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# 1 **Density and climate effects on age-specific survival and** 2 **population growth: consequences for hibernating mammals**

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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.

65 Demographic information, for example data collected by mark-recapture studies, is essential in order  
66 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*

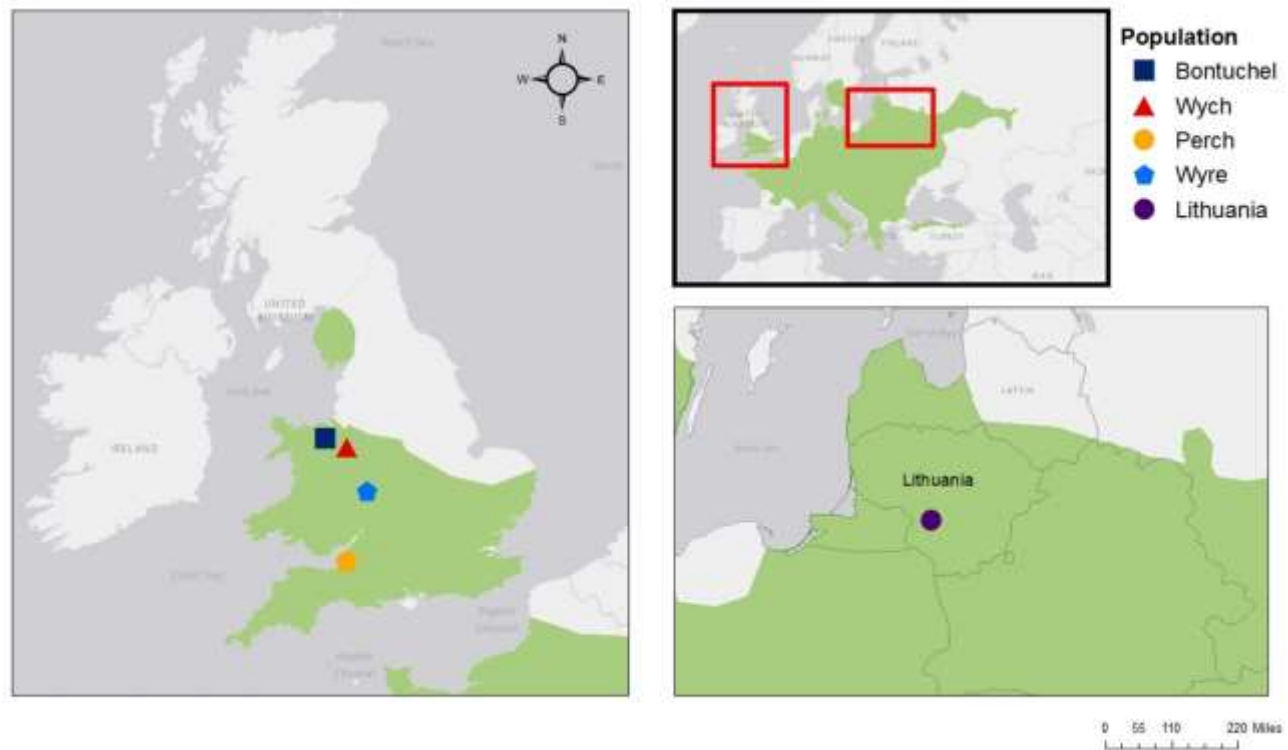
121 CMR data were collected in five hazel dormouse populations: The Perch (Somerset, UK), Wyre  
122 Forest (Worcestershire, UK), Bontuchel (North Wales, UK), Wych (reintroduction site; Cheshire,  
123 UK) and Šakiai (South West Lithuania, Šakiai district; see Fig.1). The Wych population is an  
124 established reintroduced population, part of the UK Species Recovery Program that released captive  
125 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

146



147

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 ( $< 6$  months  
 160 old) and adults ( $\geq 6$  months old). The dormouse nest survey counts and CMR data were modelled  
 161 with an IPM for each population to estimate: age-specific annual survival ( $\phi$ ), population growth rate  
 162 ( $\lambda$ ), 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-  
 165 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  
 168 winter, a juvenile was assumed to be an adult. Recapture probability was assumed to vary between  
 169 years.

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:

$$181 \quad \text{Log}(i_t) = \log(\mu_i) + \varepsilon_{i,t}$$

$$182 \quad \varepsilon_{i,t} \sim \text{Normal}(0, \sigma.\varepsilon.i)$$

183 where  $\mu_i$  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).



188

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).

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

193

$$194 N_{juv,t+1} \sim \text{Poisson}((N_{1,t}+N_{ad,t}+N_{im,t}) \times f_t/2 \times \phi_{j,t})$$

$$195 N_{ad,t+1} \sim \text{Binomial}((N_{1,t}+N_{ad,t}+N_{im,t}), \phi_{ad,t})$$

$$196 N_{im,t+1} \sim \text{Poisson}((N_{1,t}+N_{ad,t}+N_{im,t}) \times i_t)$$

197

198 where the number of 1-year old individuals in the population is denoted with  $N_{juv}$  and, the number of  
199 adults in the population with  $N_{ad,t}$  and the number of immigrants as  $N_{im}$ ,  $f_t$  was the number of  
200 offspring produced per adult female at time  $t$ ,  $\phi_{juv,t}$  and  $\phi_{ad,t}$  were the apparent survival probabilities of  
201 juveniles and adults, respectively, from time  $t$  to  $t + 1$ , and  $i_t$  is the immigration rate. The total  
202 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:

$$206 y_t \sim \text{Poisson}(N_{tot,t})$$

207 We calculated the annual population growth rate ( $\lambda_t$ ) from the estimated total population size ( $N_{tot}$ ) in  
208 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:  $\chi^2 = 17.32$ ,  $df = 10$ ;  $P = 0.098$ ; Wych:  $\chi^2 = 9.483$ ,  $df = 6$ ;  $P = 0.107$ ). 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 ( $\hat{R} \leq 1.04$ ) was evaluated for all  
224 parameter estimates and we summarized posterior distributions by their means and 95% credible  
225 intervals (CRI).

#### 226 *Density dependence*

227 To evaluate the role of population density and weather variables, we converted population abundance  
228 ( $N_{tot,t}$ ) to density of dormice per hectare for each year at each population. To test the effect of density  
229 dependence we modelled the population growth rate ( $\lambda_t$ ) as a function of population density per  
230 hectare for the previous year (Slade, 1977; Hixon & Johnson, 2009). Thus, we interpreted the  
231 regression coefficient as the strength of density dependence and evaluated it against zero. Here, a  
232 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 ( $^{\circ}\text{C}$ ) 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  $10^{\circ}\text{C}$ , 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).

243

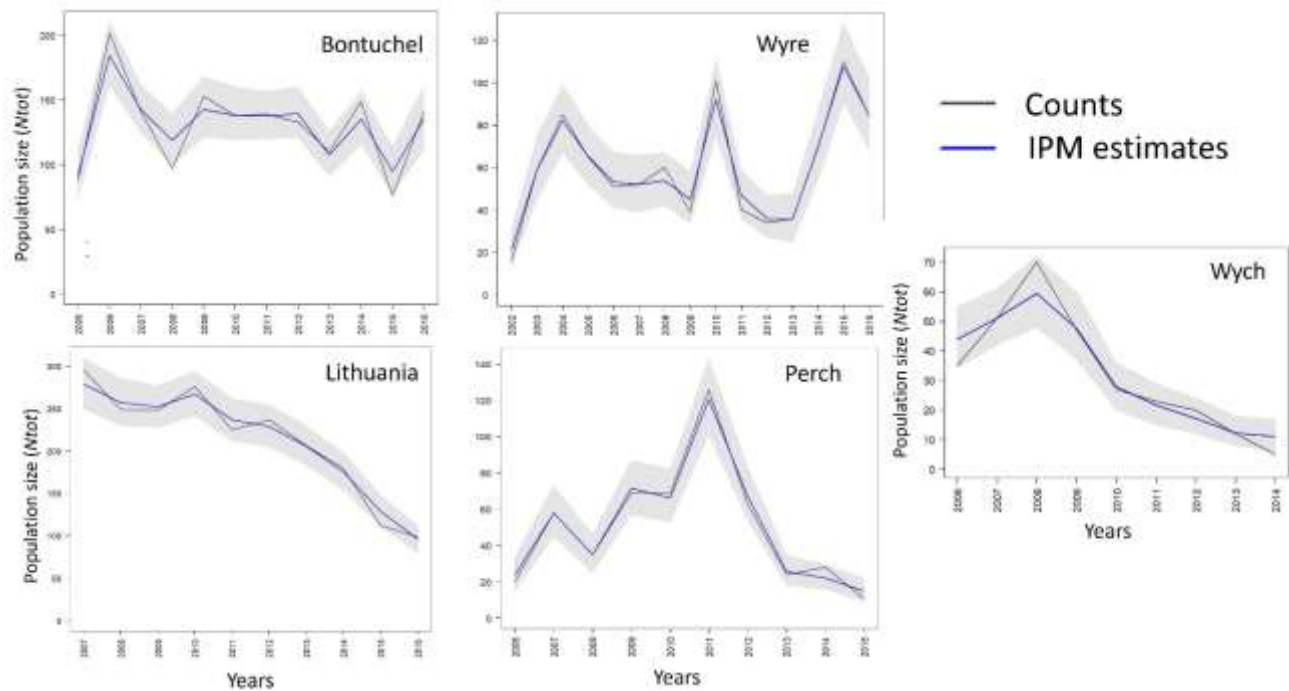
*245 Post hoc statistical analyses of weather variables and population density*

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  
265 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  
269 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  
271 individuals to a high in 2015 of 110. The populations in Perch and Wyre were both increasing in  
272 early years, however, in both populations there was a dramatic decline over the study period (Perch,  
273 high=126, low=22; Wych, high=63, low=11). In Lithuania the population fluctuated highly across

274 the study period with a rapid decline from a high of 271 in 2007 to a low of 140 in 2016. Population  
 275 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 ( $\lambda=1.116$ ,  
 277 95% CRI 0.888, 1.824) and Bontuchel ( $\lambda=1.05$ , CRI = 0.108, 0.129) both increased, while the  
 278 Lithuanian ( $\lambda=0.910$ , 95% CRI 0.778, 1.033), Perch ( $\lambda=0.949$ , 95% CRI 0.727, 1.102) and Wych  
 279 populations ( $\lambda=0.840$ , 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,  
 281 these populations declined steadily thereafter (Fig. 2).

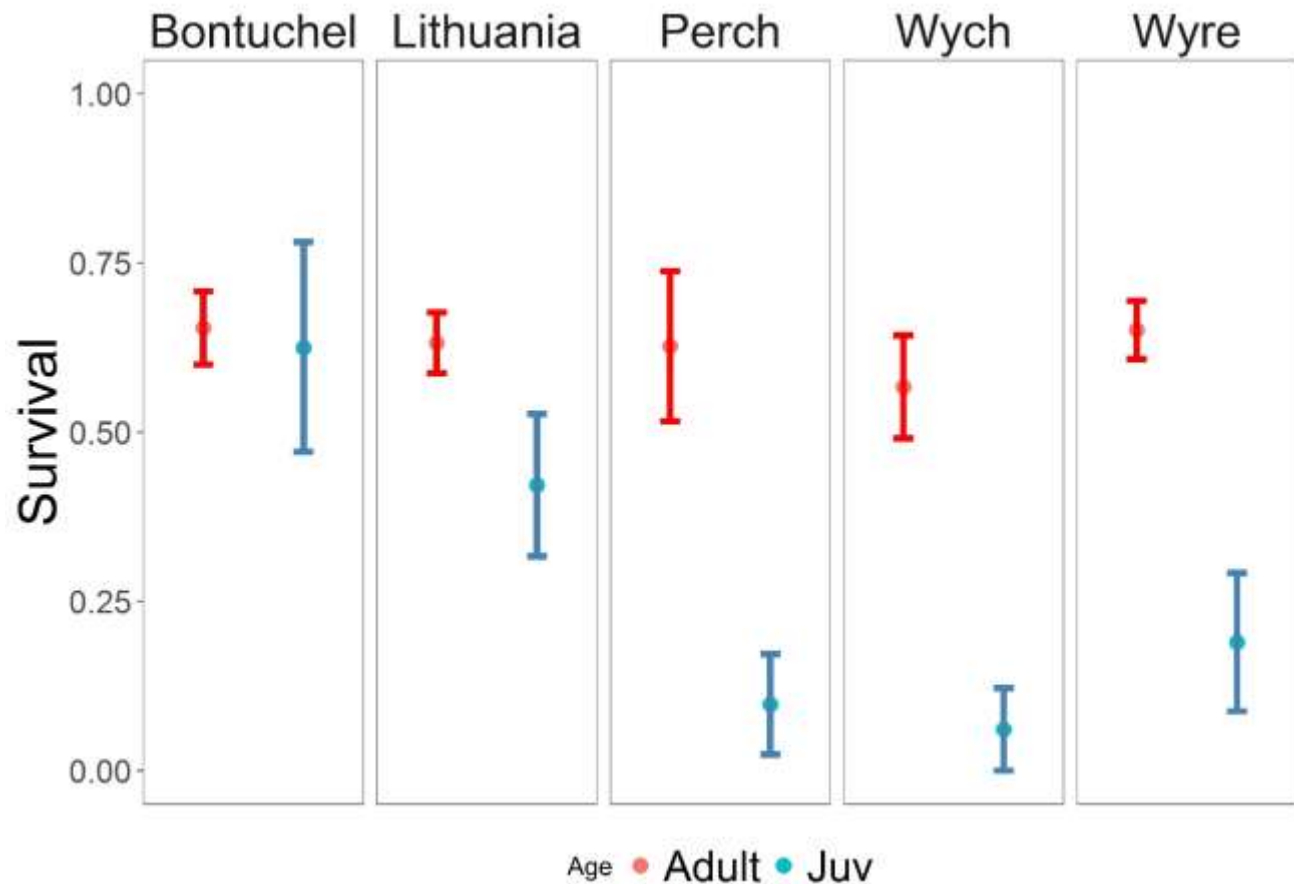


282  
 283  
 284  
 285 Figure 2. Time series of estimated total population size ( $N_{tot}$ ) of hazel dormouse for four UK  
 286 populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population, estimated with  
 287 Integrated Population Models (IPM) fit to individual and nest count, and capture-mark-recapture  
 288 data. The observed count data from surveys is the black line, the solid blue line shows the posterior  
 289 median calculated from each IPM, and the shaded grey region indicates the 95% credible interval  
 290 (CRI).

291

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.

301

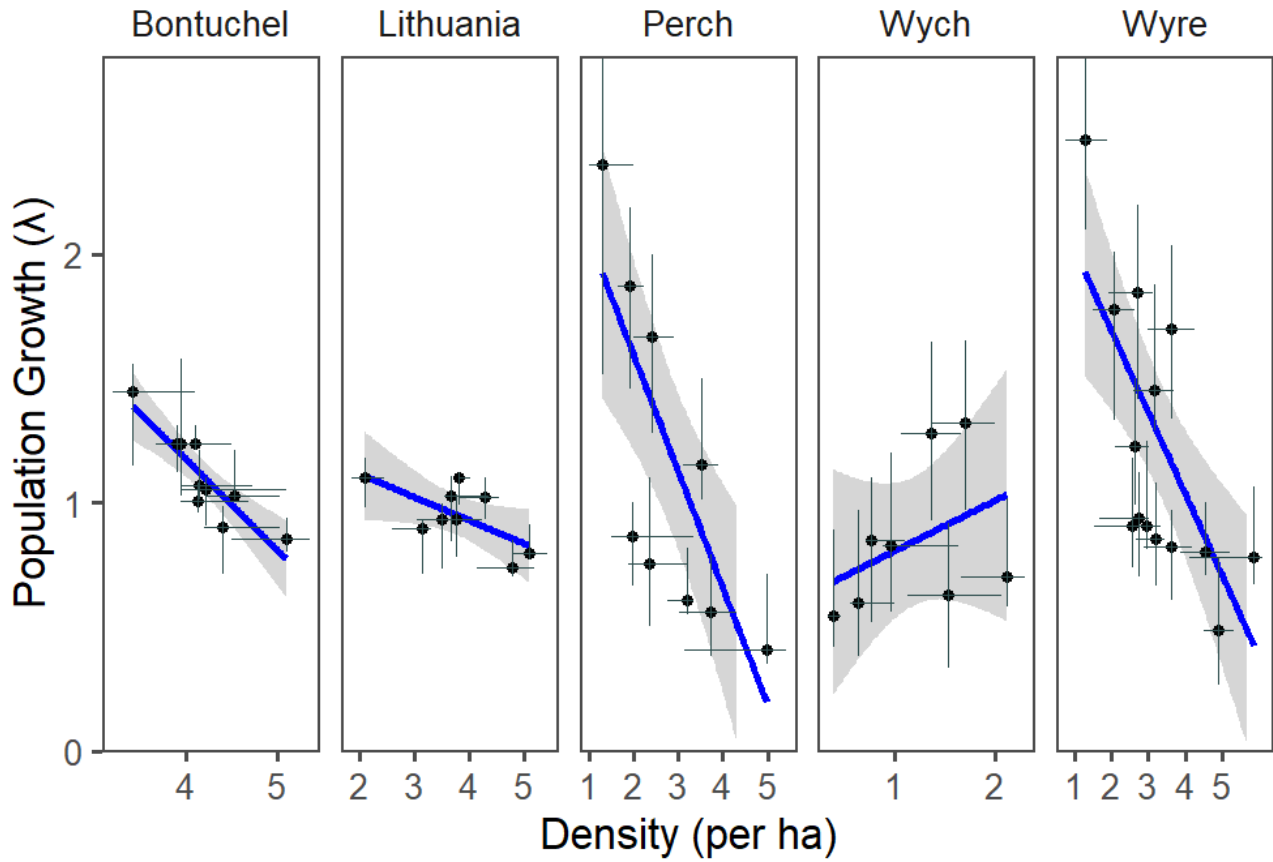


302

303 Figure 3. Juvenile (blue) and adult (red) annual survival probabilities of hazel dormice from four UK  
 304 populations (Bontuchel, Perch, Wych and Wyre) and one Lithuanian population estimated with  
 305 Integrated Population Models fit to individual and nest count, and capture-mark-recapture data. Dots  
 306 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  
 311 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  
 315 relationship between population growth and density (Slope = 0.781, P = 0.329).



316

317

318 Figure 4. Annual population growth rate ( $\lambda$ ) as a function of hazel dormouse density (per ha) in  
 319 previous year.  $\lambda$  was calculated from Integrated population models fit to individual and nest count,  
 320 and capture-mark-recapture data for four UK populations (Bontuchel, Perch, Wych and Wyre) and  
 321 one Lithuanian population. Each circle is the annual posterior mean with 95% credible interval bars,  
 322 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 to 146 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  
 330 varied widely with the UK populations, ranging from 820 to 1410 mm, and in Lithuania from 425 to

331 820 mm. During the study period, there was a small increasing trend in temperature and precipitation  
332 in all populations. For a full summary of weather variables see Supplementary table S3.

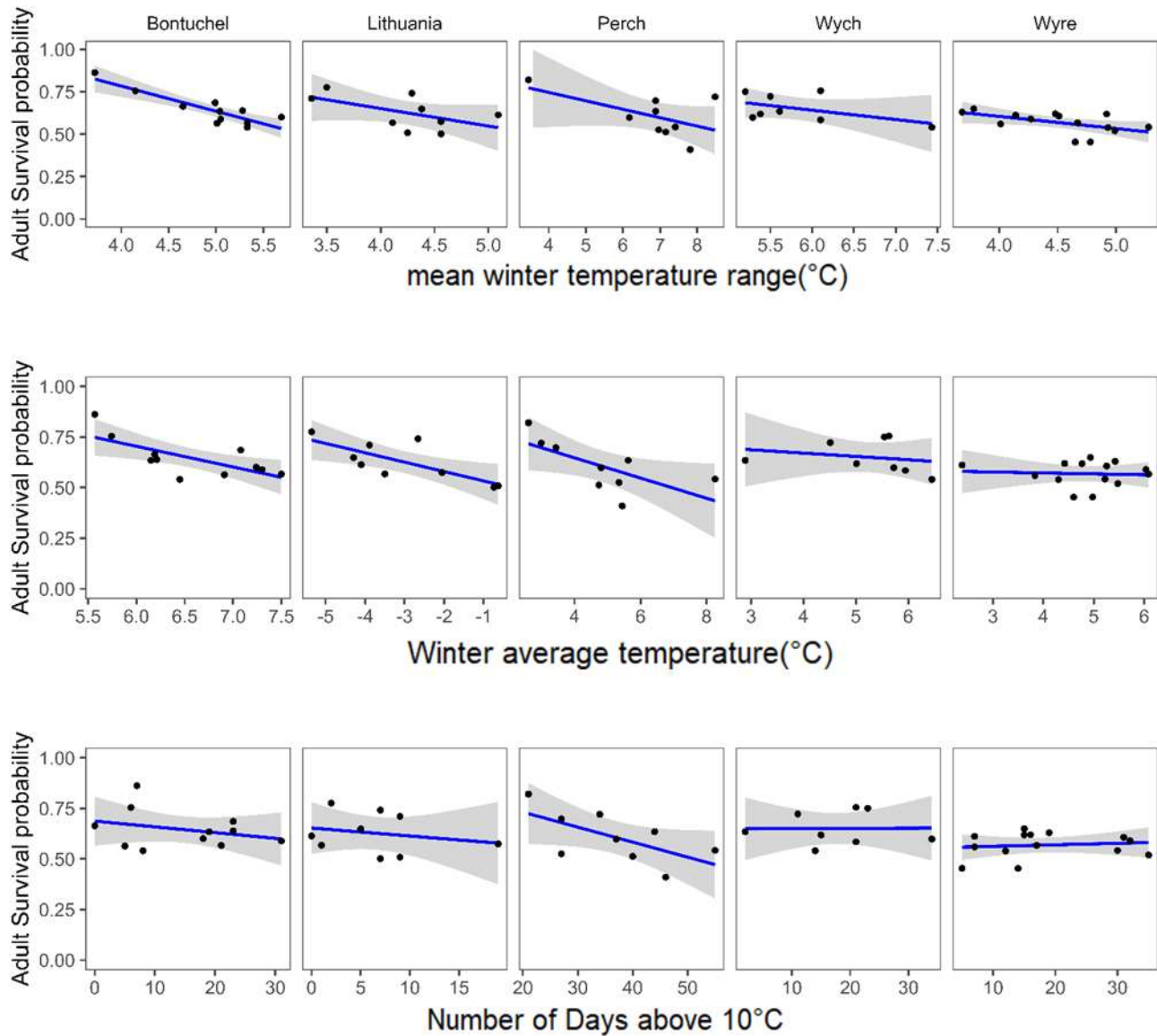
333

#### 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  
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  
345 days above 10 °C and Winter temp average (Table 1, Fig. 5). We also found a negative interaction  
346 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  
348 also found a low negative interaction effect between Density and Annual temp.





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

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359 Table 1. Parameter estimates ( $\beta$ ) 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 ( $\lambda$ ), fecundity ( $f$ ), adult and juvenile survival ( $\phi$ )) 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.

Explanatory Variable	Dependent Variable			
	Population Growth ( $\lambda$ )	Fecundity ( $f$ )	Adult ( $\phi$ )	Juvenile ( $\phi$ )
Density	<b>-0.236 (0.348/-0.121)</b>	<b>-0.182 (-0.367/-0.012)</b>	-0.094 (-0.037/-0.261)	<b>0.219 (0.065/0.372)</b>
Annual temperature	0.061 (-0.061/0.184)	<b>0.156 (0.08/0.023)</b>		<b>-0.031 (-0.065/-0.0003)</b>
MT winter	<b>-0.124 (-0.263/0.001)</b>	-0.0112 (-0.244/0.021)	<b>-0.088(-0.131/-0.039)</b>	
Max temp winter				
N of Days ^10oC			<b>-0.003 (-0.004/-0.001)</b>	
Annual PRCP		0.001 (-0.001/0.001)	0.006 (-0.002/0.009)	<b>-0.004 (-0.0032/-0.0009)</b>
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			<b>-0.031 (-0.049/-0.014)</b>	
NAO index	-0.032 (-0.07/0.006)			
Density: Annual temp				<b>-0.015 (-0.026/-0.07)</b>
Density: Winter temp			<b>-0.016 (-0.026/-0.006)</b>	

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## 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

379 strong effect in populations with high density. These findings are consistent with other studies  
380 showing population density can impact survival and reproductive rates in complicated ways  
381 (Eberhardt, 2002; Fauteux et al., 2021). While understanding the mechanisms underlying these  
382 patterns will require further study for the hazel dormouse, we suggest that they may have broader  
383 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.

403 Population density is recognized as an important factor regulating population growth in small  
404 mammal species (Erb, Boyce, & Stenseth, 2001), but it has not previously been studied in dormice.  
405 Our results are consistent with the idea that dormouse populations are intrinsically regulated by local-  
406 scale density dependence. We found a strong negative effect of density on population growth in all of  
407 our populations except Wych. However, Wych is different from the other locations in our study as it  
408 is a reintroduced population. Whilst we provide evidence that this site exhibits low productivity, poor  
409 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

441 of dormouse hibernation bouts. Increased energetic expenditure due to hibernation arousal and lack  
442 of food resources can cause reduction in fat reserves, increasing starvation risk (Pretzlaff, Rau, &  
443 Dausmann, 2014; Pretzlaff et al., 2021). While this increase in energy use over winter may negatively  
444 impact survivorship during the early active season, for those individuals that survive it may have a  
445 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  $\sim 14^{\circ}\text{C}$  and semi-torpor below  $\sim 19^{\circ}\text{C}$  (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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