



Estimating rodent population abundance using early climatic predictors

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Abstract

Climate might directly or indirectly affect the population dynamics of several rodent species including *Apodemus flavicollis*, a very common forest small mammal and an important reservoir for several emerging zoonotic pathogens. We thus investigated how climatic data alone might be useful to predict rodent population dynamics. We used rodent data gathered through a long-term monitoring effort carried out for 17 years (2000–2017) using a capture-mark-recapture method in northern Italy. Temperature and precipitation data were obtained from a weather station close to the study area. Linear models were implemented to assess how mice density was associated with weather conditions considering various time lags. We found that warmer summers 2 years before sampling were positively related to *A. flavicollis* annual average population densities. Conversely, precipitation occurring the autumn 1 year before sampling negatively influenced mice abundance. To the best of our knowledge, this is one of the first attempts at investigating how rodent abundance is associated with climatic conditions in the central European region of the Alps. Our results highlight important correlations, which eventually might be used for estimating risk of transmission of rodent-borne zoonotic pathogens.

Keywords Rodent density · *Apodemus flavicollis* · Climate · Early warning

Introduction

The abundance of rodent species is affected by many different factors such as predation, habitat suitability, and food availability. In Europe, small rodents show intense breeding activity during favorable seasons (spring and summer, sometimes autumn) when food resources are available and the climate is mild. Moreover, at central and southern latitudes, small rodents display large population outbreaks characterized by mast-driven events at irregular intervals, compared to the periodic multi-annual cycles exhibited at northern latitudes (see Andreassen et al. (2021) and references therein). Rodents include over 2200 known species encompassing approximately 42% of worldwide mammalian biodiversity (Wilson and Reeder 2005). They are vital to the maintenance of many ecosystems, but they are also important pests in agricultural and forestry productions causing severe economic losses (Meerburg et al. 2009b; Singleton et al. 2010). Moreover, rodents represent a crucial reservoir of several zoonoses, playing a major role in their transmission and

spread (Meerburg et al. 2009a). Thus, the ability to predict high densities of rodents is of economical and health importance.

Changes in climatic factors, such as temperature and precipitation, are known to directly or indirectly (quality of habitat, phenology of resources, phenology of animals) affect geographical and numerical changes of both animal and plant species. Rodents are primary consumers and fluctuating climatic conditions may affect their population size and use of resources (Ostfeld 1985) directly or indirectly by shaping the available food resources. While it is known that environmental conditions might impact rodent activity and survival in some systems (e.g., boreal forest and desert) (Korslund and Steen 2006; Kausrud et al. 2008; Previtali et al. 2010; Wróbel and Bogdziewicz 2015; Andreassen et al. 2021), little is known about this from high elevation areas in central Europe.

In the case of plants, the greatest expression of the interaction between physiological, evolutionary, and climate factors is given by masting. Mast seeding occurs in many terrestrial ecosystems, when dominant or abundant vegetation members of a community (trees, shrubs, or herbaceous plants) synchronously produce large fruit or seed crops (i.e., mast) (Pearse et al. 2016). As a consequence, these seasonal productions has been shown to be responsible for the fluctuations in several rodent species between years and geographical locations

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(Clement et al. 2009; Imholt et al. 2015; Reil et al. 2015). More specifically, in central Europe beech (*Fagus sylvatica* L.) mast is known to trigger rodent population outbreaks in the following year (Reil et al. 2015; Imholt et al. 2017). These mast events are reported to occur at irregular intervals of 3–10 years (Övergaard et al. 2007), while a warm and dry summer may trigger flowering and consequently seed production the next year (Vacchiano et al. 2017).

The rodent species most likely to respond to a mast event are trophic generalists which can rapidly switch between food resources already present in their habitat and mast produced seeds. In general, seed availability increases the length of the breeding season and facilitates winter survival of forest rodents resulting in a higher rodent density in the following spring (Pucek et al. 1993; McShea 2000; Clotfelter et al. 2007). The yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) is a widespread rodent species associated with woodlands and mature forests (Pucek et al. 1993; Mazurkiewicz and Rajska-Jurgiel 1998; Marsh and Harris 2000; Juškaitis 2002), with a preference towards forest edges (Montgomery 1999; Hille and Mortelliti 2011). This species is typically granivorous, although it has a broad food niche that includes plants, fungi, and invertebrates (Drózd 1966; Abt and Bock 1998).

The availability of quantitative data on masting is limited. Although some extensive datasets have been compiled (Ascoli et al. 2017; Hacket-Pain et al. 2022), they consist mainly of arbitrary categorical observations, which might not be easily compared (Ascoli et al. 2017) as they are observer-dependent. Consequently, the development of predictive models of rodent abundance might not rely on them.

Considering all the above-mentioned available knowledge, we hypothesized that climate might be directly linked to rodent abundance in the European Alps area, including time lags due to the non-instantaneous sequence of events from weather, flowering, fructification, resource availability, to rodent reproduction and increase in population size. We thus conducted this exploratory study to investigate if there is any straightforward relationship between meteorological conditions (temperature and rainfall) and rodent abundance at different time scales by considering a 17 years long time series of *A. flavicollis* estimated densities and meteorological data collected in northern Italy, in an area where beech trees are the dominant arboreal species and therefore their seed production might profoundly affect mice density.

Methods

Apodemus flavicollis data

Our study was carried out in the municipality of Cavedine (Province of Trento, Italy, 750 m a.s.l.; Fig. 1a). The rodent

trapping area is an isolated calcareous ridge covered with mixed deciduous coppice woodland (*Fagus sylvaticus*, *Carpinus betulus*, *Fraxinus ornus*, *Corylus avellanae*) and scattered meadows. The population dynamics of yellow-necked mice was monitored from 2000 to 2017 (2009 data missing due to logistic reasons) using four permanent trapping grids (labeled A, B, C, D; Fig. 1) distant between about 200 and 1380 m from each other. Each grid consisted of an 8 × 8 square array of trap stations set 15 m apart (with a total grid covering area of 1.1 ha). At each trap station, one multiple-capture Ugglan live trap model n. 2 (Grahnbab, Sweden) baited with sun flower seeds and a slice of potato/carrot was set and standard capture-mark-recapture techniques (CMR) were adopted (Pollock et al. 1990; Lawson et al. 1992). Overall, 220 capture sessions (3 days/2 nights) were carried out, every 2 weeks from 2000 to 2008 and every month from 2010 to 2017 from May to October. Grid sizes and locations remained constant from the whole period. At first capture, each mouse was individually marked with a subcutaneous implanted passive integrated transponder (PIT) tag (ID100 Trovan Ltd., UK). Animals were then released unharmed at the site of capture. At each sampling session, date, grid, trap station, body mass, sex, and the PIT tag number were recorded. All methods were carried out in accordance with relevant guidelines and regulations. Trapping and sampling procedures were carried out in accordance with regulations approved by the Wildlife Committee of the Autonomous Province of Trento (Prot. N. S044-5/2015/277268/2.4).

Climatic data

Daily average temperature and precipitation data were obtained from a weather station belonging to Fondazione Edmund Mach located in Cavedine near the study area (see Fig. 1a).

Statistical analysis

The raw CMR observations were used to estimate the population density, expressed as yellow-necked mice per hectare per grid and session, through the standard open population Jolly-Seber method (Schwarz and Arnason 1996). These densities were then averaged over study sites, thus obtaining a mean monthly density $M_{m,y}$. We also computed a mean yearly density M_y by averaging densities estimated between June and September, since mice were sampled in all grids and years only for these months. Both variables were transformed prior to analysis in order to normalize their distribution, following the Box-Cox method (Box and Cox 1964). We denoted with $M_{m,y}^*$ and M_y^* the transformed variables.

- Short-term analysis

We investigated the association between $M_{m,y}$ and the climatic conditions occurred during different previous

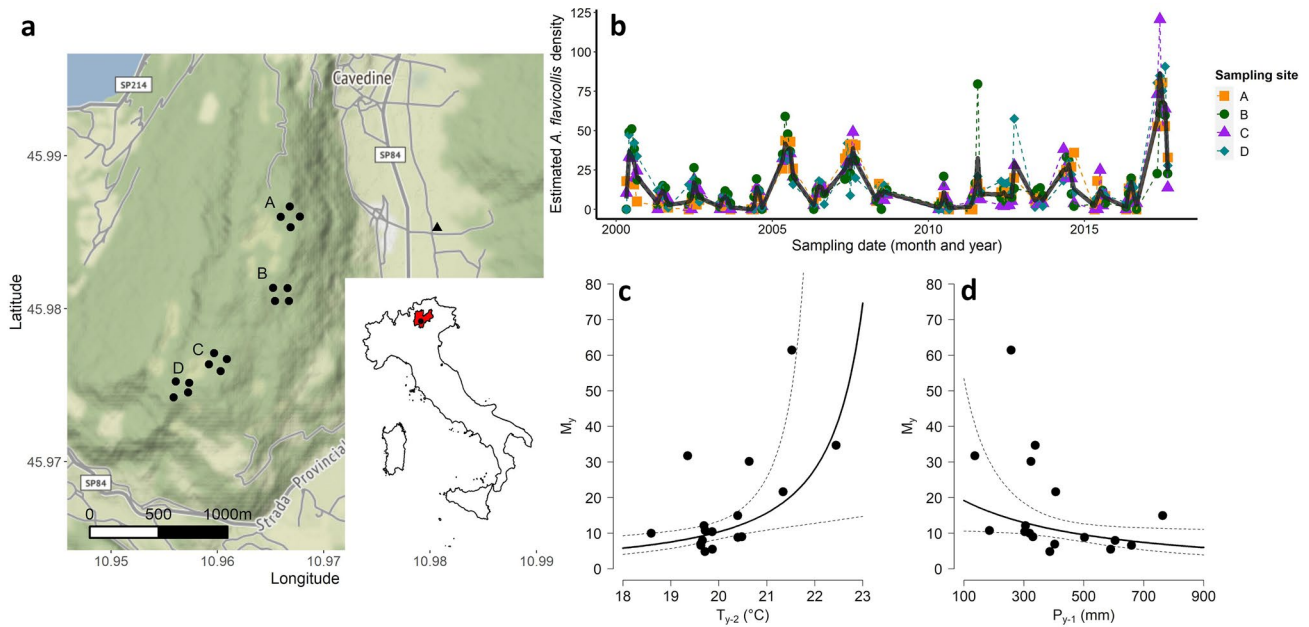


Fig. 1 **a** Map of the study area in Cavédine (Province of Trento, Italy). Trapping sites are labeled with A, B, C, D and black dots represent the corners of the grids. The triangle represents the weather station location. Map data from OpenStreetMap under the Open Database License <https://www.openstreetmap.org/copyright>. **b** Estimated *A. flavicollis* density (number of individuals per hectare) per site and sampling month (colored lines) in Cavédine (Province of Trento, Italy, 2000–2017). Dark continuous line

represents the mean monthly density ($M_{m,y}$). Data in Online Resource 1. **c** Relationship between the average yearly *A. flavicollis* density (M_y) and summer temperature 2 years before (T_{y-2}). **d** Relationship between the average yearly *A. flavicollis* density (M_y) and autumn precipitation during previous year (P_{y-1}). Dots: recorded average yearly mice density. Lines: best model predictions (back-transformed, continuous lines) with confidence intervals (dashed lines)

temporal periods by developing a linear model, named as the full model, which can be represented by the following equation:

$$M_{m,y}^* = \beta_0 + \beta_1 T_2 + \beta_2 T_3 + \beta_3 T_6 + \beta_4 P_2 + \beta_5 P_3 + \beta_6 P_6$$

where T and P denote respectively the average temperature (in °C) and the total precipitation (in mm) computed over the n months ($n=2, 3,$ and 6) preceding the sampling month, m and β_i ($i=0, \dots, 6$) are the model coefficients. In order to account for collinearity among variables, we computed the variance inflation factors (VIFs) and sequentially drop the covariate with the highest VIF, recalculate the VIFs, and repeat this process until all VIFs were smaller than 3 (Zuur et al. 2010). Starting with the VIFs-adjusted full model, we carried out a model selection by ranking all sub-models on the basis of the second-order Akaike information criterion (AICc). The model with the lowest AICc was selected as the best model (Burnham and Anderson 2002; Zuur et al. 2007).

• Long-term analysis

We investigated the association between M_y and the climatic conditions occurred during different previous seasons s (summer, autumn, and winter) up to 2 years before sampling, by developing a linear model, named as the full model, which can be represented by the following equation:

$$M_y^* = \beta_0 + \sum_{n=1}^2 \sum_s \beta_{n,s}^T T_{s,y-n} + \sum_{n=1}^2 \sum_s \beta_{n,s}^P P_{s,y-n}$$

where T and P denote respectively the average temperature and the total precipitation computed over season s during year $y-n$ ($n=1, 2$) and $\beta_0, \beta_{n,s}^T,$ and $\beta_{n,s}^P$ are the model coefficients. Similarly to the short-term analysis, we calculated the VIFs to account for collinearity. Starting with the VIFs-adjusted full model, we carried out a model selection by ranking all sub-models on the basis of the AICc. The model with the lowest AICc was selected as the best model (Burnham and Anderson 2002; Zuur et al. 2007).

All analysis, including plots creation, were carried out using R v4.0.2 (R Core Team 2022) and packages *tidyverse* (Wickham et al. 2019), *EnvStats* (Millard 2013), *MuMIn* (Barton 2020), *car* (Fox and Weisberg 2019), and *ggmap* (Kahle and Wickham 2013).

Results

A total of 3560 yellow-necked mice were individually captured. Other species such as wood mice (*A. sylvaticus*) and bank voles (*Myodes glareolus*) were only occasionally caught,

but their numbers were too low to be considered in the statistical analysis (24 and 32 in total, respectively). As shown in Fig. 1b, *A. flavicollis* density changed during the study period, ranging between 0 and 120 mice/hectare considering all months and trapping sites, while $M_{m,y}$ and M_y ranged between 0–86 and 5–61 mice/hectare, respectively. *Apodemus flavicollis* raw CMR observations, the estimated densities for each grid and trapping month, and the average densities per year and grid are presented in Online Resource 1.

The coefficients of the best selected models are presented in Table 1 while estimates for all possible models built after the VIFs computation, ranked by AICc, are presented in Online Resource 2. Interestingly, we did not find any significant relationship when performing the short-term statistical analysis (all p values of the climatic covariates coefficients are greater than 0.05). The coefficients of the selected best model, which includes only T_2 (the average temperature of the 2-month period before the month of the sampling) with a coefficient which is not statistically significantly different from zero, are presented in Table 1.

Conversely, we found mice yearly density, M_y , to be significantly associated both with $T_{summer,y-2}$ and $P_{autumn,y-1}$. Specifically, through the best selected model (coefficients shown in Table 1, $R^2=0.44$), described by the equation $M_y^* = -0.14 + 0.07 \cdot T_{summer,y-2} - 2.9 \cdot 10^{-4} \cdot P_{autumn,y-1}$, we found that summer temperature was positively associated with rodent average yearly density 2 years later (Fig. 1c) while autumn precipitation negatively affected mice population the following year (Fig. 1d).

Discussion

Climate variables (temperature and precipitation) can affect seed production (Piovesan and Adams 2001; Övergaard et al. 2007; Vacchiano et al. 2017) and rodent survival (Korslund and Steen 2006), ultimately affecting rodent abundance and potentially rodent-borne pathogens' circulation (Bregnard

et al. 2020, 2021). In this exploratory study, we provide important evidence, using abundance data from a long-term live trapped rodents dataset, on how seasonal climatic conditions could be associated with *A. flavicollis* abundance in the Eastern Italian Alps.

In Italy, this rodent species avoids the plain areas, being widespread in the Alps in deciduous and mixed forests from the bottom of the valley to the upper tree limit (Mitchell-Jones 1999). To the best of our knowledge, in the Alps area no studies describing the effect of abiotic variables on its abundance have ever been carried out. From previous observations (Guzzetta et al. 2017; Rosà et al. 2019) at our study site and from literature (Flowerdew et al. 1985), *A. flavicollis* breeding season lasts from March to October and winter reproduction does not occur, except during heavy mast years. Its abundance is typically characterized by an intra-annual fluctuation with a summer peak, followed by a sharp decrease in winter and then a rise in spring. During the study period, we observed 4 beech mast events (1999, 2004, 2013, and 2016, authors' personal observations) which were always followed by an increase in the number of animals the following year (Fig. 1b). Interestingly, also in 2007 mice population was very abundant although no presence of higher production of beech seeds was observed.

It is noteworthy that in our study site (old coppice beech stand) *A. flavicollis* was the dominant captured species. In such context, additional interspecific competition with the other common forest rodent species, i.e., *M. glareolus* (bank vole), can be ruled out. Moreover, the effect of predators in response to rodent abundance was not assessed, although in years with high density of mice, many animals were predated in traps by foxes (authors' personal observation).

Our results show that summer temperatures might have a positive effect on *A. flavicollis* density 2 years later, consistently with similar association found for mast events. Indeed, it has been shown that dry and warm summers are usually followed by a larger production of beech seeds the following year (Piovesan and Adams 2001; Övergaard et al. 2007; Vacchiano et al. 2017). Thus, a particularly warm summer during year y is more likely to be followed by a mast event during year $y+1$, eventually leading to a larger availability of food resources allowing rodent population to thrive during year $y+2$. Moreover, an abundant food supply can lead to an earlier onset of breeding in rodents or winter breeding (Eccard and Ylönen 2001) or to positively affect overwinter survival (Johnsen et al. 2017). A similar positive relationship was also found between summer temperature and bank voles abundance observed 2 years later in Germany (Imholt et al. 2015).

Our findings highlight a negative association between autumn precipitation and yellow-necked mice density the following year. Although some authors reported an increased activity of this mice species during rainy days (Wróbel and

Table 1 Estimates, standard errors, t values, and p values of the parameters of the best linear models for $M_{m,y}^*$ and M_y^* . The equations for the models after back-transformation of the dependent variable are $M_y^* = (-0.69 \cdot (-0.14 + 0.07 \cdot T_{summer,y-2} - 2.9 \cdot 10^{-4} \cdot P_{autumn,y-1}) + 1)^{\frac{1}{0.69}}$ and $M_{m,y}^* = (0.1 \cdot (1.92 + 0.05 \cdot T_2) + 1)^{\frac{1}{0.1}}$

Parameter	Coefficient estimate	Standard error	t value	p value
Short-term model ($M_{m,y}^*$)				
Intercept	1.92	0.52	3.71	<0.001
T_2	0.05	0.03	1.5	0.14
Long-term model (M_y^*)				
Intercept	-0.14	0.48	-0.29	0.77
$T_{summer,y-2}$	0.07	0.02	2.99	0.01
$P_{autumn,y-1}$	$-2.9 \cdot 10^{-4}$	$1.3 \cdot 10^{-4}$	-2.25	0.04

Bogdziewicz 2015), the negative effect of precipitation on mice abundance at our site could be linked to the simultaneous effect of rain and temperature during the autumnal season which could affect *A. flavicollis* survival, for instance by making difficult food search or possibly by limiting aggregation (Andreassen et al. 2021). The effect of these climatic variables on mice survival will be further analyzed in order to settle this question. Similarly, in Clement et al. (2009), the authors hypothesized that in Belgium milder conditions during autumn (e.g., warmer temperatures) might result in a higher survival of bank voles, eventually leading to a larger number of nephropathia epidemica infections in humans occurring the following year.

Since the response of rodents to climate and food resource changes is generally fast, we also considered the effect of climatic variables over a shorter time interval. Nonetheless, as observed also by Giraudoux et al. (2019) in France in common voles (*Microtus arvalis*), climate variables did not correlate significantly with rodent density over a short-term period, supporting the hypothesis that demographic processes need some time to respond to the new conditions.

One source of weakness in this study is the relative short time span: 17 years might still offer a limited and biased overview of the mice population dynamics. For instance, we conducted a sensitivity analysis by removing 2017 from our observations (the year characterized by the highest observed population density as shown in Fig. 1b) and we found the same best model for the long-term analysis, but autumnal precipitation of the previous year was not significant. Thus, a longer time series might be required to validate our findings. Moreover, samplings were carried out only during the summer months, so we did not measure rodents' abundance during the other seasons. Finally, an in-depth insight into the demographic structure of the mice population is necessary to better describe the possible underlying processes generating the observed patterns. Despite its exploratory nature and potential limitations, our investigation might provide useful insights on important aspects of rodents' ecology in the Alps area. *A. flavicollis* is an important reservoir for several pathogens which can be transmitted to humans, including bacteria (e.g., *Borrelia* spp.), viruses (e.g., tick-borne encephalitis virus, Dobrava virus, lymphocytic choriomeningitis virus (Schmaljohn and Hjelle 1997; Lindquist and Vapalahti 2008; Tagliapietra et al. 2018)), but also fungi, helminths, and protists (Han et al. 2015). It is generally assumed that the greater the abundance of rodent reservoirs, the higher the potential delivery rate of pathogens from rodents into vectors (e.g., ticks) or the environment, and therefore the higher the risk to people of contracting diseases (Davis et al. 2005; Rosà et al. 2007, 2019; Kiffner et al. 2011; Krawczyk et al. 2020). In this context, the ecological factors that affect the population dynamics of rodents may have consequences on public health disease burden. Moreover, if our findings are

validated with a spatially and temporally broader dataset, which might be used also to evaluate forecasting potential, climatic indicators might act as an early warning signal for the risk of transmission of directly transmitted rodent-borne pathogens or by mean of a vector such as tick-borne diseases.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10344-023-01666-2>.

Author contribution Conceptualization: Giovanni Marini, Annapaola Rizzoli, Valentina Tagliapietra; data curation: Giovanni Marini, Valentina Tagliapietra; formal analysis: Giovanni Marini; investigation: Valentina Tagliapietra, Daniele Arnoldi; software: Giovanni Marini; writing—original draft: Giovanni Marini, Valentina Tagliapietra; writing—review and editing: Giovanni Marini, Daniele Arnoldi, Annapaola Rizzoli, Valentina Tagliapietra.

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Data availability All data generated or analyzed during this study are included in this published article and its Supplementary Information files.

Declarations

Ethics approval All rodent trapping and sampling procedures were approved by the Wildlife Committee of the Autonomous Province of Trento (Prot. n. S044-5/2015/277268/2.4).

Competing interests The authors declare no competing interests.

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