

Juvenile survival of little owls decreases with snow cover

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Abstract

Global environmental changes are predicted to lead to warmer average temperatures and more extreme weather events thereby affecting wildlife population dynamics by altering demographic processes. Extreme weather events can reduce food resources and mortality, but the contribution of such events to demographic processes are poorly understood. Estimates of season-specific survival probabilities are crucial for understanding mechanisms underlying annual mortality. However, only few studies have investigated survival at sufficient temporal resolution to assess the contribution of extreme weather events. Here, we analysed biweekly survival probabilities of 307 radio-tracked juvenile little owls (*Athene noctua*) from fledging to their first breeding attempt in the following spring. Biweekly survival probabilities were lowest during the first weeks after fledging in summer and increased over autumn to winter. The duration of snow cover in winter had a strong negative effect on survival probability, while being well fed during the nestling stage increased survival during the first weeks after fledging and ultimately led to a larger proportion of birds surviving the first year. Overall annual survival probability over the first year varied by 34.3 % between 0.117 (95 % credible interval 0.052 – 0.223) and 0.178 (0.097 – 0.293) depending on the severity of the winter, and up to 0.233 (0.127 – 0.373) for well-fed fledglings. The season with the lowest survival was the post-fledging period (0.508; 0.428 – 0.594) in years with mild winters, and the winter in years with extensive snow cover (0.481; 0.337 – 0.626). We therefore show that extreme weather events reduced the proportion of first-year survivors. Increasingly warmer winters with less snow cover may therefore increase annual survival probability of juvenile little owls in central Europe, but environmental changes reducing food supply during the nestling period can have similarly large effects on annual juvenile survival and therefore the viability of populations.

1 Introduction

Global environmental change is predicted to lead to warmer average temperatures, and more extreme weather events (Stott 2016). If these extreme weather events affect demographic processes, such as the reproduction, survival or dispersal of individuals, environmental changes may contribute directly to wildlife population dynamics (Shriver 2016; Saracco & Rubenstein 2020). In birds, juvenile life stages are often critical to the growth rate of populations (Newton 1989; Robinson et al. 2004; Clark & Martin 2007; Finkelstein et al. 2010), and to understand the consequences of environmental change on populations, we require a better understanding to what extent extreme events affect juvenile survival.

The survival of juvenile birds from fledging to their first reproduction is generally lower than the survival of adults (Maness & Anderson 2013; Naef-Daenzer & Grüebler 2016; Newton et al. 2016). Because juveniles are more susceptible to extreme weather events (Robinson et al. 2007), juvenile survival can vary enormously among years partly due to environmental conditions (Gaillard & Yoccoz 2003; Harris et al. 2007; Souchay et al. 2013).

The period from fledging to first reproduction in young birds includes several distinct life-history stages such as the post-fledging period in the natal home-range, dispersal and migration, wintering, and habitat selection and settlement at the first breeding site. All these different stages involve distinct challenges and therefore may impose differential costs on juvenile survival (Robinson et al. 2004; Ward et al. 2004; Grande et al. 2009; Gruebler et al. 2014a; Buechley et al. 2021). Environmental conditions are known to affect survival during certain life-history stages more than others (Reid et al. 2008; Dybala et al. 2013; Maness & Anderson 2013), and the effects of anthropogenic environmental changes on juvenile survival may therefore differ between the life-history stages of the pre-recruiting phase. To understand which life-history stages are particularly important for population dynamics, and to predict the consequences of environmental changes on populations, the contribution of environmental variation in each life-history stage to pre-reproductive survival must be understood (Robinson et al. 2004; Low & Pärt 2009; Cox et al. 2014; Gruebler et al. 2014a).

The life-history transition of fledging generally results in high mortality as fledged birds need to survive independently in unfamiliar environments (Low & Pärt 2009; Cox et al. 2014; Naef-Daenzer & Gruebler 2016). Following that period, young birds departing from their natal site face two further significant challenges in consecutive life-history stages. First, they move through and explore new, unfamiliar, and potentially inhospitable environments during natal dispersal (Robinson et al. 2004; Bowler & Benton 2005; Low & Pärt 2009; Clobert et al. 2012; Roque et al. 2021; Stillman et al. 2021). Second, they face the reduced availability and accessibility of food, and simultaneously increased thermoregulatory costs during winter (Altwegg et al. 2006; Thorup et al. 2013; Rubáčová et al. 2021). However, whether mortality is mainly associated with the post-fledging and dispersal phases, or with the environmentally challenging period during winter is poorly studied and may vary among species (Dybala et al. 2013; Gruebler et al. 2014a).

Here we examined the first-year survival of little owls (*Athene noctua*) at biweekly temporal resolution to determine season-specific survival probabilities from fledging to the first reproductive attempt. The little owl is a small generalist mesopredator, inhabiting various open landscapes of Europe and Asia (Glue & Scott 1980). Many populations of little owls in central Europe have decreased in recent decades, and harsh winters with extended periods of snow cover have resulted in occasional population collapses (Van Nieuwenhuyse et al. 2023). Demographic analyses have indicated that juvenile survival and immigration are key demographic factors explaining differences in population growth rates (Schaub et al. 2006; Le Gouar et al. 2011). Therefore, it is important to understand the critical bottlenecks in the first year of the little owls' life (Thorup et al. 2013; Tschumi et al. 2019) and to identify the environmental factors affecting survival in different juvenile life-history stages (Thorup et al. 2010; Le Gouar et al. 2011; Perrig et al. 2014). We have previously shown that survival of juvenile little owls was very low just after fledging, varied with fledgling body condition associated with nestling food supply, and increased over the first two months post-fledging (Perrig et al. 2017). However, it is unclear whether the subsequent dispersal and wintering stages impose an equal or different toll on the survival of juvenile little owls, and what effect extreme winter weather events have on the number of little owls surviving the first year.

In this study, we investigated two main hypotheses considering the period between independence and the first breeding season. First, we hypothesized that survival during autumn, when juveniles dispersed from parental territories, would be lower than in winter and the following spring because of the risk of exploring unfamiliar environments. Second, we predicted that survival during winter would be reduced depending on the severity of winter conditions because of limited access to food resources (Altwegg et al. 2006; Le Gouar et al. 2011; Rubáčová et al. 2021). We estimated survival probabilities from the post-fledging period to the first breeding season and could thus identify the most important seasonal bottleneck within the first year of juvenile little owls. This information will be critical to understand the potential future effects of a changing climate on population dynamics of little owls.

2 Methods

2.1 Study population

The study was conducted in southwestern Germany (Landkreis Ludwigsburg, Baden-Württemberg, 48°53'43"N, 9deg11'45"E) in an area of ~700 km² at elevations ranging from 120 to 250 m above sea level. The landscape in the study area is composed of intensively used agricultural fields, meadows, orchards, and vineyards (56%), forests (25%), and urban settlements (17%), containing a high density and diversity of small structural elements and management regimes (Perrig et al. 2014; Fattebert et al. 2018; Fattebert et al. 2019; Hauenstein et al. 2019; Tschumi et al. 2020).

The little owl is a small (160 – 250 g) nocturnal bird breeding in tree cavities and nest boxes in orchards of traditional agricultural landscapes (Van Nieuwenhuysen et al. 2023). Fledglings disperse from their natal territory usually within 65 days after fledging (Perrig et al. 2017; Fattebert et al. 2019). First reproduction normally occurs at the age of one year, following the initial dispersal from the natal territory, and a stationary period during winter (Exo 1992; Hauenstein et al. 2019). Survival of adults and the quality of fledged offspring are strongly linked to habitat quality and food availability (Schaub et al. 2006; Thorup et al. 2010; Perrig et al. 2014; Michel et al. 2022).

2.2 Monitoring survival

From 2009 to 2011, 93 broods were closely monitored from egg laying until fledging by conducting regular brood controls and using camera traps (Perrig et al. 2014; Perrig et al. 2017). Prior to fledging, at an average age of 28.7 days (+/- 2.93 standard deviation), all 307 chicks of these broods were tagged with VHF radio transmitters (Naef-Daenzer et al. 2005) using backpack harnesses. The total tag mass (including harness) was 6.9 – 7.2 g (3-5% of the birds' body mass), the expected life span of the battery was 400 days and the detection range of the VHF signals was up to 40 km (for details see Perrig et al. 2017).

We used hand-held antennas to locate all individuals at least three times per week throughout the study period from May 2009 until May 2012, except during four two-week intervals in winter 2009 and early spring 2010 when no radio-tracking could be carried out. In an additional six two-week intervals (mid-winter 2009 and late winter 2010) the tracking effort was reduced, and individuals were located less than three times per week.

2.3 Temporal, individual, and environmental variables affecting survival

To quantify seasonal variation in survival, we defined four discrete seasons by date that correspond to differences in environmental conditions and the typical behaviour of juvenile birds: (1) summer (15 May until 1 August): the post-fledging phase after juveniles first leave the nest (previously analysed in Perrig et al. 2017); (2) autumn (2 August – 23 October): the dispersal period when individuals permanently depart from their natal territory, and environmental conditions change to shorter days and cooler temperatures; (3) winter (24 October – 12 March): the period when birds establish and occupy a winter home-range, and endure occasionally cold winter weather during which food can become inaccessible; (4) spring (13 March – 15 June): the first breeding period when birds acquire and occupy the first territory and breed during gradually warming weather with longer day lengths. Note that our season definition includes a deliberate overlap of 4 weeks between subsequent years to accommodate the staggered fledging date of juveniles and staggered onset of first reproduction.

Besides temporal variation, survival may also differ by age, sex, and body mass (Le Gouar et al. 2011; Tschumi et al. 2019). We therefore measured body mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm) at the day of tagging, and corrected these measurements for the age of the bird at the time of measurement (Perrig et al. 2014). We specified the age of juveniles in days based on standard pictures and the known fledging date (Perrig et al. 2017). In addition, feather samples were obtained for genetic sex determination of the nestlings (Tschumi et al. 2019). In 2010 and 2011 roughly half of the monitored broods were provided with supplementary food during the nestling stage (Perrig et al. 2017), and we recorded whether individuals had benefitted from supplementary feeding or not.

To investigate the effect of winter conditions on survival probabilities, we extracted daily snow depths from the weather station Sachsenheim (Germany, station ID: 04349, downloaded from:

https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/daily/kl/historical/, accessed 16 Oct 2023). Snow depth is known to limit owl's access to food and is therefore a primary indicator for winter harshness and food availability that would influence survival (Altwegg et al. 2006; Le Gouar et al. 2011; Thorup et al. 2013). We calculated the number of days with a snow cover [?] 1 cm for each two-week encounter occasion.

2.4 Estimating survival probabilities

Radio-tracking data were aggregated into encounter histories of biweekly intervals. The encounter histories were used in a Cormack–Jolly–Seber (CJS) mark–recapture model estimating biweekly survival while controlling for variation in detection probability and individual variability (Lebreton et al. 1992; Kéry & Schaub 2012).

Because our key interest was to quantify seasonal differences in survival, our survival model included a fixed intercept for each of the four seasons (summer, autumn, winter, spring), as well as fixed effects to account for the mass and sex of each fledgling (Tschumi et al. 2019), and whether the fledglings came from broods that were provided with supplementary food (Perrig et al. 2017). We also included a fixed effect that explored whether duration of snow cover could explain variation in survival. Because body mass and size were highly correlated, and the variables age and body size did not affect survival in preliminary explorations, we retained the most parsimonious combination of variables (Hooten & Hobbs 2015), and neither age nor size were retained in our survival model. We fitted three models to include the variables body mass and supplementary feeding in three alternative model formulations: either by affecting survival only in the immediate post-fledging period (Perrig et al. 2017), or by allowing body mass and supplementary feeding to affect survival in every season over the first year of life (Catitti et al. 2022; Nageli et al. 2022; Mainwaring et al. 2023).

To estimate detection probability, we included temporal variation in tracking effort as an explanatory variable due to the unequal tracking efforts across years and tracking periods. We specified that detection probability was zero during four intervals when no tracking effort occurred. For the remaining intervals we estimated two distinct detection probabilities, one for those six biweekly periods with reduced effort in winter 2009 and 2010, and another for the remaining 80 periods with full tracking effort. We also included a random individual effect to account for residual variability in detection probability among individuals. Because severe winter weather may not only affect survival, but may also lead to temporary escape movements to more benign areas (Sonerud 1986; Mysterud 2016; Gura 2023), we included the same snow cover variable that we assumed to affect survival also for detection probability to account for possible temporary emigration and low detection probability during severe winter weather.

We used a Bayesian approach for inference to include existing prior information on the survival probability of little owls (Schaub et al. 2006; Le Gouar et al. 2011; Thorup et al. 2013). We fit the models in software JAGS v. 3.3. (Plummer 2012) called from R 4.1.3 (R Core Team 2023) via the ‘runjags’ library (Denwood 2016). We used a mildly informative prior for the biweekly survival probability (beta distribution with $\alpha = 95$ and $\beta = 10$) given previous information on little owl survival (Le Gouar et al. 2011; Thorup et al. 2013), and a similarly informative prior for the detection probabilities during occasions with normal (random uniform 0.7 – 1) and reduced effort (random uniform 0.3 – 0.9). We used vague normally distributed priors for all other parameters, and conducted a prior sensibility test to ensure that biologically plausible survival estimates resulted from our prior distributions (Banner et al. 2020). We ran three Markov chains for 3,500 iterations each, discarded the first 200 iterations and used every sixth iteration for inference. Convergence of the three chains for all monitored parameters was visually inspected using trace plots and tested using the Gelman–Rubin diagnostic (Brooks & Gelman 1998) to confirm that all parameters had an R-hat of < 1.02 . We implemented posterior predictive checks to assess the goodness-of-fit of the survival model (Gelman et al. 1996; Kéry & Schaub 2012; Conn et al. 2018), and confirmed that there was no evidence for a lack of fit (Bayesian p-value = 0.427). Code to replicate these analyses can be found at <https://github.com/Vogelwarte/LittleOwlSurvival> and in the Supplementary Material.

We present median parameter estimates (β) for covariates on the logit scale with 95% credible intervals. We also present posterior estimates of biweekly survival probability with 95% credible intervals for each of the four seasons based on birds of average body mass that did not receive supplementary food as nestlings. To facilitate interpretation and comparison with other survival estimates, we calculated season-specific survival by raising biweekly survival to the power of the length of each season (summer: 4 periods, autumn: 6 periods, winter: 10 periods, spring: 6 periods). To predict survival in severe winters, we used the maximum length of intense snow cover periods during our study to decompose the 10 winter periods into 2 periods with extreme snow cover, 3 periods each with high and intermediate snow cover, and 2 periods without snow cover (resulting in 43% of 140 winter days experiencing snow cover), and we multiplied the respective survival probabilities to estimate overwinter survival. To estimate annual survival, we multiplied the four seasonal survival probabilities, which represents the annual survival probability from 1 July to 30 June of the following year. To visualise what proportion of juveniles survived over the first year of life, we simulated the proportion of 100 juveniles of average body mass that survived 26 fortnightly periods from one summer to the next by multiplying the number of live birds by the fortnight-specific survival probability. We present this proportion for four scenarios, namely for birds that did and did not receive supplementary food as nestlings during either a mild or a harsh winter.

3 Results

Of the 307 individuals that left their nest, 46 (15%) survived to the end of the brood-rearing stage in the following year. Our survival model estimated that biweekly survival was lowest in the summer post-fledging season (0.844; 0.809 – 0.878), and substantially higher in autumn (0.936; 0.916 – 0.953), snow-free winter (0.970; 0.954 – 0.981), and the following spring (0.945; 0.921 – 0.964; Fig. 1) seasons. Accounting for the different duration of the seasons, the overall survival was lowest for the summer post-fledging season despite its short duration (0.508), with the autumn dispersal seasons (0.673) having marginally lower survival than mild snow-free winters (0.734) and the following springs (0.712; Table 1).

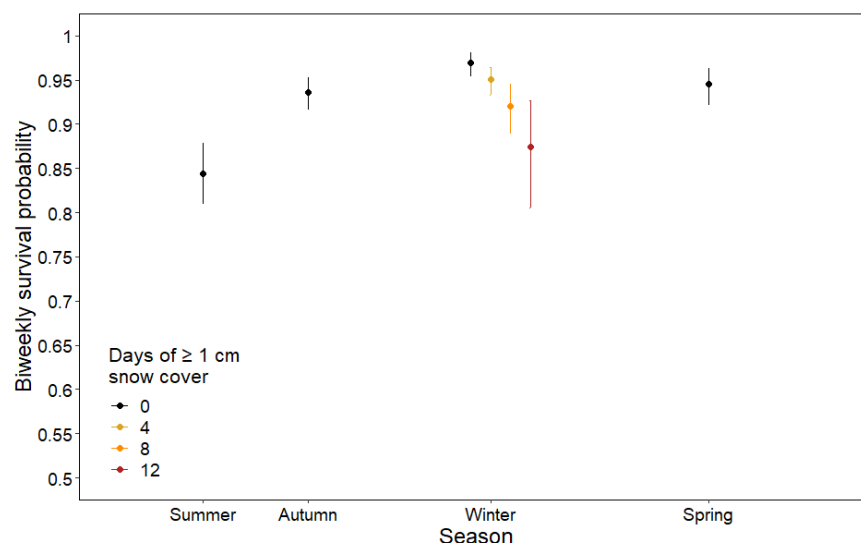


Fig. 1. Estimated median survival probabilities of juvenile little owls of average body mass during the four seasons across their first year of life. Survival probability is scaled to biweekly encounter occasions, and therefore comparable across seasons despite the different duration of each season. Error bars represent 95% credible intervals.

Biweekly survival decreased strongly with an increasing duration of snow cover ($\beta = -0.389$; 95% credible interval -0.571 – -0.201; Fig. 1, Fig. S1). By contrast, we found only a weak negative effect of snow cover

on detection probability ($\beta = -0.229; -0.468 \text{ } 0.022$; Fig. S1), and detection probability was very high (in periods with normal effort: $0.994; 0.989 \text{ } 0.996$; in periods with reduced effort: $0.803; 0.625 \text{ } 0.892$). In winters with extreme snow cover, biweekly survival decreased from 0.971 to 0.879 (Fig. 1), and the survival over an entire harsh winter season was therefore even lower than during the post-fledging summer (0.481; Table 1). In total, the annual survival probability of little owls during their first year of life ranged from 0.117 to 0.178 depending on the severity of the winter (Table 1). Thus, in years with long periods of snow cover, the winter period reduced first-year survival by 34.3% compared to a snow-free winter (Fig. 2).

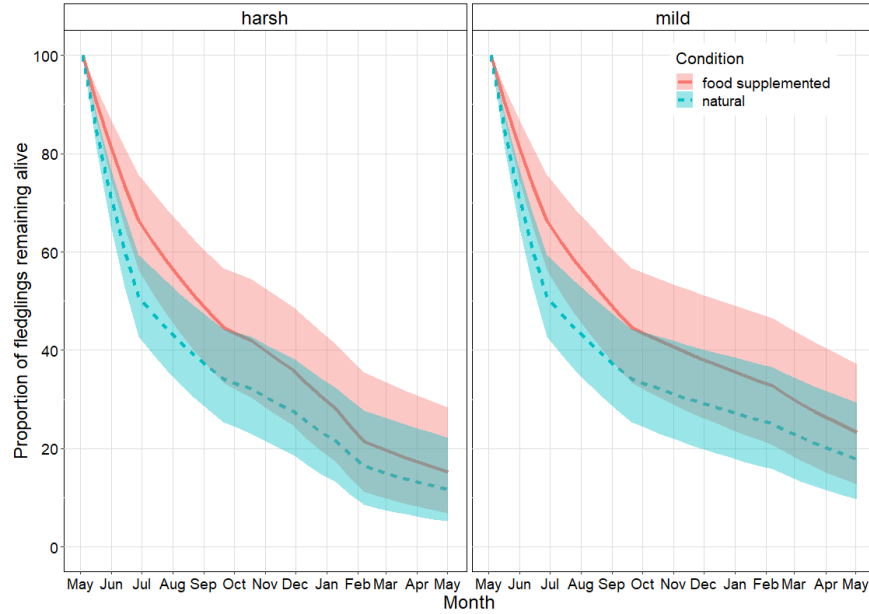


Fig. 2. Estimated median proportion (and 95% confidence intervals) of juvenile little owls surviving from fledging in May until the first breeding season in the following year depending on the harshness of winter (left panel: harsh winter with 60 days of snow cover, right panel: mild winter with no snow cover), and whether they received supplementary feeding as nestlings (blue: unfed natural nestlings; red: nestlings provided with supplementary food).

Besides the effect of snow cover, we also found evidence that survival increased with body mass ($\beta = 0.480; 0.290 \text{ } 0.670$), and with supplementary food provided to nestlings ($\beta = 0.345; -0.073 \text{ } 0.758$). Survival was only marginally higher for males than for females ($\beta = 0.153; -0.256 \text{ } 0.521$; Fig. S1). We found that the effects of body mass (Fig. S2) and food supplementation (Fig. S3) on survival only occurred during the post-fledging period, but not later in the first year of juvenile little owls. However, those differences resulted in a 23.5% lower proportion of juveniles surviving the first year depending on whether nestlings had received supplementary food (annual survival 0.233; $0.127 \text{ } 0.373$) or not, solely due to the difference in post-fledging survival (Fig. 2). Out of all the juveniles that died during the first year, the greatest proportion (39.7% – 59.9%) perished during the post-fledging period, while even harsh winters accounted for only 11.1% – 27.3% of annual mortality (Table 2). Extrapolated seasonal survival estimates for birds of specific mass, sex, and feeding status are provided in Table S1.

Table 1. Estimated survival probabilities of juvenile little owls of average body mass in southwestern Germany during the four seasons of their first year, and cumulative annual survival. Mild winter refers to winters without snow cover, harsh winter refers to 60 winter days experiencing snow cover of $[?] \text{ } 1 \text{ cm}$.

Season	Duration (weeks)	Survival probability (mild winter)	Survival probability (harsh winter)
Summer	8	0.508 (0.428 - 0.594)	0.508 (0.428 - 0.594)
Autumn	12	0.673 (0.592 - 0.748)	0.673 (0.592 - 0.748)
Winter	20	0.734 (0.624 - 0.823)	0.481 (0.337 - 0.626)
Spring	12	0.712 (0.611 - 0.801)	0.712 (0.611 - 0.801)
Annual Survival	52	0.178 (0.097 - 0.293)	0.117 (0.052 - 0.223)

Table 2. Seasonal contribution to the overall annual mortality over the first year of life of little owls. Numbers represent the proportion of juveniles that died in a given season out of all birds that died during the first year for mild and harsh winters and for birds that received supplementary food as nestlings or not. Mild winter refers to winters without snow cover, harsh winter refers to 60 winter days experiencing snow cover of [?] 1 cm.

Season	natural	natural	supplementary fed	supplementary fed
	mild winter	harsh winter	mild winter	harsh winter
Summer	59.9	55.7	43.9	39.7
Autumn	20.2	18.8	28.3	25.6
Winter	11.1	20.1	15.5	27.3
Spring	8.8	5.4	12.3	7.3

4 Discussion

We show that winter survival in juvenile little owls was highly dependent on the number of days with snow cover, but that annual survival in years with mild winters was characterized by remarkably equal survival probabilities throughout seasons once individuals had survived the first weeks after fledging. Overall, only a fifth of juvenile little owls survived to the age of one year, and harsh winters with extended periods of snow cover reduced annual survival probability by > 30%. However, the most important mortality bottleneck was the month after fledging, which accounted for 40-60% of the total first year mortality. Supplementary food provided to nestlings increased annual survival by 23.5% due to its beneficial effect on post-fledging survival. A changing climate and food supply during the nestling stage may therefore have similarly large effects on the survival of juvenile little owls during their first year of life.

Our results are consistent with previous findings that harsh winters affect survival of little owls (Le Gouar et al. 2011; Thorup et al. 2013; Michel 2016), but our study was able to disentangle mortality during the post-fledging period in summer, during dispersal in autumn, and in winter. We show that winters with constant snow cover over two months result in less than half of juveniles surviving a winter (Table 1). Snow cover and frosty conditions are widely known to prevent owls and other resident bird species from accessing food, thus leading to reduced body condition and increased foraging efforts, which ultimately result in increased mortality rates (Sonerud 1986; Kostrzewa & Kostrzewa 1991; Altwegg et al. 2006; Riegert & Fuchs 2011; Naef-Daenzer & Gruebler 2016). Young owls may also become more vulnerable to predators when they struggle to find suitable shelters and suffer from excessive thermoregulation costs (Bock et al. 2013; Gruebler et al. 2014b; Naef-Daenzer & Gruebler 2016). As juvenile survival represents a key factor in little owl population dynamics (Schaub et al. 2006; Le Gouar et al. 2011), our results suggest strong population effects of extended periods of snow cover in this species, which is consistent with past evidence of population collapses after harsh winters from the last century (summarized in Van Nieuwenhuyse et al. 2023).

We found that survival increased for food supplemented and for heavier birds, but these effects occurred only in the post-fledging period and were not detectable in subsequent seasons. A previous study revealed that early-life effects associated with nestling food supplementation affected departure decisions from the

parental home-range, but not movement decisions during natal dispersal after departure (Fattebert et al. 2019). Similarly, early-life conditions affected survival primarily during the post-fledging period, but not afterwards, and we speculate that the selection imposed by early post-fledging mortality reduces the influence of early-life conditions at later stages in life (Sergio et al. 2014; Sergio et al. 2019). Nonetheless, given the magnitude of the difference in survival between food-supplemented and un-supplemented (natural) little owl fledglings during the post-fledging period, 23.5% more food-supplemented fledglings survived the first year (Fig. 2). Thus, favourable natal conditions in our study species may affect population level processes mainly by non-random selection of juveniles in the nestling and post-fledging period, with an effect of similar magnitude as that imposed by harsh winters.

Increased predation risk of inexperienced birds is widely known as a main factor for lower juvenile than adult survival probability during the first year of life in general (Clutton-Brock et al. 1985; Sunde 2005; Maness & Anderson 2013; Naef-Daenzer & Gruebler 2016), and in little owls in particular (Naef-Daenzer et al. 2017; Šálek et al. 2019). Juvenile predation rate is often further increased under poor food conditions (Rohner & Hunter 1996; Coles & Petty 1997) and when juveniles explore unknown areas (Bélichon et al. 1996; Lima 1998; Yoder et al. 2004). Elevated costs during natal dispersal have led to the theory that the dispersal stage is a bottleneck with respect to survival and evolutionary ecology (Bowler & Benton 2005; Benard & McCauley 2008; Bartoń et al. 2012; Bonte et al. 2012; Hardouin et al. 2012; Väli et al. 2021). Our results show that in little owls the survival during the autumn dispersal season was not noticeably reduced. However, because we focused on a fixed temporal definition of the autumnal dispersal season, we were not able to investigate survival during the actual dispersal movement of individuals. Main natal dispersal movements are generally of short duration in little owls (median = 10 days; Fattebert et al. 2019). Mortality might be considerably increased during the few days of active dispersal without affecting our overall survival probability of the season. More detailed investigations of survival in relation to individual movements may reveal more nuanced patterns in survival probability and will illuminate the costs of dispersal in little owls (Yoder et al. 2004). Nestling food supply and its effects on post-fledging survival may therefore be a more important factor for juvenile survival and the growth rate of populations than the dispersal or wintering stages (Low & Pärt 2009; Cox et al. 2014; Gruebler et al. 2014a; Naef-Daenzer & Gruebler 2016; Martin et al. 2018).

We found only a relatively small and uncertain effect of increased snow cover on detection probability, which was generally very high in our study. Thus, while some temporary emigration is possible and accounted for by our model, we can be confident that our estimate of lower survival in harsh winters is not affected by little owls temporarily leaving the study area during periods with extensive snow cover. We cannot exclude the possibility that little owls performed permanent escape movements that have been recorded in other owl species during severe winter conditions (Sonerud 1986; Myrsetrud 2016; Gura 2023), because permanent emigration out of the monitored area and mortality are confounded in our data set. However, permanent emigration would be most likely during the autumn dispersal phase (Hauenstein et al. 2019; Van Nieuwenhuyse et al. 2023), but we did not find a reduction in apparent survival during this season with the highest mobility of juveniles. We therefore suggest that permanent emigration likely only accounts for a small proportion of the estimated mortality.

In summary, the survival of little owls during the first year can be characterized by two bottlenecks, differing in the underlying mechanisms. Juveniles first encounter a survival bottleneck in summer immediately after fledging from the nest, and another bottleneck in winter if environmental conditions reduce the accessibility of food. Contrary to the general hypothesis of elevated costs during natal dispersal, our results indicate that the autumn dispersal season in little owls is not more hazardous than other seasons during the first year of life. Increasingly warmer winters with less snow cover, which are expected under climate change, will therefore likely have beneficial effects on the juvenile survival probability and thus, on population dynamics of little owls.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available in GitHub (<https://github.com/naefdaenzer/little-owl>)

[ps://doi.org/10.5281/zenodo.10714914](https://doi.org/10.5281/zenodo.10714914)).

AUTHOR CONTRIBUTIONS

Marco Perrig: Conceptualization (Equal)

Data curation (Equal)

Formal analysis (Lead)

Methodology (Lead)

Software (Equal)

Writing – original draft (Lead)

Writing – review & editing (Equal)

Steffen Oppel: Formal analysis (Equal)

Writing – review & editing (Equal)

Matthias Tschumi: Data curation (Equal)

Investigation (Equal)

Project administration (Equal)

Writing – review & editing (Equal)

Herbert Keil: Conceptualization (Equal)

Funding acquisition (Supporting)

Investigation (Equal)

Methodology (Supporting)

Project administration (Equal)

Validation (Equal)

Writing – review & editing (Supporting)

Beat Naef-Daenzer: Conceptualization (Lead)

Funding acquisition (Equal)

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Resources (Equal)

Supervision (Lead)

Writing – original draft (Equal)

Writing – review & editing (Equal)

Martin U. Gruebler: Conceptualization (Equal)

Formal analysis (Supporting)

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Investigation (Equal)

Methodology (Equal)

Project administration (Equal)

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Supervision (Equal)

Writing – original draft (Equal)

Writing – review & editing (Equal)

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

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Supplementary Material

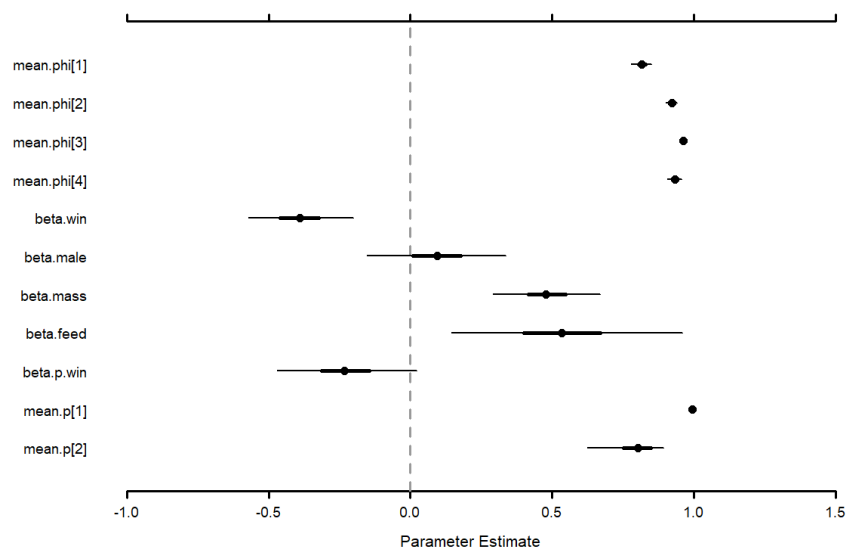


Fig. S1: Parameter estimates of the Cormack-Jolly-Seber model estimating biweekly survival and detection probability of radio-tracked little owls in Germany between 2009 – 2011. Mean.phi are survival probability intercepts for summer [1], autumn [2], winter [3], and spring [4], mean.p are detection probability intercepts for periods with full effort [1] and reduced effort [2], and 'beta' are parameter estimates for the linear predictors of winter snow cover (win), sex (male), body mass (mass), and supplementary feeding during the nestling phase (feed) on survival probability, and for the linear predictor of winter snow cover on detection probability (p.win).

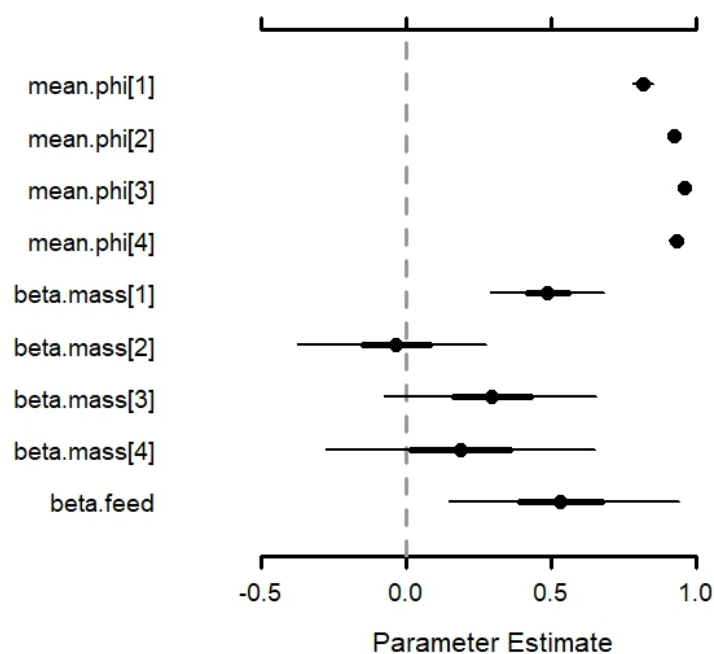


Fig. S2: Parameter estimates of a Cormack-Jolly-Seber model estimating biweekly survival and detection probability of radio-tracked little owls in Germany between 2009 – 2011, assuming that body mass affected survival in all seasons. Mean.phi are survival probability intercepts for summer [1], autumn [2], winter [3], and spring [4], and 'beta' are parameter estimates for the linear predictors of body mass (mass, for summer [1], autumn [2], winter [3], and spring [4]), and supplementary feeding during the nestling phase (feed) on survival probability.

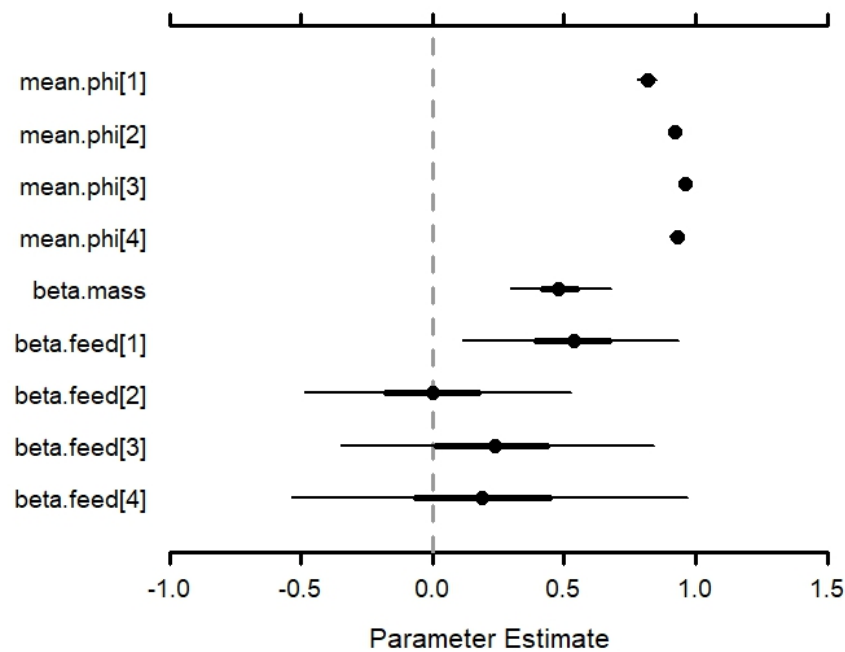


Fig. S3: Parameter estimates of a Cormack-Jolly-Seber model estimating biweekly survival and detection probability of radio-tracked little owls in Germany between 2009 – 2011, assuming that supplementary feeding affected survival in all seasons. Mean.phi are survival probability intercepts for summer [1], autumn [2], winter [3], and spring [4], and ‘beta’ are parameter estimates for the linear predictors of body mass (mass), and supplementary feeding during the nestling phase (feed, , for summer [1], autumn [2], winter [3], and spring [4]) on survival probability.

Table S1: Seasonal survival probabilities of radio-tracked little owls in Germany given as the median and 95% credible interval of survival estimates derived from a Cormack-Jolly-Seber model. Because the model accounted for sex, size, winter severity and supplementary feeding, survival estimates are provided for all possible parameter combinations. Food supplementation was provided during the chick-rearing period only, for details see (Perrig et al. 2017)

Food Suppl.	Sex	Mass	Season	Survival probability (mild winter)	Survival probability (harsh winter)
No	Female	light	Summer	0.196 (0.109 - 0.317)	0.196 (0.109 - 0.317)
No	Female	light	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
No	Female	light	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
No	Female	light	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)
No	Female	average	Summer	0.494 (0.421 - 0.567)	0.494 (0.421 - 0.567)
No	Female	average	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
No	Female	average	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
No	Female	average	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)
No	Female	heavy	Summer	0.752 (0.636 - 0.838)	0.752 (0.636 - 0.838)
No	Female	heavy	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
No	Female	heavy	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
No	Female	heavy	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)

Food Suppl.	Sex	Mass	Season	Survival probability (mild winter)	Survival probability (harsh winter)
No	Male	light	Summer	0.222 (0.122 - 0.345)	0.222 (0.122 - 0.345)
No	Male	light	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
No	Male	light	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
No	Male	light	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)
No	Male	average	Summer	0.523 (0.444 - 0.605)	0.523 (0.444 - 0.605)
No	Male	average	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
No	Male	average	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
No	Male	average	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)
No	Male	heavy	Summer	0.771 (0.652 - 0.858)	0.771 (0.652 - 0.858)
No	Male	heavy	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
No	Male	heavy	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
No	Male	heavy	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)
Yes	Female	light	Summer	0.355 (0.192 - 0.544)	0.355 (0.192 - 0.544)
Yes	Female	light	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
Yes	Female	light	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
Yes	Female	light	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)
Yes	Female	average	Summer	0.652 (0.554 - 0.742)	0.652 (0.554 - 0.742)
Yes	Female	average	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
Yes	Female	average	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
Yes	Female	average	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)
Yes	Female	heavy	Summer	0.845 (0.767 - 0.901)	0.845 (0.767 - 0.901)
Yes	Female	heavy	Autumn	0.661 (0.586 - 0.732)	0.661 (0.586 - 0.732)
Yes	Female	heavy	Winter	0.723 (0.615 - 0.812)	0.465 (0.324 - 0.608)
Yes	Female	heavy	Spring	0.701 (0.601 - 0.789)	0.701 (0.601 - 0.789)
Yes	Male	light	Summer	0.387 (0.214 - 0.568)	0.387 (0.214 - 0.568)
Yes	Male	light	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
Yes	Male	light	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
Yes	Male	light	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)
Yes	Male	average	Summer	0.676 (0.579 - 0.766)	0.676 (0.579 - 0.766)
Yes	Male	average	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
Yes	Male	average	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
Yes	Male	average	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)
Yes	Male	heavy	Summer	0.857 (0.781 - 0.912)	0.857 (0.781 - 0.912)
Yes	Male	heavy	Autumn	0.684 (0.604 - 0.757)	0.684 (0.604 - 0.757)
Yes	Male	heavy	Winter	0.743 (0.638 - 0.829)	0.497 (0.354 - 0.636)
Yes	Male	heavy	Spring	0.723 (0.623 - 0.808)	0.723 (0.623 - 0.808)

Code S1: JAGS model code for the Cormack-Jolly-Seber model estimating biweekly survival and resighting frequency of radio-tracked little owls in Germany between 2009 – 2011. Data and R code to run this model are available at <https://github.com/Vogelwarte/LittleOwlSurvival>

```

model {
# Priors and constraints
for (i in 1:nind){
for (t in f[i]:(n.occasions)){
logit(phi[i,t]) <- mu[season[t]] +
beta.mass*weight[i]*pf[t] +

```

```

beta.feed*feeding[i]*pf[t] +
beta.win*env[year[i],t] +
beta.male*sex[i]
logit(p[i,t]) <- mu.p[recap.mat[i,t]] + beta.p.win*env[year[i],t] + epsilon.p[i]
} #t
} #i
for (i in 1:nind){
epsilon.p[i] ~ dnorm(0, tau.p)
}
for (s in 1:4){ ### baseline for the 4 seasons summer, autumn, winter, spring
mean.phi[s] ~ dbeta(95, 10) # Prior for mean biweekly survival from Thorup et al. 2013, converted to beta
mu[s] <- log(mean.phi[s] / (1-mean.phi[s])) # Logit transformation
}
mean.p[1] ~ dunif(0.7, 1) # Prior for mean recapture during full effort periods
mean.p[2] ~ dunif(0.3, 0.9) # Prior for mean recapture during reduced effort periods
for (y in 1:2) {
mu.p[y] <- log(mean.p[y] / (1-mean.p[y])) # Logit transformation
}
mu.p[3] <- -999999999999999999 # recapture probability of zero on logit scale
sigma.p ~ dunif(0, 2) # Prior for standard deviation for random detection effect
tau.p <- pow(sigma.p, -2)
beta.mass ~ dnorm(0, 1) # Prior for mass effect
beta.male ~ dnorm(0, 1) # Prior for sex effect (for males, females are 0)
beta.win ~ dunif(-2, 2) # Prior for winter weather effect, which we know is negative
beta.p.win ~ dnorm(0, 1) # Prior for winter weather DETECTION effect
beta.feed ~ dnorm(0, 1) # Prior for effect of supplementary feeding
# Likelihood
for (i in 1:nind){
# Define latent state at first capture
z[i,f[i]] <- 1
z.rep[i,f[i]] <- 1 # replicate z (true state)
y.rep[i,f[i]] <- 1 # replicate y (data)
for (t in (f[i]+1):n.occasions){
# State process

```

```

z[i,t] ~ dbern(phi[i,t-1] * z[i,t-1])
z.rep[i,t] ~ dbern(phi[i,t-1] * z.rep[i,t-1]) # replicate z (true state)
# Observation process
y[i,t] ~ dbern(p[i,t] * z[i,t])
y.rep[i,t] ~ dbern(p[i,t] * z.rep[i,t]) # replicate y (observations)
} #t end
#Derived parameters
## GOODNESS OF FIT TEST SECTION
## Discrepancy observed data
E.obs[i] <- pow((sum(y[i,(f[i]+1):n.occasions]) - sum(p[i,(f[i]+1):(n.occasions)] * z[i,(f[i]+1):n.occasions])), 2)
/ (sum(p[i,(f[i]+1):n.occasions] * z[i,(f[i]+1):n.occasions]) + 0.001)
## Discrepancy replicated data
E.rep[i] <- pow((sum(y.rep[i,(f[i]+1):n.occasions]) - sum(p[i,(f[i]+1):(n.occasions)] * z.rep[i,(f[i]+1):n.occasions])), 2) / (sum(p[i,(f[i]+1):(n.occasions)] * z.rep[i,(f[i]+1):n.occasions]) + 0.001)
} #i end
fit <- sum(E.obs[])
fit.rep <- sum(E.rep[])
}

```