



Recent large-scale range expansion and outbreaks of the common vole (*Microtus arvalis*) in NW Spain

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Abstract

Irruptive populations of rodents cause damage to agriculture worldwide. By the end of the last century, the distribution range of *Microtus arvalis* in NW Spain greatly expanded to encompass agricultural habitats, with the appearance of crop damaging population outbreaks. The absence of long term vole monitoring data has so far precluded outbreak forecasting, which might help mitigating associated bioeconomic costs. We used non-standard and diverse sources of information, including newspaper and national technical reports, to describe the vole expansion and outbreak dynamics in NW Spain since the late 1960s. We illustrate a rapid (<20 years) and large scale (ca. 5 million ha) colonisation of agricultural lowlands, and suggest a pattern of westward expansion emanating from the peripheral mountains. Crop damaging outbreaks directly followed range expansion and our analyses indicate that they have occurred at approximately 5-year intervals since the early 1980s. This is the first description of long term (>40 years) regional scale vole dynamics reported for the Iberian Peninsula. We suggest that expansion from (humid) mountains to (dry) plains may be related to recent changes in land use. If confirmed at a local scale, the apparent cyclicity of outbreaks would provide a basis for forecasting outbreak risk in NW Spain and may help managers adjust current control strategies.

Zusammenfassung

Nagetierpopulationen, die sich explosionsartig vermehren, verursachen weltweit Schäden in der Landwirtschaft. Am Ende des letzten Jahrhunderts dehnte sich das Verbreitungsgebiet von *Microtus arvalis* in NW Spanien weitläufig aus und es gab Populationsexplosionen, welche die Ernte minderten. Das Fehlen langfristiger Monitoringdaten für die Wühlmäuse schloss bisher Vorhersagen über die Ausbrüche aus, die möglicherweise helfen, die bioökonomischen Kosten zu senken. Wir nutzten nicht-standardisierte und vielfältige Informationen, wie z. B. Zeitungen und nationale, technische Berichte, um die Ausbreitung und Ausbruchsdynamik der Wühlmäuse in NW-Spanien seit den späten 60er Jahren zu beschreiben. Wir beschrieben eine schnelle (<20 Jahre) und großräumige (ca. 5 Millionen ha) Besiedlung des landwirtschaftlichen Tieflandes und vermuten ein Muster der westlichen Expansion ausgehend von den umgebenden Bergen. Ausbrüche, welche die Ernte minderten, folgten

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direkt der Ausbreitung des Vorkommens und unsere Analysen lassen vermuten, dass sie in etwa 5-jährigen Intervallen seit den frühen 80er Jahren auftreten. Dies ist die erste Beschreibung einer langfristigen (>40 Jahren) regionalen Wühlmausdynamik, die von der Iberischen Halbinsel bekannt ist. Wir vermuten, dass die Ausbreitung von den (feuchten) Bergen in die (trockenen) Ebenen mit aktuellen Veränderungen in der Landnutzung zusammenhängen. Wenn das auf einer lokalen Ebene bestätigt wird, könnte die Regelmäßigkeit der Ausbrüche eine Basis für eine Vorhersage des Ausbruchsriskos in NW Spanien darstellen und könnte daher den Landwirten helfen, die derzeitigen Kontrollmethoden anzupassen.

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Introduction

Rapid human-induced changes in land use are strongly influencing the composition and functioning of ecosystems across Europe (Young et al. 2005). For instance, agriculture intensification is a main driver of biodiversity loss in European ecosystems (Osvaldo et al. 2000). Such changes in biological communities often translate in increases of environmental risks, including the (re)emergence of zoonotic diseases (Jones et al. 2008), biological invasions (Lockwood, Hoopes, & Marchetti 2007) and population outbreaks of species that may then be considered as pests (Singleton, Belmain, Brown, & Hardy 2010). Rodents are among the most important vertebrate pests to agriculture worldwide, and they are often associated with environmental, socioeconomic and health issues (Ostfeld & Mills 2007; Singleton et al. 2010).

In Europe, the common vole (*Microtus arvalis*) is a major vertebrate pest for plant production that can cause important economic losses during outbreaks (Jacob & Tkadlec 2010). Although outbreaks are regularly recorded in Europe (Jacob & Tkadlec 2010), a weakening of cyclic dynamics has been reported for common vole populations in its western range during recent decades (Lambin, Bretagnolle, & Yoccoz 2006). These observations fit a geographically widespread pattern of dampening cyclic dynamics amongst small herbivores across Europe, explanations for which invoke human-induced land use shifts, sometimes coupled with climate change (Ims, Henden, & Killengreen 2008).

In sharp contrast to seemingly fading out of rodent cycles elsewhere in Europe, hitherto unseen outbreaks of common vole populations have erupted in recent decades in agricultural areas of NW Spain (Castilla y León autonomous region, CyL hereafter; Fig. 1A and B), following a regional scale colonisation event at the end of the XXth century (González-Esteban & Villate 2007). Unprecedented socioeconomic impacts are now recurrent in recently colonised agricultural habitats, including significant crop damage episodes (Jacob & Tkadlec 2010) and zoonotic outbreaks of *Francisella tularensis*, the etiological agent of tularaemia (Vidal et al. 2009). As is often the case (Singleton et al. 2010), management of vole outbreaks in CyL mainly relies on rodenticides spread over crops and/or in vole burrows. Such poison-based control practices notoriously produce undesired secondary poisoning of non-target fauna, including

protected species (Olea et al. 2009; Mougeot, García, & Viñuela 2011; Sánchez-Barbudo, Camarero, & Mateo 2012). Rodenticides add to the cost of farming by individuals or local governments (Stenseth et al. 2003; Jacob & Tkadlec 2010). For instance, during the 2007 outbreak in CyL, the cost to the public purse of emergency vole management using rodenticides was estimated at 15 million € (Jacob & Tkadlec 2010). In this context, the ability to forecast rodent outbreaks could contribute to reducing their economic and ecological impacts by allowing informed control decisions (Davies, Leirs, Pech, Zhang, & Stenseth 2004).

Long-term data sets of vole abundance are an essential starting point to assess whether outbreaks occur with a regular period and to study their causal factors, two key aspects to developing predictive models and mitigate bioeconomic costs (Stenseth et al. 2003; Davies et al. 2004; Imholt, Esther, Perner, & Jacob 2011). Unfortunately, long-term vole monitoring studies in NW Spain are limited to one study in a non-agricultural mountainous area located in Segovia Province to the south of CyL, belonging to the historical distribution range (Fargallo et al. 2009). This leads to a limited understanding of the emergence of outbreaks in farmland areas, which has so far precluded attempts to predict vole outbreaks.

Here, we used non-standard and complementary data sources to reconstruct the historical *colonisation process* of the region and *regional outbreak dynamics* of common voles in CyL, NW Spain, over 40 years. In the absence of long term monitoring data on vole populations in agricultural areas, such as available elsewhere in Europe, we combined information from public annual agricultural reports and news in a main daily regional newspaper extracted using keyword based search of archives. Combining these sources of information, we provide the first historical reconstruction of past outbreaks in this region and use time series analyses to test for regularity in outbreaks. We also assess whether vole outbreaks have been consistently accompanied by the use of rodenticides and outbreaks of tularaemia.

Materials and methods

Study area

Our study area comprises the region of Castilla y León in the north-plateau of the Iberian Peninsula (Fig. 1), an

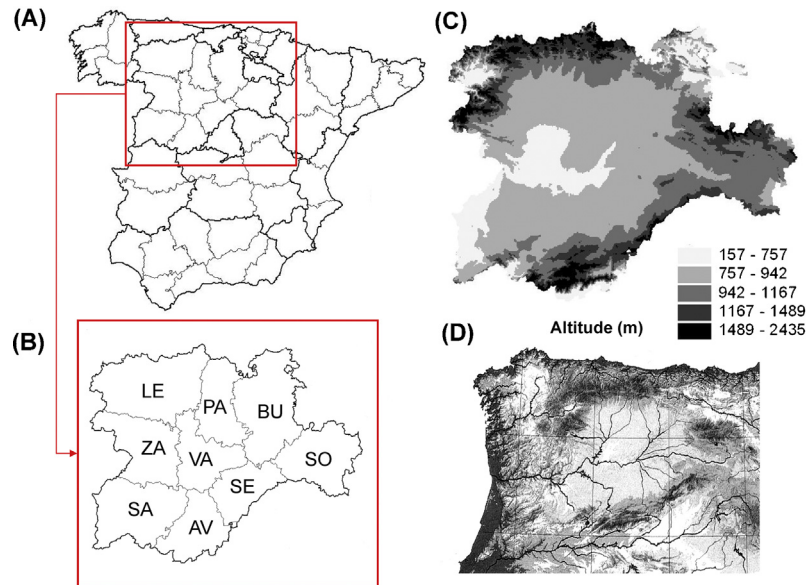


Fig. 1. (A) Boundaries of autonomous regions (dark lines) and provinces (light lines) of mainland Spain (the square frames the Castilla y León autonomic region); (B) Provinces of Castilla y León: Ávila (AV), Burgos (BU), León (LE), Palencia (PA), Salamanca (SA), Segovia (SE), Soria (SO), Valladolid (VA) and Zamora (ZA); (C) Elevations of Castilla y León, highlighting the central plains (lighter colours) and surrounding mountain ranges (darker colours); (D) location of the river Duero catchment within the region.

autonomous region of Spain (9,422,100 ha) that is divided in 9 administrative provinces (Fig. 1B). The region holds almost the entire catchment of the river Duero and includes central plains surrounded by mountain ranges (Fig. 1C and D). The region is mainly characterised by a Mediterranean climate in terms of annual precipitation (equinoctial rains, summer droughts) but less so in terms of temperatures (wide seasonal temperature oscillation, strong and frequent winter frosts). The mountainous belt is dominated by woodlands whilst the central plains are dedicated to agriculture (ca. 3.7 million ha) (Gil & Torre 2007).

Regional colonisation process

The distribution of common voles in Spain up to the early 1970s was limited to mountainous landscapes (Rey 1973). In order to reconstruct changes in vole distribution in CyL, we compiled data from published distribution maps of *M. arvalis* from 5 papers published in local scientific and technical journals (Rey 1973; Delibes & Brunett-Lecomte 1980; Palacios et al. 1988; González-Esteban, Villate, & Gosálbez 1994; González-Esteban, Villate, & Gosálbez 1995) and a book on Spanish mammals (González-Esteban & Villate 2002). We additionally searched for all publications in Zoological Record (search in topic field: [Microtus arvalis OR Common vole OR Topillo campesino] AND Spain), but found no references adding any geographically significant information to the papers mentioned above at the scale of this study. The map published by Rey (1973), a review of common vole distribution based on trapping data and raptor pellet surveys, was considered as the starting point to evaluate range expansion. We built sequential presence/absence maps between 1973 and

2002 by overlaying distribution information. The maximum spatial resolution for presence maps was set at the level of agrarian county (*comarca agraria* in Spanish); each province (see Fig. 1B) holds several agrarian counties, with surface area ranging from 473 to 3045 km² (1597 ± 609 , $n=59$). Published maps typically presented higher spatial resolution distribution data (UTM 10×10 km²) than our county grid, but with a greater level of error as not all UTM were surveyed.

Outbreak dynamics and related impacts

We used data that reported explicit spatial and temporal information on the occurrence of outbreaks (defined as unusually high vole densities creating crop damages or the risk of those). Data were compiled from two different sources that we treated as complementary in assessing the status of voles in a given year and province (i.e. our unit of analysis): (a) national technical reports from the series on plant protection and pest control (*Reuniones Anuales de los Grupos de Trabajo Fitosanitarios*) published irregularly by the Ministry of Agriculture (“Ministry of Agriculture Reports”: “MARs”); and (b) digital archives of daily issues (published regularly) of the main regional newspaper, *El Norte de Castilla* (Norte de Castilla News: NCN).

We reviewed 19 “MARs” from 1989 to 2008 (except for 1992 as no issue exists), seven of which contained explicit information (province, year) about vole outbreaks (MAR issues: 1989, 1994–96, 1998–99 and 2007–08). Not all reports referred to vole outbreaks occurring in the year of publication; indeed, the first outbreak mentioned was dated in 1968, but this reference occurred in the MAR issue of 1989. When a province was reported to be affected by an

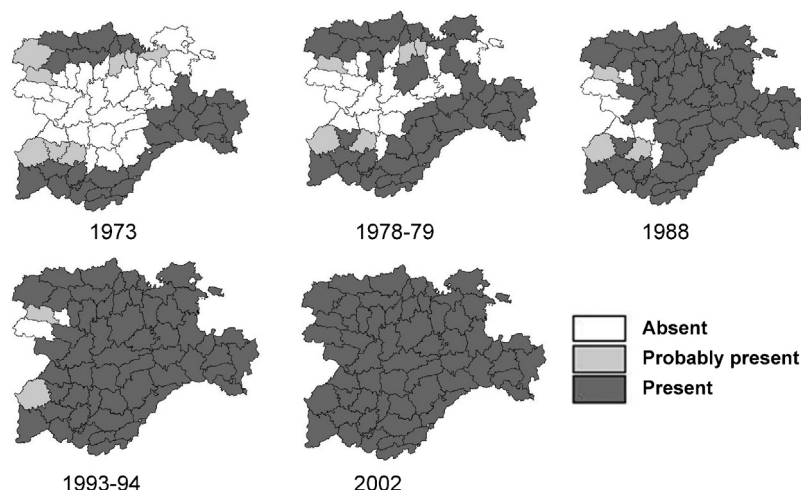


Fig. 2. Colonisation process of *Microtus arvalis* in the Castilla y León region, NW Spain, over 29 years. The maps show presence or absence of *M. arvalis* in agrarian counties (*comarcas agrarias*; $n = 59$) according to published distribution records (Rey 1973; Delibes & Brunett-Lecomte 1980; Palacios et al. 1988; González-Esteban et al., 1994, 1995; González-Esteban & Villate 2002).

ongoing outbreak in two successive years, a single MAR entry contributed 2 positive values for that province in our historical reconstruction series. However, even though the consequences of vole damage reported in one calendar year may have in part stemmed from damage that started in the previous calendar year, we did not record this unless both years were mentioned.

Instead of searching the freely available web version of the regional newspaper, we accessed the now digitised archives of the printed version of daily news from *El Norte de Castilla*, through its own dedicated software (localised at the Hemeroteca de *El Norte de Castilla*, Valladolid, Spain), between 1960 and 2009. This was in order to obtain a long time span of data and non-abridged versions of the paper content. Following initial keyword-based searches for voles and rodent terms, we restricted our search of the archives to the keywords “ratilla” and “topillo” (the old and more recent names of voles in Spanish, respectively). We avoided using less specific terminology such as “ratones” (mice) or “roedores” (rodents) in order to avoid picking up items referring to murid species other than the focal common vole. Coupling of the dynamics of coexisting cyclic and non cyclic rodents is an ecological phenomenon geographically widespread in Europe (e.g. Korpimäki, Norrdahl, Klemola, Pettersen, & Stenseth 2002; Lambin et al. 2006). We thus ensured all reports and newspaper items that we used in this study referred explicitly to common voles. Search for the keyword “topillo” yielded a total of 984 independent news items (the first dated in 1969), of which 371 (38%) provided spatial information on vole outbreaks that could be attributed to a specific province and calendar year. We excluded from analyses entries referring to regions wider than a province, and natural history accounts not relevant to outbreaks. None of the articles containing the word “ratilla” was relevant to this study according to these criteria.

As no single source of information yielded an exhaustive coverage, we combined the information from both sources (MAR and NCN) to produce a synthetic reconstruction of vole outbreaks. We thus constructed a combined data set, considering as years of outbreak those for which the evidence came from at least one information source, and considering the maximum number of provinces reported to have been affected. In order to investigate the spatial distribution of outbreaks, we also split the time series spatially into 3 geographical groups of provinces with different regional colonisation histories: (i) North (LE, PA, BU) and (ii) South (SA, AV, SE, SO), were occupied by voles before 1973; while (iii) the Central provinces comprised agricultural lowlands colonised by voles after 1973 (ZA, VA) (see Fig. 1B).

We also quantified changes in the frequency of reports reporting vole outbreaks in terms of public health (cases of tularaemia among local human populations) and environmental impacts (primary or secondary poisoning of non-target fauna; reports on chemical campaigns as management measures to control local rodent numbers, or public debates on the use of rodenticides). Among the 984 NCN items containing the keyword “vole”, 87 contained the keyword “tularaemia” (*tularemia*, in Spanish) and 257 contained reports on use or impacts of rodenticide (keywords “rodenticide” *rodenticida*, “poison” *veneno*, “raticide” *raticida*, “anticoagulant” *anticoagulante*, “chlorophacinone” *clorofacinona*, and “bromadiolone” *bromadiolona*).

Statistical analyses

We generated two data sets spanning from 1967 to 2009 to characterise past outbreaks. The first contained binary data: presence, 1, or absence, 0, of reported outbreak in a given year. The second consisted of the number of provinces within

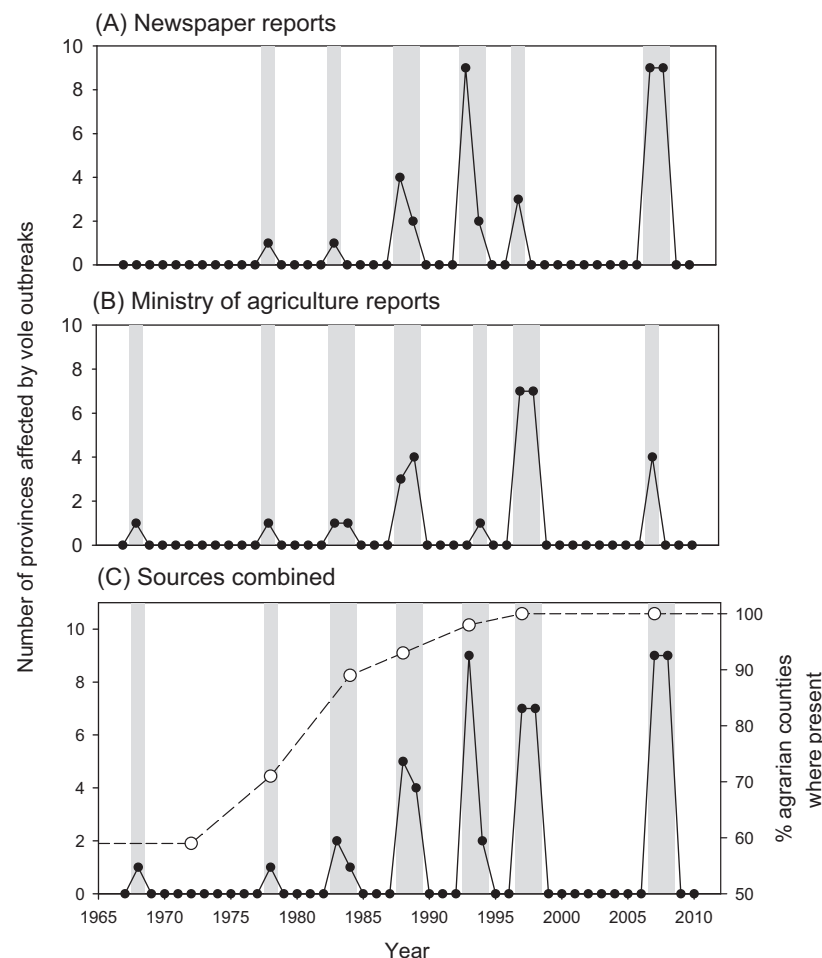


Fig. 3. Reconstruction of past common vole outbreaks in Castilla y León provinces ($n=9$), NW Spain. The graphs show the number of provinces in which outbreaks were documented in a given year (black dots), according to two sources of information: (A) Regional newspaper *El Norte de Castilla* news archives (NCN) and (B) “Ministry of Agriculture Reports” (“MARs”), and (C) for the two sources combined. In (C), the percentage of agrarian counties occupied by the common vole over the study period (see Fig. 2) is also shown (secondary y-axis). Grey bars indicate years with documented outbreaks (see main text for details).

the CyL region where outbreaks had been reported in a given year. We used the Walsh transform for a spectral analysis of the binary data, looking for evidence of periodicity in the occurrence of past outbreaks and an autocorrelation analysis to look for periodicity in the area affected by outbreaks. We used wavelet analysis to investigate whether any periodicity in the occurrence of past outbreaks changed through time. Time series analyses were performed with the software “PAST” (Hammer & Harper 2005).

Results

Regional colonisation process

Starting from a distribution restricted to the peripheral mountainous areas of CyL up to the early 1970s (Fig. 2, 1973), common voles had colonised locations north and south of the main river Duero at lower altitudes (see Fig. 1C and

D) by the late 1970s, suggesting a descending expansion pattern from mountains on both sides of the Duero river (Fig. 2, 1978–79). At that time, central and western agrarian counties at lower elevations still appeared free of common voles. Ten years later however, most of these lowland areas were colonised and voles were seemingly absent from only a few western counties (Fig. 2, 1988). By the early 1990s, colonisation of the region was almost complete (Fig. 2, 1993–94). The presence of the species in the entire region was confirmed by 2002 and remained unchanged thereafter (100% occupation in 2007) (González-Esteban & Villate 2007). The species’ distribution thus expanded from 40% up to >90% of the agrarian counties in ca. 20 years (Fig. 2 and synthesis in Fig. 3C).

Past outbreak occurrences

Our two sources of information allowed reconstruction of past outbreaks at temporal and spatial resolution levels of year

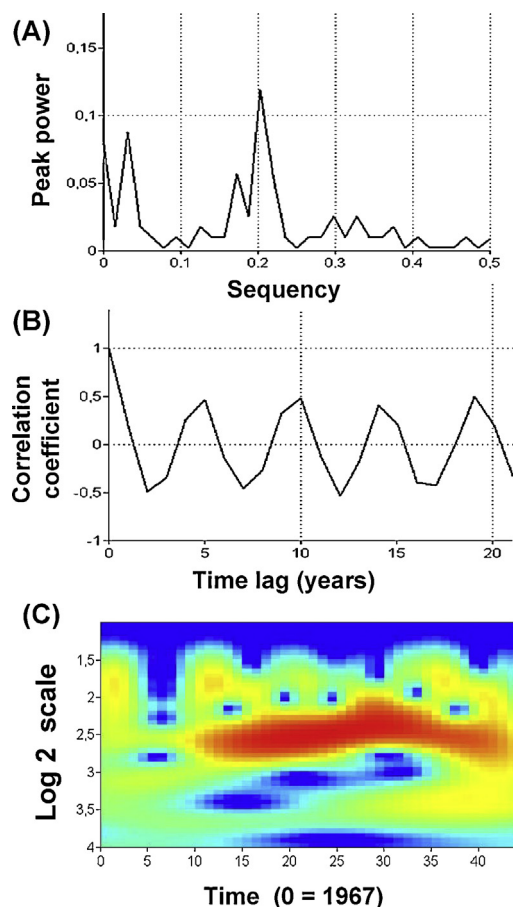


Fig. 4. Results of time series analyses of the occurrence of common vole outbreaks in Castilla y León, NW Spain. (A) Walsh transform analysis for the occurrence of outbreaks within the whole region between 1967 and 2009, showing a power peak at 0.2 frequency (corresponding to a 5-year period); (B) auto-correlogram for the number of provinces with outbreaks showing a 5-year period; and (C) wavelet analysis showing evidence of a 5-year period from 1980 onwards (darker band at 2.3–2.6 on the log-2 scale y-axis).

and province (Fig. 3C; Synthesis). Both sources were consistent in reporting six outbreaks in 1978, 1983, 1988–89, 1993, 1997 and 2007, but not always in the same provinces. The oldest outbreaks were reported in 1968 (MAR) and 1978 (MAR and NCN). Outbreaks were reported in only a few provinces until the mid-1980s, but once common voles were present in all the agricultural plains of CyL, outbreaks affected all nine provinces (Fig. 3C).

The Walsh transform analysis of the binary data 1967–2009 gave statistical evidence for cyclicity in outbreaks with a 5-year period (Fig. 4A: peak power of 0.119 for a sequence of 0.203, indicative of a 5-year period). In our reconstruction, we omitted evidence for vole outbreaks in “Tierra de Campos” in 2006 (1 NCN), which was excluded because it was not spatially explicit at the province level (see above), but was corroborated by sources other than those used in our reconstruction (Olea et al. 2009; Vidal et al. 2009). If we include this evidence for outbreaks in the region in

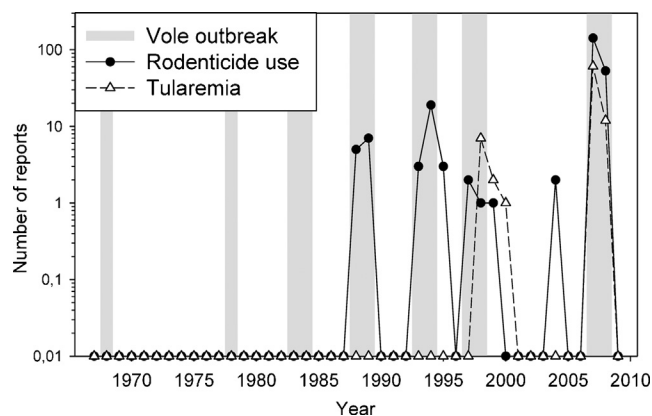


Fig. 5. Temporal pattern of reports in the main regional newspaper (*El Norte de Castilla*, NCN) related to incidents of tularaemia or rodenticide use over the study period. Grey bars indicate years with common vole outbreaks.

2006 and repeat our analysis, we still obtain a similar result (Walsh transform; peak power of 0.141 for a sequence of 0.203). When considering changes in the number of provinces with outbreaks (data in Fig. 3C), an autocorrelation analysis showed significant positive correlations for a time lag of 5 years ($R=0.409$; $p=0.05$) and 10 years ($R=0.513$; $p<0.05$; Fig. 4B), also indicative of a 5-year period. We further conducted a wavelet analysis to investigate whether the period was stationary (constant) through time in 1967–2009. The analysis showed a maximum power for a 5-year period (around 2.5 on a log-2 scale; y-axis) from 1980 until 2009 (Fig. 4C). We therefore had no evidence that the period of outbreak occurrence at regional level changed over time; newsworthy outbreaks occurred every 5 years from 1980, when most of the region was already colonised.

Splitting the binary data time series by groups of provinces shows that the oldest outbreaks (1968 and 1978) were restricted to the southern group, but that from the 1980s onwards vole outbreaks affected all 3 groups synchronously. Noticeably, outbreaks occurred in the central group of provinces as soon as voles colonised the area whereas vole outbreaks were not recorded in the northern group of provinces before the 1980s (see Appendix A).

Bioeconomic impacts related to outbreaks

Newspaper articles indicate that control campaigns using rodenticides took place at least since the 1988–89 outbreak, and in all subsequent ones, including in 2004 despite a lack of reports of a significant (regional) outbreak in our data. Newspaper articles also contained reports of cases of tularaemia associated with the 1997–98 and 2007–08 outbreaks (Fig. 5). The number of news items published in *El Norte de Castilla* dealing with impacts of vole outbreaks (tularaemia or environmental impacts) increased exponentially over the course of the most recent outbreak (Fig. 5; note the log-scale on the y-axis).

Discussion

Range expansion and outbreak occurrence in agricultural landscapes

The massive range expansion of common voles in NW Spain only took about 20 years, consistent with estimates of expansion range from other invasive rodents (e.g. Andow, Kareiva, Levin, & Okubo 1990). Populations in CyL expanded from peripheral higher elevation areas towards central lower altitude areas, probably through tributary river valleys (Delibes & Brunett-Lecomte 1980) and the whole colonisation proceeded mainly from east to west (Fig. 2, and see González-Esteban et al., 1995). Common voles typically depend on moist grassy habitats (González-Esteban et al., 1994; Delattre, Giraudoux, Baudry, Quéré, & Fichet 1996), and the observed colonisation of (dry) agricultural plains from (humid) nearby mountains runs counter to the observed increasing aridity of Iberian climate (Moreno 2005). Thus instead of responding to a climatic trend, we hypothesise that common vole populations from the mountains surrounding CyL plains have responded to land use changes that facilitated their expansion, namely an increase in moist (irrigated) grassy crops (González-Esteban et al., 2011; López-Gunn, Zorrilla, Prieto, & Llamas 2012). Thus, a potential link with an expansion of crop irrigation at regional level deserves further attention.

It has been suggested that the irruptive dynamics of common voles may have contributed to accelerating colonisation of agricultural landscapes (González-Esteban & Villate 2007). Locally high population densities during early outbreaks (1978, 1983–84) may have indeed contributed to a fast colonisation of neighbouring areas (Gauffre, Petit, Brodier, Bretagnolle, & Cosson 2009). It is striking that large-scale fluctuations of common voles were recorded immediately after the colonisation of central agricultural lowlands (see Fig. 3C), so outbreaks in agricultural landscapes of NW Spain may ultimately be a consequence of the range expansion in an area where ecological conditions for cyclicity were present. Outbreaks in CyL typically reach maximum densities (and bioeconomic impacts) in central agricultural steppes such as the continuous and homogeneous landscapes of herbaceous habitats without tree cover (Jacob & Tkadlec 2010). Such intensive agricultural landscapes are notoriously the scene of large-scale rodent outbreaks elsewhere (Singleton et al. 2010).

Past outbreak dynamics and forecasting future outbreaks

In agreement with our reconstruction, vole outbreaks had been reported or suggested in the Spanish scientific-technical and/or popular science literature in 1983, 1988, 1993–1994, 1997, and 2007 (Delibes 1989; Sunyer & Viñuela 1994; González-Esteban et al., 1995; García Calleja 1999; Olea

et al. 2009; Vidal et al. 2009). Some local outbreaks reported in a scientific paper (1985–1986 and 1990; González-Esteban et al., 1995) were not confirmed by our sources. However, the information used to describe these local outbreaks came mostly from interviews with farmers, who may have over-interpreted unusual densities of a new species as outbreaks, or reported them incorrectly. Alternatively, these discrepancies may reflect an asynchrony of outbreaks at a local scale.

Overall, this study sets a new southern limit for common vole outbreaks in Europe (Jacob & Tkadlec 2010). We found that outbreaks in NW Spain seemingly fit a 5-year cyclic pattern at the regional scale, which contrasts with the most common 3-year cycle documented in agricultural areas from the west to the east of Europe (Mackin-Rogalska & Nabaglo 1990; Lambin et al. 2006; Jacob & Tkadlec 2010). However, this pattern may not be fixed (e.g. outbreaks in 1993 and 1997) and more detailed data at smaller scales would be needed. Geographic variability at relatively short distances in cycle period length has been described in France, associated to differences in habitat quality (Delattre et al. 1996). Cyclic populations of common voles may show wide variation in period length; for example, studies from Eastern Europe have shown that cyclicity can range from 2 to 10 years, although in most cases (65%) it ranges between 3 and 4.9 years (Mackin-Rogalska & Nabaglo 1990).

Previous work from northern and central Europe has successfully used alternative sources of information to reconstruct past rodent cycles in the absence of monitoring data. For instance, a 79-year reconstruction from binary series of outbreak occurrence in Norway based on bounties paid for predators (one information source) facilitated the demonstration of temporal changes in cyclic dynamics across the whole country (Steen, Yoccoz, & Ims 1990). Geographical variation in cyclic periodicity of common voles was also evaluated in Poland using published local information (up to 39 data sets) (Mackin-Rogalska & Nabaglo 1990).

The main limitation of our methodology compared to quantitative population monitoring based on dedicated protocols is its limited resolution in space and time, precluding analyses of population variation at local and crop levels. For instance, whereas our results suggest that outbreaks typically last two years at the regional level (Fig. 3C), they were not as long at each locality: where information about agrarian counties existed, different counties were affected in each year of the outbreak. Maximal abundances have been reported in summer-autumn of the outbreak year, with a subsequent decline in the winter of the next year (e.g. Delibes 1989; Sunyer & Viñuela 1994; García Calleja 1999; Olea et al. 2009). Indeed, the highest frequency of NCN news items corresponded to the months of August to October (unpublished data). Therefore, outbreaks reported during the second consecutive year probably correspond to the decline phase of the outbreak or to peripheral pockets of high vole density. The observation that fewer provinces were always affected in the second year (Fig. 3C) is consistent with this idea. Additionally, outbreaks may have occurred even when they do not

reach a threshold of causing damage, thus not being widely reported in the media. Our approach is also limited in that it does not include quantitative information on the presence of a threshold vole density when an outbreak and associated crop damage are perceived. Yet, such quantitative information should be a cornerstone of local adaptive management and control.

Nevertheless our reconstruction indicates that the risk of vole outbreaks in the region may increase every ~5 years, consistent with the only trapping study in Segovia Province (Fargallo et al. 2009). While these results could provide the basis for forecasting outbreaks (Davies et al. 2004), our inference of cyclical dynamics remains tentative, as the time span of our data is short relative to the estimated cycle length, and other vole species have had initial evidence of cyclic dynamics contradicted by subsequent data (Zhang et al. 2003).

Rainfall is a known trigger of rodent outbreak dynamics in arid and semi-arid ecosystems worldwide (Brown & Singleton 1999; Zhang et al. 2003; Kausrud et al. 2007). Accordingly, it could be postulated that common vole outbreaks in arid CyL are associated with total previous year rainfall, as was the case in *Mus domesticus* in arid cereal crops in SE Australia (Brown & Singleton 1999). Indeed, uptake of common voles by long-eared owls (*Asio otus*) (Veiga 1986) and vole population density in Segovia Province (Fargallo et al. 2009) positively correlate with previous year rainfall. Thus the cyclical outbreaks could reflect a (possibly temporary) 5-year periodicity in above-average rainfall. Alternatively, common vole populations may have an inherent tendency to exhibit regular cyclical fluctuations but their amplitude (and hence damage to crops) might be modulated by rainfall. For example, contrary to expectation under a ~5-year periodicity, no outbreak was reported between 2002 and 2004. However, long term common vole trapping data indicated localised peak abundance in 2003–04 in Segovia province (Fig. 1B), but with lower densities than in 1997 and 2007 (Fargallo et al. 2009). In addition, NCN articles picked up farmer demands for vole control in a different province (Zamora) in 2004 (see ‘Bioeconomic impacts related to outbreaks’ above and Fig. 5), although no significant (regional) outbreak was reported during that or the previous year. In climatic terms, 2003 was a significantly abnormal year across Europe, and strong heat waves and continued drought strongly affected primary productivity (Fink et al. 2004). It is thus plausible that the severe 2003 drought precluded growth in vole density in CyL. Further studies of the role of climate in driving (or modulating the amplitude of) vole dynamics in NW Spain are required.

Bioeconomic impacts of vole outbreaks in agricultural areas

Media coverage of vole related issues (the occurrence of tularaemia events or issues related to the impacts of rodenticide use) increased over time, this being particularly marked

in the outbreak of 2007. Analysing the discourses of this coverage could reveal changes in attitudes towards the species or its outbreaks. Indeed, vole outbreaks and their management have social as well as agronomical or ecological impacts. These have led in the past to, sometimes extremely heated, conflicts between actors with opposing views on how to manage, or even on the nature of the problem (Delibes-Mateos, Smith, Slobodchikoff, & Swenson 2011). These conflicts emphasise the need to manage vole populations more effectively. They also highlight that multiple approaches need to be taken simultaneously (ecological, agronomical, social) to develop sustainable, acceptable and environmentally friendly solutions to minimise crop damage by voles in this recently colonised area.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2013.04.006>.

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