

GRADUAL AND ERUPTIVE DYNAMICS OF RODENT PESTS:

Outbreaks in house mice in Australia and common voles in Spain



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Theory without practice is fantasy, practice without theory is chaos

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Resumen

Las plagas de roedores son habituales en los cultivos de todo el mundo, causando grandes daños económicos y problemas de salud por zoonosis. Este proyecto de tesis trabajó con dos plagas de roedores: el ratón doméstico australiano y los topillos españoles por ser plagas que generan pérdidas económicas en los cultivos, tener dinámicas de población complejas con influencia de factores endógenos y exógenos, y la ausencia de un mecanismo explicativo causal. Para analizar los brotes poblacionales de ratones domésticos en Australia se usaron datos de abundancia de la plaga en tres sitios productores de trigo (Victoria, Sur de Australia y Queensland) junto con variables climáticas y depredadores generalistas para identificar los factores causantes del incremento poblacional. Para analizar las dinámicas se emplearon modelos estacionales y anuales para comprender los factores que impulsan el aumento y la disminución de la población (fase de brote y colapso). Se evaluaron los efectos de las variables climáticas en la tasa de crecimiento de la población a través de sus efectos potenciales en el suelo, capacidad para cavar madrigueras, y datos de abundancia relativa de aves para entender el papel de los depredadores y la existencia de umbrales de escape. La tasa de aumento de las poblaciones de ratones en el sureste australiano (Victoria y Sur de Australia) se explicó mejor por la baja evaporación en verano, las altas precipitaciones acumuladas de invierno en los dos años anteriores al brote y un índice de abundancia de los depredadores Nankeen kestrel (Walpeup) y Brown falcon (Sur de Australia) durante el verano al otoño. En cuanto a Queensland los factores más importantes fueron las precipitaciones de los dos años anteriores y factores denso-dependientes de las estaciones previas. El rol de los depredadores no fue evidente. El colapso poblacional en el sureste australiano y en Queensland se explicó por la abundancia poblacional de los ratones domésticos en la fase de brote y la abundancia de depredadores. Por lo tanto, se evidenció que las poblaciones de ratones en Australia presentan dos estructuras de brote diferentes: el sureste australiano se caracteriza por

tener brotes de tipo eruptivo dependientes del clima y con umbrales de escape a los depredadores, y brotes de tipo gradual en Queensland dependientes del clima y densidades previas de ratones domésticos, lo cual influye en el tipo de manejo y predicción de estas plagas. Estos resultados son útiles para predecir brotes futuros y reducir su impacto económico en los cultivos de trigo australianos.

Los topillos en España son un ejemplo de una especie plaga que cada 3 o 4 años alcanza grandes números en cultivos de alfalfa y cereales causando daños considerables en los cultivos. Para analizar los brotes poblacionales se usó una serie de tiempo de 11 años de abundancia de topillos en la región de Castilla y León (Zamora, Valladolid y Palencia), factores climáticos, abundancia de competidores como el ratón de madera, ratón argelino y musaraña, y la abundancia de comadrejas para examinar el papel de los depredadores. Para el análisis se emplearon modelos estacionales y anuales para comprender los factores que impulsan el aumento y la disminución de la población. La tasa de aumento de las poblaciones de ratones se explicó mejor por las altas precipitaciones acumuladas (otoño a primavera) en los dos años previos al brote, la humedad de primavera a verano y la abundancia de comadrejas en primavera. La tasa de disminución de la población se explicó mejor por la abundancia en la temporada de brote (denso-dependencia) y la precipitación en otoño. En conclusión, los brotes de topillos españoles fueron clasificados como eruptivos, al depender no solo de factores exógenos como la precipitación y la humedad, si no de un umbral de escape a las comadrejas en primavera. Estos resultados son útiles para predecir brotes futuros y reducir el impacto económico de los topillos en los cultivos de alfalfa y cereales.

Abstract

Rodent plagues are usual on crops around the world causing severe economic damage and health problems by zoonoses. The thesis project worked on two rodent plagues: Australian house mouse and Spanish voles which generate economic loss on crops. They have complex population dynamics with endogenous and exogenous influence factors, and an absence of a causal explanatory mechanism to predict their outbreaks. House mice in Australia are a plague with irregular population dynamics and cause considerable damage on cereal crop systems. We used a 20-year mouse mark-recapture dataset from Walpeup (Victoria), Roseworthy (South Australia) and Darling Downs (Queensland), and climatic and predator variables. We employed seasonal and annual models to understand the increase and decrease of the population through different drivers. In south-eastern Australia, the rate of increase was best explained by low evaporation in summer, high cumulative winter rainfall, and an index of abundance of the Nankeen kestrel (Walpeup), and the Brown falcon (Roseworthy) during summer to autumn. The Queensland mouse outbreaks were explained by spring to summer rainfall from two years before the plague, and previous mouse abundances. On the other hand, the South-eastern decline rate was explained by outbreak abundance and predators like the Barn owl to Walpeup and Swamp harrier to Roseworthy. The Queensland collapse was related to outbreak abundance (density-dependence) and Barn owl density. We conclude that South-eastern mouse dynamics can be defined as an eruptive dynamic caused by weather triggers that allow the population to obtain more and better resources avoiding being consumed by predators. Queensland outbreaks can be defined as gradual because they are generated by changes in rainfall and a strong density-dependence. These results are useful to explain and predict the outbreaks, understanding the mechanisms that cause the mice explosion on wheat production sites.

The common voles in Spain are an example of an irruptive species that every three or four years reaches plague numbers and causes considerable damage in cropping systems. We used an 11-year mark-recapture dataset from Castilla y León region (Zamora, Valladolid, and Palencia) and various climatic, competitors and predator variables, employing seasonal and annual models to understand the drivers of the population increase and decrease. We examine the climatic effects, interspecific competition (Wood mouse, Algerian mouse, and Shrew), and weasel's abundance to examine the predators' role. The rate of increase of vole populations was best explained by high cumulative rainfall (autumn to spring) in the two years prior to the outbreak, spring and summer humidity, and spring weasel's abundance. The rate of population decline over winter was best explained by abundance in the peak season (density-dependence) and autumn precipitation. We conclude that the outbreaks of Spanish voles are classified as eruptive because depended on precipitation and humidity, an index of food supply and burrows, and weasel's density. The results are useful to predict future outbreaks to reduce their economic impact on alfalfa and cereal crops.

General introduction

Many agroecosystems suffer economic damage by the presence of pests that consume the harvest and destroy the crops. The standard solution is to attack the plagues through agrochemicals, natural enemies and other controls (mechanical, physics, cultural) (Berryman 1999a). Still, we forget that crops are an agroecosystem regulated by interactions and feedbacks. If we understand the relationship between them and identify the factors that cause the pest, it is possible to predict them (Royama 1992, Berryman 1995). This approach is possible by applying through population dynamic models that describe the changes in a population density and allow us to understand the pest increase rate and the relationship with the environmental carrying capacity and limiting resources, the inter and intraspecific competition, and the predation role (Berryman 1995, Berryman 2003).

Small rodents have been a focus of human interest because they carry diseases and cause economic damage in crops (Krebs 2013). House mouse in Australia and common voles in Spain are examples of classic outbreaks on crops and zoonosis. They are at low densities most of the time due to interactions with limiting resources or predators, but they can quickly increase cause devastation. The outbreak of the house mouse can reach 800 to 1000 mice/ha in wheat, maize, sorghum, barley, and rice causing losses of \$40 million USD per year due to seeds consumption along the wheat belt (Singleton et al. 1999, Singleton et al. 2001, Singleton et al. 2005). They are considered non-cyclic or irregular because the low density is constant most of the years but increases suddenly. On the other hand, Spanish common voles are usually found in alfalfa, cereals, legumes, and potatoes causing losses of 20 million euros per year due to the consumption of stems and leaves on crops (Jacob et al. 2004, Jacob 2008, Cornulier 2013). Voles are vectors and reservoirs of tularemia, an infectious disease caused by *Francisella tularensis*, which generates mortality in voles and humans

(Rodriguez et al. 2017). The vole outbreaks are considered cyclic or a regular dynamic because their population increases every three or four years throughout Europe.

The economic, epidemiological, and social impact of mice and voles have been promoting research into the causes of increased density through different hypotheses proposed to explain and predict the rodent outbreaks (Pech et al. 1999, Jacob & Tkadlec 2010). Some hypotheses have been proposed like food supply, rainfall, and droughts (French & Schultz 1984, Krebs et al. 2004), food quality (Babinska-Werka 1979, White 2002, Heroldova et al. 2004), cover, refuge and burrows (Mutze 1991, Singleton et al. 2007, Brugger et al. 2010, Blank et al. 2011), social behaviors (Krebs 1995, Krebs 2003), predator and diseases regulation (Andersson & Erlinge 1977, Sinclair et al. 1990, Pech et al. 1999, Hankki et al. 2001), weather influences (Krebs et al. 2005, Ims et al. 2007, Brommer et al. 2010), and others (Pech et al. 1999, Jacob & Tkadlec 2010).

The most relevant hypotheses are three: food supply, soil conditions to burrows and predators. First, food supply has been one of the hypotheses that has been most evaluated because it provides energy to grow and reproduce, and probably inducing an early litter. Consequently, females could have a larger litter size, and juveniles can mature quickly to have more offspring. Then, the population density will increase, causing an outbreak (Boonstra and Redhead 1994, Brown and Singleton 1999, Jacob et al. 2002, Tkadlec et al. 2006). Food supply can be measured through food addition directly or using precipitation, like an index, because of influences on soil conditions and the capture of nutrients and water by plants. Thus, the crop yield improves (Newsome 1969, Saunders and Giles 1977, Redhead 1982, Singleton 1989, Mutze et al. 1990, Cantrill 1992, Twigg and Kay 1994, Pech et al. 1999, Krebs et al. 2004). However, the house mouse and common vole

outbreaks do not always occur following rainfall, meaning that other factors might also be necessary.

Second, the precipitation effect on soil conditions could be a driver of rodent population increases (Newsome 1969, 1970, 1971, Newsome & Corbett 1975, Blank et al. 2011). Burrows availability and cover can be considered a limiting resource that rises when environmental conditions are better (Jacob 2008, Esther et al. 2014, Giradoux et al. 2019, Imnholt et al. 2011). Soil conditions could be improved due to the influence of precipitation. Increasing humidity and decreasing evaporation enable easier digging of burrows for nesting and to avoid predation. These conditions increase the enemy-free space, reduce predation risk, and increase the rodent density (Airoldi and Werra 1993, Brugger et al. 2010, Brommer et al. 2010). Third, the escape from predator regulation, establish how rodents obtain more and better resources increasing their density to escape predators through the co-operation principle, where individuals benefit from the presence of others (Berryman 1999 a). The possible mechanisms could be the predator saturation by rodent explosion growth, where they are less likely to be killed when they are in a crowd (Sinclair and Pech 1996, Berryman 1999 a,b). Generalist predators that switch between dense alternative prey instead of consuming mice and voles (Holling 1966, Murdoch 1969, Goud et al. 1990, Berryman 1999 a,b). Or, that environmental conditions improve, influencing limiting resources for rodents, generating a density raise (Sinclair et al. 1990, Berryman 1999 a,b, Berryman 2003, Sinclair 2003, Korpimäki et al. 2004).

Some of these hypotheses have been tested and achieved a prediction of more than 50% of mouse outbreaks, being a challenging dynamic to explain and predict. They have never been tested in the common vole outbreaks in Spain. Therefore, the specific mechanism behind these outbreaks is not

clear yet, and it is necessary to identify the factors that cause the rodent increase and how they operate (Chitty 1960, Krebs 2013). For this purpose, this thesis used the outbreak theory proposed by Berryman, who establish an outbreak as a population transition between low to high density when a harmless population due to a disturbance ‘environmental favorability’ becomes a pest, causing economic damage to crop (Berryman et al. 1984, Berryman et al. 1987, Berryman 1999b). Berryman proposed an outbreak classification to define the factors and mechanisms to cause the population increase, dividing the outbreaks into gradient and eruptive to understand pest the structure dynamic and manage them (Berryman 1987).

Gradient outbreaks depend on exogenous factors exclusively, where the population needs a large disturbance to move their equilibrium point from low to high density. This kind of pests depends on the increase of limited resources (Royama 1992, Berryman 1999 a,b, Lima 2006). For example, the rainfall in Chilean semiarid ecosystem improves the biomass of seed (bamboo flowering), making the rodents increase and generate ratadas. When the rain disappears, the rodent outbreak too (Jaksic and Lima 2003). Pests are regulated through competition for resources (food, cover, habitat) and negative feedback. They tend not to spread to new and unfavorable environments (Berryman 1981, 1988, 1989, 1999b, DeAngelis et al. 1986, Berryman & Kindlmann 2008). On the other hand, eruptive outbreaks do not depend on exogenous factors exclusively, being a complex dynamic with more than one factor involved. They can spread from local epicenters to cover large areas (Berryman & Kindlmann 2008). This kind of dynamic is caused by positive feedback that amplifies the response to obtain more and better resources, avoiding the regulation by predators (Berryman & Stark 1985, Berryman 1989). Eruptive dynamics have an escape threshold where pests increase above them and decline below it. The threshold can be overcome due to saturation of predator functional response, abundant alternative prey, or the trigger influence

on the population that allows the density increase, avoid the predators attack, and cause an outbreak (May 1977, Berryman et al. 1987, Sinclair et al. 1990, Berryman 1996, Berryman 1999b, Sinclair 2003, Groffman et al. 2006).

The outbreak theory is useful for improving our knowledge about the Australian house mouse and Spanish voles and identify whether the populations' increase depends on a pulse of resources or triggers that allow their escape from predators. The aim is analyzing if rodents could respond differently or not to a wide range of soil types, rainfall regimes, and cropping systems, generating an outbreak through diverse mechanisms. The results will help predict future outbreaks to reduce their economic impact on wheat and alfalfa crops.

Paper 1: Mouse outbreaks in Walpeup (Victoria, Australia).

Complex dynamics of Australian house mice: Could the weather and predators cause outbreaks?

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Abstract

House mice in Australia are an example of an irruptive species that irregularly reaches plague numbers and causes considerable damage in cropping systems. We used a 20-year mouse mark-recapture dataset from Walpeup (Victorian Mallee) and various climatic and predator variables, employing seasonal and annual models to understand the drivers of the population increase and decrease. Previous analysis has shown that the mouse outbreaks often occur in years following good winter rain, but the mechanisms are not yet clear. We examined the effects of climatic variables on population growth rates (via their potential effects on soil that might influence the ability of mice to dig burrows) and use relative abundance of birds to examine the predators' role and the existence of escape thresholds related to the principle of co-operation. The rate of increase of mouse populations over the summer breeding season was best explained by low evaporation in summer, high cumulative winter rainfall in the two years prior to the outbreak, and an index of abundance of the Nankeen kestrel (predator) during January to June. The rate of population decline over winter was best explained by the starting abundance in autumn (density dependence) and an index of Barn owl abundance during autumn and winter. There were limitations with the predator abundance data, but they provide a hint that reduced predation pressure is important prior to an outbreak, which needs further research. We conclude that the population dynamics of house mice

we studied are complex and that multiple factors are interacting in the system to generate mouse outbreaks. The results are useful to predict future outbreaks to reduce their economic impact on wheat crops.

Keywords: Mouse outbreaks; drivers; mathematical models; population dynamics.

Introduction

The transition from low-density to very high-density populations is known as an outbreak (Berryman 1999), turning a harmless population into a potential pest population capable of causing significant economic losses on crops (Berryman 1984). An impressive outbreak example is the Australian house mouse (*Mus musculus*), which maintains low densities due to interactions with limiting resources or predators, but they can increase their population rapidly during ‘good’ years (Singleton et al. 1999, Singleton et al. 2001, Singleton et al. 2005). Mouse plagues usually occur in grain-growing regions causing considerable economic damage (losses of 40 million AUD per year) (Singleton 1997, Singleton et al. 2010). Since 1900, the house mouse has been a problem for farmers and ecologists in the main wheat production areas (New South Wales, Victoria, South Australia, and Queensland). Because their population dynamics are irregular with outbreaks not constant across time, i.e., not cyclic (Stenseth et al. 2003), making it difficult to achieve an accurate prediction. Therefore, researchers have been looking for factors that could explain and predict the outbreaks, yet there is no consensus regarding satisfactory explanatory mechanisms to understand these outbreaks (Pech et al. 1999, Krebs et al. 2004).

The likely causes of mouse outbreaks have been analyzed using a range of different approaches, which have also been used to improve predictions. Some hypotheses proposed to explain the

population growth and collapse are food supply, environmental factors (i.e., climatic or soil conditions), social behaviors, habitat and refuges, and predation (regulation) (Table 1). Food supply has been one of the most evaluated hypotheses due to their importance for mice to provide energy to grow, establish nesting sites and reproduce, and escape from predators (Newsome and Crowcroft 1971, Boonstra and Redhead 1994, White 2002). One mechanism states that increased precipitation generates permeable soil where the plants can capture more nutrients, thereby improving crop yield. This increases the seed biomass providing the population enough food resources to increase, causing an outbreak. For outbreaks of mice in Southern Australia, this approach uses the April to October rainfall (in-crop rainfall) as an index of crop productivity (Pech et al. 1999), due to the positive relationship between rainfall and crop yield (Seif and Pederson 1978, Redhead 1982). Statistical analysis shows that the rainfall acts as an outbreak driver, accounting for 50% of the variation in mouse peak (Krebs et al. 2004). However, outbreaks do not always occur following good rainfall, meaning that other factors might also be important.

The precipitation impact on population abundance of mice is irrefutable (Newsome 1969, Saunders and Giles 1977, Redhead 1982, Singleton 1989, Mutze et al. 1990, Cantrill 1992, Twigg and Kay 1994, Pech et al. 1999, Krebs et al. 2004), but the specific mechanism behind the outbreaks is not clear yet. Newsome (1969, 1970, 1971) and Newsome and Corbett (1975) considered the effect of precipitation on soil conditions as a driver of mouse population increases. They suggested that soil conditions are improved as a result of increased humidity and decreased evaporation to enable easier digging of burrows for nesting and to avoid predation. This proposal has not been evaluated through experimental, statistical or mathematical approaches.

In other approaches, Sinclair et al. (1990), Sinclair (2003) and Korpimäki et al. (2004) consider that predators' influence on outbreaks of the house mouse would be through regulation and their escape. This idea is based on an experimental observations of mouse and predator population behaviors (Sinclair et al. 1990), where the first phase of the experiment showed a density-dependent functional response of predators on the mouse population, invoking population regulation, and a second phase characterized by a large increase of mouse density, where the functional response was density-independent without regulation, due to mouse densities escape from predation pressure because their populations became too high (Sinclair et al. 1990, Sinclair and Pech 1996). Furthermore, a possible mechanism could be the co-operation principle (Berryman 1999, Holling 1959), where the mice can escape from regulation through rainfall, burrows, or food supply acting on the increased mouse population. Thus, being a high population, it is less likely to be killed by predators. The limitation of this approach is the absence of rigorous field experiments or predator's monitoring to calculate their impact on mouse populations. Currently, the only available predator data are occurrence or relative abundance available from online portals contributed by the general public.

We may well ask whether anything more needs to be said about mouse outbreaks. Given their complex nature, there are likely to be several factors involved, which need to be explored. We think that there are additional reasons to demonstrate that simple population models can help understand the causes of population outbreaks and can make reasonable predictions. We will use a 20-year mouse population abundance dataset as well as climatic, soil, and predator data to investigate the influence on mouse population dynamics. Our idea is to determine whether the explosion depends on a pulse of resources due to weather factors (gradual dynamic), or an eruptive dynamic through mice escaping from predator regulation. Through this approach, we will use theoretical ecology

and pest management models to identify which factors are important to generate the mouse outbreaks and reduce their economic impact in Australian grain crops.

Materials and Methods

Study area

Mouse population abundance data were collected from farms near (within 5 km) the Mallee Research Station at Walpeup, Victoria (35°08'S, 142°01'E), which is a major cereal production area in Australia and experiences periodic house mouse outbreaks. The area has a mean annual rainfall of 336 mm falling mainly in winter (the crop growing season), mean maximum temperature of 30.4° C in summer and mean minimum temperature 5.4° C in winter. Principal crops are winter cereals such as wheat, canola and barley. Soils are yellowish-brown sands and reddish-brown sandy loams which is very different from the hard-cracking clays that Newsome (1965) worked on (Brown and Singleton 1999, Singleton et al. 2005).

Longworth live-capture traps (Longworth Scientific, Abingdon, UK) were used to trap mouse populations. These traps were baited with wheat and set for three to ten consecutive nights in an arrangement of trap grids and trap lines in key habitats with traps spaced at 10 m intervals in different sites such as paddocks, pastures, and fencelines between 1983 and 2002 (detailed methodology in Singleton 1989; Brown and Singleton 1999). The mouse abundance data are expressed as an adjusted trap success (captures per 100 trap nights) using the frequency-density transformation of Caughley (1977). Traps that have fired but have not caught a mouse are subtracted from the total number of traps set to give an adjusted number of traps (Caughley et al. 1998). Absolute densities of mouse populations in fields were estimated by mark-recapture using the Petersen method (Krebs 1999).

$$\% \text{ trap success} = \frac{\# \text{ mice caught} \times 100}{\text{Adjusted \# traps}}$$

The time series has abundance gaps in some seasons where no monitoring was conducted. These gaps occur in low-density years and were filled-in using the mean abundance of non-outbreak years. To characterize the time series, we used the population rate of change (R_t) or reproduction function (Berryman 1999) as a function of population size (N_t) to show the process of individual survival and reproduction (Berryman and Kindlmann 2008).

$$R_t = \ln N_t - \ln N_{t-1} = \ln \left(\frac{N_t}{N_{t-1}} \right)$$

Weather data (precipitation, humidity, temperature, and evaporation) and the productivity of wheat crop (yield) were obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/data>) and AGSURF Data (<https://apps.agriculture.gov.au/agsurf/agsurf.asp>). The predator numbers were acquired from the e-bird database (www.ebird.org) using the relative abundance data (average number of birds reported on all checklists). The checklists used in the calculation include those that reported a species 'absence' providing a gross measure of relative abundance or how commonly the bird is reported. The predator species examined were *Elanus axillaris* (Black-shouldered Kite), *Tyto alba* (Barn owl), *Ninox novaeseelandiae* (Boobook), *Falco berigora* (Brown falcon), *Falco cenchroides* (Nankeen kestrel), *Circus approximans* (Swamp harrier), and *Circus assimilis* (Spotted harrier) based on knowledge of birds known to frequent Walpeup (Brown et al. 2002). These are all

relatively common species readily identifiable by the bird observers, and all of them are generalist predators of mice.

Seasonal models

We refer to the southern hemisphere seasons of summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). We estimated the exponential rate of population change (R) during the summer increase (spring to autumn) and winter decrease (autumn to spring) phases, using an autoregressive model (Hansen et al. 1999, Merritt et al. 2001). Population growth rates in summer (R_{summer}) and winter (R_{winter}) are modelled as a linear function of their seasonal densities using minimum value per year log abundance in spring (Sp_t), and maximum value per year in autumn (A_t) because trapping effort varied each year, the monitoring timing was different each year, and the breeding season was different lengths (Singleton et al. 2005). Furthermore, we used the minimum and maximum abundance in spring and autumn to standardize low and high population periods for analysis. Also, we include the endogenous feedbacks like previous densities in each season, R_{summer} used spring and autumn (Sp_{t-1} , A_{t-1}), and autumn and spring to R_{winter} (A_{t-1} , Sp_{t-1}).

Population abundance and climatic variables were standardized to have 0 mean and variance equal to 1. To analyze the summer growth rate, we used winter rainfall (April to October; equivalent of “in crop rainfall”) and their lag of the last year ($t-1$), and summer (January to March, t) average humidity, evaporation, soil moisture, soil temperature, the number of days $\geq 35^\circ$ C and number of days with >1 mm rain. We used the same factors to analyze the winter growth rate plus winter (June to August) average minimum temperature, minimum soil temperature, and the number of

days with a minimum $\leq 0^{\circ}\text{C}$. We included the predators' relative abundance as a proxy of predation risk using the maximum value in summer-autumn abundance to explain the rate of population growth, and maximum value in autumn-winter abundance during the decrease phase.

To find the most parsimonious model for seasonal dynamics, we used the corrected Akaike information criterion AICc (Hurvich and Tsai 1989, Burnham and Anderson 2003). We fitted models, including climatic and predator effects using glm package in R (R Development Core Team 2004). As the incorporation of climate and predator variables produced a large number of possible models, we only present the best models according to the AICc. No more than three independent variables were used in any model to reduce the risk of over-parameterization. Parameter estimates from the best models were used to simulate population trajectories and predict when outbreaks would occur. We used a one-step-ahead simulation (OSA) that recalculates the abundance of each year according to the observed previous data and the model parameters (Turchin 2003).

Annual models

A discrete-time logistic model (Ricker 1954) was used to evaluate the influence of precipitation, humidity, temperature, evaporation, and productivity of wheat crop on the annual intrinsic rate of change of the mouse population. Maximum abundance of mice was identified and used for each calendar year irrespective of month for Walpeup. The logistic equations included the weather factors in two ways to evaluate the mechanism according to Royama (1992): lateral effect to analyze the influence of weather on carrying capacity of the mouse population (Equation 1 a), and

vertical effect to model the weather impact on the mice rate of change (Equation 1 b). We tested in the models all possible combinations between climatic factors.

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K+Z}\right)^Q \quad (\text{a}).$$

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K}\right)^Q + Z \quad (\text{b}).$$

Equation 1. R_t is the population rate of change; R_m is the maximum finite reproductive rate, and was fixed at 2.5 derived from the linear equation (R_t vs. N_{t-1}); N_{t-1} is the mouse abundance; K is the environment carrying capacity; Z is the environmental factor; and Q is the non-linearity of the curve: a value of $Q > 1$ indicates a convex shape and $Q < 1$ indicates a concavity. a. Lateral effect. b. Vertical effect.

To model the predation impact on the mouse populations a discrete time predator-prey model with a functional response type III was used (Holling 1959, Berryman 1999, 2003). We used house mouse abundance and predator relative abundance using the maximum value per year ($t-1$). To understand the predator's impact on mice, we tested each predator independently or the sum of all species (Equation 2 a). We also evaluated the predator effect with precipitation and evaporation (Berryman 1987, 1999, Berryman et al. 1987) (Equation 2 b).

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) - W \left(\frac{N*D}{h^2 + N^2}\right) \quad (\text{a}).$$

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) + Z - W \left(\frac{N*D}{h^2 + N^2}\right) \quad (\text{b}).$$

Equation 2. R_t is the population rate of change; R_m is the maximum finite reproductive rate, and was fixed at 2.5 according to R function (R_t vs. N_{t-1}); N_{t-1} is the mouse abundance; K is the environment carrying capacity; Z is precipitation and evaporation; W is the predators attack rate; D_{t-1} is the predators' abundance; and h^2 is the predator's saturation rate. a. The logistic model with functional response type III. b. The functional response model with precipitation and evaporation.

We used non-linear regression (Bates and Watts 1988) to determine the best fitted model with mouse abundance, predator relative abundance and weather data. To analyze the mathematical models, we used the nls function (Nonlinear least squares) in the R program (R Development Core Team 2004). The most parsimonious models were selected using the AICc (Burnham and Anderson 2003). Parameter estimates from the best models were used to simulate population trajectories and predict when outbreaks would occur. In the first case we performed a complete simulation taking just the first observed abundance as a starting point and ran the models for successive years. The second case we used a one-step-ahead simulation that recalculates the abundance of each year according to the observed previous data (Turchin 2003).

Results

There were five outbreaks across our time series (1983 to 2002) which demonstrated an irregular pattern in population abundance (Fig. 1 a). The relative abundance of Nankeen kestrel (t_1) (*Falco cenchroides*) was dynamic and also showed peaks in the year with mouse outbreaks (Fig. 1 b). The precipitation varies between 170 mm to 350 mm and shows peaks one year before each outbreak (Fig. 1 c). Mean summer evaporation tended to be lower in mouse outbreak years (Fig. 1 d).

Seasonal model

The rate of increase of mouse populations over the summer breeding season was best explained by lower evaporation in summer, the cumulative winter higher rainfall in the two years before the outbreak, and a minor negative contribution from Nankeen kestrel abundance (*F. cenchroides*), where a high density of Nankeen kestrel cause a low mice density and vice versa (Table 2, Figure 2). The best model included high winter precipitation (Figure 2 a), low summer evaporation (Figure

2 b), and low predator abundance positively affecting the rate of change (R) (Figure 2 c), and explained 61% of the variation in R . The results showed that when Nankeen kestrel abundance was low or better environmental conditions occurred, the mouse numbers were increasing rapidly. When Nankeen kestrel abundance was high, the mouse abundance was not overgrowing to predation pressure. It allows us to understand a possible mechanism from mice escaping predation to generate an outbreak. Although predation was a very small component, it could be important to predict the mouse outbreak dynamics. The next best models included rainfall and evaporation but only explained 52% of the variation in R , and a model including the previous two years rainfall explained only 50% (Figure 2 d). The simulation to predict the mouse outbreaks showed that correlation between predicted and empirical data of the weather model was 65% (Figure 3 a) and 71% in the predator and weather model (Figure 3 b), which is a significant improvement in the prediction of the magnitude of the outbreaks in comparison with weather model. The rate of population decline over winter was best explained by the starting abundance in autumn (Figure 2 e), and higher Barn owl abundance (*Tyto alba*, Figure 2 f) which explained 65% of the variation in R , but this was not better than the simple model with autumn abundance only.

Annual models

The models with vertical effect (equation 2 b) showed a better performance than the models with lateral effect (equation 2 a) where lateral effect analyzed the influence of weather on carrying capacity of the mouse population, and vertical effect modeled the weather impact on the mouse rate of change. The best vertical model was precipitation and evaporation achieving a 68.33 AICc and a prediction of 66% among simulated and observed abundance (Figure 3 c). This model correctly predicted the seven outbreaks (1984, 1987, 1988, 1993, 1994, 1997, 2001) in the Walpeup mouse abundance data. The result supports the mechanism proposed, where the precipitation and

evaporation could improve the soil conditions, becoming more permeable. Thus, this allows mice to dig their burrows (enemy-free space) and escape predators, leading to an outbreak. Likewise, the influence of precipitation and evaporation on the maximum rate of change of the mouse population is through vertical effect, directly affecting the maximum rate of change (more reproduction).

The model selection process indicated that the relative abundance of the predators, precipitation, and evaporation factors resulted in the lowest AICc compared to the rest of the models. These results establish a relationship between the possible causes of mouse outbreaks. The best model included Nankeen kestrels (*Falco cenchroides*) and weather factors acting together achieving a 74.18 AICc (Table 2). The correlation between predicted and empirical data was 73% (Figure 3 d), which is a significant improvement in the prediction of the magnitude of the outbreaks in comparison with models of weather alone.

Discussion

Australian mouse populations were analyzed using seasonal and annual models of population change to understand the influence of endogenous and exogenous factors on the rodent populations (Berryman and Kindlmann 2008). There is controversy about which is the best approach to analyze the outbreaks of small mammals. Seasonal models enabled an evaluation of mouse eruption phases separately, to observe the outbreak increase phase from the breeding to peak phase, and the collapse phase from the peak to the lowest point (Merritt et al. 2001). Likewise, it includes the endogenous feedback (density dependence) which allowed the effect of the previous abundances to be tested and the density influence on the populations to be identified. For example, the spring mouse abundance is crucial to trigger the outbreak and the autumn mouse abundance to understand the

collapse. Furthermore, seasonal models identify the relationship between the weather or predators' factors and the mouse rate of change, eliminating the autocorrelation variables. The outputs improve our understanding of how the outbreak is generated, when the various factors are important, and when each factor should be monitored. Also, the results help determine which months are more critical to monitoring and predict them. For example, our results identified spring to autumn seasons (September to May) as the increase phase which is relevant to monitoring because the favorable environmental conditions before the breeding season support the mouse density increase and their litter size (Singleton & Redhead 1990, Singleton et al. 2001).

The annual models were used to understand the mechanism of the exogenous factors through a vertical and lateral effect on the pest population (Royama 1992, Lima et al. 2002). Our best model was precipitation and evaporation in a vertical effect, meaning the exogenous variables influenced the maximum rate of change directly (increased reproduction), being independent of population density, $R_t = R_m * (X_{t-1}) + Z$ (Royama 1982, Stenseth et al. 2002). On the contrary, the lateral effect would have been on carrying capacity or some limiting resource, and the population density ($X_{t-1}/K+Z$), but this is not the case in the mice population (i.e. rainfall influences the food supply). Additionally, the annual models were able to determine the influence of endogenous and exogenous feedbacks on the rate of change ($R_t = R_{t-1}$) to estimate mouse abundance through a simulation-based approach using fitted models and cross-validation (Lima 2003, Turchin 2003).

We evaluated some hypotheses proposed to explain the population growth: soil conditions, rainfall and food supply, dry and wet years, and predators (Table 1). Weather models allowed us to conclude that rainfall and food supply are both necessary but not sufficient to generate a plague (Bomford and Redhead 1987, Ylonen et al. 2003, Korpimaki et al. 2004, Jacob et al. 2007, Brown

et al. 2010). Many researchers have focused their modeling efforts only on precipitation through an index of crop yield because high seed availability and quality food could trigger an early breeding season and cause an outbreak. Still, our results showed that using only rain is not sufficient to predict the outbreaks (Saunders and Giles 1977, Redhead 1982, Singleton 1989, Mutze et al. 1990, Cantrill 1992, Twigg and Kay 1994, Pech et al. 1999, Krebs et al. 2004). The response of abundance in south-eastern Australia is not due to a pulse of resources because the population does not vary directly with rainfall and food supply fluctuations alone (Berryman 1999, Singleton et al. 2001, Krebs et al. 2004). Nevertheless, the precipitation role on mouse populations is evident due to its influence on soil conditions, the attack rate of predators, or water availability (Mutze 1989, Mutze et al. 1990, 1991, Pech et al. 1999, Krebs et al. 2004, Brown et al. 2008).

Several authors have proposed additional factors that could act with rainfall like soil conditions, predators, social structure, and others since a single factor has not been able to explain and predict the mouse dynamics correctly (Mutze et al. 1990, Brown and Singleton 1999, White 2002). The seasonal and annual models showed that high winter rainfall (t_1 and t_2) and low summer evaporation best explained the outbreaks. The outbreak mechanism consists of winter and spring rainfall that promotes the growth of plants to provide the mouse food supply (crops and weeds), moist soil conditions ideal for digging mouse burrows for shelter, and low evaporation to prevent the drying out of the soil. The Victoria soils are calcareous or sandy loam with low water storage capacity, poorly aerated and with poor drainage, and they are compact (Isbell 2016). Their evaporation is high, retaining little moisture, and when the soil dries it forms clods. Thus, soil conditions are essential to dig the burrows. Abundant mouse burrows mean that mice can avoid predators, and as a consequence, increase the reproduction leading to an outbreak (Newsome 1969, Saunders 1986).

Some studies have established the relevance of soil conditions and precipitation for building mouse burrows leading to an outbreak in dry-arid lands in south-eastern Australia (Newsome 1969 a,b, Newsome 1970, Saunders and Giles 1977, Cantrill 1992, Twigg and Kay 1994, Mutze et al. 1991, Boonstra and Redhead 1994). For example, Newsome and Corbett (1975) registered the highest mouse numbers when the soil was wet, unlike when the soil was hard and dry in summer; Twigg and Kay (1994) predicted an outbreak in the Macquarie Valley using food supply, clay soils, temperature, and burrow number; and Singleton et al. (2001) mentioned the importance of dry years followed by wet years (good rainfall) for generating better food and cover. However, we should keep in mind that first, the weather model tries to predict most of the outbreaks, but the magnitude accuracy is not enough. Hence, the outbreak may depend on triggers such as weather that protect mice from regulation by predators turning it into a complex eruptive dynamic. Second, the burrows and precipitation (food supply) must be available, abundant, and simultaneous for the mouse population, but this coincidence is rare. Perhaps, for this reason, mouse outbreaks are irregular (Newsome and Corbett 1975, Krebs et al. 1995). Also, there could be other factors that we are not totally aware of.

The best model for the increase phase included winter rainfall, summer evaporation, and relative abundance (low) of Nankeen kestrels (*Falco cenchroides*) with a negative relationship between predator-prey due to a predation effect on the intrinsic growth rate of the mouse. Therefore, mice could potentially escape a threshold through increased rainfall and decreased evaporation which acts as a trigger for outbreaks, by allowing the mice to make more burrows due to the improved soil conditions. In the same way, the mouse population could escape regulation by predators because of the rapid population increase causing prey saturation (considered a co-operative

mechanism by many authors) (Berryman 1987, 1999, Berryman et al. 1987). Also, the seasonal and annual model accomplished an accurate outbreak prediction in comparison with precipitation and evaporation model. These results suggest the regulation by predators is weak at low-intermediate mouse densities, which then disappears with better environmental conditions, i.e., precipitation and evaporation, and as mouse abundance escapes from regulation and crosses the population threshold (Newsome and Corbett 1975, Sinclair et al. 1990, Brown and Singleton 1999). Mice can escape from predator control due to weather triggers and the functional response of generalist predators that adapt quickly to changes according to prey availability (Sinclair 1996). The triggers and predator mechanism could enhance mice reproductive performance because good rainfall and low evaporation allow mice to build their burrows; as a consequence, mice can escape from predators, particularly when predator numbers are low (Figure 4) (Newsome and Corbett 1975, Sinclair et al. 1990, Berryman 1990, Krebs 2001).

The generalist predator's regulation often does not respond to high mouse density. Experiments have observed a mouse mortality rise (regulation) at low-density, where it is usual that the predator switches to alternative prey. When this occurs, it is possible that mouse density will increase. As a consequence, predator control diminishes (Sinclair et al. 1990, Krebs et al. 1995, Hanski and Korpimäki 1995, Sinclair and Pech 1996, Korpimäki and Norrdahl 1998). The non-regulation phase can occur through predator saturation or high consumption of alternative prey that diminishes the impact on mice (Holling 1966, Murdoch 1969, Newsome and Corbett 1975, Gould et al. 1990, Berryman 1999b, Sinclair 2003). Our results suggest mice may be held in a predator pit (Berryman 1999, 2003, Sinclair 2003) especially if outbreak related climatic triggers are absent. However, if there are few predators and a large climatic trigger event leading to good food and cover conditions, then an outbreak can be generated.

We need to comprehend the interactions between species as predator-prey to analyze the potential influences on the mouse population as a complex system. Few studies have examined the predator role on house mouse outbreaks because we do not have adequate measures of predator abundances across time. We used secondary data from e-bird online databases. We need more precise data and experiments to clarify the predators' role because they are a common factor operating on small mammals (Krebs 2001). We think that the first step is to identify the predators' tendencies on the mouse population using relative abundance. Our data are from different checklists in Australia that report the presence or absence of a diverse range of predators in the Victorian Mallee. Our results show an additive effect of generalist predators with weather factors. Demonstrating a different structure of population dynamic than other rodent pests, where predators or resources regulated the population, mice can escape their controlling factors due to weather triggers and erupt to high densities (Berryman 1982). The models suggest it is worth an effort to explore further the role of predators on mouse population abundance.

We propose an outbreak mechanism in a stepwise manner. For an outbreak to occur, the mice population needs different favorable conditions before the breeding season commences to provide food supply, cover, and water availability. The low summer evaporation and winter rainfall (t_1 and t_2) may improve soil conditions for mice to dig burrows to escape from predator regulation. Followed by abundant food supply through breeding season to maintain a high reproduction rate to generate an outbreak (Figure 4). (Newsome 1969, 1970, 1971, Newsome and Corbett 1975, Mutze et al. 1991, Singleton et al. 2001, White 2002, Brown et al. 2008). Subsequently, the strong autumn density-dependence, absence of good conditions, i.e. food because the crops are sown in the autumn season, social stress like aggression or territorialism, and diseases will cause an outbreak

collapse (Singleton 1989, Sinclair 1989, Singleton and Redhead 1990, Brown and Singleton 1999). Finally, mice return to low densities where predators may consume the mouse population as we showed with the Barn owl (*Tyto alba*), faster rates of decline are associated with higher predator numbers (Singleton and Redhead 1990, Singleton et al. 2001, Singleton et al. 2005, Brown and Singleton 1999).

To forecast outbreaks of the house mouse, it is essential to choose a model that predicts the onset, magnitude, and duration accurately (Pech et al. 1999). Our results showed that the best of the annual models to explain the outbreaks was precipitation and evaporation, but the best prediction was in the predator and weather model. We must choose the weather model like a quick tool to predict the outbreaks because the weather data is cheaper, easier to work with, more reliable, and more robust (centrally collected through the Australian Bureau of Meteorology) than predator abundance data. It would, however, be useful to include predators to understand the ecological processes of mice outbreaks as a complex eruptive dynamic, but more work is required to achieve this aim.

Conclusions

The weather model identified the possible mechanisms behind the outbreaks with high precipitation and low evaporation which improve the soil conditions potentially creating more enemy-free space. Also, predators and trigger model improved the prediction capacity of the simulation because of the relationship between weather and predators. Better monitoring data is needed to test the relationship between predator and prey. According to our results the Australian mouse population dynamics can be defined as “eruptive” because the outbreaks are initiated by a trigger followed by positive feedback processes that allow the population to obtain more and better resources and escape a predator threshold by increasing population density. Furthermore, rodent

abundance dynamics are complex, non-linear, and depend on seasonal patterns such as precipitation and evaporation, and other factors such as predator abundance.

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Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors designed the study and wrote the manuscript. The first author collected and analyzed the data.

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Table 1. Factors previously proposed to explain and predict the mouse outbreaks in Australia. Y = yes, N = no.

Hypothesis	Description	Tested	References
Soil conditions and nesting sites	Rainfall events and good soil conditions provide burrowing and nesting sites in cracking soils. Weather provides abundant home-sites.	Y	Newsome 1969 a, b, Newsome 1970, Saunders and Giles 1977, Cantrill 1992, Twigg and Kay 1994, Mutze et al. 1991, Boonstra and Redhead 1994.
Rainfall and food supply	Rainfall is a surrogate for food supply that is essential for mice reproduction and survival.	Y	Redhead 1982, Redhead 1982, Redhead 1988, Singleton 1989, Mutze et al. 1990, Brown and Singleton 1999, Dickman et al. 1999, Pech et al. 1999, Singleton et al. 2001, Kenney et al. 2003, Ylonen et al. 2003, Krebs et al. 2004, Jacob et al. 2007, Brown et al. 2008.
El Niño/Southern Oscillation (ENSO)	Climatic variability is affected by El Niño-Southern Oscillation (ENSO) events, and large-scale weather variables could explain outbreaks.	N	Krebs et al. 2004, Letnic and Dickman 2006.
Dry and wet years	Drought-breaking rain and good winter rainfall generate better environmental conditions for crop growth.	Y	Saunders and Giles 1977, Mutze et al. 1990, Boonstra and Redhead 1994, Brown and Singleton 1999.
Predators	Predators regulate mice at low-density when predators can aggregate in high numbers.	Y	Saunders and Giles 1977, Redhead 1982, Sinclair et al. 1990, Sinclair 2003, Arthur et al. 2004, Korpimäki et al. 2004, Arthur et al. 2005.
Social behaviour	Social interactions affect the timing of sexual maturation affecting the breeding season. Mice switch from an asocial structure at low densities to a social system as abundances increase. Disruption of social regulation could be a condition to generate a plague.	N	Vandenbergh et al. 1972, Lidicker 1976, DeLong 1978, Drickamer 1984, Krebs et al. 1995, Oli and Dobson 1999, Chambers et al. 2000, Sutherland et al. 2005, Sutherland and Singleton 2006.
Food quantity and quality	Food is essential for mice reproduction and survival. High-quality food could extend the breeding season into winter in refuge habitats.	Y	Redhead 1982, Redhead 1982, Bomford 1985, Redhead et al. 1985, Bomford 1987 a, b, c, Bomford and Redhead 1987.
Habitat and refuges	Mice disperse from refuges into other areas; induced-donor habitats. Mice occur in crops when crop conditions are favorable. Habitats with structural complexity could increase the mouse density and protect them of predation risk.	N	Redhead 1982, Singleton 1989, Dickman 1992, Boonstra and Redhead 1994, Boonstra and Redhead 1994, Twigg and Kay 1994, Chambers et al. 1996, Arthur 2001, Arthur et al. 2003, Arthur et al. 2004, Jacob et al. 2004, Arthur et al. 2005.

Table 2. The most parsimonious population dynamic models for mouse outbreaks using the seasonal model from Merritt et al. (2001), logistic growth from Ricker (1954), and functional response model from Berryman (2003). R^2 : Adjusted R-squared, AICc: Akaike information criteria, OSA: Simulation One step ahead (Turchin 2003).

Model	Autoregressive coefficients	R^2 (%)	AICc	OSA (%)
<i>Increase phase</i>				
Weather	$R_{\text{summer}} = 0.170 + 0.002 \text{ Precipitation} + (-0.074) \text{ Evaporation}$	52	-7.939	65
Predators and Weather	$R_{\text{summer}} = 0.417 + 0.002 \text{ Precipitation} + (-0.082) \text{ Evaporation} + (-0.182) \text{ Nankeen kestrel}$	61	-9.381	72
Dry and Wet years	$R_{\text{summer}} = 0.311 + 0.002 \text{ Precipitation} + (-0.077) \text{ Evaporation} + (-0.0003) \text{ Precipitation}_{t-1}$	50	-4.573	59
<i>Decrease phase</i>				
Density-dependence	$R_{\text{winter}} = 0.221 + (-0.183) \text{ Autumn abundance}$	63	11.455	74
Density-dependence and Predators	$R_{\text{winter}} = 0.194 + (-0.160) \text{ Autumn abundance} + (-0.087) \text{ Barn owl}$	65	12.597	78
<i>Annual models</i>				
Weather	$R_t = R_m * (1 - (X_{t-1}/10)^{0.341}) + 0.014 \text{ Precipitation} + (-0.655) \text{ Evaporation}$	85	68	66
Predator and Weather	$R_t = R_m * (1 - (X_{t-1}/179.167)) + 0.009 \text{ Precipitation} + (-0.772) \text{ Evaporation} + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$	89	75	73

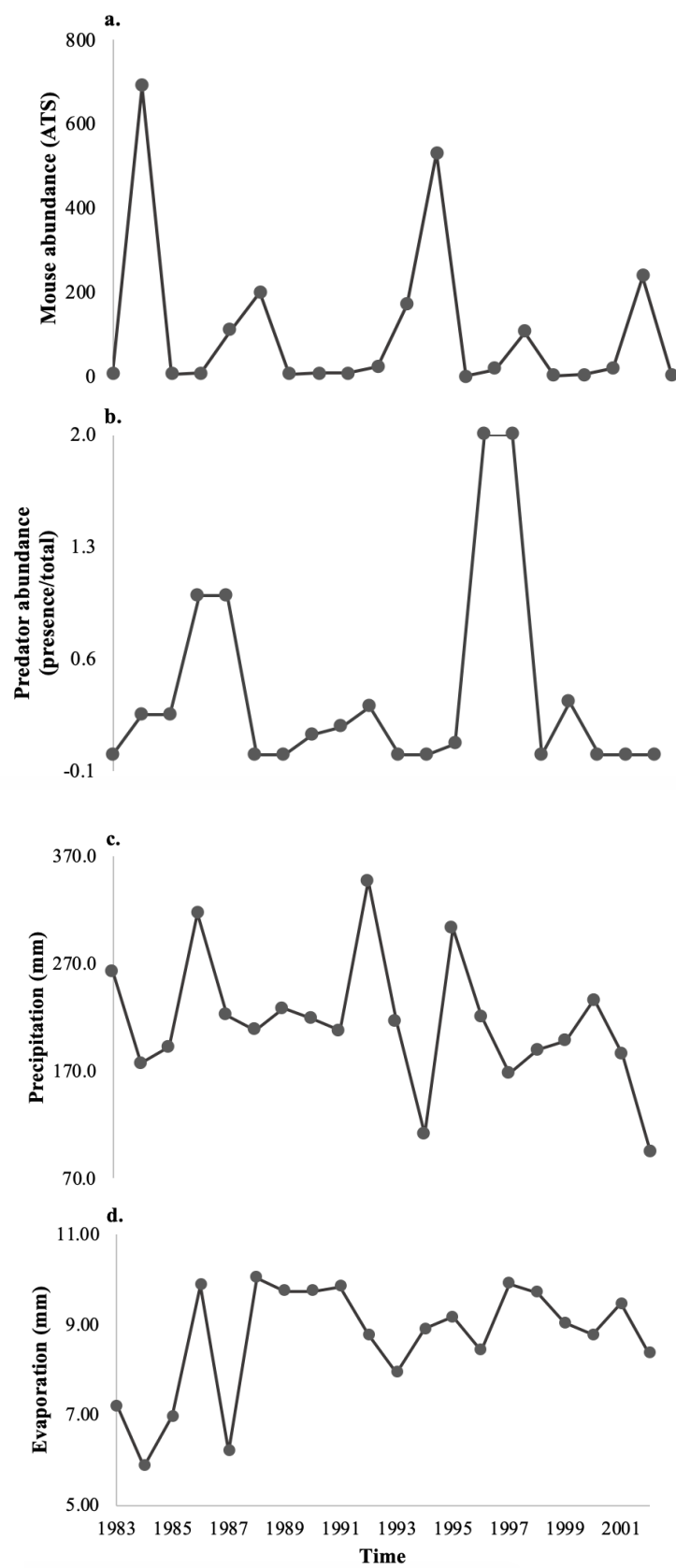


Figure 1. Time series of factors proposed to explain and predict the mouse outbreaks. A. House mouse abundance (ATS: adjusted trap success); B. Relative abundance of Nankeen kestrel (positive observations / total observations, January to July); C. Accumulative precipitation (mm, April to October); D. Average evaporation (mm, January to March).

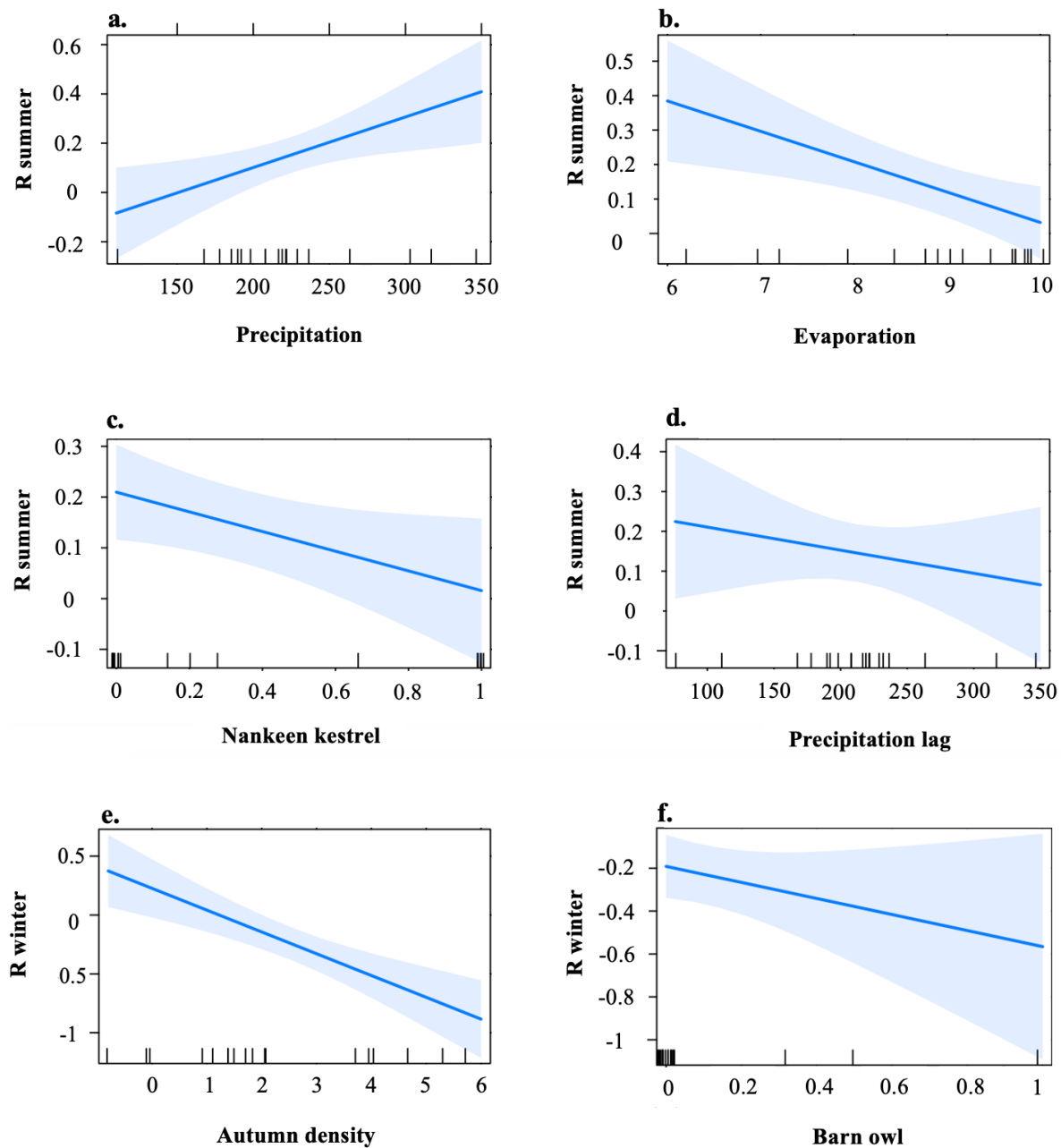


Figure 2. Predictor variables on mouse rate of change (R_{summer}/R_{winter}) show the relationship between endogenous and exogenous factors and the increase and decrease phases. The figures a, b, c, and d. correspond to R_{summer} or increase phase with precipitation (mm), evaporation (mm), Nankeen kestrel (positive observations / total observations), and precipitation with lag (t_{-1}), respectively. The figures E and F correspond to R_{winter} or decrease phase with autumn abundance (Adjusted trap success) and the Barn owl (positive observations / total observations).

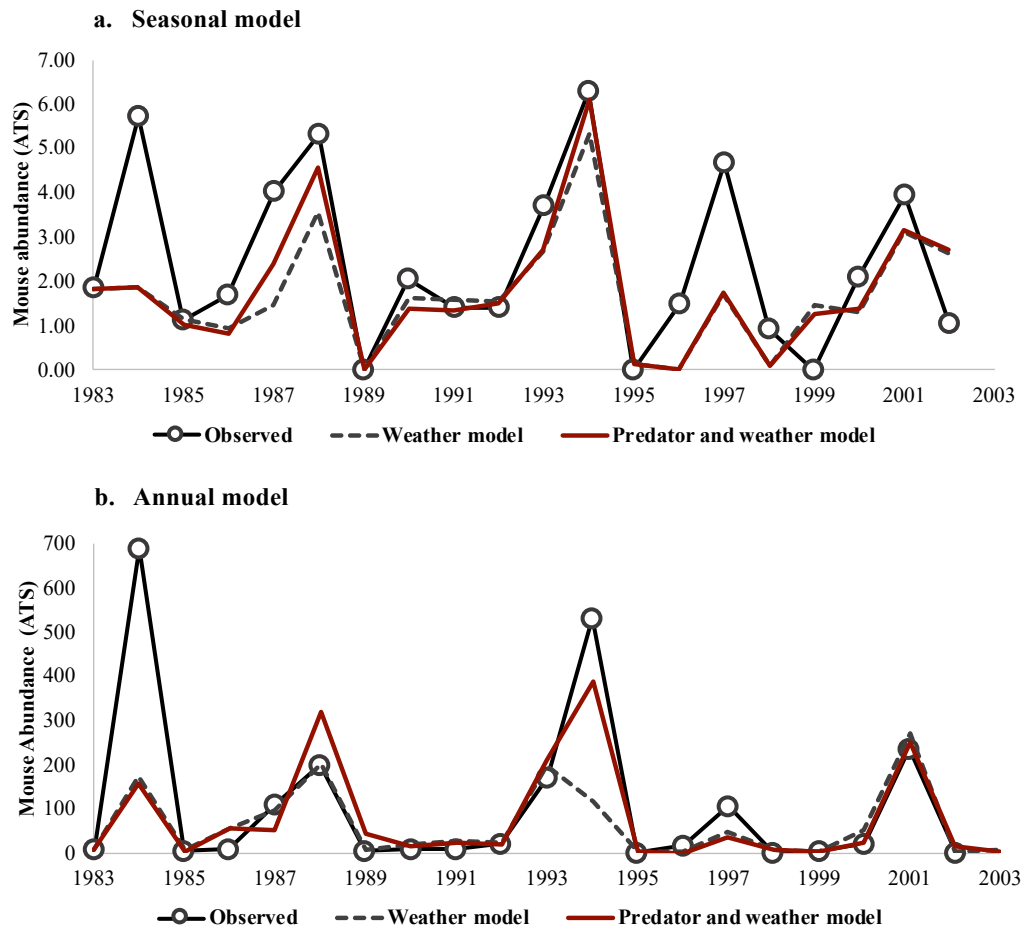


Figure 3. Prediction of mouse abundance using the seasonal model from Merritt et al. (2001), logistic growth from Ricker (1954), and functional response model from Berryman (2003). a. Precipitation and Evaporation model; mouse abundance is represented in log scale, b. Nankeen kestrel (*Falco cenchroides*) and weather model.

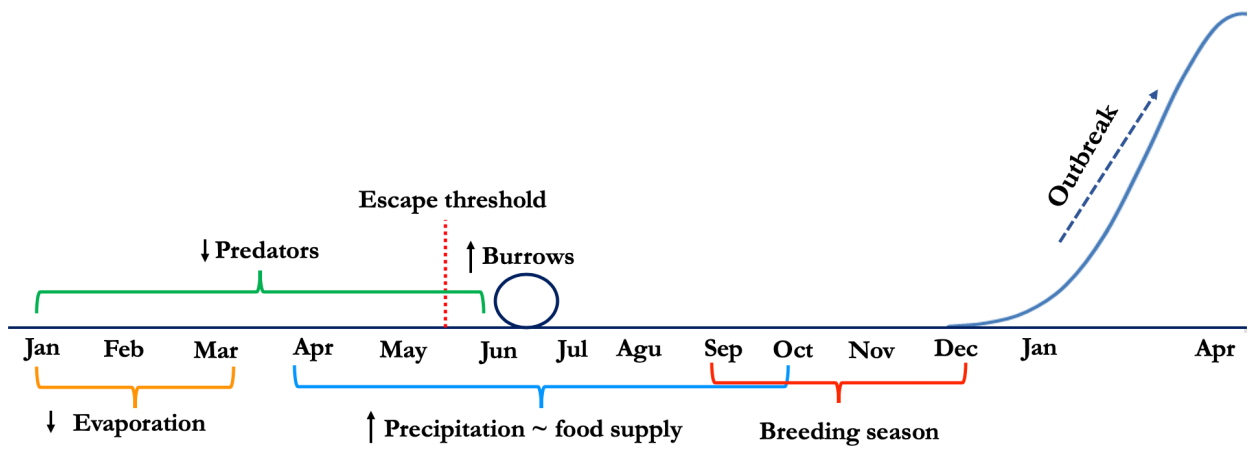


Figure 4. Outbreak mechanism to explain increased mouse density in Walpeup (Victoria). Mice need favorable conditions before the breeding season (spring) such as low summer evaporation and good winter rainfall that improves soil conditions for mice to dig burrows to escape from predators, and abundant food supply to generate an outbreak.

Paper 2: Mouse outbreaks in Walpeup (Victoria), Roseworthy (South Australia) and Darling Downs (Queensland).

Gradual and eruptive outbreaks in South-eastern Australia and Queensland

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Abstract

House mice in Australia are a plague with irregular population dynamics and cause considerable damage in cropping systems. We used a 20-year mouse mark-recapture dataset from Walpeup (Victoria), Roseworthy (South Australia) and Darling Downs (Queensland), and climatic and predator variables. We employed seasonal and annual models to understand the increase and decrease in population through different drivers. For South-eastern Australia, the rate of increase was best explained by low evaporation in summer, high cumulative winter rainfall, and an index of abundance of the Nankeen kestrel (Walpeup) and the Brown falcon (Roseworthy) during summer to autumn. The mouse outbreaks in Queensland were explained by spring to summer rainfall from the two years before the plague, and also by previous mouse abundances. The rate of declines in the Southeast is explained by mouse outbreak abundance and an index of Barn owl abundance in Walpeup and Swamp harrier in Roseworthy. The collapse phase in Queensland is related to outbreak abundance (density-dependence) and Barn owl density. We conclude that Southeast mouse dynamics can be defined as an eruptive dynamic caused by weather triggers that allow the population to obtain more and better resources while avoiding being consumed by their predators. Queensland outbreaks can be defined as gradual because they are generated by changes in rainfall and a strong density-dependence. These results are useful to explain and predict the

outbreaks, understanding the mechanisms that cause the mouse explosion on wheat productive sites.

Keywords: Australian house mouse; irregular dynamics; gradual and eruptive outbreaks; population dynamic; predator-prey; weather drivers.

Introduction

House mouse populations in Australia are a potential pest capable of causing significant economic losses (65 million AUD per year) on grain-growing because of their rapid increase (Singleton 1989, Caughley et al. 1994, Singleton et al. 1999, Singleton et al. 2001, Singleton et al. 2005). Pests can occur from South Australia through the grain belt up to the Darling Downs in Queensland or sometimes occur in smaller, localized areas. House mouse outbreaks are not constant across time, but rather they can occur every four or five years in South-eastern Australia or every two to three years in Queensland (Redhead and Singleton 1988, Singleton 1989, Mutze 1991, Singleton et al. 2005, Pople et al. 2013). The Australian grain belt has many regions with various soil types, cropping systems and climates (Table 1). The different mouse dynamics imply that the main regulating factors may not be uniform between regions, and mice could respond to favourable conditions through one or another mechanism depending on the environment. Thus, the differences can make it challenging to propose a single model to explain and predict mouse outbreaks for all the grain-growing belts.

The Southeast has had several house mouse outbreaks, where Walpeup in Victorian Mallee and Roseworthy in South Australia have had the biggest explosions (Singleton et al. 2001). The climate is semi-arid with hot summers and cold winters. The crops are winter cereals due to the maximum

rains in winter, and they grow in the same paddock only once every two to three years. The differences between Walpeup and Roseworthy are the rain levels, 215 mm in Walpeup and 335 mm in Roseworthy, and type of soil. Walpeup has calcarosols such as sandy loam or red-brown soils with low water holding capacity needing optimal conditions of humidity (Isbell 2016). Roseworthy has chromosols such as red-brown lands which are clay and poorly aerated but better drained than Walpeup soils (Jacquier et al. 2001). On the other hand, Darling Downs in Queensland has had house mouse outbreaks more consistently over time in the winter season and less severe, which makes it difficult to separate outbreak years from non-outbreak years (Pech et al. 1999). Darling Downs has a humid subtropical climate with hot humid summers and cold dry winters. The rainfall is 473 mm approximately from October to April. The crops are planted in winter and summer due to the climate, which grow continuously on self-mulching cracking dark clay soils (vertisols) with a great available water capacity and moisture retention in comparison with southeastern soils. This kind of soil is exposed to irregularities such as droughts or floods and becomes tough during droughts and very sticky when flooded (Past 1998, Isbell 2016).

Robust predictive models are required for effective management of eruptions of mice and to prevent the economic losses on crops. Pech et al. (1999) did an extensive review of the regional and local models in New South Wales, Victoria, South Australia and Queensland proposing food supply, rainfall and droughts, soil conditions, predators and diseases as different hypotheses to predict the occurrence and abundance of mice. The models above for Southeastern Australia and Queensland have only predicted outbreaks in 50% (mice abundance/occurrence), showing that the causal mechanisms are not yet identified. All models have been developed using location-specific data, and none have directly addressed the extent of the geographic range of their predictions.

In southeastern Australia, the food supply hypothesis has been tested to provides energy for growth during the breeding season, increasing the mice reproduction rate and the litter size (Bomford 1987, Bomford and Redhead 1987, White 2002), and the precipitation as an index of food supply because the rain improves the crop yield (biomass of seed), soil conditions, and breaks the drought (Seif and Pederson 1978, Redhead 1982, Singleton 1989, Singleton and Redhead 1989, Boonstra and Redhead 1994). Also, the severe droughts one or two years earlier were related to the reduction of predators and a delayed response in mice (Saunders 1986, Saunders and Giles 1977). Moreover, the favorable soil conditions have been proposed to allow mice to dig burrows and increase their nesting sites, decreasing the predation risk and raising the reproduction rate, but not tested yet (Newsome 1969, 1970, 1971, Newsome and Crowcroft 1971, Newsome and Corbett 1975, Cornish et al. 1980, Redhead 1982, Veit and Anderson 1985, Mutze 1989, 1991, Mutze et al. 1990, Twigg and Kay 1994). Finally, the predator's regulation of mice at low-intermediate densities is other hypothesis proposed but not tested, where they can escape through triggers that increase a limiting factor, or by saturation of the functional response of the predator, or predators switching between abundant alternative prey, allowing the population of mice to rise with a high reproduction rate and cause the outbreak (Holling 1959, Dawey and Fullagar 1986, Sinclair et al. 1990, Key et al. 1994, Sinclair and Pech 1996, Berryman 1999, Sinclair 2003, Korpimaki et al. 2004).

Queensland has studied the main extrinsic mechanisms to predict the mice eruptions such as food supply, precipitation and a density-dependence process in the major habitat types such as crops, fencelines, and fallow. The central hypothesis has been that rainfall influences crops, providing a finite amount of food that is exhausted by mice, where the time to depletion is a function of the trigger size (Cantrill 1992, Pople et al. 2013). The pulse of food depends on the duration and magnitude by the rainfall. Pople et al. (2013) proposed an index of abundance using the

precipitation (specifically autumn-winter rain in the previous year), crop yield, winter temperature and past mouse abundance. Rainfall in Queensland was the best correlation of seasonal mouse abundance, similar to the southeastern. Also, Cantrill (1992) assessed spring to summer rains relation to flooding which had the potential to suppress the mice rate of increase and increase juvenile mortality, avoiding an outbreak. Moreover, the endogenous factors have been evaluated through spring abundance of mice finding a negative correlation with abundance in the preceding winter which suggests a density-dependence process (Cantrill 1992, Caughley 2001). Still, the soil conditions and the predator hypotheses have not been tested yet.

The southeast and Queensland have divergent patterns and environment and crop conditions that could influence outbreaks through diverse mechanisms. This study will analyze the Australian house mice through a different perspective using population dynamics models and the outbreak theory to find the causal mechanisms behind the explosions (Berryman 1999a). The outbreak theory classified the population explosions in two types: gradient and eruptive according to their causes.

Gradient outbreaks depend exclusively on exogenous factors and they do not disperse to new and unfavourable environments (Berryman 1999b). The populations are dominated by the principle of competition for limited resources but as the environment improves, the density increases, generating an outbreak (Berryman 1999a). These dynamics depend on pulse gradients which are induced when environments in particular areas change from low to high favorability and back, depending on the increase in the resources and the duration of the exogenous factors. To identify this dynamic is through the lateral or vertical effect (Figure 1 A and B) which define the mechanisms of the exogenous factors on the limiting resource (lateral effect) or on the maximum

rate of change of the pest (vertical effect) (Royama 1992, Lima 2006). The exogenous factor moves the population density laterally or vertically on the curve of the rate of change causing an outbreak, when limiting resources rise, and collapsing when favourable conditions disappear (Royama 1992).

Eruptive outbreaks are characterized by pests spread over large areas, and their explosions do not depend on exogenous factors exclusively. The dynamics are dominated by the principle of co-operation and positive feedback processes which allows organisms to obtain more and better resources or avoid consumption by their predators through the increase in the density of the pest (Berryman & Stark 1985, Berryman 1999 a,b). The eruptive dynamics have a low-density stable equilibrium by negative feedback due to predator regulation, an escape threshold or unstable equilibrium at intermediate pest density caused by predator saturation, and a high-density stable equilibrium regulated by the shortage of food (Figure 1 C) (Holling 1965, Morris 1963, Takahashi 1964, Isaev and Khlebopros 1977, Sinclair et al. 1990, Berryman 1996, Sinclair 2003). The populations grow when pests are above escape threshold and decline when under it, separating two different states: one of growth and the other of collapse (Berryman et al. 1984, Berryman et al. 1987, Berryman 1999b). This kind of dynamics can use triggers as exogenous factors to increase the population density of pests allowing them to escape from predator regulation (May 1977, Groffman et al. 2006).

Gradual and eruptive outbreak theory can be useful to improve the knowledge of the Australian house mouse and identify whether the population increase depends on a pulse of resources, gradual outbreak, or through triggers that allow mice to escape from predators, eruptive outbreak. Establishing whether a single model or more than one can potentially predict the house mouse outbreaks for all Australia.

Materials and Methods

Study area

We used three-time series of mouse abundance along the Australian wheat belt: Walpeup in Victoria, Roseworthy in South Australia, and Darling Downs in Queensland, a major cereal production area in Australia and which experiences periodic house mouse outbreaks.

Walpeup

Mouse population abundance data were collected from farms near (within 5 km) the Mallee Research Station at Walpeup, Victoria (35°08'S, 142°01'E). The area has a mean annual rainfall of 336 mm falling mainly in winter, a mean maximum temperature of 30.4° C in summer, and a mean minimum temperature of 5.4° C in winter. Principal crops are winter cereals such as wheat, barley, and rice. Soils are yellowish-brown sands and reddish-brown sandy loams, characterized as calcarosols (Brown and Singleton 1999, Singleton et al. 2005). Longworth live-capture traps (Longworth Scientific, Abingdon, UK) were used to trap mouse populations. These traps were baited with wheat and set for three-ten consecutive nights in an arrangement of trap grids and trap lines in key habitats with traps spaced at 10 m intervals in different sites such as paddocks, pastures, and fence lines between 1983 to 2002 (detailed methodology in Singleton 1989; Brown and Singleton 1999). The mouse abundance data are expressed as an adjusted trap success (captures per 100 trap nights) using the frequency-density transformation of Caughley (1977). The time series has gaps in some seasons where there was no monitoring. These gaps occurred in low-density years and were filled-in using the mean of non-outbreak years.

Roseworthy

Mice were captured near Roseworthy (34°30'S, 138°41'E) in South Australia, in remnant woodland, adjoining crop paddocks and grassland along a railway line. The area has a mean annual rainfall of 440 mm falling mainly in winter, a mean maximum temperature of 22.4° C in summer, and a mean minimum temperature of 9.7° C in winter. Most paddocks are cropped with winter-growing cereals every second year. Soils are red-brown sands, sandy to loamy Mallee, and heavy clay loams, characterized as chromosols (Mutze et al. 1990, Mutze 1991). The live-trapping was with Elliott traps baited with peanut butter and rolled oats. These consisted of 13 trapping stations spaced at 10-m intervals with three traps at each trap station, which were checked for three consecutive nights each four to six weeks from autumn 1980 to winter 2000, along 130-m transects (two in the crop, one in nearby woodland, and one along the fence line). Before May 1986, three traps per trapping station, which were spaced at 10-m intervals. After May 1986, 1-3 traps were set per station to effectively maintain trap success below 30 % (methodology details Mutze 1991). Trap success for all periods is presented relative to the trapping effort with three traps per station. Combined data are presented as mean captures per 100 trap-nights in each habitat type.

Darling Downs

Mice have been trapped at 47 sites along a 32-km transect between Cecil Plains (27°30'S, 151°1'E) and Mount Tyson (27°34'S, 151°34'E) in Queensland, over 1989–2008. The area has a mean annual rainfall of 588 mm falling mainly in spring to summer, a mean maximum temperature of 27° C in summer, and a mean minimum temperature of 11.9° C in winter. Most paddocks are cropped with summer and winter cereals. Soils are cracking clay soils, which crack open when there are dry conditions, characterized as vertosols (Mutze et al. 1990, Mutze 1991). Trap-site locations are a variety of habitats used by mice in the district, including cultivated paddocks

(regardless of cropping stage), roadside verges, and native grasslands. Each site had 20 break-back traps baited with bacon, placed 10 m apart along a line, and left overnight (methodology detailed in Pople et al. 2013). Trapping data can be expressed as the number caught per 100 trap-nights ('unadjusted' trap success) (Cantrill 1992). The proportion of traps capturing mice (P) can be adjusted to an index of density (I) to account for trap saturation (Caughley 1977) as $I = -\ln(1-P)$ (adjusted trap success).

To characterize the time series, we used the reproduction function, which represents the population rate of change as a function of population size (Berryman 1999a, Berryman and Kindlmann 2008).

$$R_t = \ln N_t - \ln N_{t-1} = \ln \left(\frac{N_t}{N_{t-1}} \right)$$

The weather data (precipitation, humidity, temperature, and evaporation) were obtained from the Australian Bureau of Meteorology. The predator numbers were acquired from the e-bird database (www.ebird.org) using the relative abundance data like the average number of birds reported on all checklists, including those that reported a species absence, providing a gross measure of relative abundance. The predator species examined were *Elanus axillaris* (Black-shouldered Kite), *Tyto alba* (Barn owl), *Ninox novaeseelandiae* (Boobook), *Falco berigora* (Brown falcon), *Falco cenchroides* (Nankeen kestrel), *Circus approximans* (Swamp harrier), and *Circus assimilis* (Spotted harrier) based on knowledge of birds known to frequent Walpeup (Brown et al. 2002), Roseworthy and Darling Downs. These are all relatively common species readily identifiable by the bird observers.

Seasonal models

The rate of population change (R) was estimated during the summer increase (spring to autumn) and winter decrease (autumn to spring) in south-eastern Australia (Walpeup and Roseworthy), and the autumn increase (summer to winter) and spring decrease (winter to summer) in Queensland (Darling Downs). We used the maximum value of autumn in the south-east, and winter in Queensland. We employed the minimum value for the rest of the seasons. Southern hemisphere seasons were used, where summer (S) is December to February, autumn (A) is March to May, winter (W) is June to August, and spring (Sp) is September to November. The population rates were modeled as a linear autoregressive function, calculating the rate of change (R) as the following season's abundance minus the last season's abundance. The independent variables (g) were the previous densities and the exogenous factors like weather and predators (Hansen et al. 1999).

$$R_{summer} = A_t - Sp_{t-1} = Sp_{t-1} + A_{t-1} + g$$

$$R_{autumn} = W_t - S_{t-1} = S_{t-1} + Sp_{t-1} + g$$

$$R_{winter} = Sp_t - A_{t-1} = A_{t-1} + Sp_{t-1} + g$$

$$R_{spring} = S_t - A_{t-1} = W_{t-1} + A_{t-1} + g$$

The rate of increase (R_{summer}) was analyzed through winter cumulative rainfall in the south-eastern and spring cumulative rainfall in Queensland, average summer humidity, mean evaporation, mean soil moisture and temperature, number of days $> 35^\circ\text{C}$, and number of days with $> 1\text{ mm}$ rain. We used the same factors to analyze the decrease phase (R_{winter}) plus the winter average minimum temperature and minimum soil temperature, and the number of days with a minimum $< 0^\circ\text{C}$. We included the predators' relative abundance as a proxy of predation risk using the maximum value in summer-autumn abundance to explain the rate of population growth and maximum value in the autumn-winter abundance during the decrease phase. Previous house mouse population

abundances and various climatic variables were standardized to have 0 mean and variance equal to 1 on population growth and the decrease rate.

To find the most parsimonious model for seasonal dynamics, we used the corrected Akaike information criterion AICc (Hurvich and Tsai 1989, Burnham and Anderson 2003). We fitted the weather and predator models using the glm package in R (R Development Core Team 2004). As the incorporation of climate and predator variables produces a large number of possible models, we only present the best models according to the AICc. No more than three independent variables were used in any model to reduce the risk of over-parameterization.

Annual models

A discrete-time logistic model (Ricker 1954) was used to evaluate the precipitation, humidity, temperature, and evaporation on the annual house mouse rate of change. Maximum abundance was used for any calendar year irrespective of month. The logistic equations included the weather factors in two ways according to Royama (1992): a lateral effect to analyze the influence of weather on the carrying capacity of the mouse population (Equation 1 A), and a vertical effect to model the impact of weather on the rate of change (Equation 1 B). The models' assessment for each factor was considered alone and in interaction with each other.

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K+Z}\right)^Q \quad (\text{A}).$$

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K}\right)^Q + Z \quad (\text{B}).$$

Equation 1. R_t is the population rate of change; R_m is a positive constant that represents the maximum finite reproductive rate, and was fixed with maximum value of the rate of change according to each time series derived from the linear equation (R_t vs. N_{t-1}); N_{t-1} is the mouse

abundance; K is the environment carrying capacity; Z is the environmental factor; and Q is the non-linearity of the curve: a value of $Q > 1$ indicates a convex shape and $Q < 1$ indicates a concavity. A. Lateral effect. B. Vertical effect.

A discrete-time predator-prey model with a functional response type III was used to model the predation on mouse populations (Holling 1959, Berryman 1999a, 2003). We used the maximum value per year of each predator's relative abundance (*Elanus axillaris*, *Tyto alba*, *Ninox novaeseelandiae*, *Falco berigora*, *Falco cenchroides*, *Circus approximans*, and *Circus assimilis*). The models' assessment for each predator was tested alone or in interaction with others (Equation 2 A). Also, we evaluated the effect of predators and weather factors as complex dynamics (Berryman 1987, 1999a, Berryman et al. 1987) (Equation 2 B).

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) - W \left(\frac{N * D}{h^2 + N^2}\right) \quad (\text{A}).$$

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) + Z - W \left(\frac{N * D}{h^2 + N^2}\right) \quad (\text{B}).$$

Equation 2. R_t is the population rate of change; R_m is a positive constant that represents the maximum finite reproductive rate, and was fixed with maximum value of rate of change (R_t vs. N_{t-1}); N_{t-1} is the mouse abundance; K is the environment carrying capacity; Z is rainfall and evaporation; W is the predators attack rate; D_{t-1} is the predators' abundance; and h^2 is the predator's saturation rate. A. The logistic model with functional response type III. B. The functional response type III and the weather effect.

We used nonlinear regression (Bates and Watts 1988) to determine the model of best fit with mouse abundance, predator, and weather factors. To analyze the mathematical models, we used the nls function (Nonlinear least squares) in the R program (R Development Core Team 2004). The most parsimonious models were selected using the AICc (Burnham & Anderson 2003). The parameter estimates from the best models were used to predict the population trajectories and determine when outbreaks would occur. We performed a complete simulation taking just the first observed data

abundance as a starting point and ran the models for successive years, and a one-step-ahead simulation that recalculates the abundance of each year according to the observed previous data (Turchin 2003).

Results

Time series of mouse populations showed different outbreaks across time in Walpeup (Victoria), Roseworthy (South Australia), and Darling Downs (Queensland). South-eastern Australia had five similar events of outbreaks within a comparable period. Victoria presented outbreaks in 1984, 1987/1988, 1993/1994, 1997, and 2001 with a maximum amplitude of 800 mice/ha. South Australia had outbreaks in 1980, 1984, 1988, 1993, 1996/1997 with a maximum amplitude of 500 mice/ha. The south-eastern showed an irregular outbreak pattern (Fig. 2 A). Queensland has different behavior because the period is regular, with outbreaks every two years in 1989, 1993, 1995, 1997, 1999, 2001, 2003, and 2008, with a maximum amplitude of 80 mice/ha (Fig. 2 A). Some relevant variables in the models were predators, precipitation, and evaporation. The relative abundance of predators, Nankeen kestrel in Walpeup, Brown falcon in Roseworthy, and Spotted harrier in Darling Downs was dynamic, showing peaks in the years with mouse outbreaks and before each one (Fig. 2 B). The precipitation showed different patterns between productive wheat sites. Walpeup had the lowest values (90 to 350 mm), followed by Roseworthy (250 to 480 mm) and Queensland with the highest values (270 to 690 mm). All the sites showed high precipitation one year before each outbreak (Fig. 2 C). Evaporation tended to be steady. Walpeup had an interval between 6 to 10 mm, Roseworthy 6.5 to 9.5 mm, both sites with low evaporation values in the outbreak year, and Darling Downs with 5 to 9.5 mm without any significant pattern (Fig. 2 D).

Seasonal model

The weather model evidenced precipitation and evaporation as the main drivers to generate the outbreaks in south-eastern Australia. They obtained 52% in Walpeup and 57% in Roseworthy of the variance explanation (Figure 3 A and B, Table 2). The models improved when including the predator's role on house mouse dynamics. The rate of increase over summer was best explained by high winter precipitation, low summer evaporation, and low predator abundance affecting the rate of change positively (Figure 3 A and B, Table 2). These models achieved 61% and 59% of the variation in R in Walpeup and Roseworthy, respectively. Also, the spring abundance or 'breeding season' was a relevant factor to predict the outbreaks, with a negative density-dependence. The rate of population decline over winter was best fitted by the mouse autumn abundance (peak phase) and Barn owl in Walpeup explaining 65%, and 61% in Roseworthy by autumn abundance and Swamp harrier influence (Table 2). On the other hand, the rate of increase in Queensland over autumn was best explained by the cumulative spring and summer rainfall two years before the outbreak and previous summer and winter mouse abundance, achieving 54% (Figure 3 C, Table 2). The predator role plus the weather factors was not evident, achieved 51%. The rate of population decline over spring was best explained by house mouse winter abundance (peak phase) and the Barn owl, explaining 73% of the outbreaks (Table 2).

Annual models

The best weather model in south-eastern Australia was precipitation and evaporation which achieved the lowest AICc value (68) in Walpeup (Figure 4 A, Table 3), and 72 AICc in Roseworthy (Figure 4 B, Table 3), and a prediction of 66% and 70% among predicted and observed abundance. This model correctly predicted most of the outbreaks in the Walpeup and Roseworthy mouse population data. The result supports the mechanism proposed, where the precipitation and

evaporation could improve the soil conditions, allowing mice to dig their burrows. The models with a vertical effect showed better performance than the models with a lateral effect. Likewise, the influence of precipitation and evaporation on the maximum rate of change of the mouse population is through a vertical effect, affecting directly the maximum rate of change. The predator and weather model showed the relative abundance of the predators, precipitation, and evaporation factors obtained the lowest AICc related to models that used predators or weather alone. The best model was a Nankeen kestrel (Walpeup) and Brown falcon (Roseworthy) acting together with weather factors, achieving a 68 and 71 AICc (Table 3), respectively. The outbreak prediction showed a 73% value in Walpeup, and 75% in Roseworthy, accomplishing a significant improvement in the prediction of the magnitude of the outbreaks (Figure 4 A and B).

The best model for Queensland was precipitation two years before the outbreaks and winter and summer mouse abundance, achieving 60 AICc (Table 3), and a prediction of 60% among simulated and observed abundance (Figure 4 C). This model correctly predicted most of the outbreaks in the Darling Downs mouse population. The result supports the mechanism where precipitation offers more and better-quality food acting together with an early breeding season from winter to summer. The model selection process indicated that the relative abundance of the predators does not influence the house mouse population dynamics (Table 3, Figure 4 C).

Discussion

We analyzed whether the house mouse increases are caused by weather factors or an escape threshold from predators to establish if the Australian mice can be explained with the same model or if it needs more than one to predict them (Berryman 1999b). Southeastern Australia and Queensland showed different patterns in their mouse explosions, environment and the mechanisms

that operate. Eruptive outbreaks with predator and weather roles in Southeast and gradual outbreaks with the weather and endogenous factors in Queensland. Several authors have discussed if there is a single mechanism or explanation for the same pattern of rodent explosions (Forster and Sorber 1994, Lambin et al. 2000, Turchin and Hanski 2001, Hanski and Henttonen 2002, Lambin et al. 2006). On that basis, Lambin et al. (2006) mentioned that the rodent cycles could be different or similar in their patterns independently of their location and they can be unleashed by diverse mechanisms that depend on the substantial ecological differences between the ecosystems involved.

The southeast had winter rainfall, one and two years before the outbreak, summer evaporation and summer to autumn abundance of generalist predators like Nankeen kestrel (*Falco cenchroides*) in Walpeup and Brown falcon (*Falco berigora*) in Roseworthy as the best models to explain and predict the outbreaks. Southeast populations are not due to a pulse of resources or gradual outbreak because they do not vary directly with rainfall or food fluctuations uniquely, and the generalist predators seem to play an important role when the mice are in low density (Holling 1965, Morris 1963, Takahashi 1964, Isaev and Khlebopros 1977, Berryman 1999a, Singleton et al. 2001, Krebs et al. 2004). Therefore, the outbreaks are classified as eruptive because they do not depend on exogenous factors exclusively, depending on more than one factor involved, and they are caused by positive feedbacks that amplifies the response to obtain more and better resources, avoiding regulation by predators through the escape threshold (Berryman et al. 1984, Berryman and Stark 1985, Berryman et al. 1987, Berryman 1989, Berryman 1999b, Berryman & Kindlmann 2008). The threshold can be overcome due to saturation of the predator, alternative preys, or the influence of triggers on the population that allows the density increase and avoid the predators attack (May 1977, Berryman et al. 1987, Sinclair et al. 1990, Berryman 1996, Berryman 1999b, Sinclair 2003,

Groffman et al. 2006). This escape happens when the weather factors move the curve of population dynamic approaching the escape threshold and low mice density, making the population cross the threshold and raise density becoming a plague (Figure 1 C) (May 1977, Berryman 1982, 1984, 1986).

Our mechanism proposed for southeast mice is based on favourable conditions before the breeding season to provide a food supply, burrows, and water availability. Low summer evaporation and winter rainfall may improve soil conditions to dig warrens and escape from predator regulation, followed by an abundant food supply in the breeding season to increase the litter size and generate an outbreak (Figure 5 A) (Newsome 1969, Mutze et al. 1991, Cantrill 1992, Caughley 2001, Singleton et al. 2001, White 2002, Brown et al. 2008). The positive feedback amplifies the disturbance in the system, where food supply and nesting increase due to weather influences, enabling the mice increases and which escape of negative feedback from predators (Figure 6 A) (Berryman 1999 a,b, Berryman and Kindlmann 2008). Subsequently, the strong autumn density-dependence and predators such as the Barn owl in Walpeup and the Swamp harrier in Roseworthy look to be the factors responsible for collapsing the outbreak because high densities of pest cause food depletion, generating a negative regulation together with social stress and diseases that spread quickly (Singleton 1989, Sinclair 1989, Singleton and Redhead 1990, Brown and Singleton 1999, Singleton et al. 2005).

The outbreak mechanism in southeast is based in three principles: rainfall promotes the growth of plants offering food for mice, moist soil conditions to dig their burrows and low evaporation to prevent the drying out of the soil in the arid lands, and weather triggers enable that mice escape from predators (Newsome 1969, 1970, 1971, White 2002, Brown et al. 2008). The effect of food

on mice is well known for providing energy to grow, find a mate and reproduce. It is a limiting resource especially in winter and the breeding season, where the rainfall improves the availability of seeds (Singleton et al. 2001). Rainfall could affect the soil and burrow conditions too. Burrows are a limiting resource because they offer protection from predators and a refuge for feeding and reproduction. They are critical in winter due to the minimum temperatures, depletion of food and predation risk in searching for food (Newsome 1969, Newsome and Corbett 1975, Saunders 1986, Mutze et al. 1991, Twigg and Kay 1994, Singleton et al. 2001). Finally, generalist predators have a negative impact on mice but due to weather triggers, precipitation and evaporation, influences the burrows increase, allowing the escape of mice from predator regulation (Holling 1966, Murdoch 1969, Sinclair et al. 1990, Krebs et al. 1995, Brown and Singleton 1999, Krebs 2001, Sinclair 2003). Additionally, the escape threshold is possible because the generalist predators do not have a numerical response with mice so that their offspring and reproduction rate do not depend uniquely on mouse population feeding (Hanski and Korpimäki 1995, Korpimäki and Norrdahl 1998, Berryman 1999 a,b).

Darling Downs had rainfall in spring to summer, one and two years before the outbreaks and a strong density-dependence in summer and winter as the best model to explain and predict the outbreaks. The response of the mouse population in Queensland is due to a pulse of resources by the influence of rainfall on yield crop, that is a gradual outbreak because the population varies directly with duration and magnitude of rainfall fluctuations. Thus, mouse population in Darling Downs depends on the weather factors exclusively with a strong density-dependence, where the population needs a large disturbance to move their equilibrium from low to high density (Royama 1992, Berryman 1999 a,b, Lima 2006). The Queensland mice are regulated through competition for resources through negative feedback that keeps the population at low density without rainfall.

Still, if the precipitation appears, move the population density through a vertical effect on the rate of change, generating an outbreak (Berryman 1981, 1988, DeAngelis et al. 1986, Berryman 1989, Royama 1992, Berryman & Kindlmann 2008).

Our mechanism proposed for Queensland mice is based on good rainfall to provide abundant food supply and density dependence of mice before the breeding season to generate an explosion (Figure 5 B) (Cantrill 1992, Singleton et al. 2001, White 2002, Pople et al. 2013). The positive feedbacks involved in the population dynamics acting with high rainfalls that increases the food resource, increasing the mice population density (Figure 6 B). Subsequently, the strong outbreak density dependence causes the collapse because high densities generate food depletion and mice population return to original conditions when the rainfall disappears (Singleton 1989, Sinclair 1989, Singleton and Redhead 1990, Brown and Singleton 1999, Singleton et al. 2001, Singleton et al. 2005). At the same time, predators (Barn owl) take advantage to consume mice (Singleton & Redhead 1990, Singleton et al. 2005, Brown and Singleton 1999).

The outbreak mechanism in Queensland is based in two principles: first, rainfall could provide enough food to mice, influencing the growth and reproduction rate, population density, recruitment, and breeding season, generating an early and prolonged litter, larger reproduction, and decreased mortality, causing an outbreak (Singleton and Brown 1999, Davis et al. 2004). Our results showed that precipitation in spring to summer and mice density dependence as the best predictors for the Darling Downs outbreaks. Cantrill (1992) and Pople et al. (2013) found that spring mouse abundance and autumn to winter rainfall in the previous year were the best predictors to this population in Australia. Second, previous densities of mice have a negative relationship between the rate of increase, where mice likely show changes in the timing of reproduction, body

and litter size related to the past densities (Bomford and Redhead 1987, Singleton 1989, Mutze et al. 1990, Cantrill 1992, Burgman et al. 1993, Pech et al. 1999, Ylonen et al. 2003, Jacob et al. 2007, Brown et al. 2010). Besides, Scanlan and Farrell (2005) identified rainfall and summer mouse abundance as a predictor to the outbreaks, similar to our results, with strong seasonal cycles and a positive correlation at two years before the explosions (Cantrill 1992, Caughley 2001).

The house mouse in southeast and Queensland have divergent patterns and environments that can influence the outbreaks through diverse mechanisms. This makes some factors to be more critical in one location than in another. Australian grain belt has many regions with various soil types, cropping systems and climates, making it difficult to predict the outbreaks with a single model. These differences affect in a distinct way the limiting resources like food supply and burrows. For example, Queensland has humid subtropical climate and vertosols with good field capacity and available water, that seems to be better to mice than semi-arid climate with the calcarosols and chromosols from southeastern Australia. Perhaps for this reason, moist soil conditions, low evaporation and predators were not relevant factors there (Newsome 1969, Newsome and Corbett 1975, Saunders 1986, Twigg and Kay 1994, Singleton et al. 2001).

Pest management is different depending on the structure dynamic. Australian mice have two different structures: southeast has eruptive outbreaks and Queensland has gradual. The first one is much harder to predict and control than gradual because the first has three states or critical points: a low-density stable equilibrium by negative feedback due to predator regulation, an escape threshold or unstable equilibrium at intermediate pest density, being a challenge identify it, and a high-density stable equilibrium regulated by the shortage of food. The predator issue is based on it being hard to monitor them because it is expensive and requires a huge logistics. Few studies have

examined the predator role because they do not have adequate predator abundances across time. We need more precise data and experiments to clarify the predators' role because they are a common factor operating on small mammals (Krebs 2001). In comparison, the gradual outbreaks are easier to predict because only depend on exogenous factors, majority weather data are a quick tool to predict the explosions, and they are cheaper, easier to work with, more reliable and robust.

It is essential to employ the outbreak theory to identify the causes and mechanisms behind the mice population increase to know their structure dynamic and understand how we can control them. These results are useful for predicting future outbreaks and reducing their economic impact on Australian wheat crops. Establishing that it is hard to predict the mice dynamics in the Australian grain-belt with one unique model, due to there being different environmental conditions that influence the outbreak mechanisms and that mice have different structure in their dynamics.

Conclusions

Australian mice have two different structures: southeast has eruptive outbreaks, and Queensland has gradual, where the weather factors as the main driver of outbreaks with predator intervention in some productive sites. South-eastern outbreaks were explained by the rainfall and evaporation, improving the soil conditions to create more enemy-free space, increasing the mouse growth rate. Queensland outbreaks were explained by rains and by the density-dependence of the previous mouse abundance, where rainfall improves the food supply and crop cover to breeding season to generate the outbreak. The collapse in all Australia was explained by the mice abundance in the outbreak and predator abundances.

Australian grain belt has many regions with various soil types, cropping systems and climates, making it difficult to predict the outbreaks with a single model. Gradual and eruptive outbreak theory showed us that it is useful to improve our knowledge about the Australian house mouse, identifying that populations depend on a pulse of resources in Queensland, and triggers that allow their escape from predators in the southeast. Thus, the Australian house mouse has divergent patterns and environments that influence outbreaks through diverse mechanisms.

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Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors designed the study and wrote the manuscript. The first author collected and analyzed the data.

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Table 1. Characteristics of environmental and house mouse outbreaks in South-east Australia: Walpeup (1983 to 2002) and Roseworthy (1980 to 2000), and Queensland: Darling Downs (1989 to 2008).

Characteristics	Walpeup	Roseworthy	Darling Downs
Outbreaks	5	6	9
Breeding season	Spring	Spring	Spring-Summer
Peak	Autumn	Autumn	Winter
Collapse	Winter	Winter	Spring
Crops	Winter	Winter	Summer-Winter
Rainfall (mm)	215	335	473
Temperature (° C)	30	29	31
Humidity (%)	61	56	69
Evaporation (mm)	8.7	8	7.8
Soil	Calcarosols	Chromosols	Vertosols
Climate	Semi-arid	Semi-arid	Humid subtropical

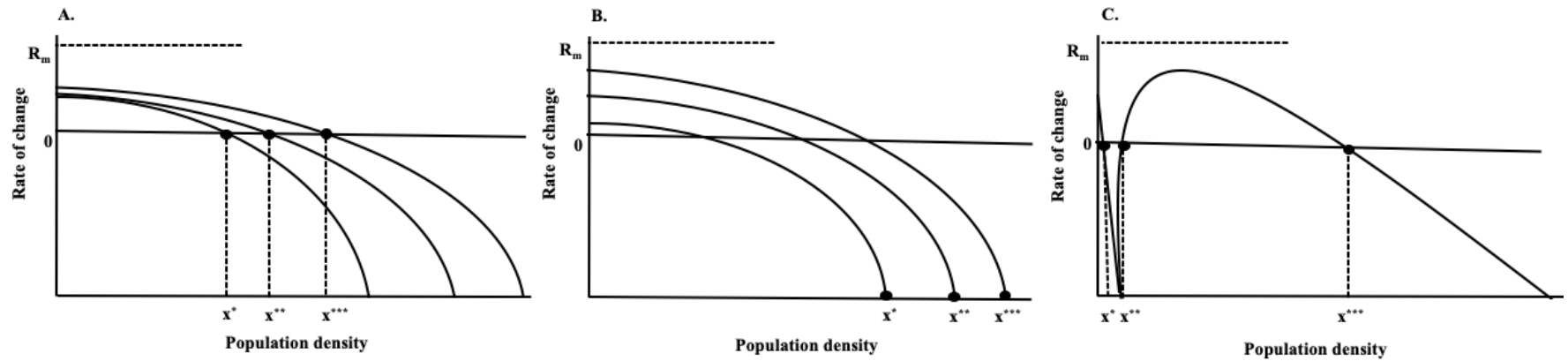


Figure 1. **A.** Gradual outbreak with a lateral effect: exogenous variables influence carrying capacity or some limiting resource and the population density directly $R_t = R_m \cdot (X_{t-1}/K + Z)$. **B.** Gradual outbreak with vertical effect: exogenous variables influence the maximum rate of change directly (increased reproduction), being independent of population density $R_t = R_m \cdot (X_{t-1}) + Z$. In A. and B. the environmental factor increase shifts the population density to the right generating an outbreak, while a decrease shifts to the left causing the collapse. **C.** Eruptive outbreak with an escape threshold of predators: the curve presents low and high density divided by an escape threshold. The low density enforced by predation could be closer to the threshold when predators are low or when some trigger increases the density of prey.

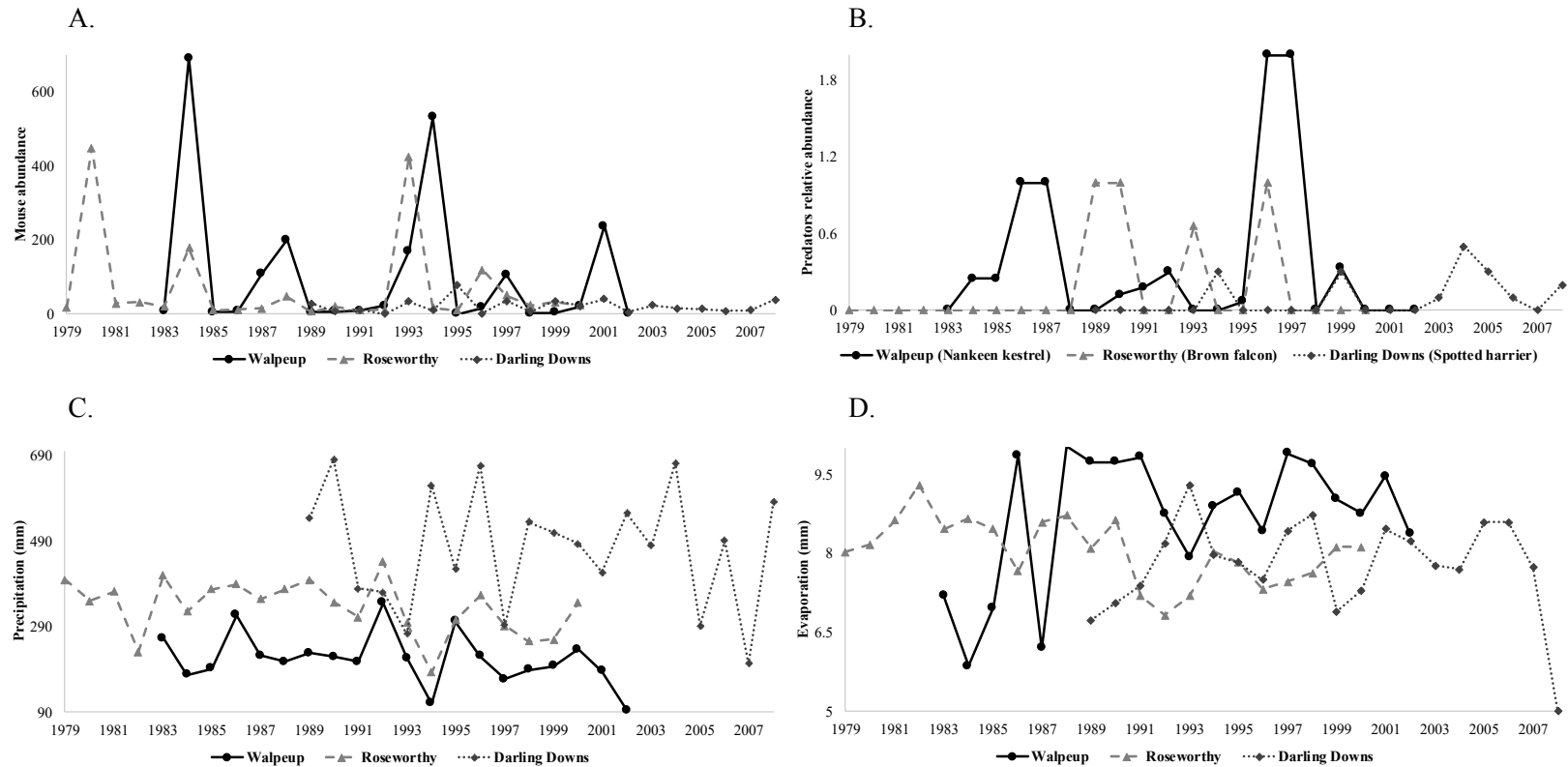


Figure 2. Time series of factors proposed to explain and predict the mouse outbreaks on wheat productive sites (Walpeup 1983-2002, Roseworthy 1979-200, and Darling Downs 1989-2008). A. House mouse abundance (adjusted trap success); B. Relative abundance of predators (positive observations / total observations, January to July); C. Accumulative precipitation (mm); D. Average evaporation (mm).

Table 2. Optimal population dynamics models for house mouse outbreaks using the seasonal model $R_{\text{summer}} = A_t - S_{p,t-1} = S_{p,t-1} + A_{t-1} + g$, $R_{\text{autumn}} = W_t - S_{t-1} = S_{t-1} + S_{p,t-1} + g$, and $R_{\text{winter}} = S_{p,t-1} - A_{t-1} = A_{t-1} + S_{t-1} + g$ from Merritt et al. (2001). R^2 : Adjusted R-squared, AICc: Akaike information criteria, OSA: Simulation One step ahead (Turchin 2003).

	Seasonal model	Autoregressive coefficients	R^2 (%)	AICc
<i>Walpeup</i>				
<i>Increase phase</i>	Weather	$R_{\text{summer}} = 0.170 + 0.0027 \text{ Precipitation} + (-0.074) \text{ Evaporation}$	52	-7.9
	Weather and predator	$R_{\text{summer}} = 0.417 + 0.002 \text{ Precipitation} + (-0.082) \text{ Evaporation} + (-0.182) \text{ Nankeen krestel}$	61	-9.3
<i>Decrease phase</i>	Density-dependence	$R_{\text{winter}} = 0.221 + (-0.183) \text{ Autumn abundance}$	63	11.4
	Density-dependence and predator	$R_{\text{winter}} = 0.194 + (-0.160) \text{ Autumn abundance} + (-0.087) \text{ Barn owl}$	65	12.5
<i>Roseworthy</i>				
<i>Increase phase</i>	Weather	$R_{\text{summer}} = -1.741 + (-0.471) \text{ Spring abundance} + 0.010 \text{ Precipitation} + (-0.303) \text{ Evaporation}$	57	59.4
	Weather and predators	$R_{\text{summer}} = 0.100 + (-0.463) \text{ Evaporation} + 0.010 \text{ Precipitation} + (-0.003) \text{ Brown falcon}$	59	58.7
<i>Decrease phase</i>	Density-dependence	$R_{\text{winter}} = 1.516 + (-1.123) \text{ Autumn abundance}$	57	63.8
	Density-dependence and predator	$R_{\text{winter}} = 1.439 + (-1.057) \text{ Autumn abundance} + (-0.486) \text{ Swamp harrier}$	61	63.5
<i>Darling Downs</i>				
<i>Increase phase</i>	Density-dependence and weather	$R_{\text{autumn}} = 0.157 + (-0.052) \text{ Winter abundance} + (-0.050) \text{ Summer abundance} + 0.0004 \text{ Precipitation } t_2$	54	-25.4
	Weather and predators	$R_{\text{autumn}} = 0.205 + (-0.046) \text{ Spring abundance} + 0.0003 \text{ Precipitation} + (-0.355) \text{ Spotted harrier}$	51	-24.2
<i>Decrease phase</i>	Density-dependence	$R_{\text{spring}} = 0.244 + (-0.204) \text{ Winter abundance}$	64	-1
	Density-dependence and predator	$R_{\text{spring}} = 0.237 + (-0.180) \text{ Winter abundance} + (-0.836) \text{ Barn owl}$	73	-4.4

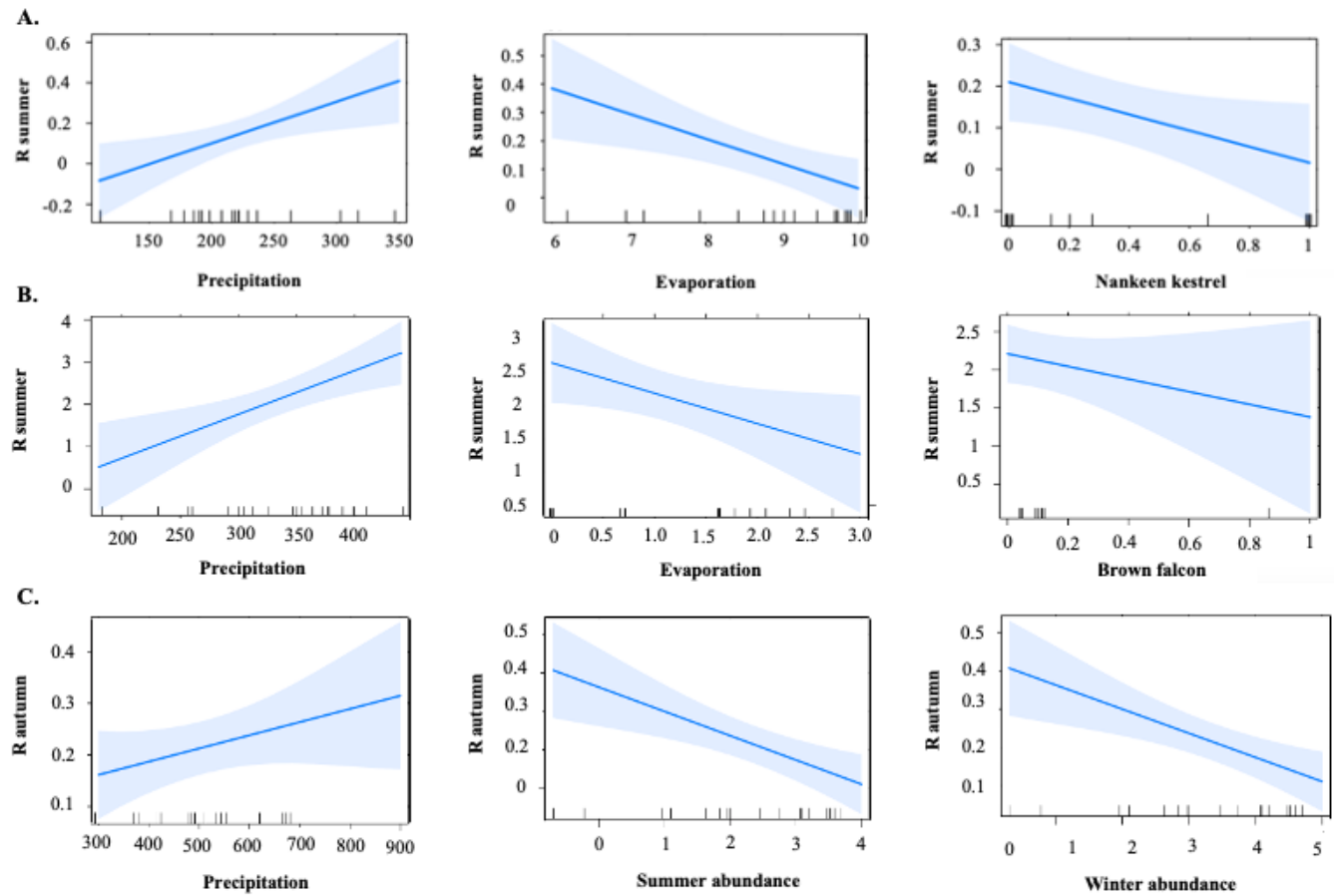


Figure 3. Predictor variables on the rate of change of mouse abundance on wheat productive sites show the positive or negative relationship between endogenous and exogenous factors. A. Walpeup (Victoria). B. Roseworthy (South Australia). C. Darling Downs (Queensland).

Table 3. Optimal population dynamics models for mouse outbreaks using the annual model from Ricker (1954) $R_t = R_m * (1 - X_{t-1}/k)^Q$, and functional response model from Berryman (2003) $R_t = R_m * (1 - (X_{t-1}/k)) + Z + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$. R^2 : Adjusted R-squared, AICc: Akaike information criteria, OSA: Simulation One step ahead (Turchin 2003).

Annual model		Coefficient values	AICc	OSA
<i>Walpeup</i>				
	Weather	$R_t = 2.5 * (1 - (X_{t-1}/10) ^ 0.341) + 0.014 \text{ Precipitation} + (-0.655) \text{ Evaporation}$	68	66
	Weather and predator	$R_t = 2.5 * (1 - (X_{t-1}/177.428)) + 0.010 \text{ Precipitation} + (-0.814) \text{ Evaporation} + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$	75	73
<i>Roseworthy</i>				
	Weather	$R_t = 4 * (1 - (X_{t-1}/50) ^ 0.267) + 0.010 \text{ Precipitation} + (-0.475) \text{ Evaporation}$	72.4	70
	Weather and predator	$R_t = 4 * (1 - (X_{t-1}/375.714)) + 0.013 \text{ Precipitation} + (-0.928) \text{ Evaporation} + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$	72.7	73
<i>Darling Downs</i>				
	Weather	$R_t = 4 * (1 - (X_{t-1}/10 + 0.054 \text{ Precipitation}) ^ 0.383) + (-0.002) \text{ Precipitation } t_{-2}$	61.5	60
	Weather and predator	$R_t = 4 * (1 - (X_{t-1}/10 + 0.099 \text{ Precipitation})) + (-0.003) \text{ Precipitation } t_{-2} + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$	64.3	55

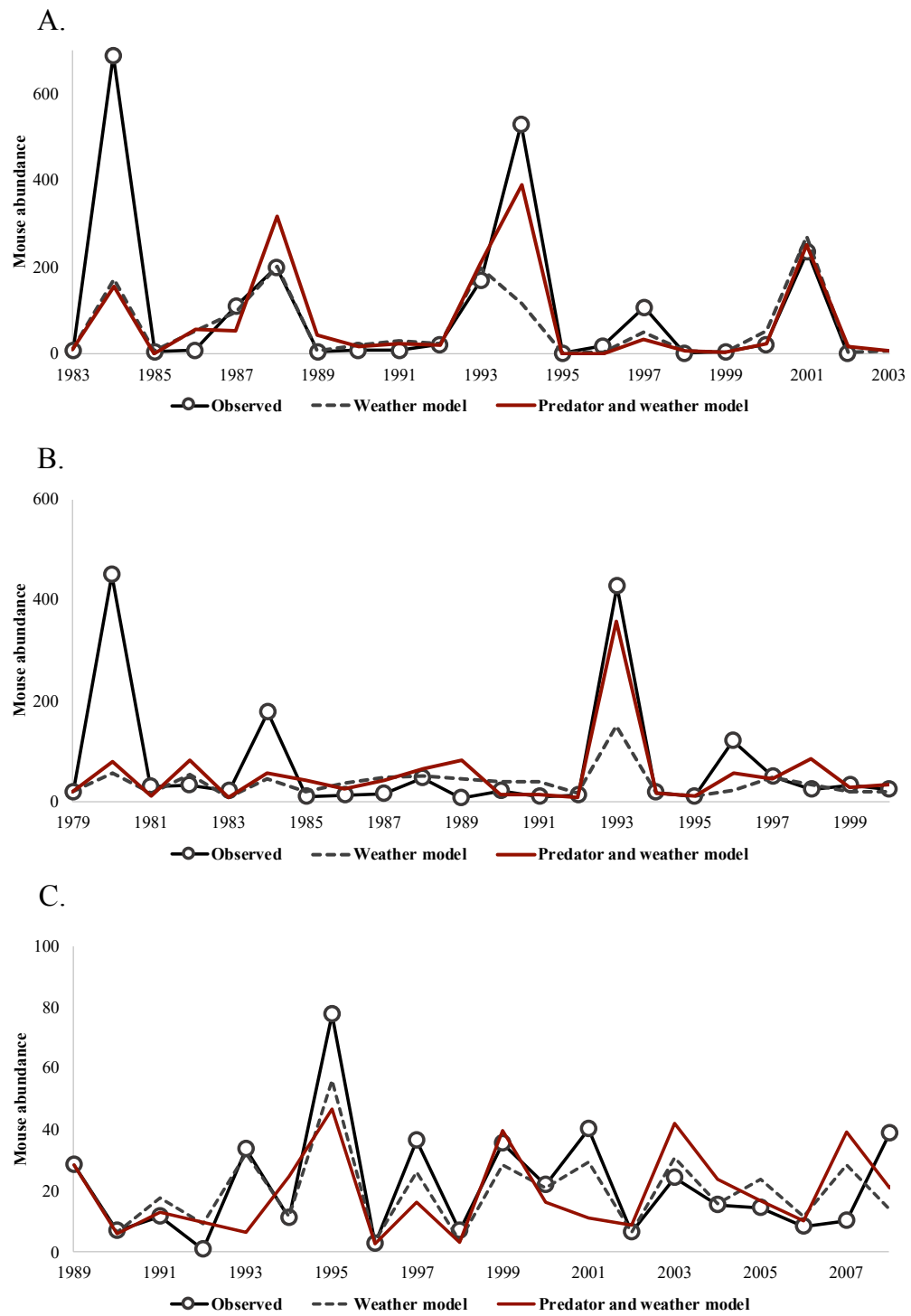


Figure 4. Mouse abundance prediction according to the weather model and the predators and weather model. A. Walpeup (Victoria). B. Roseworthy (South Australia). C. Darling Downs (Queensland).

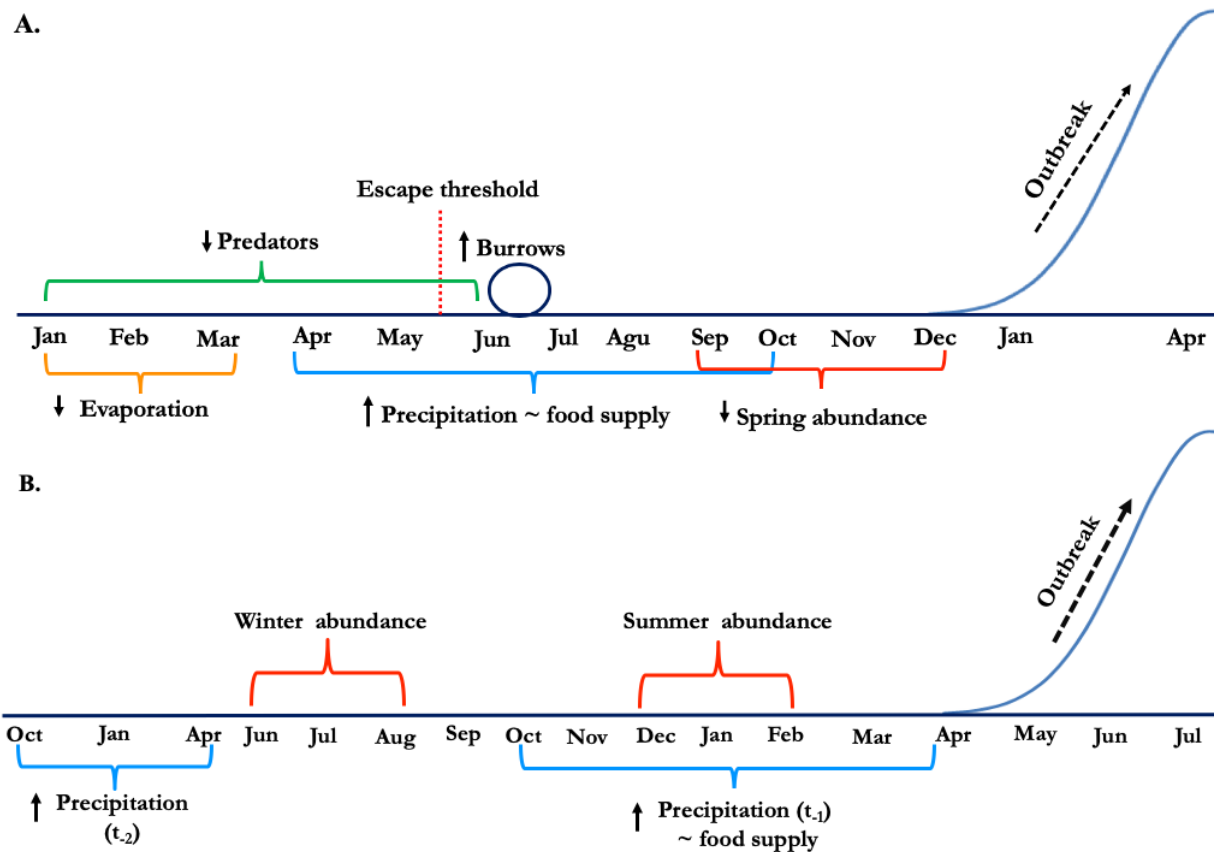


Figure 5. Outbreak mechanism to explain increased mouse density in Australia. **A.** South-eastern Australia: Walpeup (Victoria) and Roseworthy (South Australia). Mice need favorable conditions before the breeding season (spring) such as low summer evaporation and high winter rainfall that improves soil conditions enabling mice to dig burrows to escape from predators and generate an outbreak. **B.** Queensland: Darling Downs. Mice need favorable conditions before the breeding season (spring) such as high winter rainfall (t_1 and t_2) that improves crop conditions, like food supply, plus winter and summer previous abundance.

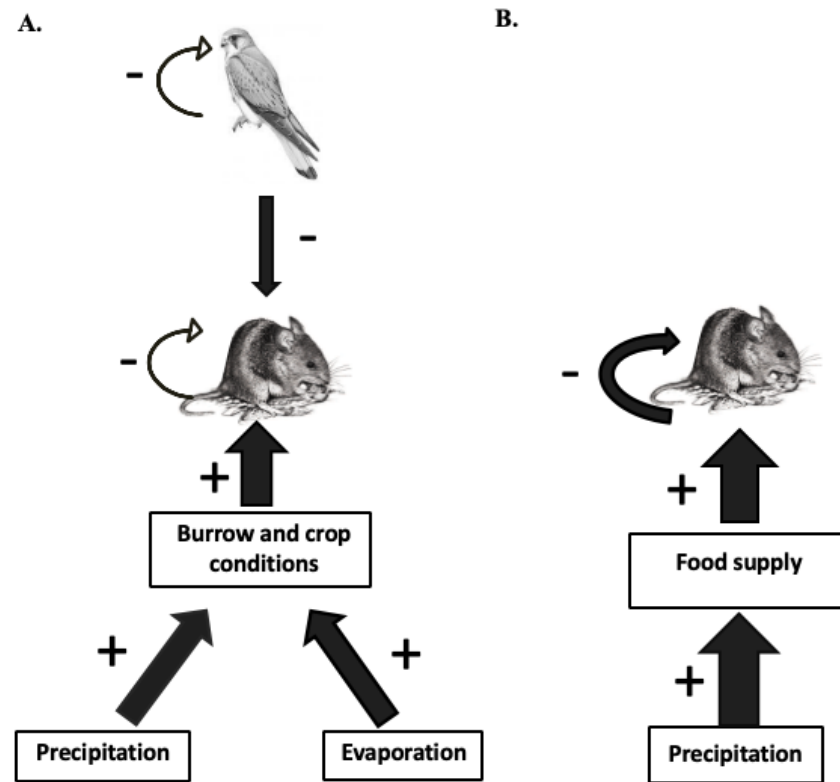


Figure 6. Feedback structure of mice outbreaks in Australia. A. Eruptive outbreak in south-eastern Australia. B. Gradual outbreak in Queensland.

Paper 3: Voles outbreaks in North-western Spain (Palencia, Valladolid, and Zamora).

Seasonal and annual models to predict the outbreaks of common voles in NW Spain

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Abstract

Common voles in Spain are an example of an irruptive species that every 3 or 4 years reaches plague numbers and causes considerable damage in cropping systems. We used an 11-year vole mark-recapture dataset from the Castilla y León region (Zamora, Valladolid, and Palencia) and various climatic and predator variables, employing seasonal and annual models to understand the drivers of vole outbreaks. We examine the effects of precipitation, temperature, evaporation, humidity, competitor's abundance of the wood mouse, Algerian mouse, shrews, and the weasel's abundance to examine the predators' role. The rate of increase of vole populations was best explained by high cumulative rainfall (autumn to spring), two years before the outbreak, spring and summer humidity, and spring weasel's abundance. The population decline rate over winter was best explained by abundance in the peak season (density-dependence) and autumn precipitation and temperature. Spanish vole outbreaks are classified as eruptive and dependent on rainfall and humidity, as an index of food supply and cover, increasing the burrows, and the escape of regulation from weasels. The results are useful to predict future outbreaks to reduce their economic impact on alfalfa and cereal crops.

Keywords: Voles outbreaks; drivers; mathematical models; population dynamics; weather; predator-prey.

Introduction

The common vole population (*Microtus arvalis*) in Spain are found most of the time at low densities due to interactions with limiting resources, food or shelter, or through predators as birds or mammals. Still, outbreaks are caused suddenly when their density increases (Berryman 2002, Turchin 2003, Luque-Larena et al. 2011, Luque-Larena et al. 2013, Paz et al. 2020). An outbreak can be defined as an explosive population increase that occurs over a relatively short time, and they have often devastated economically important human resources (Berryman 1982, Berryman 1987, Berryman et al. 1987). Vole outbreaks are usually around 500 to 1000 rodents/ha in alfalfa, cereals, legumes, potatoes, among others causing losses of 20 million euros per year due to the consumption of stems and leaves on crops (Korpimäki et al. 2004, Jacob and Tkadlec 2010, Jacob et al. 2014, Rodríguez et al. 2016). Also, voles are vectors and reservoirs of tularemia, infectious disease caused by *Francisella tularensis*, which generates mortality in voles and humans (Luque-Larena et al. 2015, Rodríguez et al. 2017, Rodríguez 2018).

Voles invaded the central plains autonomous communities of Castilla y León region (Valladolid, Palencia, and Zamora) at the end of the twentieth century rapidly (1970 to 1990). Castilla y León is located in northwestern Spain in a semi-arid agricultural area of 50.000 km² (Luque-Larena et al. 2011, 2013, Jareño et al. 2015). Usually, vole outbreaks begin in the breeding season in spring followed by a density explosion from summer to autumn, and a collapse in winter due to the depletion of food or diseases (Luque-Larena et al. 2011, Jacob et al. 2014,

Jareño et al. 2015). Several authors have proposed different factors as being responsible for causing the European vole outbreaks like weather, quantity and quality food, burrows, cover and habitat, predator and diseases regulation, and others (Andersson and Erlinge 1977, Desy et al. 1990, Airoidi and Werra 1993, Lambin et al. 2000, Turchin and Batzli 2001, Hanski et al. 2001, Huitu et al. 2003, Heroldova et al. 2004, Korpimaki et al. 2005, Lambin et al. 2006, Brugger et al. 2010, Blank et al. 2011, Esther et al. 2014, Giraudoux et al. 2019). Despite decades of research in Europe, a consensus has not been reached among ecologists as to what factors cause these outbreaks (Batzli 1992, 1996, Stenseth and Ims 1993, Norrdahl 1995, Korpimaki and Krebs 1996, Krebs 1996, Boonstra et al. 1998, Lindstrom et al. 2001). Also, none of these drivers has been tested in Spain through population dynamics models to explain and predict the outbreaks.

We will focus in three possible hypothesis that could cause the vole outbreaks in Spain: First, the hypotheses of food supply and predation are more strongly evaluated as causes of the outbreaks in most of Europe (Desy et al. 1990, Hornfeldt 1994, Krebs 2003, Turchin 2003). Food supply influences vole growth and reproduction rate, population density, recruitment, and breeding season. The effects of food probably could induce an early and prolonged litter, larger reproductive output, and decreased mortality (Ford and Pitelka 1984, Batzli 1986, Desy and Batzli 1989, Boutin 1990, Tkadlec and Zejda 1995). As a consequence, females could have a larger litter size, and juveniles can mature quickly to have more offspring, causing an outbreak (Huitu et al. 2003, Heroldova et al. 2004, Lantova and Lanta 2009). Usually, food supply can be evaluated using rainfall as an index because the relationship between crop yield and precipitation is well documented on rodents (Seif and Pederson 1978, French and Schultz 1984,

Brown and Singleton 1999, Singleton et al. 2001, Kenney et al. 2003, Krebs et al. 2004). Further, rainfall can influence crop, soil conditions, and drought breaks in the semi-arid agroecosystem.

Second, precipitation can influence soil conditions through humidity and evaporation to become a more permeable surface and easy to dig the burrows (Blank et al. 2011). Soil type is closely associated with plant production, which affects the availability and quality of food and shelter (Knoepp et al. 2000). The burrows availability can be considered a limiting resource because the voles are highly social and form large groups of related individuals inhabiting underground burrows (Frank 1957, Blank et al. 2011, Brugger et al. 2010, Brommer et al. 2010). Thus, the weather factors could increase the number of burrows (enemy-free space), decreasing predation risk (Anderson 1986, Arthur et al. 2004), increasing the voles reproduction rate and generate an outbreak (Laundre and Reynolds 1993, Imholt et al. 2011, Giraudoux et al. 2009).

The last possible cause of the vole outbreak is the escape from regulation by predators due to satiety in the predator functional response as a consequence of the rapid vole population growth (Hanski et al. 2001). Regulation of prey is unlikely at high densities because the growth rate of rodents is higher than predators, and they never reach the same rate (Hanski et al. 2001). Vole populations may be regulated by generalist predators, sustained at low abundance (Anderson and Erlinge 1977, Erlinge et al. 1983, 1984, 1988, Erlinge 1987, Hansson 1971, 1979, 1987). Still, the switching between voles and abundant alternative preys could contribute to relaxing the regulation and increase the vole density. Another possibility is that pests increase through triggers such as weather that raise limiting resources, where the predator cannot consume the prey for the saturation rate (Berryman et al. 1987, Berryman et al. 1984, Berryman 1999 a,b).

Common vole populations have a complex nature, and their population dynamics could involve several factors that need to be explored. We used population models to understand the causes of vole outbreaks and to be able to make reasonable predictions. We will use an 11-year vole population abundance dataset as well as climate, small rodents' abundance, and weasel's data. Our idea is to identify whether the outbreaks depend on a pulse of resources due to weather factors, or an escape threshold from predator regulation. We will use theoretical ecology and pest management models to identify which factors are important to generate the vole outbreaks and reduce their economic and social impact in Spain.

Materials and Methods

Study area

Voles population data were collected from the large intensive agricultural region of NW Spain (Castilla y León) a major alfalfa production area. Fieldwork was conducted in three study areas (40 km² each) located in the provinces of Palencia (42°01'N, 4°42'W), Valladolid (41°34'N, 5°14'W) and Zamora (41°50'N, 5°36'W) (Jareño et al. 2014), and were 55-80 km apart from each other (Rodríguez-Pastor et al. 2016). The farming landscapes consist of a mosaic of crops dominated by non-irrigated cereals mainly wheat and barley, irrigated and non-irrigated alfalfa crops, and other herbaceous crops (natural or semi-natural habitats, such as uncultivated lands, meadows, pastures or set asides) (detailed methodology in Jareño et al. 2015). The Castilla y León climate is denominated the continental Mediterranean with cold and humid winters, and dry and hot summers with a variable drought period and reduced natural green vegetation (Jareño et al. 2015, Rivas-Martínez and Loidi 1999).

The monitoring was conducted in March, July, and November, referred to as spring, summer, and autumn from July 2009 to November 2019. Our trapping method was extractive, removing voles from sampled fields could influence subsequent local vole abundance. Each field had a set-up of 35 live traps (8 cm x 9 cm x 23 cm; LFAHD Sherman) spaced every 2 m and forming a “T”-shape, 10 traps were placed along a 20-m transect line in the field margin, and 25 traps were placed along a 50-m transect line perpendicular to the field margin and going towards the field center. Each trap was baited with apple or carrot and water for trapped individuals. Traps provide hydrophobic cotton inside to increase vole survival when temperatures were low. In each study site (Zamora, Valladolid, and Palencia), we trapped in two different areas denominated experimental and control (2000 ha each), located 4 km apart. The first one was provided with nest-boxes (100 nest boxes installed on artificial poles throughout the area) to increase the local abundance of raptors (Paz et al. 2013), and control without nest-boxes used as a control. Traps were set up in the morning, were inspected after 24 h and were subsequently removed. The vole’s abundance was estimated as the number captured divided by the number of traps available for capture and multiplied by 100 (vole numbers/100 traps/24 h).

The weather data (precipitation, humidity, temperature, and evaporation) were obtained from the Agencia Estatal de Meteorología (AEMET, www.aemet.es). The predator and competitors' abundance were measured using from the same monitoring as the voles. We used the weasels population (*Mustela nivalis*) as a predator of voles and small mammals like the Wood mouse (*Mus spretus*), Algerian mouse (*Apodemus sylvaticus*), and shrew (*Crocidura russula*) as competitors of voles for space or transmission of tularemia (*Francisella tularensis*).

Seasonal models

We used the northern hemisphere seasons of summer (June to August), autumn (September to November), winter (December and February), and spring (March to May). We estimated the exponential rate of population change (R) during summer, autumn, and winter, using an autoregressive model (Hansen et al. 1999, Merritt et al. 2001). Population growth rates are modeled as a linear function, including the endogenous feedbacks like previous densities in each season, and exogenous factors (g) such as weather, competitors, and predators.

$$R_{summer} = S_t - Sp_{t-1} = Sp_{t-1} + A_{t-1} + g$$

$$R_{autumn} = A_t - S_{t-1} = S_{t-1} + Sp_{t-1} + g$$

$$R_{winter} = Sp_t - A_{t-1} = A_{t-1} + S_{t-1} + g$$

Population abundance of voles, weasels, and small mammals (mice and shrew population), and climatic variables were standardized to have 0 mean and variance equal to 1. We employed the weasels, and small mammals spring abundance to analyze their impact on the growth rate of voles in R_{summer} and R_{autumn} . The exogenous factors, precipitation (mm), humidity (%), evaporation (mm), and temperature (°C), were calculated from March to July data in R_{summer} , July to November in R_{autumn} , and November to March in R_{winter} . We calculated the sum of precipitation and the mean of humidity, evaporation, and temperature in each period, and the respective lags (six months before). Additionally, we tested cumulative precipitation from autumn to spring and cumulative temperature from winter to spring.

To find the most parsimonious model for seasonal dynamics, we used the corrected Akaike information criterion AICc (Hurvich and Tsai 1989, Burnham and Anderson 2003). We fitted models using a Generalized Linear Mixed Models in R (R Development Core Team 2004).

Handling the sites (Zamora, Valladolid, and Palencia) and populations (control and experimental) as a random effect, and previous densities, weather, competitors, and predators as fixed effects. The incorporation of climate, competitors, and predators' variables produced a large number of possible models. We only present the best models according to the AICc and adjusted R^2 .

Annual models

A discrete-time logistic model (Ricker 1954) was used to evaluate the precipitation, humidity, temperature, and evaporation on the voles rate of change. We used the summer abundance for each calendar year for Zamora, Valladolid, and Palencia. To characterize the time series, we used the reproduction function, which represents the population rate of change as a function of population size (Berryman 1999, Berryman and Kindlmann 2008).

$$R_t = \ln N_t - \ln N_{t-1} = \ln \left(\frac{N_t}{N_{t-1}} \right)$$

To evaluate the mechanisms of weather on voles rate of change, we tested the influence of weather on the carrying capacity of the voles population denominated as the lateral effect (Equation 1 a), and the weather impact on the voles rate of change called the vertical effect (Equation 1 b) (Royama 1992, Lima 2006). The models' assessment for each weather factor was considered alone and in interaction with each other.

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K+Z}\right)^Q \quad (\text{a}).$$

$$R_t = R_m * \left(1 - \frac{N_{t-1}}{K}\right)^Q + Z \quad (\text{b}).$$

Equation 2. R_t is the population rate of change; R_m is the maximum finite reproductive rate, and was fixed at 2.5 derived from the linear equation (R_t vs. N_{t-1}); N_{t-1} is the voles abundance; K is the environment carrying capacity; Z is the environmental factor; and Q is the non-linearity of the curve: a value of $Q > 1$ indicates a convex shape and $Q < 1$ indicates a concavity. a. Lateral effect. b. Vertical effect.

The predation impact on vole populations was modeled using a discrete-time predator-prey model with a functional response type III because the weasels have alternative prey like other small mammals (Holling 1959, Berryman 1999, 2003) (Equation 2 A). We employed the summer value per year to voles and predator abundance. We tested the weasels' abundance on population dynamics of voles alone (Equation 2 a), and the additive effect of predators with precipitation and humidity (Berryman 1987, 1999, Berryman et al. 1987) (Equation 2 b).

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) - W \left(\frac{N*D}{h^2 + N^2}\right) \quad (\text{a}).$$

$$R_t = Rm_N * \left(1 - \frac{N_{t-1}}{K_N}\right) + Z - W \left(\frac{N*D}{h^2 + N^2}\right) \quad (\text{b}).$$

Equation 3. R_t is the population rate of change; R_m is the maximum finite reproductive rate, and was fixed at 2.5 according to R function (R_t vs. N_{t-1}); N_{t-1} is the voles abundance; K is the environment carrying capacity; Z is precipitation and humidity; W is the predator's attack rate; D_{t-1} is the predators' abundance; and h^2 is the predator's saturation rate. a. The logistic model with a functional response type III. b. The functional response model with precipitation and humidity.

We used non-linear regression (Bates and Watts 1988) to determine the best model fitted with vole abundance, predators' and competitors' abundance and weather data. To analyze the mathematical models, we employed the nls function (Nonlinear least squares) in the R program

(R Development Core Team 2004). The most parsimonious models were selected using the AICc (Burnham and Anderson 2003). Parameter estimates from the best models were used to simulate population trajectories and determine when outbreaks would occur. We performed a complete simulation taking just the first observed abundance data as a starting point and ran the models for successive years, and the one-step-ahead simulation that recalculates the abundance of each year according to the observed previous data (Turchin 2003).

Results

The time series of vole populations showed five outbreaks across our period (2009 to 2019) demonstrating a regular pattern in population dynamics, every two to three years in Palencia, Valladolid, and Zamora (Fig. 1 A). The weasel abundance was dynamic and showed peaks in the outbreak year and the following (Fig. 1 B). The precipitation was constant, with values between 150 mm to 550 mm, but showed peaks one year before each outbreak (Fig. 1 C). Mean humidity tended to be higher in voles outbreak years and one year before with a mean between 52 to 80% (Fig. 1 D).

Seasonal model

The rate of increase of vole populations over the summer (R_{summer}) was best explained by the cumulative autumn to spring rainfall, evaporation in spring to summer, and the spring abundance of mice (Wood mouse and Algerian mouse), explained 38% of the variation in R_{summer} (Table 1, Figure 2 A). The rate of the population increase over autumn (R_{autumn}) was explained by cumulative precipitation, spring to summer humidity, weasel abundance, and the starting abundance in summer, explaining 74% of the variation in R_{autumn} (Table 1, Figure 2 B). Finally,

the rate of population decrease over winter (R_{winter}) was explained by summer to autumn precipitation and temperature and the starting abundance in summer and autumn (peak phase), explaining 52% of the variation in R_{winter} (Table 1, Figure 2 C).

Annual models

The best weather model was precipitation and humidity, achieving the lowest AICc value (230) and a prediction of 67% among simulated and observed abundance (Table 1, Figure 3). This model correctly predicted most of the outbreaks in the Palencia, Valladolid, and Zamora voles population data. The result supports the proposed mechanism where the precipitation and humidity could improve the soil conditions, allowing voles to dig their burrows and escape predators. The models with a vertical effect showed better performance than the models with a lateral effect. Likewise, the influence of precipitation and humidity on the maximum rate of change of the vole population is through a vertical effect, affecting the maximum rate of change directly. On the other hand, the best predator model were weasel abundance, precipitation, and humidity, which obtained the lowest AICc (227) related to models that used predators or weather alone (Table 1). The correlation between predicted and empirical data was 79% (Figure 3), which significantly improved the magnitude of the prediction of the outbreaks in comparison with models of weather alone. These results establish a relationship between the possible causes of vole outbreaks related to the escape threshold and escape from predator's regulation.

Discussion

There are different explanations and mechanisms regarding vole fluctuations depending on their location in southern and northern Europe (Lambin et al. 2006). Common vole populations have

been analyzed to explain and predict their outbreaks through several factors like food supply, weather, predators, maternal effect, habitat, cover and burrows, diseases or social structure (Hanski et al. 1991, Inchausti and Ginzburg 1998, Hanski et al. 2001, Huitu et al. 2003, Blank et al. 2011, Esther et al. 2014, Jareño et al. 2015, Rodríguez et al. 2016, Rodríguez et al. 2018). Still, Spain was colonized recently by common voles (1970 to 1990) and neither of these hypotheses has been tested yet. Apparently, high autumn and winter temperatures, high autumn precipitation, and low winter precipitation allowed that voles colonized (Jareño et al. 2015). Therefore, weather factors seem the main drivers for vole colonization in Spain through their effect on crops, and perhaps they influence the outbreaks (Veiga 1986, Tkadlec et al. 2006, Fargallo et al. 2009, Jareño et al. 2015).

Cumulative precipitation, evaporation, and humidity were the best weather factors to predict the outbreaks in NW Spain. Rainfall has been a relevant factor to increase the rodent abundances in arid and semi-arid ecosystems because of the effects on crop productivity, soil conditions, water availability and its ability to end droughts (Seif and Pederson 1978, Singleton et al. 2001, Krebs et al. 2004, Brown et al. 2008, Fargallo et al. 2009). Castilla y León in NW Spain has the highest precipitation from autumn to spring contributing to crop growth, offering high-quality food, a large percentage of cover and soil stability to voles (Veiga 1986, Janova et al. 2008, Fargallo et al. 2009, Lantová and Lanta 2009). Our models demonstrated that rainfall, one and two years before the outbreak, are essential to the vole's increase, as the studies by Veiga (1986) and Fargallo et al. (2009) suggest.

Rainfall mechanism is usually related with food supply to explain the rodent outbreaks because rain positively influences crop yield. Thus, the biomass increases positively affecting the vole reproduction, overwinter survival and litter size. Also, food supply can generate an early breeding season and decrease the mortality rate (Hansson 1979, Cole and Batzli 1979, Ford and Pitelka 1984, Boutin 1990, Huitu et al. 2003). However, some experimental studies have demonstrated that food does not limit the vole population growth (Babinska-Werka 1979, Desy et al. 1990, Huitu et al. 2003, Heroldova et al. 2004, Lantova and Lanta 2009). Our results showed that Spanish vole populations do not depend on a pulse of food because it does not vary directly with rainfall and food uniquely. The possible reason is due to the multiannual perennial alfalfa crop in Spain that has been increasing over time and stays at least five years without being ploughed providing a stable habitat for voles underground breeding colonies, burrows and protective cover against predators (Korpimäki et al. 2004, Jacob et al. 2007, Luque-Larena et al. 2018).

Our weather mechanism proposes that high rainfall (autumn-spring) promotes the growing plants in crops to provide food supply to rodents together with significant humidity (spring-summer) to keep soil permeable and high evaporation (spring-summer) to avoid flooding. These favourable environmental conditions allow voles to dig their burrows for shelter, food storage, protection from extreme environmental conditions and a decreased predator risk. As a consequence, the reproduction rate and population density increase causing an outbreak (Newsome 1969, Saunderson & Giles 1977, Airolidi and Werra 1993, Brommer et al. 2010, Brügger et al. 2010, Blank et al. 2011). Burrow systems could be considered a limiting resource to voles because they spend most of their lives in these systems (Mackin-Rogalska et al. 1986,

Aschwanden et al. 2005, Jacob 2008, Brugger et al. 2010). Vole outbreaks occur most of the time in wet soils rather than hard and dry soils with many roots, stones and high density that impede well depth. For this reason, some authors have established the relevance of soil conditions for building burrows in dry-arid lands (Delattre et al. 1992, Laundre and Reynolds 1993, Delattre et al. 1999, Jacob and Brown 2000, Romañach et al. 2005, Hinze et al. 2006, Luna and Antinuchi 2006, Torre et al. 2007, Brugger et al. 2010, Blank et al. 2011, Rodríguez et al. 2016). Spanish alfalfa crops typically hold well-established vole colonies over long periods, indicating that voles obtain good soil stability and a high protein source from the crops (Rodríguez et al. 2016). Then, soft soils with little hardness and compaction create favourable habitat conditions, resulting in an outbreak as our models showed (Luna and Antinuchi 2006, Albanese et al. 2010, Blank et al. 2011, Imholt et al. 2011).

Undoubtedly the weather affects vole populations, influencing the reproduction rate, litter size and population density of the following year, which could unleash an outbreak (Imholt et al. 2011, Esther et al. 2014, Giraudoux et al. 2009). Nevertheless, environmental factors are not the only ones that cause outbreaks and our models showed that when including predators, the outbreak prediction improves. The predator-vole relationship has been well studied in northern Europe. Diverse studies have established the increase in vole density when predators were removed, evidencing a predation pressure on the low-intermediate density of voles (Desy and Batzli 1989, Desy et al. 1990, Hanski et al. 1993, 2001, Krebs et al. 1995, Korpimäki and Norrdahl 1998, Klemola et al. 2000, 2003, Korpimäki et al. 2002, Norrdahl and Korpimäki 2002, Huitu et al. 2003). Our best predator and weather model were the rainfall (autumn-spring), humidity and evaporation (spring-summer), and weasel's spring abundance. The mechanism

proposes how the voles could escape from weasel's regulation due to the influence of weather factors which trigger outbreaks by allowing the voles to make more burrows by improving soil conditions. More enemy-free space and food decreasing the predation risk and the effects of extreme environmental conditions on the survival rate of rodents. Then, the population density of voles rises, causing saturation in the functional response of weasels, generating an outbreak (Hanski et al. 1993, 2001, Korpimäki and Norrdahl 1998, Klemola et al. 2000, 2003, Korpimäki et al. 2002, Norrdahl and Korpimäki 2002).

Saturation happens because weasels cannot consume a high vole density as vole growth rates are at their highest, thus the weasels never catch up unless some factor like the weather slows down the vole's population growth (Hanski et al. 2001). Although weasels cannot prevent the vole's population from increasing, they can suppress the population after the decline, and delay its recovery (Erlinge et al. 1983, 1984, 1988, Erlinge 1987, Hansson 1971, 1979, 1987, Hansson and Henttonen 1985). As a consequence of predator saturation, voles can escape and cross the threshold to generate an outbreak (Ryszkowski et al. 1971, 1973, Sinclair et al. 1990). Another possibility to escape from weasels is the appearance of alternative prey. The weasel can adapt quickly to changes in prey availability, allowing an increase in vole density that causes predators to lose the regulation (Anderson and Erlinge 1977, Sinclair et al. 1990, Korpimäki et al. 1991, 2002, Hanski and Korpimäki 1995, Sinclair 1996, Sinclair and Pech 1996, Boonstra et al. 1998, Korpimäki and Norrdahl 1998, Huitu et al. 2003). Our results exhibited a positive impact of Algerian and Wood mice on voles, possibly acting as alternative prey for weasels, increasing their densities in autumn to spring in Spain (Erlinge 1975, Korpimäki and Norrdahl 1989).

The seasonal model results allowed us to propose a succession of factors to understand how the outbreak built up. Voles need a low-intermediate density during spring ‘breeding’ and favourable environmental conditions, before and during the breeding season, to generate large litter size, increase the reproduction rate and raise the population density (Hansson 1984, Lambin and Krebs 1991, Krebs 2003, Huitu et al. 2003). The high evaporation, humidity and rainfall could improve soil conditions for voles to dig burrows, and escape from predator regulation. Followed by an abundant food supply this would enable an increase in vole reproduction rate and generate an outbreak (Figure 4) (Newsome 1969, Singleton et al. 2001, Hanski et al. 2001, Huitu et al. 2003, Heroldova et al. 2004, Korpimäki et al. 2004, Brugger et al. 2010, Blank et al. 2011). Subsequently, the strong outbreak density-dependence, absence of food, social stress, diseases, precipitation and temperatures in the outbreak season will cause the collapse (Sinclair 1989, Singleton and Redhead 1990, Ims et al. 2007). Our results exhibited a negative influence of weather factors on the mortality rate of voles which might be due to a short pulse of flooding in the outbreak season, and this could cause hypothermia and drowning in voles (Jacob 2003). Also, the high temperatures from summer to autumn can increase the vole’s mortality by affecting body growth and fertility (Daksetse and Martinet 1977, Norrdahl 1995). Another form to analyze the outbreak dynamic is through the feedback structure which shows the positive feedback of weather factors (precipitation and humidity) on burrows and crop conditions generating an increase in the reproduction rate of voles, allowing them to escape from weasels’ regulation (Figure 5).

Regarding the endogenous factors, our population models identified them involved in the generation the outbreak from the breeding season to the peak (spring to autumn) and the collapse

(winter), testing the effect of the previous abundances on the populations. Spanish vole populations presented the highest density in summer and autumn in Zamora, Valladolid, and Palencia (Castilla y León). Summer outbreaks can keep until autumn, and autumn outbreaks can last up to nine months depending negatively on summer abundance. We evidenced a strong density-dependence to predict the autumn outbreaks which showed a negative relationship between the reproduction and survival of individuals and the summer population density (Krebs 2003, Jacob et al. 2014). Collapse has had the density-dependence of outbreak seasons with a high density of voles. The highest level of vole density can generate negative effects like food depletion, competition, territorialism or aggression between them, and diseases can spread quickly in a dense population increasing the mortality rate (Desy et al. 1990, Krebs 2003, Ims et al. 2008).

The results showed a complex population dynamic of voles with endogenous and exogenous factors which cause the outbreaks in NW Spain.

Conclusions

Spanish common vole dynamics evidenced the weather factors and predators as the main driver of outbreaks. The vole outbreaks were explained by cumulative rainfall, humidity, and weasel abundance. The mechanism involved is that weather factors act as a trigger to improve the soil conditions, creating more enemy-free space and food supply. Consequently, the predation risk decreases and allows voles to escape from weasel's regulation. The vole population density increases and generates the outbreak. The collapse outbreaks were explained by the strong density-dependence of outbreak density in the previous season and precipitation and

temperature in the outbreak season. Spanish voles need weather triggers that allow the population to obtain more and better resources, avoiding being consumed by their predators. Our results may help design decision support systems that provide information to farmers, foresters, health officials and conservationists etc. about the risk of common vole outbreaks.

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Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors designed the study and wrote the manuscript. The first author collected and analyzed the data.

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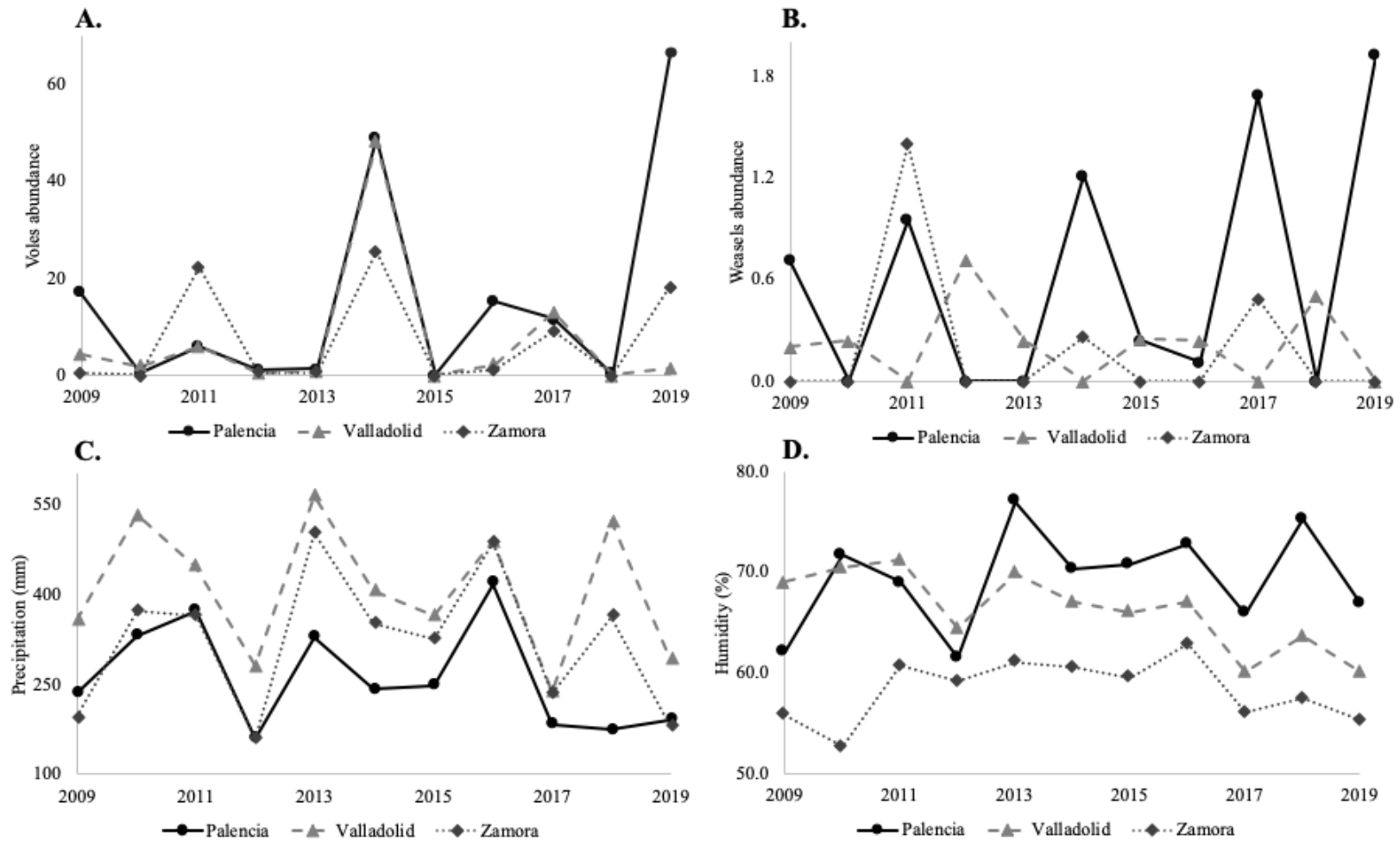


Figure 1. Endogenous and exogenous variables across time (2009-2019). A. Voles abundance (vole numbers/100 traps/24 h); B. Weasels abundance (vole numbers/100 traps/24 h); C. Accumulative precipitation (Autumn to Spring); D. Average humidity (mm, Spring to Summer).

Table 1. Optimal population dynamics models for voles outbreaks using the seasonal model $R_{\text{summer}} = S_t - Sp_{t-1} = Sp_{t-1} + A_{t-1} + g$, $R_{\text{autumn}} = A_t - S_{t-1} = S_{t-1} + Sp_{t-1} + g$, and $R_{\text{winter}} = A_{t-1} - S_{t-1} = S_{t-1} + Sp_{t-1} + g$ from Merritt et al. (2001), logistic growth from Ricker (1954) $R_t = R_m * (1 - X_{t-1}/k)^Q$, and the functional response model from Berryman (2003) $R_t = R_m * (1 - (X_{t-1}/k)) + Z + W * (X_{t-1} * Y_{t-1} / h^2 + X_{t-1}^2)$. R^2 : Adjusted R-squared, AICc: Akaike information criteria, OSA: Simulation One step ahead (Turchin 2003).

Model	Autoregressive coefficients	R^2 (%)	AICc
Seasonal models			
<i>R_{summer}</i>			
Endogenous	$R_{\text{summer}} = 0.817 + 0.049 \text{ Autumn } t-1 + (-0.062) \text{ Spring } t-1$	2	176.8
Weather	$R_{\text{summer}} = -3.285 + 0.001 \text{ Evaporation spring-summer} + 0.002 \text{ Cumulative precipitation}$	30	156.3
Predator + competitors	$R_{\text{summer}} = 0.653 + 0.092 \text{ Mice spring}$	10	171.7
Weather + competitors	$R_{\text{summer}} = -3.436 + 0.001 \text{ Evaporation spring-summer} + 0.004 \text{ Cumulative precipitation} + 0.083 \text{ Mice spring}$	38	150.3
<i>R_{autumn}</i>			
Endogenous	$R_{\text{autumn}} = 1.227 + (-0.628) \text{ Summer } t-1 + (-0.396) \text{ Autumn } t-1$	62	192.2
Weather	$R_{\text{autumn}} = 3.937 + 0.003 \text{ Cumulative precipitation} + (-0.005) \text{ Cumulative precipitation } t-1 + (-0.454) \text{ Cumulative temperature}$	36	211.3
Predator + competitors	$R_{\text{autumn}} = 0.792 + (-2.644) \text{ Weasels spring} + (-0.192) \text{ Mice spring}$	18	227.3
Endogenous + weather + predator	$R_{\text{autumn}} = -3.436 + 0.001 \text{ Summer } t-1 + 0.001 \text{ Humidity spring-summer} + 0.004 \text{ Cumulative precipitation} + 0.083 \text{ Weasels spring}$	74	170.6
<i>R_{winter}</i>			
Endogenous	$R_{\text{winter}} = 1.227 + (-0.628) \text{ Summer } t-1 + (-0.396) \text{ Autumn } t-1$	45	172.9

Weather	$R_{winter} = 2.646 + 0.007 \text{ Precipitation autumn-spring} + (-0.007) \text{ Precipitation summer-autumn} + (-0.239) \text{ Temperature summer-autumn}$	42	192.2
Predator + competitors	$R_{winter} = 0.653 + 0.092 \text{ Weasels autumn}$	12	203.0
Weather + competitors	$R_{winter} = 5.054 + (-0.256) \text{ Summer t-1} + (-0.457) \text{ Autumn t-1} + (-0.004) \text{ Precipitation summer-autumn} + (-0.280) \text{ Temperature summer-autumn}$	52	168.2
Annual models		AICc	OSA
Weather	$R_t = 2.5 * (1-(X_{t-1}/21.845)) + (-0.011) \text{ Precipitation t-1} + 0.035 \text{ Humidity}$	230	67
Predator	$R_t = 2.5 * (1-(X_{t-1}/10)) - W * (X_{t-1} * Y_{t-1}/h^2 + X_{t-1}^2)$	271	11
Competitors	$R_t = 2.5 * (1-(X_{t-1}/15.631)) - 0.207 \text{ Mice abundance}$	291	2
Weather + predator	$R_t = 2.5 * (1-(X_{t-1}/21.690)) + (-0.011) \text{ Precipitation t-1} - W * (X_{t-1} * Y_{t-1}/h^2 + X_{t-1}^2)$	226	79

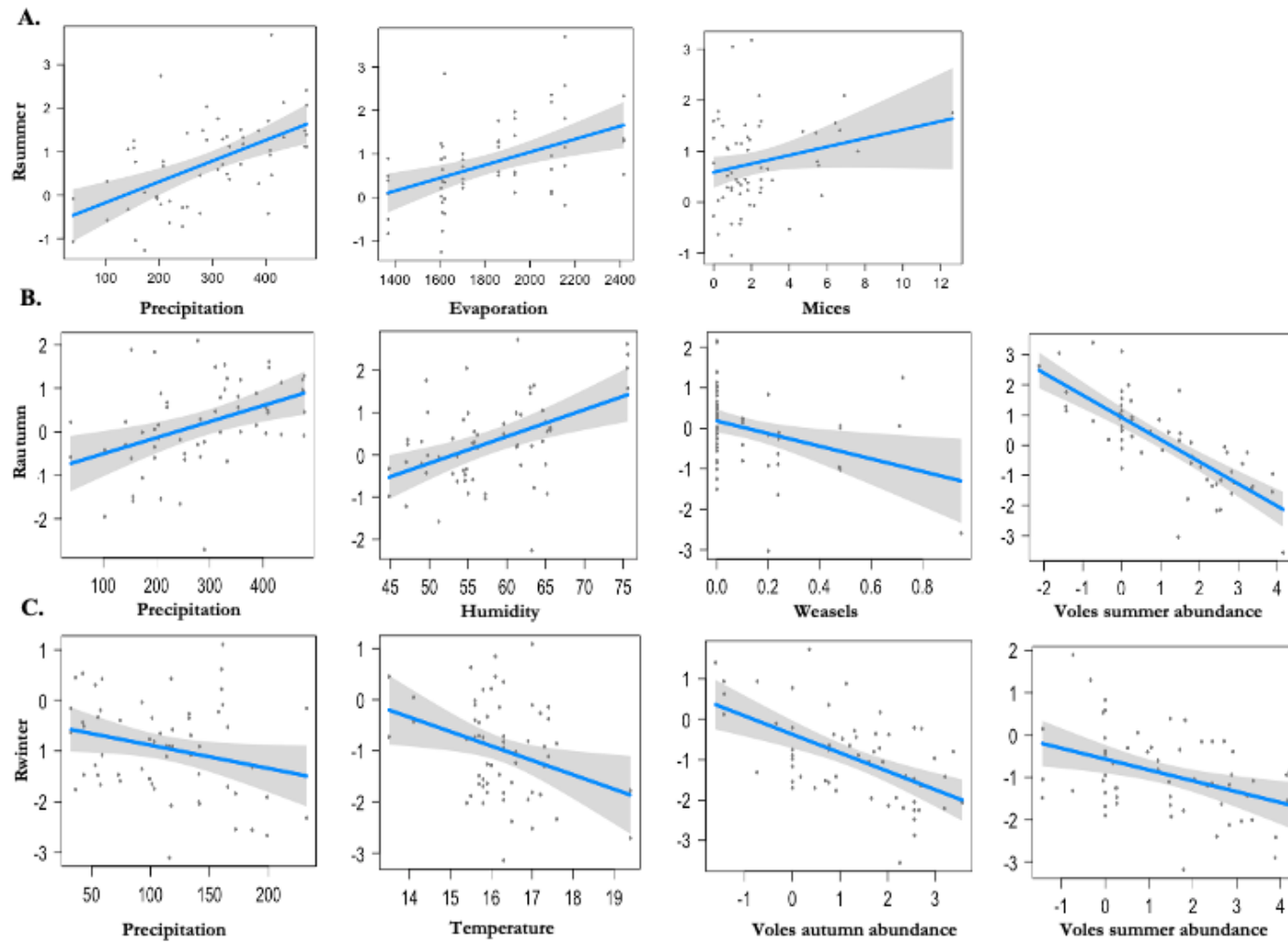


Figure 2. Predictor variables on vole rate of change show the relationship between endogenous and exogenous factors and the increase and decrease phases. A. R_{summer} , B. R_{autumn} , C. R_{winter} .

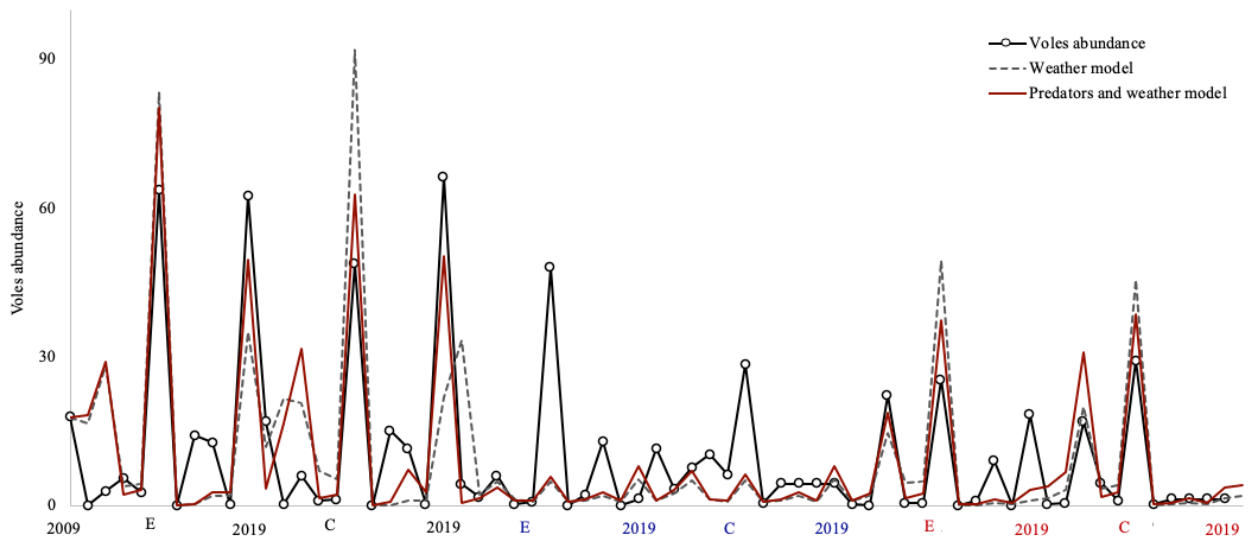


Figure 3. Prediction of vole abundance according to the weather model (precipitation and humidity) and the predators and weather model (weasels and precipitation and humidity). E= experimental population, C= control population in Palencia (axis black), Valladolid (axis blue) and Zamora (axis red).

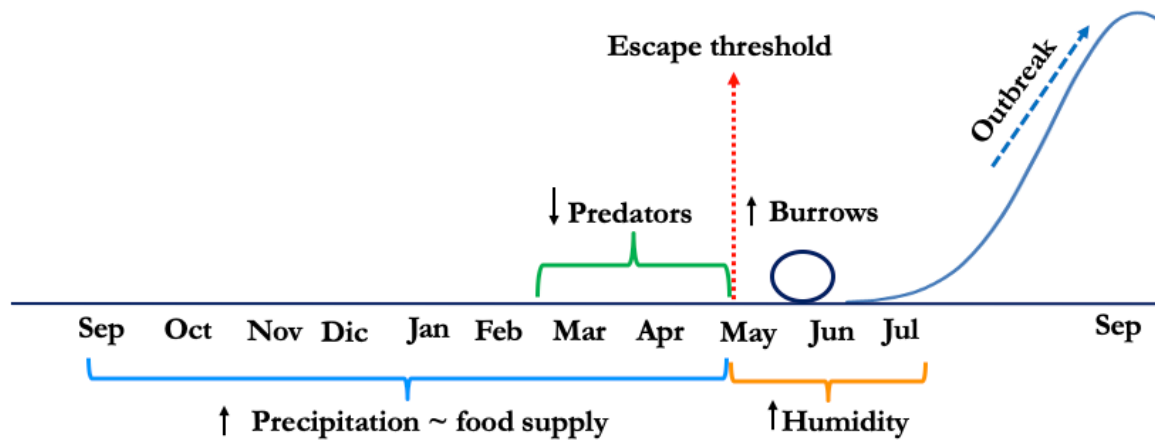


Figure 4. Outbreak mechanism to explain increased voles density in NW Spain. Voles need favorable soil conditions such as high autumn to spring rainfall and high humidity in spring that improves soil conditions for mice to dig burrows to escape from predators to generate an outbreak.

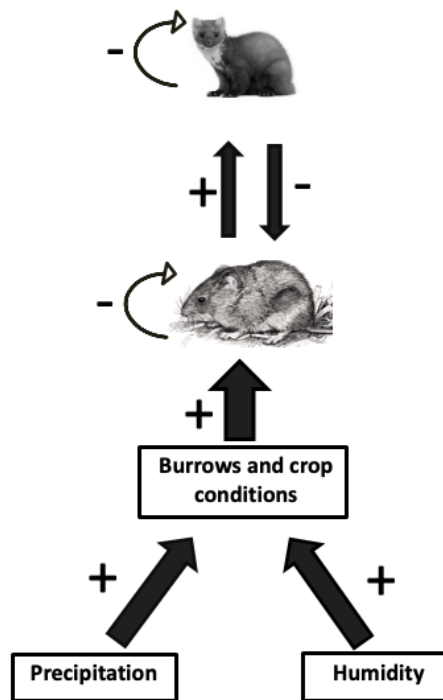


Figure 5. Feedback structure of vole outbreaks in NW Spain.

General discussion

This thesis worked with two small rodent populations which caused economic damage in crops: the house mouse in Australia and common voles in Spain. Both are at low densities most of the time due to interactions with food supply, cover or predators, but they can quickly increase and cause devastation to wheat and alfalfa crops. Small rodents have different dynamic patterns (cyclical or irregular) worldwide, where some pests increase quickly and stay sustained for many years or others that rise but very quickly collapse. Analyzing the Australian mouse population dynamics, we establish non-cyclic or irregular dynamics in the southeast population because the low density is constant most of the year but increases suddenly. In contrast, the outbreaks in Queensland occur every two to three years, which is considered more regular (Redhead and Singleton 1988, Singleton 1989, Mutze 1991, Singleton et al. 2005, Pople et al. 2013). Also, Spanish common voles are considered cyclic in Europe because their population increases every three or four years. However in Spain, the population dynamic study began ten years ago, and it is still premature to say that it is cyclical.

According to the information above, the *first general point* to discuss is that it is essential to identify the limiting factors involved in the outbreak process to manage the pest, determining the influences on the growth rate and their operation. The population pattern does not matter (cyclic or non-cyclic), but rather the factors and mechanisms that cause the population to increase and connect with the environmental conditions must be understood (Chitty 1960, Krebs 2013). Independent if the population is cyclic or irregular, some pests can share the same mechanisms to cause population increase, like mice in southeastern Australia and common voles in Spain.

Several authors have mentioned that pest rodents can have different or similar patterns in their population dynamics. Still, they can be independent of the mechanisms that unleash the outbreaks, depending on the ecological differences between the ecosystems involved (Forster and Sorber 1994, Lambin et al. 2000, Turchin and Hanski 2001, Hanski and Henttonen 2002, Lambin et al. 2006). Our results showed that the major factors leading to outbreaks depend on two things: first, the influence of the diverse regions where the outbreaks happen and their environmental characteristics, which will be discussed in the next paragraph, and second the population dynamic models and the outbreak theory (gradual and eruptive) that choose to find the mechanisms behind the rodent explosion. To discuss the first point, the focus should be on the similarities and differences of the environment along the Australian grain-belt and how that influences mouse dynamics and compare this analysis with the vole dynamics in NW Spain.

The *second general point* to discuss is how the environmental conditions and the agroecosystem affect the outbreak mechanism. Our models of Australian mice showed differences between populations, such as cyclical or irregular, environments and the mechanisms that cause the mice to increase. Mice from the southeast (Walpeup and Roseworthy) were classified as eruptive outbreaks with predator and weather factors (precipitation/evaporation) which cause the outbreak. Unlike the southeast, mice from Queensland (Darling Downs) were defined as having gradual outbreaks with precipitation and endogenous factors. It is considered that these results are supported by the environmental differences between sites and their dynamic behaviours (gradual/eruptive) that allow some factors to be more critical in one location than in another.

Australian grain belt has many regions with various soil types, cropping systems and climates, making it difficult to predict the outbreaks with a single model. Southeastern soils are calcareous or sandy loam with low water storage capacity, poorly aerated and poor drainage, and compact (Isbell 2016). Also, evaporation is high, retaining little moisture, and when the soil dries, it forms clods. Thus, soil conditions are essential to dig the burrows, as our models and precipitation showed. The southeast has 200 to 350 mm of rains, which is a critical factor to food supply and soil conditions (Newsome 1969, Saunders 1986). In contrast, Queensland has a humid subtropical climate with hot and humid summers, cold and dry winters, and 400 to 500 mm of rain. Crops are planted in winter and summer due to the climate, doubling the food and cover for the mice as compared to the southeast, which grows continuously on self-mulching cracking dark clay soils with a great available water capacity and moisture retention (Past 1998, Isbell 2016). Then, predator and soil conditions (burrows) were not an obvious factor due to the environmental conditions of Queensland. In comparison, NW Spain had a similar mechanism to the one that caused the outbreaks in southeastern Australia with weather factors (precipitation/humidity) and predator role. Although the dynamic pattern of voles seems cyclic, which is different than mice from southeastern Australia (irregular), the environment is very similar with a semi-arid ecosystem, soil conditions with poorly drained soil and low rains (Luque-Larena et al. 2011, 2013, Jareño et al. 2015). Thus, the climate and environment conditions differences could influence the rodent outbreak mechanisms and development distinctly with the predator role the strongest.

The *third, fourth and fifth general points* to discuss are analyzing the rodent time series through population dynamic models, the outbreak theory and its application in management (gradual

and eruptive) to identify which factors cause the outbreaks and the pests' dynamic structure to predict and manage them. There is a discussion about which are the best models to study the outbreak causes. We decided to employ the seasonal and annual models and take advantage of each one's benefits, and test if both models deliver the same results. Seasonal models enabled an evaluation of the outbreak phase (breeding season to peak) and collapse phase (peak to low density); identifying the factors that explain the increase and decrease of rodents (Merritt et al. 2001). Our new and relevant findings to house mouse and vole outbreak phase were precipitation, evaporation/humidity and predators (birds and mammals) as exogenous factors in Southeastern Australia and Northwestern Spain, and precipitation and density dependence as endogen factors in Queensland. The collapse phase was similar in Australia and Spain, explained by the rodent abundances in the peak and the profit that predators get. The strong density-dependence may be caused by the intraspecific competition for food and territorialism issues (Sinclair 1989, Singleton and Redhead 1990, Ims et al. 2007).

The seasonal model allowed for the inclusion of the density dependence feedback, testing the effects of the previous abundances. The finding for the mice and voles was to discover the importance of the spring abundance or 'breeding season' to trigger the outbreak and the favourable environmental conditions before this period to provide enough food supply, burrows, and water availability (Singleton & Redhead 1990, Singleton et al. 2001). This result supports the management decision taken by CSIRO in Australia to monitor the mice in September, that is the breeding season because it is a crucial time where the population is beginning to increase, and it could be an alert of a new pest. Also, this suggestion applies to the monitoring of voles in Spain during their breeding season.

The annual models were used to understand the exogenous factors' mechanism through a vertical and lateral effect on the rodent populations (Royama 1992, Lima et al. 2002). Coincidentally, maybe due to the similarities of the environment, the best models in Southeastern Australia and Northwestern Spain were precipitation and evaporation/humidity in a vertical effect. Meaning the exogenous variables influenced the maximum rate of change directly (increase reproduction), independent of population density (Royama 1982, Stenseth et al. 2002). The exogenous factor mechanism in Queensland was mixed because rainfall two years ago acts in a vertical effect on the maximum rate of change. Before the outbreak the rain acted in a lateral form on population density and limited resources like food supply. Annual models were also able to determine the influence of endogen and exogenous factors on the rate of change to predict the rodent abundances through a simulation-based approach using fitted models and cross-validation that verifies the model accuracy (Lima 2003, Turchin 2003). Our seasonal and annual models predict most of the outbreaks in Australia and Spain. For this reason, we recommended using both kinds of models to analyze rodent pests.

The *four general point* is about the advantage of using the outbreak theory on pests (gradual and eruptive) to identify the factors and mechanisms and the dynamic structure to predict and manage them. Berryman's theoretical outbreak approach mentioned two outbreak types according to their characteristics, behaviour, causes and the processes to build it (Berryman et al. 1984, 1987). Gradual and eruptive outbreak theory showed us that it is useful to improve our knowledge about the Australian house mouse and Spanish voles and identify whether the population increase depends on a pulse of resources or the triggers that allow their escape from

predators. Evidencing that rodents can respond differently to a wide range of soil types, rainfall regimes, and cropping systems, an outbreak can be generated through diverse mechanisms.

Southeast mice and Northwestern voles presented factors related to eruptive outbreaks that were not dependent on exogenous factors exclusively. These complex dynamics with more than one factor involved, such as weather and predators (Berryman 1989, 1996), influence the management that should be proposed to decision-makers. According to Berryman, these dynamics were likely caused by positive feedbacks that amplified the response to obtain more and better resources avoiding the regulation from predators through an escape threshold by three potential mechanisms: saturation in the functional response of generalist predators due to the increase in rodent density, abundant alternative prey, or in our cases the influence of weather triggers which allowed the equilibrium at low rodent density to move closer to the threshold and escape from regulation (May 1977, Berryman & Stark 1985, Sinclair et al. 1990, Sinclair 2003, Groffman et al. 2006). The eruptive outbreaks in Australia and Spain suggest that predator regulation could be weak at low-intermediate rodent densities, which then disappears with better environmental conditions, i.e., precipitation and evaporation/humidity, and as rodent abundance escapes from regulation and crosses the population threshold (Newsome and Corbett 1975, Sinclair et al. 1990, Brown and Singleton 1999).

The Queensland population showed a possible cause related to the gradual outbreak that depends on exogenous factors exclusively. This population needs a large and lasting disturbance such as precipitation, one and two years before the explosion, to moved from low density to high density, increasing the limited resources as food supply (Royama 1992, Berryman 1999 a,b,

Lima 2006). Unlike southeast mice and voles, the Queensland population appears to be dominated by the principle of competition for limited resources. Still, as environmental conditions improve, the density increases, generating an outbreak (Berryman 1999 a). They depend on pulse gradients, magnitude and duration, which are induced when environments in particular areas change from low to high favorability and back when favourable conditions disappear (Berryman 1981, 1988, Royama 1992, Berryman 1999 a,b, Lima 2006). Then, depending on the structure dynamic, it is governed by eruptive or gradual outbreak, the pest management will be different.

The *last general point* to discuss is about applying the outbreak theory in pest management because after classifying the outbreaks, eruptive or gradual; we have to predict and avoid future explosions. Eruptive outbreaks are much harder to predict and control than gradual ones because the first has three states or critical points: a low-density stable equilibrium because of negative feedback due to predator regulation, an escape threshold or unstable equilibrium at intermediate pest density, making it a challenge identify it, and a high-density stable equilibrium regulated by the shortage of food; this means that pests have a different structure dynamic and possibly depend on more than one factor. Now, understanding the eruptive outbreaks including the predators was essential because they could keep regulating the pest at low density having a role in their population dynamic. Predator interaction with weather improves the outbreak explanation and prediction in Southeastern Australia and NW Spain due to the rainfall and evaporation/humidity which act like a triggers to improve the soil conditions, generating more burrows, allowing more rodent increase to escape from predators.

The predator issue is based on it being hard to monitor because it is expensive and requires more logistics. Few studies have examined the predator role on Australian house mouse and Spanish vole outbreaks because they do not have adequate predator abundances across time. We need more precise data and experiments to clarify the predators' role because they are a common factor operating on small mammals, such as bird and mammal abundance data in Australia and bird data in Spain (Krebs 2001). In comparison, the gradual outbreaks are easier to predict because they only depend on exogenous factors, primarily weather data that is a quick tool to predict the explosions, and it is cheaper, easier to work with, and more reliable and robust. It would, however, be useful to include predators to understand the ecological processes of outbreaks.

In conclusion, it is considered that to study the rodent outbreaks: it is essential to understand the ecosystem and the environmental conditions at the outbreak site, employing seasonal and annual models to test the endogen and exogenous factors in different ways and temporal scales, and finally, most importantly, use the outbreak theory to classify them and find their causes and mechanisms, with the final purpose to predict and manage rodent outbreaks.

General conclusions

Rodent population outbreaks are affected by multiple factors that must be involved. At present, weather factors and predation appear to be the dominant mechanisms of regulation on mice and common vole dynamics. The driver explanations are similar in both pests, it does not matter that mice dynamics are irregular or non-cyclic, and the vole dynamics are regular or cyclic. It is the same explanation for both patterns.

Australian house mouse dynamics show evidence that the weather factors act as the main driver of outbreaks with predator intervention in some productive sites. The South-eastern outbreaks were explained by the rainfall and evaporation, improving the soil conditions to create more enemy-free space. Thus, the mice growth rate increases and generates the outbreak. However, the Queensland outbreaks were explained by rainfall, and by the density-dependence of previous mice abundance. The rainfall mechanism improves food supply and covers crops through breeding season, occurring every two years to generate the outbreak. On the other hand, the South-eastern collapse was explained by outbreak abundance and Barn owl abundance from Victoria and Swamp harrier to South Australia. The Queensland collapse was explained by the mice autumn abundance (outbreak season) and the Barn owl predator.

To understand the mouse outbreaks, it was essential to include the generalist predator of mouse dynamics because they keep regulating the pest at low density. In the south-east, the predator interaction with the weather factors improves the outbreak explanation and prediction because the rainfall and evaporation act like a trigger to create more enemy-free space which allows mice to escape from regulation. The predator role was not evident in Queensland, it could be

the burrows are not a limiting factor there due to the soils having good water holding capacity rather than South-eastern soils with low water storage and poor soil drainage. However, we need better data on predators, from monitoring or experiments, to confirm the predator-prey relationship. According to our results, the south-eastern mouse outbreaks can be defined as eruptive because mice cross the threshold and increase. They need weather triggers that allow the population to obtain more and better resources, avoiding being consumed by their predators. The mouse dynamics of Queensland can be defined as gradual due to outbreaks that are generated by changes in rainfall that allow the population to obtain more and better food supply and cover.

Spanish common vole dynamics evidenced the weather factors and predators as the main driver of outbreaks. The vole outbreaks were explained by cumulative rainfall, humidity, and weasel's abundance. The mechanism involved weather factors that act as a trigger to improve the soil conditions, creating more enemy-free space. Consequently, the predation risk decreases and allows voles to escape from weasel's regulation. The vole's population density increases and generates the outbreak. The collapse outbreaks were explained by the strong density-dependence of outbreak density in the previous season and precipitation and temperature in the outbreak season. According to our results, the common vole outbreaks can be defined as eruptive because voles cross the threshold and increase. Spanish voles need weather triggers that allow the population to obtain more and better resources (burrows), avoiding being consumed by their predators.

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