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Density and climate effects on age-specific survival and 1

population growth: consequences for hibernating mammals 2

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20 Abstract

21 The impact of factors such as density dependence, food availability, and weather are known to be 22 important for predicting population change in a wide range of species. However, a challenge in 23 ecology is understanding the contributory and interactive role of these drivers on populations. This is 24 necessary to design effective conservation and management strategies. Using data from long-term 25 studies of five hazel dormouse populations in Europe, we tested the relationship between population 26 density and weather and their impact on demographic rates. We used an integrated population 27 modelling approach, estimating age-specific overwinter survival, annual population growth, and 28 fecundity rates. We found strong negative effects of population density, precipitation, and winter 29 temperature on population growth rates. This suggests that warmer and wetter weather negatively 30 affects dormouse survival for both adults and juveniles, but we found subtle differences in these 31 effects between age classes. We also identified an interaction between weather measures and 32 population density on age-specific survival, possibly as a result of weather impacts during 33 hibernation. Although we found low winter temperature was positively associated with population 34 growth, we found evidence consistent with density-dependence. We discuss our results in the context 35 of woodland habitat conservation management.

36 Introduction

37 Understanding the mechanisms underlying animal abundance is fundamental to ecology. This 38 understanding is necessary to predict population growth and therefore to inform species conservation 39 management (Krebs, 2002; Hastings, 2010). This is especially true in fragmented landscapes where 40 populations vary in size, demographic composition and connectivity, factors which are of key 41 importance for population persistence (Fahrig & Paloheimo, 1988; Boyce & McDonald, 1999; 42 Mackey & Lindenmayer, 2001). Thus, effective conservation monitoring requires data on abundance, 43 population growth, age specific survival, reproductive success, and dispersal in order to evaluate 44 population trends and identify factors influencing changes in population growth (Magurran et al., 45 2010; Keith et al., 2015). Population size is expected to show temporal and spatial variance due to 46 extrinsic factors, such as resource availability, predation, and local weather conditions, as well as 47 intrinsic factors such as population density (Bjørnstad & Grenfell, 2001; Melbourne & Hastings, 48 2008). These factors impact populations through their effects on demographic parameters such as 49 fecundity, survival, immigration and emigration, in turn driving variation in population growth rates. 50 Thus, the estimation of demographic rates through population monitoring can play a pivotal role in 51 understanding the complex interactions between demography and the environment in order to predict 52 population change and inform conservation management of at-risk species.

53 Conservation monitoring of populations is a challenge for many species owing to logistic constraints. 54 This is exacerbated for rare or elusive species which may be relatively difficult to detect or identify, 55 or which occur at low density (Lomba et al., 2010; Harris, Combe, & Bird, 2015). Further, some 56 species exhibit variation in their life history or conservation status over a wide geographical range, 57 leading to impediments in the collection of basic data, or spurious extrapolation due to difficulty in 58 long term monitoring of populations or sampling biases from small population sizes. As a result of 59 these issues, the basic population abundance for many species of conservation concern is uncertain 60 even when monitoring is conducted, due to lack of long-term data sets (Flowerdew, Amano, & 61 Sutherland, 2017). Because populations are expected to respond to conservation management, it is 62 critical to monitor this response to measure its impact (Buckland et al., 2007). Thus, a basic 63 requirement to measure conservation impact is population monitoring data and the biological and 64 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,

67 there is a history of debate surrounding the contribution of multiple environmental and density-68 dependent processes which act on population vital rates such as survival, recruitment and fecundity 69 (Andrewartha & Birch, 1954; Leirs et al., 1997; Nowicki et al., 2009; Ohlberger, Rogers, & Stenseth, 70 2014). However, ecological theory generally recognises population density dependence as an integral 71 process that often has a role in regulating population abundance (Henderson & Magurran, 2014). 72 Virtually all habitats are subject to environmental stochasticity in temperature and precipitation, often 73 at a local scale (Walther et al., 2002; Wilson et al., 2005), which may sometimes be extreme (Barker, 74 2007). Weather conditions may directly impact survivorship or fecundity due to changes in the 75 availability of food, shelter, or water (Vasseur & Fox, 2007; Loreau & de Mazancourt, 2013). There 76 is evidence that environmental stochasticity can alter the relationship between population density and 77 population vital rates (Miller, 2007; Richard et al., 2014; Manning, Medill, & Mcloughlin, 2015). 78 Such weather impacts may also interact with density dependence, e.g., through availability of 79 resources, leading to increased competition, that can strongly affect population dynamics. Such 80 processes can be complex (Coulson, 2001; Boyce et al., 2006), but may be essential to understand 81 population dynamics (Gamelon et al., 2017). As such, we require an understanding of how weather 82 factors, density dependence and the strength of interaction between these factors influence population 83 vital rates.

84 Weather conditions also may have a large impact on hibernating species (Inouye et al., 2000;

85 Nowack, Stawski, & Geiser, 2017), for example by altering the date of emergence or phenology, and 86 subsequently impacting survival or fecundity. Temperature variation may affect energetic state, water 87 reserves and thermoregulation during hibernation (Seebacher, 2009; Boyles et al., 2011). There is 88 evidence that hibernating species are susceptible to changes in precipitation and through phenological 89 changes in their active season, e.g. affecting mating activities or hibernation survival (Falvo, Koons, 90 & Aubry, 2019; Cordes et al., 2020; Johnston et al., 2021). Thus, in hibernating species it is 91 particularly important to consider the role of environmental conditions in maintaining homeostasis or 92 body mass for reproduction (Humphries, Thomas, & Kramer, 2003; Fietz et al., 2004; Pretzlaff et al., 93 2021). Finally, spatial variation in population demographics caused by environmental stochasticity is 94 poorly understood, motivating the study of demographic variation in replicated subpopulations that 95 may vary biologically and environmentally.

96 The hazel dormouse (*Muscardinus avellanarius*) is a small, semi-arboreal mammal associated with
97 deciduous and mixed coniferous woodlands in Europe that exhibits a long hibernation period (~ 6

98 months). The duration of hibernation varies geographically, being longer in more northern European 99 populations (Juškaitis, 2014). The hazel dormouse is characterised as having a small home range with 100 low dispersal, low fecundity and occurring at low population density in comparison to other small 101 mammals (Bright, Morris, & Mitchell-Jones, 2006). Because of a decline in its northern range due to 102 climate change and habitat degradation (Goodwin et al., 2017; 2018), it is a species of conservation 103 concern and strictly protected in Europe (Habitat Directive Annex IV, Bern Convention Annex III). 104 Hazel dormice are also known to be sensitive to seasonal variation in weather with high mortality in 105 variable winters, and reductions in activity and food availability during wetter spring and summer 106 periods (Juškaitis, 1999, 2013; Bright, Morris, & Mitchell-Jones, 2006). For these reasons, this 107 species has been the subject of long-term population monitoring and require active management and 108 habitat alteration over a wide geographical range, making it an ideal model to test the role of weather 109 in relation to population growth, survival and reproduction patterns.

110 This study aimed to investigate the importance of population density and weather conditions

111 associated with population size change in the hazel dormouse. We assessed these effects using long

112 term capture mark recapture (CMR), productivity and population count data across five populations

113 in the UK and Lithuania that vary in size, woodland management, and habitat composition.

114 Specifically, we compared variation in population growth and age-specific annual survivorship and

115 investigated the association between population density and climate variation with variation in

116 population size change. We discuss our findings in the context of conservation management for

117 hibernating mammals in the face of ongoing climate change.

118

119 Materials and Methods

120 Study sites and data sources

121 CMR data were collected in five hazel dormouse populations: The Perch (Somerset, UK), Wyre

122 Forest (Worcestershire, UK), Bontuchel (North Wales, UK), Wych (reintroduction site; Cheshire,

123 UK) and Šakiai (South West Lithuania, Šakiai district; see Fig.1). The Wych population is an

124 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

126 to 40-m intervals as part of the UK National Dormouse Monitoring program (NDMP) (White, 2012),

127 whilst the Lithuania boxes were spaced in a grid system at 50-m intervals. Each site was the subject

128 of long-term surveys of nest box occupancy to monitor trends in dormouse number and distribution. 129 Nest boxes were at a height of 2-4m mounted on posts or trees and distributed along transects. In the 130 UK populations, dormice were marked with 8mm passive implanted transponder (PIT) tags and in 131 the Lithuania population, dormice were marked with aluminum leg bands (inner diameter 2.5mm, 132 height 3.5mm). During each survey period nest boxes were checked for occupancy and individual 133 dormice were checked for PIT tag presence. For each captured individual we recorded age-class 134 (adult or juvenile), sex (in adults only), litter size (number of juveniles per female) and weight (g). 135 Unmarked individuals were marked with PIT tags or rings. All sites were monitored between May 136 and October. Wyre data were available for the period 2002-2016, Perch and Lithuania data were 137 available for 2007-2016, and Bontuchel and Wych data were available for 2005-2016. We analyzed 138 capture data for Wyre and Perch from monthly records taken for all 6 months between May and 139 October, inclusive. For Bontuchel and Wych, monthly records were available for the months May, 140 June, September and October. For Lithuania, records were available for the months April-October 141 inclusive. To facilitate direct comparison of the populations, and because the expected lifespan of 142 dormice in the wild is known to reach up to six years (Juškaitis, 2014), capture histories were 143 collapsed to yearly bins.

144

145





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

150 Bayesian integrated population model

- 151 Integrated population modeling (IPM) allows the simultaneous analysis of CMR and nest survey data
- 152 consisting of annual counts of dormice (unique individuals), to estimate spatial and temporal
- 153 demographic variation, and uncertainty in population parameter estimates (Zipkin & Saunders,
- 154 2018). This can compensate for variation in data by reducing biases inherent in small data sets and
- 155 can provide more precise estimates of demographic vital rates compared to CMR data alone (Schaub
- 156 & Abadi, 2011; Harris, Combe, & Bird, 2015). The nest survey data used in the IPM consisted of
- 157 annual number of uniquely identified adults (y), annual number of young produced (J), and the total
- 158 number of breeding adults (calculated from the annual total number of nests found, R). We
- 159 transformed the CMR data in the m-array format (Burnham et al., 1989) for juveniles (< 6months
- 160 old) and adults (\geq 6months old). The dormouse nest survey counts and CMR data were modelled
- 161 with an IPM for each population to estimate: age-specific annual survival (ϕ), population growth rate
- 162 (λ) , fecundity (f) and population sizes (N_t) (Supplementary Fig. S1).
- 163 Estimation of model parameters

164 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

166 estimate the survival probability of juveniles born in year t to become one year old in year $t+1 \phi_{juv,t}$,

167 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 betweenyears.

170 The annual number of young produced were analysed to estimate fecundity (f_t) , the number of

171 offspring per adult female, which was considered a latent variable. We assumed a Poisson

172 distribution with the expected value being the product of fecundity and the annual number of

173 surveyed nests (R_t): $J_t \sim \text{Poisson}(R_t f_t)$.

174 Between-year variation in fecundity was modelled as: $log(f_t) = log(\mu_f) + \varepsilon_{f,t}$,

175 where $\log(\mu_f)$ denotes the natural logarithm of average fecundity and $\varepsilon_{f,t}$ the year-specific deviation 176 from this value. We model these deviations as random effects and hence $\varepsilon_{f,t} \sim \text{Normal}(0, \sigma.\varepsilon)$, where 177 $\sigma. \varepsilon$ is the temporal variability of fecundity. In order to make the immigration process comparable to 178 survival and fecundity, we specified annual immigration as a rate (i_t) , which is the proportion of 179 immigrants in year *t*+1 with respect to the population size in year *t*. Again, we modelled immigration 180 with temporal random effects:

181 $\operatorname{Log}(i_t) = \log(\mu_i) + \varepsilon_i_t$

- 182 $\varepsilon i_t \sim \text{Normal}(0, \sigma.\varepsilon.i)$
- 183 where μ_i is the average immigration rate and $\sigma.\varepsilon.i$ is the temporal variability of immigration rate.

184

185 Thus, we assumed that the populations were open to unobserved movement of young individuals

186 (Juškaitis, 1997) to and from the monitored populations (N_{im}) to prevent overestimation when

187 immigration is relatively small (Schaub & Fletcher, 2015).

- 189 To estimate model parameters we used an IPM that was defined by the joint likelihoods of all the 190 available data sets (population counts, CMR, productivity data).
- We used a pre-breeding census population model that included demographic and environmentalstochasticity:
- 193
- 194 $N_{juv,t+1} \sim Poisson((N_{1,t}+N_{ad,t}+N_{im,t}) \ge f_t/2 \ge \phi_{j,t})$
- 195 $N_{ad,t+1} \sim Binomial((N_{1,t}+N_{ad,t}+N_{im,t}), \phi_{ad,t})$
- 196 $N_{im,t+1} \sim Poisson((N_{1,t}+N_{ad,t}+N_{im,t}) \times i_t)$
- 197

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:

203

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

204 The annual counts (*y*_t) were modelled with a Poisson distribution conditional on the estimated

- 205 populations size, hence:
- 206 $y_t \sim \text{Poisson}(N_{\text{tot},t})$

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*:

209 $\lambda_t = (N_{tot,t}+1)/(N_{tot,t})$

- 210 Model implementation
- 211 We first ran goodness-of-fit tests on our CMR model using the R package R2ucare version 1.02
- 212 (Gimenez et al., 2018), with the results suggesting a good fit across sites for use in the IPMs
- 213 (Bontuchel: $\chi 2 = 10.531$, df = 6; P = 0.105, Lithuania: $\chi 2 = 2.821$, df = 6; P = 0.508; Wyre: $\chi 2 = 5.99$,

214 df = 6; P = 0.424; Perch: χ^2 = 17.32, df = 10; P = 0.098; Wych: χ^2 = 9.483, df = 6; P = 0.107). We 215 obtained posterior distributions of population growth rate, fecundity and survival for each population 216 separately from the IPM as defined above, using Markov chain Monte Carlo (MCMC) simulation 217 implemented in JAGS version 3.4.0 (Plummer, 2003) called from R version 4.0.5 (R Core Team, 218 2021) with the R package jagsUI version 1.5.2 (Kellner, 2019). For all parameters we defined vague 219 priors (see code for details). To assess convergence, we ran four independent chains of 400,000 220 MCMC iterations with different starting values, with a burn-in of 50,000 iterations, thinning every 221 100th observation resulting in 3,500 posterior samples. We confirmed model convergence using the 222 Gelman-Rubin statistic (Gelman & Rubin, 1992) and visual inspection of chains (JAGS code for 223 fitting the IPM is available in Appendix S2). The R-hat score ($\hat{R} \le 1.04$) was evaluated for all 224 parameter estimates and we summarized posterior distributions by their means and 95% credible

225 intervals (CRI).

226 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

233 growth rate as population abundance increases.

234 Weather data

235 Annual mean temperature (°C) and precipitation (mm) data (within 10km of each site) were obtained 236 from the R package weatherData version 0.6 (Narasimhan, 2014). We compiled the weather data for 237 spring (March-May), summer (June-August), autumn (September-November) and winter (December-238 February). Thus, temperature and precipitation data were grouped by season and year. Additional 239 weather variables were compiled for winter months, including temperature range and maximum, and 240 the number of days above 10 °C, and NAO (North Atlantic Oscillation) index scores. Explanatory 241 variables did not exhibit significant multicollinearity, and thus they were retained in our analysis (for 242 definition of weather variables see appendix S1).

245 Post hoc statistical analyses of weather variables and population density

246 We analyzed the association of environmental variables with our estimates of population density (per 247 hectare), fecundity and survival. To identify a subset of variables of high explanatory value, we used 248 the R package RandomForest version 4.7 for variable selection (Genuer, Poggi, & Tuleau-Malot, 249 2010). We ranked weather variable importance against parameter estimates and retained the ten most 250 important ones for further analysis (Supplementary Table S1). We used model averaging on the 251 remaining explanatory variables in a mixed effect framework for all further analyses, using the R 252 package lme4 version 1.1 (Bates et al., 2015) and the dredge and model.avg functions of the package 253 MuMin version 1.47 (Barton, 2015; Burnham & Anderson, 2002; Harrison et al., 2018), treating both 254 year and population as random effects. We included two-way interactions in our models (i.e., 255 between density and each weather variable) to investigate whether density mediated the effect of 256 weather variables (or vice versa) on demographic rates. We tested each linear model met normality 257 and homoscedasticity testing assumptions using the R package lme4 version 1.1 (Bates et al., 2015) 258 before continuing data analyses (Supplementary Figure S2). We log transformed fecundity and 259 Juvenile survival to meet the test of normality assumptions. Wych and Perch were excluded from 260 analysis of juvenile survival due to low number of captured juveniles. We highlight model estimates 261 with 95% confidence intervals not intersecting zero (e.g. as used in Grueber et al., 2011).

262 **Results**

263 Demographic estimates from the IPMs

264 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.

266 The other three populations, Wyre, Perch and Wych, had 850 (number of marked individuals = 464),

267 314 (number of marked individuals = 192) and 298 (number of marked individuals = 273) capture

268 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
- 270 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
- 276 growth rates over all years showed strong spatio-temporal variation. Populations in Wyre (λ =1.116,
- 277 95% CRI 0.888, 1.824) and Bontuchel (λ =1.05, CRI = 0.108, 0.129) both increased, while the
- 278 Lithuanian (λ =0.910, 95% CRI 0.778, 1.033), Perch (λ =0.949, 95% CRI 0.727, 1.102) and Wych
- 279 populations (λ =0.840, 95% CRI 0.565, 1.304) declined. Both Wyre and Perch showed a rapidly
- 280 increasing population trajectories in the first two years of study as seen in the growth rates however,
- these populations declined steadily thereafterFig.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).

292	Annual adult ($\phi_{ad,t}$) and juvenile survival ($\phi_{juv,t}$) estimates are shown for each population in Figure 3.
293	Adult survival was similar among populations, while juvenile survival varied between populations,
294	with much lower estimates in the Perch populations. Mean fecundity (f) was highest in Bontuchel
295	(4.33, CRI=3.02, 4.74) followed by Lithuania (3.21, 95% CRI 3.04, 3.7), Wyre (2.803, 95% CRI
296	2.401, 3.235), Perch (1.830, 95% CRI 1.508, 2.212) and Wych (0.844, 95% CRI 0.589, 0.989).
297	Estimates of immigration rate adult individuals was low among all populations (Bontuchel = 0.490
298	95%, CRI, 0.309, 1.326, Wyre = 0.98 95% CRI, 0.77, 3.803, Perch = 0.178 95% CRI 0.00, 0.810,
299	Wych = $0.165\ 95\%\ CRI\ 0.00,\ 0.493$); Lithuania estimates indicated zero immigration over the study
300	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.

307 *Density dependence in growth rate*

308 Annual population growth rates in relation to density of hazel dormouse (per hectare) are shown in

309 Fig. 4. Four out of the five populations showed a significant negative relationship between population

310 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

312 Perch (Slope = -0.456, P = 0.024) and Wyre (Slope = -1.376, P = 0.014) both exhibited a less

313 pronounced but significant negative relationship between population growth and density (for full

314 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).



317

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.

323

324 Observed weather variation

325 During the study period 2002-2016, yearly average temperature in the UK ranged from 9.2 to 11.1

326 °C, and in Lithuania from 6.3 to 8.2 °C. In winter, average temperature in the UK was 5.3 °C, and in

327 Lithuania was -2.3 °C. Winter precipitation in the UK ranged from 176 to 556 mm, and in Lithuania

328 from 98 to146 mm. The range of mean winter temperatures varied from 3.7 °C in Bontuchel to a

329 maximum of 8.5 °C in Perch with a mean range for all populations of 5.2 °C. 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 precipitationin all populations. For a full summary of weather variables see Supplementary table S3.

333

334 Weather effects on demography

335 Population density) and MTR winter (mean temperature range winter) had a negative association 336 with population growth (Table 1). Meanwhile, effect estimates of Winter PRCP and NAO index were 337 negligibly different from zero. Density and Annual temperature were the most important predictors 338 for fecundity (Table 1). Density had a strong negative effect on fecundity whilst annual temperature 339 had a positive effect on fecundity. Annual PRCP and MT winter had only a weak effect. We found 340 no evidence of an interaction effect for population growth or fecundity with weather explanatory 341 variables. 342 Our main results for adult and juvenile survival are as follows (a complete account of results is

342 Our main results for adult and juvenile survival are as follows (a complete account of results is

343 available in Supplementary Table S4). We found density had a negative effect on adult survival and

344 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

347 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.



350

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 (°C), winter average temperature (°C) and number of days above 10 °C. Black dots show data points, blue line indicates linear trend and grey shaded area indicates the standard error.

356

357

359 Table 1. Parameter estimates (β) and 95% confidence intervals from model averaging results using 360 mixed effect models of each explanatory weather variable for each dependent variable (population 361 growth (λ), fecundity (f), adult and juvenile survival (ϕ)) and interaction effects between density and 362 weather variables. Dependant variables were calculated from Integrated population models fit to 363 individual and nest count, and capture-mark-recapture data for four UK populations (Bontuchel, 364 Perch, Wych and Wyre) and one Lithuanian populations of hazel dormice. Model terms with 95% 365 confidence intervals not intersecting zero are shown in **bold**. For definition of explanatory variables 366 see Supplementary table S1.

		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				
Explanatory	N of Days ^10oC			-0.003 (-0.004/-0.001)	
Variable	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)	

Dependent Variable

368

367

369

370 Discussion

371 We investigated the effects of population density and weather on the population dynamics in the 372 Hazel dormouse and found evidence that density dependence is very important for dormouse survival 373 for both juveniles and adults, and for fecundity. These results suggests that available resources such 374 as food or overwinter nest sites may limit individual reproduction and survival. We found that 375 precipitation and winter temperature had strong negative associations with population growth, 376 suggesting that warmer and wetter winters during hibernation periods have negative impacts on 377 populations reducing population growth rates. We found a negative interaction between temperature 378 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.

384 There is a breadth of research focusing on understanding density dependence in populations 385 (Turchin, 2003; Churcher, Filipe, & Basáñez, 2006; Morris & Maceachern, 2010). However, less 386 well understood is how density dependence may interact with environmental variation, such as 387 climate change or habitat structural complexity, to drive population abundance (Griffith et al., 2016). 388 As long-term and large spatial scale data become available, scientific understanding of causation in 389 population ecology and these environmental interactions is improving. Survival rates often vary 390 between sexes and age classes (Lebreton et al., 1992), e.g. in mammals, (Gaillard et al., 2013) and 391 birds (Payo-Payo et al., 2016). While we found negative effects of population density and 392 temperature on survival in both adults and juveniles, in adults we found that winter temperature and 393 precipitation negatively affected over-winter survival in this hibernating species. In juveniles, we 394 found annual temperature and precipitation to be negatively associated with survival (with a low 395 effect size). These results suggest that weather variation can affect adult and juvenile survival in 396 subtle and complex ways, possibly by imposing negative constraints on life-history traits associated 397 with hibernation. On the other hand, we found an interaction between weather and density in 398 association with survival. As a consequence the cumulative effect of poor weather conditions 399 interacting with periods of high density may have a much stronger negative effect, such as population 400 crashes during these time periods (Fauteux et al., 2021). However, further research on the interaction 401 between climate and density in relation to individual energetic states is required to fully understand 402 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 localscale 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

410 other sites, such as low shrub density and woodland dominated by holly and sycamore that are

411 considered less favorable habitat.

412 Implications of weather variability

413 We found that an increase in environmental climatic variation per se (e.g. temperature ranges in 414 winter) was negatively associated with population growth rate and that this explained a significant 415 part of the variability of survival and fecundity in the hazel dormouse. While the mean of weather 416 variables has been implicated in negative impacts on vital rates, the mechanisms underlying climate-417 induced population change are poorly understood (McLaughlin et al., 2002). While our results 418 suggests that warmer winter weather, comprising increased average temperatures and rainfall during 419 winter, negatively affect dormouse survival for adults, for juveniles we found they were negatively 420 impacted by warmer and wetter weather during the annual time period. A cause for this age specific 421 difference may be the energetic expenditure of reproduction and overwintering in adults (Pretzlaff et 422 al., 2021) whilst juveniles may be more susceptible to more sudden local climate variability due to 423 building of energy reserves for their first year. Global warming in the northern latitudes during winter 424 months is thought to have negative consequences for many species, and this trend may continue as 425 mean winter temperatures are predicted to rise and winter periods shorten in duration (Turbill & 426 Prior, 2016) with global warming of 1.5 °C observed since pre-industrial levels (Allen et al., 2018). 427 Under a regime of warming winter temperatures, there are a suite of changes such as the timing of 428 food availability, lengthening growth periods and earlier reproduction. This has implications for 429 hibernating species that may emerge earlier in spring and observe shifts in availability of seasonal 430 food resources (i.e flowering plants) with uncertain effects on reproductive success and survival 431 (Inouye et al., 2000; Koppmann-Rumpf, Heberer, & Schmidt, 2003; Adamík & Král, 2008). Thus, 432 while climate change has been widely shown to affect species range limitations (e.g. Parmesan & 433 Yohe, 2003), climate variation during winter may also have more direct negative consequences for 434 hibernating species, such as the hazel dormouse with a relatively short active season in order to breed 435 and gain enough weight to survive the following winter (Pretzlaff & Dausmann 2012).

436 Over winter survival is considered to be relatively high in hibernating small mammal species,

437 (Turbill, Bieber, & Ruf, 2011) such as garden dormouse (Schaub & Vaterlaus-Schlegel, 2001) and

438 edible dormouse (Lebl et al., 2011). Our results suggest that an increase in rainfall and temperature

- 439 during the winter months are negatively correlated with adult survivorship. This decrease in
- 440 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.

446 Juvenile survival exhibited a significant negative association with weather, yearly average 447 temperature, and annual precipitation. The negative impact of increasing temperature we observed on 448 juvenile survival over their first winter could be due to a reduction in torpor duration and being 449 abnormally active while food is scarce. This is important given the general trend in increased annual 450 temperature across all study sites. Dormice go into torpor during spring and summer when 451 temperatures are less than ~14°C and semi-torpor below ~19°C (Juškaitis, 2005). Torpor reduces 452 energy expenditure allowing individuals to shorten foraging times and possible exposure to predators 453 (Liow et al., 2009). Thus, as a consequence of climatic changes such as rising temperatures, our 454 results are consistent with the idea that species such as dormice may suffer from a deficit in energy 455 reserves under conditions of erratic or increased winter and spring temperatures leading to a negative 456 impact on fitness related traits.

457 Management implications

458 Forest management can impact animal abundance by affecting habitat complexity and the availability 459 of nest sites or food resources (Chaudhary et al., 2016). Thus, management can have a major role in 460 shaping the pattern of population demographics of the species which inhabit these forests 461 (Lindenmayer, Franklin, & Fischer, 2006; Lacerda & Nimmo, 2010). Forest management is 462 considered to have important effects on the population parameters of hazel dormice populations 463 (Juškaitis, 2008; Sozio et al., 2016; Goodwin et al., 2018). Despite sometimes being associated with 464 ancient, mature woodland habitat (Bright et al. 2006), across their range they are also associated with 465 early, successional woodland (Juškaitis, 2014) where there is complex, woody understory and an 466 abundance of food. We found that the Wyre population exhibited an increasing trend in abundance 467 and survival. A former conifer plantation, Wyre has undergone management to restore deciduous 468 woodland during the time period of our study (Trout et al. 2018), possibly creating more favorable 469 conditions and increasing the availability of resources for hazel dormice. Hazel coppicing is a forest 470 management practice that is considered to benefit dormice maintaining successional stasis that is 471 ideal for the species (Bright et al. 2006) and small-scale felling has been shown to have positive

472 impact on hazel dormice abundance in Lithuania (Juškaitis, 2020). However, there is still a lack of 473 good evidence about the effectiveness of these practices for dormice or for other woodland species 474 and, more broadly, there is a lack of evidence for the specific effectiveness of management practice 475 for many specific species (Lindenmayer et al. 2006). Thus, while we identify some factors associated 476 with population regulation in the hazel dormouse, we lack specific understanding for the role forest 477 management practice may have for population change in dormice or other species.

478 Our results suggest that aspects of weather conditions are negatively associated with survivorship and 479 fecundity in the hazel dormouse. While short term weather changes such as these can be shown to 480 have a negative effect, it is important to consider long term patterns. Winter is a key season for 481 hibernating species and fluctuations in temperature during this time can have serious consequences 482 for individual fitness, due to a decreased in hibernation bouts, early emergence, and abnormal activity 483 during periods of lower food availability. Our results are consistent with the expectation of negative 484 impacts of climate change on hibernating species; these effects could be particularly important in 485 species such as dormice that are sensitive to fragmentation, and changes in quality, of habitats that 486 are essential to provide energy resources to survive winter and early spring (Fedyń, Figarski, & 487 Kajtoch, 2021). Local conservation efforts can potentially mitigate these effects. In the hazel 488 dormouse this may include tree felling and coppicing to increase forage and hibernation sites or 489 improving woodland resilience through landscape management such as improving hedgerow quality 490 and connectivity. Our analysis demonstrates that the pattern of population vital rates can broadly 491 differ between populations in space and time, representing a great challenge for the future.

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498 Author contribution

499 FJC and EW and JE conceived the ideas and designed methodology; RJ and RT, SB, NF and

500 IW collected the data; FJC and DN and EH analysed the data; FJC and EH led the writing of the

501 manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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