Journal of Ornithology
https://doi.org/10.1007/s10336-018-1619-z

ORIGINAL ARTICLE

Long-term decline of juvenile survival in German Red Kites

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Received: 11 June 2018 / Revised: 5 December 2018 / Accepted: 13 December 2018
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Abstract

The Red Kite (*Milvus milvus*) is a raptor species of conservation concern in Europe and especially in Germany, where about 50% of all breeding pairs are found. Agricultural intensification and deteriorating food availability, but also anthropogenic mortality due to poisoning and collisions, are major threats for the species throughout its strongly restricted distributional range. Despite the great influence of mortality on the population size of the long-lived Red Kite, information on current age-specific survival probabilities and their change over time is lacking. We analyse a long-term dataset of > 29,000 Red Kites marked with metal rings and about 1500 recoveries of dead birds from 1970 to 2015 with a multinomial ring-recovery model. We model age-dependent recovery probability, based on separate datasets of birds marked as nestlings and as adults/immatures, and thereby estimate juvenile, subadult and adult survival probability over nearly 50 years for a major part of the German Red Kite population. The results show a substantial long-term decline in juvenile survival of more than 40% from the 1970s until today. Furthermore, from 1974 to 2014, adult survival probability shows a consistently decreasing trend (-0.26% year^{-1}). We estimate the recovery probability for dead Red Kites in the first year (as juveniles) to be two times lower than that for birds that reach subadult/adult age. Also, the recovery probabilities of all age classes show a decreasing trend over time except for the last years. The spatial and temporal distributions of juvenile Red Kite recoveries suggest an increase in mortality at the breeding grounds, but in > 60% of cases the cause of death is unknown. The age-structured differences in recovery probability potentially highlight differences in the most important causes of mortality; however, further investigation of the cause of death in all ages classes is required to gain a more accurate picture. Our study provides valuable data for a better understanding of Red Kite demography and ongoing changes in population size.

Keywords *Milvus milvus* · Mortality · Multinomial ring-recovery model · Poisoning · Agricultural intensification · Resource availability

Zusammenfassung

Langfristiger Rückgang der Überlebensraten erstjähriger Vögel in der deutschen Rotmilan-Population

Der Rotmilan (*Milvus milvus*) ist eine fast ausschließlich in Europa beheimatete Greifvogelart von der etwa 50% des Bestands in Deutschland brüten. Landwirtschaftliche Intensivierung und Verschlechterung der Nahrungsverfügbarkeit, aber auch anthropogene Mortalität durch Vergiftungen und Kollisionen sind wesentliche Bedrohungen für die Art in ihrem stark begrenzten Verbreitungsgebiet. Trotz des großen Einflusses der Sterblichkeit auf die Populationsgröße des langlebigen Rotmilans fehlen Informationen über aktuelle altersspezifischen Überlebensraten und deren Veränderungen im Laufe der Zeit. Wir analysieren einen langfristigen Datensatz von > 29.000 mit Metallringen markierten Rotmilanen und etwa 1500 Wiederfunde von toten Individuen von 1970–2015 mit einem multinomialen Ring-Wiederfund-Modell. In unserem Modell berücksichtigen wir altersbedingte Wiederfundwahrscheinlichkeiten, basierend auf getrennten Datensätzen sowohl von Vögeln die als Nestling und von solchen die als adulter/immaturer Vogel beringt wurden. So erlaubt unsere

Communicated by O. Krüger.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10336-018-1619-z) contains supplementary material, which is available to authorized users.

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Auswertung eine robuste Schätzung der Überlebensraten von erstjährigen, subadulten und adulten Vögeln über fast 50 Jahre in einem wesentlichen Teil der deutschen Rotmilan-Population. Die Ergebnisse zeigen einen erheblichen langfristigen Rückgang des Überlebens erstjähriger Rotmilane um mehr als 40% von den 1970er Jahren bis heute. Darüber hinaus zeigt die Überlebenswahrscheinlichkeit der Altvögel in den Jahren 1974–2014 einen abnehmenden Trend (− 0.26% p.a.). Die Wiederfundwahrscheinlichkeit für tote Rotmilane im ersten Jahr lag zwei Mal niedriger als für Vögel, die die subadulte/adulte Altersklasse erreichten. Im Verlauf der Zeit zeigten die Wiederfundwahrscheinlichkeiten beider Altersklassen, mit Ausnahme der letzten Jahre, einen rückläufigen Trend. Die räumliche und zeitliche Verteilung der Totfunde erstjähriger Rotmilane deutet auf eine erhöhte Sterblichkeit im Brutgebiet hin, allerdings war in > 60% der Fälle die Todesursache unbekannt. Die altersstrukturierten Unterschiede in der Wiederfundwahrscheinlichkeit zeigen potenziell Unterschiede in den wichtigsten Mortalitätsursachen in den verschiedenen Altersklassen, jedoch ist eine weitere Untersuchung der Todesursachen erforderlich, um ein genaueres Bild zu erhalten. Unsere Studie liefert wichtige Daten für ein besseres Verständnis der Rotmilan-Bestandsdynamik und für laufende Veränderungen der Bestandsgröße.

Introduction

Studying demography is central to the conservation of animal populations because effective management, aiming to improve population viability, depends on identifying which demographic parameters (e.g. survival, reproduction) limit population size (Newton et al. 2016). A method widely used to gain reliable estimates of survival in wild birds is the marking of individuals with metal rings, to monitor the fate of individuals and infer from their lifetime the survival probabilities of different age classes of a population (Baillie 2001).

The Red Kite (*Milvus milvus*) is a raptor species with a highly restricted distribution. It occurs almost exclusively in Europe and has a world population of only about 30,000 pairs (BirdLife International 2016). The main breeding grounds are in central Europe, with the stronghold in Germany harbouring roughly 50% of all Red Kite breeding pairs (Gedeon et al. 2014; BirdLife International 2016). Because such a large proportion of the breeding population is based in Germany, the conservation of the species is an important aim on both national and federal levels, and the Red Kite is prioritised as an umbrella species for agricultural habitats (Achtziger et al. 2004). Population trends of the species differ within Europe, but declines in the core states of Germany, France and Spain have only been partly offset by increases in other countries within the last decades (Knott et al. 2009). Within Germany, the Red Kite population is concentrated in the central and eastern parts of the country, but field surveys in the last 6–12 years have shown that population size is gradually decreasing in these high-density areas, while apparently increasing in the south west (Gedeon et al. 2014). Most of the German Red Kites migrate to France and the Iberian Peninsula in autumn, while only a small part of the breeding population overwinters in the country (Schönfeld 1984; Pfeiffer and Meyburg 2009).

Red Kites are known to be long-lived, with maximum ages for wild birds of up to 30 years (Pfeiffer 2009; Bairlein et al. 2014). The life cycle of Red Kites can be partitioned into three stages: first-year juveniles, second-year subadults and all ages above 2 years as adults (Mammen et al. 2014). Previous studies show that Red Kite survival varies with age and between different regions throughout Europe (Aebischer 2009; Newton et al. 2016). The ring-recovery studies by Schönfeld (1984) and Pfeiffer (2009) investigated Red Kite survival in Germany with data from the 1960s to 1970s, while a local study from 2000 to 2005 by Nachtigall (2008) additionally marked birds with wing tags for survival estimation. Approximation from these studies suggests that in Germany > 60% of the Red Kite juveniles survive the first year of life, while in the second year about 75% survive to reach the adult age class, where survival is then around 80% or more (Schönfeld 1984; Nachtigall 2008; Pfeiffer 2009). However, these survival estimates were gained using dated methods, which did not take into account imperfect detection (Kéry and Schaub 2012). If recovery probability differs according to age, but this is not considered during analysis, the resulting survival estimates either under— or overestimate true survival (depending on whether, for example, juveniles are more or less often recovered than older birds). Analyses of ringing data in Switzerland showed that juvenile Red Kites are found dead much less often than individuals that have completed their first year of life (Aebischer 2009; Kéry and Schaub 2012).

The German Red Kite population has declined by 20–30% since the early 1990s; however, over the past two decades, although fluctuating, it has remained relatively stable (Gedeon et al. 2014; Mammen 2016). A decrease in reproductive productivity is suspected as a main reason for the population decline in Germany (Mammen et al. 2014). The reduced productivity is attributed to agricultural intensification, which reduces foraging possibilities for the opportunistically scavenging Red Kite during the critical time of chick rearing in late spring (Nachtigall et al. 2010). The German reunification in 1989–1990, entailing profound changes in land use and agriculture in eastern Germany, is perceived as a major turning point for the Red Kite population (George 1995; Mammen et al. 2014). Especially the loss of feeding habitats following unification of the two German states is often linked to the population decline in the 1990s (George 1995; Mammen et al. 2014).

In recent years, the species has also been identified as being under threat of collision with wind turbines, with the continuing expansion of onshore wind farm development possibly reaching demographically relevant levels of mortality for the Red Kite population (Bellebaum et al. 2013; Grünkorn et al. 2016; Busch et al. 2017). Other important causes of anthropogenic mortality threatening the survival of individuals are poisoning and direct persecution, both along flyways and on breeding grounds (Knott et al. 2009; Hirschfeld 2011). The use of rodenticides in agriculture especially threatens Red Kites by secondary poisoning (Berny and Gaillet 2008; Coeurdassier et al. 2012; Montaz et al. 2014; Molenaar et al. 2017). However, up-to-date population-level estimates of mortality for different age classes in the German breeding population are still lacking (Bezzel 2010).

During the last 50 years, great efforts by both professionals and volunteers have been undertaken in Germany to mark nearly 30,000 Red Kites in the nest with metal rings—allowing the study of individual survival histories and migratory behaviour after ring recovery (Schönfeld 1984; Pfeiffer 2009; Bairlein et al. 2014). Using current methods to draw on this wealth of existing long-term ringing data, the aim of this study was to estimate age-specific survival probabilities of the Red Kite population in Germany from 1970 until 2015. Reliable estimates of survival are one crucial parameter needed to inform the discussion about ongoing changes in population size.

Methods

Bird ringing data

Data on the number of Red Kites fitted with metal rings in Germany and recoveries of dead birds were collated from the regional authorities Vogelwarte Hiddensee, Vogelwarte Helgoland and Vogelwarte Radolfzell. From 1970 to 2015 approximately 29,800 Red Kite juveniles (range per year, 140–1290; median, 690) were ringed in Germany. Most individuals (> 90%) were marked in eastern Germany with Vogelwarte Hiddensee rings. Ring recoveries from 1970 to 2015 provided data for 1470 marked Red Kites. Dead birds were recovered opportunistically, by noting casualties with their ring number and cause of death (if known) from reports by the general public. Most of the recovered birds (89%) were marked with Hiddensee rings in eastern Germany, but among them were birds from the whole distributional range within Germany (Fig. S1, Supplement 1). Of all 1470 recoveries, 1426 were birds marked as juveniles (1412 marked while still in the nest), of which 461 were recovered dead in the first year of life. Because it is much more difficult to capture and mark individuals once they have left the nest, the number of birds fitted with rings as adults or immatures represents only a small proportion of total marking effort. In this case, around 900 adult/immature Red Kites were marked with Hiddensee or Helgoland rings from 1970 to 2015, of which 44 were recovered dead. Information on ringing effort was fully digitised in Hiddensee from 1977 onwards (U. Köppen, personal communication); however, the number of marked Red Kites in 1970–1976 presented in Schönfeld (1984) were used for reconstruction. Annual marking effort with rings was available in detail from Vogelwarte Helgoland for 2000 onwards (O. Geiter, personal communication). Since these data only represent a marginal number of all Red Kites ringed in Germany, an approximation of the number of birds marked with Helgoland rings was used for 1970–1999, according to summary statistics presented in Foken (2000). From a total of 2424 marked Red Kites (Foken 2000), we approximated an annual average of 44 ringed birds in 1945–1999, with a percentage of immatures and adults of 12% (the average value from all three ringing authorities). This approximation was similar to the annual average of 38 birds marked with Helgoland rings thereafter (in the period 2000–2015). To assign the age of individuals since marking, first of June was used as the start of a new year. If the exact age at marking was unknown (for all immatures and adults), ages represent the minimum age since marking. To assure that nestling mortality did not affect the analysis, we checked how many recoveries of juveniles were made in May–July close to the nest after being ringed in the same year. This amounted to 44 recoveries of which 80% were made after 2000. Of these 44 recoveries, only 29% were made shortly after ringing (2 weeks) and this only occurred in 2005–2015. We are therefore certain that late nestling mortality did not substantially affect our analysis.

Multinomial ring-recovery model

A Bayesian implementation of a ring-recovery model (Brownie et al. 1985) with Markov chain Monte Carlo sampling was used to estimate survival and recovery probabilities for the different Red Kite age classes following Kéry and Schaub (2012). If survival and recovery probability are age dependent and individuals are only marked as juveniles, only adult survival is identifiable (Anderson et al. 1985). However, with a different number of age classes for survival and recovery probability and data on marked adults, juvenile survival can be estimated (Kéry and Schaub 2012). We thus modelled the survival of the three age classes juveniles (calendar year 1), subadults (calendar year 2) and adults (calendar year > 2) separately, while recovery probability was distinguished between juveniles (calendar year 1) and the two older age classes combined (calendar year > 1) (Kéry and Schaub 2012). To show that all parameters are identifiable when using this model formulation and can be estimated from ring-recovery data similar to our dataset, we include the results from simulations, and the code to reproduce these, as supplementary materials (Supplement 2). All individuals marked at the same age and in the same year were treated as a release cohort. A non-informative prior (uniform distribution, interval 0–1) was used for all parameters. The likelihood was calculated from the number of birds recovered in each age class in each year modelled as a multinomial trial, with index equal to cohort size and cell probabilities as a function of survival and recovery parameters (Table 1). All models were run in JAGS version 4.2.0 (Plummer 2003) via R version 3.3.2 (R Core Team 2017) and package jagsUI version 1.4.4 (Kellner 2016). The mixing of three chains was inspected visually and convergence was confirmed by *R*-hat values < 1.01 (Brooks and Gelman 1998; Kéry and Schaub 2012). To estimate annual survival probabilities from 1970 to 2015, independent survival for each year and age class was fitted for adult, subadult and juvenile survival, while recovery probabilities were modelled with a random year effect. The random year effect was specified on the logit scale as a normal distribution with mean zero and the between-year variance. For the latter, a uniform prior distribution between 0 and 5 was used for the SD. To test if the mean annual survival probabilities of each age class showed a trend over time, we used a precision-weighted linear regression. We implemented this with the metafor R package (Viechtbauer 2010), using the SD of the posterior distribution as weights for the mean of the posterior distribution and report the slope estimate with a 95% confidence interval. To gain reliable estimates of survival for different time periods, allowing for age-specific recovery probabilities, we used a model with 5-year periods from 1970 to 2015 for survival and the same random time-effect formulation as before. To investigate if changes in survival probabilities over time are robust according to the assumption that recovery probability differs with age, we fitted the same model estimating survival over the 5-year periods while assuming an identical recovery probability for all age classes, once again with recovery probability varying over time with a random year effect.

Results

Annual Red Kite survival and recovery probabilities

The estimated annual survival probabilities of all Red Kite age classes showed a substantial amount of variability between years, with the highest survival probabilities seen in the late 1970s and early 1980s (Fig. 1). Annual survival probabilities for most age classes could not be reliably estimated for the first and the last 1 or 2 years from the time series (Fig. 1) and were thus not used for trend estimation. The adult survival estimates for 1972–1973 seem unrealistically low and thus should be treated with caution. Survival of adult birds (in the third year and older) fluctuated between 0.79 and 0.85 until the mid-1980s, slightly decreased and remained stable around 0.79 until 1990, slowly increased up to 0.83 throughout the 1990s and then declined steadily to values near 0.75 after 2000 (Fig. 1). Based on data for the period 1972–2014, adult survival did not show a consistent trend with a slope of − 0.17% and 95% confidence interval (CI) of − 0.37 to 0.04%. Excluding the unrealistic first two estimates (1972–1973) for trend estimation, however, showed that from 1974 to 2014 adult survival declined annually by a mean of 0.26% (95% CI: − 0.47 to − 0.05%). Subadult birds in the second year of life varied

Table 1 Cell probabilities for multinomial trial used to estimate likelihood for the parameters juvenile survival (*sjuv*), subadult survival (*ssub*), adult survival (*sad*), juvenile recovery (*rjuv*) and adult recovery probability (*rad*)

Recoveries marked as juveniles (with year *t*)					
Age	1	2	3	≥ 4	Never recovered
Probability	$(1-\text{sjuv}_t)\times \text{rjuv}_t$	$\text{sjuv}_t\times(1-\text{ssub}_{t+1})\times\text{rad}_{t+1}$	$\text{sjuv}_t\times\text{ssub}_{t+1}\times(1-\text{sad}_{t+2})\times\text{rad}_{t+2}$	$\text{sjuv}_t\times\text{ssub}_{t+1}\times\text{prod}(\text{sad}_{t+2:\text{age-1}})\times(1-\text{sad}_{\text{age}})\times\text{rad}_{\text{age}}$	1 − rowsum

Recoveries marked as adults (with year t)			
Age (since marking)	1	≥ 2	Never recovered
Probability	$(1-\text{sad}_t)\times\text{rad}_t$	$\text{prod}(\text{sad}_{t:\text{age}-1})\times(1-\text{sad}_{\text{age}})\times\text{rad}_{\text{age}}$	1 − rowsum

Subscripts denote an index of time for each parameter

prod Product

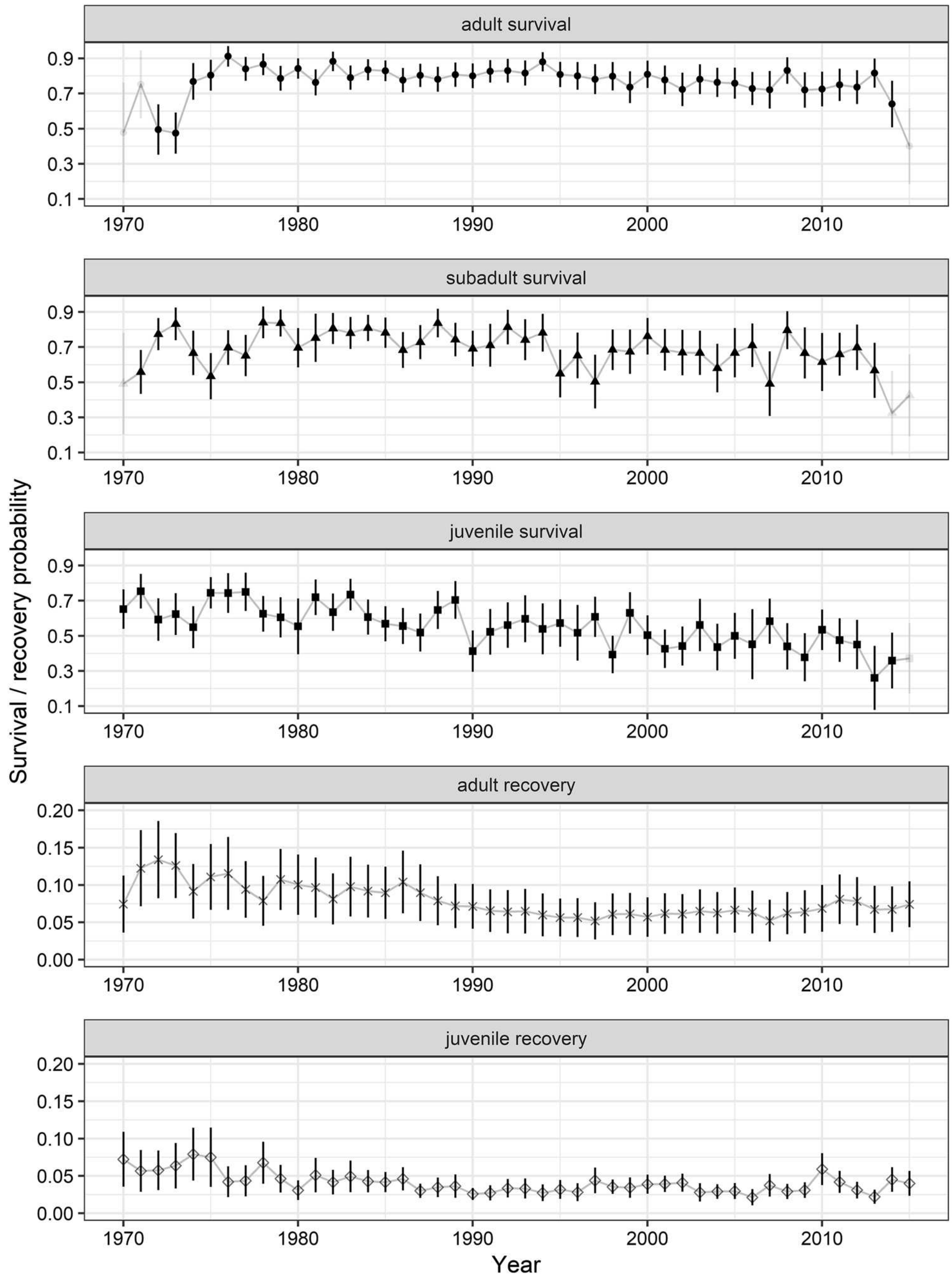

Fig. 1 Estimated annual survival probabilities for adult, subadult and juvenile Red Kites from 1970 to 2015. The survival estimates are conditional on estimates of recovery probabilities for juvenile birds and birds older than 1 year in the respective year. Error bars show ± 1 SE around the posterior mean (note the differing *y*-axes for survival and recovery probabiltiy). Light grey values could not be estimated precisely and are only shown for the sake of completeness. The adult survival estimates for 1972–1973 seem unrealistically low and thus should be treated with caution

strongly in their survival probabilities from year to year, with annual estimates spread around an average near 0.74 until 1995 and thereafter fluctuating around a lower average near 0.65 (Fig. 1). Subadult survival did not show a consistent trend from 1971 to 2013 (slope, − 0.26%; 95% CI, − 0.54 to 0.02%). Juvenile survival was relatively high (average 0.65) until the mid-1980s, declined to 0.51 after 1984, briefly recovered, and then dropped further in 1990 close to 0.4 (Fig. 1). Thereafter, survival of first-year birds fluctuated slightly at around 40–50% survival probability, declining in the late 1990s and reaching a minimum of 26% in 2013. From 1970 to 2014 juvenile survival showed a negative trend with an annual decrease of 0.66% (95% CI: − 0.94 to − 0.39%). Recovery probability for Red Kites older than 1 year (adults and subadults) continually declined from near 12% in the early 1970s to a minimum near 5% in 1997, showing a slightly increasing trend again after 2005 (Fig. 1). Across all years, mean adult recovery probability was 7.2% (SE 0.8%). The annual mean of juvenile recovery probability also declined markedly from 1970 to 1997; it was approximately two times lower than adult recovery probability and similarly increased slightly after 2005 (Fig. 1). The estimated mean of juvenile recovery for 1970–2015 was 3.7% (SE 0.5%).

Red Kite survival probabilities in different time periods

To reliably assess the temporal development of survival rates in the German population we estimated mean Red Kite survival over 5-year periods, together with the associated uncertainty and considering changing recovery probability. Mean survival probabilities were relatively high for all three age classes in 1970–1984, showing decreases over the following periods for all parameters but with differing magnitudes (Fig. 2). Adult survival probability dropped by 4.9 percentage points (p.p.) from 81.3% after 1984, then increased up to 82% in the early 1990s and then declined again below 80% after 2000. The uncertainty around the mean estimate increased over time and the 95% credible interval (CrI) for all periods overlapped (Fig. 2). Survival of subadult birds declined by 6.4 p.p. from 77.5% after 1984, in the late 1990s it reached a minimum near 63%, but subsequently increased again up to 70%. As for adult survival, the 95% CrIs of each other period overlapped (Fig. 2). In contrast, a substantial decline in survival was seen for birds in the first year of life. Survival of juveniles in the 1970s was estimated to be high, with mean values above 68% and lower 95% CrIs near 58% (Fig. 2). Thereafter, during the 1980s, mean juvenile survival dropped in total by 24 p.p., and after 1984 showed no overlap of its upper 95% CrI at 56.7% with the previous decade (Fig. 2). In the following period, after German unification, mean juvenile survival decreased by another 13.9 p.p. and thereafter remained at a minimum near 35% survival probability until 2009 (Fig. 2). The uncertainty in regard to the mean estimate of juvenile survival also increased towards the end of the time series. In the last 5-year period until 2014, mean juvenile survival was estimated to increase up to 40% (Fig. 2), but this suggestion of a positive development contrasts with declines in annual estimates of juvenile survival after 2012 (Fig. 1). The increasing uncertainty and some differences between annual and periodic survival estimates towards the end of the time series indicated that not enough data were available to precisely estimate survival after 2010. Estimation of survival in the same 5-year periods with a model assuming identical recovery probability for all ages confirmed the long-term decrease of juvenile survival, but without separating recovery of first-year birds in the model the onset of the decline was only seen later in the 1990s and at a smaller magnitude (decrease by 17 p.p.; Table S1).

Spatial and temporal patterns and causes of juvenile mortality

The recovery dataset showed two Red Kites that reached a record age of 34 years, after being marked as nestlings in 1973 and 1978. Further analysis of the juvenile recoveries revealed that over time the proportion recovered dead near the location where they were marked strongly increased (Figs. 3, 4). In the period 1970–1985 a total of 112 birds ringed in Germany were recovered dead as juveniles, in 1986–2000 this amounted to 185 individuals and in 2001–2015 there were 165 recoveries of juveniles. Between 34 and 51% of the recoveries of dead juveniles were along the migratory route in France, Spain or Portugal during all time periods (Fig. 3); however, over time more and more

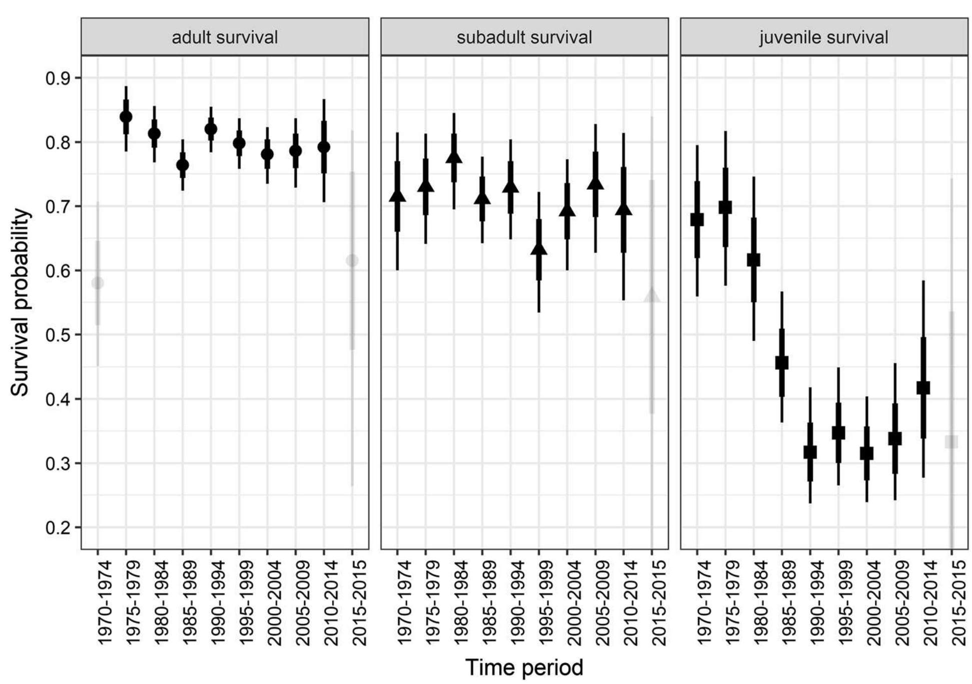

Fig. 2 Survival estimates of adult, subadult and juvenile Red Kites in 5-year periods from 1970 to 2015. The periodic survival estimates are conditional on annual estimates of recovery probability for juvenile birds and birds older than 1 year, as shown in Fig. 1. Inner error bars show ± 1 SE around the posterior mean, while outer error bars show the 95% credible interval. Values in light grey could not be estimated precisely

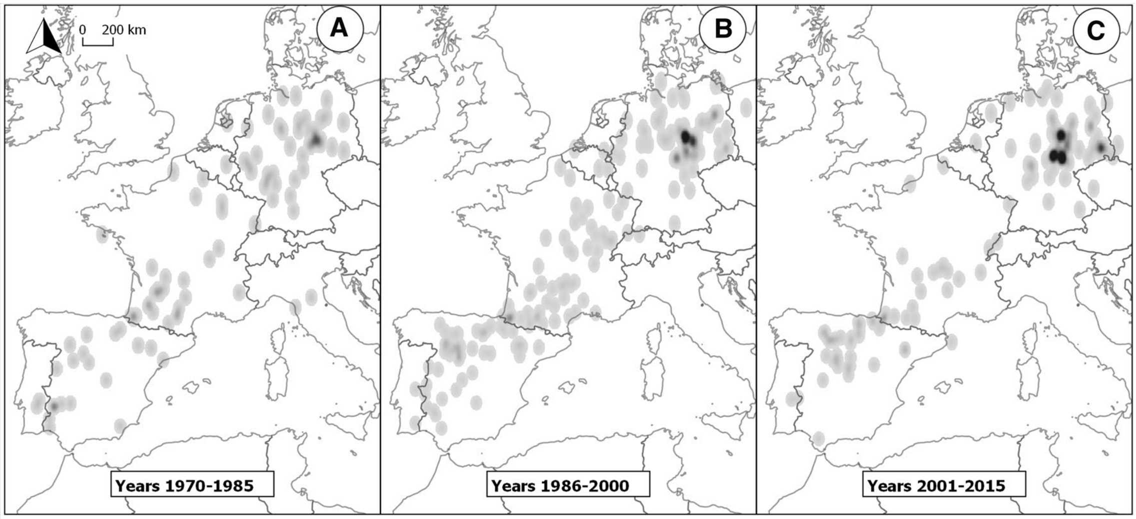

Fig. 3 Decrease in recovery distance for juvenile Red Kites marked in Germany and found dead from 1970 to 2015. **a**–**c** Kernel density heat maps with dark shading indicating areas with highest proportions of recoveries

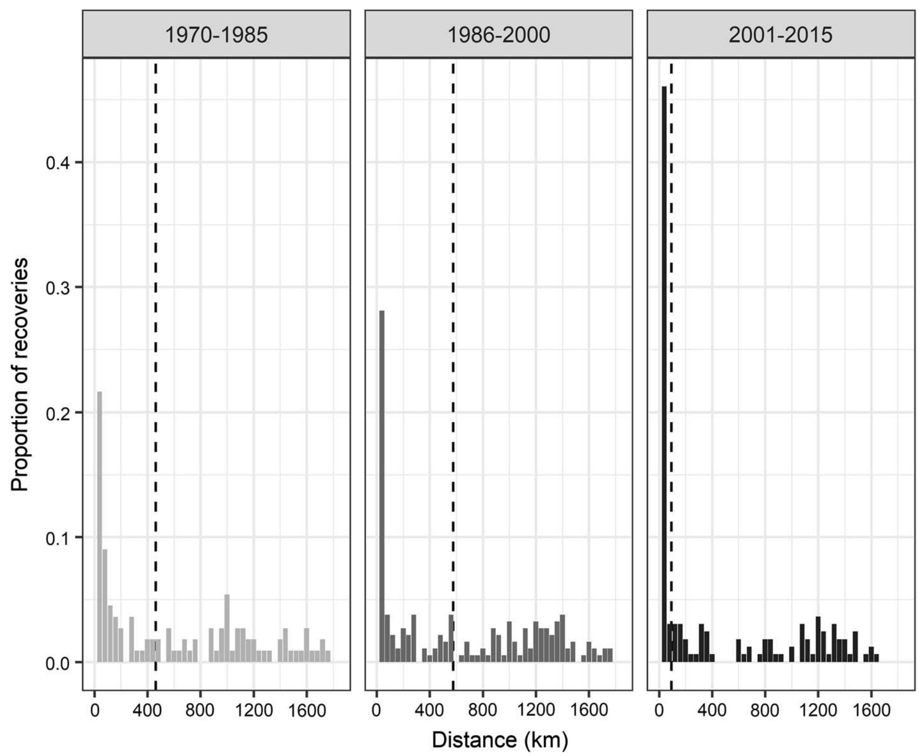

Fig. 4 Recovery distances of juvenile Red Kites ringed in Germany in three time periods from 1970 to 2015 (bin width 50 km). Vertical dashed lines show the median recovery distance for each time period

fatalities were reported less than 50 km from the ringing location in Germany (Fig. 4). Correspondingly, the distance of recovery to ringing location for dead juvenile Red Kites decreased significantly from 1970 to 2015 ($F_{1408} = 7.8$, $p = 0.005$; Fig. S2). The distribution of juvenile recoveries throughout the year showed a bimodal pattern in all time periods, with peaks in April and October (Fig. 5). In the last period, 2001–2015, there was a clear increase in the recovery of juvenile fatalities in the fledging period at the end of the breeding season (late June, early July; Fig. 5).

The cause of death reported for the ring recoveries of the juvenile Red Kites also changed over time, with mortality from collisions, poisioning and predation increasing (Fig. 6). For fatalities of first-year birds within Germany (up to 50 km distance to their origin), reported predation

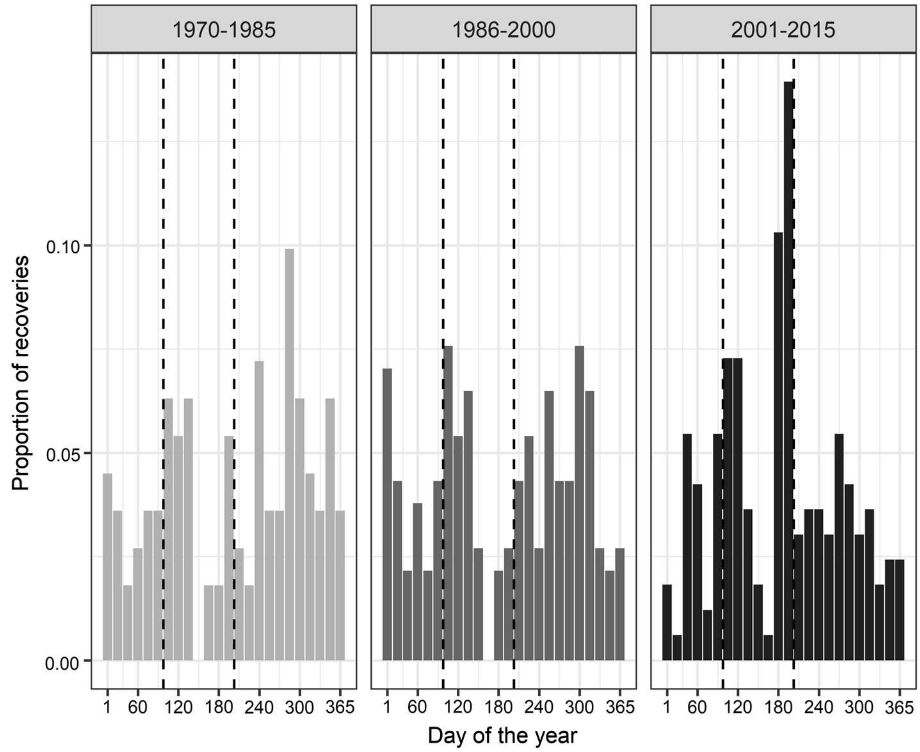

Fig. 5 Temporal distribution of juvenile Red Kite recoveries throughout the year in three time periods from 1970 to 2015 (bin width 14 days). Vertical dashed lines mark the approximate start (1 April) and end (15 July) of the breeding season

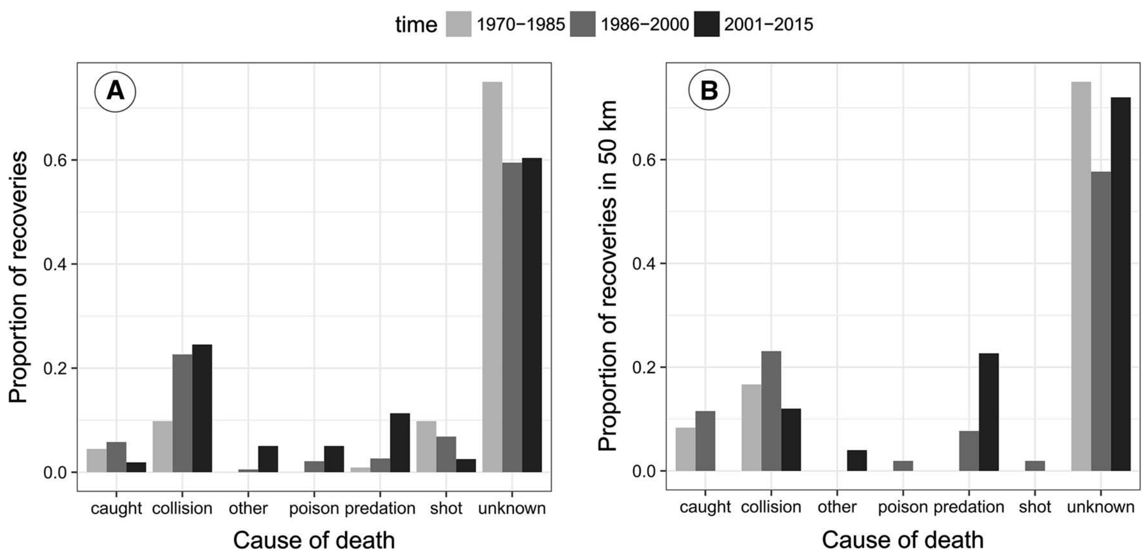

Fig. 6 Reported cause of death for juvenile Red Kites ringed in Germany recovered from 1970 to 2015. **a** Proportion of recoveries for all juveniles in the three periods. **b** Only recoveries within 50 km of ringing location. Category ‘other’ is the sum of all cases which did not apply to further categories, while ‘unknown’ shows cases where the cause of death is either not reported or was reported as unknown

showed an especially strong increase for 2001–2015 (Fig. 6b). However, in 60% or more of cases the cause of death for the juvenile birds was unknown or not reported, which meant there was only limited explanatory power to reliably assess causes of mortality.

Discussion

Our results reveal for the first time a substantial long-term decline in the survival of juvenile Red Kites in the German breeding population, with more than 40% reduction from the 1970s until the present day (Fig. 2). Additionally, we demonstrate that adult survival probability also shows a decreasing trend; however, this is associated with a higher uncertainty (Fig. 2). The key to these new results is the estimation of age-specific recovery probabilities from the existing long-term ringing data on Red Kites, which was achieved by implementing a multinomial ring-recovery model. As the results were gained from analysing recovery data of dead birds, they represent robust information on true survival of the marked Red Kites, in contrast to results from mark-recapture studies, which usually derive biased 'apparent' survival of the population under study (Kéry and Schaub 2012; Gilroy et al. 2012).

Decreasing survival rates are known to be highly influential for long-lived species like the Red Kite, but their effects can take several years to manifest as these birds only recruit to the breeding population after a minimum of 2–3 years (Pfeiffer 2009; Bellebaum et al. 2013). In Germany, the species is of central conservation importance and a decline in population size throughout the 1990s has been documented and discussed (Bezzel 2010; Gedeon et al. 2014; Mammen 2016). The decline of the Red Kite population in the eastern part of Germany after reunification in 1990 has often been related to deteriorating conditions in the agricultural landscape during the breeding season and decreased reproductive productivity (Nachtigall et al. 2010; Mammen et al. 2014). Such a temporal pattern is also visible in our survival estimates, where juvenile survival decreased further in the years following reunification (Figs. 1, 2). However, our results also suggest that the survival of all age classes already decreased markedly in a short period of time (1986–1990) before reunification of East and West Germany (Fig. 2). Our study thus suggests an additional, yet unconsidered, driver of change in the German Red Kite population throughout the 1980s and thereafter.

Estimation of age-specific recovery probabilities

The estimation of age-specific recovery probabilities for the Red Kite population from the long-term ringing data in Germany is an important step towards more reliable survival estimates. In previous analyses of Red Kite survival using ringing data in Germany, imperfect detection and possible age dependence were ignored, and survival rates were estimated simply from the life histories of the recovered individuals (Schönfeld 1984; Nachtigall 2008; Pfeiffer 2009). In our analysis, data on individuals that were not recovered also contribute towards estimating more reliable survival rates, and changes in recovery probabilities of different age classes can highlight differences in demographic processes. We demonstrate that, without considering age-specific recovery probabilities, the long-term decline of juvenile survival could have also been observed, but at a smaller magnitude. Ignoring the age dependence of recovery would have also masked the temporal pattern of decreasing survival probabilities well before the reunification in 1990 that we have been able to show.

Estimation of recovery probabilities for juveniles and older birds is difficult if most individuals are marked as juveniles, as it requires additional ring recoveries from birds marked as adults or immatures (Kéry and Schaub 2012). Although catching and marking adult Red Kites is relatively difficult, the data generated by doing so allow a more detailed analysis of demographic processes, and it is thus highly important and useful to also ring adult individuals. Ring recovery rate of all Red Kites marked in Germany over the last decades was previously estimated as 4.9% (Bairlein et al. 2014); our model without age-specific differences in recovery probability estimated a similar 5.6% from 1970 to 2015 (Table S1). However, it is known that ring recovery probability is lower for juvenile Red Kites than for older birds in Switzerland, where recovery probability for adults is around 10% and for juveniles near 5% (Aebischer 2009; Kéry and Schaub 2012).

Age-dependent recovery probabilities can occur if the main cause of mortality changes with age and if different causes of mortality are associated with different recovery probabilities (Schaub and Pradel 2004; Kéry and Schaub 2012). Most causes of death for the Red Kite are thought to be anthropogenic (Schönfeld 1984; Knott et al. 2009; Langgemach et al. 2010), but depending on whether humans are directly involved or not, the recovery rate for different causes of mortality will differ. Thus, the generally lower recovery probability of dead Red Kites in the first year indicates a cause of death that is less often discovered than others. Another potential reason for age-structured differences in recovery rate could be related to juvenile dispersal and the location of death. If the recovery probability decreases with distance from the place of ringing, as seen with other species, the lower probability of recovery for juveniles could also hint at, on average, more distal fatalities for this age class. The median recovery distance of birds older than 1 year in our dataset was approximately only half that of the juvenile age class, which supports this hypothesis.

Survival probabilities over time in the German Red Kite population

In long-lived birds, the conditions experienced by the chicks during rearing and in early life can affect fitness and juvenile survival—mediated by natal habitat quality and resource availability (Van De Pol et al. 2006; Payo–Payo et al. 2016). The decrease in Red Kite juvenile survival could therefore reflect a deterioration in habitat quality experienced by the breeding population. As such, it seems plausible that food availability that is reduced due to agricultural intensification not only affects the reproductive output of breeding Red

Kites, but also lowers fitness and survival of the fledging juveniles. Additionally, resource availability for territorial birds of prey can be density dependent, where an increase in population size approaching carrying capacity can decrease juvenile survival (Nicoll et al. 2003). Throughout the second half of the twentieth century, the German Red Kite population slowly recovered from persecution and increased in size (Ortlieb 1989; Nicolai and König 1990; Bezzel 2010). Monitoring data are only available from 1988 onwards, but until 1991 the breeding population was still continually growing (Mammen 2016). That the fitness of Red Kite nestlings in fact deteriorated after the German reunification is known from studies by Pfeiffer (2000), who detected a declining trend in the relative body weight of nestlings from 1989 to 1999 and related this to decreased food availability.

Another likely factor that can explain increased mortality in Red Kites is poisoning, especially with agricultural pesticides. This is a well-established problem for raptors in general, and in particular for the Red Kite (Berny and Gaillet 2008; Coeurdassier et al. 2012; Montaz et al. 2014; Molenaar et al. 2017), which has however received relatively little attention in Germany (but see Hirschfeld 2011). Moreover, the rapidly decreasing trend in recovery probability that we found for both juvenile and subadult/adult Red Kites in the mid-1980s (Fig. 1) could indicate a change in the dominant causes of mortality, leading gradually to fewer and fewer dead birds being recovered. Fatalities after poison ingestion or accumulation of poison over time would most likely lead to such a trend (Cox 1991) because birds that die from poisoning without direct human contact are much less likely to be found than those casualties which directly involve humans or ones which ocurr near inhabited areas (e.g. collisions on roads or with infrastructure; Wayland et al. 2003).

Environmental contamination in East Germany and the fatal non-target effects of agricultural pesticide application were extensively documented in the former German Democratic Republic (GDR) (Grün et al. 1982; Riedel et al. 1988). Between 20 and 30% of the agricultural area was regularly treated with organochloride pesticides (mainly Toxaphene/Camphechlor) to control rodent pests, while 1983/1984 saw a strong increase of aerial dichlorodiphenyltrichloroethane (DDT) application in forestry to cope with pest infestation (Heinisch et al. 1994). Although DDT is mainly known for its detrimental effects on reproduction, dichlorodiphenyldichloroethylene (DDE; a DDT metabolite) and other organochloride compounds applied at high concentrations can also have lethal toxic effects (Beitz et al. 1991; Cox 1991; Newton 2013). From 1984 onwards, a new strategy for the use of first-generation anticoagulant rodenticides (especially Chlorophacinone) was applied in the GDR, by provisioning bait at lower levels of pest infestation, over a 30% larger area and over longer periods of the year (Wieland and Schellenberg 1984). This strategy was devised in response to several years of high abundance of the Common Vole (*Microtus arvalis*), which is considered a pest (Sellmann 1991). This led to 221 recorded fatal non-target poisoning events affecting wild mammals from 1981 to 1990 in the GDR, of which 49% were caused by chlorophacinone bait intake due to mishandling and bait attraction (Beitz et al. 1991). Such poisoned carcasses represent an enormous threat to scavengers, like the Red Kite, which feed on them and then are poisoned themselves. For scavenging birds of prey the direct consumption of poisoned rodents, targeted during pest control operations, is another major pathway of intoxication with pesticides (Berny and Gaillet 2008; Coeurdassier et al. 2012; Montaz et al. 2014). This process was also documented throughout the 1980s in the GDR, and included kites (*Milvus* spp.) as fatalities (Beitz et al. 1991). Stubbe (1982) already suspected that contamination and the resulting poisoning could affect Red Kite survival in the GDR. Considering the scale of pesticide and especially anticoagulant rodenticide application throughout the 1980s, it is highly likely that this affected Red Kite survival rates through secondary poisoning.

Throughout the 1990s the amount of pesticides used in plant protection generally decreased in Germany (Schmidt 2003). The number of anticoagulants registered for plant protection, however, increased strongly until after 2000, but data on agricultural use are unfortunately not publicly available (Jacob and Buckle 2017). In recent years, EU legislation has restricted the use of anticoagulant rodenticides (Luque-Larena et al. 2018). This has led to constraints in their agricultural use for plant protection, but biocidal applications have risen (Jacob and Buckle 2017), which also hold potential for secondary poisoning of farmland scavengers like the Red Kite (Ntampakis and Carter 2005; Jacob et al. 2018).

Since 2000 there has been a particular increase in adult bird mortality (Figs. 1, 2). During the same time period, an increasing number of wind turbines were erected in Germany, leading to additional mortality due to collision for the Red Kite population (Dürr 2009; Bellebaum et al. 2013). In fact, from 2001 to 2015 more than 300 Red Kites, mostly adults, were discovered dead as victims of wind turbine collisions in Germany (Langgemach and Dürr 2018). This number, however, is only a small proportion of the true number of collisions, since it is based on chance encounters of dead birds, i.e. carcasses are known to disappear quickly after a collision event and are thus seldom found (Bellebaum et al. 2013; Grünkorn et al. 2016). So far, the impact of collision mortality on the Red Kite population has only been assessed on a regional level (Bellebaum et al. 2013), but the potential for a substantial impact on the national population has recently been demonstrated (Busch et al. 2017). Even though proportionally fewer juvenile Red Kites collide with wind turbines, an increasing collision risk may contribute to their decreasing survival rates in the last decades. The increase in awareness of this potentially problematic additional cause of mortality and the ensuing increase in search effort most likely contributed to the generally increasing trends in both adult and juvenile Red Kite recovery probabilities after 2005 (Fig. 1).

A natural cause of death that mainly affects Red Kite nestlings or fledglings is predation, especially by other raptors but also by predatory mammals (Langgemach et al. 2010). Most predation is by Northern Goshawks (*Accipiter gentilis*), which preyed on almost 30% of 40 nestlings studied with nest cameras (Gottschalk et al. 2015). The reported causes of Red Kite juvenile mortality clearly show an increase in predation over time (Fig. 6), and the increase in mortality in recent years near the end of the breeding season (Fig. 5) could also be related to fledgling predation. With an increasing population density of Northern Goshawks, the proportion of other raptors in their diet also increases (Hoy et al. 2017), thus the long-term population recovery of Northern Goshawks after their persecution in the twentieth century could have also had a negative effect on the survival rate of the Red Kite due to superpredation. Similarly, superpredation by the Eagle Owl (*Bubo bubo*) on the Red Kite seems to be more common than previously thought (Lourenço et al. 2018).

Causes of Red Kite mortality

Obtaining an accurate picture of the most important causes of death affecting survival of individuals in a population is difficult, particularly when this is based on opportunistically collected and unstructured ring recoveries. Proportional changes in the reported causes of death should therefore be viewed with caution, and rather suggest patterns that need further investigation. We can also see from our results on juvenile mortality that in nearly 60% of cases the cause of death is simply unknown (Fig. 6). It is thus at present unclear which combination of factors has led to the long-term decrease in juvenile survival of the German Red Kite population. We can, however, see a trend in the recovery data showing that more juveniles were found dead close to their place of birth in Germany, just after the end of the breeding season (Figs. 3, 4). A better understanding of the dominant causes of mortality of the Red Kite in different age classes is therefore urgently needed, to ensure that effective conservation measures can be put in place at the breeding grounds in Germany. The most reliable way to gain such unbiased estimates is by telemetry of a suitable number of individuals of all age classes and a thorough investigation of carcasses to determine the cause of death.

Acknowledgements We gratefully acknowledge the efforts of all the voluntary Red Kite ringers in Germany that allowed the study of ring recovery data over such a long period. We thank Vogelwarte Hiddensee (U. Köppen, C. Herrmann; Ringfundmitteilung der Beringungszentrale Hiddensee no. 09/2018), Vogelwarte Helgoland (F. Bairlein, O. Geiter) and Vogelwarte Radolfzell (W. Fiedler) for data provision, and F. Bairlein and C. Herrmann for helpful comments that improved the quality of the manuscript. For comprehensive advice on how to best analyse the data and comments on an earlier draft of the manuscript, we are deeply grateful to M. Schaub. The detailed comments by F. Korner-Nievergelt, J. Bellebaum and an anonymous reviewer greatly helped to further improve our manuscript.

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