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Demographic effects of extreme winter weather in the barn owl

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Abstract Extreme weather events can lead to immediate catastrophic mortality. Due to their rare occurrence, however, the long-term impacts of such events for ecological processes are unclear. We examined the effect of extreme winters on barn owl (*Tyto alba*) survival and reproduction in Switzerland over a 68-year period (~20 generations). This long-term data set allowed us to compare events that occurred only once in several decades to more frequent events. Winter harshness explained 17 and 49% of the variance in juvenile and adult survival, respectively, and the two harshest winters were associated with major population crashes caused by simultaneous low juvenile and adult survival. These two winters increased the correlation between juvenile and adult survival from 0.63 to 0.69. Overall, survival decreased non-linearly with increasing winter harshness in adults, and linearly in juveniles. In contrast, brood size was not related to the harshness of the preceding winter. Our results thus reveal complex interactions between climate and demography. The relationship between weather and survival observed during regular years is likely to underestimate the importance of climate variation for population dynamics.

Keywords Catastrophes · Climate change · Climate variability · Matrix population model · Population dynamics

Introduction

The effect of extreme weather events on ecological processes has recently become a central concern in climate change research, because organisms are now more frequently exposed to weather events that they used to experience only rarely in the past (Easterling et al. 2000; Parmesan et al. 2000; Stenseth et al. 2002). Extreme weather events can lead to high immediate mortality (e.g. Tompa 1971; Garel et al. 2004), but it is currently unknown whether they affect ecological processes in similar ways to regular environmental variation or have a qualitatively different impact.

Environmental variation affects population dynamics through its effect on survival and reproduction. However, not all life stages are equally important for population dynamics (Crouse et al. 1987; Caswell 2001). The effect of weather on population dynamics thus depends on which life stage is affected, and on whether several life stages are affected at the same time. Any factor that affects several life stages in similar ways will cause positive correlations between the associated fitness components at the population level, thereby increasing the variability in population dynamics and decreasing the expected time to extinction (Lande et al. 2003). Factors that only affect one life stage tend to decrease correlations between fitness components at the population level and thus lead to more stable population dynamics.

Recent studies show that vertebrate population dynamics are strongly influenced by weather, and that different age groups within the same population are susceptible to different weather patterns (Sæther et al. 2000; Coulson et al. 2001; Clutton-Brock and Coulson 2002; Altwegg et al. 2005). In this case, the effect of climate on overall population dynamics is dampened by demography. In contrast, extreme events may affect all

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individuals regardless of their age and condition, and, in such situations, the dampening effect of demography breaks down.

The observed variance in biological time series generally increases with the length of the study, partly because longer studies are more likely to encompass extreme events (Pimm and Redfearn 1988). Since populations of more variable size face a higher extinction risk (Lande and Orzack 1988; Dennis et al. 1991; Foley 1994), population viability analyses obtained from short-term studies tend to be too optimistic about the fate of the population in question (Reed et al. 2003). Just how long studies need to be to reliably estimate variability in demographic rates is not known because long-term demographic data are particularly sparse (but see Franklin et al. 2002).

Here, we present an unusually long time series of detailed demographic data for barn owls (*Tyto alba*) ringed over most of their breeding range in Switzerland between 1934 and 2001. Earlier studies indicated that winters with long-lasting snow cover decrease barn owl survival (Altwegg et al. 2003), and catastrophic reductions in population size have been observed after extremely harsh winters (Sauter 1956; Güttinger 1965). We ranked the years of our study according to the duration of snow cover during the winter. Then, we examined the effects of the 1, 2, 5, 10, and 20 most extreme years on demographic rates and their temporal variance. The generation time of barn owls in western Switzerland was 3.6 years (calculated following Lande et al. 2003, and using survival estimates from Altwegg et al. 2003), and the most extreme year is thus an event that occurred once in 19 generations. On the other hand, barn owls experienced years of the harshness of the ten most extreme years every second generation.

Materials and methods

Data collection

Between 1934 and 2001, 23,010 barn owls were ringed in Switzerland over an area of ca. 9,500 km². For some of the birds that were encountered again we lacked exact information on the date of death (e.g. if only the ring was found) or the finder did not report the fate of the encountered individual. After excluding these doubtful cases, we were left with 22,709 individuals (21,099 ringed as nestlings and 1,610 ringed as adults). Of these, 3,311 (2,864 and 567, respectively) were later re-encountered at least once (1,420 live recaptures in total and 2,869 dead recoveries). We included data on re-encountered individuals collected until the end of February 2002.

Survival analysis

We used combined live-recapture and dead-recovery models. These models allow estimation of survival while

accounting for the fact that not every surviving bird was recaptured, and not every dead bird was recovered (Burnham 1993). We refer to recapture rate as the probability of capturing and subsequently releasing a previously ringed live individual at time t , given that it is alive at this time, whereas the recovery rate is the probability of a ringed individual being found and reported dead. Survival cannot reliably be estimated if only recovery data of individuals ringed as juveniles are available (Anderson et al. 1985). However, we had enough data on birds ringed as adults and subsequent live recaptures to estimate survival for each year except 1934, 1938 and from 1940 to 1945. We can only report mean values for those years. In an earlier study, we reported survival rates for the Payerne region in western Switzerland from 1990 to 2001 (Altwegg et al. 2003). Here, we used the same statistical procedures as in our earlier study, and our starting models accounted for the factors found to be important in this earlier study. These factors were independent time variability in juvenile and adult survival rates, constant recapture rate, and independently time-variable recovery rates in juveniles and adults. In addition, the models used in the current study accounted for the anticipated lower recapture rate outside the area and time span of our earlier intensive study in the Payerne region. We did not have enough data to examine full time variability in the recapture rate. However, the recaptures in relation to releases were evenly distributed over the years, and assuming a constant recapture rate thus seems justified.

Our modelling approach assumes that each individual marked at time t has the same probability of surviving to time $t+1$, and that the individuals are identical in their probability of being recaptured or recovered dead on a particular occasion (Brownie et al. 1985; Lebreton et al. 1992). Even though our earlier spatially restricted study found good agreement of our data with these assumptions (Altwegg et al. 2003), we expected some deviation due to potential spatial heterogeneity in our present analysis. We estimated the fit of our most general model (described in the previous paragraph) using the bootstrap goodness-of-fit test provided by program MARK 4.2 (White and Burnham 1999). Based on 100 simulations, this test suggested moderate overdispersion (mean and range of deviance 1,909.55; 1,670.26–2,110.07; observed deviance 2,683.19). Such overdispersion does not affect the maximum likelihood estimates of the survival, recapture and recovery rates, but leads to an underestimation of their confidence intervals (Burnham et al. 1987), which we corrected by multiplying the variance-covariance matrix for the parameter estimates by an overdispersion factor $\hat{c}=1.40$ (Burnham et al. 1987, obtained by dividing the observed deviance by the mean deviance of the bootstrap simulations). Program MARK offers a second way of calculating \hat{c} , called the median- \hat{c} approach. This approach simulates data sets over a range of overdispersion levels and compares the deviance- \hat{c} (model deviance divided by degrees of freedom) of the simulations to the observed

deviance- \hat{c} . Running six simulations each at seven levels of overdispersion between 1 and 1.6 yielded $\hat{c}=1.37$ (SE=0.02), an estimate close to the one obtained by the bootstrap procedure. We retained the latter, slightly more conservative estimate, but this choice did not qualitatively affect our results, and the quantitative differences were small.

All models were run in program MARK 4.2 (White and Burnham 1999). We followed basic capture-mark-recapture methodology (Lebreton et al. 1992), and based model selection on Akaike's information criterion, adjusted for overdispersion and sample size (QAICc) (Burnham and Anderson 2002). The model with the lowest QAICc is the most parsimonious one (Burnham and Anderson 2002).

This study focussed on time variation in survival, and examined to what extent it was affected by catastrophic weather events. We considered the effects of snow cover, which we previously found to affect barn owl survival (Altwegg et al. 2003). As in our previous study, we measured snow cover as the number of days per winter with more than 5 cm of snow, which makes small mammals unavailable to hunting barn owls (see Roulin 2002). The weather data were obtained from the Swiss Meteorological Institute at a station near Bern in the centre of our study area and at a representative altitude (46.55°N, 7.25°E, altitude 565 m). We used ultrastructural models within program MARK to model survival as a linear or quadratic (on the logit scale) function of snow cover. Then, we calculated the amount of variation in survival explained by snow cover using random effects models (Link and Nichols 1994; Burnham and White 2002; Loison et al. 2002; Altwegg et al. 2003). We followed the procedures detailed in Loison et al. (2002). This method allows distinguishing between sampling variance and variance caused by biological processes, and only the latter is relevant for population dynamics (for a detailed description, see Hilborn and Mangel 1997; Franklin et al. 2000). We first obtained the total process variance (σ^2) by fitting a random effects model that assumed a constant mean survival. Then we fitted a random effects model assuming that mean survival depended on snow cover and estimated the residual variance (σ_{res}^2). The percentage of variance explained was then calculated as $(\sigma^2 - \sigma_{\text{res}}^2) / \sigma^2$. These calculations were based on the model with independent juvenile and adult survival.

We estimated σ^2 using the method of moments procedure available in program MARK. This procedure does not, however, allow the estimation of the process correlation between juvenile and adult survival. We estimated this correlation using the Bayesian Markov Chain Monte Carlo (MCMC) module also implemented in program MARK (see Gilks et al. 1996). In this module, we built hierarchical models where annual juvenile and adult survival rates are assumed to be realisations of two random processes with a mean and variance each (μ and σ^2), and we allowed the processes to be correlated (ρ). The hyperparameters μ , σ^2 and ρ

can be estimated directly from the data. We chose flat prior distributions [normal prior with standard deviation = 100 for the logit transformed μ , recapture and recovery rates; a gamma prior with both scale and shape parameters = 0.001 for σ ; and a uniform prior over (-1,1) for ρ]. Then, we ran one chain of 11,000 iterations, and discarded the first 1,000 iterations (burn-in). From our other analyses, we had estimates for all parameters except ρ , and we verified that they were nearly identical to the ones we obtained from the Bayesian analysis. We then repeated this analysis excluding the two most extreme winters to examine how they affected ρ . Note that the MCMC module in MARK is based on the logit-transformed parameters, and ρ estimates the correlation of these rather than the real parameter values. Estimating ρ on the untransformed or logit-transformed parameter estimates is equivalent in principle, but the latter approach is preferable because the transformed survival rates are not bounded between zero and one.

Reproduction

Starting in 1945, the ringers recorded the number of nestlings in the brood at the time of ringing, even if they did not ring all nestlings. We used these records as an estimate of brood size, and separated the variance into within-year and between-year components using linear mixed effects models in procedure lme of program R 1.8.1 (Pinheiro and Bates 2000; R Development Core Team 2003). Brood size ranged from 1 to 12 (mean = 4.5, median = 5), and the residuals were normally distributed. We estimated the variance components by restricted maximum likelihood (REML).

Reconstruction of population trajectory

We reconstructed the population trajectory from our estimated survival rates and brood size using a two-stage projection matrix, A , with post-breeding census (Caswell 2001). Taking the survival estimates from model 2 (Table 1; and thus not imposing any constraint on the correlation between juvenile and adult survival), we projected the numbers of juveniles and adults (the elements of the vector n of length two) in year $t+1$ from the numbers in year t . We used the following model:

$$n_{t+1} = A_t \times n_t \quad (1)$$

$$A_t = \begin{pmatrix} (b_{t+1} \times \text{nbj} \times 0.5 \times \text{sj}_t) & (b_{t+1} \times \text{nba} \times 0.5 \times \text{sa}_t) \\ \text{sj}_t & \text{sa}_t \end{pmatrix}, \quad (2)$$

where sa is adult survival, sj is juvenile survival, b is brood size, nbj and nba = number of successful annual broods for first time breeders (0.4) and adults (0.9), and the brood sex ratio is set to 0.5 (A. Roulin, unpublished

Table 1 Summary of model selection for estimating survival of Swiss barn owls (*Tyto alba*) from 1934 to 2002

Survival model	Recovery model	QAICc	Δ QAICc	w	K	QDeviance
1 Independent time variation in juveniles and adults	Parallel time variation in juveniles and adults	20,788.16	69.82	0.000	184	1,909.474
2 As 1	Quadratic trend over time	20,733.43	15.09	0.012	130	1,964.208
3 Parallel time variation in juveniles and adults	As 2	20,718.34	0.00	0.988	71	2,068.137
4 Juveniles constant, adults variable over time	As 2	20,862.29	143.95	0.000	71	2,212.091
5 Juveniles variable over time, adults constant	As 2	20,915.71	197.37	0.000	71	2,265.512
6 Juveniles variable over time, adults linearly dependent on snow	As 2	20,797.08	78.74	0.000	72	2,144.866
7 As 6, but quadratic relationship between adult survival and snow	As 2	20,788.19	69.85	0.000	73	2,133.966
8 Juveniles linearly dependent on snow, adults variable over time	As 2	20836.85	118.51	0.000	72	2,184.633
9 As 8, but quadratic relationship between juvenile survival and snow	As 2	20,837.66	119.32	0.000	73	2,183.431

The models use combined live-recapture and dead-recovery data. All models account for differences between adults and juveniles in both survival and recovery rates. In addition, all models account for differences in recapture rates between western Switzerland after 1990, and the rest of the study (see [Materials and methods](#)). Other models accounted for independent time variation of the two age classes in the recovery rate, but were poorly supported and not shown. Model selection is based on Akaike's Information Criterion, corrected for overdispersion (QAICc, using $\hat{c}=1.4$), and a lower value indicates a better model. Δ QAICc gives the difference in QAICc between the current model and the best model (in bold); the Akaike weights (w) assess the relative support that a given model has from the data, compared to the other models in the set; K is the number of parameters. Finally, the QDeviance is the difference in $-2 \log$ Likelihood between the current model and the saturated model, where the saturated model is the one where the number of parameters equals the number of cells

data; we considered females only). Broods can fail completely, and barn owls can breed twice in a season. However, we do not have annual data for the number of successful broods and our model thus underestimates the true variability in population size. The objective of the matrix model was to visualise the population-level effects of the variation in survival and brood size that we estimated here. Note that the model reconstructs relative changes in population size, rather than absolute population densities, since precise data on the latter are lacking.

Results

Survival, recovery and recapture rates

Between 1934 and 2002, juvenile and adult survival varied around the mean values of 0.294 and 0.570, respectively (Fig. 1b, c), with estimated process variance 0.0148 (corrected for sampling variance, see [Materials and methods](#)) and 0.0228. The most parsimonious model constrained juvenile and adult survival to vary synchronously (model 3, Table 1), showing that there was temporal correlation in these two fitness components. The Markov Chain Monte Carlo analysis estimated the process correlation between juvenile and adult survival at $\rho=0.69$.

Overall, juvenile and adult survival was lower in years with longer lasting snow cover (Fig. 2). For juveniles, the best relationship was linear with a slope on the logit scale -0.018 (95%CI: -0.023 to -0.012) (model 8, Table 1, change per additional day of snow). For adults,

the best relationship was quadratic, with coefficients -0.004 (-0.018 to 0.010) and -0.030 (-0.046 to -0.015) for the linear and quadratic terms, respectively (model 7, Table 1). Harsher winters thus had a progressively worse impact on adult but not juvenile survival (Fig. 2). These models were, however, considerably less well supported than the fully time variable ones, showing that snow cover could not account for a major part of the temporal variance. Snow cover explained 18.6 and 49.1% of the temporal process variance in juvenile and adult survival, respectively. Nevertheless, the variance accounted for by snow cover was highly significant (Analysis of Deviance, juveniles: $F_{1,58}=7.23$, $P=0.009$; adults: $F_{2,57}=22.08$, $P<0.001$).

To examine the effect of years with extreme winters on the temporal variance in survival, we estimated this variance after excluding progressively less harsh winters. While the temporal variance in juvenile survival appeared to be little affected by extreme winters, the variance in adult survival tended to decrease when the years with extreme weather were excluded from the calculation (Fig. 3). The process correlation between juvenile and adult survival dropped to $\rho=0.63$ when we omitted the two most extreme winters, associated with population crashes.

The probabilities of finding a dead owl (recovery rates) were lower for juveniles than adults and were best modelled as a quadratic trend over time (Table 1: Delta QAICc = 54.73, comparing model 1 and 2). For juveniles, the recovery rate was 0.124 (SE = 0.014) in 1934, increased to 0.218 (SE = 0.008) in 1959, and slowly decreased to 0.041 (SE = 0.002) in 2002. The corresponding values for adults were 0.210 (SE = 0.022), 0.343

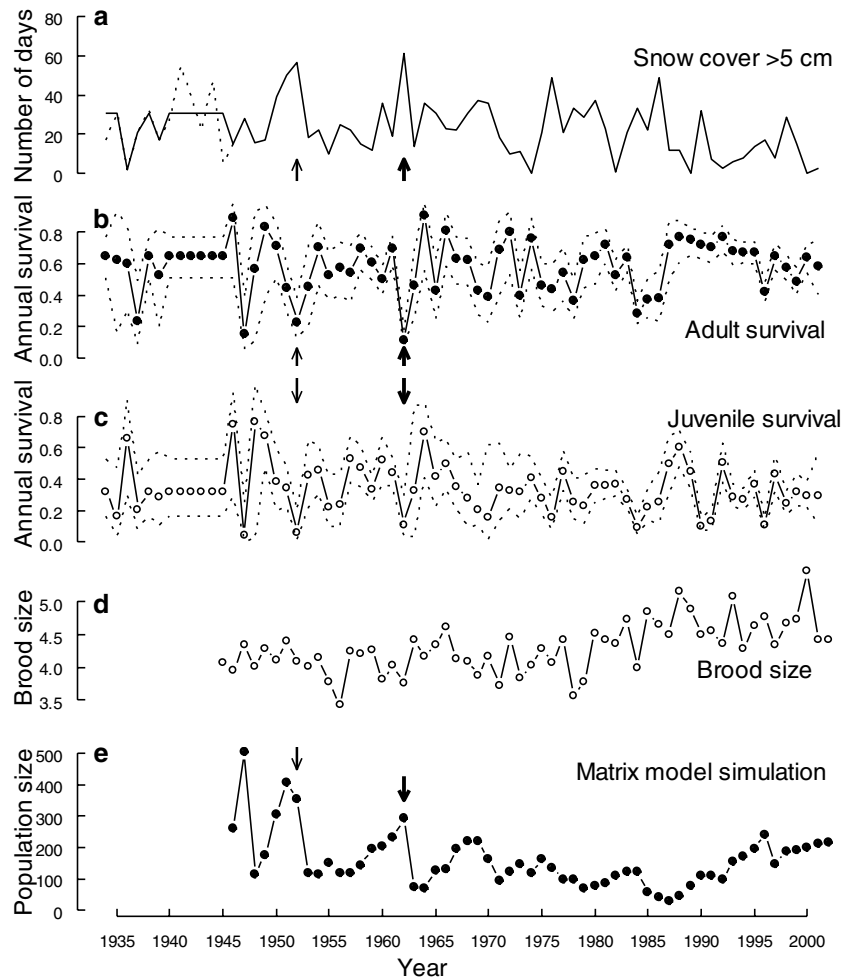


Fig. 1 Time series for weather, survival, brood size, and a projected population trajectory of Swiss barn owls (*Tyto alba*) from 1934 to 2002. **a** Number of days with more than 5 cm of snow cover at the meteorological station Bern. When relating weather to survival, we used the average measurements over the years 1934, 1938, and from 1940 to 1945, for which we did not have enough data to investigate time variation in survival. The actual measurements during this period are shown as *dotted lines*. The *arrows* highlight the 2 years with the longest snow cover (the *bold arrow* highlights 1962-1963 with the most extreme value).

b, c Adult and juvenile annual survival rate, with 95% confidence interval. For the years 1934, 1938, and from 1940 to 1945, only the mean estimate can be given. Estimates from model 2, Table 1. **d** The estimates are the best linear unbiased predictors (BLUP) for brood size estimated from a mixed effects model with the overall mean as fixed effect and between-year variation as random effect. **e** Projected trajectory of a population started at 100 adults and 140 juveniles (ratio corresponding to a stable age distribution for the initial matrix)

(SE = 0.014), and 0.074 (SE = 0.0052). The probability of capturing and subsequently releasing a live bird was 0.792 (SE = 0.017) for the Payerne region during 1990 to 2001, and 0.112 (SE = 0.013) for the remainder of the study.

Reproduction

The overall mean brood size at the time of ringing between 1945 and 2002 was 4.3 (SE = 0.07). The between-year variance was 0.204 (95% CI: 0.127–0.329, coefficient of variation: 10.51%), and the within-year (residual) variance was 2.207 (CI: 2.119–2.300). Brood

size significantly increased over time (Fig. 1d), and a linear trend explained 24.8% of the between-year variance (slope: 0.019, SE = 0.003, $P < 0.0001$). This trend was not an artefact of the more detailed data from the Payerne region dominating the analysis during later years. Entering region as a fixed effect into the mixed effects model showed that mean brood sizes were nearly identical in the Payerne region as compared to the rest of the study area (difference = 0.021, SE = 0.078, $P = 0.79$). Snow cover had no significant effect on brood size in the subsequent breeding season ($P > 0.15$), and explained less than 3.5% of the between-year variance regardless of whether or not the time trend was accounted for in the model.

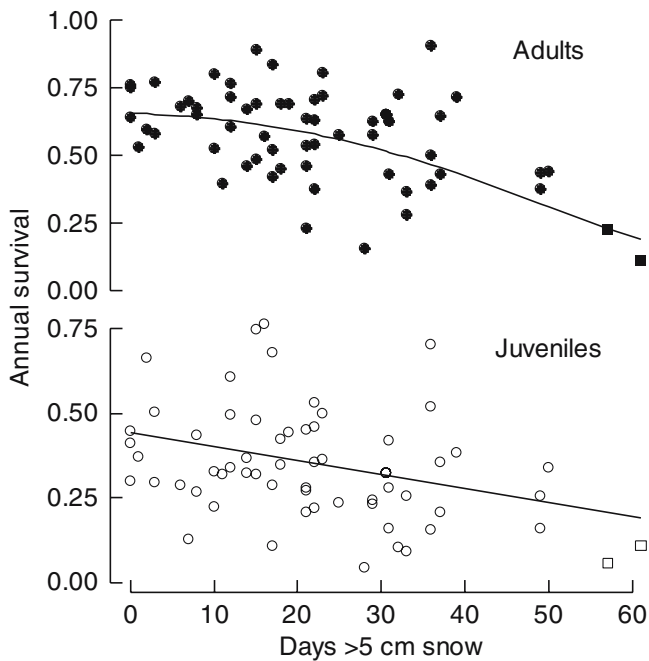


Fig. 2 Adult and juvenile survival in relation to winter harshness, measured by the number of days with more than 5 cm of snow. The two most extreme winters led to population crashes, and are highlighted by *square symbols* in this figure. The regression lines were taken from models 7 and 8 (Table 1) for adults and juveniles, respectively

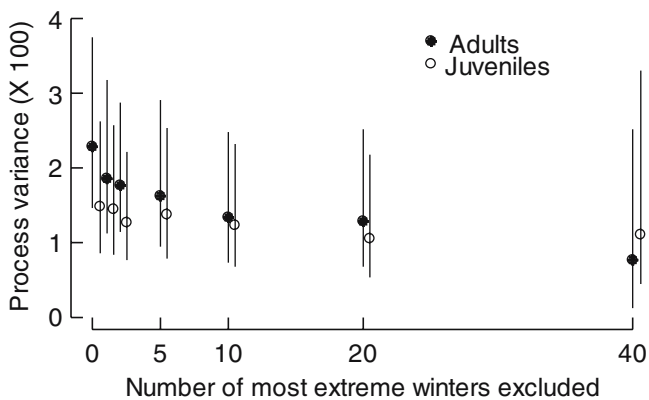


Fig. 3 Change in temporal variance in survival when years with extreme winters were excluded. Winter harshness is defined by the number of days with more than 5 cm of snow. The estimates are corrected for sampling variance and thus show process variance only. Vertical bars show 95% confidence intervals

Population trajectory

We reconstructed the trajectory of the Swiss barn owl population from the observed fitness components using projection matrices (Caswell 2001). This simple population model recovered the salient features previously known for this population, and demonstrates the negative effect of catastrophic winters on population densities (Fig. 1e). First, the population density declined over

most of the last century and then slowly increased over the last two decades, in accordance with field data (Schmid et al. 2001). And, second, there were catastrophic declines in the winters 1947-1948 (Schifferli 1949), 1952-1953 (Sauter 1956), and 1962-1963 (Güttlinger 1965). The low survival rate that we found for 1947-1948 may have been due to exceptional food shortage unrelated to snow cover, or due to a disease outbreak (Schifferli 1949).

Discussion

Using modern statistical tools and ringing data, we estimated annual survival of Swiss barn owls from 1934 to 2002, and brood size for the period 1945 to 2002. The length of our study permitted us to examine the effect of rare catastrophic weather events on these fitness components. Winters with long-lasting snow cover are catastrophic for barn owls because their main prey, rodents, become unavailable under the snow. Our results show that the two harshest winters over the past 70 years (1952-1953 and 1962-1963) had devastating effects on the Swiss barn owl population, because survival of both juveniles and adults was unusually low during these years (see Figs. 1, 2). With 57 and 61 days of snow, these two winters were considerably harsher than the rest (Fig. 2). Three more years with around 50 days of snow also stood out as being more extreme than the rest (Fig. 2), but they did not lead to equally low survival or population crashes, as did the two most extreme years.

The profound effects of catastrophic winters could not easily have been anticipated from normal weather effects since snow cover explained only a minor part of the variance in survival over the whole length of our study (19 and 49% for juveniles and adults, respectively). It was rather the coincidence of very low juvenile and adult survival that led to population crashes. The result that snow explained a higher proportion of variance in adult survival compared to juvenile survival is in contrast to our earlier study, where we found that weather explained a higher proportion in juvenile survival in the Payerne region between 1990 and 2001 (Altwegg et al. 2003), a period that did not encompass any exceptionally harsh winters. Adults appear to be less sensitive than juveniles to regular levels of weather fluctuations.

Both in our earlier and the present study, adult survival had a higher temporal variance than juvenile survival. These variances may not be directly comparable, however, because the mean values differ. Like in other binomial processes the maximum possible variance is determined by the mean survival rate, s , as $s \times (1-s)$. The variance in survival thus necessarily goes to zero as survival goes towards zero or one. Gaillard and Yoccoz (2003) and Morris and Doak (2004) therefore suggested using the ratio of the observed variance to the maximum

possible variance [i.e. $\sigma^2/s \times (1-s)$] to compare the variability of survival rates. By this measure, the variability in juvenile and adult survival was similar (0.071 and 0.093). Earlier studies found that fitness components are less variable when they are more strongly related to population dynamics and fitness (Pfister 1998; Gaillard et al. 2000; Sæther and Bakke 2000; Gaillard and Yoccoz 2003; Morris and Doak 2004). Population dynamics in Scottish barn owls are almost equally sensitive to variation in adult and juvenile survival (Hone and Sibly 2002), and our results are thus consistent with theory.

Using random effects models, our estimates of the long-term variance in survival are not confounded by sampling variance. Few other avian studies report estimates of demographic rates for more than 20 years (Peach et al. 1994; Frederiksen and Bregnballe 2000; Blums et al. 2002; Franklin et al. 2002; Loison et al. 2002; Robinson et al. 2004). Franklin et al. (2002) and Loison et al. (2002) give estimates of temporal variance in survival corrected for sampling variance. Using the ratio of observed variance to the maximum possible variance, we find that our estimate for adult barn owls (0.093) was intermediate between 11 American waterfowl species on the one hand (mean 0.030; Franklin et al. 2002) and the European dipper on the other hand (0.176; Loison et al. 2002). Our estimate of variance for survival of juvenile Swiss barn owls (0.071) was higher than the one for juvenile European dippers (0.011; Loison et al. 2002). In our study, the variance in adult but not juvenile survival appeared to be inflated by rare extreme events (Fig. 3). Short-term studies not running long enough to encompass extreme weather events may thus underestimate the temporal variance in fitness components.

Biological systems have been globally observed to respond to climatic trends, such as global warming (Parmesan and Yohe 2003). However, in addition to trends, recent climate models predict extreme events to change in frequency in the near future (Easterling et al. 2000). The biological implications of this latter prediction are poorly understood. Our results show that extreme events can have profound effects on populations by affecting all segments of the population simultaneously. In our example, the extreme events were harsh winters, which have become less frequent over the last decades. Other natural disasters, such as droughts or heat waves, which are predicted to become more frequent (Easterling et al. 2000), are likely to have similar effects as extreme winters. They may affect all individuals regardless of age and sex, even if they differ in their susceptibility to weather during regular years. Catastrophic events may thus have qualitatively different ecological effects than regular environmental variation.

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