Erschienen in: Journal of Avian Biology ; 48 (2017), 2. - S. 266-274
https://dx.doi.org/10.1111/jav.00947

Bias in ring-recovery studies: causes of mortality of little owls *Athene noctua* and implications for population assessment

Beat Naef-Daenzer, Fränzi Korner-Nievergelt, Wolfgang Fiedler and Martin U. Grüebler

B. Naef-Daenzer (beat.naef@vogelwarte.ch), F. Korner-Nievergelt and M. U. Grüebler, Swiss Ornithological Inst., Sempach, Switzerland. FK-N also at: OIKOSTAT, Ettiswil, Switzerland. – W. Fiedler, Max Planck Inst. of Ornithology, Vogelwarte Radolfzell, Radolfzell, Germany.

Recoveries of marked animals hold long-term, large-scale information on survival and causes of mortality, but are prone to bias towards dead recoveries and casualties in the range of presence of potential finders. Thus, accounting for circumstance-related recovery probabilities is crucial in statistical approaches. For the little owl, a species of conservation concern in central Europe, raw ring recoveries suggested a strong human-related impact on survival. We analysed the proportions of the main causes of death using a large sample of radio-tracked birds as a reference. We compared ring recoveries in southern Germany collected 1950–2012 (n = 465 dead recoveries of 2007 recoveries of 30 623 ringed birds) with data from a radio-tracking study in the same region 2009–2012 (n = 177 dead recoveries of 377 tagged individuals). Two assumptions of multi-state ring recovery modelling were unrealistic. First, not all dispatched rings remained available to potential finders. Instead, 34% of tracked birds were displaced to sites where rings were irretrievable, resulting in biased estimates of recovery probability. Second, the proportions of irretrievable rings were disproportional, with 48% in predated birds and 5% in human-induced mortality. Consequently, the sample of rings from which recoveries were drawn differed from the sample of dispatched rings. Accounting for these biases in a multi-state model, we estimated the frequencies of main causes of mortality to 45% for predation, 20% for casualties due to traffic and at buildings and 34% for all other causes. In radio-tracked birds, predation was even more dominant (76%). Integrating mark–recapture data and telemetry observations allowed detecting and quantifying so far unknown recovery bias and resulted in improved estimates of key population parameters. The demography of little owls likely depends mainly on predator–prey relationships rather than on human-induced deaths.

Ringing of birds has been used for roughly a century to assess migration routes and to estimate demographic rates of populations. Very large samples of individuals have been tagged at a continental scale. Thus, ringing data bases hold information that could not be acquired using alternative techniques. However, drawing conclusions on the importance of causes of mortality and related conservation measures from raw recovery frequencies can be misleading (Peach et al. 1994, Bowker et al. 2007). Only 0.5–2% of the tagged birds are ever recovered, most of them dead (Baillie and Green 1987). Resolving the methodological problems with analysing ring recoveries and quantifying the major determinants of survival and the proximate causes of mortality is important for understanding demographic patterns, ecological relationships (such as trophic webs) and life-history bottlenecks (such as age-stage-specific survival). A likely source of bias is that ring recoveries are inevitably related to the spatial and temporal variation in human activities (more recoveries at places where many potential finders are present). The conspicuousness of birds or carcasses may further affect the probability of recoveries (more recoveries of large birds and of conspicuous casualties). Furthermore, rings may be displaced to sites where a recovery is factually impossible. Therefore, recovered rings are likely a non-representative sample from the population of dispatched rings (Perdeck 1977).

Statistical modelling of demographic rates takes into account that the recovery probability may vary with the abovementioned circumstances (Newton and Lakhani 1983, Anderson et al. 1985, Brownie et al. 1985, Schaub and Lebreton 2004). However, these techniques are limited in that they cannot account for causes of death that are not represented in recoveries. This bias may occur in relation to casualties where rings disappear from the surface (under-representation, if birds are consumed by predators or perish while crossing water). Moreover, recoveries may be closely related to specific human activity (over-representation, e.g. hunting). A persisting issue is that the application of multistate mark–recovery models to quantifying the sources contributing to overall mortality is restricted to specific cases, e.g. where the contribution of one particular cause of mortality is addressed (Schaub and Pradel 2004).

Radio-tracking appears an ideal recovery technique to acquire calibration data for testing ring recovery models.

Provided the absence of adverse tagging effects, it allows individuals to be recovered quickly and independently of visibility (Kenward et al. 1999, Kenward 2001, Naef-Daenzer et al. 2001). If large samples can be included (Naef-Daenzer and Grüebler 2014), radio-tracking data offer a valuable complement to large-scale, long-term recoveries of marked birds.

Here we determine and compare the frequencies of various sources of mortality in the little owl *Athene noctua* as obtained by radio-tracking and from ring-recovery data from the same area. This allowed testing for potential bias in ring recoveries and according improvement of multi-state modelling approaches. The main aim of the study was to quantify the major causes of death in little owls and to test earlier notions that mortality caused by human infrastructure and traffic is a major factor for the demography of the species in central Europe (Exo and Hennes 1980, Van Nieuwenhuyse et al. 2008, Le Gouar et al. 2011).

Methodologically, we show that two assumptions of multi-state recovery models are unrealistic, at least in the case of the little owl. First, it is assumed that all released rings remain available to potential finders for long periods. We show, that for dead recoveries a substantial proportion of rings is displaced to sites where recovery is virtually impossible, resulting in underestimation of recovery probability. Second, the proportions of irretrievable rings are biased in relation to the cause of death, namely predation. Thus, the fundamental assumption that the sample of rings from which recoveries are drawn is representative for the original sample of ringed birds is violated. To our knowledge, these additional sources of bias in ring recovery data have so far not been quantified.

Methods

Study species

The little owl is a small nocturnal, sedentary raptor. In central Europe it inhabits open agricultural landscapes such as orchards and other habitats with scattered groups of trees. These are frequently located close to settlements, urban infrastructure and traffic. The species forages frequently on the ground and feeds on a large variety of prey, particularly small mammals and birds, large insects and earthworms. The birds roost in tree tops, hedges or isolated buildings and frequently enter natural cavities and nest boxes (Van Nieuwenhuyse et al. 2008, Bock et al. 2013).

Ring recoveries and radio-tracking data

The sample of ring recoveries of little owls was obtained from the Max Planck Inst. of Ornithology (Vogelwarte Radolfzell) and included all dead recoveries in southern Germany from 1955 to 2012 (n = 30 623 ringed birds, n = 2682 recoveries, of which n = 465 reported dead, W. Fiedler, counties Baden-Württemberg, Hessen, Rheinland-Pfalz, Saarland).

The radio-tracking data were collected in a study of little owl dispersal in Württemberg, Germany (district of Ludwigsburg). In total, 377 birds (239 juveniles, 138 adults) were radio-tagged from 2009–2012. Little owls were tagged with transmitters of own design (Naef-Daenzer et al. 2005) with an operational range of over 30 km. Including a figure-8 harness (Kenward 2001) the tags weighed 6.8–7.5 g (i.e. < 5% of minimum body mass of 150 g), and lasted for 270–450 d (depending on duty-cycles). The owls were located at least once weekly throughout the year. The analysis includes the 177 animals that were recovered dead until end of 2012. 179 birds were known alive at the end of the period of data collection. The fate of 21 birds (5.5%) remained unknown because they were lost before the minimum expected life of the transmitters.

Classification of causes of mortality

The EURING code includes numerous potential causes of mortality, some of them not applying to the little owl (North 1990; <www.euring.org/data-and-codes/euring-codes>). The circumstances of mortality as described in the ring recoveries and in telemetry data had to be aggregated into a standard categorisation. We classified the recovery circumstances of radio-tagged birds and ring recoveries into 11 categories given in the EURING codes for finding circumstances. Using all available evidence from the recovery sites, data from radio-tagged birds were also assigned to one of these categories. As radio-tracked animals could be recovered within hours to days, the circumstances of mortality could be determined in detail in most of the cases. An overview of the classes and observed frequencies are given in Supplementary material Appendix 1, Table A1. In a second step the causes of mortality were further aggregated into the 5 general classes used in the analysis (traffic, human-built structures, predation, various, unknown).

Analysis

Telemetry data

Analyses of re-encounter histories of the radio-tagged birds revealed that the probability to relocate a bird within a 2-week interval exceeded 0.95 throughout the observation period. (detailed analysis in Perrig 2015). Given the high recovery probability and the small number of individuals whose fate was unclear, we analysed the raw frequencies of causes of mortality in adults and juveniles.

Potential bias in telemetry data

Dead radio-tracked birds may have been collected by scavengers or predators before the individuals were located, falsely suggesting a predation incidence. We hypothesise that in presence of a scavenger-effect the proportion of apparent predation in the telemetry data increases in relation to the time elapsed between the last live observation and the dead recovery. The median recovery time of dead radio-tagged individuals was 7 d (quartile range 4–12 d, range 0–106 d). For statistical tests we categorized the telemetry data according to recovery time into 2 classes (≤ 7 d, > 7 d). In ringed birds the median time between ringing and (dead) recovery was 248 d (quartile range 91–733 d, range 0–5765 d).

Radio-tags inevitably add weight and may cause various adverse effects (review by Murray and Fuller 2000, Kenward 2001) including reduced manoeuvrability and associated effects on mortality. Studies addressing tagging effects in owls came to contrasting conclusions, even within species (Petty et al. 2004, Sunde 2006). In little owls, no tagging effect on survival could be detected in a Danish study (Sunde et al. 2009). Comparisons of our survival estimates of tagged birds with evidence from ringed animals (Schaub and Lebreton 2004, Thorup et al. 2010, Le Gouar et al. 2011, German ringing data) do not suggest a tagging effect on long-term survival in adults and juveniles. The respective evidence is given in the results section. Moreover, reduced manoeuvrability likely would affect various kinds of causes of death.

Multi-state model

To analyse the ring recovery data we used a multi-state mark–recovery model (below 'ring recovery model') to estimate recovery probabilities for each cause of death and to account for these in estimates of the proportions of the different causes of death, as has been done by (Schaub and Lebreton 2004). The ringing and recovery data were arranged in two-dimensional arrays with 55 release (years 1957–2011) and 55 recovery (1958–2012) occasions. Within each recovery occasion, the array contained three cells for each of three causes of death (predation, human and other, Table 1).

For each cohort of ringed individuals i (individuals ringed in year i), we formulated a multinomial model, $\mathbf{R}_{i,1:166} \sim \text{Multinom}(\mathbf{p}_i, N_i)$. With cell probabilities $\mathbf{p}_{i,1:165} = S^{(v-1)}(1 - S)m_{v,k}r_k$, where S is the annual survival probability (S_{ad} in all cases except during the first year of juveniles, where it was S_{juv}), $m_{age,v,k}$ is the proportion of death cause k in year v for adults and juveniles, and r_k is the probability that an individual that has died due to the cause k is found and its ring number reported. The last cell probability $p_{i,166}$ is $1 - \sum_{j=1}^{165} p_{i,j}$. We formulated separate multinomial cell probabilities for individuals ringed as juveniles and adults. For the juveniles, we estimated a different annual survival probability during their first year. The likelihood of the model was obtained as the product of the multinomial likelihoods formulated for each cohort and each age class (Supplementary material Appendix 1, Table A2). We used Markov chain Monte Carlo simulations as implemented in WinBUGS (Spiegelhalter et al. 2003) to fit the model. The BUGS code including technical and diagnostic information on the Markov chains is provided in Supplementary material Appendix 1.

We used flat prior distributions for all model parameters, i.e. $r_k \sim \text{Beta}(1,1)$, $S_{age} \sim \text{Beta}(1,1)$, and $\mathbf{m}_{age,v,1:3} \sim \text{Dirichlet}(1,1,1)$.

The model assumes that an individual can die only of one cause and cannot change this state. It further assumes that annual survival probability is constant from the second year onward (Newton et al. 2016) and we do not include individual heterogeneity in any parameter. The model estimates the recovery probability for each class of cause of mortality, but it assumes that ring recovery probability is constant over time and independent of age.

Accounting for retrievability of rings

As an important modification of the multi-state model, we adjusted the estimates of recovery probabilities for each cause of death according to the proportion of rings that were irretrievable post-mortem. We qualitatively assessed for each radio-tagged individual the probability that it may have been recovered without the aid of telemetry. We denoted individuals 'retrievable' if remains were found on the surface, at sites where potential finders may occur (even if only very few small parts were present). We denoted individuals 'irretrievable' where both the occurrence of potential finders was extremely improbable and the conspicuousness of potential remains of the bird was extremely poor. We classified in this category for example a dead bird located in the vertical wall of a quarry (predation by eagle owl), carcasses or transmitters found completely buried or inside a den (predation by red fox), or tags located in trees (nest of common buzzard, hollow tree) or in high-grown cultures (rape, maize prior to harvest, with subsequent mechanical treatment). Assuming that the sample of radio-tagged birds is representative for the population we adjusted the estimates of recovery probabilities and frequencies of causes of mortality according to the proportions of retrievable rings. Detailed information is given in the BUGS code provided in Supplementary material Appendix 1.

Results

Estimates of ring recovery and survival probabilities

Using the multi-state model approach (accounting for irretrievable birds), we estimated the average annual survival of adults to 0.71 ($\pm$ 0.02 SE). Juvenile annual survival was estimated to 0.35 ($\pm$ 0.03 SE).

Survival of radio-tagged juveniles and adults did not deviate from the rates calculated from ring recoveries and those reported in other studies (Table 1). In juveniles, the survival to recruitment was 0.37 ± 0.06 (i.e. first full year survival 0.30 ± 0.08). In adults the annual survival rate was 0.64 (males 0.70 (0.60–0.78 CRI), females 0.59 (0.50–0.68 CRI), V. Michel pers. comm.). These rates suggest that

Table 1. Survival rates of juvenile and adult little owls as estimated from ring recoveries and telemetry data (this study) and compared to results from other studies using ring recovery data.

Study	Juveniles	Adults
DE, NL (Exo and Hennes 1980)	0.299	0.648 ± 0.058
NL (Le Gouar et al. 2011)	0.258 ± 0.047	0.753 ± 0.019
DK (Thorup et al. 2010)	0.15	0.68
DE (Schaub and Lebreton 2004)	0.06 ± 0.02 to 0.19 ± 0.002	0.61 ± 0.04 to 0.69 ± 0.07
DE (own study, ring recoveries)	0.35 ± 0.03	0.71 ± 0.02
DE (own study, unpublished telemetry data, Perrig 2015)	0.30 ± 0.075	0.64 (provisional)

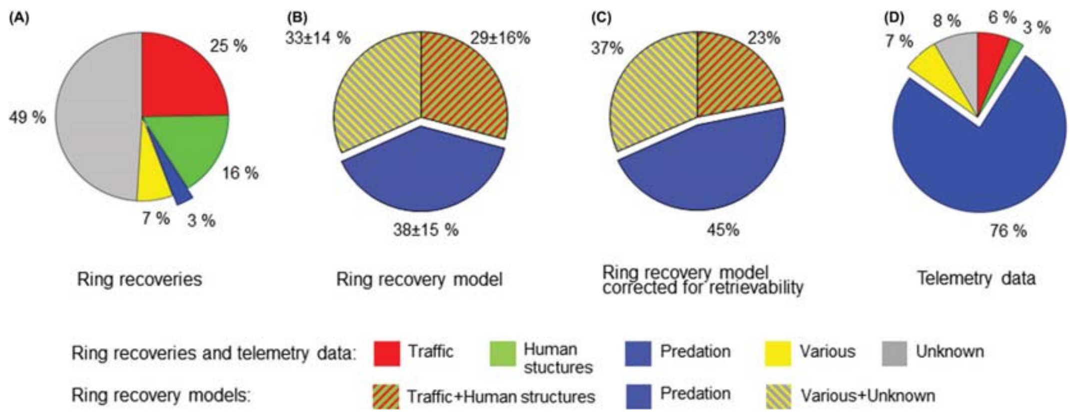

Figure 1. Proportions of the main categories of causes of death in little owls as assessed by four approaches. (A) Raw ring recoveries, (B) multistate recovery model on the basis of ring recoveries with no correction for irretrievables, (C) multistate recovery model corrected for irretrievables, (D) telemetry data. For raw data and definition of categories see Table 1, for frequency numbers and statistical results, see Table 2. Both multistate models did not fully correct for the bias in the raw recovery data.

radio-tagging had no significant effect on the survival of juvenile and adult little owls.

The estimated recovery probabilities varied strongly between the categories of causes of mortality. The recovery probability for casualties at human structures was 0.022 (± 0.003 SE). The recovery probability for predation was 0.003 (± 0.001 SE). The recovery probability for all other causes was 0.041 (± 0.006 SE). Predated individuals were therefore retrieved by a factor 7–14 less frequently compared to other causes. Estimates for the proportions of irretrievable individuals for each cause of mortality are given in the analysis of potential biases.

Raw ring recoveries and telemetry data

The major result is a marked and highly significant difference in the frequency distributions of the five general categories of causes of mortality between the raw ring recoveries and the raw telemetry data (Fig. 1, statistical results given in Table 2, Pearson $X^2 = 358.29$, DF = 4, $p < 0.0001$). If cases with undetermined cause of death were excluded, these strong disproportionalities persisted (Pearson Chi-square: 238.23, DF = 3, $p < 0.0001$). This indicates that the difference in observed frequencies is not related to the fact that in ring recoveries the cause of death cannot often be determined from the remains found with the ring. In particular, raw ring recovery data were composed of 25% traffic casualties and 16% accidents at buildings and other human-built structures. Thus 41% of the dead recoveries were directly human-induced. Three per cent of cases were assigned to predation and 7% to various other causes. In a large proportion of 49% the cause of death was undetermined (Fig. 1A). In sharp contrast to this figure, the frequencies of causes of mortality in the telemetry data set were 6 and 3% for traffic victims and casualties at human-built structures, respectively. Thus, human-induced causes totalled to only 9%. However, 76% of the cases were due to predation, and 7 and 8% were due to various and unknown causes (Fig. 1D, statistical results given in Table 2). In summary, the frequencies of causes of death from raw ring recoveries suggest that close to half of the reported casualties were human-induced, whereas telemetry recoveries indicate that three quarters of deaths were due to predation.

Table 2. Frequencies of causes of mortality as determined from ring recoveries and telemetry data (5 categories).

	Ring recoveries		Telemetry data		Row total
Category	n	%	n	%	n
Traffic	115	24.7	11	6.2	126
Human structures	76	16.3	6	3.4	82
Predation	15	3.2	135	76.2	150
Various	31	6.7	11	6.2	42
Unknown	228	49.0	14	7.9	242
Column total	465		177		642

Pearson Chi-square = 389.6, DF = 4, $p < 0.0001$; excluding unknown causes: Pearson Chi-square: 245.8, DF = 3, $p < 0.0001$.

The closer examination of frequencies revealed further evidence that predation was strongly under-represented in the set of ring recoveries. Figure 2 illustrates the monthly distribution of cases of predation in ring recoveries and telemetry data. Although the set of dead recoveries of ringed birds was considerably larger than that of radio-tagged birds, only a total of 15 birds were assigned to predation (ten of these reported by one person). Of these, 13 (82%) were recovered in May and June, when nest box controls are carried out. Only three out of 30 623 ringed birds were denoted predation victims outside the season of nest box controls. In contrast, the number of predation victims in radio-tracked birds was large, and the peak frequency (63% of deaths) was in June–August, when chicks and fledglings spend much time outside nest boxes or cavities. These differences in the annual distribution of cases of predation were highly significant (Pearson $X^2 = 46.72$, DF = 11, $p < 0.0001$).

The frequency distributions of ring recoveries showed a significant difference between age classes (juveniles, adults). The frequencies suggest that the proportion of juvenile birds that died due to traffic casualties (33%) was almost twice the proportion in adult owls (17%, Pearson $X^2 = 23.70$, DF = 4, $p < 0.0001$, Fig. 3). Again, we found a strong contrast to this figure in the telemetry data set. Here, the frequency distribution among categories were very similar and did not differ significantly from proportionality (Pearson $X^2 = 3.08$, DF = 4, $p = 0.57$, Fig. 3, Table 4).

Table 3. Frequencies of causes of mortality as reported from ring recoveries in different regions of southern Germany. No significant differences in the proportions of the 5 categories were found.

	Württemberg		Baden		Hessen, Saar, Pfalz		Other		Row total	
Category	n	%	n	%	n	%	n	%	n	%
Traffic	44	24.0	34	27.6	11	15.1	26	30.2	115	24.7
Human structures	25	13.7	14	11.4	16	21.9	21	24.4	76	16.3
Predation	6	3.3	6	4.9	2	2.7	1	1.2	15	3.2
Various	18	9.8	6	.9	3	4.1	4	4.7	31	6.7
Unknown	90	9.2	63	51.2	41	56.2	34	39.5	228	49.0
Column total	183		123		73		86		465	

Pearson $X^2 = 21.06$, $DF = 12$, $p = 0.14$.

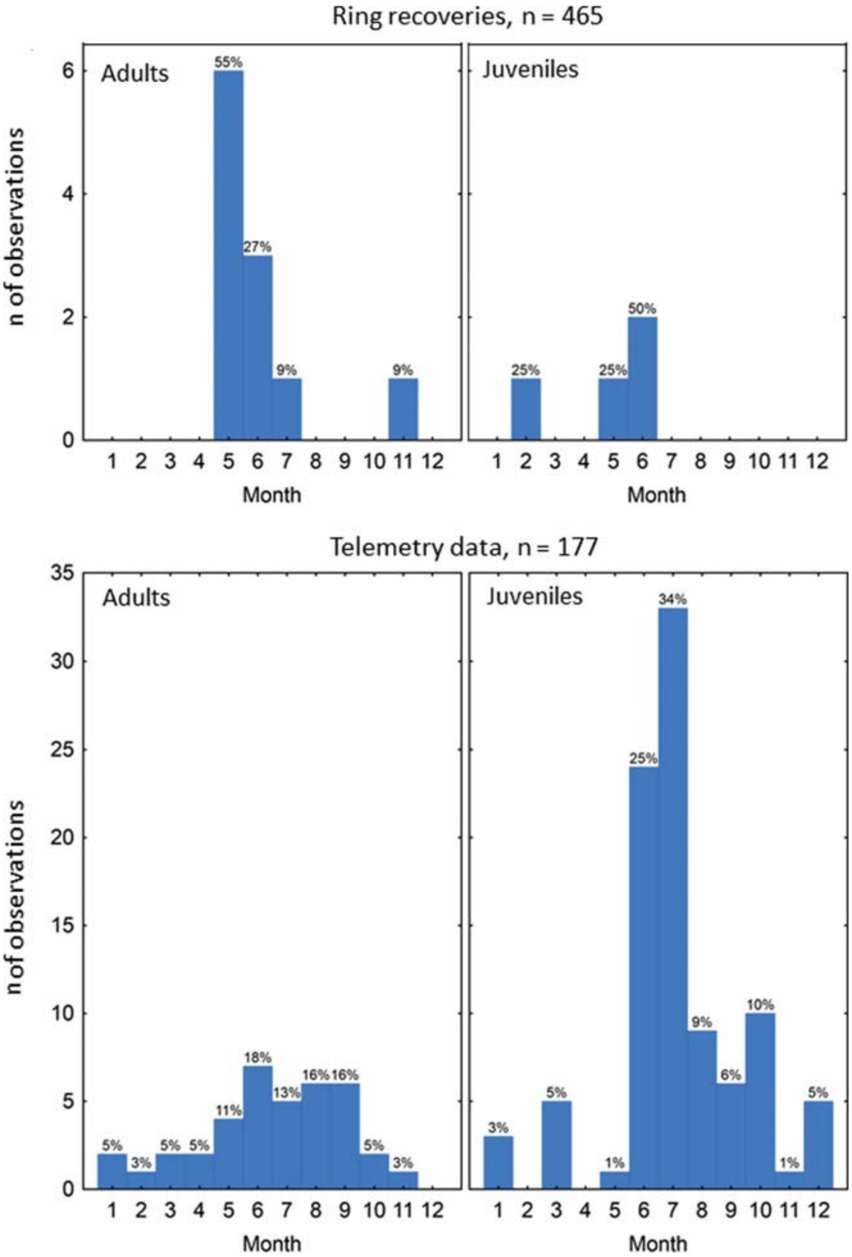

Figure 2. Monthly frequencies of dead recoveries considered to be due to predation for ring recoveries (top panels) and telemetry data (bottom panels), and for juveniles (left column) and adults (right column). In ring recoveries, most cases of predation were reported in May–June when nest controls are carried out. Only 3 cases were reported outside the breeding season. For telemetry data, predation cases were reported throughout the year with a peak in July–September when juveniles are newly fledged. For statistical tests see text.

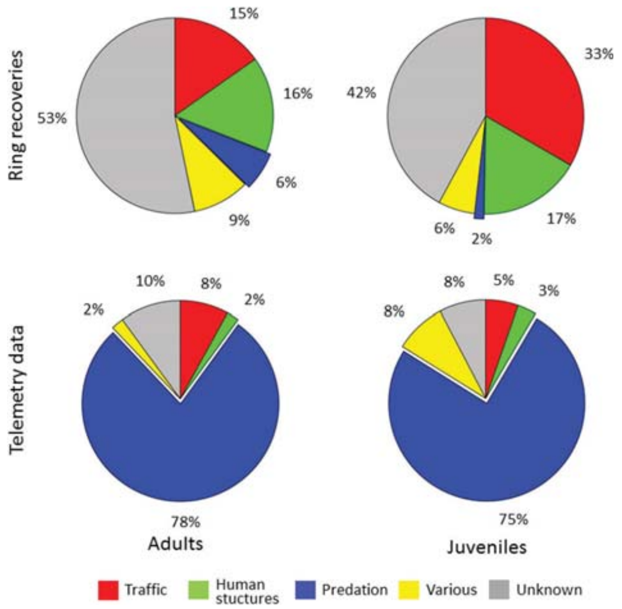

Figure 3. Frequencies of causes of death in ring recoveries and telemetry data as specified for juveniles and adults, respectively. Ring recovery data suggest that compared to adult birds about twice as many juveniles were killed in traffic accidents. In telemetry data, no significant deviation from proportionality amongst adults and juveniles was found. For statistical tests see text.

To test whether the proportion in frequencies of the 5 categories of causes of mortality may differ between regions in southern Germany we analysed the distribution amongst four separate regions (Württemberg, Hessen-Saar-Pfalz, Baden, other counties). We found no significant spatial variation in these frequency distributions, which signifies that ring recovery data from Württemberg did not deviate from the figures found for the entire set of ring recoveries (Pearson $X^2 = 20.28$, DF = 12, p = 0.062, Table 3).

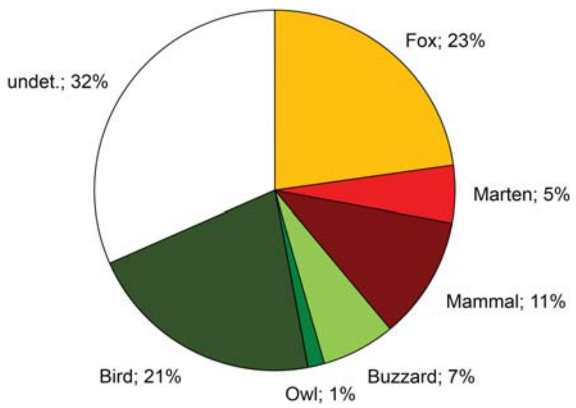

Figure 4. Frequencies of casualties due to various predators of little owls (n = 135, telemetry recoveries). In about one third of cases predators could not be determined. 39% of the birds were taken by mammals, and 29% by birds. The red fox *Vulpes vulpes* was the main mammalian, the common buzzard *Buteo buteo* the main avian predator. Fox = red fox; marten = any mustelid species; mammal = undetermined mammal; buzzard = common buzzard; owl = tawny owl *Strix aluco* or eagle owl *Bubo bubo*.

Table 4. Frequencies and proportions of detailed causes of death in radio-tracked juvenile and adult little owls. No significant difference between juveniles and adults were detected. For statistical details see text.

	Juveniles		Adults	
Category	n	%	n	%
Traffic	7	5.4	3	6.3
Human structures	2	1.5	0	0.0
Predation (mammal)	48	37.2	19	39.6
Predation (bird)	33	25.6	15	31.3
Predation (undetermined)	16	12.4	4	8.3
Weather, starvation	9	7.0	0	0.0
Drowned	2	1.5	1	2.1
Unknown	10	7.8	5	10.4
Column total	129		48	

Pearson $X^2 = 5.52$, DF = 8, p = 0.70.

Red foxes *Vulpes vulpes* accounted for some 20% of predation cases (e.g. birds were found buried in fields, near or in dens). In 5% of casualties martens *Martes* sp. and other mustelids were the guessed predators (e.g. predation inside cavities or nest boxes, in buildings), and in 10% of the cases an undetermined mammalian predator was assumed (bitten feathers). In 6% of the cases the common buzzard *Buteo buteo* was observed (visual observations, tags in or below nests). In total, 36 and 29% of the predation reports were attributed to mammalian and avian predators, respectively. The data suggest that little owls are day and night under considerable predation pressure (Fig. 4).

Multi-state model

The basic ring recovery model (not accounting for irretrievable birds) estimated the proportion of human-induced deaths to 29%, predation 38% and various and unknown causes 33%. (Fig. 1B). The ring recovery model (accounting for irretrievable birds) estimated the proportions of human-induced casualties to 22 ± 13% and 18 ± 14% for juveniles and adults respectively, predation 45 ± 15% and 44 ± 17% and various and unknown causes to 34 ± 14% and 38 ± 15 %, respectively (Fig. 1C). Therefore, accounting for the large difference in recovery rates and additional bias in ring retrievability resulted in a 13-fold increase in the estimate of the proportion of predation (raw ring: 3% vs model: 45%) and in a marked decrease of the estimate of the proportion of human-related causes (raw ring: 41% vs model: 20%). Similar to the telemetry data, the model results suggest that predation was the most frequent cause of mortality.

Potential bias in ring recoveries and telemetry data

Retrievability of rings

The proportion of individuals that were denoted 'irretrievable' amounted to 34.0% (of n = 177). The proportions of irretrievables in the three categories of cause of mortality were 48% for predation, 5% for human-induced causes, and 40% for other causes. Accordingly, accounting for these proportions had a substantial effect on the result of the multi-state models. Estimates for the uncorrected and corrected multi-state model are given in Fig. 1B and C.

Time-dependent bias in proportions of predation

We found no significant difference in the proportions of the five causes of mortality between birds that were recovered within 7 d from the last live observation and birds for which the recovery time exceeded 7 d (Pearson $X^2 = 4.83$, $DF = 4$, $p = 0.31$). The residual frequencies in the category 'predation' indicate a slight increase in frequencies (–7% in quick vs + 6% in late recoveries), and suggest that a potential time-related bias in telemetry recoveries is too small to explain the marked differences between telemetry data and model results.

Discussion

Causes of mortality

From radio-tracking a large sample of adult and juvenile little owls we conclude that the major cause of death of both adults and juveniles was predation by diurnal and nocturnal birds and mammals. Similarly, other radio-tracking studies of owls and other taxa have also revealed predation as an important proximate cause of death (Naef-Daenzer et al. 2001, Sunde 2006). Conversely, the results suggest that casualties due to traffic and human infrastructure were much less important than presumed from analysing ring recoveries. Accordingly, the little owl appears to be a meso-predator that is under considerable pressure from superior trophic levels. Hence, trophic relationships rather than human-caused kills may be the most important proximate mechanisms determining mortality rates and in turn, may influence demographic trends. Although juvenile survival was substantially lower compared to adults (Table 1), the observed proportions of causes of death did not differ with age classes (Fig. 3). These results suggest that directly human-caused deaths are not negligible (Van Nieuwenhuyse et al. 2008, Le Gouar et al. 2011) but have inferior impact compared to causes of death that are related to the trophic web within the habitat. Thus, local demographic structures and trends may primarily depend on both predator abundance (Michel et al. 2016) and on the availability of crucial resources (such as cavities and food, Thorup et al. 2010, Bock et al. 2013, Perrig et al. 2014).

The large proportion of predation in dead recoveries does not necessarily imply high predation-induced mortality rates. Our results were obtained in a rapidly increasing population and juvenile survival was markedly higher than in other populations (Table 1, H. Keil pers. comm.). Thus, this study evaluates the proximate mechanisms underlying mortality in little owls irrespective of the magnitude of survival rates. While the distribution of causes of death reveals the relative importance of proximate mechanisms affecting mortality, the combination of causes of death and mortality rates determines the effect of proximate mechanisms at the population level. Given equal mortality rates, our study suggests that the impact of human structures (including traffic) on our little owl population is considerably lower than previously assumed. Thus, for conservation measures knowing both the proximate causes of death and the ecological mechanisms determining mortality rates is important and further corroboration of our result would be welcome. Although the multi-state model showed that predation was a major cause of mortality, the estimated proportions were not as high as in the telemetry data set. Thus, the estimates obtained by telemetry and ring recoveries vary in a relatively large range. In summary the ranges are 45–76% for predation, 9–20% for human-induced mortality and 15–36% for other causes, respectively. Here, we do not address the ultimate determinants of mortality. Factors such as body condition, food and roost availability and winter conditions have been shown to exert significant effects on survival rates (Thorup et al. 2010, Perrig et al. 2014, Perrig 2015) and occupancy patterns (Michel et al. 2016). The results of our study imply that these factors operate mainly via differential predation.

Methodological issues

The two data sets on causes of mortality in little owls represent two statistically significantly different entities. The differences in reported frequencies are so large that the results suggest intriguing methodological problems. We discuss these issues under the assumption that potential bias in the detection of causes of death from radio-tracking data is small, and that tags did not affect mortality. Regarding the telemetry data as a reference, the estimate of the proportion of predation on little owls as based on ring recoveries appears to be underestimated even if differential recovery probabilities are accounted for (Fig. 1).

We interpret the patterns as follows: first, in ringed birds the recovery probability of predated individuals is very low. As only few recoveries were reported the uncertainty of estimates of recovery probability is large, which has implications for the accuracy of the estimate of the proportion of predated birds. A second issue has, to our knowledge, not been quantified so far. In little owls a third of recovered radio-tracked birds was located at sites where rings are irretrievable, and rings of predated individuals disappeared disproportionally from the population of recoverable rings. Under the common model assumption that all released rings are available to potential recovery, this causes considerable underestimation of recovery probabilities and thus biased frequencies of causes of mortality. Third, times to recovery of ringed birds are normally fairly high. Therefore, it is difficult to detect predation reliably. For various reasons, cases of predation are often incorrectly assigned to the categories of various or unknown causes. This results in additional, observer-related bias. Furthermore the categories 'predation', 'various' and 'unknown' are not mutually exclusive. In contrast, the finding circumstances in casualties due to traffic and due to human-built are more evident. Over-all the compound effects of recovery probability, differential recoverability of rings and differential detectability of causes of death may have caused the almost complete lack of reports of predation incidents and likely reduce the power of multi-state models in accounting for variation in recovery probabilities.

Dead recoveries of radio-tracked birds are not free from potential bias, too. Although birds were recovered quickly, the time lag between a bird's death and its recovery allows for biasing incidents: an individual killed on a road may be picked by a predator-scavenger, eventually suggesting predation as the cause of mortality. However, our results showed no significant change in the proportion of predation in relation to the time to recovery. We estimate a potential bias to be below 10%. A recent review of survival rates in raptors and owls (Newton et al. 2016) also addresses similar bias in ring recovery studies due to differential recovery probability particularly in relation to estimating first-year and adult survival. Provided that radio-tagging has no deleterious effects on the manoeuvrability and survival of individuals, radio-tracking offers scope to more accurate evidence on causes of death and in turn, stage- and time-specific survival rates.

Conservation implications

Our study indicates that the decline of little owl populations in central Europe since ca 1950 may be less strongly affected by human-induced mortality than previously assumed (i.e. by road/rail kills and casualties in/at human-built structures). As predation was found to be the major cause of death, the little owl appears to be a meso-predator in a trophic web including avian and mammalian predators. Thus, both bottom-up factors (habitat and food resources, winter climate (Perrig 2015)) and top-down effects (predation and non-lethal predator effects (Michel et al. 2016)) may be the central determinants of local demography and population dynamics. Although human-related mortality of little owls should not be neglected, a main conservation implication is that a direct human impact has likely been overestimated. Since in central Europe much of the remaining potential habitat for little owls is in close proximity of settlements and traffic infrastructure (Van Nieuwenhuyse et al. 2008), the results may encourage conservation measures in areas that have so far been considered too exposed to presumed major causes of mortality.

Acknowledgements – We thank all assistants and volunteers for their effort in collecting data. We are grateful to H. Keil for providing information on 11 radio-tracked birds from an earlier study in the same area. The Max Planck Inst. of Ornithology provided logistic and administrative support. Capture and tagging of birds was permitted by the Council of Baden-Württemberg, Germany (no. 35-9185-81/0188). Radio-tracking was conducted under license of Deutsche Bundesnetzagentur (no. 37 55 5413). This research was funded by the Swiss National Science Foundation (grant 3100A 132951/1 to BN-D and MUG), the Hirschmann Foundation and the Karl Mayer Foundation.

References

Anderson, D. R., Burnham, K. P. and White, G. C. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. – J. Anim. Ecol. 54: 89–98.

Baillie, S. R. and Green, R. E. 1987. The importance of variation in recovery rates when estimating survival rates from ringing recoveries. – Acta Ornithol. 23: 41–60.

Bock, A., Naef-Daenzer, B., Keil, H., Korner-Nievergelt, F., Perrig, M. and Grüebler, M. U. 2013. Roost site selection by ittle owls *Athene noctua* in relation to environmental conditions and life-history stages. – Ibis 155: 847–856.

Bowker, G., Bowker, C. and Baines, D. 2007. Survival rates and causes of mortality in black grouse *Tetrao tetrix* at Lake Vyrnwy, North Wales, UK. – Wildl. Biol. 13: 231–237.

Brownie, C., Anderson, D. R., Burnham, K. P. and Robson, D. S. 1985. Statistical inference from band-recovery models – a handbook. –U.S. Fish and Wildlife Service.

Exo, K. M. and Hennes, R. 1980. Beitrag zur Populationsökologie des Steinkauzes (*Athene noctua*) – Eine Analyse deutscher und niederländischer Ringfunde. – Die Vogelwarte 30: 162–179.

Kenward, R. E. 2001. A manual for wildlife radio tagging. – Academic Press.

Kenward, R. E., Marcström, V. and Karlbom, M. 1999. Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. – J. Anim. Ecol. 68: 1020–1033.

Le Gouar, P., Schekkerman, H., Van der Jeugd, H., Boele, A., Fuchs, P., Stroeken, P. and van Noordwijk, A. J. 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.

Michel, V. T., Jiménez-Franco, M. V., Naef-Daenzer, B. and Grüebler, M. U. 2016. Intraguild predator drives forest edge avoidance of a mesopredator. – Ecosphere 7: e01229.

Murray, D. L. and Fuller, M. R. 2000. A critical review of the effects of marking on the biology of vertebrates. – In: Boitani, L. and Fuller, T. K. (eds), Research techniques in animal ecology: controversies and consequences. Columbia Univ. Press, pp. 15–16.

Naef-Daenzer, B. and Grüebler, M. U. 2014. Effects of radio-tag characteristics and sample size on estimates of apparent survival. – Anim. Biotelem. 2: 2.

Naef-Daenzer, B., Widmer, F. and Nuber, M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. – J. Anim. Ecol. 70: 730–738.

Naef-Daenzer, B., Früh, D., Stalder, M., Wetli, P. and Weise, E. 2005. Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters. – J. Exp. Biol. 208: 4063–4068.

Newton, I. and Lakhani, K. H. 1983. Estimating age-specific bird survival rates from ring recoveries – can it be done? – J. Anim. Ecol. 52: 83–91.

Newton, I, McGrady, M. J. and Oli, M. K. 2016. A review of survival estimates for raptors and owls. – Ibis 158: 227–228.

North, P. M. 1990. The statistical investigation of avian population dynamics using data from ringing recoveries and live recaptures of marked birds. Proceedings of the EURING technical conference and meeting of the mathematical ecology group of the Biometric Society (British region) and British Ecological Society, Sempach, Switzerland, 12–14 April 1989. – The Ring 13: 314.

Peach, W. J., Thompson, P. S. and Coulson, J. C. 1994. Annual and long-term variation in the survival rates of British lapwings *Vanellus vanellus*. – J. Anim. Ecol 63: 60–70.

Perdeck, A. C. 1977. The analysis of ringing data: pitfalls and prospects. – Die Vogelwarte 29: 33–44.

Perrig, M. 2015. Juvenile survival and onset of natal dispersal in little owls (*Athene noctua*) in relation to nestling food supply. – PhD thesis, Univ. of Zürich.

Perrig, M., Grüebler, M. U., Keil, H. and Naef-Daenzer, B. 2014. Experimental food supplementation affects the physical development, behaviour and survival of little owl *Athene noctua* nestlings. – Ibis 156: 755–767.

Petty, S. J., Appleby, B. M., Coles, C. F. and Juillard, R. 2004. The long-term effect of fitting back-mounted radio tags to juvenile tawny owls *Strix aluco*. – Wildl. Biol. 10: 161–170.

Schaub, M. and Lebreton, J.-D. 2004. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. – Anim. Biodivers. Conserv. 27: 73–85.

Schaub, M. and Pradel, R. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. – Ecology 85: 930–938.
Spiegelhalter, D., Thomas, A., Best, N. and Lunn, D. 2003. WinBUG user manual, version 1.2. – MCR Biostatistics Unit., Cambridge, <www.mrc-bsu.cam.ac.uk/bugs>.
Sunde, P. 2006. Effects of backpack radio tags on tawny owls. – J. Wildl. Manage. 70: 594–599.
Sunde, P., Thorup, K., Jacobsen, L. B., Holsegard-Rasmussen, M. H., Ottessen, N., Svenne, S. and 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, L. B. and Rahbek, C. 2010. Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. – Ibis 152: 803–814.
Van Nieuwenhuyse, D., Génot, J. C. and Johnson, D. H. 2008. The little owl: conservation, ecology and behavior of *Athene noctua*. – Cambridge Univ. Press.