, *Strix aluco*. Oikos 110:461–472

Sunde P, Thorup K, Jacobsen LB, Holsegård-Rasmussen MH, Ottesen N, Svenné S, Rahbek C (2009) Spatial behaviour of little owls (*Athene noctua*) in a declining low-density population in Denmark. J Ornithol 150:537–548

Thorup K, Sunde P, Jacobsen LB, Rahbek C (2010) Breeding season food limitation drives population decline of the Little Owl *Athene noctua* in Denmark. Ibis 52:803–812

Todd LD, Poulin RG, Wellicome TI, Brigham RM (2003) Post-fledging survival of burrowing owls in Saskatchewan. J Wildl Manag 67:512–519

Tucker GM, Heath MF (1994) Birds in Europe: their conservation status. Birdlife International, Cambridge

Ullrich B (1980) Zur Populationsdynamik des Steinkauzes (*Athene noctua*). Die Vogelwarte 30:179–198

Van Nieuwenhuyse D, Génot JC, Johnson DH (2008) The little owl. Conservation, ecology and behaviour of *Athene noctua*. Cambridge University Press, Cambridge

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139