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Density and climate effects on age-specific survival and population growth: consequences for hibernating mammals

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Abstract

The impact of factors such as density dependence, food availability, and weather are known to be important for predicting population change in a wide range of species. However, a challenge in ecology is understanding the contributory and interactive role of these drivers on populations. This is necessary to design effective conservation and management strategies. Using data from long-term studies of five hazel dormouse populations in Europe, we tested the relationship between population density and weather and their impact on demographic rates. We used an integrated population modelling approach, estimating age-specific overwinter survival, annual population growth, and fecundity rates. We found strong negative effects of population density, precipitation, and winter temperature on population growth rates. This suggests that warmer and wetter weather negatively affects dormouse survival for both adults and juveniles, but we found subtle differences in these effects between age classes. We also identified an interaction between weather measures and population density on age-specific survival, possibly as a result of weather impacts during hibernation. Although we found low winter temperature was positively associated with population growth, we found evidence consistent with density-dependence. We discuss our results in the context of woodland habitat conservation management.

Introduction

Understanding the mechanisms underlying animal abundance is fundamental to ecology. This understanding is necessary to predict population growth and therefore to inform species conservation management (Krebs, 2002; Hastings, 2010). This is especially true in fragmented landscapes where populations vary in size, demographic composition and connectivity, factors which are of key importance for population persistence (Fahrig & Paloheimo, 1988; Boyce & McDonald, 1999; Mackey & Lindenmayer, 2001). Thus, effective conservation monitoring requires data on abundance, population growth, age specific survival, reproductive success, and dispersal in order to evaluate population trends and identify factors influencing changes in population growth (Magurran et al., 2010; Keith et al., 2015). Population size is expected to show temporal and spatial variance due to extrinsic factors, such as resource availability, predation, and local weather conditions, as well as intrinsic factors such as population density (Bjørnstad & Grenfell, 2001; Melbourne & Hastings, 2008). These factors impact populations through their effects on demographic parameters such as fecundity, survival, immigration and emigration, in turn driving variation in population growth rates. Thus, the estimation of demographic rates through population monitoring can play a pivotal role in understanding the complex interactions between demography and the environment in order to predict population change and inform conservation management of at-risk species.

Conservation monitoring of populations is a challenge for many species owing to logistic constraints. This is exacerbated for rare or elusive species which may be relatively difficult to detect or identify, or which occur at low density (Lomba et al., 2010; Harris, Combe, & Bird, 2015). Further, some species exhibit variation in their life history or conservation status over a wide geographical range, leading to impediments in the collection of basic data, or spurious extrapolation due to difficulty in long term monitoring of populations or sampling biases from small population sizes. As a result of these issues, the basic population abundance for many species of conservation concern is uncertain even when monitoring is conducted, due to lack of long-term data sets (Flowerdew, Amano, & Sutherland, 2017). Because populations are expected to respond to conservation management, it is critical to monitor this response to measure its impact (Buckland et al., 2007). Thus, a basic requirement to measure conservation impact is population monitoring data and the biological and environmental correlates of variation in population growth.

Demographic information, for example data collected by mark-recapture studies, is essential in order to assess extinction risk in small or declining populations (Bonebrake et al., 2010). In this context, there is a history of debate surrounding the contribution of multiple environmental and density-dependent processes which act on population vital rates such as survival, recruitment and fecundity (Andrewartha & Birch, 1954; Leirs et al., 1997; Nowicki et al., 2009; Ohlberger, Rogers, & Stenseth, 2014). However, ecological theory generally recognises population density dependence as an integral process that often has a role in regulating population abundance (Henderson & Magurran, 2014). Virtually all habitats are subject to environmental stochasticity in temperature and precipitation, often at a local scale (Walther et al., 2002; Wilson et al., 2005), which may sometimes be extreme (Barker, 2007). Weather conditions may directly impact survivorship or fecundity due to changes in the availability of food, shelter, or water (Vasseur & Fox, 2007; Loreau & de Mazancourt, 2013). There is evidence that environmental stochasticity can alter the relationship between population density and population vital rates (Miller, 2007; Richard et al., 2014; Manning, Medill, & Mcloughlin, 2015). Such weather impacts may also interact with density dependence, e.g., through availability of resources, leading to increased competition, that can strongly affect population dynamics. Such processes can be complex (Coulson, 2001; Boyce et al., 2006), but may be essential to understand population dynamics (Gamelon et al., 2017). As such, we require an understanding of how weather factors, density dependence and the strength of interaction between these factors influence population vital rates.

Weather conditions also may have a large impact on hibernating species (Inouye et al., 2000; Nowack, Stawski, & Geiser, 2017), for example by altering the date of emergence or phenology, and subsequently impacting survival or fecundity. Temperature variation may affect energetic state, water reserves and thermoregulation during hibernation (Seebacher, 2009; Boyles et al., 2011). There is evidence that hibernating species are susceptible to changes in precipitation and through phenological changes in their active season, e.g. affecting mating activities or hibernation survival (Falvo, Koons, & Aubry, 2019; Cordes et al., 2020; Johnston et al., 2021). Thus, in hibernating species it is particularly important to consider the role of environmental conditions in maintaining homeostasis or body mass for reproduction (Humphries, Thomas, & Kramer, 2003; Fietz et al., 2004; Pretzlaff et al., 2021). Finally, spatial variation in population demographics caused by environmental stochasticity is poorly understood, motivating the study of demographic variation in replicated subpopulations that may vary biologically and environmentally.

The hazel dormouse (*Muscardinus avellanarius*) is a small, semi-arboreal mammal associated with deciduous and mixed coniferous woodlands in Europe that exhibits a long hibernation period (~ 6 months). The duration of hibernation varies geographically, being longer in more northern European populations (Juškaitis, 2014). The hazel dormouse is characterised as having a small home range with low dispersal, low fecundity and occurring at low population density in comparison to other small mammals (Bright, Morris, & Mitchell-Jones, 2006). Because of a decline in its northern range due to climate change and habitat degradation (Goodwin et al., 2017; 2018), it is a species of conservation concern and strictly protected in Europe (Habitat Directive Annex IV, Bern Convention Annex III). Hazel dormice are also known to be sensitive to seasonal variation in weather with high mortality in variable winters, and reductions in activity and food availability during wetter spring and summer periods (Juškaitis, 1999, 2013; Bright, Morris, & Mitchell-Jones, 2006). For these reasons, this species has been the subject of long-term population monitoring and require active management and habitat alteration over a wide geographical range, making it an ideal model to test the role of weather in relation to population growth, survival and reproduction patterns.

This study aimed to investigate the importance of population density and weather conditions associated with population size change in the hazel dormouse. We assessed these effects using long term capture mark recapture (CMR), productivity and population count data across five populations in the UK and Lithuania that vary in size, woodland management, and habitat composition. Specifically, we compared variation in population growth and age-specific annual survivorship and investigated the association between population density and climate variation with variation in population size change. We discuss our findings in the context of conservation management for hibernating mammals in the face of ongoing climate change.

Materials and Methods

Study sites and data sources

CMR data were collected in five hazel dormouse populations: The Perch (Somerset, UK), Wyre Forest (Worcestershire, UK), Bontuchel (North Wales, UK), Wych (reintroduction site; Cheshire, UK) and Šakiai (South West Lithuania, Šakiai district; see Fig.1). The Wych population is an established reintroduced population, part of the UK Species Recovery Program that released captive bred dormice in 1996. Each population contains approximately 250 wooden nest boxes placed at 20 to 40-m intervals as part of the UK National Dormouse Monitoring program (NDMP) (White, 2012), whilst the Lithuania boxes were spaced in a grid system at 50-m intervals. Each site was the subject of long-term surveys of nest box occupancy to monitor trends in dormouse number and distribution. Nest boxes were at a height of 2-4m mounted on posts or trees and distributed along transects. In the UK populations, dormice were marked with 8mm passive implanted transponder (PIT) tags and in the Lithuania population, dormice were marked with aluminum leg bands (inner diameter 2.5mm, height 3.5mm). During each survey period nest boxes were checked for occupancy and individual dormice were checked for PIT tag presence. For each captured individual we recorded age-class (adult or juvenile), sex (in adults only), litter size (number of juveniles per female) and weight (g). Unmarked individuals were marked with PIT tags or rings. All sites were monitored between May and October. Wyre data were available for the period 2002-2016, Perch and Lithuania data were available for 2007-2016, and Bontuchel and Wych data were available for 2005-2016. We analyzed capture data for Wyre and Perch from monthly records taken for all 6 months between May and October, inclusive. For Bontuchel and Wych, monthly records were available for the months May, June, September and October. For Lithuania, records were available for the months April-October inclusive. To facilitate direct comparison of the populations, and because the expected lifespan of dormice in the wild is known to reach up to six years (Juškaitis, 2014), capture histories were collapsed to yearly bins.

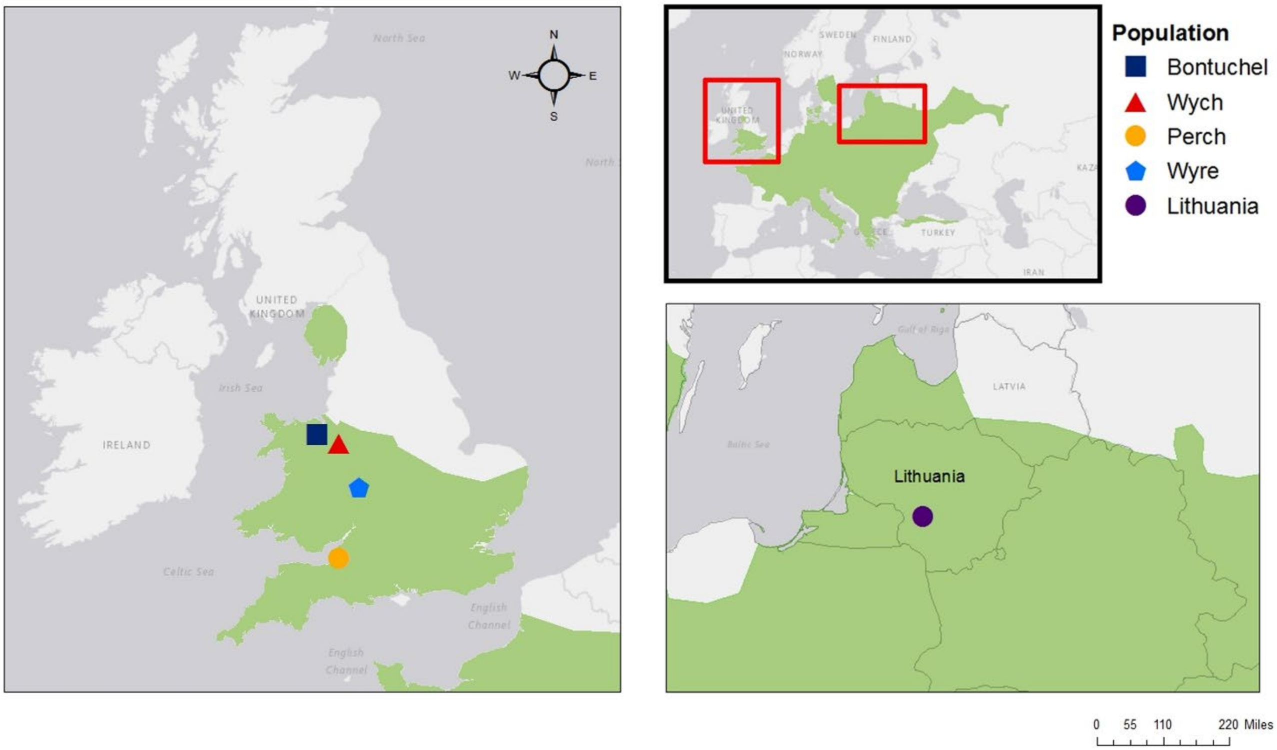

Figure 1. Geographical location of hazel dormouse capture-mark-recapture sites in the UK and Lithuania. The distribution range of the species is indicated in green.

Bayesian integrated population model

Integrated population modeling (IPM) allows the simultaneous analysis of CMR and nest survey data consisting of annual counts of dormice (unique individuals), to estimate spatial and temporal demographic variation, and uncertainty in population parameter estimates (Zipkin & Saunders, 2018). This can compensate for variation in data by reducing biases inherent in small data sets and can provide more precise estimates of demographic vital rates compared to CMR data alone (Schaub & Abadi, 2011; Harris, Combe, & Bird, 2015). The nest survey data used in the IPM consisted of annual number of uniquely identified adults (y), annual number of young produced (J), and the total number of breeding adults (calculated from the annual total number of nests found, R). We transformed the CMR data in the m-array format (Burnham et al., 1989) for juveniles (< 6months old) and adults ($\geq$ 6months old). The dormouse nest survey counts and CMR data were modelled with an IPM for each population to estimate: age-specific annual survival (ϕ), population growth rate (λ), fecundity (f) and population sizes (N_t) (Supplementary Fig. S1).

Estimation of model parameters

We used the Cormack-Jolly-Seber (CJS) model with a multinomial distribution to estimate time-specific apparent survival probability for juveniles, $\phi_{juv,t}$ and adults, $\phi_{ad,t}$ (Kéry & Schaub, 2012). To estimate the survival probability of juveniles born in year *t* to become one year old in year *t+1* $\phi_{juv,t}$, we used all individuals marked as juvenile in the annual encounter histories. After surviving the first winter, a juvenile was assumed to be an adult. Recapture probability was assumed to vary between years.

The annual number of young produced were analysed to estimate fecundity (f_t), the number of offspring per adult female, which was considered a latent variable. We assumed a Poisson distribution with the expected value being the product of fecundity and the annual number of surveyed nests (R_t): $J_t \sim \text{Poisson}(R_t f_t)$.

Between-year variation in fecundity was modelled as: $\log(f_t) = \log(\mu_f) + \varepsilon_{f,t}$, where $\log(\mu_f)$ denotes the natural logarithm of average fecundity and $\varepsilon_{f,t}$ the year-specific deviation from this value. We model these deviations as random effects and hence $\varepsilon_{f,t} \sim \text{Normal}(0, \sigma.\varepsilon)$, where $\sigma.\varepsilon$ is the temporal variability of fecundity.

In order to make the immigration process comparable to survival and fecundity, we specified annual immigration as a rate (i_t), which is the proportion of immigrants in year *t*+1 with respect to the population size in year *t*. Again, we modelled immigration with temporal random effects where $\sigma.\varepsilon$ is the temporal variability of fecundity.

$$i_t = {}^{N_{im,t+1}}\!\big/_{N_{tot,t}}\,.$$

Thus, we assumed that the populations were open to unobserved movement of young individuals (Juškaitis, 1997) to and from the monitored populations (N_{im}) to prevent overestimation when immigration is relatively small (Schaub & Fletcher, 2015).

To estimate model parameters we used an IPM that was defined by the joint likelihoods of all the available data sets (population counts, CMR, productivity data).

We used a pre-breeding census population model that included demographic and environmental stochasticity:

$$N_{juv,t+1} \sim \text{Poisson}((N_{1,t}+N_{ad,t}+N_{im,t}) \text{ x } f_t/2 \text{ x } \phi_{j,t})$$
$$N_{ad,t+1} \sim \text{Binomial}((N_{1,t}+N_{ad,t}+N_{im,t}), \phi_{ad,t})$$
$$N_{im,t+1} \sim \text{Poisson}((N_{1,t}+N_{ad,t}+N_{im,t}) \text{ x } i_t)$$

where the number of 1-year old individuals in the population is denoted with N_{juv} and, the number of adults in the population with $N_{ad,t}$ and the number of immigrants as N_{im}, f_t was the number of offspring produced per adult female at time t, $\phi_{juv,t}$ and $\phi_{ad,t}$ were the apparent survival probabilities of juveniles and adults, respectively, from time t to $t + 1$, and i_t is the immigration rate. The total population size in year t was represented as the sum of individuals in all age classes:

$$N_{tot,t} = N_{juv,t} + N_{ad,t} + N_{im,t}$$

The annual counts (y_t) were modelled with a Poisson distribution conditional on the estimated populations size, hence:

$$y_t \sim \text{Poisson}(N_{tot,t})$$

We calculated the annual population growth rate (λ_t) from the estimated total population size (N_{tot}) in year $t+1$ compared to that in year t:

$$\lambda_t = (N_{tot,t}+1) / (N_{tot,t})$$

Model implementation

We first ran goodness-of-fit tests on our CMR model using the R package R2ucare version 1.02 (Gimenez et al., 2018), with the results suggesting a good fit across sites for use in the IPMs (Bontuchel: $\chi2$ = 10.531, df = 6; P = 0.105, Lithuania: $\chi2$ = 2.821, df = 6; P = 0.508; Wyre: $\chi2$ = 5.99, df = 6; P = 0.424; Perch: $\chi2$ = 17.32, df = 10; P = 0.098;Wych: $\chi2$ = 9.483, df = 6; P = 0.107). We obtained posterior distributions of population growth rate, fecundity and survival for each population separately from the IPM as defined above, using Markov chain Monte Carlo (MCMC) simulation implemented in JAGS version 3.4.0 (Plummer, 2003) called from R version 4.0.5 (R Core Team, 2021) with the R package jagsUI version 1.5.2 (Kellner, 2019). For all parameters we defined vague priors (see code for details). To assess convergence, we ran four independent chains of 400,000 MCMC iterations with different starting values, with a burn-in of 50,000 iterations, thinning every 100th observation resulting in 3,500 posterior samples. We confirmed model convergence using the Gelman-Rubin statistic (Gelman & Rubin, 1992) and visual inspection of chains (JAGS code for fitting the IPM is available in Appendix S2). The R-hat score ($\hat{R} \leq 1.04$) was evaluated for all parameter estimates and we summarized posterior distributions by their means and 95% credible intervals (CRI).

Density dependence

To evaluate the role of population density and weather variables, we converted population abundance ($N_{tot,t}$) to density of dormice per hectare for each year at each population. To test the effect of density dependence we modelled the population growth rate (λ_t) as a function of population density per hectare for the previous year (Slade, 1977; Hixon & Johnson, 2009). Thus, we interpreted the regression coefficient as the strength of density dependence and evaluated it against zero. Here, a negative coefficient indicates negative density dependence characterised by a decrease in population growth rate as population abundance increases.

Weather data

Annual mean temperature (ºC) and precipitation (mm) data (within 10km of each site) were obtained from the R package weatherData version 0.6 (Narasimhan, 2014). We compiled the weather data for spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). Thus, temperature and precipitation data were grouped by season and year. Additional weather variables were compiled for winter months, including temperature range and maximum, and the number of days above 10 ºC, and NAO (North Atlantic Oscillation) index scores. Explanatory variables did not exhibit significant multicollinearity, and thus they were retained in our analysis (for definition of weather variables see appendix S1).

Post hoc statistical analyses of weather variables and population density

We analyzed the association of environmental variables with our estimates of population density (per hectare), fecundity and survival. To identify a subset of variables of high explanatory value, we used the R package RandomForest version 4.7 for variable selection (Genuer, Poggi, & Tuleau-Malot, 2010). We ranked weather variable importance against parameter estimates and retained the ten most important ones for further analysis (Supplementary Table S1). We used model averaging on the remaining explanatory variables in a mixed effect framework for all further analyses, using the R package lme4 version 1.1 (Bates et al., 2015) and the dredge and model.avg functions of the package MuMin version 1.47 (Barton, 2015; Burnham & Anderson, 2002; Harrison et al., 2018), treating both year and population as random effects. We included two-way interactions in our models (i.e., between density and each weather variable) to investigate whether density mediated the effect of weather variables (or vice versa) on demographic rates. We tested each linear model met normality and homoscedasticity testing assumptions using the R package lme4 version 1.1 (Bates et al., 2015) before continuing data analyses (Supplementary Figure S2). We log transformed fecundity and Juvenile survival to meet the test of normality assumptions. Wych and Perch were excluded from analysis of juvenile survival due to low number of captured juveniles. We highlight model estimates with 95% confidence intervals not intersecting zero (e.g. as used in Grueber et al., 2011).

Results

Demographic estimates from the IPMs

Bontuchel and Lithuania had high numbers of capture events with 2,017 (number of marked individuals = 1216) and 3,265 (number of marked individuals = 2,065) total captures respectively. The other three populations, Wyre, Perch and Wych, had 850 (number of marked individuals = 464), 314 (number of marked individuals = 192) and 298 (number of marked individuals = 273) capture events, respectively. Annual estimates of the number of dormice in Bontuchel fluctuated from a high of 181 (2006) to a low of 86 individuals (2015) (Fig. 2). The Wyre population also fluctuated but overall, the number of individuals increased over the study period from a low in 2002 of 23 individuals to a high in 2015 of 110. The populations in Perch and Wyre were both increasing in early years, however, in both populations there was a dramatic decline over the study period (Perch, high=126, low=22; Wych, high=63, low=11). In Lithuania the population fluctuated highly across the study period with a rapid decline from a high of 271 in 2007 to a low of 140 in 2016. Population size estimates were relatively similar to the observed population size data. The average population growth rates over all years showed strong spatio-temporal variation. Populations in Wyre (λ=1.116, 95% CRI 0.888, 1.824) and Bontuchel (λ=1.05, CRI = 0.108, 0.129) both increased, while the Lithuanian (λ=0.910, 95% CRI 0.778, 1.033), Perch (λ=0.949, 95% CRI 0.727, 1.102) and Wych populations (λ=0.840, 95% CRI 0.565, 1.304) declined. Both Wyre and Perch showed a rapidly increasing population trajectories in the first two years of study as seen in the growth rates however, these populations declined steadily thereafter, with declines observed in population sizes (Fig.2).

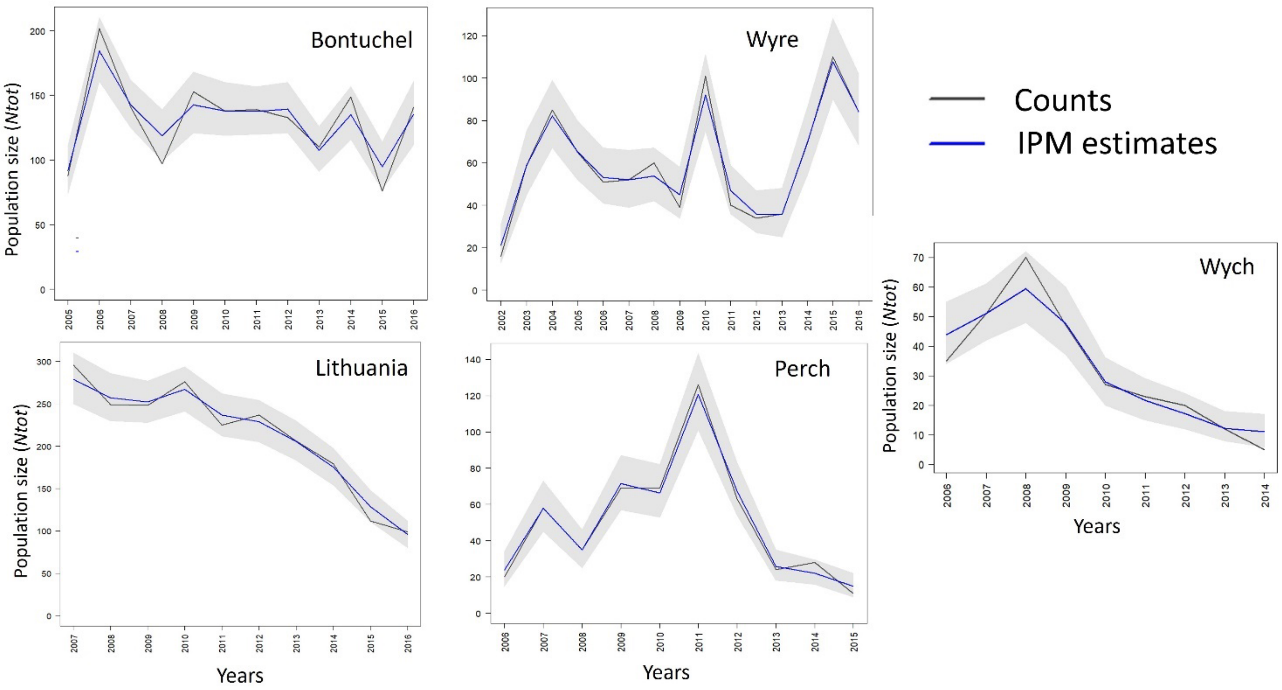

Figure 2. Time series of estimated total population size (N_{tot}) of hazel dormouse for four UK populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population, estimated with Integrated Population Models (IPM) fit to individual and nest count, and capture-mark-recapture data. The observed count data from surveys is the black line, the solid blue line shows the posterior median calculated from each IPM, and the shaded grey region indicates the 95% credible interval (CRI).

Annual adult ($\phi_{ad,t}$) and juvenile survival ($\phi_{juv,t}$) estimates are shown for each population in Figure 3. Adult survival was similar among populations, while, juvenile survival varied between populations, with much lower estimates in the populations Perch. Mean fecundity (f) was highest in Bontuchel (4.33, CRI=3.02, 4.74) followed by Lithuania (3.21, 95% CRI 3.04, 3.7), Wyre (2.803, 95% CRI 2.401, 3.235), Perch (1.830, 95% CRI 1.508, 2.212) and Wych (0.844, 95% CRI 0.589, 0.989). Estimates of immigration rate adult individuals was low among all populations (Bontuchel = 0.490 95%, CRI, 0.309, 1.326, Wyre = 0.98 95% CRI, 0.77, 3.803, Perch = 0.178 95% CRI 0.00, 0.810, Wych = 0.165 95% CRI 0.00, 0.493); Lithuania estimates indicated zero immigration over the study period.

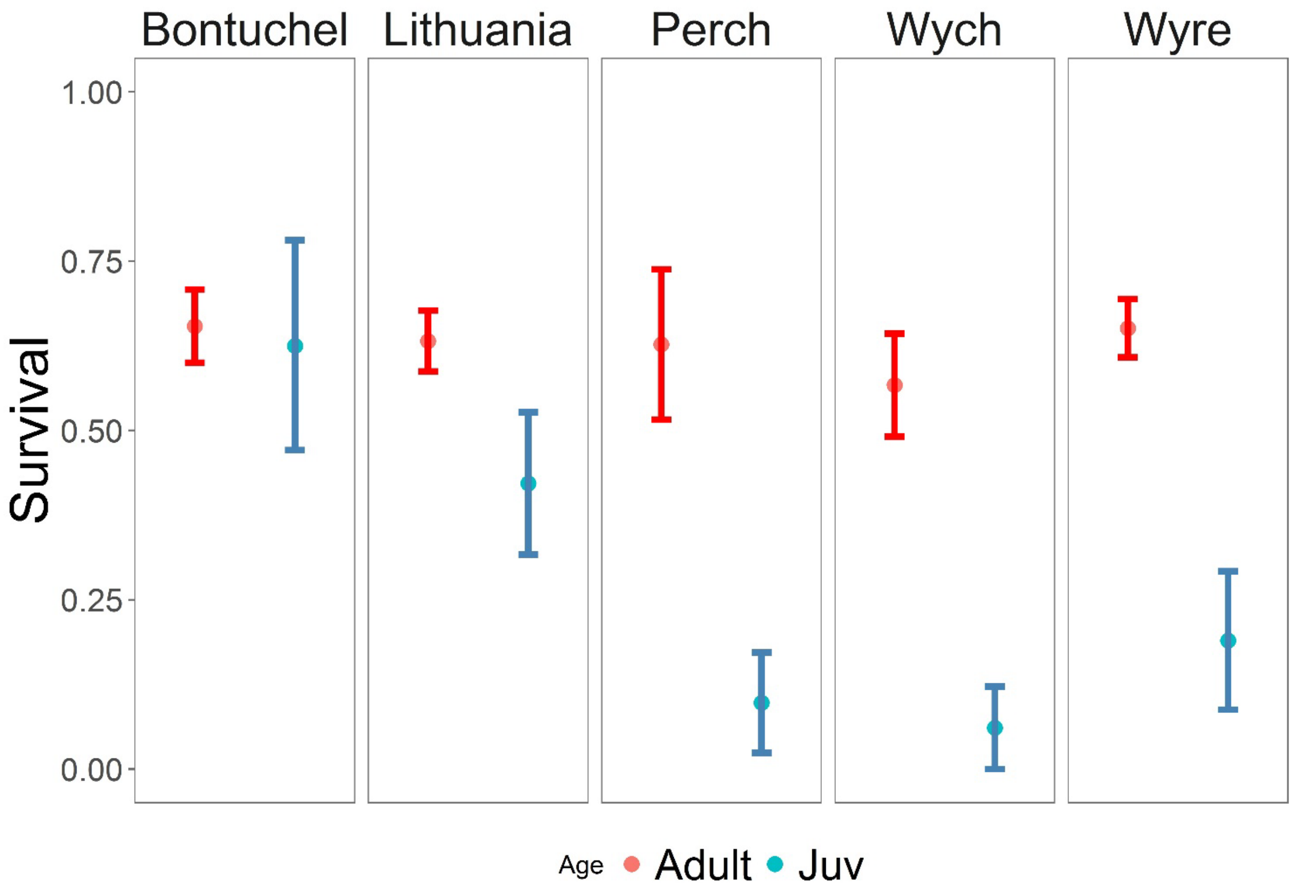

Figure 3. Juvenile (blue) and adult (red) annual survival probabilities of hazel dormice from four UK populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population estimated with Integrated Population Models fit to individual and nest count, and capture-mark-recapture data. Dots show posterior means, the vertical lines show the limits of the 95% credible intervals.

Density dependence in growth rate

Annual population growth rates in relation to density of hazel dormouse (per hectare) are shown in Fig. 4. Four out of the five populations showed a significant negative relationship between population growth rate and density. The largest populations, Bontuchel and Lithuania, showed a strongly negative slope (Bontuchel, Slope = -2.373, P = 0.023; Lithuania, Slope = -2.013, P = 0.004), while Perch (Slope = -0.456, P = 0.024) and Wyre (Slope = -1.376, P = 0.014) both exhibited a less pronounced but significant negative relationship between population growth and density (for full output see Supplementary Table S2). However, the Wych population did not show a significant relationship between population growth and density (Slope = 0.781, P = 0.329).

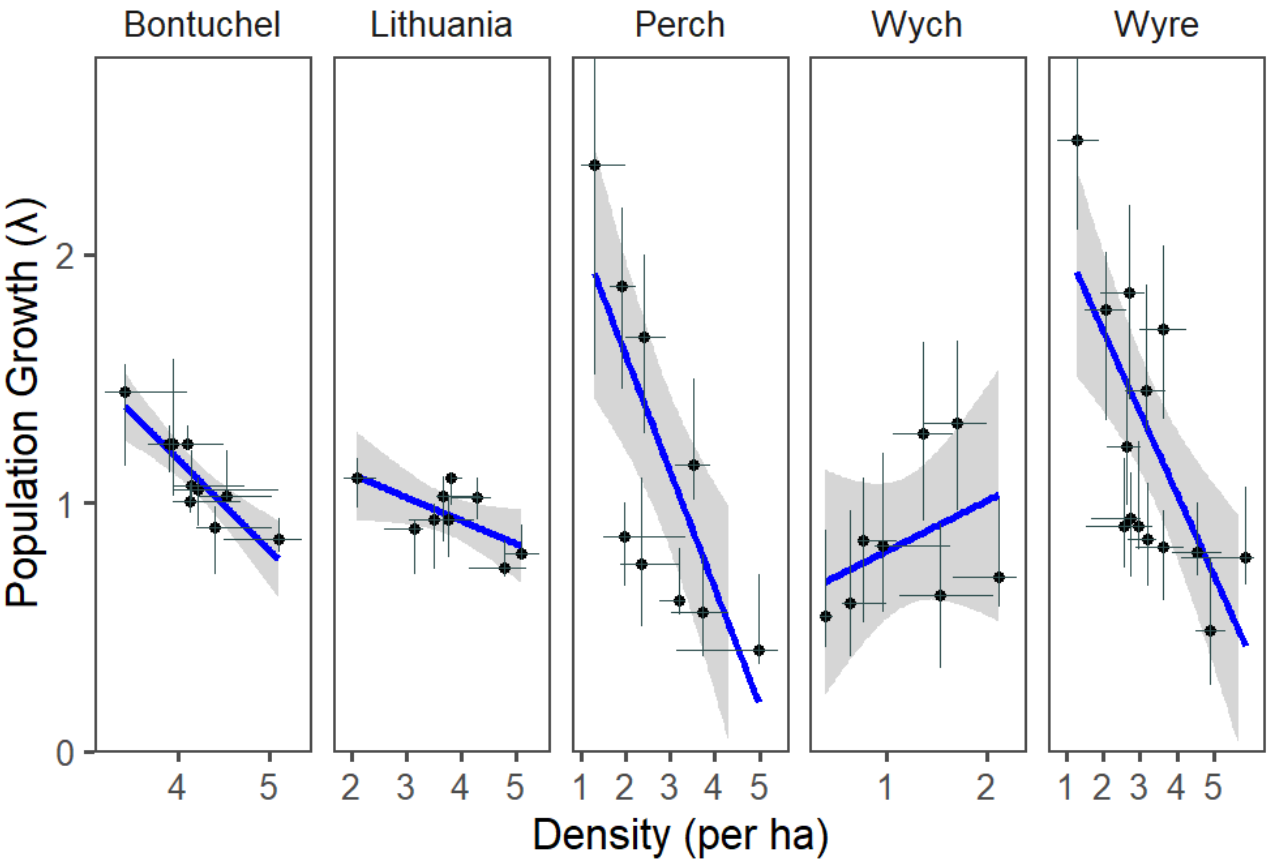

Figure 4. Annual population growth rate (λ) as a function of hazel dormouse density (per ha) in previous year. λ was calculated from Integrated population models fit to individual and nest count, and capture-mark-recapture data for four UK populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population. Each circle is the annual posterior mean with 95% credible interval bars, the blue line represents the linear fit and shaded area is the standard error.

Observed weather variation

During the study period 2002-2016, yearly average temperature in the UK ranged from 9.2 to 11.1 ºC, and in Lithuania from 6.3 to 8.2 ºC. In winter, average temperature in the UK was 5.3 ºC, and in Lithuania was -2.3 ºC. Winter precipitation in the UK ranged from 176 to 556 mm, and in Lithuania from 98 to146 mm. The range of mean winter temperatures varied from 3.7 ºC in Bontuchel to a maximum of 8.5 ºC in Perch with a mean range for all populations of 5.2 ºC. Annual precipitation varied widely with the UK populations, ranging from 820 to1410 mm, and in Lithuania from 425 to

820 mm. During the study period, there was a small increasing trend in temperature and precipitation in all populations. For a full summary of weather variables see Supplementary table S3.

Weather effects on demography

Population density) and MTR winter (mean temperature range winter) had a negative association with population growth (Table 1). Meanwhile, effect estimates of Winter PRCP and NAO index were negligibly different from zero. Density and Annual temperature were the most important predictors for fecundity (Table 1). Density had a strong negative effect on fecundity whilst annual temperature had a positive effect on fecundity. Annual PRCP and MT winter had only a weak effect. We found no evidence of an interaction effect for population growth or fecundity with weather explanatory variables.

Our main results for adult and juvenile survival are as follows (a complete account of results is available in Supplementary Table S4). We found density had a negative effect on adult). We observed a negative association of adult survival with the climatic variables, MTR winter, number of days above 10 °C and Winter temp average (Table 1, Fig. 5). We also found a negative interaction between density and Winter temp average. For juvenile survival Density had a positive effect. We observed a low negative effect of average annual temperature and annual precipitation (Table 1). We also found a low negative interaction effect between Density and Annual temp.

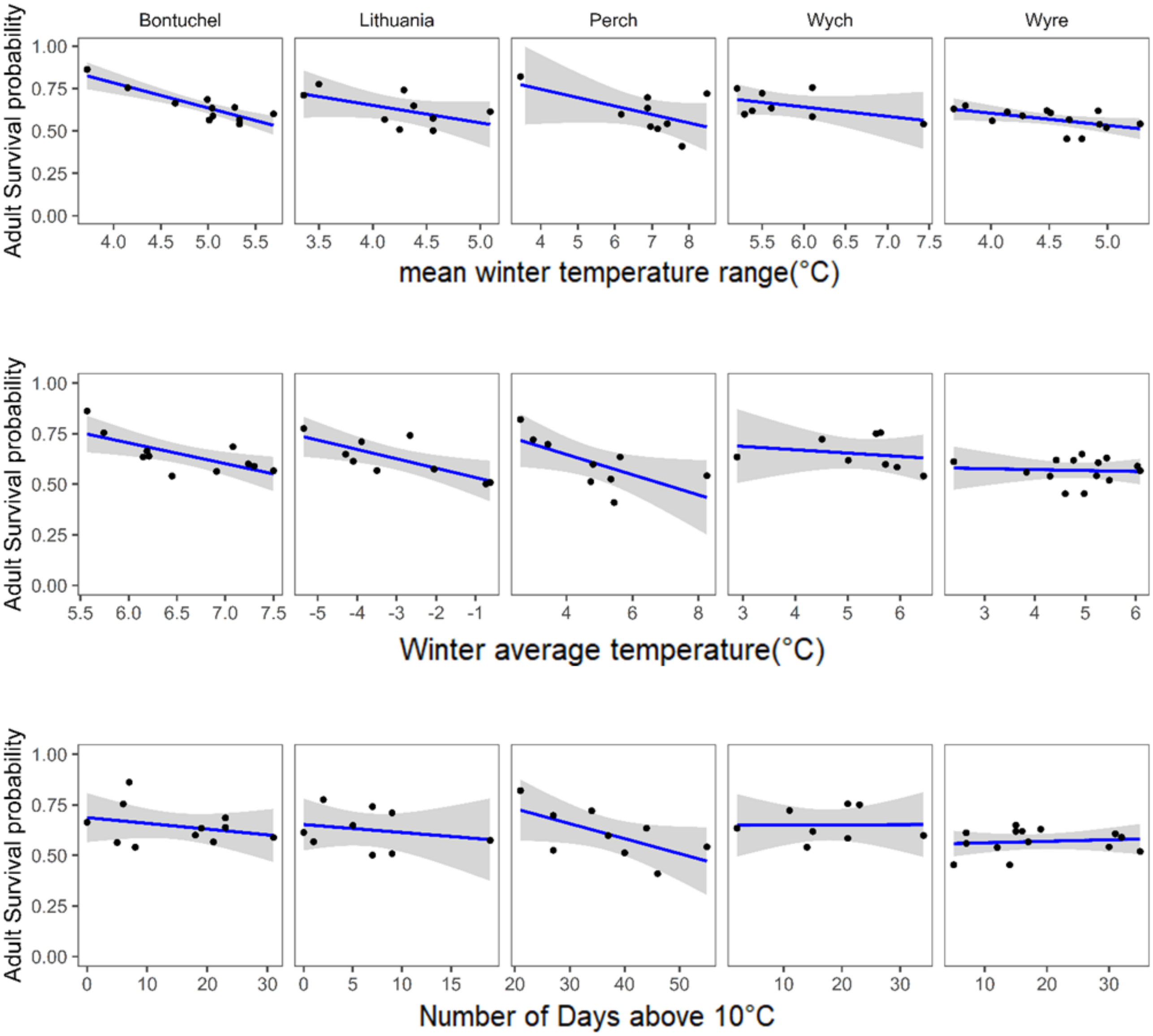

Figure 5. Adult dormouse survival plotted against the significant environmental variables in model averaging mixed effect models for the four UK populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population. Mean temperature range winter (ºC), winter average temperature (ºC) and number of days above 10 ºC. Black dots show data points, blue line indicates linear trend and grey shaded area indicates the standard error.

Table 1. Parameter estimates (*β*) and 95% confidence intervals from model averaging results using mixed effect models of each explanatory weather variable for each dependent variable (population growth (λ), fecundity (*f*), adult and juvenile survival (*ϕ*)) and interaction effects between density and weather variables. Dependant variables were calculated from Integrated population models fit to individual and nest count, and capture-mark-recapture data for four UK populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population. Model terms with 95% confidence intervals not intersecting zero are shown in bold. For definition of explanatory variables see Supplementary table S1.

Explanatory Variable	**Dependent Variable**			
	Population Growth (λ)	Fecundity (*f*)	Adult (φ)	Juvenile (φ)
Density	**-0.236 (0.348/-0.121)**	**-0.182 (-0.367/-0.012)**	**-0.094 (-0.037/-0.261)**	**0.219 (0.065/0.372)**
Annual temperature	0.061 (-0.061/0.184)	**0.156 (0.08/0.023)**		**-0.031 (-0.065/-0.0003)**
MT winter	**-0.124 (-0.263/0.001)**	-0.0112 (-0.244/0.021)	**-0.088(-0.131/-0.039)**	
Max temp winter				
N of Days ^10oC			**-0.003 (-0.004/-0.001)**	
Annual PRCP		0.001 (-0.001/0.001)	0.006 (-0.002/0.009)	**-0.004 (-0.0032/-0.0009)**
Winter PRCP	0.0004 (-0.001/0.001)			-0.014 (-0.036/0.0001)
Spring PRCP				-0.0058 (-0.010/0.001)
AUT PRCP			0.006 (-0.001/0.0006)	
Winter temp average			**-0.031 (-0.049/-0.014)**	
NAO index	-0.032 (-0.07/0.006)			
Density: Annual temp				**-0.015 (-0.026/-0.07)**
Density: Winter temp			**-0.016 (-0.026/-0.006)**	

Discussion

We investigated the effects of population density and weather on the population dynamics in the Hazel dormouse and found evidence that density dependence is very important for dormouse survival for both juveniles and adults, and for fecundity. These results suggests that available resources such as food or overwinter nest sites may limit individual reproduction and survival. We found that precipitation and winter temperature had strong negative associations with population growth, suggesting that warmer and wetter winters during hibernation periods have negative impacts on populations reducing population growth rates. We found a negative interaction between temperature and population density in association with survival, suggesting that weather may have a particularly strong effect in populations with high density. These findings are consistent with other studies showing population density can impact survival and reproductive rates in complicated ways (Eberhardt, 2002; Fauteux et al., 2021). While understanding the mechanisms underlying these patterns will require further study for the hazel dormouse, we suggest that they may have broader conservation implications, which we discuss below.

There is a breadth of research focusing on understanding density dependence in populations (Turchin, 2003; Churcher, Filipe, & Basáñez, 2006; Morris & Maceachern, 2010). However, less well understood is how density dependence may interact with environmental variation, such as climate change or habitat structural complexity, to drive population abundance (Griffith et al., 2016). As long-term and large spatial scale data become available, scientific understanding of causation in population ecology and these environmental interactions is improving. Survival rates often vary between sexes and age classes (Lebreton et al., 1992), e.g. in mammals, (Gaillard et al., 2013) and birds (Payo-Payo et al., 2016). While we found negative effects of population density and temperature on survival in both adults and juveniles, in adults we found that winter temperature and precipitation negatively affected over-winter survival in this hibernating species. In juveniles, we found annual temperature and precipitation to be negatively associated with survival (with a low effect size). These results suggest that weather variation can affect adult and juvenile survival in subtle and complex ways, possibly by imposing negative constraints on life-history traits associated with hibernation. On the other hand, we found an interaction between weather and density in association with survival. As a consequence the cumulative effect of poor weather conditions interacting with periods of high density may have a much stronger negative effect, such as population crashes during these time periods (Fauteux et al., 2021). However, further research on the interaction between climate and density in relation to individual energetic states is required to fully understand the effects of weather variation on individual survival.

Population density is recognized as an important factor regulating population growth in small mammal species (Erb, Boyce, & Stenseth, 2001), but it has not previously been studied in dormice. Our results are consistent with the idea that dormouse populations are intrinsically regulated by local-scale density dependence. We found a strong negative effect of density on population growth in all of our populations except Wych. However, Wych is different from the other locations in our study as it is a reintroduced population. Whilst we provide evidence that this site exhibits low productivity, poor breeding conditions and low juvenile survival, Wych also exhibits habitat differences compared to other sites, such as low shrub density and woodland dominated by holly and sycamore that are considered less favorable habitat.

Implications of weather variability

We found that an increase in environmental climatic variation *per se* (e.g. temperature ranges in winter) was negatively associated with population growth rate and that this explained a significant part of the variability of survival and fecundity in the hazel dormouse. While the mean of weather variables has been implicated in negative impacts on vital rates, the mechanisms underlying climate-induced population change are poorly understood (McLaughlin et al., 2002). While our results suggests that warmer winter weather, comprising increased average temperatures and rainfall during winter, negatively affect dormouse survival for adults, for juveniles we found they were negatively impacted by warmer and wetter weather during the annual time period. A cause for this age specific difference may be the energetic expenditure of reproduction and overwintering in adults (Pretzlaff et al., 2021) whilst juveniles may be more susceptible to more sudden local climate variability due to building of energy reserves for their first year. Global warming in the northern latitudes during winter months is thought to have negative consequences for many species, and this trend may continue as mean winter temperatures are predicted to rise and winter periods shorten in duration (Turbill & Prior, 2016) with global warming of 1.5 ^{o}C observed since pre-industrial levels (Allen et al., 2018). Under a regime of warming winter temperatures, there are a suite of changes such as the timing of food availability, lengthening growth periods and earlier reproduction. This has implications for hibernating species that may emerge earlier in spring and observe shifts in availability of seasonal food resources (i.e flowering plants) with uncertain effects on reproductive success and survival (Inouye et al., 2000; Koppmann-Rumpf, Heberer, & Schmidt, 2003; Adamík & Král, 2008). Thus, while climate change has been widely shown to affect species range limitations (e.g. Parmesan & Yohe, 2003), climate variation during winter may also have more direct negative consequences for hibernating species, such as the hazel dormouse with a relatively short active season in order to breed and gain enough weight to survive the following winter (Pretzlaff & Dausmann 2012).

Over winter survival is considered to be relatively high in hibernating small mammal species, (Turbill, Bieber, & Ruf, 2011) such as garden dormouse (Schaub & Vaterlaus-Schlegel, 2001) and edible dormouse (Lebl et al., 2011). Our results suggest that an increase in rainfall and temperature during the winter months are negatively correlated with adult survivorship. This decrease in survivorship could be attributable to a range of factors, such as a decrease in the length or continuity of dormouse hibernation bouts. Increased energetic expenditure due to hibernation arousal and lack of food resources can cause reduction in fat reserves, increasing starvation risk (Pretzlaff, Rau, & Dausmann, 2014; Pretzlaff et al., 2021). While this increase in energy use over winter may negatively impact survivorship during the early active season, for those individuals that survive it may have a double negative impact of reduced fecundity.

Juvenile survival exhibited a significant negative association with weather, yearly average temperature, and annual precipitation. The negative impact of increasing temperature we observed on juvenile survival over their first winter could be due to a reduction in torpor duration and being abnormally active while food is scarce. This is important given the general trend in increased annual temperature across all study sites. Dormice go into torpor during spring and summer when temperatures are less than ~14ºC and semi-torpor below ~19ºC (Juškaitis, 2005). Torpor reduces energy expenditure allowing individuals to shorten foraging times and possible exposure to predators (Liow et al., 2009). Thus, as a consequence of climatic changes such as rising temperatures, our results are consistent with the idea that species such as dormice may suffer from a deficit in energy reserves under conditions of erratic or increased winter and spring temperatures leading to a negative impact on fitness related traits.

Management implications

Forest management can impact animal abundance by affecting habitat complexity and the availability of nest sites or food resources (Chaudhary et al., 2016). Thus, management can have a major role in shaping the pattern of population demographics of the species which inhabit these forests (Lindenmayer, Franklin, & Fischer, 2006; Lacerda & Nimmo, 2010). Forest management is considered to have important effects on the population parameters of hazel dormice populations (Juškaitis, 2008; Sozio et al., 2016; Goodwin et al., 2018). Despite sometimes being associated with ancient, mature woodland habitat (Bright et al. 2006), across their range they are also associated with early, successional woodland (Juškaitis, 2014) where there is complex, woody understory and an abundance of food. We found that the Wyre population exhibited an increasing trend in abundance and survival. A former conifer plantation, Wyre has undergone management to restore deciduous woodland during the time period of our study (Trout et al. 2018), possibly creating more favorable conditions and increasing the availability of resources for hazel dormice. Hazel coppicing is a forest management practice that is considered to benefit dormice maintaining successional stasis that is ideal for the species (Bright et al. 2006) and small-scale felling has been shown to have positive impact on hazel dormice abundance in Lithuania (Juškaitis, 2020). However, there is still a lack of good evidence about the effectiveness of these practices for dormice or for other woodland species and, more broadly, there is a lack of evidence for the specific effectiveness of management practice for many specific species (Lindenmayer et al. 2006). Thus, while we identify some factors associated with population regulation in the hazel dormouse, we lack specific understanding for the role forest management practice may have for population change in dormice or other species.

Our results suggest that aspects of weather conditions are negatively associated with survivorship and fecundity in the hazel dormouse. While short term weather changes such as these can be shown to have a negative effect, it is important to consider long term patterns. Winter is a key season for hibernating species and fluctuations in temperature during this time can have serious consequences for individual fitness, due to a decreased in hibernation bouts, early emergence, and abnormal activity during periods of lower food availability. Our results are consistent with the expectation of negative impacts of climate change on hibernating species; these effects could be particularly important in species such as dormice that are sensitive to fragmentation, and changes in quality, of habitats that are essential to provide energy resources to survive winter and early spring (Fedyń, Figarski, & Kajtoch, 2021). Local conservation efforts can potentially mitigate these effects. In the hazel dormouse this may include tree felling and coppicing to increase forage and hibernation sites or improving woodland resilience through landscape management such as improving hedgerow quality and connectivity. Our analysis demonstrates that the pattern of population vital rates can broadly differ between populations in space and time, representing a great challenge for the future.

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Author contribution

FJC and EW and JE conceived the ideas and designed methodology; RJ and RT, SB, NF and IW collected the data; FJC and DN and EH analysed the data; FJC and EH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

Adamík, P., & Král, M. (2008). Climate- and resource-driven long-term changes in dormice populations negatively affect hole-nesting songbirds. *J. Zool.* **275**, 209–215.

Allen, M., Babiker, M., Chen, Y., Taylor, M., Tschakert, P., Waisman, R., Warren, P., & Zhai, P. (2018). Global warming of 1.5° C. An IPCC Special Report on the impacts of global warming of 1.5° C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate chang. Vol. 32.

Andrewartha, H. G., & Birch, L. C. (1954). The distribution and abundance of animals. *Chicago Univ. Press Chicago 37*.

Barker, T. (2007). Climate Change 2007 : An Assessment of the Intergovernmental Panel on Climate Change. *Change* **446**, 12–17.

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Softw.* **67**, 1–48.

Bjørnstad, O. N., & Grenfell, B. T. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science (80-.).* **293**, 638–43.

Bonebrake, T. C., Christensen, J., Boggs, C. L., & Ehrlich, P. R. (2010). Population decline assessment, historical baselines, and conservation. *Conserv. Lett.* **3**, 371–378.

Boyce, M. S., Haridas, C. V., Lee, C. T., Boggs, C. L., Bruna, E. M., Coulson, T., Doak, D., Drake, J. M., Gaillard, J. M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T., Mastrandrea, M., Menges, E. S., Morris, W. F., Pfister, C. A., & Tuljapurkar, S. D. (2006). Demography in an increasingly variable world. *Trends Ecol. Evol.* **21**, 141–148.

Boyce, M. S., & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends Ecol. Evol.* **14**, 268–272.

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integr. Comp. Biol.* **51**, 676–690.

Bright, P. W., Morris, P. A., & Mitchell-Jones, A. . (2006). The dormouse conservation handbook. *English Nat.* 75.

Buckland, S. T., Newman, K. B., Fernández, C., Thomas, L., & Harwood, J. (2007). Embedding Population Dynamics Models in Inference. *Stat. Sci.* **22**, 44–58.

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). *Ecol. Modell.* Vol. 172. New York, USA: Springer Science & Business Media.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., & Pollock, K. H. (1989). Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. *Am. Fish. Soc. Monogr.* **5**, 437.

Chaudhary, A., Burivalova, Z., Koh, L. P., & Hellweg, S. (2016). Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs. *Sci. Rep.* **6**, 23954.

Churcher, T. S., Filipe, J. A. N., & Basáñez, M. G. (2006). Density dependence and the control of helminth parasites. *J. Anim. Ecol.* **75**, 1313–1320.

Cordes, L. S., Blumstein, D. T., Armitage, K. B., CaraDonna, P. J., Childs, D. Z., Gerber, B. D., Martin, J. G. A., Oli, M. K., & Ozgul, A. (2020). Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc. Natl. Acad. Sci.* **117**, 18119–18126.

Coulson, T. (2001). Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. *Science (80-.).* **292**, 1528–1531.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841–2854.

Erb, J., Boyce, M. S., & Stenseth, N. C. (2001). Population dynamics of large and small mammals. *Oikos* **92**, 3–12.

Fahrig, L., & Paloheimo, J. (1988). Effect of spatial arrangement of habitat patches on local population size. *Ecology* **69**, 468–475.

Falvo, C. A., Koons, D. N., & Aubry, L. M. (2019). Seasonal climate effects on the survival of a hibernating mammal. *Ecol. Evol.* **9**, 3756–3769.

Fauteux, D., Stien, A., Yoccoz, N. G., Fuglei, E., & Ims, R. A. (2021). Climate variability and density-dependent population dynamics: Lessons from a simple High Arctic ecosystem. *Proc. Natl. Acad. Sci.* **118**, 2106635118.

Fedyń, I., Figarski, T., & Kajtoch, Ł. (2021). Overview of the impact of forest habitats quality and landscape disturbances on the ecology and conservation of dormice species. *Eur. J. For. Res.* **140**, 511–526.

Fietz, J., Pflug, M., Schlund, W., & Tataruch, F. (2004). Influences of the feeding ecology on body mass and possible implications for reproduction in the edible dormouse (Glis glis). *J. Comp. Physiol. B* **175**, 45–55.

Flowerdew, J. R., Amano, T., & Sutherland, W. J. (2017). Strong "bottom-up" influences on small mammal populations: State-space model analyses from long-term studies. *Ecol. Evol.* **7**, 1699–1711.

Gaillard, J. M., Mark Hewison, A. J., Klein, F., Plard, F., Douhard, M., Davison, R., & Bonenfant, C. (2013). How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecol. Lett.* **16**, 48–57.

Gamelon, M., Grøtan, V., Nilsson, A. L. K., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S., Røstad, O. W., Slagsvold, T., Walseng, B., Stenseth, N. C., & Sæther, B.-E. (2017). Interactions between demography and environmental effects are important determinants of population dynamics. *Sci. Adv.* **3**.

Gelman, A., & Rubin, D. B. (1992). Inference from Iterative Simulation Using Multiple Sequences. *Stat. Sci.* **7**, 457–472.

Genuer, R., Poggi, J. M., & Tuleau-Malot, C. (2010). Variable selection using random forests. *Pattern Recognit. Lett.* **31**, 2225–2236.

Gimenez, O., Lebreton, J. D., Choquet, R., & Pradel, R. (2018). R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models. *Methods Ecol. Evol.* **9**, 1749–1754.

Goodwin, C. E. D., Suggitt, A. J., Bennie, J., Silk, M. J., Duffy, J. P., Al-Fulaij, N., Bailey, S., Hodgson, D. J., & McDonald, R. A. (2018). Climate, landscape, habitat, and woodland management associations with hazel dormouse Muscardinus avellanarius population status. *Mamm. Rev.* **48**, 209–223.

Griffith, A. B., Salguero-Gómez, R., Merow, C., & Mcmahon, S. (2016). Demography beyond the population. *J. Ecol.* **104**, 271–280.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711.

Harris, W. E., Combe, F. J., & Bird, S. (2015). Using integrated population modelling in conservation monitoring: A case study in the common dormouse (Muscardinus avellanarius). *Folia Zool.* **64**, 330–336.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* **6**, e4794.

Hastings, A. (2010). Timescales, dynamics, and ecological understanding. *Ecology* **91**, 3471–3480.

Henderson, P. A., & Magurran, A. E. (2014). Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. *Proc. R. Soc. B Biol. Sci.* **281**, 20141336.

Hixon, M. A., & Johnson, D. W. (2009). Density Dependence and Independence. *Encycl. Life Sci.*

Humphries, M. M., Thomas, D. W., & Kramer, D. L. (2003). The Role of Energy Availability in Mammalian Hibernation: A Cost-Benefit Approach. *Physiol. Biochem. Zool.* **76**, 165–179.

Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. U. S. A.* **97**, 1630–1633.

Johnston, A. N., Christophersen, R. G., Beever, E. A., & Ransom, J. I. (2021). Freezing in a warming climate: Marked declines of a subnivean hibernator after a snow drought. *Ecol. Evol.* **11**, 1264–1279.

Juškaitis, R. (1997). Ranging and movement of the common dormouse Muscardinus avellanarius in Lithuania. *Acta Theriol. (Warsz).* **42**, 113–122.

Juškaitis, R. (1999). Winter mortality of the common dormouse (Muscardinus avellanarius) in

Lithuania. *Folia Zool.* **48**, 11–16.

Juškaitis, R. (2005). Daily torpor in free-ranging common dormice (Muscardinus avellanarius) in Lithuania. *Mamm. Biol.* **70**, 242–249.

Juškaitis, R. (2008). Long-term common dormouse monitoring: effects of forest management on abundance. *Biodivers. Conserv. 2008 1714* **17**, 3559–3565.

Juškaitis, R. (2013). Summer mortality in the hazel dormouse (Muscardinus avellanarius) and its effect on population dynamics. *Acta Theriol. (Warsz).* **59**, 311–316.

Juškaitis, R. (2014). The Common Dormouse Muscardinus avellanarius: Ecology, Population structure and Dynamics. 2nd Editio. Institute of Ecology of Vilnius University Publishers, Vilnius.

Juškaitis, R. (2020). Hazel dormice (Muscardinus avellanarius) in a regenerating clearing: the effects of clear-felling and regrowth thinning on long-term abundance dynamics. *Eur. J. Wildl. Res. 2020 664* **66**, 1–8.

Keith, D., Akçakaya, H. R., Butchart, S. H. M., Collen, B., Dulvy, N. K., Holmes, E. E., Hutchings, J. A., Keinath, D., Schwartz, M. K., Shelton, A. O., & Waples, R. S. (2015). Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa. *Biol. Conserv.* **192**, 247–257.

Kellner, K. (2019). jagsUI: a wrapper around ‘rjags’ to streamline ‘JAGS’ analyses. R package version 1.5.1.

Kéry, M., & Schaub, M. (2012). Bayesian Population Analysis using WinBUGS. *Bayesian Popul. Anal. using WinBUGS* 463–477.

Koppmann-Rumpf, B., Heberer, C., & Schmidt, K. H. (2003). Long term study of the reaction of the Edible Dormouse Glis glis (rodentia: gliridae) to climatic changes and its interactions with hole-breeding passerines. In *Acta Zool. Acad. Sci. Hungaricae*. Vol. 49, pp. 69–76.

Krebs, C. J. (2002). Two complementary paradigms for analysing population dynamics. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **357**, 1211–1219.

Lacerda, A. E. B. d, & Nimmo, E. R. (2010). Can we really manage tropical forests without knowing the species within? Getting back to the basics of forest management through taxonomy. *For. Ecol. Manage.* **259**, 995–1002.

Lebl, K., Bieber, C., Adamík, P., Fietz, J., Morris, P., Pilastro, A., & Ruf, T. (2011). Survival rates in a small hibernator, the edible dormouse: A comparison across Europe. *Ecography (Cop.).* **34**, 683–692.

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.

Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R., & Verheyen, W. (1997).

Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* **389**, 176–180.

Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol. Conserv.* **131**, 433–445.

Liow, L. H., Fortelius, M., Lintulaakso, K., Mannila, H., & Stenseth, N. C. (2009). Lower Extinction Risk in Sleep-or-Hide Mammals. *Am. Nat.* **173**, 264–272.

Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., & Guisan, A. (2010). Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biol. Conserv.* **143**, 2647–2657.

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecol. Lett.* **16**, 106–115.

Mackey, B. G., & Lindenmayer, D. B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *J. Biogeogr.* 1147–1166.

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M. P., Elston, D. A., Scott, E. M., Smith, R. I., Somerfield, P. J., & Watt, A. D. (2010). Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. *Trends Ecol. Evol.* **25**, 574–582.

Manning, J. A., Medill, S. A., & Mcloughlin, P. D. (2015). Climate fluctuations interact with local demography and resources to predict spatially dynamic adult sex ratios in a megaherbivore. *Oikos* **124**, 1132–1141.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L., & Ehrlich, P. R. (2002). Climate change hastens population extinctions. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 6070–6074.

Melbourne, B. A., & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**, 100–103.

Miller, T. E. X. (2007). Demographic models reveal the shape of density dependence for a specialist insect herbivore on variable host plants. *J. Anim. Ecol.* **76**, 722–729.

Morris, D. W., & Maceachern, J. T. (2010). Active density-dependent habitat selection in a controlled population of small mammals. *Ecology* **91**, 3131–3137.

Nowack, J., Stawski, C., & Geiser, F. (2017). More functions of torpor and their roles in a changing world. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **187**, 889–897.

Nowicki, P., Bonelli, S., Barbero, F., & Balletto, E. (2009). Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. *Oecologia* **161**, 227–239.

Ohlberger, J., Rogers, L. A., & Stenseth, N. C. (2014). Stochasticity and determinism: How density-independent and density-dependent processes affect population variability. *PLoS One* **9**, 6.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Payo-Payo, A., Genovart, M., Bertolero, A., Pradel, R., & Oro, D. (2016). Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. *Proc. R. Soc. B Biol. Sci.* **283**, 20153042.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proc. 3rd Int. Work. Distrib. Stat. Comput. (DSC 2003)* 20–22.

Pretzlaff, I., & Dausmann, K. (2012). Impact of Climatic Variation on the Hibernation Physiology of Muscardinus avellanarius. In *Living a Seas. World*. pp. 85–97. Berlin, Heidelberg: Springer.

Pretzlaff, I., Radchuk, V., Turner, J. M., & Dausmann, K. H. (2021). Flexibility in thermal physiology and behaviour allows body mass maintenance in hibernating hazel dormice. *J. Zool.* **314**, 1–11.

Pretzlaff, I., Rau, D., & Dausmann, K. (2014). Energy expenditure increases during the active season in the small, free-living hibernator Muscardinus avellanarius. *Mamm. Biol.* **79**, 208–214.

R Core Team. (2021). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing URL http://www.R-project.org/.

Richard, E., Simpson, S. E., Medill, S. A., & Mcloughlin, P. D. (2014). Interacting effects of age, density, and weather on survival and current reproduction for a large mammal. *Ecol. Evol.* **4**, 3851–3860.

Schaub, M., & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* **152**, 227–237.

Schaub, M., & Fletcher, D. (2015). Estimating immigration using a Bayesian integrated population model: choice of parametrization and priors. *Environ. Ecol. Stat.* **22**, 535–549.

Schaub, M., & Vaterlaus-Schlegel, C. (2001). Annual and seasonal variation of survival rates in the garden dormouse (Eliomys quercinus). *J. Zool.* **255**, 89–96.

Seebacher, F. (2009). Responses to temperature variation: integration of thermoregulation and metabolism in vertebrates. *J. Exp. Biol.* **212**, 2885–2891.

Slade, N. A. (1977). Statistical Detection of Density Dependence from a Series of Sequential Censuses. *Ecology* **58**, 1094–1102.

Sozio, G., Iannarilli, F., Melcore, I., Boschetti, M., Fipaldini, D., Luciani, M., Roviani, D., Schiavano, A., & Mortelliti, A. (2016). Forest management affects individual and population parameters of the hazel dormouse Muscardinus avellanarius. *Mamm. Biol.* **81**, 96–103.

Trout, R. C., Brooks, S., Combe, F. J., & Rudlin, P. (2018). The different effects of periodic experimental tree removal patterns on the population demography of the hazel dormice (Muscardinus avellanarius) in a conifer plantation. *Folia Zool.* **67**, 110–119.

Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc. R. Soc. B Biol. Sci.* **278**, 3355–3363.

Turbill, C., & Prior, S. (2016). Thermal climate-linked variation in annual survival rate of hibernating rodents: shorter winter dormancy and lower survival in warmer climates. *Funct. Ecol.* **30**, 1366–1372.

Turchin, P. (2003). Complex Population Dynamics: A Theoretical/Empirical Synthesis. *Monogr. Popul. Biol.* Princeton University Press.

Vasseur, D. A., & Fox, J. W. (2007). Environmental fluctuations can stabilize food web dynamics by increasing synchrony. *Ecol. Lett.* **10**, 1066–1074.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395.

White, I. (2012). The National Dormouse Monitoring Programme in Britain. *Peckiana* **8**, 103–107.

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., & Monserrat, V. J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–1146.

Zipkin, E. F., & Saunders, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. *Biol. Conserv.* **217**, 240–250.