Density-dependent age of first reproduction as a key factor for population dynamics: stable breeding populations mask strong floater declines in a long-lived raptor

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Abstract
The age at which individuals reproduce for the first time is a key demographic factor impacting population dynamics and is subject to substantial variation across animal populations. There is also widespread empirical evidence that age of first reproduction responds to changes in population density over time, especially for long-lived birds and mammals. The density dependence in age of first reproduction has profound impacts on the size of the non-breeding (’floater’) part of the population. A better understanding of floater dynamics in raptor populations is urgently needed for comprehensive assessments of conservation status and management. We use the European near-endemic red kite Milvus milvus, a long-lived raptor of conservation concern, as an example to investigate total population dynamics with an age-structured demographic model. Using published estimates of survival and reproduction, we model the red kite population in Germany over four decades, considering also density dependence in the age of first reproduction in different model scenarios. Based on the literature and the results of our simulations, we show that age of first reproduction for the red kite most likely responds non-linearly to density and that this general feedback mechanism should regularly be considered in demographic simulations. Our model results have far-reaching implications for the conservation status of the red kite, as they highlight a drastic decrease of juvenile and non-breeding individuals in the population over time – driven both by declining vital rates and a density-dependent shift towards a younger age of first breeding. This process is not visible when judged only by the size of the breeding population, which our model estimates to be of similar size today as in the 1980s. The total red kite population reconstructed for Germany, however, seems diminished to nearly 50% of its former size.

Introduction
Management and conservation of animal populations critically rely on an understanding of the key vital rates that impact population dynamics, especially for building robust models of population development (Pe’er et al., 2013; Reed et al., 2002). Apart from survival, reproduction, emigration and immigration, the age at which individuals first reproduce is a key demographic factor (Clotet et al., 1990; Neubert and Caswell, 2000; Oli and Dobson, 1999; Pradel et al., 1997). The absolute limits of minimum and maximum reproductive age (sexual maturation and senescence) for a species are determined by physiology, but the individual age of first reproduction can vary spatially or temporally across animal populations (e.g. Antor et al., 2007; Furness, 2015; Langvatn et al., 1996). Especially for long-lived vertebrates with age-structured populations, variation in the age of first reproduction can substantially affect the total number of reproducing individuals and thus overall productivity (Ferrer, Otalora, and García-Ruiz, 2004; Morandini et al., 2019). We hypothesize that density-dependent variation in age of first reproduction can buffer breeding population size, potentially masking total population declines.

A density-dependent feedback mechanism acting on age of first reproduction, where an increase in population density leads to a delayed age of first reproduction, is well grounded...
in ecological theory and population biology (Eberhardt, 2002; Neubert and Caswell, 2000; Oli and Dobson, 1999; Stearns, 1992; Tavecchia et al., 2007). Empirical studies of this relationship largely support the theory; especially for long-lived birds and large herbivores there is clear evidence for a positive density effect on age of first reproduction (Bonenfant et al., 2009; Borowik and Jędrzejewska, 2018; Croxall et al., 1990; Ferrer, Otalora, and García-Ruiz, 2004; Jorgenson et al., 1993; Krüger, 2005; Tavecchia et al., 2007). Such a density feedback on age of first reproduction is also well documented for smaller, short-lived bird and mammal species (Clòbert et al., 1990; Cooper et al., 2009; Ergon et al., 2016; Melero, Robinson, and Lambin, 2015). However, the variation in age of first reproduction does not always follow the expected relationship with population density, which could be due to overriding environmental factors or because density effects are restricted to specific age or sex classes (Fay et al., 2017; Furness, 2015; Gamelon et al., 2016; Millsap, 2018; Trites and York, 1993). For example, the albatross population studied by Fay et al. (2017) only initially showed the expected decrease in age of first reproduction with decreasing population size; later on recruitment age still declined even with increasing density – which according to the authors could be explained either by non-linear density regulation, an Allee effect on mating processes or the effect of climatic variables on body condition (Fay et al., 2017).

Especially for larger birds, like raptors, it is evident that a density dependence in the age of first reproduction is also directly linked to the size of the non-breeding (‘floater’) part of the population (Antor et al., 2007; Elliott et al., 2011; Ferrer, Otalora, and García-Ruiz, 2004; Morandini et al., 2019; Ortega et al., 2009; Penteriani, Otalora, and Ferrer, 2006), and a better understanding of floater dynamics is essential for conservation and management of these bird populations (Carrete, Donázar, and Margalida, 2006; Hunt, 1998; Penteriani, Ferrer, and Delgado, 2011). Despite its clear relevance, empirical data about the variation in age of first reproduction in animal populations are often severely limited and therefore this aspect is also often ignored in demographic simulations and population viability analyses (PVAs) (cf. Ferrer, Otalora, and García-Ruiz, 2004; Morandini et al., 2019; this study). The reliability and robustness of PVAs, however, depends critically on the assumptions made and many PVAs need to be improved in this regard (Chaudhary and Oli, 2020; Pe’er et al., 2013).

Here, we investigate the population dynamics of the European near-endemic red kite Milvus milvus, a medium sized but remarkably long-lived raptor of conservation concern (Bird et al., 2020; BirdLife International, 2019), in the centre of its breeding range. Both juvenile survival and productivity of the red kite population in its breeding stronghold Germany are showing long-term declines (Hoffmann et al., 2017; Katzenberger et al., 2019; Mammen, Stark, and Stubbe, 2017). We highlight that existing studies indicate a substantial, but widely overlooked, density-dependent variation in age of first reproduction for the red kite (but see Walz, 2005; Table 1). Based on two case studies, we formulate a simple function to include density dependence in the age of first reproduction into matrix population models. Using published estimates of red kite survival and reproduction and an age-structured matrix model, we then reconstruct key aspects of the population dynamics from 1975 to 2015 in Germany – adjusting the age of first reproduction in different scenarios. Finally, we compare the resulting simulations to red kite breeding bird surveys in Germany, to investigate the interacting effects of density-dependent variation in age of first reproduction and declining vital rates on the temporal dynamics of the breeding and the non-breeding part of the population.

Materials and methods

Estimating density-dependent age of first reproduction for the red kite

Several studies used demographic models to analyse red kite population dynamics, but they differed widely in the assumptions made about the age of first reproduction and also in red kite population density (Table 1). Throughout the paper we use a general expression of density as the ratio of the total population size (N) to carrying capacity (K), rather than defining it as local breeding density in pairs per 100 km² or a similar spatial measure. The absolute population size is, therefore, not important because it is used as a relative value. We use the term breeding individuals to describe birds that have acquired a breeding territory (including ‘territorial individuals’ that may or may not lay eggs in a given year), while the term non-breeding individuals describes birds in the age classes 2–6 years which have not acquired a breeding territory. In the previous studies modelling red kite populations, the age of first reproduction is usually set to a constant age (2 or 3 years) or as fixed proportions in different age classes (ages 2–3 or 2–5 years; Table 1). A potential variation in age of first reproduction over time is only partly considered by Tenan et al. (2012), where the mean proportion of breeders is estimated as a latent variable in the model and thus reflects the best fit to the data and not an a priori assumption.

To describe density dependence in the age of first reproduction for the red kite, we used two empirical case studies, as also communicated in German language by Katzenberger and Gottschalk (2019). For details about the matrix models applying this density-dependent age of first reproduction, please see the next section ‘simulation models’. To estimate a situation under high density, we used published data on the red kite population in the surroundings of Weimar, Germany (Pfeiffer, 2009). This population showed a long-term stable development from 1988 to 2008, fluctuating mostly between 40 and 50 breeding pairs (Pfeiffer, 2009), and we, therefore, assumed that the population was breeding near the local carrying capacity. For a sample of 44 individuals from this population, Pfeiffer (2009) reported the age while breeding (not age of first breeding); birds aged 7 years made up the highest proportion in this sample (16% or seven individuals; Table 2). As older individuals generally represent an
increasingly smaller proportion in the population and earliest breeding in red kites usually occurs with 2 or 3 years of age (rarely after the first year; Evans et al., 1999; Newton et al., 1989; Pfeiffer, 2009), we assumed from these data that by 7 years of age all birds had recruited as breeders. This assumption is in line with other studies on the red kite in Wales (Newton et al., 1989) and the closely related black kite Milvus migrans (Sergio, Blas, and Hiraldo, 2009), where by 7 years all individuals were breeding as well. With this assumption, and a proportion of 4.7% for the age class 7 years in the red kite population obtained from ringing data (Pfeiffer, 2009), we calculated a total population size of 149 individuals for this model population (seven individuals aged 7 years/proportion 0.047 = 149). This total population size was then used to construct the age structure of a model population under high density (based on the proportional data in Pfeiffer 2009; Fig. 1) and to calculate the percentage of non-breeding birds in the age classes 2–6 years (Table 3). To infer a situation of breeding under low density, with a population much below carrying capacity, we used the data from the successful re-introduction project of the red kite in the United Kingdom (UK). For the phase of recolonization, the proportion of individuals breeding for the first time at age 2 years is estimated at 80%, while at 3 years of age all birds are expected to breed (Evans et al., 1999; Smart et al., 2010).

From these two case studies, we derived a simple density-dependent formula for red kite age of first reproduction in different age classes, adapted from the standard formula used in the VORTEX software (Lacy and Pollak, 2018):

$$Ba(N) = Ba(0) - \left[ \left( \frac{Ba(0) - Ba(K)}{N} \right) \times \left( \frac{N}{K} \right)^x \right].$$

Here, $Ba(N)$, the percentage of breeders in age class a at total population size $N$, is calculated from the percentage breeding at low density ($Ba(0)$) and the percentage breeding near carrying capacity $K$ ($Ba(K)$) in the respective age class and with a density dependence component modulated by the exponent $x$. At low densities, the resulting percentage of breeders for each age class approaches the values from Smart et al. (2010), while at high densities the percentages reach the values estimated here (Table 3). With an increasing value of the exponent $x$ in the formula, the age of first

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### Table 1

Assumptions on age of first reproduction in previous studies using demographic models for the red kite Milvus milvus. The density simply reflects a general approximation of red kite population size in relation to carrying capacity.

| Study                  | Reference for breeding age | Location          | Density          | Age first reproduction |
|------------------------|----------------------------|-------------------|------------------|------------------------|
| Hotker et al. (2005)   | standard textbooks         | Germany           | High, core breeding area | 2y                     |
| Smart et al. (2010)    | 80%, 2y, 100%, 3y          | Spain (Mallorca)  | Higb, core breeding area | 2y, 3y                 |
| Schaub (2012)          | —                          | central Europe    | Low, reintroduction | 2y                    |
| Tenan et al. (2012)    | —                          | Spain             | Low, reintroduction | 2-5y, 3-5y             |
| Bellebaum et al. (2013)| fixed proportions per age class, based on field data (telemetry) | Germany, Italy, UK | High, core breeding area | 2y                     |
| Ceccoloni et al. (2013)| fixed proportions per age class chosen after Newton et al. (1989); Nachtigall (2008) | Germany, Italy, UK | High, core breeding area | 2y, 3y, 4y             |
| Mammen et al. (2014)   | 80%, 2y, 100%, 3y          | Germany           | High, core breeding area | 2y, 3y, 4y             |
| Meyer et al. (2016)    | 80%, 2y, 100%, 3y          | Germany           | High, core breeding area | 2y, 3y, 4y             |
| Ponsom et al. (2019)   | fixed proportions per age class, based on field data from 18 individuals | Spain, Spain     | Low               | 2y                     |

### Table 2

Ages of 44 breeding red kites by Pfeiffer (2009). The individuals were sampled from the local population from 1991 to 2008, see also Pfeiffer (2009)

| Age class (years) | No. of Individuals |
|-------------------|--------------------|
| 2                 | 4                  |
| 3                 | 5                  |
| 4                 | 6                  |
| 5                 | 5                  |
| 6                 | 6                  |
| 7                 | 7                  |
| 8                 | 3                  |
| 9-18              | 8                  |
reproduction is only regulated substantially at higher densities (Fig. 2). For an example how to include this formula as a function in a VORTEX model see Table S1 (Supporting information).

**Simulation models**

Fundamentally, the size of a population is determined by mortality, reproduction, emigration and immigration. As far as currently known, the red kite is a species showing high natal philopatry as well as high adult breeding-site philopatry (Newton et al., 1989; Nachtigall, 2008; Pfeiffer, 2009) and thus emigration and immigration processes should mainly take place within the large-scale population that we are addressing here. We, therefore, did not consider emigration and immigration further in the population models. For local or regional studies however, this assumption may not hold and should be further investigated.

To model population development of the red kite population in Germany from 1975 to 2015, we used 1,000 stochastic simulations with VORTEX (v. 10.3.5.0, Lacy and Pollak, 2018), based on the values in Table S1. Because the first timestep in the model (1975 to 1976) is needed to constitute the correct proportions of the different age groups in the total population, we only display model results from 1976 onwards. Age-dependent mortality for individuals in the first year, second year and third year and older was taken from the 5-year periods reported in Katzenberger et al. (2019). The annual productivity of the breeding population (number of young/all breeding pairs) from 1988 to 2012 is published by the MEROS project (Mammen, Stark, and Stubbe, 2017). For years where no productivity estimates were reported (1975–1987 and 2013–2014), the average of the nearest 5 years in the existing data was used. The starting population was set to 400 individuals and a capacity of 1000 (initial density = 0.4). The absolute number of breeding individuals is of course much higher in Germany (Grüneberg and Karthäuser, 2019); we focus here only on the relative changes in the population over time. To set up the initial density, we used existing long-term population estimates for the red kite in Germany: In the 1970s, the population was estimated to number 4,000–6,000 breeding pairs, approximately half of its previous maximum estimated in the 19th century and one-third of its later maximum in the early 1990s (Mammen et al., 2014; Nicolai and Kostrzewa, 2001). Based on this information, we assumed the initial density to be in a range of 0.3–0.5 and used a mean value of 0.4 as described above. To test the effect of the initial density
assumption on our results, we replicated all analyses with starting populations of 200 and 600 individuals (density 0.2 and 0.6 respectively).

We simulated five scenarios using different formulations for the age of first reproduction (Table 4): scenario ‘3y’ used the common assumption that all birds start breeding at 3 years of age, scenarios ‘D-E1’ to ‘D-E8’ all used the density-dependent formula of breeding age described above (min. breeding age 2 years), but differed in the exponent used (1, 2, 4 or 8; Fig. 2). Independently of age, we added a stochastic variation in the annual percentage of breeding individuals (std. dev. 10%). As the actual relationship between density and age of first reproduction remains currently unknown, the scenarios with the differing exponents were used to test different functional forms of the relationship between density and age of first reproduction. The standard population size reported in VORTEX is the total population, but separate values for the different age groups (first year, non-breeding, breeding individuals) at each time step can be extracted from the optional census files (.yr file format). From the 1,000 stochastic simulations for each scenario, we calculated the average and standard deviation of population size at each time step in the different age groups using R (v. 3.5.2, R Core Team, 2018). The number of non-breeding individuals was calculated by subtracting the number of breeders from the sum of all individuals older than 1 year.

Table 4 Description of the model scenarios with different assumptions on age of first reproduction

| Scenario | Description (see also Fig. 2) |
|----------|--------------------------------|
| 3y       | This scenario uses the common assumption of a fixed age of first reproduction at 3 years, without any density-dependent regulation. |
| D-E1     | In this scenario, age of first reproduction is regulated linearly by density (exponent 1 in density function). An increase in density, thus, has the same effect on recruitment age at low and at high densities and already at very low densities (<0.15) a slight density regulation takes effect. |
| D-E2     | In this scenario, age of first reproduction is regulated non-linearly by density (exponent 2 in density function). Under low densities (<0.25), the effect of density on age of first reproduction is minimal, but at densities > 0.25 the regulation increasingly affects recruitment age. |
| D-E4     | In this scenario, age of first reproduction is regulated non-linearly by density (exponent 4 in density function). Until intermediate densities (<0.45), the effect of density on age of first reproduction is minimal, but at densities > 0.45 the regulation shows a strongly increasing effect on recruitment age. |
| D-E8     | In this scenario, age of first reproduction is regulated non-linearly by density (exponent 8 in density function). Until high densities (<0.75), the effect of density on age of first reproduction is minimal, but at densities > 0.75 the regulation shows a very rapidly increasing effect on recruitment age. |
The model estimates for the breeding part of the population in each scenario were compared based on relative annual changes (%) to published estimates of red kite breeding population size in Germany for 1988–2014 (Mammen, 2016). These estimates of red kite breeding population size are based on field surveys of breeding individuals and reported as index data by the MEROS project (Mammen, 2016). Comparing the model predictions of breeding individuals to the index data based on relative annual changes assured that the choice of a base year for indexing did not affect the comparison. To quantify the difference between the model scenarios and the breeding population index data, we used the root mean square error (RMSE). Because the RMSE in this case is calculated from relative annual changes, it describes the overall annual prediction error expected to occur when making a model prediction for a single year (in percent).

**Results**

**Model-based reconstruction of red kite breeding population**

The red kite breeding population reconstructed in the different model scenarios generally increased until the early 1990s and then showed either continuing or gradually slowing declines thereafter (Fig. 3a). Changing the age of first reproduction in the different model scenarios showed a

![Figure 3](https://zslpublications.onlinelibrary.wiley.com)

**Figure 3** Part A: Number of breeding red kites predicted by the different matrix population model scenarios over time without (‘3y’) and with (‘D-E1’ to ‘D-E8’) density dependence in age of first reproduction. The numbers at the start of the time series differ according to the density-dependent model formulation. Part B: Number of breeding individuals in the matrix population model scenarios indexed to year 2010, for comparison with long-term breeding population estimates for the German red kite population (grey shading) reported in Mammen et al. (2014) based on Nicolai and Kostrzewa (2001). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]
considerable effect on the development of the breeding population over time. In comparison with existing breeding population estimates for the German red kite population, the scenarios ‘D-E4’ and ‘D-E8’ best reflected the long-term development (Fig. 3b). The scenario ‘D-E4’, with a noticeable regulation of age of first reproduction occurring at intermediate densities, also showed the best fit to the annual index data from breeding population surveys from 1988 to 2014 (RMSE: 8.11). Scenario ‘3y’, assuming a fixed age of first reproduction at 3 years, showed the worst fit to the annual breeding population index (RMSE: 8.84). Based on the difference in RMSE, scenario ‘D-E4’ improved the prediction error of the model for a single year by about 8% compared to scenario ‘3y’. When projecting a population development over 30 years, the annual prediction error accumulates and the number of breeding individuals at the end of the time series would be expected to differ on average by 22% between the two scenarios. The RMSE for the other scenarios was 8.48 for ‘D-E8’, 8.20 for ‘D-E2’ and 8.19 for ‘D-E1’. Replicating the simulations with differing starting densities of 0.2 and 0.6 always showed the lowest RMSE for scenario ‘D-E4’ or ‘D-E2’ and the highest RMSE for scenario ‘3y’. Comparing the annual relative changes between the index data and the model scenarios ‘3y’ and ‘D-E4’ showed that the changes in breeding population size from year to year were often stronger in the index data from population surveys than in the model population (Fig. 4). Scenario ‘3y’ reflected the initial breeding population changes until the late 1990s relatively well, but thereafter strongly deviated from the population index. Scenario ‘D-E4’ generally reflected the alternating phases of declines and increases in the breeding population index better.

**Population dynamics and density-dependent age of first reproduction**

Based on the model scenario ‘D-E4’, which represents a noticeable regulation of age of first reproduction starting only at intermediate densities, the development of the breeding and the non-breeding part of the population can be viewed separately (Fig. 5). Under the conditions at the beginning of the time series, an increase and overall a very high proportion of non-

![Figure 4](https://example.com/figure4.png)

**Figure 4** Comparison between annual relative change in the number of breeding red kites from 1989 to 2014 based on index data from MEROS breeding population surveys (Mammen 2016) and matrix population model predictions without (‘3y’) and with (‘D-E4’) density dependence in age of first reproduction. Lines show a 3-year moving average of annual change. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]
breeding birds in the model population was observed. Thus, by the mid-1980s, the capacity limit of the total population was reached, despite the relatively low number of breeding birds. Already from 1985 onwards, a continuous decline of the non-breeding and the total population became apparent (Fig. 5). However, due to the high number of individuals recruiting as breeders for the first time during this period, the breeding population in the model continued to increase until the early 1990s (Fig. 5). From 1995 onwards, the breeding population also started to decline, but gradually stabilized after the year 2010. At the end of the time series, the total population was about 50% lower than the maximum in the early 1980s, while the breeding population was only slightly smaller than in the 1980s but about 33% lower than the maximum in the early 1990s (Fig. 5).

The density-dependent proportion of breeding individuals aged 2 and 3 years in the population decreased sharply at the beginning, as high total densities were reached (Fig. 6). With the decline of the total population, however, more and more birds aged 2 and 3 years started to breed, and the proportion of breeding birds in these age groups reached a plateau near their maximum values by the year 2005 (Fig. 6). Under the given vital rates and a density-dependent regulation of age of first reproduction, the proportion of non-breeders in the population was largely minimized over time. The number of first year birds in the model in 2015 was nearly 50% lower than in the early 1980s, while the mean number of non-breeding individuals (ages 2–6 years) even decreased by 90% during this period (Fig. 5).

In the model scenario ‘3y’, without a density-dependent regulation of age of first reproduction, the breeding population showed extremely rapid changes over time, nearly doubling in size within 5 years from 1976 to 1981 and declining by almost 50% from the early 1990s until just after the year 2000 (Fig. S1). The total population in scenario ‘3y’ also supported few non-breeding individuals and they were minimized over time.

**Discussion**

Using an age-structured demographic model and published estimates of survival and reproduction, we were able to reconstruct key features of the population dynamics of the red kite in Germany over four decades. A substantial growth of the breeding population throughout the 1970–1980s, in part due to legal protection of the red kite and other raptors, is documented by large-scale field surveys in Germany (Aebischer, 2009; Nicolai and König, 1990). Our model also reproduces the peak of the red kite breeding population size in the early 1990s and the following decline and stabilization, known from annual field surveys starting in the late 1980s (Mammen, 2016). We also reconstruct a strong decline of the total red kite population in Germany by nearly 40% from the early 1990s to the early 2000s (Fig. 5). Because most of the German red kite population winters on the Iberian Peninsula, this could to a large extent explain the recorded 50% decrease of the species’ wintering population in Spain during same time period (Cardiel, 2006; Viñuela...
et al., 1999). Since the German breeding population of the red kite declined approximately by 20% during this time period (Mammen, 2016), only the consideration of simultaneous cryptic declines in juvenile and non-breeding individuals based on demographic data reveals the full magnitude of the decrease during this time period. In addition, we show that the age of first reproduction in a red kite population is most likely density dependent and that incorporating this into model projections yields more accurate results.

Density-dependent age of first reproduction

The existing data on red kite age of first reproduction clearly suggest such a density dependence (Table 1) – as already proposed by Walz (2005), but has largely been overlooked in previous simulation studies. Also, the first results from telemetry studies tagging juvenile red kites under a high density situation in juvenile and non-breeding individuals indicate a strongly increased recruitment age and considerable floating behaviour: a large proportion of individuals has not yet settled in a breeding territory at ages up to the sixth calendar year (Scherler, 2020). Despite extensive scientific evidence that age of first reproduction frequently responds to changes in population size, both in long- and short-lived species, this process is often not considered in PVA assessments or other demographic simulations (cf. Ferrer, Otalora, and García-Ruiz, 2004; Morandini et al., 2019). Yet, variation in age of first reproduction can have a substantial impact on the structure and temporal development of animal populations. We show here that for raptors this not only applies to small populations, where changes in age of first reproduction affect productivity and thus extinction risk (Morandini et al., 2019), but that also the dynamics of larger populations can be affected via effects on non-breeding floaters. The existing knowledge about density feedbacks on age of first reproduction in a variety of animal species highlights the generality of this process, which means it should also be considered more often to improve the robustness of demographic simulations and projection models (Chaudhary and Oli, 2020).

Population dynamics and conservation status

In the case of the German red kite population, our model allows for the first time to investigate the likely long-term changes in the total population, including a separate consideration of juveniles and non-breeding individuals. This model framework allows a more comprehensive assessment of the conservation status for the species and highlights changes in population size that go unnoticed if only the breeding part of the population is being considered. As such, our results have far-reaching implications for the conservation status of the red kite in Germany, because they suggest a drastic long-term decrease in the number of juveniles and non-breeding individuals in the population. The demographic drivers of this process are, on the one hand, the observed substantial declines in juvenile survival rates and breeding productivity (Katzenberger et al., 2019; Mammen, Stark, and Stubbe, 2017), which are both at least partly connected to decreased...
food availability during the breeding season (Nachtigall, Stubbe, and Hermann, 2010; Pfeiffer, 2000). Declining survival rates are surely also impacted by direct mortality – how different causes contribute to this quantitatively remains, however, currently unclear (Katzenberger et al., 2019). On the other hand, a density-dependent shift towards a younger age of first breeding has likely eroded the non-breeding part of the red kite population over time (Walz, 2005). This continuous shrinkage of floaters, however, is not visible when judged only by the stabilized trend of the breeding population. This also indicates that the capacity to buffer further negative effects, that exists to some degree in a healthy raptor population (Ferrer, Otalora, and García-Ruiz, 2004; Hunt, 1998), could be largely eroded at least in parts of the German red kite population. In a healthy raptor population, the ratio of breeding to non-breeding individuals can be expected as nearly 1:1 (also known as “Moffat's equilibrium”; Hunt, 1998; Newton, 1988); a situation that our model suggests occurred only in the 1980s for the red kite in Germany. This floater-to-breeder ratio can help to assess the health of a raptor population (Penteriani, Ferrer, and Delgado, 2011), while an increased proportion of immature birds recruiting as breeders can act as a warning sign of further population declines (Ferrer et al., 2003). However, these metrics need to be combined with other information to reliably assess population health and to predict the risk of decline (Monzón and Friedenberg, 2018). Another important consideration is that breeding attempts by younger, inexperienced individuals tend to produce less offspring in the red kite (Evans et al., 1999; Pfeiffer, 2009), which could further affect the productivity of the population.

Because formerly marginal breeding populations of the red kite in Europe are increasing, for example, in the UK, in Switzerland and in Sweden, the global conservation status of the species has recently been down listed from “Near Threatened” to “Least Concern” by BirdLife International (BirdLife International, 2020). This assessment is most likely only based on nest counts and the number of breeding pairs in the different European countries of the species’ range – which potentially overlooks demographic changes in population structure and the non-breeding parts of the red kite populations. It was acknowledged in the recategorization process that the documented long-term decline of red kite survival in Germany (Katzenberger et al., 2019) could limit the recovery of the European population (BirdLife International, 2020). However, as we show here, and as also demonstrated by Sergio et al. (2020), a focus on breeding individuals alone fails to account for substantial decreases in the juvenile and non-breeding age classes of the red kite. If this more comprehensive view is taken, and cryptic population declines inferred from demographic data are considered, the major part of the European red kite population in Germany is still decimated well below its numbers from 30 years ago. Since the major threats in the breeding and wintering areas of the species also persist (BirdLife International, 2020), we argue that the European conservation assessment of the red kite should also consider this new information. Generally, our example shows that conservation status assessments for long-lived bird species, with potentially large non-breeding proportions and known floating behaviour, could benefit from including further demographic data and modelling procedures to allow a more comprehensive view on total population size (Lee, Reid, and Beissinger, 2017; Penteriani, Ferrer, and Delgado, 2011; Piper et al., 2020; Tanferna et al., 2013).

**Future research needs**

The density dependence function that we used here to reconstruct red kite population dynamics is based on case studies and empirical data. Yet, the exact functional form of the relationship between age of first reproduction and population density in the red kite remains currently unknown. By including different assumptions about the form of the relationship (exponent 1–8) in our model scenarios, we could show that density most likely has a non-linear effect on age of first breeding. This needs further empirical study to improve demographic simulations and model projections for red kite population studies. Especially the satellite telemetry of juvenile red kites, which allows to determine the exact location and age of first breeding for an individual, promises further insights here. Generally, a better understanding of individual life-history effects on reproduction and survival but also of sex-specific strategies would be needed to further improve the demographic models for the red kite. For example, breeding performance improves in early-life and senescence with age differently for male and female white-tailed eagles *Haliaeetus albicilla* (Murgatroyd et al., 2018), while reproduction of blackrowhawks *Accipiter melanoleucus* shows no increase in early-life but senescence with age for both sexes (Sumasgutner, Koeslag, and Amar, 2019). For the red kite, it remains currently unclear if, or how, breeding performance declines with increasing age. Also, sex-specific strategies in age of first reproduction have received little attention for raptors but they could markedly affect demographic models (Millsap et al., 2019). If such individual life-history effects explain much of the variation in population dynamics, the effect of density-dependent variation in age of first reproduction could be smaller than suggested here.

Our reconstruction of the red kite population in Germany also assumes the dynamics of a single, nation-wide population. Of course, the national red kite population consists in reality of a number of local or regional subpopulations, with differing densities, vital rates and trends. As neither the likely exchange and interplay between these subpopulations nor their vital rates remain currently known, especially not the by far most important parameter adult survival (Sergio et al., 2019), we can only reconstruct a hypothetical large-scale population at the moment. The major data source for estimating local survival rates is individual marking, but with feasible additional efforts field surveys of breeding territories can also elucidate individual identity by non-invasive feather collections (Brune et al., 2019) or survival can even be estimated without individual identification (Oppel et al., 2016; Roth and Amrhein, 2010). Future studies should also aim for a better understanding of emigration and immigration in local red kite populations, which can be achieved by...
combining different data sources in an integrated population model (Pladl et al., 2019; Schaub and Abaci, 2011).

If we consider the simplification to a nation-wide population, the uncertainty about individual life-history effects, as well as the use of time-aggregated survival estimates, our model cannot be expected to fully reproduce the annual variation in population size of the red kite in Germany. Rather, the results should be seen as a long-term reconstruction of key features of the species’ population dynamics. In comparison with the annual changes from index data (Fig. 4), which are imputed to the national scale but likely subject to observation error and site-level effects as well, some temporal mismatch and differences in the magnitude of annual changes need to be expected. We, therefore, focus our results on the relative improvement in prediction error related to the assumption on age of first reproduction when forecasting a time series over several decades.

Finally, when using density-dependent models, the assumed capacity has an influence on the resulting projections. It is currently not clear how to measure a realistic landscape capacity on the local scale; one approach to get an objective estimate of the potential for red kite breeding territories in a landscape could be to apply habitat suitability models, taking into account breeding and feeding habitats, in conjunction with population surveys to account for social attraction and philopatry (Heuck et al., 2013; Katzenberger, 2019).

Conclusions

We could show, based on a review of existing population studies and our simulations, that the age of first reproduction for the red kite most likely responds non-linearly to population density. Such a density feedback, seen in a variety of animal populations, should be considered more often in demographic simulations and PVA studies to further improve the robustness of model projections. For the red kite and other raptors, the existing evidence strongly supports a substantial effect of variation in age of first reproduction on population productivity, but also on the proportion of non-breeding floaters in the total population. This means that judging the conservation status of long-lived raptor populations only by changes in the number of breeding individuals is prone to overlooking substantial changes in the dynamics of floaters and of total population size. For a better understanding of the population dynamics of the red kite and other raptors, we need more empirical research on the age of first reproduction in relation to population density, but also more demographic data on the dispersal and survival of individuals.

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Data Availability Statement

Our results can be fully replicated with the VORTEX software, the input data given in Table S1 and the cited references. The simulation results for the different model scenarios are available under this link: https://doi.org/10.6084/m9.figshare.14207939

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Mean number of red kites in different age groups from 1000 simulations with the model scenario ‘3y’, assuming a fixed age of first reproduction with 3 years.
Table S1. Values used to parameterize the VORTEX population model.