POPULATION ECOLOGY AND DYNAMICS OF AN IRRUPTIVE SMALL MAMMAL PEST SPECIES

A thesis presented for the degree of Doctor of Philosophy at the University of Aberdeen

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Declaration of authenticity

I, Deon Roos, hereby declare that the work presented in this thesis has been carried out and written by myself, and has not been submitted in any previous application for a higher degree. All quotations have been distinguished by quotation marks and all sources of information have been specifically acknowledged.

Deon Roos: ..............................................

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In memory of A3.
Preface

This thesis is presented as a series of four distinct papers (chapters II to V), that are linked by a common theme of pest population dynamics in an agri-environmental setting. There is, however, some unavoidable repetition between chapters due them being prepared as standalone articles for submission.

I am the first author on all chapters, and Xavier Lambin, Beatriz Arroyo, Francois Mougeot, Juan Jose Luque-Larena and Constantino Caminero Saldaña are contributing authors on all data analysis chapters. David Elston also contributed to chapters III and IV. Pablo García-Díaz contributed to the statistical analysis in chapter II. Juan Romairone contributed to data collection for chapter II. Maria Carmen García Ariza contributed to data collection and curation for chapters II, III and IV. Javier Rojo Revilla contributed to data collection and curation for chapter III and IV.

Chapter II is published in Agriculture, Ecosystems and Environment, and is included in this thesis as per the guidelines of Elsevier Publishing. All other data chapters are in preparation for submission.

Supplementary material for the relevant chapters can be found at the end of the thesis.
Chapter I
General Introduction
Background

Agriculture supplies the majority of food for the global human population. Following the green revolution of the 1960s, farming intensified across the developed and an increasing proportion of the developing world (Evenson & Gollin, 2003). These advancements have allowed the agricultural industry to keep pace with an increasing human population and shifts in dietary habits (e.g. increasing use of animal protein in many areas). However, due to the widespread application of such methods, the effects of the green revolution may have reached diminishing returns (World Bank, 2020). As a result, there are three possible options for agriculture to keep pace with increasing demand. These include dedicating more land to agriculture, global dietary shifts to less resource-intensive food sources, or reducing the amount of yield lost at the farm scale (Godfray et al., 2010). As the first two options are either undesirable or unreliable, ensuring current land is as productive as possible will aid in balancing increasing food supply with biological and conservation concerns.

Pest species, whether insects, mammals, or birds, can have large impacts on crop yields. For instance, in Malaysia, farmers can lose up to 60% of their harvest to rodent crop pests (Lam, 1990, in Singleton et al., 1999). Such losses demonstrate the impact pest species may have on reducing the efficiency of farms and suggest that control of pests is an important aspect in increasing crop yields. Invertebrate pest managers have long been the leaders in pest control research, with well-developed methods in biological and chemical forms (Roitberg, 2007). Conversely, understanding the management and the underlying applied ecology of specific rodent crop pests is comparatively less well understood, though this is changing (see Singleton et al., 1999). However, despite the advancements, outbreaks and irruptions of rodents are still widespread and common.

Within the rodent crop pest problem lies the potential and requirement (Singleton et al., 1999) to understand their ecology. As these species represent an economic threat, there often exist several large-scale, long-term datasets on pest species abundance (Stenseth et al., 2003; Bjørnstad, 2001), which are well suited for developing ecological knowledge. Furthermore, many rodent crop pests display cyclical or irregular irruptive dynamics, which, from an applied perspective, means that their impacts on crops may not be felt for many years but can become highly pronounced during peak or outbreak years (Jacob et al. 2014). Therefore, the aim of cyclic rodent crop pest management should be viewed as an attempt to dampen the amplitude of a cycle, or more broadly, to maintain densities below a defined critical damage-inducing density. This necessitates understanding the core fundamental aspects of the species' ecology and their population cycles. However, understanding the underlying cause(s) of population cycles and outbreaks has been an enigma in population ecology for nearly a century (see Krebs, 2013; and Oli, 2019 for thorough reviews).

Knowledge to enable effective management

This goal highlights an issue surrounding applied research that can occasionally be overlooked; whether scientific research is applicable and actionable. For applied ecology to be actionable, in a pest management context, the first crucial piece of information is to develop a management objective (Yoccoz, Nichols & Boulinier, 2001).
In pest management, this objective will state a density of pests below which damage is negligible and by which the success of control actions can be gauged. Such information is vital for determining the efficacy of control methods, as without an objective, the unstated goal is to kill an unspecified number of pest animals with no understanding of whether this would be sufficient or not to limit damage. Further, by understanding the density-to-damage relationship, the focus shifts from managing the pest in a vacuum to managing the pest with regards to its impact. Such an impact-focussed approach has been advocated in the invasive alien species’ literature (García-Díaz et al., 2021) but appears to be often lacking in pest management research.

Once an objective is in place, the focus can move to actions that can either reduce densities or predict in advance when an outbreak (i.e., densities able to influence yields negatively) may occur. Control actions are an attractive option for research, though their feasibility and effectiveness can either be overstated or overlooked. For instance, a commonly researched rodent pest control option is the promotion of avian predators, often by placing nest boxes or perches in and around fields. Studies investigating the viability of these methods most often consider some measure of the proportion of pest in the predator’s diet. Inevitably, such studies find that predators eat a commonly available prey species (see Labuschagne et al., 2016 for a meta-analysis), which is then portrayed as evidence of avian control viability. However, such claims confuse any predation with sufficiently intense predation - that is, predation capable of lowering a pest density to a pre-determined density objective. Therefore, an answer to the following question should always accompany such research; “Has predation reduced the population sufficiently to prevent damage?” Simply finding that predators eat abundant prey does not amount to evidence of effectiveness as a control method (Labuschagne et al., 2016).

Similarly, even when the impact, i.e. crop damage, is recorded, the reduction of any damage is also portrayed as evidence of avian control effectiveness. In a rare instance where a study related *Tyto alba* presence to impacts on crop yields, it was found that *T. alba* presence enhanced yields by 3.24% (Motro, 2011). A decrease in damage of 3% represents a trivial reduction in crop loss, where the same pest may cause losses of up to 100% (see chapter II). Such research highlights the importance of determining a management objective, often lacking in the literature.

Avian predation represents a constant control method, i.e., perches and nest boxes are installed and always present. However, other control actions can be more reactive to perceived increased risk or the onset of an outbreak (e.g. destruction of field margins or mechanical destruction of rodent burrows). Such reactive approaches necessitate some ability to predict when an outbreak will occur, as the alternative is to apply control at peak or outbreak densities (i.e. when the problem is visible). Implementing such reactive control methods may appear highly effective, when, in fact, they are not:

“The affair runs always along a similar course. Voles multiply. Destruction reigns. There is dismay, followed by outcry, and demands to Authority. Authority remembers its experts or appoints some: they ought to know. The experts advise a Cure. The Cure can be almost anything: golden mice, holy water from Mecca, a Government Commission, a culture of bacteria, poison, prayers denunciatory or tactful, a new god, a trap, a Pied Piper. The Cures have only one thing in common: with a little patience they always work. They have never been known entirely to fail.
Likewise they have never been known to prevent the next outbreak. For the cycle of abundance and scarcity has a rhythm of its own, and the Cures are applied just when the plague of voles is going to abate through its own loss of momentum.”

C. S. Elton, 1942

Assuming an outbreak was predictable, however, there is a strict requirement that those predictions must be actionable. For predictions to be actionable requires three features to be met. The first is that the prediction must allow sufficient time for actions to be carried out, be that implementation of a Cure or changes to farming practices (e.g. early harvesting). For instance, a prediction that states an outbreak will occur tomorrow is not actionable, while one which says an outbreak will occur in 60 days may be.

Additionally, predictions of outbreaks must have a sufficiently high probability of being correct. For any predictions to be useful in an applied setting and therefore acted upon by stakeholders requires trust in the prediction from those stakeholders. Analysis that correctly predicts an outbreak 50% of the time would eventually be ignored by stakeholders. They could just as well flip a coin.

Finally, the temporal uncertainty of predicted risk is important in terms of stakeholders making use of the predictions for decision making. For instance, if early harvesting were to be suggested as a mitigation strategy, farmers would want to leave this as late as possible to give their crops as much time as possible to reach full maturity. Even if the prediction were 100% accurate, if this comes with an uncertainty period of two months (e.g. you will experience an outbreak on the 1st of June ± 1 month), it leaves a farmer in a difficult position where they must balance the benefits of letting their crop mature versus experiencing the outbreak on the 1st of May. Improving this prediction to an uncertainty period to within, e.g., two weeks, would dramatically impact its usefulness to farmers.

An ability to accurately predict outbreaks or peaks is, therefore, highly desirable. However, a crucial assumption of such attempts is to assume that outbreaks or peaks are perfectly synchronized over space, i.e., all populations will outbreak simultaneously (Andersson & Jonasson, 1986; Hanski & Henttonen, 2002). Such perfect synchrony is a strong assumption and, if violated, may lead to predictions with wide temporal uncertainty, and lowered accuracy in parts of the landscape, leading to the problems mentioned above for stakeholder use. Worryingly for such an objective, is that there is increasing evidence that true spatial synchrony may be unlikely for cyclic species (Lambin et al., 1998; Berthier et al., 2014). As such, determining the presence and form of any spatio-temporal asynchrony (e.g. partial synchrony, see chapter IV and V) would grant an understanding of how the risk of outbreak changes over time and space. Thus, describing the spatio-temporal asynchrony and refining our understanding of these processes is crucial for allowing more considered attempts at predicting outbreaks.

**Microtus arvalis as a model system**

**Natural history**

*Microtus arvalis* ("common vole" in English, "topillo campesiño" in Spanish, family *Cricetidae*, subfamily *Arvicolinae*) are small (ca. 30 g) microtine rodents, common
throughout continental Europe, extending eastwards to the Altay mountains. Beyond the continental population, endemic and isolated populations exist in Orkney (Haynes, Jaarola & Searle, 2003; Berry & Rose, 1975), the Channel Islands (UK), and the Iberian Peninsula (Spain) (Jacob et al., 2014).

Common voles are fossorial species living within excavated simple burrow networks, typically ca. 15 cm deep (Brügger et al., 2010). They are broadly considered folivores (Jacob et al. 2014) and show good ability for thriving in agricultural landscapes (see chapter II [Roos et al., 2019]; Rodríguez-Pastor et al., 2016; Heroldová et al., 2018). In combination with their herbivorous diet and ability to inhabit agricultural landscapes, common voles have a high reproductive capacity. The species can begin breeding within two weeks of birth, with 5-6 pups per litter after a three week gestation period, allowing, on average, four to five litters per season (Jacob et al., 2014 and references therein). To demonstrate reproductive potential, if we assume no mortality occurs during a breeding season and all females maximally breed, then a single pregnant female can give rise to ca. 250 female offspring in a single breeding season (i.e. daughters, granddaughters, etc.) \[n_{t+1} = n_t + n_t \times F \times \sigma,\] where \(n\) is the female population size and \(n_1 = 1\), \(t\) is period [1,5], \(F\) is a fecundity of six, and \(\sigma\) is a sex ratio of 0.5]. This combination of herbivory, adaptation to agri-ecosystems and high reproductive potential leads common voles to being a pest species throughout much of their range (Jacob et al., 2014).

A complication for management purposes is that the population dynamics of common voles show either population cycle dynamics or irruptive dynamics. The management implications of either cycling or irruptive dynamics impart additional difficulties and constraints on management. For example, a broadly stable pest population requires constant ongoing management, and in turn, leads to a faster accumulation of cultural experience and knowledge in dealing with the pest. Conversely, pests with population cycles or irruptive dynamics, by definition, mean that years may pass between instances where management needs to occur, slowing experience gain and hindering familiarity with the problem. Further, any spatio-temporal lag in outbreaks may lead to stakeholders' misconceptions that management attempts were either partially successful or unsuccessful (as the reverse scenario suggested by Fournier et al., 2019 for species of conservation concern). This is without mentioning the various failed attempts to stop populations from cycling and the uncertainty of the cycles' underlying cause (reviewed in Krebs 2013 and Oli 2019). These factors may converge to a scenario where pests can cause severe damage, and practitioners have a limited understanding of how to deal with the issue, with this being exacerbated in systems where the pest species has newly arrived.

Topillo campesiño

Before the 1970s, *Microtus arvalis* in Spain were restricted to the mountain ranges encircling the wider region of Castilla-y-León. However, following ambiguous land-use changes, voles began colonizing from the mountain ranges into the central plateau (Luque-Larena et al., 2013) and are now present throughout the region. Since the region’s colonization, recurrent outbreaks have occurred roughly every three to five years (Luque-Larena et al., 2013; Mougeot et al., 2019). Given the extensive agriculture in the region, these outbreaks have created social tension and conflict between various
stakeholders (Olea et al., 2009; Lauret et al., 2019), in part exacerbated by human outbreaks of tularemia which occur in concert with common vole outbreaks (Luque-Larena et al., 2015). Indeed, tularaemia and bartonellosis prevalence have been shown to be vole density dependant (Rodríguez-Pastor et al., 2019).

With this backdrop, common voles in Spain represent an instance where a novel pest occupied a previously naive region, whereby locals had no cultural experience in dealing with a pest with complex population dynamics. The result is that in the early days of pest management, no clear course of action was known or even the extent of the problem. The uncertainty gave rise to conspiracy theories, use of poisoning with unknown effectiveness (in terms of halting an outbreak), resentment and anger amongst different interest groups, to name a few. However, this has improved in the past decade, thanks in no small measure to the work of my co-authors in the following chapters.

ITACyL monitoring

In 2007, a large scale, high amplitude common vole outbreak occurred in Castilla-y-León, which led to the creation of a team tasked with monitoring and managing the pest problem. The team decided to use an abundance index to monitor vole populations, based on a method developed in France (DeLattre et al., 1990a; DeLattre et al., 1990b). Initially focused in and around the most affected area, the monitored region was gradually expanded over time to the extent that it now reaches ca. 32,000 km². To do so required a large team, which at maximum had ca. 50 technicians who carried out these surveys. However, due to additional demands, the surveying took on a semi-reactive adaptive approach, where more resources (i.e. technicians) are deployed for monitoring when outbreaks appear to be more likely. During the data collection period used in this thesis, the monitoring resulted in > 80,000 abundance indices across the region. The semi-reactive nature of the monitoring proved to be a benefit of the dataset. In order to detect and describe the travelling waves in chapters III and IV required high temporal resolution, afforded by the semi-reactive sampling over time (albeit at the occasional cost to spatial resolution). As discussed in chapter III, a lack of spatial resolution can be a substantial barrier when describing subtle forms of synchrony. Given that the synchrony described in chapter III shows subtle within-year variation, this semi-reactive monitoring design is likely the reason we can even detect this variation. An alternative, highly structured sampling design, e.g., 10,000 locations sampled twice per year, may well have limited the detail we could extract in the form of synchrony.

Precis of chapters

With this in mind, I structure the thesis by presenting the first two chapters with a strong applied focus, intent on resolving two aspects I view as crucial for aiding management. The two following basic science chapters may provide the foundation for more considered solutions to the pest problem, as well as developing theoretical understandings of spatio-temporal phenomena. The first data chapter (chapter II) focuses on a fundamentally important piece of information, the damage to density relationship between crop yield and common vole density. Chapter III focuses on understanding what agricultural practices exacerbate the risk of having pests occupy a given field. In Chapter IV I seek to develop an understanding of spatio-temporal lags in
population cycles. Finally, in chapter V, I consider whether a commonly invoked feature in theoretical explanations of the spatio-temporal lags is represented in empirical data.

Rodent pests; Applied focus

Chapter II

A truly fundamental piece of information for managing any species, whether species of conservation concern or pests, is determining the metric by which the success of management will be gauged. Without this information, management will inevitably be ad hoc and inconsistent. The importance of determining objectives to enable evidence-based management is well known in the broader literature (Yoccoz, Nichols & Boulinier, 2001; Junker et al., 2020), but there is a lack of knowledge regarding at what densities rodent pest species become economically detrimental, presumably because determining such information can be challenging (e.g. Huitu et al., 2009). Further, the relationship as a whole between density and damage is especially lacking across the field, with researchers generally preferring to describe the overall relationship with a particular threshold (e.g. Ramsden et al., 2017). While thresholds have clear value, they ignore the benefits of understanding the whole relationship. For instance, identifying the shape of the damage to density relationship can be especially useful for distinguishing between a linear relationship, where control could be applied at a proportional rate, or non-linear, which presents various threshold objectives to gauge success or failure. To determine this, we used two experimental datasets whereby voles were excluded, or not, from crops, and a secondary dataset consisting of insurance claims of vole damage and an independent dataset of vole abundance indices. In doing so, we suggest that the relationship is likely non-linear and very tentatively suggest the inflexion point may occur at densities above 250 to 300 voles per ha.

Chapter III

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An additional understanding required for informed decision-making rests on the notion that agricultural landscapes can be dynamic from one year to the next, whereby crops are harvested, fields are tilled, new crops are sown, and so forth. In these agricultural environments, fields that may superficially appear equivalent, for instance, planted with the same crop, may differ in various ways due to the diverse suite of agricultural practices that a particular farmer may employ. As such, we may expect that the risk of pest occupancy varied with these features. The risk here is that any such practices, which encourage persistent occupancy, may translate into either increased likelihood of adjacent fields being occupied and/or higher densities during outbreaks due to more optimal habitats. Once identified, any practices which increase the "attractiveness" of a particular field may be used to either focus management resources on those most at risk (reactive) or to reduce their risk by favouring alternative practices (preventative). Using a factorial experimental field with different farming practices and crops, we show that certain farming practices and specific crops can greatly increase the risk of vole occupancy.
Rodent dynamics; Pure focus

Chapter IV

The ability to predict when an outbreak will occur would be an incredibly powerful tool for managing a cyclic pest species. Unfortunately, given that ecologists have been attempting to explain the cause of cyclicity for a century now, resulting in greater understanding (reviewed in Krebs, 2013; Oli 2019) but no ability to reliably predict when a peak will occur, attempting to do so seems unlikely to prove fruitful. However, a feature of many, if not all, cyclic systems is the propagation of those cycles through space and time, referred to as periodic travelling waves. Through travelling waves, distant populations become synchronized with each other through local dispersal, trophic interactions, and the interaction of the two. The greater the speed of a travelling wave through a landscape, the closer to true synchrony the system becomes. However, simply determining the presence or absence of travelling waves requires large datasets spanning a suitable length of time and large spatial scales (Koenig, 1999). Due to the requirement of such rare datasets, empirical descriptions and understandings of travelling waves are limited (Lambin et al., 1998; Johnson, Bjørnstad and Liebhold, 2004; Berthier et al., 2014), though a substantial pool of theoretical literature compliments them. A challenge, however, is to marry empirical and theoretical works, owing to empiricists using limited datasets (relative to the spatial scale of the pattern) to phenomenologically describe travelling waves and theorists using biologically unfeasible settings to simulate the spatial patterns (i.e. impossible to determine, e.g. carrying capacity, see Lambin et al., 2002 for a general discussion of the value of theoretical models for generating testable hypotheses).

Nevertheless, attempting to bring the two fields together with a suitable dataset would represent one route to improve our understanding of these spatial dynamics. Using an exceptionally large-scale dataset spanning 2011 to 2017, we estimate the presence of two radial travelling waves, which we posit represent activator and inhibitor properties, respectively. In doing so, we test the empirical support for a variety of hypotheses generated by empiricism and theory, culminating in an understanding that provides parsimony between travelling wave theory and the fundamental relationship with population cycles.

Chapter V

Improving understanding of travelling waves is important for both theoretical understandings, but also for improving any attempts at predicting outbreaks. A common assumption in empirical research is that the speed of the waves is invariant, while theory suggests this is not the case. Instead, there is an implication that the speed of a travelling wave may vary with pest population density. For applied considerations, for instance, if the waves (and any resulting patterns) travel through a landscape very rapidly (i.e. approaching true synchrony), this may not provide practitioners with enough time to act but would mean that purely temporal predictions are spatially more accurate, due to little to no spatial lag. Therefore, understanding what features influence the speed may lead to greater usefulness in any forecasts to farmers of encroaching pest outbreaks. Dispersal and trophic interactions are believed to be responsible for the
formation of travelling waves (Blasius, Huppert & Stone, 1999; chapter IV), where we may expect the speed of a wave to be determined by the dispersal of each trophic layer.

However, we consider dispersal itself an incomplete variable. For instance, electrons travelling (i.e. dispersing) in a wire move excruciatingly slow, roughly two seconds to move the distance of the thinnest human hair. Nevertheless, when a light switch is flicked, a light bulb turns on without any perceived delay. This is due to each small dispersal event resulting in neighbouring electrons also dispersing, essentially culminating in a snowball effect of slow, small scale dispersal events. However, this “snowballing” results in a pattern that spreads much greater than any individual electron. The key takeaway from this analogy is two-fold. First, slow local dispersal events can result in spatial patterns that move much faster than an individual. Second, the “snowballing” relies on neighbours that can be "hit" and can then disperse themselves. Indeed, this analogy seems well reflected in the theoretical parameterisations of travelling waves, where the propagation of a wave relies on dispersal combined with density (see, e.g., Smith, Sherratt and Lambin, 2008; Johnson, Bjørnstad and Liebhold, 2006). Thus, we anticipated that the speed of travelling waves might be density-dependent. Further, given that we found what appears to be activator-inhibitor travelling waves, theory has made predictions that the respective dispersal ability of activators (e.g. "victim" in this case) and inhibitors (e.g. "enemy") is what can lead to the cumulative spatio-temporal patterns seen in systems with travelling waves. Thus, we tested for density-dependent relationships with speed, using extensions to the models described in chapter IV.

**Scientific philosophy adopted in this thesis**

Popperian falsification is broadly upheld within the scientific community as the preferred prescription of the scientific method, allowing the demarcation between science and pseudo-science. Popper believed that scientists should be engaged in falsification and argued that pseudo-scientists are not. The core rationale behind his view was the science should exclusively use deductive logic (i.e., where the premise/hypothesis is unquestionably true, meaning that the conclusion is guaranteed) and should not make use of inductive logic (where the validity of the premise cannot be guaranteed, therefore neither could the conclusion). This mantra is most often taught to students as the principle by which to guide their research. Yet, Popper’s philosophy is, arguably, a poor representation of how science occurs and has an important logical flaw.

Popper believed that scientists do not rely on logical induction to reach their conclusions. To make his point, he used the white and black swan analogy, where the toy hypothesis was that *all* swans are white. This theory, he argued, was unprovable, as not all swans could be observed to confirm it. Instead, Popper proposed that scientists instead set out to falsify the hypothesis. In doing so, scientists would not need to use inductive logic (as the premise that all swans are white cannot be guaranteed) and instead use deductive logic. If ever a black swan were observed, the hypothesis would be proven false, resulting in a new hypothesis to take its place. In many instances, this process of falsification will be highly instructive and a worthwhile endeavour (Lambin et al., 2002), but an example from the movie Pink Panther Strikes Again (1976) illustrates a potential flaw with a Popperian view. The script from a scene reads:
[Pink Panther] Does your dog bite?
[Hotel receptionist] No.
[Pink Panther attempts to pet dog.]
[Pink Panther] Nice doggy.
[Dog bites him.]
[Pink Panther] I thought you said your dog did not bite.
[Hotel receptionist] That is not my dog.

We could reconstruct this scene as a deductive argument using Popperian falsification:

Premise: This dog will bite me.
Observation: Informed that the dog will not bite.
Conclusion: The dog will not bite me.

The premise is falsified, and Pink Panther concludes that he may pet the dog. However, the falsification was incorrect due to unspecified conditions not being met, meaning that the truth of the premise could not be guaranteed. Namely, there was an assumption within the premise that was untrue.

The problem with Popper’s portrayal of the scientific method is that it inherently relies on many assumptions, where Popper believed that such inductive logic had no role to play in science, hence the need for deductive falsification. As such, falsification covertly relies on assumptions that cannot be guaranteed, and hence relies on inductive reasoning, the very form of logic that Popper wanted to avoid. In essence, Popper believed that data could not be wrong, only theories.

This if the premise is true, then I predict this outcome (i.e. inductive logic), arguably used more commonly in science (i.e. being reliant on generalizations, e.g. I assume Microtus arvalis are multicellular, carbon-based organisms without attempting to falsify it), is better encapsulated by Thomas Khune’s notion of paradigms. Khune’s description (as opposed to Popper’s prescription) includes four stages of science. Given that this thesis includes a cyclic species, the stages will be described using population cycles as the backdrop.

Pre-paradigmatic phase: Before a paradigm emerges, science appears chaotic, with no unified theory, concept or methodology. However, with the development of a paradigm comes a unified set of theories, concepts, and methods, forming the foundation for subsequent research. For instance, the paradigm that population cycles in Fennoscandinavia are unique to Fennoscandinavia (e.g., Hanski & Henttonen, 2002).

Normal science: Research then occurs, accepting without critique the paradigm that, e.g. specialist predator and prey interactions cause population cycles, a component of the Fennoscandivian paradigm). The field develops and becomes more refined, but always without being highly critical of the paradigm. Khune states this uncritical acceptance of the paradigm allows scientific progression, as science can occur without the constant need to guarantee the truth of all assumptions. For instance, work investigating whether specialist predator removal influences a cycle (e.g. Graham & Lambin, 2002 [an example of
Popperian falsification of one theory] is carried out without having to confirm the existence of population cycles themselves.

**Crisis:** The crisis phase is entered once an observation is made, which calls into question the paradigm (e.g. Lambin, Bretagnolle & Yoccoz, 2006; Graham & Lambin, 2002). At this point, the anomaly (i.e. a problem within the paradigm that scientists are unable to solve) is explored, with one result being that the observation is explained, meaning the paradigm can be maintained and normal science resumes. Alternatively, if the anomaly cannot be explained, then faith in the paradigm deteriorates, and scientists begin exploring more radical alternatives to explain the anomaly, resulting in a scientific revolution.

**Scientific revolution:** A new set of theories, concepts, and methods emerge to replace the old paradigm (a “paradigm shift”). This new paradigm is embedded, and normal research resumes under the new theories, concepts and methods.

Khune’s view (as well as Foucault’s extension of epistemes; briefly, epistemes are unconscious paradigms) of science appears a much closer match to reality, where the focus is more often on knowledge gaps, than Popper’s idealized view. Strong support of this view is the trust scientists place in paradigms. Indeed, much of the early stages of a PhD and part of a supervisor’s role is to ensure consistency between the work produced by the student and the existing paradigm(s).

Statistical analysis forms part of most scientific paradigms. Indeed, Khune’s notion that paradigms can be trusted during the normal phase appears to be reflected in approaches to statistics. For example, at the start of my PhD, I was told that I did not need to know or understand all of the details in a statistical model to use it (for clarity, none of my supervisors said this). The analogy used was, “You do not need to understand all of the mechanical engineerings of a car to drive it down a road”. This analogy follows Khune’s description of the scientific method and faith in the paradigm. However, adherence to the paradigm concerning statistics may represent a scenario where there should be additional scepticism. Why should scepticism of the paradigm be applied predominantly with statistical methods and not with, e.g., ecological theories? Because ecological paradigms will be developed over time by those well educated in ecology, but not necessarily in statistics. Indeed, instances of misuse or misunderstanding of statistics in ecology have long been known (e.g. Yoccoz, 1991 [an example of suggesting a crisis with the paradigm]).

The analogy that, arguably, should be taught to young researchers (and the one I used when I taught a quantitative course) is: “You are going to build a car, with little to no training, using parts developed by others in ways you do not know or understand, and then drive down a busy road.” Indeed, I believe many of the issues surrounding the misuse and overuse of significant tests (Yoccoz, 1991) could stem from a substantial lack of paradigm scepticism. The dogmatic use of familiar statistical methods in fields where statistics is not the primary focus of the education necessitates particular scepticism of the paradigm. The approach developed over the course of this PhD was to approach statistical analysis with a desire to try and understand as many of the details as possible. The ultimate objective of this approach is to do a piece of analysis without using any code written by someone else. I have not, and likely never will, achieve this,
but it is an aspiration to ensure that I am not overly reliant on a paradigm I do not fully understand.

The philosophy adopted in this thesis

In this thesis, I have carried out research with an appreciation that Popper’s prescription of the scientific method allows robust conclusions to be achieved but acknowledge the limitations of his prescription for science. While I believe this prescription should be strived for, I believe that Khune’s description of the scientific method is closer to reality. Therefore, in an attempt to include the benefits of Popper’s prescription with Khune’s description of paradigms, I apply additional scepticism to statistical analysis. I do so to develop solutions that I intend to be relevant to applied problems and hope that I may impact the development of scientific knowledge.

References


Chapter II

Characterizing the crop damage to pest density relationship with a fluctuating rodent population in NW Spain
Effective pest species management requires an understanding of when and how increasing pest species densities impact crop yields. Of equal importance, for the timing of management in relation to outbreak dynamics, is understanding what form this relationship takes, as different shapes call for divergent management strategies. For instance, a curved (e.g. sigmoidal) damage-density relationship would mean that control actions are least cost-effective at low or high densities, while a linear relationship permits control at any density. Using two small-scale experiments and a large-scale insurance claim dataset, we sought to describe the functional relationship between the density of an agricultural pest species, the common vole (*Microtus arvalis*), and its impacts on crop yields in NW Spain. Our analyses of the two experimental datasets show that at low densities (< ca. 270 individuals per ha) the pest does not cause damage above that of background yield variation. Our analysis of the insurance claims suggested that increasing pest densities led to yield reductions with up to ca. 50% of...
yields lost when pests are at outbreak densities. However, in 3% of all claims, exceptional circumstances led to fields experiencing 100% loss. The functional form in this analysis suggested a linear shape, though only when considering all three analyses together can the shape be characterised as curved, likely sigmoidal. Additionally, our insurance claim analysis highlighted potential difficulties stakeholders have in correctly attributing damage to common voles; with either claimants or assessors potentially misattributing the cause or over- or under-estimating the extent of damage in 43% of all claims. Our description of the relationship will allow for informed decisions to be made by both practitioners and individual stakeholders, enabling more effectively timed control and, in turn, reducing risk to non-target species.

**Keywords:**

density dependence | economic impacts | species management | pest species | crop damage | rodent pests

**Introduction**

Problematic species, such as pests and invasive species, cause damage to a quantity of interest, either social, economic, or environmental assets (Bradley et al., 2019; Pedigo, Hutchins & Hugins, 1986). The management response to both pests and invasive species requires an understanding of both the strength and shape the relationship between a given species density and damage caused, in order for control actions to be timely and cost-effective (Bradley et al., 2019; Pedigo, Hutchins & Hugins, 1986; Choquenot & Parkes, 2001; Norbury et al., 2015; Yokomizo et al., 2009). While the direction of the density-impact relationship for non-native species may be context-specific (i.e. positive, neutral, or negative impacts, see Bradley et al., 2019), for pest species it is intuitive that greater densities of pests will cause increasing amounts of damage. An additional difference between pest and invasive species damage-density relationships is that, while it may takes years or decades for invasive species to establish and reach critical densities, such processes can act out in a single harvesting season for pest species. Regardless, the shape of the relationship remains of paramount interest for pest management (Pedigo, Hutchins & Hugins, 1986) as the severe damage to crops caused by agricultural pests is a well-known case of a socio-economic impact. Yield losses can represent a substantial economic burden to farmers, whilst control methods can be socially and ecologically controversial.
In studies relating pest abundance to yield losses, no clear consensus appears as to what the shape of the relationship is (sometimes referred to as “damage curves” Pedigo, Hutchins & Hugins, 1986 or “damage-impact functions” Norbury et al., 2015) as many relationships appear to be context specific (Norbury et al., 2015). For instance, some find the relationship is best approximated as linear (Rogers & Brier 2010a; Brown et al., 2007; Forsyth et al., 2015; Choquenot, Lukins & Curran 1997), others that the form is non-linear, of varying strength (Brown et al., 2007; Meheretu et al., 2014; Rogers & Brier 2010b; Tammes 1961), whilst others find both non-linear and linear possible (Hone 1995). The lack of generality on the shape of the relationship is particularly limiting, as this is an essential piece of information for practitioners when making decisions as to when to apply control actions (Pedigo, Hutchins & Hugins, 1986). For instance, where the shape is non-linear, e.g. sigmoidal, then control should be avoided at both low and high densities as these are comparatively ineffective densities at which to do control. However, given many pest densities are highly dynamic over time (Jacob & Tkadlec, 2010), such advise must be refined by expectations of outbreak likelihoods. That is, if an outbreak is likely, control should be initiated immediately while the pest is at low densities (Liers et al., 1999). Conversely, if pests remain at low densities until harvesting, then only minor or no damage will occur. In cases where outbreaks do not materialise then carrying out control at low densities is unlikely to be cost-efficient, either economically or ecologically, in relation to the amount of damage they prevent. Additionally, at high densities, the damage has either already occurred, or for regenerative crops, the density must first be reduced by a given amount before crops can recover (Nugent, Fraser & Sweatapple, 2001), though the regenerative abilities of some crops appear to diminish over the course of multiple harvests (Babińska-Werka, 1979). In contrast, applying control actions prior, or possibly even during the early stages of the increase phase of would likely provide the best return for a limited amount of investment in control, but such strategies would require a high degree of assurance that both an outbreak will occur and that control methods are capable of reducing pest densities. Considerations based on such presumed inflection points must be made with the understanding that pest densities can be dynamic over time, meaning that such decisions would be made with uncertainties regarding density trajectories. Conversely, if the relationship is strictly linear, then management is simplified as there would be no need to time control actions with specific densities. Misunderstanding this relationship
risks giving detrimental advice to stakeholders and may reduce trust between management and individuals (Norbury et al., 2015).

Studies investigating pest economic damage thresholds, where a specific amount of damage is estimated at which farmers no longer make a profit, have been documented for many invertebrate pests (reviewed in Ramsden et al., 2017), though studies determining the entire shape of the pest-specific damage-density relationship are comparatively limited (but see e.g. Hughes & McKinlay, 1988; Rogers & Brier 2010; Rogers & Brier 2010b), especially for rodent pests in Europe (Jacob & Tkadlec, 2010). In some studies, it is not possible to make inferences regarding the shape of the relationship; for example, where experiments measure the impacts of species presence or absence on crop yields (Grisley, 1997; Borowski 2007), or in studies limited to low densities of the pest species (Meheretu et al., 2014). Studies which explore the relationship under a full range of abundances are rarer, though, in the few existing examples, data on either densities or damage require indirect measurements or approximations. For example, agricultural models are often used to predict yields to infer damage-density relationships (Pathak & Dyck 1973; Pinnschmidt, Batchelor & Teng, 1995; Brown et al., 2007). Even rarer still, are examples testing a wide range of abundances against directly measured yields (but see Huitu et al., 2009 who used stakeholder assessments of damage).

While some pests with stable populations can reliably be expected to cause some amount of damage from one year to the next (Kiritani 1979; Wang et al., 2015; Pfeffer et al., 2021), other species with high growth rates are irruptive where years may pass with no outbreaks occurring (Huitu et al., 2009; Jacob et al., 2014; Jacob & Tkadlec, 2010). If pest damage occurs with regularity (i.e. every harvesting season), then practitioners may be expected to build experience and knowledge in dealing with pests and become less reliant on a description of the shape of the relationship over time. For instance, Japanese farmers, experienced in dealing with the pest Nilaparvata lugens, learnt to apply whale oil on to paddy surface water to reduce pest damage ca. 300 years ago (Kiritani 1979). However, for pest species which are both irruptive and have population cycles, meaning that years can pass without an outbreak occurring, then control strategies necessarily become more nuanced as control actions need not, or cannot, be applied routinely. In such cases, the length of time between outbreaks may be suitably long that any experiences learnt from previous outbreaks are diminished over time (e.g.
A lack of experience in dealing with pests, and reliance on understanding the damage-density relationship, would be exemplified in systems where the pest is newly arrived. Doubly so when the newly arrived pest is irruptive. In such scenarios, emphasising management strategies could be required each outbreak, resulting in increased reliance on the description of the shape of the relationship.

Here we carried out three analyses from two independent manipulative experiments and a regional observation dataset to determine the shape and strength of the relationship between *Microtus arvalis* (common vole) densities and the damage caused to crop yields in the recently colonised region of NW Spain (Luque-Larena et al., 2013). Using two experimental datasets, we described these relationships at relatively low vole densities (i.e. < 300 per ha compared to outbreak densities of ca. 1000 per ha [Jacob et al., 2014; Jacob & Tkadlec, 2010]). While we were unable to explore the impact across the whole range of vole densities, the presence or lack of damage at these densities can provide strong inference as to whether the shape is linear or non-linear. We then made use of a large-scale observational dataset on vole density estimates from regional monitoring and assessed claims of damage made by subscribing farmers to an insurance company, to examine the shape of the relationship over a wide range of densities, including two outbreak periods. Using all three analyses, we sought to distinguish between a linear and non-linear relationship and use this knowledge to offer suggestions for the control of this pest species.

**Materials and Methods**

**Study species**

The common vole is a widespread pest species across Europe (Jacob & Tkadlec, 2010; Jacob et al., 2014). The species exhibits population cycles with peaks occurring once every three years (Mougeot et al., 2019) in a recently colonised part of their range in NW Spain (Luque-Larena et al., 2013). During outbreaks, vole densities may reach between ca. 800 to 1,000 individuals per ha (Bryja et al., 2001; Jacob et al., 2014), with observations suggesting near-complete yield loss at such densities (pers. obs. CCS). Common voles prefer perennial crops and field margins with vegetation cover though will spread into all available fields during outbreaks (Rodríguez-Pastor et al., 2016; Roos et al., 2019; Heroldova et al., 2018; Santamaría et al., 2019), similar to voles in N Europe (Huitu et al., 2009).
Data collection

We conducted our research in the central plateau of Castilla-y-León, NW Spain, where 35,750 km² is dedicated to the production of cereals (mostly wheat and barley), alfalfa, sunflower, and grain legumes. Farmers in the region can broadly sustain 15 to 20% damage before no longer making a profit in a given field (CCS pers. obs.). We conducted two experiments within a region known to experience high-density outbreaks (Tierra de Campos). Complementarily, we accessed a third dataset that contained assessed claims of damage collected and released for this study by the Spanish Association of Combined Agricultural Insurance Companies (hereafter Agroseguro), from customers across the entire region.

The first experiment (Experimental Field, hereafter) was carried out in a 1 ha experimental field belonging to the University of Valladolid, planted with non-irrigated alfalfa (*Medicago sativa*, Aragón variety) two years prior to the experiment start date. We built 12 exclosures, each 1 m², within the field to exclude voles by using wire mesh (either 10 or 8 mm mesh) buried approximately 25 cm deep to prevent voles from burrowing in (where Brügger et al., 2010 suggested that mean common vole burrow depth was 15 cm). The top 5 cm of the mesh was cut and folded outwards to discourage climbing. We paired each exclosure with a 1 m² control area where voles were able to enter and leave at will. We checked all exclosures for signs of entry by voles (namely presence of burrows, vegetation clippings, or grazed alfalfa) every 4 weeks, with no evidence found to suggest voles had entered. We determined the placement of exclosures and controls by segregating the field into 12 grid cells during Spring 2016, with one exclosure and control per cell.

We carried out simultaneous spatially explicit capture-recapture trapping, which occurred every four weeks to estimate vole densities (see Romairone et al., 2019 for details). For our crop yield measurements, we harvested all alfalfa, ca. 5 cm above ground (equivalent to farming practices and as used by Babińska-Werka, 1979), from each exclosure and control pairings to coincide with trapping to allow accurate estimation of vole density. We collected the data from late March until mid-June in 2017 (5 occasions), and from early May until late July 2018 (4 occasions). We delayed harvesting in 2018, following a large-scale drought in the late summer of 2017. Vole densities ranged between 0 and 53.9 voles per ha over the course of data collection. Harvested alfalfa was dried overnight in a 60° C oven and weighed the following
morning. Each month, we randomly chose three exclosure-control pairs for harvesting. As alfalfa is regenerative and is harvested multiple times a season by farmers, all previously harvested pairs were re-harvested to replicate farming practices. The final dataset consisted of 114 samples of alfalfa yields (Fig. 1).

To encompass a wider range of densities, in 2018 we relocated the experiment into eight active, farmer-owned alfalfa fields in areas where common vole were reported as being present at unknown densities (Active Fields, hereafter). In each of the eight fields, we erected four exclosure-control pairs using the same design as in the Experimental Field, except for pair placement. Pairs were arranged in a line, alternating between exclosure and control, all placed ca. 5 m parallel to the field margin. We did so both to maximise density as common voles tend to occur at higher densities in margins than in fields (Rodríguez-Pastor et al., 2016) but also to minimise adverse impacts on farming. Exclosures and controls were separated from each other by ca. 10 m. Four of the eight Active Fields had been harvested within a week before we installed the enclosures. Vole density was estimated using a single trapping event where 35 Sherman traps, arranged in a T shape, were placed parallel to the field margin, extending outwards into the field. Traps were left for 24 hours, baited with apples and carrots. The proportion of captures was used to estimate density (see Jareño et al., 2014 for details) and indicated vole densities ranged between 2.5 and 269.4 voles per ha. The exclosure-control pairs were left in situ for one month before data collection. After one month, we harvested half of the pairs in each field with the remaining pairs harvested four weeks later.

We placed a single INRA trap within each exclosure to determine if they were successfully preventing voles from entering. Simultaneously, we checked for visual signs of vole presence as in the Experimental Field. INRA traps were operational and checked every two days the week before and during harvesting. Only a single vole was caught in an exclosure, though no sign of damage to the alfalfa was observed. The final dataset consisted of 64 samples of alfalfa (Fig. 1).
Figure 1: Data collected from both the Experimental (grey) and Active Fields (black). A shows the distributions of vole densities per ha in both datasets. B shows regional captures per 100 traps from surrounding areas, with the black line showing a thin-plate regression spline with 4 knots (model unverified and included only as visual aid). Red dots indicate points within the same municipality as the Experimental and Active Fields. Grey areas indicate data collection periods (unpublished data, JJLL & FM). C shows the distribution of alfalfa yield, in g per m², from both datasets, with the mean yield in Experimental Field equal to 82.11 g per m² +/- 10.23 SE and Active Fields equal to 82.09 g per m² +/- 8.29 SE regardless of treatment. D shows alfalfa yield again, but faceted by treatment level Voles Absent (exclosures) and Voles Present (controls). Note that the bar positions have been dodged to allow easier comparisons between the two datasets.

In order to characterise the relationship at outbreak densities (i.e. ca. 1,000 per ha [Jacob & Tkadlec, 2010]) that were absent from the experimental datasets, we used a dataset collected by Agroseguro S.A., on claims of damage by customers and assessed by their technicians from 2012 until 2016. Information collected as part of the claim assessments included: estimated proportion of the yield lost to voles; crop type; year and location. Due to customer privacy concerns, the claim location was only known to an administrative region level, (“municipality”, hereafter). The data set included information from 124 municipalities (from a total of 2248 municipalities in CyL). The full data generating process was likely; a farmer was insured for vole damage by
Agroseguro, they then made a claim, possibly based on perceived vole presence and/or related damage, and subsequently, based on the amount of damage, an assessment was made. However, given we did not have access to the total number of customers in the region (and therefore data on those who never claimed), we were unable to take the full data generating process into account. As such, this dataset and results must be interpreted as being conditional on a farmer having made a claim.

We complemented the insurance data using a regional common vole monitoring program carried out by the Ministry of Agriculture, Livestock and Rural Development of Castilla y León, coordinated by Instituto Tecnológico Agrario de Castilla y León (ITACyL). Vole abundance indices have been collected from across the region from 2011 onwards. The method involves surveying three 99 m transects per field, with each transect split into 33 sections. One of the three transects is conducted in the field margin, and the other two within the target field, forming a Π shape. The vole abundance index (hereafter ITACYL index) for field margin or for the field was then calculated by finding the mean proportion of sections showing signs of vole activity (burrows with fresh droppings, vegetation clippings and/or recent digging). As only the year, and not the season or month, of each claim was known, we opted to include vole transects from March until August inclusive, as it is during this period when claims are most likely to occur. While less accurate than direct estimates of density, the method has proven robust when tested (Caminero-Sadaña et al., 2015; Jareño et al., 2014), is widely employed in the study site, and is well-known to practitioners.

While the exact locations of each ITACyL transect were known, the location of insurance claims was only known to a municipality. As such, we were unable to match a specific vole index to a specific claim at field level. Instead, we opted to calculate a mean vole index per municipality and assign those values to a relevant claim. We expected that doing so likely created measurement error, as claims presumably occurred in fields experiencing higher-than-municipality-average vole densities, which we attempted to account for in the statistical analysis (see details below). The final dataset consisted of 3104 observations (Fig. 2).
Figure 2: Data used for the insurance analysis. A shows the distribution of assessed proportion of damage to yields, not including claims assessed as 0 or 1, coloured according to crop type (where *Other Cereals* included rye, oats, and triticale; *Other Legume* included ervil, chickpeas and peas; and *Root* included sugar beets and potatoes. Note that rape seed is not included in the legend as all rape seed claims were assessed as 0, but is included in B). B shows the same data but includes claims assessed as 0 and 1. C shows the distribution of number of ITACyL index surveys in each municipality. D shows the mean vole index per municipality. E shows boxplots of abundance index over the years of data collection, where points are jittered, and a trend line fit using a thin-plate spline with 4 knots (spline fit was not checked for assumptions, included only as a visual aid). In multiples A to D, the vertical dashed lines represent the mean value for the respective x axis.

**Analysis**

A logNormal Bayesian regression was fitted to the Experimental Field dataset with dry alfalfa weight as the response, conditioned on a vole density-experimental treatment (exclosure and control) interaction. Sigma was regressed against vole density to account for apparent heteroscedasticity.
\[ y_i \sim \text{Normal}(\mu_i, \sigma_i) \]  
\[ \log(\mu_i) = \beta_0 + \beta_1 \text{Density}_{\text{Present}_i} + \beta_2 \text{Density}_{\text{Absent}_i} \]  
\[ \sigma_i = \gamma_0 + \gamma_1 \text{Density}_i \]

Where \( y \) is the measured dried alfalfa weight (g) with \( i \) denoting each row of data, \( \mu \) and \( \sigma \) are the mean and standard deviation of the normal distribution, \( \beta_0 \) is the intercept, \( \beta_1 \text{Density}_{\text{Present}} \) is the slope of vole density per ha for control treatments (i.e. where voles were present), \( \beta_2 \text{Density}_{\text{Absent}} \) is the slope of vole density per ha for exclosure treatments (i.e. where voles were absent), \( \sigma \) is the standard deviation of dried alfalfa weight, \( \gamma_0 \) is the sigma intercept, \( \gamma_1 \text{Density} \) is the slope of vole density per ha.

We used uninformative normal priors for all the parameters in our model with a mean of zero and standard deviation of 10. We set the Stan No-U-Turn sampler (NUTs) to use four chains, each with a warmup period of 10,000 iterations and 15,000 sampling iterations. The sampler was altered to use a smaller step size, with an adapt delta value of 0.9, and maximum tree depth of 15 to avoid divergent transitions and improve sampler efficiency, respectively. We visually checked for the convergence and mixing of the chains.

The Active Field dataset used the same structure as the Experimental Field model (Eq. 1-3).

We used the same prior structure as the Experimental Field analysis, as well as using the same sampler adjustments with the only difference being that we used 20,000 sampling iterations as opposed to 25,000.

We used a Beta distribution for modelling the insurance data, in a Bayesian framework, as insurance technicians assessed crop damage as a continuous proportion (Douma & Weedon, 2019). However, damage assessments also included absolute 0s (i.e., where no damage was detected) and absolute 1s (i.e. fields which had lost all crops). Thus, a zero-one-inflated-beta distribution was used for the regression to allow the inclusion of both 0s and 1s. Doing so allowed for distinct data generating processes to account for 0s, 1s, and all values in between (Martin et al., 2005). To account for the presumed measurement error in vole index, described above, we estimated the true vole index by assuming observed indices were drawn from a normal distribution where the mean was
the true mean vole index for a municipality and the standard deviation was the standard deviation from all observed vole indices (Eq. 6).

Our model included two terms varying the intercept (Eq. 7 and 8). The first was for each municipality in each year, noted as ID (166 levels). We opted to differentiate each municipality by year, given the agricultural landscape can be highly dynamic from one year to the next, due to, e.g. crop rotations etc. The second term was the crop type the damage claim was made in (10 levels) as we were interested in the general damage-density relationship, not specific to any one crop. Both varying terms also allowed the imbalanced sample sizes, by ID and crop type (Fig. 3), to be accounted for. We opted to use an informative prior for the intercept as the regressions for Experimental and Active Fields suggested no damage was detectable at low densities (see Results) as well as if there are no voles present, this strictly necessitates that no damage can be caused by voles, hence a normal distribution with a mean of -4 and standard deviation of two was used for α (Eq. 9).

\[
y_i \sim \text{ZeroOneInflatedBeta}(\mu_i, \phi, p, q) \tag{Eq. 4}
\]

\[
\logit(\mu_i) = \alpha + \alpha_{ID[i]} + \alpha_{CROP[i]} + \beta_1 \text{Vole}_{Est,i} \tag{Eq. 5}
\]

\[
\text{Vole}_{obs,i} \sim \text{Normal}(\text{Vole}_{Est,i}, \sigma) \tag{Eq. 6}
\]

\[
\alpha_{ID} \sim \text{Normal}(0, \sigma_{ID}) \tag{Eq. 7}
\]

\[
\alpha_{CROP} \sim \text{Normal}(0, \sigma_{CROP}) \tag{Eq. 8}
\]

\[
\alpha \sim \text{Normal}(-4,2) \tag{Eq. 9}
\]

\[
\beta_1 \sim \text{Normal}(0,5) \tag{Eq. 10}
\]

\[
\sigma_{ID} \sim t(3,0,2.5) \tag{Eq. 11}
\]

\[
\sigma_{CROP} \sim t(3,0,2.5) \tag{Eq. 12}
\]

\[
\phi \sim \text{Gamma}(0.01,0.01) \tag{Eq. 13}
\]

\[
p \sim \text{Beta}(1,1) \tag{Eq. 14}
\]

\[
q \sim \text{Beta}(1,1) \tag{Eq. 15}
\]

Where \(y\) is the proportion of damage to a field, with \(i\) denoting each row of data, \(\mu\) and \(\phi\) are the mean and precision of the Beta distribution, \(\alpha\) is the intercept, varied by
municipality-year ID ($a_{ID}$) according to the respective amount of variation ($\sigma_{ID}$), as well as varied by crop ($a_{CROP}$) according to the respective amount of variation ($\sigma_{CROP}$). $\beta_1$ is the slope for estimated true vole index ($Vol_{Est}$), which was inferred from mean observed vole indices ($Vol_{Obs}$), and $\sigma$ is the standard deviation of all $Vol_{Obs}$. Eq. 13, 14 and 15 were the priors used for the family specific parameters, where $\phi$ is the precision of the beta distribution, $\rho$ is the probability of having either a 0 or 1, and $q$ is the conditional probability of having a 1.

We set the Stan No-U-Turn sampler (NUTs) to use four chains, each with a warmup period of 5,000 iterations and 10,000 sampling iterations across four chains. The sampler was altered to use a smaller step size, with an adapt delta value of 0.99, and maximum tree depth of 15 to avoid divergent transitions and improve sampler efficiency, respectively.

We fit each regression using Stan (Stan Development Team), as implemented in R (R Core Team 2020) via brms (Bürkner 2017). Additional R packages used were tidybayes (Kay 2020), bayesplot (Gabry 2020), and ggplot2 (Wickham 2016). Code for the analysis is included in the Supplementary Material.

All model fits and sampler performances were checked using both Stan diagnostics and posterior predictive checks (via bayesplot) and were deemed to show good mixing of chains, ability to simulate the response variable based on model fit, and Stan specific checks (see Supplementary Material).

**Results**

Our results for both the Experimental Field (Fig. 1 and Table 1) and the Active Fields (Fig. 2 and Table 2) suggested no detectable damage occurred when voles were present at low densities, between 0 and 53.9 voles per ha and between 2.5 and 269.4 voles in the Experimental and Active Fields respectively.
Figure 3: The relationship between yield and vole density in the Experimental Field. The posterior mean (lines) and 95% Credible Intervals (grey ribbons) for two treatments as estimated by our Bayesian model.

Table 1: Parameter estimates from the Experimental Field analysis on log link scale.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>4.84</td>
<td>4.51</td>
<td>5.10</td>
</tr>
<tr>
<td>$\beta_1 Density_{Present}$</td>
<td>-0.17</td>
<td>-1.40</td>
<td>-0.01</td>
</tr>
<tr>
<td>$\beta_2 Density_{Absent}$</td>
<td>-0.23</td>
<td>-1.54</td>
<td>-0.02</td>
</tr>
<tr>
<td>$\gamma_0$</td>
<td>4.86</td>
<td>4.69</td>
<td>5.05</td>
</tr>
<tr>
<td>$\gamma_1 Density$</td>
<td>-0.02</td>
<td>-0.02</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

Our results from the Active Fields indicated that while there was no apparent difference in yields between plots with and without voles, the fit suggested that there were slightly higher yields when we excluded voles (Fig. 4). The slight difference may represent the start of the inflection point where vole densities become high enough to impact yield for those fields in a given municipality at a given time, though note that the credible intervals still comfortably overlap each other. We may discount the influence of noise
related to phenology, given the short period in which samples were collected relative to alfalfa growth.

Figure 4: The relationship between yield and vole density in the Active Fields. The posterior mean (lines) and 95% Credible Intervals (grey ribbons) for two treatments as estimated by our Bayesian model.

Table 2: Parameter estimates from the Active Fields analysis on log link scale.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>4.63</td>
<td>4.37</td>
<td>4.86</td>
</tr>
<tr>
<td>$\beta_1 \text{Density}_{\text{Present}}$</td>
<td>-0.01</td>
<td>-0.04</td>
<td>0.00</td>
</tr>
<tr>
<td>$\beta_2 \text{Density}_{\text{Absent}}$</td>
<td>-0.01</td>
<td>-0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>$\gamma_0$</td>
<td>4.33</td>
<td>4.10</td>
<td>4.58</td>
</tr>
<tr>
<td>$\gamma_1 \text{Density}$</td>
<td>0.00</td>
<td>-0.01</td>
<td>0.00</td>
</tr>
</tbody>
</table>

We found a substantial variation in alfalfa yield regardless of vole densities in both the Experimental and Active Fields analyses. Hence, even though voles will undoubtedly eat and damage crops regardless of densities, their effect on yield is so minimal as to be negligible, compared to the background crop yield variation.
Our zero-one-inflated-beta model results showed a likely increasing amount of damage with increasing estimated true vole indices (Fig. 3). Even at apparently low abundances, mean damage exceeded profit thresholds of farmers (profit thresholds are between 15 to 20% in the region [REF]), indicating that when damage occurs, it quickly reaches these thresholds. We also found that 43% of claims were assessed as having no damage, while 3% of claims were deemed to have experienced total yield loss (visible in Fig. 2D and summarised in Table 3), calculated as 0.46 (probability of getting either a 0 or 1) multiplied by 0.07 (conditional on 0.46, 0.07 of those were awarded 1).

![Graph showing the relationship between true vole index and proportion of crop yield damaged.](image)

**Figure 5**: The relationship between the proportion of a crop yield damaged and estimated “true” vole abundance index (as approximated by Eq. 9). The posterior mean (solid line) and 95% CI (grey ribbon) were estimated from our zero-one-inflated beta model of the insurance claims. The horizontal dark grey shaded area represents threshold of damage that can be sustained by farmers in the region before no longer making a profit (CSS pers. obs.).

**Table 3**: Parameter estimates from the insurance claim analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>-1.07</td>
<td>-2.69</td>
<td>0.53</td>
</tr>
<tr>
<td>$\beta_1 Vole_{Est}$</td>
<td>3.31</td>
<td>-5.02</td>
<td>11.74</td>
</tr>
</tbody>
</table>
While the posterior of the insurance claim regression suggested an increasing relationship ($\beta_1 \text{Vol}_{\text{Est}}$), most likely linear (Fig. 5), the results were far from conclusive with a slope of 0 being comfortably within the credible intervals.

**Discussion**

Our experimental results revealed that, at low densities (< ca. 270), common voles do not cause noticeable reductions in yield above the inherent stochasticity in crop yields. This finding strongly implies a curved relationship between vole density and crop damage, as a linear relationship can be ruled out. That is, if the relationship were linear, it would mean no damage could occur regardless of density. Further, the relationship between damage assessed by insurance investigators with vole abundance indices (at municipality level) indicated a likely increasing linear trend (posterior mean $\neq 0$, Fig. 5), though this effect was uncertain as the 95% CI overlapped zero. The upper 95% credible interval suggested that when at high-density (i.e. indices $> 0.6$, equivalent to $> 350$ voles per ha), voles may damage ca. 60% of the crop in individual fields. However, across all abundance indices, the mean posterior suggested there was sufficient damage to prevent profits being made by individual farmers, highlighting that the results must be interpreted as being conditional on a claim being made. That is, we find that when damage is detected by assessors, it exceeds the profit threshold of farmers. In a small fraction of claims (3%) voles were deemed to have caused complete crop loss in a field, though in 43% of all claims, assessors deemed that no vole damage could be identified.

If we were to use only the insurance analysis, we may infer that the relationship as a whole was most likely linear. However, given the results from both experimental datasets, which showed no damage occurs at low densities, this necessitates a curved relationship (Fig. 6).

We suspect this discrepancy, where the experimental results suggest a curved relationship while insurance suggests a linear one, is due to the aforementioned caveat.
of the insurance data, whereby it is conditional on a claim being made. This caveat likely
impacts a sampling bias in the insurance dataset. This may mean, that in municipalities
with low mean vole indices, most insured farmers do not claim, though a minority who
experienced substantial damage presumably due to high vole abundances at the field
scale, did claim. This bias would then, in some cases, translate into observations of low
mean municipality vole abundance, but would only include information from a handful
of farmers experiencing higher-than-average densities.

Additionally, assessments of damage may have been more or less reliable depending
on unknown circumstances. We find suggestions that assessors bin their estimates of
damage (possibly into 25, 33, 50 and 90%) (Fig. 2A). While such binning of percentages
is common and understandable, it suggests some degree of inaccuracy in the damage
assessments. A lack of reliability of stakeholder damage estimates has previously been
observed by Huitu et al., (2009) and we find similar suggestions.

Similarly, despite attempts to estimate the true vole index, it appears as though the
analysis under-estimated vole abundances, as may be expected from the sampling bias
mentioned above. Such inaccuracies of indices have been found to occur for alternative
methods for inferring abundances (Byrna et al., 2001), though calibrations of the method
used by ITACyL have proven relatively robust (Jareño et al., 2014). As such, we do not
believe this is a result of inaccuracies with the index per se, but rather in trying to infer
abundances experienced by individual farmers using municipality averaged
abundances, mirroring previous findings (Huitu et al., 2009; Pfeffer et al., 2021). As
suggested above, it may be likely, that at the municipality-scale (i.e. large-scale), the
indices were approximately correct, though were inaccurate at the local-scale where the
damage occurred. Given evidence of spatially and temporally asynchronous population
dynamics in the region are emerging (Santamaria et al., 2020; chapter IV) such highly
variable abundances at relatively local-scales may be expected (Jacob & Tkadlec, 2010).
If true, these approximately correct large-scale values would be inaccurate at the small-
scale, resulting in underestimates of the abundances experienced by farmers suffering
from damage. We believe this is exemplified by the result that economically significant
damage was predicted at abundance indices of zero, despite using an informative prior
for the intercept.

Part of the lack of damage at low densities may be due to some crops being able to
rejuvenate (Jacob & Tkadlec, 2010). Previous research has either suggested such
possibilities (Huitu et al., 2009) or found evidence of this (Babińska-Werka, 1979). Huitu et al., (2009) suggested that the lack of a definitive relationship in their study of vole damage to silviculture was due to instances where damage was initially detected by stakeholders, but by the time assessments were carried out, the plants had compensated. Such a trend is likely within our system as well, and may partly explain both why 43% of claimants were rejected and why, in the experimental analyses, no damage was detected at low vole densities despite voles being present.

![Figure 6](image)

**Figure 6:** Inferred overall relationship between damage to yield across varying densities of voles based on all three analyses. Boxes contain regression fits for Experimental and Active Fields (left) and insurance claims (right). We assume, from the conditional nature of the insurance analysis, that the municipality-level vole indices underestimated field-level indices in damaged fields.

We also find evidence which suggests that stakeholders, either farmers or assessors, may misattribute the cause and/or the severity of the damage. For a farmer to make a claim, it can be presumed that they believed that they had suffered sufficient damage to warrant making a claim, or that the damage observed in the field at a given time in the farming cycle would lead to an equivalent yield loss later on. Given that upon assessment, 43% of claims were rejected, suggests completely different assessments
by the two stakeholders. It is important to note that in these cases, the insurance covering wildlife damage also covers other types of loss (e.g., drought, hail, and flooding), and that in some cases the possible losses due to vole damage may be masked by other types of damage, or that the assessor judged these as more important (though this data was not provided). Such misattributions of damage are common within human-wildlife conflict systems, where stakeholders may perceive a problematic species as being a substantial cause of damage, where empirical research finds little evidence to support this (Margalida & Donázar, 2020; Chase Grey, Bell & Hill, 2017; Fernández-Gil et al., 2016; Echegaray & Vilá 2009; Suryawanshi et al., 2013; Nybakk, Kjelvik & Kvam 1999; Dickman, 2010 and references therein). From our results, the apparent disagreement when determining both the presence and extent of damage suggests either overestimated or misattributed claims or involving subsequent recoveries of the damaged plants. Farmers can make claims due to the simple presence of voles, without the existing populations being sufficient to ultimately cause significant damage, or may overestimate the level; or misattribute the cause of damage, making a claim when they see damage, which may either not ultimately lead to yield loss or be due to other causes not related to voles. Mistimed claims may be instances where there are delays from when a claim was made, to when it was assessed. In such cases, what was originally deemed to be substantial damage may not have materialised, as the crops compensated for the damage (as suggested by Babińska-Werka, 1979).

Additionally, vole outbreaks are often reported in local media (Luque-Larena et al., 2013), though evidence suggests that outbreaks in the region are spatially and temporally asynchronous (Santamaría et al., 2019; chapter IV), meaning that despite local news coverage of a regional outbreak, it is likely that at least some farmers will not be affected. Such instances of regional news coverage may serve to incorrectly reinforce the belief of an individual farmer that they will experience a vole pest problem and face crop damage. Such instances where local newspapers report predominantly on negative aspects of human-wildlife conflicts has been documented in the wolf recovery in France (Chandelier et al., 2018), which, if this also occurs in our study system, may partly explain why 43% of claims are rejected. Conversely, intense local news coverage may lead to farmers becoming more vigilant leading to previously unobserved damage being detected and reported. Given that there is already tension between stakeholders in the study site regarding pests and their control (Lauret et al., 2018), such
misattribution or overestimation of damage may only serve to exacerbate these tensions.

Economic threshold are often used when managing agricultural pests, as these indicate the extent of damage that can be sustained before no longer making a profit. Our results can be used, with caution, to suggest tentative economic threshold densities of approximately 270 voles per ha. Alternatively, a mean municipality index value of approximately 0.25 may be useable, as this is roughly where the lower credible interval reaches the economic profit threshold of farmers in the region (Fig. 6). Caution must be taken when using these values as we are unable to definitively determine exact values, so instead these values may be better suited for initial “rules of thumb” to be updated as new evidence becomes available, keeping in mind the various caveats outlined above. These results also suggest that, when practitioners or stakeholders implement vole population controls, they should be targeting densities lower than approximately 300 voles per ha. In such cases, the aim would not be to achieve a complete eradication, but rather a functional eradication by decreasing and maintaining densities below a tolerable threshold (Green & Grosholz, 2020).

It is important to add a caveat, relevant for cyclic or irruptive pests, that such control thresholds should only be used if there is a belief that densities will continue to rise and culminate in an outbreak. For instance, throughout the experimental data collection densities never reached those of an outbreak, meaning that although the “threshold” had been reached in some fields, implementing control would likely have had no benefit. This, potentially frequent, scenario strongly necessitates a viable and robust method of predicting outbreaks (Leirs et al., 1996; Jacob 2010). However, given the difficulties in predicting population peaks (Lambin et al., 2006; Jacob & Tkadlec, 2010) stakeholders may have to make decisions under the haze of uncertainty and pressure, possibly necessitating qualitative predictions given the lack of alternatives, though when such qualitative predictions prove incorrect, they may exacerbate wildlife-conflict tensions.

Additional complications for immediate use of these results for management, are the lack of empirically tested and proven efficient control options available (but see Singleton et al.). Various control methods have been proposed (Jacob & Tkadlec, 2010; Luque-Larena et al., 2013; Paz et al., 2013; Prieur & Swihart 2020), though most or all face limitations or objections (e.g. Jacob & Tkadlec, 2010; Olea et al., 2009; Luque-
Additionally, some control options currently used (field margin scraping, field margin burning, or deep ploughing) are time or context sensitive. For instance, deep ploughing has been shown to be effective at reducing vole abundances, through the destruction of their burrows and nests (Roos et al., 2019; Heroldova et al., 2018; Prieur & Swihart 2020), though the ability to plough is dependent on the amount of rainfall in our system. If there is a lack of rain, soils can become too hard to plough, meaning at certain times of the year, ploughing is not a usable control option. Alternatively, farmers may plant crops with possible repellent properties (Roos et al., 2019) or alter farm characteristics (Prieur & Swihart 2020), to reduce vole abundance, though such activities come at a cost and are not a viable short term solution to an impending outbreak. This results in a limited, time- or context-sensitive, and unproven set of tools for dealing with vole outbreaks.

**Conclusion**

We have provided evidence consistent with a non-linear, curved relationship between vole abundance and crop damage. In agreement with similar previous research, rodent pests did not cause damage at densities up to ca. 270 individuals per ha (or roughly a quarter or a third of outbreak densities), and the data indicate an inflection point past this density. This result provides a tentative guideline for the densities control actions should be able to achieve. We also find evidence of overestimating or misattribution of damage, by either assessors or claimants, suggesting that the human-wildlife-conflict may be exacerbated by difficulties in correctly identifying the cause and amount of damage associated with a pest. Additional implications suggest that the use of vole indices aggregated to a municipality scale, coupled with insurance claims may be insufficient for estimating damage at the field scale (similar to Pfeffer et al., 2021) but never-the-less provide useful insights into the system.

**Acknowledgements**

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ECOVOLE (CGL2012-35348) and ECOTULA (CGL2015-66962-C2-1-R) funded the Experimental Field and its maintenance as well as regional vole samplings shown in Fig. 1.

CRediT Author Statement

**Deon Roos**: Conceptualisation, Software, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualisation; **Beatriz Arroyo**: Conceptualisation, Data Curation, Methodology, Writing – Review & Editing, Supervision; **Juan José Luque Larena**: Conceptualisation, Methodology, Resources, Writing – Review & Editing; **François Mougeot**: Conceptualisation, Methodology, Writing – Review & Editing; **Constantino Caminero Saldaña**: Resources, Data Curation, Writing – Review & Editing; **Pablo García Díaz**: Formal analysis, Methodology, Writing – Review & Editing; **Juan Romairone**: Investigation, Data Curation, Writing – Review & Editing; **María Carmen García Ariza**: Data Curation, Writing – Review & Editing; **Xavier Lambin**: Conceptualisation, Supervision, Methodology, Project administration, Funding acquisition, Writing – Review & Editing

References


Chapter III

Unintentional effects of environmentally-friendly farming practices: Arising conflicts between zero-tillage and a crop pest, the common vole (Microtus arvalis)

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Unintentional effects of environmentally-friendly farming practices: Arising conflicts between zero-tillage and a crop pest, the common vole (Microtus arvalis)

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\textbf{ABSTRACT}

Common voles are a main European facultative, fossorial, farmland rodent pest that can greatly reduce crop yields during population outbreaks. Crop protection against common voles is a complex task that requires the consideration of a set of preventive and control measures within an integrated pest management strategy. A possible option could be to modify farming practices to reduce the availability of refuges for rodents and the damage to crops that they subsequently cause. Farming, however, must simultaneously meet multiple goals including the reduction of the carbon (C) emissions, soil erosion and water use, and the improvement of soil quality. Crop establishment through conservation agriculture strategies, like zero-tillage, would reduce crop management investment, but is also promoted in many regions to reduce C emissions and increase soil organic matter. It could, however, create favourable refuge habitats for fossorial rodent crop pests, like common voles, benefitting from reduced soil disturbance between crop rotations and thus increasing burrow persistence. Assessing the impact that tillage practices, their interaction with different crops and the influence of proximity to potential common vole source, have on common vole occupancy could provide a valuable tool within an in-tegated management strategy. Using a 2-ha experimental field with 62 plots 180 m\textsuperscript{2} (each roughly matching common vole home range size) located experimental plots in north-western Spain, we tested how tillage prac-tices, crop type (wheat, barley, veitch, Nabonne veitch, pea and fallow) and distances from possible colonization sources affect field use by common vole during low population density conditions. Our results show that tillage practices have more influence on common vole occurrence (zero tillage > reduced and conventional tillage) than other aspects such as crop type thus supporting the hypothesis that tillage practices play a key role in common vole habitat use.

1. Introduction

The increasing global human population necessitates a commensu-rate increase in crop yields, all the while doing so in increasingly dif-ficult scenarios presented by climate change (Lobell et al., 2008). However, the role of agriculture in the developed world is more nuanced than simply increasing crop yield (Godfray et al., 2010). Concerns regarding impacts on biodiversity (Tilman et al., 2011), carbon (C) and nitrogen (N) emissions (Smith et al., 2005; Tilman and Clark, 2014), or water retention (Bescansa et al., 2006; Freibauer et al., 2004) must be balanced with the need for increased yields, with no generic win-win scenarios being apparent. In order to achieve these aims, various trade-offs must be managed concerning the competing interests.

One approach to achieve these multiple aims is through the use of agricultural conservation practices which are considered to be en-vironmentally sensitive and economically viable (Soane et al., 2012). An increasingly widely used conservation practice is zero-tillage (whereby seeds are directly drilled into the soil with minimal soil dis-turbance, accompanied with remaining crop stubble, usually treated

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with herbicide prior to seeding), which is promoted in many regions in order to reduce C emissions (Lal, 2004; but see Powson et al., 2014), stabilise higher crop yields (Govaerts et al., 2005) and reduce crop management costs (Lal, 2004). However, such approaches have been suggested to correlate with higher abundance of rodent pests (Heroldová et al., 2017; Witmer et al., 2007) possibly explaining why no-tillage often results in lower yields (Pittelko\w et al., 2015b, 2015a).

Rodents are a global cause of varying degrees of crop yield losses, inflicting varying degrees of damage, including complete crop losses locally during high-density pest years (Singleton et al., 1999; Stenseth et al., 2003; Jacob et al., 2014). Difficulties concerning the control of rodent crop pests are inflated since many rodent control methods are largely untested (such as ploughing the field margins to reduce crop colonisation risk), are only locally applied (such as bounty systems, i.e. payments for capturing rodents, Singleton et al., 2003), or make use of conventional approaches which are potentially environmentally risky (such as the use of rodenticides, Buckle and Smith, 2015). In addition, control strategies are often implemented reactively, where the decision to undertake control is based on current densities of pests (Follette et al., 2016; Heroldová et al., 2017), which may reduce the potential effect-tiveness of management strategies. As such, preventative management is more likely to be sustainable in the long term and may involve the modification of farming practices.

Some farming practices have previously been identified as being able to reduce in-situ pest populations (Jacob, 2003), and may provide a basis to inform strategies which may reduce undesirable effects related to rodent crop pests. For instance, in common voles (Microtus arvalis), a fossorial species that is the main vertebrate pest of arable crops in Europe (Jacob et al., 2014), ploughing fields post-harvest was found to reduce the populations dramatically (Jacob, 2003). Two potential causes of for this may be inferred. The first being directly related with mortality and vole disturbance caused by machinery, and the second being that, through destruction of the burrows and removal of remnant vegetation, ploughed fields are no longer attractive habitats or are more difficult to persist in (see Inchausti et al., 2009). Exemplifying the po-tential of a low disturbance effect, field margins and alfalfa fields are known to be refuges for common voles (Rodríguez-Pastor et al., 2016), both of which are usually left unploughed and undisturbed for pro-tracted periods of time providing cover and habitat stability.

If the second assumption is true, then tillage practice impacts on soil may be important for common vole persistence and/or habitat pre-ference (Bonnet et al., 2013). Practices such as zero-tillage (ZT) may thus presumably increase the likelihood of common vole occupation. The relative soil stability and added residual vegetation cover of ZT compared with other forms of plot management, like reduced tillage (RT) or conventional tillage (CT), involving the movement of soil at varying depths, may further enhance the impact of tillage practices on vole occupancy risk.

Recently, research carried out in the Czech Republic has identified such a trend, where common vole densities were found to be higher in ZT fields, compared with tilled fields (Heroldová et al., 2017). Simi-larly, common voles in France were found to have disturbed life cycles in fields which experienced disruptive farming activities (such as ploughing) (Inchausti et al., 2009). Testing whether the results ob-served in temperate regions of central Europe are consistent in other more arid regions with dry, compacted soil is important to inform control strategies of the pest species which occupy large geographical areas. With a species such as the common vole, present from Spain to Mongolia (Yigit et al., 2016) across a correspondingly wide variety of soil types, achieving a broader understanding of common vole occu-pancy is of particular importance.

The influence of crop type on vole occupancy is similarly important, as well as how these may interact with tillage practices. While studies have investigated the importance of crop type for common vole abun-dances to various extents, these have either used single crop type characteristics (e.g. Fischer et al., 2017 investigated wheat height) or a small number of crops (e.g. Heroldová et al., 2017 used an interaction between wheat and rapeseed with ZT and tillage, while Rodríguez-Pastor et al. (2016) used alfalfa, fallow and a functional grouping of cereal). Gathering an understanding of how crop types interact with three commonly used tillage practices (ZT, RT and CT) would be of particular interest in an applied setting. A further consideration, equally important within an applied con-text, would be the distance between plots and linear habitat features (such as field margins), which usually harbour higher densities of voles, or from other already occupied plots, which could act as sources of colonising voles. Although the issue of distance from source habitat to field are a concern for farmers and managers of official control cam-paigns, it is not often considered within the applied rodent crop pest literature (but see Rodríguez-Pastor et al., 2016). Understanding the relationship that distance from source populations may have on mi-croscale crop colonisation events is, again, of particular importance as this would inform strategies targeting those features. Currently, control strategies focus on trying to control common voles within linear re-servoirs (e.g. field margins, Caminero Saldaña et al., 2015a), or through the use of ploughed strips around field perimeters (acting as a "fire-break" (inferred from Jacob, 2003)), though the effectiveness of both approaches are still insufficiently understood.

We hypothesised that ZT plots would have the highest likelihood of occupation in relation to other tillage practices, and when in-corporating crop types, we expected higher occupancy rates in ni-trogen-rich crops (Lantová and Lanta, 2009) and fallow, in line with the results of Rodríguez-Pastor et al. (2016). With regards to the likelihood of temporal variation in occupation, we expected occupancy to de-crease with distance from source populations, including the field margin harbouring voles as well as nearby occupied experimental plots and/or an influence of differences between crop height. Crucially, we combine these aspects, previously studied in varying degrees of isola-tion, into an integrated experiment to inform common vole manage-ment.

2. Materials and methods

2.1. Study species

The common vole is a small rodent, weighing approximately 25–30 g (Jacob et al., 2014). As with most microtines, common voles create burrows for nesting, foraging, and predator evasion, with bur-rows growing in complexity the longer they are occupied (Brügger et al., 2010). Within agroecosystems, common voles have a preference for field margins, alfalfa and fallow fields, moving into cereal crops once populations reach peak densities (Rodríguez-Pastor et al., 2016).

The semi-arid plateau in the central region of Castilla y León (CyL), located in NW Spain is dominated by farmlands. CyL has 3.6 million hectares of arable land, 84% of which is considered to be under rainfed conditions. Predominantly the crops farmed in the region are wheat and barley which are collectively farmed on 2 million hectares. The area was recently colonised by common voles. The colonisation began in the early 1980s with CyL becoming fully colonised by the mid-1990’s (Lauque-Larena et al., 2013). The range expansion was associated with an increase in irrigated herbaceous crops, in particular alfalfa (Jareño et al., 2015). By 2014 eight outbreak events had occurred at the regional scale (Lauque-Larena et al., 2015, 2013; Rodríguez-Pastor et al., 2017) with claims of substantial damage to crops, mainly in winter cereals, grain legumes and alfalfa.

2.2. Study site, experimental design and vole presence estimation

According to wide scale vole abundance monitoring across CyL, vole populations were observed growing rapidly in 2016, culminating in very high densities in field margins in early 2017. However, this high density within field margins never developed into a full outbreak as the...
voles failed to disperse into fields, likely due to a large scale drought that affected the Iberian Peninsula at that time (see Table 1) (Roos, unpublished). Additionally, in the area where the study took place, voles, including those in field margins, never showed a marked increase and the population was considered to be at relatively low abundance (Roos, unpublished).

The research was carried out in 2017, in the last week of April, May and June in a 2-ha experimental field in Zamadueñas, Valladolid (41° 39' 8" N, 4° 43' 24" W, elevation 690 m.a.s.l.). The experimental field was part of an ongoing investigation testing different soil management practices and crop rotations in a context of sustainable agriculture. The experimental field was separated from an adjoining field margin by a strip of land measuring between 3 m to 35 m (see Fig. 1). This strip was ploughed in the previous winter with a harrow disc at a depth of 10 cm to keep these areas of land devoid of vegetation. The field margin was the only nearby habitat, other than the experimental field, with plant cover and vole presence during our research in a radius of ~90 m from the experimental site.

The experimental field consisted of 18 plots arranged in a systematic layout using three tillage practices (each block has been continuously managed by the same tillage practice since 2004): ZT (n = 4 blocks, 28 plots; one block was divided in two due to the shape of the field), RT (n = 4 blocks, 28 plots) and CT (n = 1 block, 6 plots; in a 2 × 3 plot arrangement). Within the experimental field, RT block plots were ploughed before seeding with a chisel at a depth of 10 cm, whereas ploughing in the CT block plots, was carried out to a depth of 30 cm using a moldboard plough. No ploughing was applied in ZT plots. Before sowing, ZT and RT blocks were treated with glyphosate 36% at 2 kg/ha. No other pesticides were applied.

Common vole burrows have been described to be 12.6 cm below ground on average, with a maximum depth of 25 cm (Brügger et al., 2010). Thus, RT and CT may penetrate deep enough to disrupt vole burrows, though CT is more likely to destroy entire burrow complexes.

Within each block, seven experimental plots (six in CT block) were randomly allocated one of six crop types: wheat (Triticum aestivum), barley (Hordeum vulgare), vetch (Vicia sativa), Narbonne vetch (Vicia narbonensis), pea (Pisum sativum), and fallow, with wheat replicated twice per block (CT did not have a pea crop treatment). Crops used in the previous year were similarly recorded (see Table 3 in Supplementary Material). Each experimental plot measured 20 m by 9 m. Crop height (cm) was estimated for each plot at each time point (see Table 4 in Supplementary Material).

Within blocks, plots were separated by 1 m, while separation between blocks was 6 m. Both between plots and between blocks, the space was ploughed with a harrow disc at a depth of 10 cm (Fig. 1) after sowing. No vegetation was observed between blocks and plots during data collection.

The size of the plots (180 m²) roughly matches the largest measured average home range size of common voles (30 to 202 m²) (Brüner et al., 2005; Jacob and Hempel, 2003), and as such plots were assumed to be large enough to be (partially) occupied by voles. Common voles are estimated to disperse between 76 m–110 m per generation depending on sex (Gauffre et al., 2009, 2008) though alternative estimates suggest that within hours or a few days, voles can disperse several hundred meters or a few kilometers (Schweizer et al., 2007). As such voles were assumed capable of dispersing to and colonising vacant experimental plots, though this would be most pronounced during periods of high population growth (Andreasen and Ims, 2001).

The experimental plots were surveyed for signs of vole presence three times in the last week of April, May and June 2017. The experimental field was surveyed in consecutive 9 m wide transects, each be-ginning from the field margin in 3 m paced increments, resulting in the entire 2 ha surface being surveyed. In total, 1478 sections were sur-veyed over the three sampling periods. 668 of these were in ZT plots, 671 in RT and 139 in CT. Additionally, the field margin was surveyed at the same time as the field using the same transect design. In every

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**Table 1**


<table>
<thead>
<tr>
<th>Period</th>
<th>Mean daily temperature</th>
<th>Mean daily humidity</th>
<th>Mean daily precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 1&lt;sup&gt;st&lt;/sup&gt; to June 30&lt;sup&gt;th&lt;/sup&gt;, 2010-2016</td>
<td>14.8 °C</td>
<td>64.2 %</td>
<td>1.1 mm</td>
</tr>
<tr>
<td>May 1&lt;sup&gt;st&lt;/sup&gt; to June 30&lt;sup&gt;th&lt;/sup&gt;, 2017</td>
<td>17.2 °C</td>
<td>55.7 %</td>
<td>0.6 mm</td>
</tr>
</tbody>
</table>

---

Fig. 1. Map of experimental plots. The solid black line indicates the field margin. Tillage types are re-presented by grey shading (CT), black shading (RT) and white shading (ZT) background within a given plot. Crop types are represented by "W" (wheat), "B" (barley), "V" (vetch), "N" (Narbonne vetch), "P" (pea) or "F" (fallow). Grey diagonal lines represent the ploughed areas between plots.

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Andreassen and Ims, 2001
3 m x 9 m section of a transect signs of vole presence were noted. Signs included: burrowing complexes (three or more burrows), fresh latrines, fresh vegetation clippings, fresh digging activity, and runs accompanied by areas of damaged vegetation surrounding a burrow complex of three or more entrances. These indicators are routinely used in the study region (Caminero-Saldaña et al., 2015b,c; Jareño et al., 2014) and are similar to those used elsewhere (e.g. Heroldová et al., 2017). For this study, one or two burrows in a section were not considered as a sign of fresh activity as a burrow may persist for long periods of time despite no voles being present.

2.3. Statistical analysis

2.3.1. Spatial variation analysis

For each experimental plot, the proportion of occupied sections in each plot per survey (weighted by the total number of sections) was calculated and used as the response variable in Generalised Linear Mixed Models (GLMMs) analysis. To calculate proportion of usage, for each section within a plot the presence of any fresh signs resulted in that section being considered occupied. Then, the total number of occupied sections per plot was summed for the respective plot and divided by the total number of sections in a plot to give a proportion of usage per plot, weighted according to the number of sections (the latter varied among plots because the pacing out of 3 m was measured by length of stride and was therefore imprecise).

We modelled proportion of vole plot occupancy using binomial distribution GLMMs. The proportion of occupancy (a two vector response variable; number of occupied sections per plot / total number of sections per plot) was considered in relation to: tillage practice and its interaction with crop type; crop type interacting with crop height (crop height was only included as an interaction due to height being crop specific resulting in it being confounded if included as an additive effect, see Table 4 in Supplementary Material); crop type in the previous year (which may have affected persistence in plots) and distance from the field margin. We included experimental plots nested within blocks as a random effect to account for the repeated measures in each plot.
(reflecting the nested experimental design) as well as unexplained variation between blocks and plots. Plot nested within month was also tested as an alternative random effect structure. Model selection was carried out using single term deletion and subsequent AIC values. GLMM analysis was carried out in R v3.4.1 (R Core Team, 2017) using the lme4 package (Bates et al., 2015).

2.3.2. Temporal variation analysis

Simple multi-season occupancy models were used to determine in-tial
occupancy ($\Psi = \text{the probability that a plot was occupied at the first sampling occasion}$), colonisation ($\gamma = \text{the probability that voles will colonise a previously unoccupied plot}$), extinction ($\epsilon = \text{the prob-ability that a plot will no longer have voles where previously they present}$) and detection ($p = \text{the probability that if voles were present in a plot, it was correctly identified as occupied}$) rates per plot and thus the extent of temporal variation during the study period. Each plot was assigned a 1 (occupied) or a 0 (unoccupied) for each survey month, depending on if any sections within a plot had vole activity (e.g. 011 denotes absence in April, and presence in May and June, respectively). The null model, assuming constant initial occupancy $\Psi(\cdot)$, colonisation $\gamma(\cdot)$, extinction $\epsilon(\cdot)$ and detection $p(\cdot)$ rates, was compared to the full model which used the following: $\Psi$ explained by tillage type, crop type and distance from field margin; $\gamma$ explained by month and number of occupied adjacent plots (to account for colonization being dependent on distance from already occupied plots); $\epsilon$ as constant; and $p$ de-terminated by crop type. Values for occupancy rates in later time periods and lambda values for transition periods were derived as part of the analysis. Model selection was carried out using single term deletion and subsequent AIC values (Burnham and Anderson, 2004). Occupancy modelling was carried out using the Presence software, version 12.7 (Hines, 2006).

3. Results

3.1. Spatial variation

3.1.1. Tillage practice

Common vole activities were only detected in ZT plots (51 of the 84 ZT plots), with no sign of voles detected in the CT block nor the four RT blocks (see Fig. 2). Similarly, for pea plots, regardless of tillage practice, no common voles were detected (see Table 2 for summary). The complete absence of voles in plots other than ZT and pea plots (Table 2) precluded a global analysis with all the tillage regimes, re-sulting in GLMM failure to converge due to perfect separation. We therefore further investigated vole presence variation focusing within ZT plots. Accordingly, the GLMM models were fitted excluding data from CT, RT and pea crop plots. GLMM model selection resulted in the model with only crop type giving the lowest AIC value, while the model with both crop type and

3.1.2. Crop type

Spatial variation, as explained by crop type, showed higher pro-proportion of usage for vetch (0.67, 0.43 – 0.84 95% CI, Z = 2.97) and fallow (0.58, 0.35 – 0.79 95% CI, Z = 2.5), with barley (0.19, 0.08 – 0.40 95% CI, Z = -2.06), wheat (0.12, 0.06 – 0.23 95% CI, Z = -0.83), and Narbonne vetch (0.11, 0.04 – 0.29 95% CI, Z = -0.80) having lower proportion of usage (Fig. 3). As stated above, pea plots were never occupied.

3.1.3. Distance from field margin

The proportion of usage in each ZT plot, as explained by distance from the margin, showed no significant trend with increasing distance from margin (-0.0002 ± 0.032; Z = -0.032, P = 0.97).

3.1.4. Random effects

The nested random effect terms, block and plot, explained 0.76 of the variance and block explained 0.03 of the variance, suggesting that while there was variation between plots, the interaction between blocks and plots explained a greater proportion. Alternative random effects, with plots nested in month, were tested but had higher AIC scores and explained less variation, and thus were not included in the final model.

3.1.5. Occupancy variation in field margin

The field margin harboured a common vole population with an average naïve occupancy estimate of 0.63 over the three months (cal-culated as the number of sections occupied / total number of sections surveyed in the field margin) varying by month from 0.72 (0.62 – 0.80 95% CI) in April to 0.54 (0.44 – 0.64 95% CI) in May and 0.61 (0.51 – 0.71 95% CI) in June (Fig. 4). These values were similar to those ob-served in vetch and fallow plots within ZT blocks (see above).

3.2. Temporal variation

Occupancy model selection resulted in the $\Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$ model being selected, though the null model ($\Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$) had a AIC of < 2 and so could not be differentiated. In other words, the results suggested that initial occupancy was constant and not explained by tillage type, crop type or distance from field margin, whereas colo-nisation was only explained by month but not by the number of ad- jacent occupied plots. Occupancy models were not able to converge when including tillage type, crop type, and number of adjacent occup-ied plots as variables due to the aforementioned separation. Failure to converge through the inclusion of number of adjacent occupied plots in the occupancy models was likely due to this equating to the number of adjacent ZT plots leading to separation (i.e. an occupied adjacent plot is conditional on it being both occupied, but also the plot being ZT as ZT

Table 3

<table>
<thead>
<tr>
<th>Parameter Estimate</th>
<th>Std. Error</th>
<th>Z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>-1.412</td>
<td>0.671</td>
<td>-2.10</td>
</tr>
<tr>
<td>Fallow</td>
<td>1.791</td>
<td>0.715</td>
<td>2.50</td>
</tr>
<tr>
<td>Narbonne Vetch</td>
<td>-0.606</td>
<td>0.761</td>
<td>-0.80</td>
</tr>
<tr>
<td>Vetch</td>
<td>2.127</td>
<td>0.715</td>
<td>2.97</td>
</tr>
<tr>
<td>Wheat</td>
<td>-0.533</td>
<td>0.639</td>
<td>-0.83</td>
</tr>
<tr>
<td>Distance from field margin</td>
<td>-0.001</td>
<td>0.007</td>
<td>-0.06</td>
</tr>
</tbody>
</table>

distance from the margin had a AIC of +2.0 and so could be con-sidered as equally good (see Table 3 for GLMM coefficient summary). An interaction with crop height and crop type was not retained (AIC +11.52) and the previous years crop type was excluded due to being confounded with the current crop type (crop type rotation was not randomised). We therefore continued with the model with crop type and distance from margin to investigate the influence of the three hy-pothesised drivers of common vole distribution.

Table 2

<table>
<thead>
<tr>
<th>Factor</th>
<th>Number of plots occupied</th>
<th>Total number of plots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>April</td>
<td>May</td>
</tr>
<tr>
<td>Zero Tillage</td>
<td>17</td>
<td>21</td>
</tr>
<tr>
<td>Reduced Tillage</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Conventional Tillage</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wheat</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Barley</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Vetch</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Narbonne vetch</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Fallow</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Pea *</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Fig. 3. Predicted proportion of plot occupied by common voles according to crop type within ZT experimental plots with 95% CI. The dashed grey line represents the naïve 3-month average proportion occupied in the field margin. N. Vetch shortened from Narbonne vetch.

plots were the only plots occupied). The results of the final model showed an initial occupancy rate of 0.27 (0.15 – 0.38 95% CI) in April, slightly increasing to 0.34 (0.22 – 0.46 95% CI) in May and 0.36 (0.24 – 0.47 95% CI) in June (Ψ for May and June were derived estimates) (Fig. 4 and see Fig. 2 for per plot vole usage for each month). Additionally, colonisation rates during the study were 0.10 (0.01 – 0.20 95% CI) between April and May, dropping to 0.02 (0 – 0.07 95% CI) between May and June (see Fig. 2 for colonisa-tion events). Derived lambda rates (rate of change in site occupancy) gave values of 1.29 (0.94–1.63 95% CI) between April and May, and 1.04 (0.94–1.15 95% CI) between May and June. Extinction rate per site was consistently estimated at 0 (0 – 0.13 95% CI) for both April to May and May to June transition periods. Detection rate was estimated at 0.97 (0.83–1.00 95% CI).

4. Discussion

Within our experimental settings common voles, at low densities,
were only found to occupy ZT plots, and never RT nor CT. This may be the result of voles only being present in plots that had not been ploughed prior to the start of our study. Additionally, voles occurred at a higher prevalence in vetch and fallow.

While occupancy analysis showed that the population expanded, from 0.27 occupancy in April to 0.36 in June, and plot colonisation occurred with rates of 0.10 from April to May and 0.02 from May to June, this was limited and the population may be considered to have been broadly static from May, reflecting a likely aborted outbreak event (lambda decreasing from 1.29 to 1.04) as observed regionally. While colonisation rate varied temporally, we found no evidence that colonisation, nor the proportion of plot usage, was affected by distance from field margin, nor were we able to test the influence of number of ad-jacent occupied plots. Given that we do not have abundance estimates prior to seeding, we were not able to determine the relative importance of colonisation from the field margin or persistence in plots from the previous season to explain occurrence in ZT plots in our first sampling session. However, during the period when sampling occurred, it seems more likely that colonisation occurred from already occupied plots ra-ther than from the field margin (see Figs. 4 and 2).

Caution must be taken with these results owing to the small number of colonisation events which occurred during the study; however, our results match those of Heroldová et al. (2017) (see also Wittmer et al., 2007) and may provide circumstantial evidence that the rodent pest species have a preference for ZT fields. Possibly the most likely cause of occupancy in ZT alone, and not RT or CT plots, is the combined per-sistence from previous year populations and colonisation into un-occupied ZT. In fact, with a species which is controlled, a farming practice which may increase both persistence and preference should warrant further research, as the potential for ZT fields to enable per-sistence and encourage colonisation has worrying implications for management.

Owing to the small-scale nature of the experiment, caution must be taken if, or when, results from this study are extrapolated to landscape scales. For instance, although we have no data on abundance or da-mage, common voles were believed to colonise the experimental field in 2007, and practitioners at that time and subsequently in 2014 (during a period of high regional vole abundance) noted that pea crops in the experimental field were disproportionately damaged (Caminero Saldaha, unpublished), though this may reflect pea crops being more susceptible to damage as the meristem is located at the top of the plant (Yaxley et al., 2001). Regardless, similar results regarding tillage have been observed by Heroldová et al. (2017) and crop type by Rodríguez-Pastor et al. (2016), suggesting that the patterns seen in this study are consistent with observations at larger landscape scales. An additional strength of this experiment, however, has been to investigate a wider variety of both tillage practices (all three of the commonly used methods; ZT, RT and CT, where Heroldová et al. (2017) only used ZT and tillage) and crops (Heroldová et al. 2017) considered winter wheat and winter rape, while Rodríguez-Pastor et al. (2016) considered fallow, alfalfa and a functional grouping of wheat and barley). This has allowed us to gather greater insight into the relative importance of a wider array of factors determining the occurrence of common voles. For instance, the higher occurrence of voles in vetch and low occurrence in Narbonne vetch and pea is surprising as this rejects the hypothesis that the voles would occur at higher rates in legume crop types (Lantová and Lanta, 2009), indicating that functional groupings may not be appro-priate for common voles with certain crop types.

While we expected that protein-rich legumes would have had the highest occupancy, our results show the opposite, with Narbonne vetch plots having lower occupancy despite having higher crude protein content; Narbonne vetch has on average 234 ± 7 g kg⁻¹ forage dry matter crude protein (Hadjipanayiotou, 2000) compared to vetch which has 209 g kg⁻¹ (Mikić et al., 2014). A potentially exciting explanation could be that Narbonne vetch is able to repel common voles similar to how another legume is able to repel herbivory (Baldwin et al., 2018).

Indeed, previous research has identified a chemical component (γ-Glutamyl-S-ethenlycysteine, GEC) apparently specific to Narbonne vetch, that appears to act as a repellent to monogastric herbivores (Enneking et al., 1998). If the results here relate to this repellent po-tential of Narbonne vetch, then this may offer tentative evidence that an alternative crop could be used by farmers in the region during periods when an outbreak appears likely. However, caution must be made in utilising this method, as even though Narbonne vetch may be unattractive, during high densities the need to feed may compensate and overwhelm the repellent.

In any case, it is also important to mention that our study design did not allow separating the effect of either previous crop or crop height, as these were confounded with crop type. In both fallow and vetch, the crop types where higher occupancy was detected, had barley as pre-cedent crop (see Table 3 in Supplementary Material). Additionally, all the new colonisation events during our study occurred into cereal plots, where vegetation was higher than in other crop types (see Table 4 in Supplementary Material). Rodríguez-Pastor et al. (2016) found evi-dence that voles were less likely to be present when cereal height was low. Further studies should specifically assess whether previous crop type or vegetation cover are an important additive factors explaining occurrence or colonization.

The immediate implication of our results is that tillage practices must be taken into account when carrying out monitoring and in future work attempting to manage fissional rodents. Crop type has previously been viewed as the dominant farm specific variable when predicting common vole occupancy (see Follette et al., 2016), with tillage type broadly not being considered (but see Heroldová et al., 2017; Wittmer et al., 2007), though recent studies have begun including additional farming practice variables when studying the pest (Fischer et al., 2017; Jug et al., 2008; Rodríguez-Pastor et al., 2016). More broadly, our re-sults show the importance of relating farming practices in general, ra-ther than focussing on crop type alone, to vole habitat use. While our results agree that crop type is important and must be retained in monitoring efforts, tillage practice has been shown to be a greater predictor of vole presence, necessitating the inclusion of tillage practice into monitoring and, eventually, into efforts aimed at predicting common vole outbreaks.

Other factors, not assessed in our experiment, similarly warrant inclusion in future research such as the use of irrigation, which is im-portant in arid regions for increasing crop height and vegetation cover, which may soften soil allowing easier burrow creation, and allows the expansion of semi-permanent crops such as alfalfa. Alternatively, irri-gation could be considered as a control strategy, using it to flood bur-rows and, consequently, drowning voles or destroying the burrow network.

If it is possible to predict common vole outbreaks then the results presented here, combined with Rodríguez-Pastor et al. (2016) and Heroldová et al. (2017), would suggest that during outbreak-likely periods switching from ZT to a tillage form that has at least some soil movement, such as RT, may help to reduce potential common vole sources and thus the outbreak or crop damage risk. Additionally, al-though further experimental research is needed, our results suggest that switching crop types (e.g., to Narbonne vetch) could also help. Similarly, the lack of colonisation events in our study into plots separated by 6 m of ploughed ground opens the question of whether the maintenance of strips without vegetation between crops and vole reservoirs (e.g. field margins) could be used as a preventative method to reduce the colo-nisation of voles into fields. Further studies and analysis of such man-agement approaches may prove valuable for farmers.

5. Conclusion

Our results show that generalities may be drawn between arid re-gions of common vole geographic range and those from temperate regions (Heroldová et al., 2017). However, we emphasise the need to
better establish the links between a variety of farming practices holistically, including crop type, tillage type and distance from source ha-biats, especially when attempting to manage crop pests. Failure to do so risks ignoring important factors determining risks of crop damage and may lead to inefficient management plans. Recent research has moved towards this end with work showing the importance of tillage, both for biodiversity (Barré et al., 2018) and pest distribution (Heroldová et al., 2017), as well as crop type and distance from source populations (Rodríguez-Pastor et al., 2016). How such information is taken into account when attempting to manage pests is not apparent, especially when taking into account the various nuanced aims of farming as well as the trade-off between conservation benefits of VT (Barré et al., 2018) and pest risk.

Acknowledgements

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Appendix A. Supplementary data

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Chapter IV

From pattern to process? Dual travelling waves, with contrasting propagation speeds, best describe a self-organised spatio-temporal pattern in population growth of a cyclic rodent
Abstract

Observed dynamics of populations distributed in space result from the relative strength of synchronising influences (e.g., Moran effect, limited dispersal, and trophic interactions) and the limited dispersal of agents involved in ecological processes, described as activators and inhibitors, known to cause multi-annual population cycles. However, while each of these have been well studied respectively, there is limited empirical evidence that these processes, synchronisation and activation-inhibition, act together, largely owing to the scarcity of datasets with sufficient spatial and temporal scale. Additionally, when empirically detected, travelling waves (i.e., where cycle phases appear to move across space over time) have most often been characterised as constant speed, planar travelling waves, whereas theory suggests that more complex patterns could form, though often under simplified assumptions (e.g. homogenous landscapes). Here, we assessed a variety of models that could be underlying the spatio-temporal pattern, designed to capture both theoretical and empirical understandings of travelling waves using large-scale (> 35,000 km²), multi-year (2011-2017) field monitoring data of common vole (*Microtus arvalis*) abundances, a cyclic, outbreaking agricultural rodent pest. We demonstrate most support for a single pattern described
as two radial travelling waves with contrasting speeds cumulatively describing the growth rates across the region. These two waves are consistent with theoretical understanding of activator and inhibitor type dynamics with restricted dispersal, resulting in a self-organising spatio-temporal pattern playing out over an exceptionally large-scale area. Our results provide novel empirical support for theoretical understandings of both population cycles and population synchrony.

**Keywords**

Spatio-temporal | patterns | population cycles | population growth rate | synchrony

**Introduction**

Classic ecological theory assumes that population dynamics result from interacting organisms in time but in a non-spatial context (e.g. Lotka-Volterra model). However, these predictions are modified when accounting for restricted species movement by including space and dispersal (Levin 1974). When interactions between pairs of species, broadly fitting the definition of activator-inhibitor (such as predator-prey, parasite-host, etc.), result in local cycles, incorporating space and accounting for restricted dispersal can give rise to spatio-temporal patterns (de Roos, McCauley & Wilson, 1991; Bjørnstad et al., 2002; Sherratt 2001; Johnson, Bjørnstad and Liebhold, 2006). These dynamic spatial patterns can take various forms, ranging from chaos (Li et al., 2005) to perfect synchrony (Blasius, Huppert & Stone, 1999) and much in between.

Causes of synchrony have been attributed to three factors. They include, climate conditions (the Moran effect, e.g., Bogdziewicz et al., 2021), dispersal of individuals and trophic interactions. While the Moran effect is often suggested as the cause of synchrony (e.g., Fay et al., 2020), microcosm experiments have strongly implicated an interaction between dispersal of organisms and their trophic interactions through the differential depletion of denser than average prey/host populations as a potent cause of synchrony (Vasseur & Fox, 2009; Fox et al., 2013).

Synchrony itself exists on a spectrum. Of note are periodic travelling waves (termed *partial synchrony* in Fig. 1B), whereby the oscillations of population cycles seemingly travel across space over time, either in a single constant direction (i.e., anisotropic, henceforth termed *planar wave*, e.g. Lambin et al., 1998; Berthier et al., 2014; Bjørnstad et al., 2002) or in all directions (i.e., isotropic; henceforth termed *radial wave*, e.g.
John, Bjørnstad & Liebhold 2004), at a given speed. For population cycles linked via a travelling wave, all populations experience the same cycle, but do so at potentially different times. For such populations, with increasing distance between them, the cycle will become increasingly asynchronous until eventually returning to the same cycle phase. Conversely, a perfectly synchronised cycle (termed *true synchrony* in Fig. 1C) is merely one where dispersal of agents and hence, wave speed, is practically infinite (Jepsen et al., 2016; Sherratt, 2001). In a cycle with true synchrony, all populations in a landscape exhibit the same phase of the cycle simultaneously with no spatio-temporal lag. The opposing end of the synchrony spectrum would be populations that are disconnected and cycle completely independently of each other (termed *true asynchrony* in Fig. 1A).

While travelling waves appear to be routinely detected when datasets are sufficient, there remains much uncertainty. Namely, what form a travelling wave will take when spreading across a natural landscape, what features determine the source location(s) of the wave(s), and what if activator-inhibitor dynamics play a role in the underlying mechanisms generating travelling waves?

Theoretical simulations of travelling waves unfolding in homogenous landscapes suggest the spread should be radial. However, real world landscapes include habitat heterogeneity (but see Johnson, Bjørnstad & Liebhold 2006). Intriguingly, spatial inhomogeneity can lead to the formation of both radial and planar waves via either variation in productivity, connectivity or interactions with dispersal. However, theoretical work explicitly investigating the role that heterogenous landscapes have on travelling waves, via inclusion of physical features (e.g. lakes), suggest that waves may originate from these structures with an imparted directionality (Sherratt et al., 2002; Sherratt et al., 2003). If the feature preventing isotropic dispersal is itself linear, then the resulting form of the wave would be expected to be planar. Because heterogeneities are ubiquitous in real landscapes and affect both dispersal and productivity, theory offers no prediction on what pattern should unfold in any real-world landscapes and arguments on any match between empirical pattern and theory have been post-hoc.

Empirical research projects, which by their nature occur in heterogenous environments, have often used planar wave parameterisations to describe the observed travelling waves in cyclic populations (Lambin et al., 1998; Berthier et al., 2014). Such a mismatch between generally predicted (i.e., radial) and observed (i.e., planar) patterns may have
two interpretations. The first may be that the apparent planar waves are simply a feature of observing a radial wave at too small a spatial scale (feasible given the substantial data requirements [Koenig, 1999]). Alternatively, observed planar waves may reflect real world conditions which some simulations fail to account for (e.g. heterogenous landscapes with regards to the distribution of both habitats and organisms). Thus, true planar waves may arise due to approximately linear physical features in the landscape. Building on Sherratt and Smith’s (2008) theoretical work, which suggested physical features may generate travelling waves, Berthier et al., (2014) invoked quasi-linear physical features in their landscape as being potentially responsible for planar waves in cyclic montane water vole populations. However, because of necessary theoretical assumptions for how physical features interact with organisms (resulting in boundary conditions which are hard to quantify empirically) Berthier et al., (2014) could not ascertain which of two plausible features were responsible. This reflects the challenge of translating theoretical assumptions into real-world characteristics and vice-versa.

An alternative to physical features generating travelling waves is the suggestion that that they are generated in foci with particular features. Such features include: areas with high densities (Bulgrim et al., 1996); areas where predators were introduced (Sherratt et al., 1997; Gurney et al., 1998; Sherratt et al., 2000; Sherratt 2001; Sherratt 2016) and areas of high population connectivity or habitat quality (Johnson, Bjørnstad & Liebhold, 2006). The epicentre hypothesis posits that travelling waves recurrently form via epicentres. These epicentres reflect regions in space with defined characteristics (e.g., highly connected populations in high quality habitats) that give rise to waves. Johnson, Bjørnstad and Liebhold (2006) invoked the epicentre hypothesis to explain travelling waves in cyclic larch bud moths (Johnson, Bjørnstad & Liebhold, 2004), whereby they proposed that waves emanate from regions with high-quality, well connected populations which then spread to more distant populations, resulting in partially synchronous cycles.

Related to uncertainties with what generates a wave, is the ambiguity of theory on resulting direction of travel relative to the source. It has been suggested that in the larch budmoth waves, that those waves travel outwards from epicentres (Johnson, Bjørnstad & Liebhold, 2006), resulting in expanding radial travelling waves. Conversely, alternative studies have suggested the opposite may occur, whereby waves begin at hostile environment boundaries (i.e. where individuals die if entered) and contract
inwards towards a central location (Sherratt, 2003; Sherratt & Smith, 2008). There has been no empirical research with an analytical approach that explicitly tested for such expanding or contracting waves.

As a wave spreads, via dispersal and the trophic interaction causing the cycle (Vasseur & Fox, 2009) across a landscape from one population to the next, each population in turn experiences the cyclical succession of activation or inhibition of growth rates. Such changes to a population’s growth rate are, in part, dependent on neighbouring populations. For instance, inhibition may represent the spread of agents such as pathogens or predators from one population to the next, resulting in local populations being suppressed as the respective wave passes. Theoretical expectations of travelling waves have been supported by empirical evidence from a variety of fields, all of which can be considered to have such activator-inhibitor relationships; e.g., herbivore-plant, predator-prey, parasite-host, (Lambin et al., 1998; Moss, Elston & Watson, 2000; Johnson, Bjørnstad & Liebhold, 2004; Bierman et al., 2006; Mackinnon et al., 2008; Berthier et al., 2014), susceptible-recovered, (Grenfell et al., 2001; Cummings et al., 2004), death and regeneration (Sprugel, 1976), and cellular biochemistry (Müller Mair & Steinbock, 1998; Bailles et al., 2019) amongst others. Within such systems, it is the cumulative impact of both activator and inhibitor that gives rise to the overall cyclic pattern.

The conceptualisation of population cycles as activation-inhibition, as well as the wealth of theoretical literature considering the role of such activation and inhibition accompanied by restricted dispersal in spatial patterns (Levin, 1974; de Roos, McCauley & Wilson, 1991; Bjørnstad et al., 2002; Sherratt et al., 2000; Sherratt 2001; Johnson, Bjørnstad and Liebhold, 2006) implies that statistical representation of empirical data might decompose the overall pattern in growth and retrieve evidence of two contributing travelling waves, promoting and inhibiting growth, respectively, as found in non-ecological travelling waves (Kapustina, Elston & Jacobson, 2013; Martinet et al., 2017). Additionally, the interplay between dispersal abilities of activator and inhibitor have been suggested as a component which leads to the formation of radial and planar waves (Johnson, Liebhold & Bjørnstad, 2006).

Building on exceptional data, this study evaluates a suite of hypotheses, which are flexible phenomenological descriptions of travelling waves, representing theoretical or empirical work or their logical extensions. Given the richness of our dataset, we are able
to lessen requirements for simplified caricatures and consider more complex forms. Our approach considers an initial demarcation between radial and planar waves, including whether the radial waves contract or expand. These hypotheses are further divided to represent either a single travelling wave or multiple (as simulated in Johnson, Liebhold & Bjørnstad, 2006), each in turn split into whether multiple waves are isolated from each other by physical features or coalesce into a single pattern reflecting activator-inhibitor dynamics. To do so, we used abundance indices of a rodent crop pest from a study site spanning > 35,000 km² over seven years. We find evidence of a single cumulative spatio-temporal pattern consisting of two expanding radial travelling waves, which we propose may arise due to activator-inhibitor dynamics.

**Materials and Methods**

**Study species**

The common vole (*Microtus arvalis*) is a small rodent inhabiting natural grasslands and agricultural ecosystems in Europe. It is prey for both specialist and generalist predators alike (Mougeot et al., 2019) and the host of multiple direct and vector transmitted pathogens (Rodríguez-Pastor et al., 2019). Common voles are a frequent farmland pest causing both crop damages and disease spillovers during population outbreaks that occur every 3-4 years (Jacob & Tkadlec, 2010; Mougeot et al., 2019; Rodríguez-Pastor et al., 2019). Common voles have been extensively monitored for pest management across our study site (> 35,000 km²) since 2011.

**Study site**

We (ITACyL) collected data on vole abundances in Castilla-y-León [CyL], NW Spain. CyL is a large (94,226 km²), relatively flat semi-arid agro-steppe plateau encircled by mountains and is bisected east to west by the ca. 25-150 m wide Duero River (Fig. 2). As a result of land-use changes (ca. the 1970s), common voles colonised the plateau from the adjacent mountain ranges in the north, east and south (Luque-Larena et al., 2013, Jareño et al., 2015). Within the wider region, common voles are believed to occur at higher densities within the plateau than in the surrounding mountains, likely due to the region’s agricultural practices (Roos et al., 2019). A particular area in the centre of CyL (*Tierra de Campos*) is known to practitioners as problematic due to early, large or persistent outbreaks.
While not a perfectly homogenous landscape, the plateau likely presents a "best real-world match" for conditions used in most theoretical research, which do not account for landscape features (but see Sherratt & Smith, 2008). However, there are two candidate physical features: the Duero river and surrounding mountain ranges. If physical features are related to the form of a wave, we may expect either planar waves that travel north and south due to the river or a contracting radial wave resulting from the encircling mountains. The fact that the region represents the species' range limit allows us to rule out the possibility of remote radial waves presenting as a planar wave in our observations.

Data collection

We made use of a widely employed calibrated abundance index method, based on vole presence, to monitor vole abundance at large spatial scales (Roos et al., 2019; Jareño et al., 2014). Transects, up to 99 m in length (dependent on the field's length), were carried out in linear stable landscape features (field, track or ditch margins) to estimate vole abundance from winter 2011 until autumn 2017 ($n = 42,973$). Margins are known to be reservoir habitats for voles, where from voles colonise adjacent fields during outbreak periods (Rodríguez-Pastor et al., 2016). Each transect was divided into 3 m sections, with each section noting the presence or absence of one or more signs of vole activity (i.e. latrines by burrows, fresh vegetation clippings, and recent burrow excavations). The proportion of sections with signs of vole presence per transect was then used as the abundance index. The number of surveys carried out at any time varied adaptively with the perceived risk of an outbreak (according to changes in estimated abundance in previous monitoring surveys).

Analyses of travelling waves typically use some measure that can detrend from long-term temporal trends and autocorrelation, such as phase angle or log difference growth rates (Liebhold, Koenig & Bjørnstad 2004; Vindstad et al., 2019). As such, the response variable used in all models was proportional growth rate ($r_t = \ln(N_{t+1}) - \ln(N_t)$, where $N$ is the abundance index at time $t$ (Royama 2012; Berryman, 2002). A constant of 3.03 was added to $N$ to avoid zero entries (3.03 was the lowest non-zero value of $N$). A benefit of using $r_t$, rather than $\ln(N_t)$, is that any multiplicative effects of site quality are cancelled out, provided they are constant over time. To calculate $r_t$, vole abundance indices were required at the same location in subsequent time periods (i.e. $t$ and $t + 1$). To achieve this, transects were temporally aggregated into a respective yearly quarter (e.g. January
to March 2014). Transects were then spatially aggregated by using an arbitrarily chosen transect as a reference point and assigning all transects within a 5 km radius to the $i^{th}$ centroid, with any transect only assigned to a single centroid. Once complete, the mean Julian day, X and Y UTM (Universal Transverse Mercator) were calculated for each centroid.

We chose three-month intervals and 5 km centroids as these time periods and spatial scales maximised the number of centroids with successive abundance indices, increasing the number of growth rate estimates that could be calculated. The final dataset consisted of 3,751 observations of $r_t$ (SFig 1).

Analysis

Bespoke models were constructed for all considered parameterisations of the travelling waves (summarised in Fig. 1 and Table 1), based on previous models of travelling waves (Lambin et al., 1998; Moss, Elston & Watson, 2000; Berthier et al., 2014). All the travelling wave models contained at least three components. The first component estimated distance from either a planar direction or an epicentre location (Distance equation, Table 1). The next used these distances and converted them to a space-modified time variable (Space-modified time equation, Table 1), itself then used in a GAM (generalised additive models) to explain growth rates (Growth equation, Table 1). These models reflect various ways to modify space and time so that the dynamics at each location can be explained by one or two underlying cycles (see Fig. 1). The parameters defining the space-modified time variables of the travelling waves were estimated using a stochastic annealing (SANN) optimiser (Bolker 2008), using 15,000 iterations for each model. SANN initial values were determined using a direct search method to crudely characterise the parameter space. Conditional on the values of the space-modified time variables, the underlying cycles were fitted using GAMs as described below.

Three versions of a "null" model (i.e. no travelling wave pattern) were included in the analysis and fit using generalised additive models alone. These included a true null model ($N_1$), a model which assumed true synchrony ($N_2$), and a final model which proposed growth rates were explained by space alone ($N_3$) (Table 1).

All GAM components (Growth equation, Table 1) assumed a Normal distribution and included a weighting term. The weighting term was the square root of the differential
in surveys from a centroid \( w_{t,i} = \sqrt{\frac{n_{t,i} \times n_{t-1,i}}{n_{t,i} + n_{t-1,i}}} \), where \( w_i \) is the weights for centroid \( i \) at time \( t \), and \( n \) is the number of surveys in time \( t \) and \( t-1 \). The term sought to account for observation variance caused by the adaptive vole monitoring intensity, whereby the number of transects varied over time (transects per centroid ranged from 2 to 111, with a mean of 18.5). The appropriateness of the weight term was checked by plotting model residuals against the weighted term.

All bespoke models reflected either theoretically informed radial or empirically observed planar waves parameterisations (but see Johnson, Bjørnstad and Liebhold, 2004). Models P, RE and RC were the simplest and included either a single planar (P), expanding radial (RE), or contracting radial (RC) travelling wave. A further suite of models assumed the presence of two spatially isolated, i.e. non-interfering, waves separated by the Duero river, with the waves being either planar (PF), expanding radial (RFE), or contracting radial (RFC). The potential for a single pattern informed by dual additive, overlapping waves was captured by allowing models to have two waves, either planar (PD), expanding radial (RDE) or contracting radial (RDC) waves. Compared to the models with two waves isolated by a physical feature, these models assumed that both waves influenced all populations in the landscape. This suite of models represents various predicted forms of travelling waves and some logical extensions to ensure a robust number of candidate models are considered. Given the richness of our data, the panel of models considered extends previous research that has generally used a single form or descriptive methods that could not rule out competing hypotheses. Using this approach, we can quantitively assess which description of the spatio-temporal patterns are most supported by our data. Parameterisations of each travelling wave model are included in Table 1.
Figure 2: Visual representation of the various hypotheses (via simulated patterns), where yellow indicates high growth rates and blue low growth rates. A represents a truly asynchronous population cycle, where each population (line) cycles independently of its neighbours. B shows partial synchrony where the neighbouring populations' cycle almost simultaneously, though they are not perfectly synchronised (decomposed into
C is a perfectly synchronised population where each population cycles at precisely the same time (where $r_t$ should best be represented as varying with time, model $N_2$). F shows a purely spatial pattern (where any perceived spatio-temporal pattern is merely spatial, model $N_3$, as Sherratt and Smith 2008 suggested may be the case for the apparent snowshoe hare travelling wave). D is a single planar wave at a snapshot in time (as fit in Moss, Elston & Watson, 2000; Lambin et al., 1998, Bjørnstad et al., 2002, Berthier et al., 2014, model P). E represents either an expanding or contracting single radial travelling wave (radially expanding from a central location as suggested by Johnson et al., 2006 [model RE] or contracting as suggested by Sherratt & Smith 2008, [model RC]). G shows two isolated planar waves separated by a physical feature, the Duero river (inferred from Sherratt & Smith 2008, model PF). H shows two radial waves separated by the same physical feature but may be either contracting or expanding (models RFE and RFC). J represents dual overlapping planar waves, which additively form a single overall pattern (model PD). K is either dual overlapping contracting or expanding radial waves, additively forming an overall pattern (models RDE and RDC). I represents the modelling approach, represented by the borders and arrows, used by the various parameterisations for each model, described in Table 1, to recreate a synchronised cycle in order to infer the form of partial asynchrony.

**Table 2:** Summary of analysis including model label, hypothesis, and equations used to estimate distance, space-modified time and growth rate. Where $r_{t,i}$ is the log difference growth rate of centroid $i$ at time $t$, $\alpha$ is the intercept term, $\varepsilon$ is the Normal distributed residual error, $T$ is day since start of study, $f$ is used to represent thin-plate smoothing splines with a maximum of 12 bases ($f_1$, $f_2$, $f_{\text{North}}$, and $f_{\text{South}}$), $f_{\rho}$ is a thin-plate tensor product with a maximum of ten bases in each dimension, $X$ is the mean centred easting coordinate (UTM), $Y$ is the mean centred northing coordinate (UTM), $D$ is the distance of a centroid from either a planar angle or radial epicentre, $\theta$ is the angle of a planar wave (radian), $\rho$ is the space-modified time variable, $\zeta$ is the constant speed of the wave, $\gamma$ and $\psi$ are the easting and northing coordinates of a radial wave epicentre (mean centred UTM), $N$ and $S$ denote north and south of the Duero river. The number of additional travelling wave parameters for each model are included.
<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Distance equation</th>
<th>Space-modified time equation</th>
<th>Growth rate equation</th>
<th>Number of additional parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_I$ Null</td>
<td>$D_i = -\sqrt{(x_i-x_j)^2 + (y_i-y_j)^2}$</td>
<td>$\rho_{ij} = T_{ij} + \left( \frac{1}{c} \right) D_{ij}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>NA</td>
</tr>
<tr>
<td>$N_I$ Phase-locked</td>
<td>$D_i = \sqrt{(x_i-x_j)^2 + (y_i-y_j)^2}$</td>
<td>$\rho_{ij} = T_{ij} + \left( \frac{1}{c} \right) D_{ij}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>NA</td>
</tr>
<tr>
<td>$N_I$ Static spatial pattern</td>
<td>$D_i = \sin(\theta_i) x_i + \cos(\theta_i) y_i$</td>
<td>$\rho_{ij} = T_{ij} + \left( \frac{1}{c} \right) D_{ij}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>NA</td>
</tr>
<tr>
<td>$RE$ Single expanding radial wave</td>
<td>$D_i = -\sqrt{(x_i-x_j)^2 + (y_i-y_j)^2}$, if $y_i \geq 5.068m$</td>
<td>$\rho_{N,I} = T_{ij} + \left( \frac{1}{c} \right) D_{N,I}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>3</td>
</tr>
<tr>
<td>$RC$ Single contracting radial wave</td>
<td>$D_i = \sqrt{(x_i-x_j)^2 + (y_i-y_j)^2}$, if $y_i &lt; 5.068m$</td>
<td>$\rho_{N,I} = T_{ij} + \left( \frac{1}{c} \right) D_{N,I}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>3</td>
</tr>
<tr>
<td>$P$ Single planar wave</td>
<td>$D_i = \sin(\theta_i) x_i + \cos(\theta_i) y_i$</td>
<td>$\rho_{N,I} = T_{ij} + \left( \frac{1}{c} \right) D_{N,I}$</td>
<td>$r_{ij} = a_i + f(T_{ij}) + \epsilon_{ij}$</td>
<td>2</td>
</tr>
<tr>
<td>$RFE$ Two expanding radial waves separated by river</td>
<td>$D_{N,I} = -\sqrt{(y_N - x_i)^2 + (y_N - y_i)^2}$, if $y_N \geq 5.068m$</td>
<td>$\rho_{N,I} = T_{ij} + \left( \frac{1}{c} \right) D_{N,I}$</td>
<td>$r_{ij} = a_i + f_{north}(\rho_{N,I}) + f_{south}(\rho_{S,J}) + \epsilon_{ij}$</td>
<td>6</td>
</tr>
<tr>
<td>$RDE$ Dual overlapping expanding radial waves</td>
<td>$D_{1,I} = -\sqrt{(y_1 - x_i)^2 + (y_1 - y_i)^2}$</td>
<td>$\rho_{A,I} = T_{ij} + \left( \frac{1}{c} \right) D_{A,I}$</td>
<td>$r_{ij} = a_i + f_1(\rho_{A,I}) + f_2(\rho_{S,J}) + \epsilon_{ij}$</td>
<td>6</td>
</tr>
<tr>
<td>$RFC$ Two contracting radial waves separated by river</td>
<td>$D_{S,J} = \sqrt{(y_N - x_j)^2 + (y_N - y_j)^2}$, if $y_N &lt; 5.068m$</td>
<td>$\rho_{S,J} = T_{ij} + \left( \frac{1}{c} \right) D_{S,J}$</td>
<td>$r_{ij} = a_i + f_{north}(\rho_{N,I}) + f_{south}(\rho_{S,J}) + \epsilon_{ij}$</td>
<td>6</td>
</tr>
<tr>
<td>$RDC$ Dual overlapping contracting radial waves</td>
<td>$D_{1,J} = \sqrt{(y_1 - x_j)^2 + (y_1 - y_j)^2}$</td>
<td>$\rho_{A,J} = T_{ij} + \left( \frac{1}{c} \right) D_{A,J}$</td>
<td>$r_{ij} = a_i + f_1(\rho_{A,J}) + f_2(\rho_{S,I}) + \epsilon_{ij}$</td>
<td>6</td>
</tr>
<tr>
<td>$PF$ Two planar waves separated by river</td>
<td>$D_{N,J} = \sin(\theta_j) x_j + \cos(\theta_j) y_j$, if $y_N \geq 5.068m$</td>
<td>$\rho_{N,J} = T_{ij} + \left( \frac{1}{c} \right) D_{N,J}$</td>
<td>$r_{ij} = a_i + f_{north}(\rho_{N,J}) + f_{south}(\rho_{S,J}) + \epsilon_{ij}$</td>
<td>4</td>
</tr>
<tr>
<td>$PD$ Dual overlapping planar waves</td>
<td>$D_{1,J} = \sin(\theta_j) x_j + \cos(\theta_j) y_j$</td>
<td>$\rho_{A,J} = T_{ij} + \left( \frac{1}{c} \right) D_{A,J}$</td>
<td>$r_{ij} = a_i + f_1(\rho_{A,J}) + f_2(\rho_{S,J}) + \epsilon_{ij}$</td>
<td>4</td>
</tr>
</tbody>
</table>
The final model was chosen based on parsimony considerations using $\Delta AIC$ and the corresponding hypothesis selected over the alternatives (see supplementary material for each model's AIC values). AIC, as reported by the final GAM, was adjusted to incorporate the additional number of wave parameters as;

$$\text{Adjusted } AIC = AIC + 2K$$

where $K$ is the number of wave parameters (table 1).

Confidence profiles for each parameter were determined using profiling as described in Bolker (2008). All analyses and visualisations were carried out in R version 4.0.2 (R core team, 2020) using the \textit{mgcv} (Wood, 2011), \textit{emdbook} (Bolker, 2020), \textit{ggplot2} (Wickham, 2016) and \textit{patchwork} (Pedersen, 2020) packages. The code used for the analysis is embedded in Supp. 1.

To determine the statistical method's effectiveness, we carried out a brief simulation study, available in supplementary material 2. Model assumption checks, residual plots, and summaries of each model are included in supplementary material 3.

\textbf{Results}

The null models ($N_1$, $N_2$, and $N_3$) were discarded through model selection, indicating that it is unlikely that there was true synchrony ($N_2$), or that the observed growth rates are related to static environmental conditions ($N_3$). The relative lack of support for $N_2$ (true synchrony) provides evidence that large scale true synchrony is not the pattern characterising our dataset.

Of the models which assumed the presence of travelling waves, RDE (dual expanding radial travelling waves) was selected, with the next most parsimonious model (dual contracting radial, RDC) having a $\Delta AIC = 53.2$ (accounting for additional wave parameters). The final model had epicentres estimated 75.2 km apart (Fig. 2). The first was in a well-known problematic area with higher than average abundances resulting in recurrent and severe outbreaks (\textit{Tierra de Campos}). In contrast, the second was positioned further southeast, in an area that experiences lower than average abundances (see SFig. 2 for a G$i$ cluster analysis of the 42,973 abundance indices).
Figure 4: Map of the Duero basin, coloured according to elevation (m) with mountains in the north, east and south visible as bright yellow regions. The Bay of Biscay is visible in the north. Grey dots represent the sampling locations for population growth rates. Estimated epicentre locations are noted with the mustard and white points. The Duero river is visible as the turquoise line running east to west. Elevation data was downloaded from copernicus[dot]eu (EU-DEM v1.1) and waterway data from ea[dot]europa[dot]eu.

Table 3: Summary of RDE wave parameter estimates. Labels are as noted in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter label</th>
<th>Estimate</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st wave</td>
<td>Centroid (N)</td>
<td>$\gamma_1$</td>
<td>-41,723</td>
<td>-51,645</td>
<td>-33,626 UTM (mean centred)</td>
</tr>
<tr>
<td></td>
<td>Centroid (E)</td>
<td>$\psi_1$</td>
<td>28,414</td>
<td>18,556</td>
<td>29,897 UTM (mean centred)</td>
</tr>
<tr>
<td></td>
<td>Speed</td>
<td>$\zeta_1$</td>
<td>405</td>
<td>316</td>
<td>528 m per day</td>
</tr>
</tbody>
</table>
Additionally, when plotting the predicted growth rates on the space-modified time variables, the possibility that the overall pattern can be decomposed into possible activator and inhibitor influences (themselves, phenomenological statistical descriptions) on vole population growth is suggested; the first, slow wave predominantly inhibited growth and was estimated to travel radially at 148 km per year, while the second, faster wave was estimate to travel radially at 835 km per year and generally promoted growth (Fig. 3). When the effects of both of these waves are plotted over true space and time, the cumulative spatio-temporal pattern becomes apparent (Fig. 4) and the speed at which it traverses the region is approximately 0.9 km per day (or 329 km per year, calculated by extracting the furthest south predictions where $r_t > 0.5$ [i.e. the wave front] at two arbitrarily chosen times, then calculating the distance between those and dividing by the difference in time).
Figure 3: Conditional predictions, showing the contribution of the 1\textsuperscript{st} (slow) and 2\textsuperscript{nd} (fast) waves, including the intercept, to mean growth rate ($\bar{r}_t$, y-axis) over space-modified time (x-axis) represented by the solid black lines, with 95% confidence intervals represented by the grey ribbons. Horizontal black dashed line indicates a growth rate of 0. The light grey points represent the partial residuals for the respective smoothing spline.
Figure 4: Predicted cumulative spatio-temporal pattern of $r_t$ as a result of both travelling waves, each facet shows the spatio-temporal prediction over true time (i.e. days since the start of the study).

Discussion

We find clear evidence of a self-organising spatio-temporal pattern in the population growth rates of common voles in Castilla-y-León, resulting from two travelling waves spreading radially at contrasting speeds. Further, in line with Johnson, Liebhold & Bjørnstad (2004), we find that the pattern in CyL is best approximated as two expanding radial travelling waves. However, the waves detected here are not independent as in Johnson, Liebhold & Bjørnstad (2004), instead acting additively as activator and inhibitor, suggesting they may be more than phenomenological descriptions of an overall pattern. The dual expanding, fast and slow radial travelling waves, suggesting activator and inhibitor dynamics respectively, are of a form not previously observed in the empirical literature but are in line with the fundamental interactions of activators (e.g. prey) and inhibitors (e.g. pathogens) in population cycles. Such activation and inhibition, and their spatial diffusion are similarly believed to be the process generating synchrony (Vasseur & Fox, 2009). Further, activator and inhibitor dynamics are
inherently included in travelling wave simulations. As such, we find convergence between understandings of synchrony, travelling waves and cycles.

True synchrony or partial synchrony?

While we refer to the population cycle of common voles in CyL as partially synchronous, various studies have apparently demonstrated that cyclic populations, both of common voles and other cyclic species, occur synchronously. To understand this apparent contradiction, it is important to note that synchrony occurs, not as a dichotomous state but as a spectrum (Koenig, 1999; Bjørnstad, Ims & Lambin, 1999, see Fig. 1). Nevertheless, the dichotomous representation of synchrony has led to an approach whereby evidence of synchrony (notably synchrony which decays with distance) can be perceived as evidence, or lack-there-of, of true synchrony (Smith 1983; Sundell et al., 2004; Andersson & Jonasson 1986; Huitu et al., 2003; Huitu et al., 2008; Fay et al., 2020; Lambin, Yoccoz & Bretagnolle 2006; Erlinge et al., 1999). The use of the terms “synchrony” and “asynchrony”, which implies a dichotomous state, may lead to the view that there are no nuanced forms of synchrony.

If travelling waves are ubiquitous in cyclic populations, a crucial component to detecting such nuanced forms of synchrony, overcome in the present study, is the requirement for a vast amount of data to distinguish between more subtle forms (Koenig, 1999). Early descriptions of population cycle synchrony were largely limited to qualitative assessments, where populations were deemed synchronous if they peaked sometime in the same year (e.g., Andersson & Jonasson, 1986). While such qualitative assessments of synchrony may reflect genuine true synchrony, they likely suffer from temporal aggregations, i.e., where population synchrony is deemed to have occurred because the same phase is experienced within the same broad period of time (see SFig. 3 for an example of where a travelling wave could be misconstrued as true synchrony using a qualitative approach). While research on synchrony has become more quantitative, some subsequent attempts to characterise synchrony have suffered from similar issues, namely, a lack of either or both spatial and temporal resolution (Koenig, 1999).

Likely owing to the long history of time series use in population cycle literature, many datasets which test for synchrony generally last for a long period of time (e.g. 21 years in Huitu et al., 2003). However, even in long term datasets, the temporal resolution can
be severely limited. For instance, Sundell et al., (2004) used the annual breeding output of raptors in 50 x 50 km areas across Finland, as a vole abundance index to characterise synchrony across the country. While such datasets are likely able to determine if true asynchrony or true synchrony are better supported (e.g. peaks occur in the same year), they seem ill-suited for detecting more subtle forms of synchrony as any signal of a within-year spatio-temporal delay in synchrony (e.g. a travelling wave) would be obscured.

While such issues surrounding temporal resolution and aggregation may mask more subtle forms of synchrony, such as travelling waves, a lack of spatial resolution is perhaps equally detrimental. Indeed, in many instances, population synchrony has been characterised using far fewer spatial replicates than those used in this analysis (Lambin, Yoccoz & Bretagnolle 2006; Huitu et al., 2003; Huitu et al., 2008). In such cases of comparatively low spatial resolution, as with studies with a low temporal resolution, the result is likely an ability to distinguish between the two extremes of synchrony but an inability to explore where a metapopulation exists on the spectrum of synchrony.

Indeed, whenever spatio-temporal datasets have been rich in both spatial and temporal resolution, the outcome appears to be the detection of travelling waves, irrespective of the method used (Johnson, Bjørnstad & Liebhold 2004; Lambin et al., 1998; Berthier et al., 2014; Grenfell et al., 2013; Cummings et al., 2004). Such datasets tend to exist only for species with public health or economic interests, such as pest species (Bjørnstad, 2001), which may, in part, explain the relatively few examples of travelling waves in the literature compared to detections of apparent true synchrony. However, if the waves captured here do represent activator-inhibitor dynamics and their dispersal, it is logical to assume that all cyclic systems are synchronised via travelling waves, which are only subsequently modified more or less by the Moran effect (Hugueny, 2006).

**Activator-inhibitor waves**

Given the long history of using activator-inhibitor systems to model population cycles (e.g. Levin 1974), as well as the finding that trophic interactions and dispersal promote synchrony, our findings, which suggest the presence of activator and inhibitor travelling waves, provide some measure of consistency between understandings of synchrony and population cycle theory (Bjørnstad, 2001; Bierman et al., 2006). Such activator-
inhibitor travelling waves have previously been detected in cellular biology (Kapustina, Elston & Jacobson, 2013; Martinet et al., 2017) but not in ecology.

Our results are, to our knowledge, the first instance where a single spatio-temporal pattern of population cycles has been decomposed into constituent parts, which we propose, represent the influences of activator and inhibitor on population vole growth. Microcosm experiments investigating the effects of dispersal and trophic interactions (and the Moran effect) found that the synchronising effect of dispersal in the presence of predation led to greater synchrony in population cycles of protists (Vasseur & Fox, 2009), suggesting that the two waves here may partly represent the synchronising effects of dispersal of voles, dispersal of inhibitors (possibly pathogens or predators) and the interactions between them. Indeed, a potential candidate agent for an inhibitor, pathogens, are known to spread via travelling waves (Grenfell et al., 2001; Cummings et al., 2004).

The presence of two epicentres is in line with previous research on travelling waves (Johnson, Liebhold & Bjørnstad, 2004), though the finding that final cumulative pattern is dependent on both epicentres, with apparently distinct roles (i.e. activation and inhibition of growth rates) are new to the field. The positioning of the epicentres, estimated as distinct locations with no overlap in the 95% CI, may provide some support for the interpretation of activator and inhibitor dynamics. The estimated location of the inhibitor epicentre is in an area with higher-than-average abundances of voles (Tierra de Campos, see SFig. 2). This region is known locally to practitioners for recurrently experiencing severe outbreaks, which may be related to farming practices which are more suitable for voles (Roos et al., 2019). Such a location would present an area consistent with understandings of where travelling waves of diseases initiate, as pathogen travelling waves have been found to originate in areas of high density (Grenfell et al., 2001; Cummings et al., 2004). If so, this epicentre may represent the starting location for the outward spread of pathogens because of infected dispersing individuals which serve to inhibit growth rates of voles. A testable hypothesis would be that this region experiences a higher proportion of infected individuals compared to a regional average. Indeed, two pathogens, Tularemia and bartonella, are known to occur in a density dependent relationship with vole densities in Tierra de Campos (Rodríguez-Pastor et al., 2017). A consequence of being reliant on dispersers for the propagation of the disease, in combination with various delaying processes (e.g., latency to infection),
is that we would expect that the speed of the inhibitor to be slower than the activator speed, which we observe.

Conversely, the activator epicentre was located in a lower-than-average abundance region (see SFig. 2). We propose that this may be due to a slight adjustment to the epicentre hypothesis as described in Johnson, Liebhold & Johnson (2006). The epicentre hypothesis posits that emigration between close suitable habitats cause travelling waves. We consider that our epicentre meets these requirements in all but “suitable habitat” (i.e. lower-than-average densities). However, given the high reproductive capacity of common voles, we would assume they are able to produce as many offspring in a “less-suitable habitat” as elsewhere in the region, but that most of these offspring become emigrants. In this light, the core understanding of the epicentre hypothesis is maintained, that being that an epicentre is a location producing many emigrants, but altering it to take into account the reproductive ability of common voles which we do not believe has influential spatial variation. Evidence of this would come from finding a higher-than-average proportion of dispersers at this location.

The speed of the inhibitor wave was estimated at 147 km per year, while the activator was estimated at 835 km per year, which appear to be middle-ground speed estimates amongst empirical travelling wave literature (which vary from a minimum of 7-8 km per year [Berthier et al., 2014] to a maximal 1,776 km per year [Cummings et al., 2006]). Differences in speed (which include dispersal ability) offers some confirmation with simulations (Johnson, Liebhold & Bjørnstad, 2006), where differences in activator-inhibitor dispersal abilities was found to result in radial travelling waves. We propose that pathogen (i.e. a possible inhibitor) diffusion would be dependent on host dispersal, mode of transmission, latency to infection, and so forth, all possible means to impart a delay in the spread to adjoining populations. Conversely, we believe that the fast speed of the activator wave may reflect the relative ease at which voles are able to disperse (i.e., habitat connectivity, where CyL is criss-crossed by field margins) or the effectiveness of a dispersal event (related to density).

**Conclusion**

Our modelling has demonstrated evidence for both activator and inhibitor influences on population growth rates in voles. Further work is required to establish the processes underlying these influences, and to collect sufficient large-scale data on other ecological
systems to establish whether these too are underpinned by activator and inhibitor influences.

Acknowledgements

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References


Chapter V

Does density, in addition to dispersal, influence the speed at which growth rate synchronises across space?
Abstract

Travelling waves are the partial synchronisation of population cycles across space over time. These spatio-temporal patterns are commonly observed when datasets have high resolution in space and time, though such data are rare. Consequently, understandings of the underlying mechanisms of travelling waves are still in their infancy as statistical methods to describe travelling waves are phenomenological (i.e. use only space and time to explain patterns in abundance or growth rates). Research identifying waves was historically done by detecting a relationship between distance and synchrony, which was interpreted as evidence of waves. However, various phenomenological descriptions can provide more insights into components, such as the speed at which distinct populations and their cycles become synchronised over space and time. From such studies, estimates of wave speeds show large variation across study sites, ranging from a few kilometres per year to thousands of kilometres per year. The speed at which these waves synchronise populations is believed to be via a combination of dispersal plus additional features, such as population density or habitat connectivity. Indeed, both the density of activator and inhibitor (e.g., host and pathogen) and their dispersal abilities are fundamental in mathematical descriptions of travelling waves in population cycles. Here we attempt to incorporate density-dependent wave speeds to determine if...
the speed of waves is related to density. We find evidence that speed has a weak positive relationship with density but does not outperform models with constant speed, suggesting either there is no relationship with density or that density dependence is more complex than considered here. Conversely, this finding may suggest that the crucial element in travelling waves is not density-dependent speed but rather the difference in diffusion between activator and inhibitor, which determines both the form and the speed, confirming theoretical studies.

**Keywords:**
Spatio-temporal | density-dependent | population cycles | population growth rate | synchrony

**Introduction**

Travelling waves are a nuanced form of synchrony, whereby populations are neither perfectly synchronous nor asynchronous, instead occupying an intermediate state which we refer to as partially synchronous (chapter IV). Three factors are believed to promote synchrony in otherwise distinct populations and their dynamics. The first is the Moran effect, whereby stochastic climatic events bring disjunct population dynamics into synchrony. Despite often being proposed as the mechanism generating synchrony over large scales (e.g. Bogdziewicz et al., 2021; Fay et al., 2020), the Moran theorem (per Royama, 1992) underpinning the Moran effect is often violated (Hugueny, 2006). The Moran theorem assumes that: any density-dependent structures are linear; dynamics are identical in all populations (e.g. autoregressive coefficients); and that individuals do not disperse (or populations are uncoupled, e.g. via a travelling wave), which, when accounted for, show a diminished role of the Moran effect for inducing synchrony (Hugueny, 2006).

Further, the ability of the Moran effect to drive populations towards synchrony has been found to depend on the underlying life-history strategies of a species. For example, fish species dependent on flooding for breeding are driven into synchrony via the Moran effect, while species that breed regardless of flooding are not (Tedesco & Hugueny, 2006). Further, the Moran effect could be considered less crucial when travelling waves are found to be generated at specific foci in a landscape (i.e. radial waves expanding from an epicentre [chapter IV; Johnson; Liebhold & Bjornstad, 2004]). However, we are not aware of weather patterns generated at specific locations within relatively small
regions, which then spread radially outwards (small relative to the spatial scale of weather patterns). In such cases, we would rule out the Moran effect, a density-independent mechanism, as a causal driver of synchrony.

The second and third factors deemed to cause synchrony are the dispersal of organisms and their trophic interactions. Notably, the combined, interactive effect between these two factors promotes synchrony the most in a mesocosm experiment (Vasseur & Fox, 2009). While dispersal has been discounted in the past as a possible mechanism for generating synchrony, owing to the small-scale nature of dispersal and the larger scale synchrony (Huitu et al., 2003), research has demonstrated that small-scale dispersal events are capable of generating large scale synchrony (Sherratt et al., 2001; Satake & Iwasa, 2002).

While dispersal appears to be an important feature in generating synchrony, the effect is likely dependent on additional factors. When carrying out theoretical work on travelling waves, dispersal ability is often used in conjunction with density (Smith et al., 2008). For instance, Smith et al. (2008) explicitly included density-dependent dispersal in theoretical simulations to determine if density-dependent dispersal influenced the synchrony of population cycles, coupled with travelling waves (see Eq. 1a in Smith et al., 2008). Their results suggested a density-dependent relationship, but this could be superseded when the diffusion ratio (between “consumers and resource”, i.e. activator and inhibitor here) was large.

The argument that travelling waves and resulting partial synchrony may be, in part, generated by trophic interactions (see chapter IV; Vasseur & Fox, 2009) and that the influence of trophic interactions on synchrony is most pronounced when combined with dispersal strongly implicates dispersal as a necessary condition causal mechanism for travelling waves. However, the influence of dispersal (often accounted for as an all-encompassing dispersal term, including emigration, transience, and immigrations, see Smith et al., 2008) in travelling waves appears to, in part, depend on density (Smith et al., 2008). Empirical studies that have specifically estimated the speed of travelling waves show large variations in speed between and within systems. For instance: travelling waves in common voles in Spain were estimated to advance at 147 km per year and 835 km per year (chapter IV); the wave speed of field voles in the UK was estimated at 18-21 km per year (Lambin et al., 1998; MacKinnon et al., 2003); in montane water voles in France 7–8 km per year (Berthier et al., 2014); 260 km per year in measles
outbreaks in the UK (Grenfell et al., 2001); 1,776 km per year in dengue fever outbreaks in Thailand (Cummings et al., 2006); and in larch bud moths in Switzerland, ranged between 84–1593 km per year (Johnson, Liebhold & Bjornstad, 2004). Additionally, in the case of the larch bud moths, it was found that the speed varied over time and space within the same study site (Johnson, Liebhold & Bjornstad, 2004). The role of dispersal in influencing the speed of travelling waves appears to be clear. Indeed, the speed of the travelling waves in larch bud moths was related to putative dispersal ability and distance between populations (Johnson, Liebhold & Bjornstad, 2004). Further, using two moth species populations isolated by water bodies, with only one species able to disperse over the water, the difference in dispersal ability was related to a decrease in synchrony (i.e., a slower travelling wave) (Vindstad et al., 2019). Although such findings strongly implicate, qualitatively at least, that dispersal ability is an important aspect of travelling wave speeds, dispersal alone would not explain the variation in speeds between studies, given that analogous species can experience waves up to ca. 50-fold faster in different systems.

Research investigating synchrony with habitat suitability found that the synchrony in population cycles of common voles in Czechia declined in regions with a greater proportion of forested land (Gouviera et al., 2016). Furthermore, rodent (including but not limited to *M. arvalis*) populations in farmlands and forests are known to experience notable differences in densities, with up to 1,000 more rodents per ha in farmlands compared to forests (Jędrzejewski & Jędrzejewska, 1996). It is important here to bear in mind that differences in synchrony reflect differences in the speed of travelling waves; a wave with infinite speed would result in truly perfectly synchronised cycles across large regions. Therefore, differences in synchrony across habitats of different quality imply that the speed of the wave declines in sub-optimal habitat, with habitat type likely to hold different densities. Indeed, Grenfell et al. (2011) proposed that the increasing spatial lags (i.e. slower speeds) imparted by a travelling wave in measles outbreaks (i.e. an inhibitor) may have been due to both distances between populations and the local density, with “smaller centres” lagging behind than larger ones, suggesting that the speed decreased in less dense areas.

Travelling waves in our study site have previously been suggested to exhibit activator and inhibitor type dynamics, with two waves promoting or inhibiting growth rates (chapter IV). The activator wave will undoubtedly represent the organisms themselves.
(common voles, *Microtus arvalis*) given their high reproductive potential, but the inhibitor is less clear. For the purposes here, given that the role of weasel as specialists predator (often invoked as the causal agent of cycles) has been refuted for this study system (Mougeot et al., 2019), we consider the inhibitor to be an unspecified pathogen. However, *Francisella tularensis* (Tularemia) is a possible candidate as it is known to occur in a density-dependent relationship with common vole abundance (Rodríguez-Pastor et al., 2017). As such, we have two predictions for what form any speed-density-dependence relationship would take; one for the activator wave and a similar for the inhibitor. The epicentre hypothesis (as described by Johnson, Liebhold & Bjornstad, 2006) suggests that dispersing individuals from high-quality patches (i.e. high density of organisms) cause travelling waves, as well as the law of “mass action” (de Roos, McCauley & Wilson, 1991), where the rate of a reaction is dependent on the mass of reaction substrate. Therefore, we would predict a positive relationship between speed and density for the activator wave. Assuming the inhibitor represents pathogen spread, partly owing to the need for host transmission for dispersal, imparting a similar form to the activator speed relationship, and also as more densely occupied areas represent larger populations of susceptible hosts (e.g. Cummings et al., 2006; Grenfell et al., 2001).

Using a rich dataset capable of identifying nuanced features of travelling waves, we build on the methods previously used in chapter IV to determine if the speed of travelling waves are density-dependent. We find evidence of a weak positive relationship between density and the speed of a travelling wave for both activator and inhibitor waves, though the relationship was not sufficiently influential to select these models based on AIC over their constant speed variants. Thus, our results suggest that wave speeds are either not direct density-dependent or that more complex forms of density dependence may be involved in determining the speed of waves than those used here.

The key message from our results is that incorporating density-dependent dispersal does did not dramatically affect the predicted spatiotemporal dynamics of our model cyclic populations: it has only a limited effect on both the shape of the wave family and the waves arising from two specific wave selection mechanisms. In particular, the effects are generally much less than those arising from variation in the ratio of the diffusion coefficients. However, these conclusions do not imply that density-dependent dispersal will not have an important role in the spatiotemporal dynamics observed in
biological systems. For example, if the observed wavelength is at the limit of what it is possible to detect in the field, then density-dependent dispersal may be the difference between detection or not (Smith et al., 2008).

Materials and Methods

Study species

This study used common voles as the model species to investigate if the speed of travelling waves are density-dependent. Common voles are agricultural pests throughout Europe (Jacob et al., 2014), where they are prey for a variety of predators (e.g. Mougeot et al., 2019) and hosts to several pathogens (Rodríguez-Pastor et al., 2017; Rodríguez-Pastor et al., 2018). In addition, the species has high reproductive potential, experiences population cycles (Lambin, Bretagnolle & Yoccoz, 2006; Mougeot et al., 2019) and exhibits travelling waves that partially synchronise those cycles (chapter IV).

Study site

Common vole abundance indices were collected throughout Castilla-y-León, Spain, from 2011 to 2017 across a ca. 32,000 km² area. Castilla-y-León is a pseudo-steppe agricultural plateau surrounded by mountains where, before the 1970s, common vole distribution was largely restricted to the mountain ranges. However, by 2000 the region had become fully colonised following land-use changes (Luque-Larena et al., 2013). As a result, voles now reach outbreak densities within the plateau roughly every three to five years (Luque-Larena et al., 2013; Mougeot et al., 2019).

Data collection

Data were collected using methods as described in Chapter IV. Briefly, 99 m transects were carried out in both fields and field margins, though only field margins were used to ensure a relatively constant habitat type. These transects were split into 33 sections measuring 3 x 1.5 m, where the presence of any signs (i.e., latrines, vegetation clippings, and excavations) were noted for that section. The abundance index was then the proportion of sections within a transect with signs of vole activity. Between 2011 and 2017, this method yielded 42,973 abundance indices (Fig. 1).
Figure 7: Spatial distribution of vole transects in field margins across Castilla-y-León. Each transect is indicated by a partially transparent light grey point, where more opaque points indicate greater sampling intensity. The background, coloured from blue to yellow, represents elevation. The Duero river is visible as the turquoise line running east to west. Elevation data was downloaded from copernicus[dot]eu (EU-DEM v1.1) and waterway data from ea[dot]europa[dot]eu.

These abundance indices were converted to log difference growth rates ($r_t = ln(N_{t+1}) - ln(N_t)$, where $N$ is the abundance index at time $t$ [Royama 1992; Berryman, 2002]) by aggregating transects into three-month periods and 5 km radii centroids (more details are provided in chapter IV). The mean UTM northing and easting, and Julian day were calculated for each centroid in each period. Aggregating in this manner yielded 3,751 values of $r_t$. 
Analysis

All models compared constant speed parameterisations (as described in chapter IV) with their respective density-dependent speeds versions. Models with varying speed included a component to estimate a latent speed variable for each wave, resulting in one additional parameter per wave compared to the constant model.

\[ \zeta_{t+1,i} = \alpha_1 + \alpha_2 N_{t+1,i} \]

If we assume the speed of a travelling wave (\( \zeta \)) is determined by density, then let \( \alpha_1 \) be the speed of the wave travelling through location \( i \) when voles are at mean centred density (\( N \)), and \( \alpha_2 \) be the slope in location \( i \) at time \( t_{+1} \). \( N \) is mean centred (Fig. 2) so that the initial parameterisation reflects the version of each model where speed is assumed to be constant. In this way, we initialised \( \alpha_1 \) to the speed estimated in chapter IV for the respective travelling wave model and \( \alpha_2 \) to zero.

![Distribution of mean centred abundance indices](image)

**Figure 8**: Distribution of mean centred abundance indices.

The density-dependent speed models were fit using a stochastic annealing (SANN) optimiser (Bolker 2008), using 15,000 iterations for each model. SANN initial values were determined using estimated parameter values from chapter IV.
All analyses and visualisations were carried out in R version 4.0.2 (R core team, 2020) using the \textit{mgcv} (Wood, 2011), \textit{emdbook} (Bolker, 2020), \textit{ggplot2} (Wickham, 2016) and \textit{patchwork} (Pedersen, 2020) packages. The code used for the analysis is embedded in the supplementary material.

\textbf{Results}

The best performing density-dependent wave speed model, by AIC, was the dual radial expanding activator and inhibitor travelling wave model, as in chapter IV (table 1). The estimates suggested a very weak positive relationship between the two wave speeds (Fig. 3); $\alpha_{I,1} = 393$ m per day (95% CI 326 and 631) and $\alpha_{I,2} = 0.001$ m per day per proportion of vole abundance index (95% CI 0.001 to 0.012) for the inhibitor, and $\alpha_{A,1} = 2,264$ m per day (95% CI 1,703 and 3,087) and $\alpha_{A,2} = 0.001$ m per day per proportion of vole abundance index (95% CI 0.001 and 0.008) for the activator (where the $I$ and $A$ subscripts denote the inhibitor and activator waves, respectively).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{Figure9.png}
\caption{Predicted relationships between the speed of each travelling wave and density. The black line shows the estimated fit and the grey ribbons show the 95\% confidence intervals.}
\end{figure}

Due to the weak relationship, AIC suggested that the additional parameters were not worth accounting for (table 1). None of the models showed improved AIC values when
including density-dependent speed compared to their constant speed alternatives. The estimation method returned intercepts equivalent to the constant speed parameterisations and slopes practically indistinguishable from zero (see Supp. 1 for details).

**Table 4:** Models fitted for travelling waves with speed varying according to mean centred vole density (see chapter IV for a full description of parameterisation of constant speed models). Includes the -2 log likelihood, the additional number of parameters for the travelling waves (includes an additional parameter for speed in each wave), adjusted AIC (see chapter IV) and delta AIC.

<table>
<thead>
<tr>
<th>Model</th>
<th>-2lnL</th>
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<th>ΔAIC</th>
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<td>Single planar wave</td>
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**Discussion**

Given various implications that the speed of travelling waves may be directly density-dependent, we expected to find a signature of such an effect when speed was linearly regressed against density. While we find weak evidence of positive density dependence, the effect is insufficient to improve upon constant speed model specifications. While this may be considered statistically significant, owing to the 95% CI not overlapping zero, it is important to note that this represents a maximum increase in speed of 10 cm per day at maximum abundance index value, where the intercept is estimated at 2.3 km per day. This slope, while significantly different from a slope of zero, is biologically insignificant (Yoccoz, 1991). Nevertheless, this result suggests one of the following: the
speed of travelling waves are i) not direct density-dependent, instead influenced by other features; ii) non-linearly density-dependent, or iii) influenced by more complex forms of density dependence (i.e. both temporally and spatially density-dependent).

We that the coefficient of the linear effect of density on speed is unlikely to have a practical effect on speed. This may suggest that the speed of travelling waves is not related to density, though the question then becomes: what modifies the speed of a travelling wave? Variation in speed has been observed only once to our knowledge, in Johnson, Liebhold & Bjornstad (2004), where the speeds across space mirrored spatial variations in connectivity between populations. The authors defined connectivity as the average potential for immigrants to disperse into a suitable habitat (i.e. preferred) from another suitable habitat (see Eq. (1) in Johnson, Liebhold & Bjornstad, 2004). This measure of connectivity considers only the distance between suitable locations and moth dispersal ability. While variations in connectivity are present in the highly heterogenous Alps and thus likely to affect the larch bud moth wave, similar dramatic variations in connectivity, and a subsequent relationship with speed, are more difficult to envisage for common voles in CyL. Common voles occur at the highest densities in field margins (Rodríguez-Pastor et al., 2016), reflecting a preference for these habitats (i.e. suitable habitats as per Johnson, Liebhold & Bjornstad, 2004). However, the region is well connected via these same field margins (see Fig. 1, where all data points come from sampled vole populations in field margins). The specific circumstances in CyL would seem to rule out the potential for connectivity (assumed to be constant across the region) between high-quality sites (present throughout the region) to generate variation in speed. However, if the speed of the waves were related to connectivity, this may suggest why speed is both apparently constant and relatively fast in the highly connected region compared to analogous species.

While the relationship between speed and direct density dependence is not linear, it is tempting to consider the potential for non-linear forms of density dependence (as considered in Barraquand et al., 2014 for describing the underlying population cycles). However, given the lack of any negative or positive linear relationship, the only non-linear form we can envisage that would result in a straight line with a zero gradient is a U-shaped relationship (Fig. 4). While such a relationship is statistically feasible given the non-relationship in the linear form, we are not aware of any theoretical justification for why the speed of a wave would have such a relationship with density, though,
conceptually, this may represent an interaction between density and dispersal. For such a relationship to be feasible, dispersal rates would need to be high at both low and high densities, possibly due to a lack of resources at low densities (e.g. mates) or a lack of access to those resources at high densities. Meanwhile, low dispersal would be required at intermediate densities.

Given that the density-dispersal relationship appears to be inconclusive, with results suggesting a variety of positive and negative density-dependent dispersal (Aars & Ims, 2000; Ims & Andreassen, 2001; Matthysen, 2005), with recent research finding a U-shaped relationship (Sutherland, Elston & Lambin, in prep), a U-shaped relationship between speed and dispersal-density is, at least, feasible. Further, if inhibition represents the spread of pathogens, we would expect a mirrored density-speed relationship to that of the activator. However, given pathogens rely on hosts (either or both the activator and other species [see Luque-Larena et al., 2017]) to spread across space into new populations, but once in a new population, must also infect susceptible and only then propagate into new areas, we may expect the speed to be slower. If true, this would imply that if a U-shaped relationship described the relationship for the hosts, so too may it describe the relationship for pathogens.
Figure 10: Simulated U-shaped relationship between the speed of a wave and density, with arbitrary units, which could lead to a misconstrued non-relationship when fitting a linear regression (black line with 95% CI grey ribbons). Here the speed of the wave is fast at low density, reflecting greater dispersal due to, e.g., low mate availability. The speed decreases at intermediate densities owing to resources being sufficient within the patch, meaning dispersal decreases. Finally, speed increases at high densities, reflecting higher competition for access to resources. The inset shows another non-linear form, which given the lack of a linear relationship found here, we can rule out.

The form of density dependence considered here is comparatively simple. Since population cycles may be, in part, generated by mixtures of delayed and direct density dependence, which are phase-specific (Barraquand et al., 2014), it seems reasonable to explore more complex forms of density dependence influencing the speed of a wave. However, the form that delayed density dependence may take in a travelling wave could be more complex given the intrinsic link with space. Some form of spatial density dependence may play a role, given the spatial coupling of populations reflected by travelling waves. Indeed, the possible importance of a spatial density dependence relationship come from suggestions that the distance between disjoint populations may play a role in speed (e.g. Johnson, Liebhold & Bjornstad, 2004; Grenfell et al., 2001). However, such specifications, where the immediate neighbour’s density influences a given population’s growth rate, would ignore the directionality of travelling waves (i.e. 
where it is the nearest neighbours, in respect to the direction of travel, which may have the greatest influence). We are unaware of any attempts to include spatial density dependence, not to mention delayed spatio-temporal density dependence. However, given the inherent spatio-temporal linkage of populations via travelling waves, such structures may be necessary for future attempts to understand density dependence in travelling wave speeds. Before such attempts are made, we are cautious in dismissing the potential role of density in influencing the speed of travelling waves.

Conclusion

Our results suggest that the oft parameterised density-dependent nature of the speed of a travelling wave (e.g. Johnson, Liebhold & Bjornstad, 2006; Smith et al., 2008) is not supported by empirical data. However, given that the ratio of diffusion can overwhelm the influence of density-dependent dispersal on speed (Smith et al., 2008), in combination with the potential for non-linear (e.g. Barraquand et al., 2014) or more complex spatio-temporal density dependence, we are not in a position to conclusively rule out all forms of density-dependence on speed, only the form most commonly assumed in theoretical simulations. We suggest that future research into travelling waves consider some of the forms suggested herein, when exploring the influences on the speed of travelling waves.

References


Chapter VI

General Discussion
Thesis summary

Pest species pose a substantial risk to global, national, and local food security (Savary et al., 2019). In particular, rodent pest species, in the right circumstances, can represent a pronounced and significant impact on the food production chain at all stages, from seeding to distribution (Singleton et al., 1999). Thus, developing an understanding of both the ecology and the impacts that a given rodent pest has, constitutes an important step in meeting the challenge of making informed food production decisions.

Chapter II presents a rare instance where the density of a pest is related to loss of yield, a relationship that, although fundamental for any informed decision-making, yet is unknown for many pest species in general and rodent pests in particular. Chapter III shows how specific farming practices can lead to an increased proportion of land being occupied by *M. arvalis*. With this finding, I highlight the complexity of the scenario, as those practices that led to increased occupancy are simultaneously promoted for various reasons. In chapter IV, I reveal the spatio-temporal phenomena for how pest outbreaks become synchronised over space and time, with a tantalising suggestion that the same processes which may generate the underlying population cycles may be the same as those which lead to the synchronisation of them, suggesting that travelling waves could be ubiquitous in cyclic species. Finally, chapter V shows that the speed at which this synchronisation occurs is not directly density-dependent, despite a body of theoretical work indicating that it should be.

I now discuss how these findings contribute to a developed understanding of the ecology of small mammals, their current and future impacts on food security, and implications for the field of applied ecology concerning cyclic rodent pest species.

The fundamental question: how many pests are too many pests?

An agricultural pest causes damage to a crop. This much is clear and is indeed the motivating justification behind pest research. However, for effective management and informed decision making, this statement requires far greater understanding. Attempts to refine the statement of “pests cause damage” tend to result in descriptions of at what density pests cause *important* damage via economic thresholds. While this description has clear value, it is still rather simplistic and ignores valuable information (described in chapter II). Understanding this relationship has such great importance that it should, arguably, be the priority research when starting work with a pest species. This is
especially true when working with species that exhibit population fluctuations and have the capacity for rapid population growth, such as *M. arvalis*. If the focus is on describing a specific threshold, then there is a risk that without intensive monitoring, that the population may go from near absence to outbreak densities, passing the target threshold before any actions can be taken.

On the other hand, if the focus is on understanding the density damage relationship as a whole, then it may, at least, enable attempted control. For instance, focusing on a particular density threshold places a great deal of attention on a singular value, where a view may form that below the threshold, the damage is trivial, and only beyond this threshold is damage important. The obvious question, however, is how close to the threshold is considered dangerous? Conversely, understanding the relationship as a whole would allow practitioners to make more refined and detailed decisions where populations of different sizes can be evaluated. Given that rodent crop pest populations can experience rapid growth, understanding the relationship across a range of densities is essential. As such, within this thesis, chapter II likely represents the most valuable information for stakeholders.

The importance of this is perhaps made clear with an analogy. Rather than pests and crop damage, consider that this relationship described the severity of an illness in an individual with increasing pathogen load. Understanding this relationship allows better treatment of the individual through measuring levels of pathogen. For instance, early detection may enable treatment. Conversely, if the disease is progressed, and if resources are limited, triage may be utilised to prioritise those more likely to recover. As in medicine, where the progression of symptoms is used to determine treatment, so too must a density to damage relationship be used in pest management for allocating resources.

The challenge, however, is that determining this relationship is difficult. For instance, data should ideally be collected over a sufficiently long period of time to ensure outbreak densities are observed, ideally multiple times, but with a sufficiently large number of spatial replicates to allow reliable estimation. Further, estimates of damage would need to be suitably measured via experimental manipulation and not approximated. In combination with reliable estimates of damages, reliable estimates of densities would be required, ideally using capture-recapture methods. These aspects would also need to consider that damage may be variable over space within a field,
requiring that estimates of density and damage are spatially explicit. Finally, these aspects would need to be balanced with stakeholder use in mind, where decisions are made at the field level, despite damage potentially occurring at a smaller scale. These considerations, some of which were met in chapter II, would result in a research programme with high investment requirements, where the result may lack certainty (chapter II; Huitu et al., 2009; Pfeffer et al., 2021), perhaps suggesting why the question is not well represented in the literature. However, despite the difficulties associated with establishing this relationship, the fundamental importance of this strictly requires that this question be addressed within research programmes investigating pest management. Without such information, the management of pests is at risk of being qualitative, where a view forms that the removal of any pests constitutes successful management (e.g., Labuschagne et al., 2016).

**Pest outbreaks may become more common and more severe**

Conservation agriculture is defined as practices that promote minimal soil disturbance (via no-tillage) and permanent soil cover combined with crop rotations (Hobbs, Sayre & Gupta, 2007). The method is attractive to various stakeholders, though often for different reasons: for farmers in semi-arid agricultural regions, no-tillage is favoured as it increases soil water retention and reduces soil erosion (Palm et al., 2014); for conservationists, the method is favoured as it increases biodiversity (Gayer et al., 2021); for those involved with climate change, the method is favoured as it is believed to increase carbon sequestration. This has resulted in the increased and increasing adoption of conservation agriculture across the globe. However, in chapter III, I show that this method also increases the proportion of experimental plots occupied by common voles. Indeed, further research suggests this is not an isolated case study. Similar trends have been observed with the same species in Czechia (Heroldová et al., 2018), and more recently, the same relationship has been described in Australia with house mice (Ruscoe et al., 2021), which, at the time of writing, are experiencing an exceptionally large outbreak. This is highly suggestive that rodent outbreaks may become more widespread and severe in the future as conservation agriculture also becomes more widespread.

As various stakeholders promote conservation agriculture, the use of the practice becomes intertwined with ecology, economics, and sociology. Indeed, the very reason why conservation agriculture is a problem for pest management is that the method
promotes wildlife (Gayer et al., 2021), representing the justification of the method from a conservation and biodiversity standpoint. In truth, pests occurring more frequently in conservation agriculture prove that the method effectively promotes wildlife in an agri-environment. This represents a win-win scenario for climate change (Mondal et al., 2020; but see Smith et al., 2005), biodiversity, and farming economics, with the sole dissenting voice being pest management.

A further reason why outbreaks may become more common, including those mentioned above, is that they may occur infrequently. Specifically, when outbreaks may not occur for multiple years and how this may affect how individuals perceive their specific risk of pest damage. For example, in a study of flood insurance uptake, Gallagher (2014) demonstrated that homeowners in the US consistently underestimated their risk of flooding, even in flood-prone areas and despite information on flood risk being readily available. Further, with increasing time since the last flooding event (analogous to outbreaks occurring once every few years), homeowners were less inclined to insure, suggesting that people forget the lessons previously learned from a natural disaster. Indeed, the dominant driver of flood insurance appeared to be representation on media. I see no reason to believe that such a relationship does not also occur with outbreking pest species, though with a caveat that declines in perceived risk over time are likely less severe given that outbreaks are somewhat more predictable (i.e. an outbreak will occur sometime between 3-5 years) than stochastic events such as flooding. Then, it appears reasonable to assume that farmers may similarly underestimate their respective risk of experiencing an outbreak.

There appear to be various forces leading to fossorial rodent crop pests becoming a greater threat to food security. First, a farming practice, which inadvertently promotes pest occupancy, is becoming increasingly adopted. Second, the farming practice is favoured by multiple stakeholders. Third, the increased risk of outbreaks can be underestimated or forgotten. I believe these factors may culminate in rodent crop pest outbreaks becoming more severe and widespread. Indeed, evidence of this appears to be emerging (Ruscoe et al., 2021).

**The challenge of extracting predictions from theory**

Within chapters IV and V, I used the theoretical literature to inform and guide the predictions and model parameterisations and confront these with empirical data.
However, it was often the case that drawing conclusions from theoretical work was challenging for predominantly two reasons.

First, it is often unclear within the theoretical literature what prediction can be drawn from their analyses. Theoretical studies appear to come in two flavours. The first are abstract theoretical simulations whose aim is merely to describe what could happen in a given setting. More biologically relatable models can subsequently be developed, using the abstract theoretical work as their foundation. This approach often results in predictions that can be confronted with empirically collected data (e.g., Sherratt et al., 2003). The second flavour of theoretical studies are those which seek to mimic patterns observed in nature. Questions arise as to whether such studies merely represent one of a multitude of ways to generate the same pattern, which may or may not capture the biological truth, yet are undoubtedly able to imitate the same pattern. From such studies, it can be unclear if the method used to mimic the pattern reflects a genuine data generating process and, as a result, a testable hypothesis or prediction.

Second, what information is required to test a prediction? Parameters used and specifications of simulations can often include impossible or unfeasibly difficult information to gather in the real world. For instance, theory investigating travelling waves will often include a dispersal parameter, most often described as a proportion of individuals who disperse. However, dispersal itself contains three components, emigration, transience and successful immigration, where the question becomes which proportion should be measured to account for “dispersal”. The use of dispersal as a proportion then is difficult to determine in wild populations reliably, and secondly, obfuscates distinct processes of dispersal into a single catch-all term. While the use of simplified parameters which caricature ecological processes is understandable, given the complexity in nature, the use of such parameters hinders the translation from theory into operational data collection and predictions to inform empirical research. However, confounding these issues is that the predictions made, portrayed as testable, require data that is near perfect (i.e., data collected at spatial and temporal scales that are unfeasible in reality).

The importance of theoretical work for guiding empirical research is clear and well encapsulated in chapters IV and V. The above criticisms should not be viewed as a denouncement of theoretical work but rather as a plea to help empiricists make the most of the wealth of knowledge contained in theoretical studies. This is particularly
important in research concerning travelling waves, where suitable datasets are incredibly rare, meaning that much of the understanding of travelling waves originate in theory. In such a scenario, having a well-developed, prescriptive theoretical backbone is vital to ensure the most effective use of these rare datasets.

**Travelling waves in an applied context**

Because of the wealth of theoretical literature, which was able to guide and inform empirical research, in chapter VI, I highlighted that the common vole population in Spain cycles in a partially synchronous manner. An important applied implication for accurately describing the synchrony of a system is that great care must be taken when attempting temporal predictions of outbreaks of pest species across large regions if the assumption of true synchrony is incorrectly made. If a temporal prediction were made in our study site, then there would have to be an attempt to account for the spatial asynchrony caused by the waves, where common voles may be outbursting in some areas but not others (Fig. 1A). Given that predictions with assumed true synchrony could be used to determine the risk of region-wide outbreaks and offer advice to farmers at risk of crop damage, at worst, half of the farmers may prepare for an imminent outbreak that does not materialise for some time (Fig. 1B). In systems where social tension already occurs regarding pest management (Lauret et al., 2019), causing a further loss of trust due to imprecise or flawed predictions of outbreaks could be detrimental for managing pest species.

**Figure 6:** A shows the predicted growth across space on day 1639 (January 2016) for the selected travelling wave model (model RDE, see chapter IV for details), while B shows the predicted growth across space for the same day based on the model which assumed
spatial synchrony (model $N_2$), as would be used in a simple temporal prediction of growth rates. Day 1639 was chosen as this was a period when growth rates shifted towards high growth from low.

However, understanding a spatio-temporal pattern may itself offer some information for practitioners. Depending on how quickly the outbreak spreads, early preparations against the effects of an outbreak may be feasible. In cases where they are, management could use areas affected first by an outbreak as an early warning, giving others in the region time to prepare. However, this approach is highly dependent on the speed at which the pattern itself spreads. For example, the cumulative pattern described in chapter IV and V is estimated to travel at $< 1$ km per day, meaning that farms 30 km may have a 30-day grace period to prepare for an outbreak, with increasing distance increasing the grace period. Such a period may be sufficient to allow some form of preparation, dependent on the farming cycle, e.g., planting unfavourable crops (Roos et al., 2019) or harvesting slightly early.

By extension, the speed that the pattern of growth rate spreads in CyL may enable more targeted monitoring to occur. Focusing resources in the two epicentre locations, especially the one believed to be the activator epicentre, may allow this early detection of a region-wide outbreak. However, this potential is highly uncertain. Although the forms of travelling waves in chapter IV and V are more complex than previously considered, they still contain various necessary simplifications. For the purpose of using these for informing outbreak risk, a crucial simplification worth highlighting is that the epicentres are fixed in time and space. That is, epicentres were static. Similarly, speed in chapter IV was considered invariant, though chapter V sought to determine if they may be density-dependent. These simplifications mean that the models did not allow for epicentres to vary in location. It may be perceived that theory suggests that epicentres are indeed static, though, to my knowledge, this is because theory has not considered the possibility of dynamic epicentres. This oversight in theory is perhaps justifiable when the epicentre hypothesis is invoked, as some landscapes may be considered suitably static, therefore supporting the notion that epicentres too are static. However, given that agricultural landscapes are inherently dynamic, so too may the epicentre locations vary across space over time, with changes to local farming practices. The use of the spatio-temporal patterns, described in chapters IV and V, as an early warning system must be with due caution. By no means should all resources be
expended in the epicentre locations; however, some level of regular monitoring in these regions may allow the predictive ability to be tested. A benefit to the ongoing monitoring by ITACyL is that a further four years of data have now been collected. As such, future incarnations of the research presented in this thesis will have access to an ever-increasing pool of data to test the claims made herein.

Concluding remarks

Through researching the dynamics and ecology of a rodent pest, I have developed understandings that are of immediate use to practitioners and, further, laid the foundations for future work to be carried out that is better able to make actionable predictions of outbreaks. In doing so, I uncover a rarely observed spatio-temporal phenomenon but also develop our understanding of them.

References


## Additional outputs

Throughout my PhD I was involved in additional academic and scientific projects not related to my own research. Below I list those worth noting, a brief summary of the work, my role in the work, and where they can be found (if applicable).

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