POPULATION DYNAMICS IN VOLES:
Characterization and modelling of global spatio-temporal patterns

PhD Thesis

Rubén Bernardo-Madrid

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POPULATION DYNAMICS IN VOLES:
Characterization and modelling of global spatio-temporal patterns

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CERTIFY:
That the research work developed in the Doctoral Thesis Report "***Population dynamics in voles: Characterization and modelling of global spatio-temporal patterns***", are suitable to be presented by Mr. Rubén Bernardo Madrid before the committee that will be appointed in due course, to aspire to the degree of Doctor of Philosophy by the University of Seville.

And for the record, and in compliance with the legal provisions in force, they sign this document in Seville, on May 14, 2021.

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"If we wish to control outbreaks of locust, defoliating insects, or rats and mice; if we wish to conserve endangered species, manage grizzly bears and other animals in the national parks; if we wish to help politicians save our fisheries from collapse…we must first understand the principles of population ecology."

Dennis Chitty, 1996

"If I have seen further, it is by standing upon the shoulders of giants"

Isaac Newton, 1676

A mis padres,
a Susana,
a Marta,
a mí

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Abstract

Population fluctuations of rodents have always aroused human interest due to their importance in ecosystems and human welfare. However, their scientific study became especially relevant in the late 19th and early 20th centuries when Robert Collet and Charles S. Elton described periodic eruptions of lemmings and voles. Since then, hundreds of theoretical, experimental, and field works have provided a basis for understanding the mechanisms underlying the different population fluctuations observed in nature. However, the generality of these mechanisms across different species and geographic areas remains one of the greatest unknowns in ecology; posing a problem for understanding natural ecosystems, as well as for managing species and their effects on human welfare. This dissertation takes advantage of the vast amount of data and knowledge on vole population dynamics to test the existence of general demographic mechanisms, as well as to identify predictors of events such as plagues to better understand and manage these species.

This dissertation compiles nearly 70 years of capture-mark-recapture data from 17 trapping areas with weekly, biweekly and monthly sampling frequency from five populations of four vole species in North America and Europe (*M. agrestis* = 4 sampling areas or spatiotemporal replicates, *M. ochrogaster* = 4, *M. pennsylvanicus* = 5 and *M. townsendii* = 4); being to date the largest database of rodent demographic data with high temporal resolution (monthly resolution or higher).

Subsequently, this dissertation analyses whether part of the inter-annual fluctuations is produced by common demographic mechanisms in different species and geographic areas (e.g. similar variations in survival, reproduction or migration). But to do so, it first overcomes one of the main obstacles in the study of population dynamics of rodents and many other species, the relatively low number of observations to make models sufficiently complex and informative to understand population dynamics. Specifically, this thesis proposes an extension of traditional capture-mark-recapture models, using regularization techniques widely used in different fields of statistics such as in the calculation of random effects, in order to estimate demographic parameters under conditions of relatively low data availability. With this new analysis tool, whose usefulness goes far beyond the study of rodent demography (e.g. elusive species or species with low densities such as some endangered species), this dissertation estimates the abundances and vital rates of the four vole species in the 17 sampling areas at a fine enough temporal scale to study biological models that allow an adequate understanding of their population dynamics.

This dissertation uses these estimated demographic parameters to evaluate the existence of common general patterns. The results show not only the existence of such common demographic mechanisms, but also suggest their great relevance; reopening an interesting debate on the relative importance of common and specific factors in the origin of population fluctuations. Furthermore, by testing predictions of the most accepted hypotheses in the scientific community, it showed that feeding and social interactions are more likely underlying these common demographic patterns.

Finally, the dissertation shows how theoretical knowledge about population dynamics can be used to solve or mitigate a human welfare problem, such as vole outbreaks. Specifically, this dissertation identifies an early warning signal capable of predicting outbreaks of the common vole (*M. arvalis*) one year in advance in Castilla y León (Spain). This predictor facilitates farmers and regional government to take preventive measures to mitigate the impact of vole outbreaks in crop fields.

Complementarily, this dissertation proposes an approach to solve an important but little discussed problem in applied ecology, which is that erroneous predictions entail costs for users. This dissertation proposes an approach to measure the usefulness of predictors in decision making by considering their hit and error rate (statistical aspect) as well as the expenses, effectiveness, and indirect effects of the treatment to be applied based on the predictions (management aspect). This last contribution aims that scientific researches proposing predictive models explicitly indicate their usefulness for each potential user; which can enhance and improve its use in applied ecology.

In general, this dissertation focuses on vole population dynamics from a basic, theoretical, and applied ecology point of view. On the one hand, it provides fundamental theoretical knowledge to understand the generalities of vole population dynamics, as well as vole outbreaks in Mediterranean environments. On the other hand, it provides diverse conceptual and analytical approaches with great multidisciplinary utility. All this together makes the present dissertation an important key piece in future research in various fields of science.

Resumen

Las fluctuaciones poblacionales de roedores han despertado siempre el interés humano debido a su importancia en los ecosistemas y en el bienestar humano. Sin embargo, su estudio científico empezó a ser especialmente relevante a finales del siglo XIX y principios del XX cuando Robert Collet y Charles S. Elton describieron las erupciones periódicas de lemmings y topillos. Desde entonces, cientos de trabajos teóricos, experimentales y de campo han proporcionado una base para entender los mecanismos que subyacen a las diferentes fluctuaciones poblacionales observadas en la naturaleza. Sin embargo, la generalidad de estos mecanismos a lo largo de las diferentes especies y áreas geográficas sigue siendo una de las mayores incógnitas de la ecología; lo que supone un problema para comprender los ecosistemas naturales, así como para gestionar las especies y sus efectos en el bienestar humano. Esta tesis aprovecha la amplia cantidad de datos y conocimientos sobre las dinámicas poblacionales de topillos para testar la existencia de mecanismos demográficos generales, así como para identificar predictores de eventos como las plagas que permitan entender y gestionar mejor estas especies.

En primer lugar, esta tesis recopila casi 70 años de datos de captura-marcado-recaptura en 17 áreas de muestro con frecuencia de muestreo semanal, quincenal y mensual de cinco poblaciones de cuatro especies de topillos en Norteamérica y Europa (*M. agrestis* = 4 áreas de muestreo o réplicas espacio-temporales*, M. ochrogaster* = 4*, M. pennsylvanicus* = 5 y *M. townsendii* = 4); siendo hasta la fecha la mayor base de datos demográficos de roedores con alta resolución temporal (i.e., resolución mensual o mayor).

Posteriormente, esta tesis analiza si parte de las fluctuaciones interanuales se producen por mecanismos demográficos comunes en diferentes especies y áreas geográficas (e.g. variaciones similares en la supervivencia, reproducción o migración). Pero para ello, antes supera uno de los principales obstáculos en el estudio de la dinámica poblacional de los roedores y de muchas otras especies, la relativa baja cantidad de observaciones para realizar modelos lo suficientemente complejos e informativos para entender las dinámicas poblacionales. En concreto, esta tesis propone una extensión de los modelos de captura-marcado-recaptura tradicionales, mediante el uso de técnicas de regularización ampliamente utilizadas en diferentes campos de la estadística como en el cálculo de los efectos aleatorios, y así poder estimar parámetros demográficos en condiciones de relativa baja disponibilidad de datos. Con esta nueva herramienta de análisis, cuya utilidad va mucho más allá del estudio de la demografía de roedores (e.g. especies esquivas o con bajas densidades como algunas en peligro de extinción), esta tesis estima las abundancias y tasas vitales de las cuatro especies de topillo en las 17 áreas de muestro a una escala

temporal lo suficientemente fina como para poder estudiar modelos biológicos que permitan una adecuada comprensión de sus dinámicas poblacionales.

Esta tesis utiliza esos parámetros demográficos estimados para evaluar la existencia de patrones generales comunes. Los resultados muestran no sólo la existencia de tales mecanismos demográficos comunes, sino que también sugieren su gran relevancia; reabriendo un interesante debate sobre la importancia relativa de los factores comunes y específicos en el origen de las fluctuaciones poblacionales. Además, esta tesis pone a prueba las predicciones de las hipótesis más aceptadas en la comunidad científica sobre los factores causales que subyacen a las variaciones demográficas (e.g. la alimentación, la depredación o las interacciones sociales). Los resultados sugieren que el alimento y las interacciones sociales podrían ser los factores causales detrás de las variaciones en las tasas vitales que producen los patrones comunes.

Por último, la tesis muestra cómo el conocimiento teórico sobre la dinámica poblacional puede utilizarse para resolver o mitigar un problema de bienestar humano, como las plagas de topillos. En concreto, esta tesis identifica una señal de alerta temprana capaz de predecir las plagas de topillo campesino (*M. arvalis*) con un año de antelación en Castilla y León (España). Este predictor facilita que agricultores y gobierno regional tomen medidas preventivas para mitigar el impacto de las plagas de topillo en los campos de cultivo.

Complementariamente, esta tesis propone un enfoque para solventar un problema importante pero poco discutido en ecología aplicada como es que las predicciones erróneas conllevan gastos para los usuarios. En particular, esta tesis propone un enfoque para medir la utilidad de un predictor en la toma de decisiones considerando la tasa de acierto y error (aspecto estadístico) y los costes, efectividad, y efectos indirectos del tratamiento que se aplicará en base a las predicciones (aspecto de gestión). Esta última contribución tiene como objetivo que las investigaciones científicas que proponen modelos predictivos indiquen explícitamente su utilidad para cada posible usuario; lo que puede potenciar y mejorar el uso de predictores en ecología aplicada.

En general, esta tesis se centra en las dinámicas poblacionales de topillos desde un punto de vista de la ecología básica, teórica, y aplicada. Por un lado, proporciona un conocimiento teórico fundamental para entender las generalidades en las dinámicas poblacionales de topillos, así como de las plagas de topillos en ambientes mediterráneos. Por otro lado, proporciona diversos enfoques conceptuales y analíticos con una gran utilidad multidisciplinar. Todo esto junto hace que la presente tesis pueda ser una pieza importante clave en investigaciones futuras de diversos campos de la ciencia.

GENERAL INTRODUCTION

Origin of the study of population fluctuations

Population fluctuations of rodents always aroused human interest and imagination. Proofs of this are the references to lemmings scrawled in the margin of the Norwegian version of the Bible, written by its translator, or the myths about lemmings' suicide shown in documentaries and video games (e.g. Walt Disney's documentary *White Wilderness*; Stenseth and Ims 1993, Turchin 2003, Coulson and Malo 2008). Although these references are merely anecdotal, they reflect society's historical fascination with rodents' population fluctuations and their importance in society. From a scientific point of view, the main interest dates back to the early 20th century due to the studies of Charles S. Elton and his colleagues.

Elton's first contact with the "population fluctuations of wild animals" was fortuitous as undergraduate student. While returning to England in 1923 from his second expedition in Spitsbergen, Svalbard, Elton stopped at a bookstore in Tromsø and saw Robert Collett's *Norges Pattedyr* (Norwegian mammals; Collet 1912, Pond et al. 2015). Although Elton did not understand Norwegian, he noticed that Collett's data suggested regular fluctuations in the abundance of Norwegian lemmings (Turchin 2003). Elton thus decided to spend one of his last three English pounds on Robert Collett's book, and translated it himself with the help of a dictionary to understand such interesting patterns (Crowcroft 1991, Pond et al. 2015). Elton's ideas about population fluctuations were also influenced by *The Population Problem* (1922) of Alexander Carr-Saunders and *The Conservation of the Wild Life of Canada* (1921) of Gordon Hewitt, focusing respectively on human populations and population fluctuations of the snowshoe hare and the Canadian lynx in Canada (Crowcroft 1991, Pond et al. 2015). The result was one of the classic studies of ecology (Elton 1924). His growing interest led to the study of reports from the Hudson's Bay Company in North America about regular temporal fluctuations in the number of furs, which allowed studying the population dynamics of several species at large spatio-temporal scales (see details in The Elton Archive; Pond et al. 2015). In parallel, Elton, together with his colleagues John Baker and E.B. Ford, decided to study the drivers of the population fluctuations of lemmings in Norway. But due to economic constraints, they eventually focused on an equivalent in a woodland near their workplace in Oxford, Wytham woods. They chose the wood-mice and the bank-vole, which became to population ecologist what the fruit fly is to geneticists (Crowcroft 1991, Chitty 1996). Elton, Baker, and Ford trapped 2,000 wood-mice and bank-voles during 600 nights between 1925 and 1928, performing the first systematic study of population fluctuations (Pond et al. 2015). From this data, they undertook respectively the study of parasites, breeding biology, and protozoology (Pond et al. 2015). Altogether, these researches were not only the seed of the *Bureau of the Animal Population*, but also the starting point of a journey that almost 100 years later still continues, and whose destination is the understanding of population fluctuations and its drivers; what Dennis Chitty (1996) called the “pursuit of the ecological Holy Grail”.

The importance of population fluctuations in voles

Population dynamics, how and why populations change in size and structure over time, are at the core of ecology due to their influence on ecosystem and evolutionary processes and community structure (Hairston et al. 1960, Allen 1976, Gurney and Lawton 1996, Begon et al. 2006, Schowalter 2016). Nevertheless, it may not be so obvious why some scientists seem to have a certain predilection or even obsession with vole population fluctuations, especially with periodic wave-like variations in abundance (i.e., cyclic fluctuations; Clarke 1949; Krebs 1996). It could be said that there is an intellectual need to explain one of the most prominent ecological phenomena that has fascinated and tormented ecologists, mathematicians, or epidemiologists for almost a century. However, Stenseth (1999) perfectly showed the relevance of studying population fluctuations beyond cycles with his statement: "*before we properly explain why some populations exhibit cycles and others do not, we cannot honestly say that we understand population dynamics*". In addition, without this knowledge, we cannot understand more complex systems such as ecological communities (Hastings 1997). Thus, if we want to prevent and reduce the impact of pests, protect threatened species, control farming and fisheries production and conserve ecological communities, we arguably must understand the demographic and causal mechanisms of all population dynamics (Chitty 1996). Another relevant factor that explains the abundance of studies about population ecology in voles is the relative short duration of research projects such as doctoral theses. To study population fluctuations of species like mammals in short term periods, we must focus on species with rapid life cycles like voles (Krebs 2013). And last but not least, voles are one of the most abundant small mammals in many grassland communities, so their population fluctuations have important consequences on community structure and human well-being (e.g. crop damage and disease transmission; Babinska-Werka 1979, Rose and Birney 1985, Mougeot et al. 2019, Rodríguez-Pastor et al. 2019, Jacob et al. 2020). These theoretical, practical, and management reasons explain why voles are model species (Chitty 1996) and why their population fluctuations, especially those of microtines, are the most studied in ecology and the subject of study of this dissertation.

In the following sections of this introductory chapter, I will summarize the general biology of microtines, the current knowledge about demographic patterns, the gaps in knowledge that still exist, and the objectives of this dissertation.

Biology of microtines

Microtines (subfamily: *Microtinae*) are distributed in open habitats such as semi-marshy, grassy and shrubby areas and unharvested forage crops (Gromov and Polyakov 1992, Yoccoz and Ims 1993, Fergus 2003, Luque-Larena et al. 2013, see Getz 1985 for a review of habitat factors most influencing their local distribution). Most species are associated with mesic or humid habitats and feed on grasses, sedges and seeds (Getz 1985, Gromov and Polyakov 1992). Demographic rates and population growth rates vary across the phases of the inter-annual population fluctuations (i.e., increase, peak, decline, and low density phases; e.g., Stenseth 1999, Crespin et l. 2002, Klemola et al. 2002, Ozgul et al. 2004). The average life span varies between species but it is usually less than one year (Krebs 1966, Getz et al. 1960). Average adult weight is usually below 60 g (Myers and Krebs 1971, Krebs and Myers 1974, Douglass 1977, Tamarin 1977, Nadeau 1985, Balciauskas et al. 2012).

Populations are structured by age and reproductive activity, and their individuals can be classified as pups, juveniles, and reproductive and non-reproductive adults (Fig. 1.1). Because of the different reproduction and survival rates of these classes, population composition has a major influence on population dynamics. Annual survival rates at the nest (i.e. pups) are the lowest and commonly range from more than 70% to less than 30%, but can reach 0% (Boyce and Boyce 1988, Lambin 1994a, Getz et al. 2000). Juveniles have lower survival rates than adults, and both vary in the different phases of the population dynamics (see below; Boonstra and Rodd 1983, Getz et al. 2000, Norrdahl and Korpimäki 2002).

Breeding occurs mainly from early spring to late autumn, or whenever the plant growing season is, but may vary between species and years (Krebs et al. 1969, Krebs and Myers 1974, Douglass 1977, Fernández-Salvador et al. 2005, Smith et al. 2006, Myers 2018). Several species have induced ovulation (Clulow and Mallory 1970) and pregnancy varies between species but is usually about 21 days (Fitch 1957, Hasler 1975, Cowan and Arsenault 1954, Klirkpatrick and Valentine 1970, Nadeau 1985, Gustafsson et al. 1980, Yoccoz et al. 1993). The average litter size depends on the species, parity, age, season and conditions of the breeding colony, but generally ranges from two to eight pups, with the first litter being often smaller (Keller and Krebs 1970, Hasler and Banks 1975, Innes 1978, Nadeau 1985, Innes and Millar 1994, Lambin 1997). The weight of the pups at birth ranges from 2 to 3 g (see a review by Nadeau 1985) and weaning occurs at approximately 17 to 20 days of age (Clulow and Mallory 1970). Average weight at sexual maturation ranges from 20 to 40 g and may be lower for males (Nadeau 1985, Ozgul et al., 2004). However, the age of first reproduction is bimodally distributed with a large phenotypic variation depending on the biotic and abiotic factors surrounding voles. Age at first reproduction is strongly affected by the timing of delivery and the potential number of offspring that voles may have in the breeding season of their birth year (Lambin and Yoccoz 1991, Ergon 2003). During a given breeding season, overwintered females and those born early in spring have the potential to breed up to eight litters (e.g. Lambin 1997), while for females born later in the season, the number of litters produced decreases since the breeding period for those individuals is shorter. There is a trade-off between somatic growth and reproduction and survival. When individuals breed, they reach larger body sizes, but their survival decrease (Lambin and Yoccoz 1991, Roff 1992, Ergon 2003). Thus, individuals born in spring and mid-summer may follow different reproductive strategies depending on their chances of producing a larger number of offspring. Individuals in the last cohorts of the reproductive period must decide between (i) increasing their body size and reproducing quickly, producing a reduced number of cohorts due to the relatively short remaining duration with favorable conditions; or (ii) waiting their reproduction until the following year, keeping their body size small to require less energy and survive better until the next breeding season and thus have a longer period with favorable breeding conditions (Boonstra 1989, Tkadlec and Zejda 1995, 1998, Lambin and Yoccoz 1991). In some species females have a postpartum oestrus (Myllymäki 1977, Bondrup-Nielsen and Ims 1990). Under optimal conditions, females may give birth every three weeks and have at least 4-5 litters in their lifetime (Krebs and Myers 1974, Stentseth and Framstad 1980, Boyce and Boyce 1988, Lambin 1997). In addition, distribution of oestrus females can vary spatially and temporally (Ims 1987), which affects social environment for males and then social organization (Loughran 2007).

The social organization of microtines results from different behaviours associated with factors such as social structure, mating system, and parental care (see Wolff 1985 for a review). The mating system can vary between and within species, from monogamous to polygamous or promiscuous, and within a population according to population density and sex fitness (i.e., optional mating systems); but they are commonly promiscuous and polygamous (Jannett 1978, Wolff 1985, Lambin and Krebs 1991, Getz et al. 1993, Fernández-Salvador et al. 2005, Shuster et al. 2019). Range and territoriality vary according to species, sex and seasons, and play an important role in limiting the breeding of individuals (Wolff 1985, Lambin and Krebs 1991, Lambin 1994b, Wolff 2007, Andreassen et al. 2013). Female phylopatry and male biased dispersal are common (Greenwood 1980, Lambin and Krebs 1991, Lambin 1994b, Ostfeld and Canham 1995, Pusenius et al. 1998, Borkowska and Ratkiewicz 2008; Gauffre et al. 2009). Dispersal often occurs at the start of the maturation of individuals, and its intensity varies in between seasons and years according to population densities (Krebs et al. 1979, Gaines and McClenaghan 1980, Stenseth 1983, Wolf 1993, Huitu et al. 2003; see more details on vole biology in Tamarin 1985).

In general, voles are known by having one of the highest reproduction rates among mammals, allowing them to vary the size of their populations by more than 20 times in a few months (Myers and Krebs 1974, Caughley 1977). Their social structure and the high spatial-temporal variability in their demographic responses allows for complex population fluctuations, including population outbreaks and cyclical population fluctuations, two of the most interesting phenomena in population ecology.

Generality of the demographic mechanisms

Population ecology aims to discover why populations change in density and why patterns vary among different populations (Chitty 1960). Temporal variations in population growth rates results from changes in the demographic rates defined by key demographic mechanisms: survival, reproduction, immigration and emigration. Temporal variations in demographic rates result from the effect of extrinsic and intrinsic causal factors, such as predation, food availability or social interactions. Certainly, the main objective of population ecology is to understand causal mechanisms, and their generality, and thus be able to predict and manage population fluctuations. However, no attempt to disentangle the mystery of any population fluctuations can afford to ignore the demographic mechanisms. Due to different demographic processes being able to cause similar population fluctuations (e.g. a same population increases can result from higher survival, reproductive or immigration rates), and because testing hypotheses requires concrete predictions, we must first understand the demographic mechanisms (Oli and Dobson 1999, Ozgul et al. 2004, Krebs 2013).

In the last decades, and especially between the 1950s and 1980s, there was an increasing amount of research that provided insight into the role demographic mechanisms, consolidating the field of population ecology. By examining and comparing different studies, researchers have showed that the survival rates of pups, juveniles and adults are higher during the increasing phases than during the low phases, and these in turn are higher than those during the declining phases (Chitty and Chitty 1962, Krebs 1964, Krebs and Myers 1974, Gaines and Rose 1976, Beacham 1980a, Getz et al. 2000; but see Krebs and Myers 1974, Boonstra 1985, Agrell et al. 1992). In general, there is ample theoretical and observational evidence that survival of voles, and juveniles in particular, is one of the most important, if not the most important, demographic mechanism (Hoffman 1958, Krebs 1966, Krebs 1972, Norrdahl and Korpimäki 1995; but see Oli and Dobson 2003).

With regard to reproduction, previous studies have evaluated the patterns of different demographic parameters such as the length of the breeding season, pregnancy rate and litter size during different population phases. Long breeding seasons are associated with increasing phases, especially breeding periods that begin earlier and end later than normal, even continuing through the winter (Sutton and Hamilton 1932, Dunaeva and Kucheruk 1941, Nasimovich et al. 1948, Krebs 1964, Keller and Krebs 1970, Krebs and Myers 1974; but see Zejda 1962, Smyth 1966). Whereas declining phases have been related to breeding seasons that abnormally start later and end earlier (Godfrey 1955, Kalela 1957, Krebs 1966, Keller and Krebs 1970, Ergon et al. 2001, Norrdahl and Korpimäki 2002, Ergon 2003). Complementarily, peak phases have been related to breeding season that often ends abnormally early (Thomson 1955a, Kalela 1957, Koshkina and Khalansky 1962, Zejda 1967, Krebs and Myers 1974). In general, most studies agree that the length of the breeding season not only is a general demographic mechanism but also one of the most important (Koshkina and Khalansky 1962, Krebs and Myers 1974, Norrdahl and Korpimäki 2002, Krebs 2013).

Unlike the length of the breeding season, most studies did not find variations of pregnancy rates across population phases (Kalela 1957, Krebs 1964, Keller and Krebs 1970, Norrdahl and Korpimäki 2002). But there is more controversy about the general patterns in litter size. Whereas some studies support that litter size does no vary across population phases (Thompson 1955, Kalela 1957, Hoffman 1958, Krebs 1964, Koshkina 1966), other ones found that litter size is higher during the increase and peak phases (Hamilton 1937, Bodenheimer 1949, Hoffman 1958, Koshkina and Khalansky 1962, Norrdahl and Korpimäki 2002). Complementarily, another set of studies has suggested that litter size is constant in the different phases, except in the peak phase, when it is smaller (Hoffman 1958, Patric 1962, Tanaka 1964, Keller and Krebs 1970). However, due to litter size being probably affected by body size, parity, and season of the year, these results may not be conclusive and the existence of general patterns is unclear (Krebs and Myers 1974, Krebs 2013).

With regard to the age of sexual maturity, some studies have suggested a key role for understanding population fluctuations (Cole 1954, Krebs and Myers 1974, Oli and Dobson 2003). Increasing phases have been related to earlier ages in sexual maturity (Koshkina and Khalansky 1962, Krebs and Myers 1974), while declining phases have been related with sexual maturity being reached in older ages (Keller and Krebs 1970). Certainly, the absence of a general pattern when using the weight at sexual maturity, as a proxy for maturation, could question the general role of the age at maturity (e.g. Keller and Krebs 1970). However, it may be explained by the lower growth rates of individuals during the different phases (Krebs et al. 1969, Krebs and Myers 1974).

Finally, with regards to dispersal, some experimental studies have suggested that dispersal may be an important factor regulating population densities. In particular, previous studies have shown how enclosed populations reach much higher densities than those observed in natural populations (Clarke 1955, Houlihan 1963, Louch 1956). Although these densities were achieved by providing supplemental food (Krebs and Myers 1974), other studies using enclosed populations, natural forage, and allowing predators to be present observed similar results (Gentry 1968, Krebs et al. 1969). Increasing phases have been related to the highest dispersal rates, whereas declining phases to the lowest ones (Myers and Krebs 1971). In contrast, some studies support that emigration rates are not density dependent (Gaines and McClenaghan 1980, Lidicker 1985, Ostfeld 1994) and that there is a high uncertainty with the results from many studies because their lack of replicates or disparate outcomes (Ostfeld 1994).

In summary, previous studies have provided strong evidences about the existence of multiple and concrete general demographic mechanisms across populations and species in determining wide population fluctuations in voles.

Knowledge gaps

Despite the body of knowledge acquired, the role that demographic mechanisms have on inter-annual population fluctuations remains conditional on species or even population, while the general picture is still fuzzy. The lack of adequate analytical tools for early studies on population dynamics resulted in the use of indirect indices of demographic parameters (e.g. indices of abundance; Krebs et al. 1969, Gaines and Rose 1976). Although these studies provided a great deal of information and partially served to cement our knowledge of population dynamics, the reliability of their inferences could be questioned by the use of indices that are known to suffer from important biases (Anderson 2003).

The emergence of capture-recapture analysis was a turning point in allowing the estimation of demographic parameters in a more robust way. However, these analytical tools require large numbers of captures of individuals that are rarely available when studying population fluctuations of voles (Morris et al. 2006, Kéry 2018). For example, the number of available captures may be low in absolute terms in those populations during winter or during the low phase due to the natural low abundance of the population, or may be low in relative terms because we can only obtain information from one part of the population (e.g., the low capturability of pups and juveniles). To mitigate the lack of estimates in some periods or groups, it is common to pool the data and make inferences on a larger scale (e.g., Desy and Batzli 1989). However, some resolutions are often not good enough to understand the drivers of population fluctuations at some periods (Yoccoz et al. 1998, Stenseth et al. 1999).

While some more recent studies have obtained population estimates with adequate resolution to assess the demographic mechanisms of their populations (e.g. Oli and Dobson 1999), studies aiming at making inference across populations and species require a great deal of data (i.e. populations and species worldwide distributed). One possibility to achieve them is to design new studies, but there are major funding and time constraints to do this in a relatively short time. Another more plausible possibility is to re-analyse old data with modern methodologies that allow obtain new insights. Certainly, the use of these data, or at least their collection, could be a "simple" task if the data were recent, since nowadays both researchers and scientific journals are making great efforts to store the data in repositories so that they can be used by future generations (Reichman et al. 2011, Michener 2015). However, most of the data on vole population fluctuations were collected when digital repositories did not exist and most of them were in field notebooks and outdated storage systems (e.g. tapes, cards, floppy disks) that are being lost for different reasons such as loss, mismatch, or deterioration of those storage systems, as well as retirement and passing away of the owners (Vines et al. 2014). Worryingly, the rate at which these data are disappearing may be faster than the rate at which new long-term studies suitable for answering the above questions are carried out. Therefore, we run the risk of losing very valuable information, while reducing the possibility of understanding general demographic mechanisms.

On the other hand, the assessment of the existence of general patterns has been made through comparisons of individual studies by way of discussion (e.g. Myers and Krebs 1974, Graham and Lambin 2002), but no studies have assessed and quantified the existence of general demographic mechanisms statistically.

Finally, one of the objectives of understanding the mechanisms triggering population fluctuations is to mitigate the impact of population outbreaks on human welfare (e.g. crop damage and zoonotic diseases). Since the 1990s, an increasing number of studies aimed to predict rodent outbreaks (e.g. Mutze et al. 1990, Leirs et al. 1996, Pech et al. 1999, Zhang et al. 2003). But although these studies have provided very good basic knowledge about possible predictors of outbreaks, little effort has been made to show their usefulness in practical decision-making (but see Davis et al. 2004). Most studies providing predictive models have assessed model performance from a statistical point of view, without taking into account that wrong decisions based on model predictions have costs for users; and then that how good is the hit-and-error rate of a model is relative to the expenses, effectiveness and indirect effects of the preventive treatments that would be applied. Since the latter conditions may vary among users, new research approaches are needed to ensure that studies explicitly report on the usefulness of predictive models to any potential user.

In summary, during this last century a great effort has been made to improve our understanding of vole population fluctuations, but there are still methodological, theoretical and practical challenges that need to be overcome before we have a clear overview of the patterns and mechanisms behind population fluctuations in voles as well as we understand the real usefulness of predictive models in applied ecology.

Objectives

The general objective of this dissertation is to facilitate and improve the understanding of the demographic mechanisms of population fluctuations, as well as to encourage their use in practical cases. Since this is a very general issue difficult to address in one go, the dissertation has focused on four specific objectives addressed in different chapters.

In **Chapter I**, we aim to compile old capture-recapture data of vole populations in North America and Europe in order to assess whether there are general demographic patterns and mechanisms driving population fluctuations. This chapter is the result of a global collaboration with many of the researches that studied population fluctuations of voles. The chapter describes in detail the data used in **chapter III** to better understand possible inferences reached later. **Chapter I** could also be considered as part of the material section of **chapter III**, but given that the collection, standardization, and digitalization of old data is a major goal in science, and a necessary task in data about vole populations, we included their details as a separate chapter.

In **Chapter II**, we aim to provide a new statistical tool capable of providing population estimates even when data are scarce. Vole databases collected in **chapter I** have a low absolute and relative number of captures in some periods, when classical capture-recapture models may fail to estimate demographic parameters and do not allow us to answer our biological questions (**chapter III**). To overcome this limitation, we developed an extension of the existing capture-recapture models. In particular, we proposed a regularization of the demographic estimates by penalizing variation away from the assumed (constant) average with smoothing priors. The result are biased estimates into some tolerable degree in exchange for reducing their variance (Efron and Morris 1975, Efron and Hastie 2006, Greenland 2000, Greenland 2012, Cole et al. 2013), but that are useful to answer our questions. In **chapter II** we compared the demographic parameters obtained with traditional capture-recapture model and with our approach using data from simulated populations with a relative high number of captures, in simulated populations with a relative low number of captures, and in a real vole population. We aim to show the correct functioning and advantages of our approach as well as its contribution to answer questions at fine temporal resolution that could not be answered to date.

In **Chapter III**, we aim to assess whether there are general demographic mechanisms driving population fluctuations. In particular, we re-analysed the databases collected in **chapter I** with the capture-recapture model developed in **chapter II** in order to obtain adequate parameter estimates also in moments when population abundances are very low. On that basis we studied simultaneously all demographic parameters to find out if there are general demographic mechanisms across populations and species. In particular, we assessed whether population growth rate anomalies, deviations of the population growth rate to the observed common inter-annual seasonal trajectory, were caused by the same demographic mechanisms (i.e. variations in apparent survival rates and transition rates between reproductive status). To provide insights on the role of these common mechanisms in driving inter-annual populations, we quantified the proportion of population growth rate anomalies explained. Complementarily, by assuming that causal factors such as food, predation and social interactions influence demographic rates in a particular way and at particular periods of the year, we tested their predictions and provide some clues about factors behind common demographic patterns.

In **Chapter IV**, we aim to predict vole outbreaks using the knowledge available on causal mechanisms, and to increase and improve the use of predictive models in applied ecology. We used previous knowledge on the causal mechanisms of vole outbreaks to predict the population outbreaks of *Microtus arvalis* in Castilla y León (Spain). Complementarily, we proposed a methodological approach to show how and when users (farmers, managers, or policy-makers) can benefit from the use of predictive models in their decision-making.

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CHAPTER I

Metadata of capture-mark-recapture of *Microtus* species in North America and Europe

Introduction

Ecologist have long been trying to understand population fluctuations of small mammals and their generalities. To achieve this goal requires not only information on the demographic parameters of many species and geographic areas, but also at high temporal resolution. Here, we compiled a dataset that includes capture-recapture data with weekly, biweekly, and monthly resolution for 17 grids, distributed across North America and Europe, of five *Microtus* populations: *M. townsendii* (4 grids / 1 population), *M. pennsylvanicus* (5 grids / 2 populations), *M. ochrogaster* (4 grids / 1 population), and *M. agrestis* (4 grids / 1 population). See Fig. 1 for details. This metadata describes 119,535 vole captures along 67 years (i.e. the sum of the years with sampling in each grid), being the most comprehensive dataset on capture-recapture data of small mammals. This dataset will help to better understand demographic patterns of small mammals, providing essential information for basic and applied research from the local to the global perspective.

We first provide a brief description of the four *Microtus* species included in the metadata, and then describe in detail the information collected in each grid by following the recommendations of Michener et al. (1997).

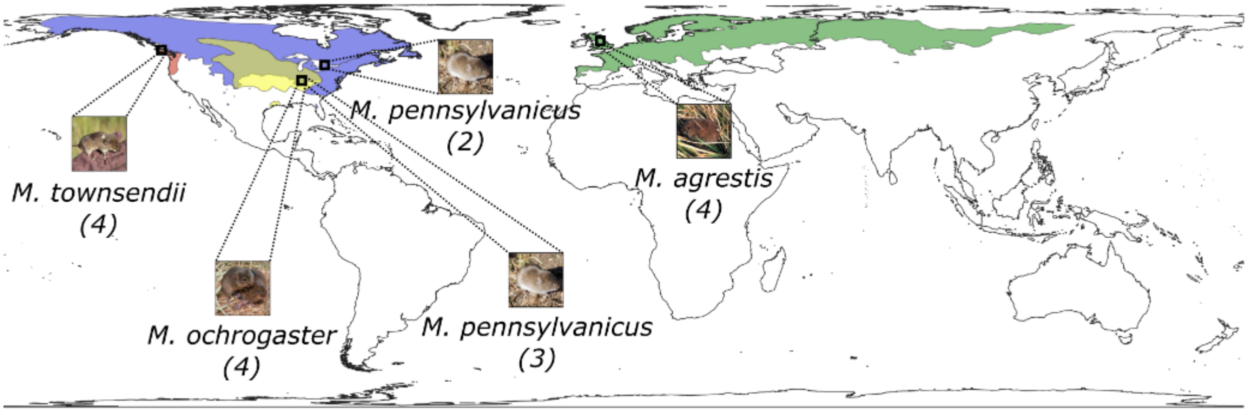

Fig. 1 | Distribution range of the four *Microtus* species described in this metadata: red polygon = Distribution range of *M. townsendii*; yellow = *M. ochrogaster;* purple = *M. pennsylvanicus*; and green = *M. agrestis.* Information obtained from the IUCN (2021). The four grids of *M. townsendii* are near Vancouver, Canada. The four grids of *M. ochrogaster* coincide with three grids of *M. pennsylvanicus* in Indiana, USA. There are two other grids of *M. pennsylvanicus* in Toronto, Canada. The four grids of *M. agrestis* are in Kielder forest, United Kingdom. See details in main text.

Species description

Microtus townsendii

The Townsend's vole (*M. townsendii*) has a relative narrow distribution restricted along the northwest coast of the United States, partially occupying the states of Washington, Oregon, and California, and along the southwest coast of Canada partially occupying the state of British Columbia (Cassola 2016; Fig. 1). *Microtus townsendii* is phylogenetically related to *M. canicaudus, M. montanus* and *M. pennsylvanicus* (Jaarola et al. 2004). Townsend's voles are in grasslands including in alpine and subalpine conditions, from sea level to elevations of 1,800 m. *M. townsendii* is a burrowing species associated with riparian zones, that inhabits mostly grasslands, but also salt and fresh marshes, moist meadows, and wetlands along streams, which are often near oak or mixed conifer forest (Cassola 2016, Fletcher 2019).

Townsend's voles are short-haired and stout-bodied rodents. Their fur is dark-brown on the back, while grey on the belly, and the fur of adolescent vole is usually darker than that of adults. The tail and feet are also black or brown. For more details on the species and the differences from other *Microtus* species, see details provided by Cornely and Verts (1988). *Microtus townsendii* is one of the largest *Microtus* spp. Adult voles have an average total length between 165 and 225mm and weight between 47 and 83g (Cornely and Verts 1988, Jones et al. 2009; Fig. 2). Previous studies have noted that Townsend's voles reach maturity at weights of 40-49 g; however, according to our data collected, females may reach maturity at lower weights (i.e. at 30 g; Table 1). Their life span in the wild is near one and half years (Fletcher 2019). Common breeding season is in April-July (Fletcher 2019; Fig. 3). Townsend's voles can have up to eight litters, varying averages across geographical areas (Anderson and Boonstra 1979, Lambin 1997, Jones et al. 2009). The gestation period ranges from 21 to 24 days, while the weaning age ranges from 13 to 17 days (Anderson and Boonstra 1979, MacFarlane and Taylor 1982, Lambin 1997).

Townsend's voles can be monogamous or polygynous, with both of these mating systems being variable throughout the year (Lambin and Krebs 1991, Boonstra 1977, Krebs 1978). Both male and female breeding Townsend's voles are territorial (Lambin and Krebs 1991). Townsend's populations have a strong sex bias towards females in their natal philopatry (i.e. a higher proportion of females remained near their natal site; Beacham and Krebs 1980, Lambin 1994a).

Species	**Male WSM (g)**	**Female WSM (g)**
M. agrestis	25	20
M. ochrogaster	28	22
M. pennsylvanicus	31	22
M. townsendii	41	30

Table 1 | Observed weight at sexual maturity (WSM) in the 17 grids of the four *Microtus* species. The values are the percentile 5th of the body mass of the breeding males and females. We considered breeding males to those males with testes in scrotal position, while breeding females to those pregnant females and females with open symphysis pubis or large nipples.

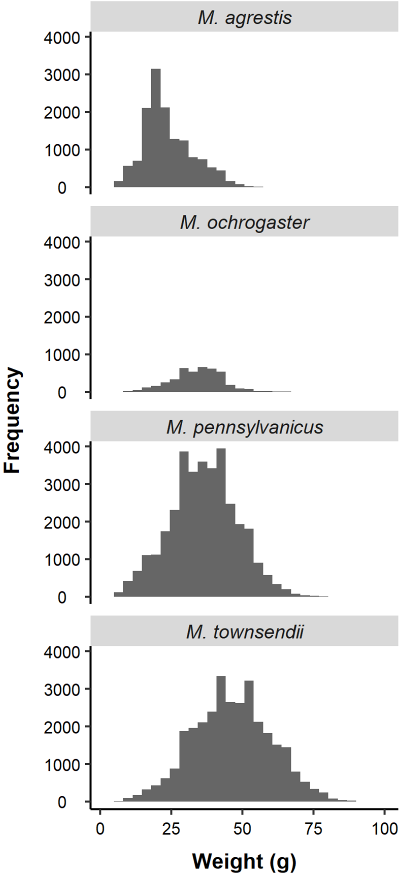

Fig. 2 | Frequency of body masses observed in the 17 grids of the four *Microtus* species (Fig. 1).

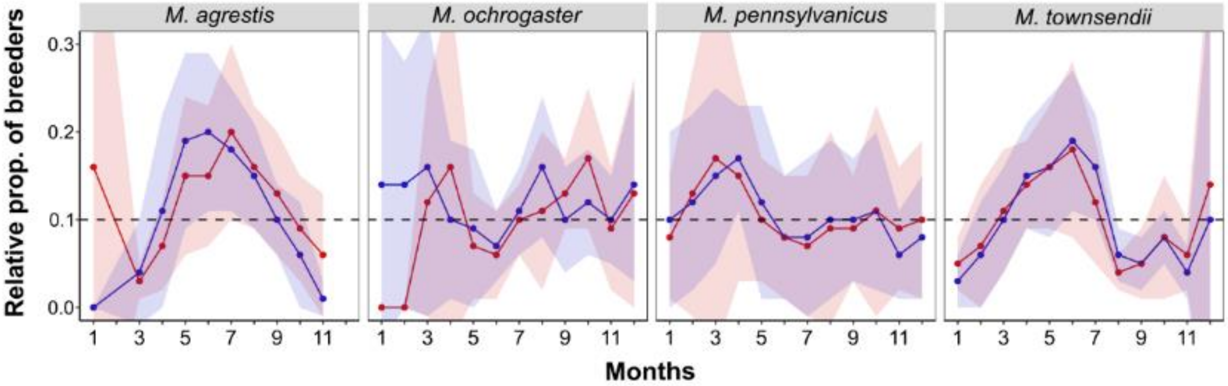

Fig. 3 | Relative proportion of breeders throughout the year. The X-axis represents the months of the year, while the Y-axis represents the proportion of breeders in a month relative to the total number of breeders in a given year. We calculated the relative proportion of breeders for each grid and year combination, and then calculated a summary of those values for the species. The dot represents the mean value, while the shaded areas represent the standard deviation. Red and blue represent, respectively, the values for females and males. The dashed horizontal line at 0.1 aims to illustrate when more than 10% of breeding males and females occur (i.e. values above the line).

M. pennsylvanicus

The meadow vole (*M. pennsylvanicus*) has a wide distribution through the northern half of North America, including northern half of United States and Canada (Reich 1981, Cassola 2016; Fig. 1). *M. pennsylvanicus* is closely related to *M. montanus, M. townsendii* and *M. canicaudus* (see Jaarola et al. 2004 for details). These voles commonly inhabit early successional habitats, such as agricultural fields, sedge marshes, open-canopied bogs, and less frequently in more densely wooded areas. These voles commonly are near to roadways when there is grass coverage for tunneling and nesting (Reich 1981, Rowe 2017).

Females and males have different coloration and their coats have two types of hair, whose coloration varies among individuals. See further details provided by Reich (1981) and Naughton (2012). Adult voles have an average total length between 140 and 195 mm (Reich 1981), and weight between 33 and 54 g (Reich 1981, Jones et al. 2009; Fig. 2). As is reflected in the weights at sexual maturation, females reach sexual maturity earlier than males (20-30 days Vs 35-45 days; Table 1; Rowe 2017). Common life span in the wild can be up to 16 months (Naughton 2012). Common breeding season is in March-November (Rowe 2017), although in our dataset there also was a large proportion of breeders in February (Fig. 1). Meadow voles have an average number of offspring of 4-6 (Rowe 2017). The average gestation period is 21 days, while the weaning age ranges from 12 to 14 days (Reich 1981, Rowe 2017). Meadow voles are polygynous (Madison 1980) and may have a polygynandrous mating system (Boonstra et al. 1993). Female meadow voles are territorial, while males have overlapping home ranges during their mating season (Madison 1980, Webster and Brooks 1981).

M. ochrogaster

The prairie vole (*M. ochrogaster*) has a wide distribution in the prairie states of the north United States and south-central of Canada (Fig. 1). For more details, see Stalling (1990) and Cassola (2016). *M. ochrogaster* is phylogenetically related to *M. californicus* (Jaarola et al. 2004, Abramson et al. 2021), but may be some uncertainty (see classification based on cytochrome b provided by Jaarola et al. 2004). Prairie voles inhabit man-made habitats such as prairies, fallow fields, roads, and agricultural fields

(Swihart and Slade 1984, Whitaker 2010). If meadow vole coexists in an area, prairie voles are restricted to patches with shorter, drier, and more diverse vegetation (Kurta 1995, Stalling 1990).

The prairie vole is a long-haired rodent, usually grayish-brown on the back, while light tan on the belly. Female and male prairie voles do not have different colorations. See Stalling (1990) and VanderLinden (2002) for more details. Adult voles have an average total length ranging from 125 to 180 mm and weight between 30 and 70 g (Stalling 1990, Stalling 1999; Fig. 2 and Table 1). The common life span in the wild is less than 1 year (Stalling 1990, Kurta 1995). The breeding season throughout the year, with the highest activity in May-October (VanderLinden 2002; but see Fig. 3). Prairie voles average four litters per year (Jones et al. 2009), and their litter size depends on the season and the age and size of the female (VanderLinden 2002). The gestation period is about 21 days, while the weaning age is 14-21 days (Stalling 1990).

Prairie voles are monogamous (Getz and Hofmann 1986, Getz and Carter 1996, Young et al. 1998). These voles can form communal groups by addition of philopatric young and unrelated adults (Getz et al. 1993).

Microtus agrestis

The field vole (*M. agrestis*) has a wide distribution through the Palearctic, ranging from western Europe eastwards through Russia to Lake Baikal in south-east Siberia (Fig. 1). See Kryštufek et al. (2017) and Mathias et al. (2017) for details. Its phylogenetical relationship with other species is unclear, but it may be related to *M. cabrerae* (Jaarola et al. 2004, Lamelas et al. 2020). It occurs from sea level to elevations of 2,100 m (Kryštufek et al. 2017). The field vole inhabits a wide range of habitats such as grasslands, woods, marshes and river-banks; but also in anthropogenic habitats such as meadows and field margins (Zima 1999).

Field voles are long-haired rodents. Their fur is grey-brown dorsally (Dienske 1969, Mathias et al. 2017). The tail has a bi-coloured tail (Bernard 1953). The colour of the dorsal surface of the tail is similar to that of the dorsal surface of the animal, while the ventral surface is more grey (Dienske 1969). Although *M. agrestis* voles are similar to *M. arvalis* and *M. oeconomus* voles (i.e. sympatric and parapatric voles; Dienske 1969, Mathias et al. 2017), there are multiple aspects that differentiate them (Dienske 1969). Adult voles have an average length of 90-120 mm and weight of 14-40 g (Krapp and Niethammer 1982, Jones et al. 2009). Female voles usually reach maturity at a weight near 30 g (Ebenhard 1990), although in our dataset females matured at weight of 20 g, while males at 25 g (Table 1). Common life span varies from 16 to 18 months in the wild (Myllymäki 1977, Andera 1981). Common breeding season is in February-October in central Europe (Alibhai and Gipps 1991), but until November or December in other regions (Saint-Girons 1973, Hansson 1984, Erlinge et al. 1990) with a reproductive peak, June–August (Krapp and Niethammer 1982; Fig. 3). Field voles have an average number of offspring of 4-7, varying across geographical regions (Mathias et al. 2017). The average gestation period is about 20 days (Ebenhard 1990, Jones et al. 2009), while the weaning age ranges is about 14 days (Jones et al. 2009). Field voles are commonly polygynous with strictly territorial males (Mathias et al. 2017). See Mathias et al. (2017) for more details about *M. agrestis.*

Metadata

In the following sections, we provide the metadata of the capture-recapture data of the 17 grids used in Chapter. *Microtus townsendii*: G1, G2, C, and E; *M. ochrogaster*: A, F, H, CARLO; *M. pennsylvanicus*: A, F, I in Indiana, and A and F in Toronto; and *M. agrestis*: BHP, KCS, PLJ and ROB. We also included the information of other grids co-occurring in the study area in order to provide all details necessary to understand the whole study system.

Microtus townsendii: grids G1 and G2

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus townsendii* collected near Vancouver, British Columbia. The capture-recapture data is the outcome of multiple studies sampling on two similar grids. The grid names used in this document match with those used in scientific publications.

2 | Information collected in the captures

Voles were marked with a fingerling fish tag into the ear in their first capture. Some individuals had also tie-grip collar radio transmitters in order to locate their nests and pups (see details in Lambin and Krebs 1991 BES). The weight of the transmitters depicted 3.5-7.9% of body mass (Lambin 1997a). Weanlings in their nests were marked by toe clipping and their age and sex determined from external appearance (e.g. visible nipples, hair growth; Lambin 1994b, c). In each capture, the ID of the individual, species name, sex, weight, breeding condition, and trap location was recorded. For females, four metrics about breeding condition were recorded: (1) vagina orifice – perforate or non-perforate, (2) nipples – small, medium, or large, (3) pubic symphysis –closed slightly open, or open, and (4) pregnancy – observed or non-observed (visually and by palpation). In addition, the date of parturition of pregnant individuals was estimated by appearance – more than seven days, between four and seven days, less than four days. For males, just the position of testes was recorded: scrotal or non-scrotal. See further details provided by Lambin (1994).

3 | Collectors of the data

Xavier Lambin

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure of each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

<u>Grid 1</u>

1. Data from January 1988 – September 1991
    1.1. Lambin and Krebs (1993) used grid 1 as an experimental grid to study the relationship between female relatedness and demography.
    1.2. Lambin (1994a) used grid 1 as an experimental grid to study the relationship between dispersal, competition and inbreeding.
    1.3. Lambin (1994b) used grid 1 as an experimental grid to study the relationship between sex ratio and female philopatry.
    1.4. Lambin (1994c) used grid 1 as an experimental grid to study the relationship between the presence of same-sex litter mates and sexual maturation.
    1.5. Lambin (1997) used grid 1 as an experimental grid to study the relationship between female's movements between litters and the settlement of her offspring in the natal range.
    1.6. Lambin and Yoccoz (1998) used grid 1 as an experimental grid to study the relationship between population structure and juvenile survival.
    1.7. Lambin and Yoccoz (2001) used grid 1 as an experimental grid to study the relationship between precocious breeding and reproductive costs.

<u>Grid 2</u>

1. Data from January 1989 - September 1991
    1.1. Lambin and Krebs (1993) used grid 2 as an experimental grid to study the relationship between female relatedness and demography.

1.2. Lambin (1994a) used grid 2 as an experimental grid to study the relationship between dispersal, competition and inbreeding.

1.3. Lambin (1994b) used grid 2 as an experimental grid to study the relationship between sex ratio and female philopatry.

1.4. Lambin (1994c) used grid 2 as an experimental grid to study the relationship between the presence of same-sex litter mates and sexual maturation.

1.5. Lambin (1997) used grid 2 as an experimental grid to study the relationship between female's movements between litters and the settlement of her offspring in the natal range.

1.6. Lambin and Yoccoz (1998) used grid 2 as an experimental grid to study the relationship between population structure and juvenile survival.

1.7. Lambin and Yoccoz (2001) used grid 2 as an experimental grid to study the relationship between precocious breeding and reproductive costs.

5 | Site description

5.1 | Location of study area

The study area was at Boundary Bay airport near Ladner, 35 km south of Vancouver, British Columbia, Canada (49°04' N, 123°00' W). Grid E was also located here (see below in section for grids E, F, U, and S). Grids 1 and 2 were separated by 125 m. They were surrounded in the south by a 7 m wide ditch, in the east by a gravel road, and in the north and west by a 2 m wide strip of grass that was cut in summer. The observation of underground runways corridors in all boundaries suggests that these "boundaries" did not prevent vole movements (Lambin 1994a).

5.2 | Site type and vegetation

The vegetation of the two grids was heterogeneous and undisturbed for more than 40 years (Lambin and Krebs 1993, Lambin 1994a).

5.3 | Geography

Flat reclaimed from the sea grassland.

5.4 | Hydrology

Grid 2 was wetter than grid 1 in winter and spring (Lambin and Krebs 1993).

5.5 | Site history

The grassland in the grids was not altered for more than four decades (Lambin 1994a).

5.6 | Climate

No information is provided.

6 | Experimental sampling design

6.1 | Permanent plots

Grids 1 and 2 were unfenced (Lambin 1997d). The grids harbored individuals of *Microtus townsendii.* But, at least, there also were *Peromyscus maniculatus, Sorex cinereus, Phalageriformes* and different mammal predators such as *Mustela frenata, Canis latrans*, *Lutrinae* spp., and many avian predators such as *Asio flammeus, Circus cyaneus, Bubo scandiacus,* and *Tyto alba*.

6.2 | Sampling design

Grids 1 and 2 had a checkerboard pattern of 170 trap stations. Trap stations were spaced 5 m apart, occupying a total surface of 0.5 ha. Each trap station had one Longworth trap covered with a 20x20 plywood board, which contained cotton and oats (Lambin 1994a). Each grid had an additional line of Longworth traps spaced 10 m apart from the edge of the checkerboard pattern to capture potential dispersal voles (Lambin and Krebs 1993).

Special trapping procedures

In addition to the Longworth traps, one pitfall trap was also located in each trapping station when water table was low, commonly from May to September (Lambin 1994a).

Grids were used in experiments about kinship. Collectors increased the matrilineal family size in one grid by removing immigrants (kin treatment) and reduced it in another by removing all individuals from a same litter, except one female, when they reached 35 g (non-kin treatment; n=106). These treatments were alternated between grids along time. The kin treatment was in grid 2 in 1989, in grid 1 in 1990, and in grid 2 in 1991, whereas the non-kin treatment was in grid 1 in 1989, in grid 2 in 1990, and in grid 1 in 1991 (Lambin 1997, Lambin and Yoccoz 1998).

In the grids with the kin treatment, collectors covered the grid in winters of 1989-90 and 1990-91 with fishing nets to prevent predation by birds, especially by *Ardea herodias* (Lambin and Yoccoz, 1998)

6.3 | Data collection period and sampling frequency

Grid 1: 15,310 records of *M. townsendii,* from February 1988 to September 1991

Grid 2: 10,418 records of *M. townsendii,* from December 1988 to September 1991

Sampling frequency

Weekly sampling during the breeding period and biweekly the rest of the year (Lambin and Krebs 1993, Lambin 1994a). In the breeding period, traps were set in the morning and checked at 2-h intervals, between three and six times per day. There also were some complementary traps outside the trapping session to capture postpartum females (Lambin 1994a). In the non-breeding period, traps were also set in the morning and checked at 5-h intervals and were left set overnight. To avoid vole deaths because capture, the traps were left closed during the day when temperature was extremely high.

Microtus townsendii: grids C, D, and W

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus townsendii* collected in a location near Vancouver, British Columbia. In the Thesis, we only used information collected in grid C. However, to understand the full details of the sampling, we also provided information on data collected in two complementary and simultaneously sampled grids located in the same study area (grids D and W). The grid names used in this document match with those used in scientific publications. Data collection in the different grids has different goals. Therefore, the design, period, and sampling frequency may partially vary between grids. See details of each grid in the specific sections below.

2 | Information collected in the captures

Voles were ear-tagged and a blood sample from the suborbital sinus was drawn at first capture. In each capture, the ID of the individual, species name, sex, weight, breeding condition, trap location and the presence of bot flies was recorded. For females, four metrics about breeding condition were recorded: (1) vagina orifice – perforate or non-perforate, (2) nipples – small, medium, or large, (3) pubic symphysis –closed slightly open, or open, and (4) pregnancy – observed or non-observed (visually and by palpation). For males, just the position of testes was recorded: scrotal or non-scrotal. The weight was measured with spring scales and rounded to the closest gram (Redfield et al. 1977, Boonstra et al. 1980). For some individuals, information about aggressiveness was also collected in laboratory conditions (see below; Krebs 1970, Krebs et al. 1978).

3 | Collectors of the data

Charles J. Krebs, James A. Redfield, Mary Taitt, Rudy Boonstra, and Terry D. Beacham

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure for each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

Grid C

1. 1971 – 1974
    1.1. Boonstra et al. (1980) used grid C as a control grid to study the impact of botfly parasitism on *Microtus townsendii* populations.
2. May 1971 - December 1973
    2.1. Krebs et al. (1976) used grid C as a control grid to study the relationship between population growth and dispersal.
3. May 1971- June 1975
    3.1. Krebs et al. (1978) used grid C as a control grid to study the relationship between dispersal and performance.
4. July 1972 - July 1974
    4.1. Redfield et al. (1977) used grid C as a control grid to study competition between *Microtus* sp. and *Peromyscus* sp.

Grid D

1. May 1971 - December 1973
    1.1. Krebs et al. (1976) used grid D as an experimental grid, i.e. removal grid, to study the relationship between population growth and dispersal.
2. May 25, 1971- June 18, 1975
    2.1. Krebs et al. (1978) used grid D as an experimental grid, i.e. removal grid, to study the relationship between dispersal and performance.
3. July 1972 - July 1974

        3.1. Redfield et al. (1977) used grid D as an experimental grid, i.e. removal grid, to study competition between *Microtus* sp. and *Peromyscus* sp.

<u>Grid W</u>

1. May 7, 1973 - June 18, 1975
    1.1. Krebs et al. (1978) used grid W as an experimental grid, i.e. pulsed removal grid, to study the relationship between dispersal and performance.

5 | Site description

5.1 | Location of study area

The three live-trapping grids were in the Serpentine Fen, south of Vancouver, British Columbia (B.C), about 5 km to the East of Ladner Airbase, where G1, G2 and grid E were located. Specifically, on the south bank of the Serpentine River, about 2.5 km east of Mud Bay. The study area was on the edge of a 200 ha marsh and was surrounded by drainage ditches on three sides (Krebs et al. 1978). Grids W and D were located at the two corners of the drainage ditches and, consequently, were surrounded by drainage ditches on two sides. See specific details on grid locations in Figure 1 provided by Krebs et al. (1978).

5.2 | Site type and vegetation

The study area was in undisturbed grasslands due to local agricultural practices (Krebs et al. 1976). There were some patches of marshy ground unsuitable for voles, such us thus surrounding grid W on the left, right and lower sides and grid C on the upper side (Krebs et al. 1978).

5.3 | Geography

No information is provided.

5.4 | Hydrology

No information is provided.

5.5 | Site history

The study area remained undisturbed for at least 10 years prior to the trapping (Redfield et al. 1977).

5.6 | Climate

The climate of coastal British Columbia with mild, wet winters and warm, dry summers (Krebs et al. 1976). Although very high and low temperatures were infrequent because the ocean moderated the temperature, in December 1971 a notable snowfall reached 80 cm and snow was on the ground for 15 days. In contrast, the following winter snowfall reached only 28 cm and snow was on the ground for 9 days. The fall of 1972 and spring of 1973 had more hours of sunshine and less rainfall than usual (Krebs eta l. 1976).

6 | Experimental sampling design

6.1 | Permanent plots

Grid C: An unfenced and unmanipulated grid that, at least, harbored individuals of *M. townsendii* but also *P. maniculatus* (Krebs et al. 1976, Redfield et al. 1977, Krebs et al. 1978). No information is provided about the species of the other individuals.

Grid D: An unfenced and manipulated, i.e. removal grid. As grid C it, at least, harbored individuals of *M. townsendii* but also *P. maniculatus* (Krebs et al. 1976, Redfield et al. 1977, Krebs et al. 1978). No information is provided about the species of the other individuals.

Grid W: An unfenced and manipulated, i.e. pulse removal grid. At least, it harbored individuals of *M. townsendii.*

6.2 | Sampling design

The three grids were sampled with Longworth traps and pitfall traps (i.e. live traps). Both types of traps were covered with a lid and board. Each Longworth trap contained rolled oats as well as cotton when set and was covered with a 30x30 cm heavy wooden board. Usually, there was one Longworth trap and one pitfall trap per trapping station (see below the spatial pattern). But, as population abundance increased, more traps were added up to a maximum of two Longworth traps per trap station (Krebs et al. 1976).

Grid C: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha.

Grid D: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha.

Grid W: This grid had 100 trap stations, but was not arranged in the shape of a square due to unsuitable marshy ground on three sides (Krebs et al. 1978). The distribution of trap stations in the grid was: rows 1-5 had trap stations in columns 1-13, rows 6-7 in columns 4-13, and rows 8-11 in columns 10-13.

Special trapping procedures

Grid D: The trapping in this grid was exactly the same as in grid C, except that voles captured were removed from the grid instead of being released.

Grid W: Trapping in this grid had a 12-week trapping cycle. Voles caught in weeks 0, 2, 4, and 6 were released as in grids C and D. In contrast, voles caught in weeks 8 and 10 were removed from the grid. Krebs et al. (1978) assumed that after week 10 there were no more voles in the grid and that voles captured two weeks later (the new week 0) constituted the initial density of the next pulse.

From July 3, 1974 until the study ended of June 1975 adult voles were sampled from the three grids to study aggressiveness in the laboratory (Krebs et al. 1978). These tests were also done on all individuals removed from the grid W. The procedure lasted about two days, and individuals from the control grid (C) were later returned to their grids (Krebs et al. 1978). For further details about the aggression tests, see the information provided by Krebs (1970).

6.3 | Data collection period and sampling frequency

Grid C: 8,071 records of *M. townsendii* from May 25, 1971 to June 18, 1975.
Grid D: 2,993 records of *M. townsendii* from May 25, 1971 to June 18, 1975.
Grid W: 3,033 records of *M. townsendii* from May 7, 1973 to June 18, 1975.

Sampling frequency

The sampling frequency was mostly the same in all grids. Trapping sessions consisted of biweekly trapping sessions. Each primary trapping session had three secondary trapping sessions consisting of three checks of the live traps (Krebs et al. 1978). Traps were opened one afternoon and checked the following morning and afternoon, and again the next morning. When an individual was detected inside a trap during a check, the collectors identified the individuals, noted different traits of the individuals and finally released them (see above). After the third control, the traps were closed until the next primary trapping session, so that voles could enter and exit freely. During the summer months, the traps were left closed during the day to avoid vole mortality due to high temperatures inside the traps.

Microtus townsendii: grids E and F

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus townsendii* collected in Ladner Airbase at Boundary Bay, British Columbia. In the Thesis, we only used information collected in grid E. However, to understand the full details of the sampling, we also provided information on data collected in one complementary and simultaneously sampled grid located in the same study area (grid F). The grid names used in this document match with those used in scientific publications. Data collection in the different grids has different goals. Therefore, the design, period, and sampling frequency may partially vary between grids. See details of each grid in the specific sections below.

2 | Information collected in the captures

Voles were ear-tagged and a blood sample from the suborbital sinus was drawn at first capture. In each capture, the ID of the individual, species name, sex, weight, breeding condition, trap location and the presence of bot flies was recorded. For females, four metrics about breeding condition were recorded: (1) vagina orifice – perforate or non-perforate, (2) nipples – small, medium, or large, (3) pubic symphysis –closed slightly open, or open, and (4) pregnancy – observed or non-observed (visually and by palpation). For males, just the position of testes was recorded: scrotal or non-scrotal. The weight was measured with spring scales and rounded to the closest gram (Redfield et al. 1977, Boonstra et al. 1980). For some individuals, information about aggressiveness was also collected in laboratory conditions (see below; Krebs 1970, Krebs et al. 1977, Krebs et al. 1978).

3 | Collectors of the data

Charles J. Krebs, James A. Redfield, Mary Taitt, Rudy Boonstra, Terry D. Beacham, Zuleyma Tang Halpin, James N.M. Smith

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure for each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

Grid E

1. 1971 – 1976
    1.1. Boonstra et al.(1980) used grid *E* as a control grid to study the impact of botfly parasitism on *Microtus townsendii* populations.
2. May 1971 - December 1973
    2.1. Krebs et al.(1976) used grid *E* as a control grid to study the relationship between population growth and dispersal.
3. January 1975 - May 1975
    3.1. Krebs et al.(1977) used grid *E* as a control grid to study the relationship between aggressiveness and spring population declines.
4. July 1972 - July 1974
    4.1. Redfield et al.(1977) used grid *E* as a control grid to study competition between *Microtus* sp. and *Peromyscus* sp.

Grid F

1. 1971 – 1976
    1.1. Boonstra et al.(1980) used grid *E* as a control grid to study the impact of botfly parasitism on *Microtus townsendii* populations.
2. May 1971 - December 1973
    2.1. Krebs et al.(1976) used grid *F* as an experimental grid, i.e. removal grid, to study the relationship between population growth and dispersal.
3. July 1972 - July 1974

3.1. Redfield et al.(1977) used grid *F* as an experimental grid, i.e. removal grid, to study competition between *Microtus* sp. and *Peromyscus* sp. All *M. townsendii* and *M. oregoni* were removed.

5 | Site description

5.1 | Location of study area

The study area was located in the southwest corner of a former airport complex called as Ladner Air Force Base, near Vancouver, British Columbia. The study area contained grids E and F. See Figure 1 provided by Redfield et al. (1977) for details about their spatial distribution.

5.2 | Site type and vegetation

The study area was in several hundred acres of grassland undisturbed by local agricultural practices (Krebs et al. 1976). The Ladner Air-base study area is a drier location than the Serpentine Fen (i.e. study area in which grid C was located; Krebs et al. 1976).

5.3 | Geography

No information is provided.

5.4 | Hydrology

No information is provided.

5.5 | Site history

The grassland area was undisturbed for at least 10 years prior to the study by Redfield et al. (1977).

5.6 | Climate

The climate of coastal British Columbia with mild, wet winters and warm, dry summers (Krebs et al. 1976).

6 | Experimental sampling design

6.1 | Permanent plots

Grid E: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. townsendii*, *M. oregoni* and *Peromiscus maniculatus* (Krebs et al. 1976, Redfield et al. 1977).

Grid F: An unfenced and manipulated grid, i.e. all *Microtus* spp. were removed. The grid harbored, at least, individuals of *M.* t*ownsendii*, *M. oregoni* and *Peromiscus maniculatus* (Krebs et al. 1976, Redfield et al. 1977).

6.2 | Sampling design

The grids were sampled with Longworth traps (i.e. live traps), which were covered with heavy board (Redfield et al. 1977). Each Longworth trap contained rolled oats as well as cotton when set and was covered with a 30x30 cm heavy wooden board. Usually, there was one Longworth trap and one pitfall trap per trapping station (see below the spatial pattern). But, as population abundance increased, more traps were added up to a maximum of two Longworth traps per trap station (Krebs et al. 1976).

Grid E: This grid had a checkerboard pattern of 5x20 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha.

Grid F: This grid had a checkerboard pattern of 5x20 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha.

Special trapping procedures

All *Microtus* spp. were removed from grid F. For the last two and a half months of the study performed by Redfield et al. (1977), *Microtus* species were no longer removed from grid F.

6.3 | Data collection period and sampling frequency

Grid E: 9,861 records of M. townsendii from June 7, 1971 to October 22, 1976.

Grid F: 1,622 records of M. townsendii from June 7, 1971 to August 13, 1975.

Sampling frequency

Trapping sessions consisted of biweekly trapping sessions. Each area was live trapped one day and two nights, except in the summer months, when only night trapping was conducted (Krebs et al. 1978). Longworth live traps were left in place between trapping periods and locked so that voles could enter and exit freely.

Microtus ochrogaster and *M. pennsylvanicus*: grids A, F, H, I Carlo, J and K (Indiana)

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus ochrogaster* and *M. pennsylvan*icus collected in a location close to Indiana University, EE.UU. In the Thesis, we only used information collected in grids A, F, H, I, and Carlo. However, to understand the full details of the sampling, we also provided information on data collected in two complementary and simultaneously sampled grids located in the same study area (grids J and K). The grid names used in this document match with those used in scientific publications. Data collection in the different grids has different goals. Therefore, the design, period, and sampling frequency may partially vary between grids. See details of each grid in the specific sections below.

2 | Information collected in the captures

Voles were ear-tagged at first capture, with a numbered and lettered fingerling fish tag into the right ear. In each capture, the ID of the individual, species name, sex, weight, breeding condition, trap location and the presence of bot flies was recorded. The weight was measured with spring scales and rounded to the closest gram. For females, four metrics about breeding condition were recorded: (1) vagina orifice – perforate or non-perforate, (2) nipples – small, medium, or large, (3) pubic symphysis –closed slightly open, or open, and (4) pregnancy – observed or non-observed (visually and by palpation). For males, just the position of testes was recorded: scrotal or non-scrotal (Krebs et al. 1969, Gaines and Krebs 1970).

3 | Collectors of the data

Charles J. Krebs, Barry L. Keller, Robert H. Tamarin, Michael S. Gaines, and Judith H. Myers.

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure for each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

Grid A

1. June 1965 - August 1967
    1.1. Krebs et al. (1969) used grid "A" as a control grid, i.e. unfenced and unmanipulated, to study demographic changes in fluctuating populations.
2. June 1965 - September 1967
    2.1. Krebs (1970) used grid "A" as a control grid, i.e. unfenced and unmanipulated, to study behavioral changes in voles because of population fluctuations.
    2.2. Tamarin and Krebs (1969) used grid "A" as a control grid, i.e. unfenced and unmanipulated, to study the relationship between the genetic composition of individuals and population fluctuations.
3. July 1967 - April 1970
    3.1. Myers and Krebs (1971a) used grid "A" as a control grid, i.e. unfenced and unmanipulated, to study the relationship between the sex ratio and population growth.
4. Period: July 1967 - August 1969
    4.1. Gaines and Krebs (1971) used grid "A" as a control grid, i.e. unfenced and unmanipulated, to study the relationship between the genetic composition of individuals and population fluctuations.
5. Undefined
    5.1. Krebs and Boonstra (1979) used grid "A" as a control grid to analyze the survival rates of large- and small-size adults in fluctuating vole populations.
    5.2. Krebs and Boonstra (1984) used trapping data from grid "A" to compare different estimates of trappability.

   5.3. Boonstra et al. (1987) used trapping data from grid “A” to study natal philopatry and dispersal in vole populations.
   5.4. Krebs (1977) used grid “A” as a control grid to study competition between *M. pennsylvanicus* and *M. ochrogaster.*

Grid B

1. June 1965 - August 1967
   1.1. Krebs et al. (1969) used grid “B” as an experimental grid to study demographic changes in fluctuating populations.
2. June 1965 - September 1967
   2.1. Krebs (1970) used grid “B” as an experimental grid to study behavioral changes in voles because of population fluctuations.
   2.2. Tamarin and Krebs (1969) used grid “B” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
3. July 1967 - August 1969
   3.1. Gaines and Krebs (1971) used grid “B” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
4. May 1969 - May 1970
   4.1. Gaines et al. (1971) used grid “B” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
5. Undefined
   5.1. Krebs and Boonstra (1984) used trapping data from grid “B” to compare different estimates of trappability.
   5.2. Boonstra et al. (1987) used trapping data from grid “B” to study natal philopatry and dispersal in vole populations.
   5.3. Krebs (1977) used grid “B” as an experimental grid to study competition between *M. pennsylvanicus* and *M. ochrogaster.*

Grid C

1. June 1965 - August 1967
    1.1. Krebs et al. (1969) used grid “C” as an experimental grid to study demographic changes in fluctuating populations.
    1.2. Krebs and Tamarin (1973) used grid “C” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
2. August 1965 - September 1967
    2.1. Krebs (1970) used grid “C” as an experimental grid to study behavioral changes in voles because of population fluctuations.
3. May 1969 to May 1970
    3.1. Gaines et al. (1971) used grid “C” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.

Grid D

1. June 1965 - August 1967
    1.1. Krebs et al. (1969) used grid “D” as an experimental grid to study demographic changes in fluctuating populations.
    1.2. Krebs and Tamarin (1969) used grid “D” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
2. June 1965 - September 1967
    2.1. Krebs (1970) used grid “D” as an experimental grid to study behavioral changes in voles because of population fluctuations.
3. July 1967 - August 1969
    3.1. Gaines and Krebs (1971) used grid “D” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.

4. May 1969 - May 1970
    4.1. Gaines et al. (1971) used grid “D” as an experimental grid to study the relationship between the genetic composition of individuals and population fluctuations.
5. Undefined
    5.1. Krebs and Boonstra (1984) used trapping data from grid “D” to compare different estimates of trappability.
    5.2. Boonstra et al. (1987) used trapping data from grid “D” to study natal philopatry and dispersal in vole populations.
    5.3. Krebs (1977) used grid “D” as an experimental grid to study competition between *M. pennsylvanicus* and *M. ochrogaster.*

<u>Grid F</u>

1. July 1967-April 1970
    1.1. Myers and Krebs (1971a) used grid “F” as a control population, i.e. unfenced and unmanipulated, to study the genetic, behavioural, and reproductive attributes of dispersing voles.
2. July 1967 - August 1969
    2.1. Gaines and Krebs (1971) used grid “F” as a control population, i.e. unfenced and unmanipulated, to study the genetic changes in fluctuating vole populations.
3. Undefined
    3.1. Krebs and Boonstra (1979) used grid “F” as a control population, i.e. unfenced and unmanipulated, to analyze the survival rates of large- and small-size adults in fluctuating vole populations.

Grid H

1. June 1967 - May 1969
   1.1. Myers and Krebs (1971b) used grid "H" as a control population, i.e. unfenced and unmanipulated, to study the relationship between the sex ratio and population fluctuations.
2. July 1967 - August 1969
   2.1. Gaines and Krebs (1971) used grid "H" as a control population, i.e. unfenced and unmanipulated, to study the genetic changes in fluctuating vole populations.
3. Undefined
   3.1. Krebs and Boonstra (1984) used trapping data from grid "H" to compare different estimates of trappability.
   3.2. Boonstra et al. (1987) used trapping data from grid "H" to study natal philopatry and dispersal in vole populations.
   3.3. Krebs (1977) used grid "H" as a control grid to study competition between *M. pennsylvanicus* and *M. ochrogaster*.

Grid I

1. July 1967- April 1970
   1.1. Myers and Krebs (1971a) used grid "I" as a control population, i.e. unfenced and unmanipulated, to study the genetic, behavioral, and reproductive attributes of dispersing voles.
2. June 1967 - May 1969
   2.1. Myers and Krebs (1971b) used grid "I" as a control population, i.e. unfenced and unmanipulated, to study the relationship between the sex ratio and population fluctuations.
3. July 1967 - August 1969

    3.1. Gaines and Krebs (1971) used grid "I" as a control population, i.e. unfenced and unmanipulated, to study the genetic changes in fluctuating vole populations.
4. Undefined
    4.1. Krebs and Boonstra (1979) used grid "I" as a control population to analyze the survival rates of large- and small-size adults in fluctuating vole populations.
    4.2. Krebs and Boonstra (1984) used trapping data from grid "I" to compare different estimates of trappability.
    4.3. Boonstra et al. (1987) used trapping data from grid "I" to study natal philopatry and dispersal in vole populations.

Grid J

1. February 1968 - April 1970
    1.1. Myers and Krebs (1971a) used grid "J" as an experimental grid to study the genetic, behavioral, and reproductive attributes of dispersing voles.

Grid K

1. June 1968 - April 1970
    1.1. Myers and Krebs (1971a) used grid "K" as an experimental grid to study the genetic, behavioral, and reproductive attributes of dispersing voles.

Grid Carlson

1. Undefined
    1.1. Myers and Krebs (1971a) used grid "Carlson" as a control grid, unfenced and unmanipulated, to study the genetic, behavioral, and reproductive attributes of dispersing voles.
    1.2. Krebs and Boonstra (1984) used trapping data from grid "Carlson" to compare different estimates of trappability.

1.3. Krebs (1977) used grid “Carlson” as a control grid to study competition between *M. pennsylvanicus* and *M. ochrogaster.*

5 | Site description

5.1 | Location of study area

The main study area harbored the grids “A”, “B”, “C”, “D”, “F”, “I”, “J”, and “K”, and was located on Kent Farm, Monroe County, Indiana, 11.3 km east of Bloomington on the Grasslands Research Area of Indiana University. The additional grid “Carlson” was close to Carlson’s Farm, approximately five km south of the Kent Farm. All those grids were located within a larger study area of Keller and Krebs (1970). Grid “H” was located ca. three km (five miles) northeast of the Kent Farm (Gaines & Krebs 1971).

Grids “A”, “B”, “C”, “D”, and “J” were contiguous on one side of a dirt road, while grids “I”, “K”, and “F” were close but not contiguous on the other side of the dirt road. Grid “A” bordered grid “B” on its east side and a dirt road on its west and north sides. Grid “B” bounded grid “C” on its east side, grid “C” bounded grid “D” on its south side, and grid “D” bounded grid “J” on its east side. Grids “A” and “J” were the farthest apart, as they were separated by almost 200m apart (Myers and Krebs 1971). On the other hand, grids “F”, “I” and “K” were on the west side of the dirt road, about 140m from the grid “A” (see Figure 1 provided by Krebs et al. (1969) and Keller and Krebs (1970) for an aerial view of the study areas, and Figure 1 provided by Myers and Krebs (1971a) for a complete illustration of the distribution of grids “A”, “B”, “C”, “D”, “F”, and “I”.

5.2 | Site type and vegetation

The vegetation of the main study area harboring grids “A”, “B”, “C”, “D”, “F”, and “I” was grassland without any manipulation in the six years prior to the first sampling (Krebs et al. 1969). The area was covered by continuous strips of grassland that allowed the dispersal of animals between unfenced grids (Myers and Krebs 1971). There were small differences in vegetation between grids. Grids “A” and “B” were dominated by fescue, i.e. *Festuca* sp., while grids “C”, and “D” were dominated by orchard grass, i.e. *Dactylis glomerata* (Krebs et al. 1969). For more details on the vegetation of grids "A", "B", "C", and "D" see Table 2 provided by Krebs et al. (1969). Some small tree seedlings colonized the grids, but were removed when they grew. The vegetation was slightly different between compared to the available vegetation (Krebs et al. 1969). No information is provided for grids "H" and "Carlson".

5.3 | Geography

The study area was located in the Norman Plateau, which is characterized primarily by highly dissected ridges with strongly defined drainage lines (Keller & Krebs 1970). Grids "A", "B", "C", "D", "F", and "I" were on terraces that hosted Illinoian outwash deposits (Keller and Krebs 1970). The soil was partially impermeable due to the presence of Mississippian siltstones, preventing rapid percolation of water and triggering flooding (Keller & Krebs 1970). No information is provided for grids "H" and "Carlson".

5.4 | Hydrology

The study area is on a flood plain that is traversed by the North Fork of Salt Creek, a tributary of the Salt Creek drainage basin".

5.5 | Site history

The vegetation of the grids "A", "B", "C", "D", "F", and "I" was unmanipulated at least six years prior to grid establishment (i.e. 1965). In 1970, construction of Monroe Reservoir affected flood and flow control of the creek (Keller and Krebs 1970). No information is provided on grids "H" and "Carlson".

5.6 | Climate

The climate of southern Indiana is continental with abundant precipitation scattered throughout the year and large seasonal fluctuations in temperature. In winter, snow was not infrequent, but its magnitude was not great enough to prevent sampling (Krebs et al. 1969). As soil was usually saturated due to low permeability (see above), local flooding occurs when it rains heavily, commonly between

December and April. Nevertheless, these floods do not substantially affect the survival of individuals (Krebs et al. 1969). Because of weather conditions, some trapping sessions were modified a week earlier or later than planned. See Table 1 provided by Krebs et al. (1969) for monthly measurements of mean temperature, precipitation, sunshine hours, and mean soil temperature for the period between January 1965 to December 1967.

6 | Experimental sampling design

6.1 | Permanent plots

Grid A: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus* (Krebs et al. 1969).

Grid F: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus* (Myers and Krebs, 1971a).

Grid H: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus* (Myers and Krebs 1971)

Grid I: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus* (Myers and Krebs 1971).

Grid J: An unfenced but manipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus, M. pinetorum* and *Synaptomys cooperii*, being these two latter rare species (Myers and Krebs 1971).

Grid K: An unfenced but manipulated grid that harbored, at least, individuals of *M. ochrogaster and M. pennsylvanicus* (Myers and Krebs 1971).

Grid Carlson: An unfenced and unmanipulated grid that harbored, at least, individuals of *M. ochrogaster* (Myers and Krebs 1971).

6.2 | Sampling design

The seven grids were sampled with live traps. In particular, collectors used Longworth traps and pitfall traps. Longworth and pitfall traps were covered with a lid and the board. Specifically, Longworth traps were placed under a 30x30 cm wooden board. We detailed just below the pattern of the live Longworth traps used to capture the individuals:

Grid A: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha (Krebs et al. 1969).

Grid F: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha (Myers and Krebs 1971)

Grid H: We do not know the concrete details about grid “H”, but basing on the comments provided by Gaines and Krebs (1971) as well as the information in the dataset about the location of the individuals (not shown here), we consider that grid “H” had a checkerboard pattern of 9x12, spaced 7.6 m apart.

Grid I: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, occupying a total surface of 0.8 ha.

Grid J: This grid had an irregular shape because the boundaries of the study area. The length of the grid was 121.6m and the width at the widest part 53.2 m. The total area was close to 0.67 ha. In grid “J” there only was 91 trap stations spaced 7.6 m apart, except the ones located in marginal areas that were placed 15.2 m apart (Myers and Krebs 1971a).

Grid K: This grid had 94 trap stations spaced 7.6 m apart, occupying a total surface of 0.73 ha. Unlike grid “F”, grid “H” mostly followed a check pattern of 10x10, but without some trap stations of some rows. Please see details provided in Figure 1 by Myers and Krebs (1971a).

Grid Carlson: We do not know the concrete details about grid “Carlson”, but basing on the comments provided by Myers and Krebs (1971a) as well as the information about the location of the individuals (not show here), we consider that grid “Carlson” also had a pattern and extension like grid “A”.

In each grid, there was a live trap per trap station, i.e. Longworth trap. Nevertheless, as population increased, more traps were added up to a maximum of two Longworth traps per trap station (Krebs et al. 1969). Traps were placed the closer to vole activity (Krebs et al. 1969). Each Longworth trap was covered with heavy board and contained crimped oats (Krebs et al. 1969).

Special trapping procedures

Grids “J”, and “K” had a different sampling frequency and procedure because of the experiment requirements.

Grid “J” was established in February 1968. During the first four consecutive weeks, all voles captured were cropped. specifically, Longworth traps were set on Friday afternoon, checked on Saturday and Sunday mornings, and then left locked open. After this first removal period of four weekends, trapping was done monthly until July 1969, when a normal schedule of biweekly trapping removing all individuals was done (Myers and Krebs 191_EM). Grid “K” was first trapped on June 5, 1968.

Grid “K” was established in June 5, 1968. During the first six weekends, all voles captured were cropped from the population. Later, grid “K” was sampled with a normal schedule of biweekly trapping removing all voles (Myers and Krebs 1971_EM).

6.3 | Data collection period and sampling frequency

Grid A: 1,534 records of *M. ochrogaster* from June 1965 to April 1970.

Grid A: 5,782 record of *M. pennsylvanicus* from June 1965 to April 1970.

Grid F: 721 record of *M. ochrogaster* from May 1967 to April 1970.

Grid F: 808 record of *M. pennsylvanicus* from March 1967 to April 1970.

Grid H: 1,353 record of *M. ochrogaster* from July 1967 to June 1969.

Grid I: 2,253 record of *M. pennsylvanicus* from June 1967 to April 1970.

Grid Carlson (C): 1,135 record of *M. ochrogaster* from March 1968 to April 1970.

Sampling frequency

Trapping sessions were conducted every two weeks, commonly referred to as primary trapping sessions in the robust design. Each primary trapping session had secondary trapping sessions over two days consisting on three live trap checks. Traps were opened one afternoon and checked the following morning and afternoon, and again on the next morning (Krebs et al. 1969, Gaines and Krebs 1970). After the third check, the traps were locked open until the next primary trapping session. During the summer months, the traps were left closed during the day to avoid vole mortality due to high temperatures inside the traps (Krebs et al. 1969).

Microtus pennsylanicus: grids A, B, C, D, E and F (Toronto)

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus pennsylvanicus* collected in two locations near Toronto, Ontario. In the Thesis, we only used information collected in grids A and F. However, to understand the full details of the sampling, we also provided information on data collected in four complementary and simultaneously sampled grids located in the same study area (grids B, C, D and E). The grid names used in this document match with those used in scientific publications. Data collection in the different grids has different goals. Therefore, the design, period, and sampling frequency may partially vary between grids. See details of each grid in the specific sections below.

2 | Information collected in the captures

Voles were ear-tagged at first capture. In each capture, the ID of the individual, sex, weight, breeding condition, and trap location was recorded (Boonstra and Rodd, 1984). For females, four metrics about breeding condition were recorded: (1) vagina orifice – perforate or non-perforate, (2) nipples – small, medium, or large, (3) pubic symphysis –closed slightly open, or open, and (4) pregnancy – observed or non-observed (visually and by palpation). For males, just the position of testes was recorded: scrotal or non-scrotal.

3 | Collectors of the data

Rudy Boonstra, F. Helen Rodd, James A. Hoyle

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure for each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

Grid A

1. June 1978 – May 1982
    1.1. Boonstra and Rodd (1984) used grid A as a control, i.e. unfenced and unmanipulated, to study enumeration efficiency of pitfall traps and live traps.
    1.2. Boonstra and Hoyle (1986) used grid A as a control grid to study competition between *Microtus pennsylvanicus* and the meadow jumping mouse *Zapus hudsonius*.
    1.3. Boonstra (1989) used grid A as a control grid to study the relationship between maturation on the natal area and population fluctuations.

Grid B

1. June 1978 – May 1982
    1.1. Boonstra and Hoyle (1986) used grid B as an experimental grid to study competition between *Microtus pennsylvanicus* and the meadow jumping mouse *Zapus hudsonius*.
    1.2. Boonstra (1989) used grid B as a control grid to study the relationship between maturation on the natal area and population fluctuations.

Grid C

1. June 1978 – May 1982
    1.1. Boonstra and Hoyle (1986) used grid B as an experimental grid to study competition between *Microtus pennsylvanicus* and the meadow jumping mouse *Zapus hudsonius*.
    1.2. Boonstra (1989) used grid C as a control grid to study the relationship between maturation on the natal area and population fluctuations.

Grid D

1. June 1978 – May 1982
    1.1. Boonstra and Hoyle (1986) used grid D as an experimental grid to study competition between *Microtus pennsylvanicus* and the meadow jumping mouse *Zapus hudsonius*.

    1.2. Boonstra (1989) used grid D as a control grid to study the relationship between maturation on the natal area and population fluctuations.

<u>Grid E</u>

1. June 1978 – May 1982
    1.1. Boonstra and Hoyle (1986) used grid E as an experimental grid to study competition between *Microtus pennsylvanicus* and the meadow jumping mouse *Zapus hudsonius*.
    1.2. Boonstra (1989) used grid E as a control grid to study the relationship between maturation on the natal area and population fluctuations.

<u>Grid F</u>

1. June 1978 - July 1981
    1.1. Boonstra and Rodd (1983) used grid F as a control grid to test the hypothesis that breeding female microtines regulate breeding density.

2. July 1978 – May 1982
    2.1. Boonstra and Rodd (1984) used grid F as a control grid to study enumeration efficiency of pitfall traps and live traps.
    2.2. Boonstra (1989) used grid F as a control grid to study the relationship between maturation on the natal area and population fluctuations

5 | Site description

5.1 | Location of study area

Two study areas grids were located near Toronto, Ontario. Grid A, and four other grids, were located 30 km north of Toronto (43°41'N, 79°38'W) near the town of Aurora; hereafter Aurora site. While grid F, and four other grids, were located adjacent to the Toronto International Airport; hereafter Toronto site (Boonstra and Rodd, 1984). The Aurora site was surrounded on three sides by roads, but only two were heavily used. In particular, grid A was bordered on the north side by a road. For a complete aerial view of the Aurora site, see Fig. 1 provided by Boonstra and Hoyle (1986). The Toronto was completely surrounded by roads, but it was not isolated due to the presence of culverts and due to voles can cross the roads (Boonstra and Rodd 1983). Grid F was located on the right side of the study area, preceded on its left side by four other contiguous but not adjacent experimental grids. Grid F was separated from the next by at least 60 m. For a complete aerial view of the study area, see Fig.1 provided by Boonstra and Rodd (1983).

5.2 | Site type and vegetation

Grids A, B, C, D, and E were located in a 10 ha meadow that had previously been pasture and was regularly mowed. Grid F was located on a 10 ha ground dominated by a former field community (Boonstra and Rodd, 1984). In grid A, approximately 60% of the cover consisted of various grasses, with *Agropyron repens* being dominant. Approximately half of grid A was occupied by a dark band of vegetation. In addition, in grid A, *Lotus corniculatus* and *Phleum pratense* was planted prior to the survey, but other invasive species appear such as *Cirsium arvense*. The grass was not mowed during the survey. In grid F, the vegetation consisted of several species of grasses (*Poa pratensis, Poa compressa, Festuca pratensis, Agropyron repens*) and herbs (*Solidago* spp. *Aster* spp. *Asclepia syriaca*, *Melilotus officinalis*, *Geum macrophyllum*, *Bidens frondosa*). For detailed information on the vegetation of grids A, B, C, D, and E, see Table 1 provided by Boonstra and Hoyle (1986).

5.3 | Geography

No information is provided.

5.4 | Hydrology

In grid A, a drainage stream flowed during the spring.

5.5 | Site history

Vegetation in grids A, B, C, D, and E was mowed annually until at least five years prior to the study, when it was abandoned. Before starting the study, *Lotus corniculatus* and *Phleum pratense* were planted (Boonstra and Hoyle 1986).

5.6 | Climate

There were deep snowfalls in all grids, but those in grid F were lower (Boonstra and Rodd 1984).

6 | Experimental sampling design

6.1 | Permanent plots

Grid A: An unfenced and unmanipulated grid that mostly harbored individuals of *Microtus pennsylvanicus*, but, at least, also individuals of *Zapus hudsonius.*

Grid B: An unfenced and manipulated (introduced small cohorts of young voles) grid that mostly harbored individuals of *Microtus pennsylvanicus*, but, at least, also individuals of *Zapus hudsonius.*

Grid C: An unfenced and manipulated (introduced small cohorts of young voles and female removal) grid that mostly harbored individuals of *Microtus pennsylvanicus*, but, at least, also individuals of *Zapus hudsonius.*

Grid D: An unfenced and manipulated (introduced small cohorts of young voles and male removal) grid that mostly harbored individuals of *Microtus pennsylvanicus*, but, at least, also individuals of *Zapus hudsonius.*

Grid E: An unfenced and manipulated (introduced small cohorts of young voles and total removal) grid that mostly harbored individuals of *Microtus pennsylvanicus*, but also, at least, individuals of *Zapus hudsonius.*

Grid F: An unfenced and unmanipulated grid that harbored, at least, individuals of *Microtus pennsylvanicus*.

6.2 | Sampling design

Grid A: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, covering an area of 0.7 ha (Boonstra and Rodd, 1984).

Grid B: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, covering an area of 0.7 ha (Boonstra and Rodd, 1984).

Grid C: This grid had an irregular spatial pattern but also contained 100 trap stations spaced 7.6 m (Boonstra and Rodd, 1984).

Grid D: This grid had an irregular spatial pattern but also contained 100 trap stations spaced 7.6 m (Boonstra and Rodd, 1984).

Grid E: This grid had a checkerboard pattern of 10x10 trap stations, less two trap stations, spaced 7.6 m apart, covering an area of 0.7 ha (Boonstra and Rodd, 1984).

Grid F: This grid had a checkerboard pattern of 10x10 trap stations, spaced 7.6 m apart, covering an area of 0.7 ha (Boonstra and Rodd, 1984).

In both grids, one Longworth live trap were located in each trap station to capture voles. As population increased, more Longworth live traps were added until a maximum of two per trap station. The Longworth trap contained oats and cotton.

Special trapping procedures

Pitfall traps were eventually used. On grid A, they were used from July through November 1978, June through mid-November 1979, June through mid-December 1980, and late May through mid-November 1981. On grid F, they were used from late May through November 1979, late May through October 1980, and May through October 1981 (Boonstra and Rodd, 1984). Pitfall traps were made up from a water light can (30 cm deep by 15 cm diameter) with a wooden cover and was supplied with oats and cotton when set (Boonstra and Rodd, 1984).

6.3 | Data collection period and sampling frequency

Grid A: 14,189 captures of *M. pennsylvanicus* from July 2, 1978 to June 4, 1982

Grid F: 11,514 captures of *M. pennsylvanicus* from May 20, 1978 to May 10, 1982

Sampling frequency

Trapping sessions consisted of biweekly traps called primary trapping sessions. Each primary trapping session had three secondary trapping sessions consisting of three live trap checks. Traps were set on Wednesday afternoon, checked on Thursday morning and afternoon, and again on Friday morning and closed for opening (Boonstra and Rodd, 1984). During the summer, trapping was limited to the evening.

Microtus agrestis: grids BHP, KCS, ROB, and PLJ

1 | Dataset

This file contains metadata of capture-recapture data of vole populations of *Microtus agrestis* collected in Kielder forest, a location near the English-Scottish border. The grid names used in this document match with those used in scientific publications.

2 | Information collected in the captures

Individuals were identified using subcutaneous micro-chip transponders (AVID plc, Uckfield, East Sussex, UK). In captures, sex, breeding condition, and weight were recorded (Burthe et al. 2006). Mass measured to the nearest 0.5 g using a Pesola spring balance (Burthe et al. 2010). Moreover, a 20–30 μL blood sample was taken from the tail tip of each individual to detect antibody to cowpox virus from sera using an immunofluorescence assay (Burthe et al. 2006).

3 | Collectors of the data

Sarah Janette Burthe, Sandra Telfer, David Carslake, Andrew Smith, Michael Begon, Pablo Beldomenico, M. Graham, James McKinnoin, and Xavier Lambin.

4 | Main scientific publications where the dataset was used and goals

To facilitate the understanding of the sampling procedure for each grid, we briefly detailed the goals of the publications that used the capture-recapture data. We ordered the publications according their publication date.

<u>Grid KCS</u>

1. May 2001 - July 2003
    1.1. Burthe et al. (2006) used grid KCS as a control grid to study the relationship between the cowpox virus pathogen and vole cycles.

  1.2. Burthe et al. (2008) used grid KCS as a control grid to study the impact of the cowpox virus pathogen on survival pKCSability.

2. May 2001 - March 2007
  2.1. Begon et al. (2009) used grid KCS as a control grid to study seasonal patterns of recurrent epidemics in comparison with those found in humans.
  2.2. Begon et al. (2009a) used grid KCS as a control grid to study the dynamics of cowpox virus.
  2.3. Burthe et al. (2010) used grid KCS as a control grid to study the relationship between individual growth rates and population density cycles.
  2.4. Telfer et al. (2011) used grid KCS to sample individuals in order to unravel if susceptibility to infection by a microparasite is influenced by other microparasites.
  2.5. Turner et al. (2014) used grid KCS to study the biology of infectious.
  2.6. Smith et al. (2008) used grid KCS to study the disease effects on reproduction and population dynamics.
  2.7. Smith et al. (2009) used grid KCS to study host-patoghens relationship and, in particular, the relationship between infection rate and host density.

3. April 2005 - May 2007
  3.1. Beldomenico et al. (2008) used grid KCS to study pathogens-hots relationship, and in particular, the influence of host condition.
  3.2. Beldomenico et al. (2009) used grid KCS to study pathogens-hots relationship, and in particular, the influence of host condition.

<u>Grid PLJ</u>

1. May 2001 - July 2003
  1.1. Burthe et al. (2006) used grid PLJ as a control grid to study the relationship between the cowpox virus pathogen and vole cycles.

   1.2. Burthe et al. (2008) used grid PLJ as a control grid to study the impact of the cowpox virus pathogen on survival pPLJability.

2. May 2001 - March 2007
   2.1. Begon et al. (2009) used grid PLJ as a control grid to study seasonal patterns of recurrent epidemics in comparison with those found in humans.
   2.2. Begon et al. (2009a) used grid PLJ as a control grid to study the dynamics of cowpox virus.
   2.3. Burthe et al. (2010) used grid PLJ as a control grid to study the relationship between individual growth rates and population density cycles.
   2.4. Telfer et al. (2011) used grid PLJ to sample individuals in order to unravel if susceptibility to infection by a microparasite is influenced by other microparasites.
   2.5. Turner et al. (2014) used grid PLJ to study the biology of infectious.
   2.6. Smith et al. (2008) used grid PLJ to study the disease effects on reproduction and population dynamics.
   2.7. Smith et al. (2009) used grid PLJ to study host-patoghens relationship and, in particular, the relationship between infection rate and host density.
3. April 2005 - May 2007
   3.1. Beldomenico et al. (2008) used grid PLJ to study pathogens-hots relationship, and in particular, the influence of host condition.
   3.2. Beldomenico et al. (2009) used grid PLJ to study pathogens-hots relationship, and in particular, the influence of host condition.

<u>Grid BHP</u>

1. May 2001 - July 2003
   1.1. Burthe et al. (2006) used grid BHP as a control grid to study the relationship between the cowpox virus pathogen and vole cycles.

   1.2. Burthe et al. (2008) used grid BHP as a control grid to study the impact of the cowpox virus pathogen on survival pBHPability.

2. May 2001 - March 2007
   2.1. Begon et al. (2009) used grid BHP as a control grid to study seasonal patterns of recurrent epidemics in comparison with those found in humans.
   2.2. Begon et al. (2009a) used grid BHP as a control grid to study the dynamics of cowpox virus.
   2.3. Burthe et al. (2010) used grid BHP as a control grid to study the relationship between individual growth rates and population density cycles.
   2.4. Telfer et al. (2011) used grid BHP to sample individuals in order to unravel if susceptibility to infection by a microparasite is influenced by other microparasites.
   2.5. Turner et al. (2014) used grid BHP to study the biology of infectious.
   2.6. Smith et al. (2008) used grid BHP to study the disease effects on reproduction and population dynamics.
   2.7. Smith et al. (2009) used grid BHP to study host-patoghens relationship and, in particular, the relationship between infection rate and host density.
3. April 2005 - May 2007
   3.1. Beldomenico et al. (2008) used grid BHP to study pathogens-hots relationship, and in particular, the influence of host condition.
   3.2. Beldomenico et al. (2009) used grid BHP to study pathogens-hots relationship, and in particular, the influence of host condition.

<u>Grid ROB</u>

1. May 2001 - July 2003
   1.1. Burthe et al. (2006) used grid ROB as a control grid to study the relationship between the cowpox virus pathogen and vole cycles.

   1.2. Burthe et al. (2008) used grid ROB as a control grid to study the impact of the cowpox virus pathogen on survival probability.

2. May 2001 - March 2007
   2.1. Begon et al. (2009) used grid ROB as a control grid to study seasonal patterns of recurrent epidemics in comparison with those found in humans.
   2.2. Begon et al. (2009a) used grid ROB as a control grid to study the dynamics of cowpox virus.
   2.3. Burthe et al. (2010) used grid ROB as a control grid to study the relationship between individual growth rates and population density cycles.
   2.4. Telfer et al. (2011) used grid ROB to sample individuals in order to unravel if susceptibility to infection by a microparasite is influenced by other microparasites.
   2.5. Turner et al. (2014) used grid ROB to study the biology of infectious.
   2.6. Smith et al. (2008) used grid ROB to study the disease effects on reproduction and population dynamics.
   2.7. Smith et al. (2009) used grid ROB to study host-patoghens relationship and, in particular, the relationship between infection rate and host density.
3. April 2005 - May 2007
   3.1. Beldomenico et al. (2008) used grid ROB to study pathogens-hots relationship, and in particular, the influence of host condition.
   3.2. Beldomenico et al. (2009) used grid ROB to study pathogens-hots relationship, and in particular, the influence of host condition.

5 | Site description

5.1 | Location of study area

The study area was located in Kielder Forest (55°13′ N, 2°33′ W), a spruce-fir forest on the border between England and Scotland. It hosted four sampling grids of similar size called: KCS (Kielder Site), PLJ (Plashett's Jetty), BHP (Black Blake Hope) and ROB (Rob's Wood). These four grids were in two cleared areas of the forest separated by about 12 km. The KCS and PLJ grids were located in the Kielder catchment and were 4 km apart, while BHP and ROB were located in the Redesdale catchment and were 3.5 km apart (Begon et al. 2009).

5.2 | Site type and vegetation

The Kielder forest is a spruce plantation covering an area of 620 km^2, dominated by Sitka spruce, *Picea sitchensis,* and Nowray spruce, *Picea abies*. The harvesting of timber creates islands of successional habitat, which change from clear-cuts, to grasslands, to pre-thicket forest, and finally to thicket stage after a period of 12-15 years. Patches ranged from 5 ha to more than 100 ha (Lambin et al. 1998).

The four grids were not placed in the forest, which is not inhabited by voles, but in grassy clearings (16-17 % of the total area) dominated by *Deschampsia caespitosa, Agrostis tenuis* and *Juncus effusus* (Petty 1992, Lambin et al. 1998, Burthe et al. 2006).

5.3 | Geography

No information is provided.

5.4 | Hydrology

There are eight valley systems that converge on Kielder Water (a reservoir of 1000 ha; Lambin et al. 1998).

5.5 | Site history

Kielder Forest is a commercially managed conifer plantation (*Picea sitchensis* and *Picea abies*) managed on a 40-60 year rotation (Petty et al. 1998), with a harvesting of timber of 750 ha yr^{-1} in the years previous to the sampled data (Petty et al. 1998).

5.6 | Climate

No information is provided.

6 | Experimental sampling design

6.1 | Permanent plots

Grid KCS: An unfenced and unmanipulated grid that harbored, at least, individuals of *Microtus agrestis*.

Grid PLJ: An unfenced and unmanipulated grid that harbored, at least, individuals of *Microtus agrestis*.

Grid BHP: An unfenced and unmanipulated grid that harbored, at least, individuals of *Microtus agrestis*.

Grid ROB: An unfenced and unmanipulated grid that harbored, at least, individuals of *Microtus agrestis*.

6.2 | Sampling design

Grid KCS: This grid had a checkerboard pattern of 100 trap stations, spaced 5 m apart, occupying a total surface of 0.3 ha (Burthe et al. 2006).

Grid PLJ: This grid had a checkerboard pattern of 100 trap stations, spaced 5 m apart, occupying a total surface of 0.3 ha (Burthe et al. 2006).

Grid BHP: This grid had a checkerboard pattern of 100 trap stations, spaced 5 m apart, occupying a total surface of 0.3 ha (Burthe et al. 2006).

Grid ROB: This grid had a checkerboard pattern of 100 trap stations, spaced 5 m apart, occupying a total surface of 0.3 ha (Burthe et al. 2006).

In each trap station there was an Ugglan Special Mousetraps (Grahnab, Marieholm, Sweden), provided with wheat, grain and carrot when set (Burthe et al. 2006).

6.3 | Data collection period and sampling frequency

In grid BHP there were 10,341 captures of *M. agrestis* from June 28, 2001 to March 15, 2007

In grid KCS there were 9,001 captures of *M. agrestis* from May 29, 2001 to March 11, 2007

In grid ROB there were 9,333 captures of *M. agrestis* from June 28, 2001 to March 14, 2007

In grid PLJ there were 7,911 captures of *M. agrestis* from May 31, 2001 to March 13, 2007

Sampling frequency

Grids were sampled every 28 days, apart from the winter when they were trapped every 56 days (i.e. from November to March). In each of the primary trapping sessions, traps were pre-baited for 3 days with a slice of carrot and a few grams of oats (Burthe et al. 2010). The traps were set at approximately 18.00 h on the first day, and checked five times (i.e. secondary trapping sessions) at approximately 12-h intervals at dawn and dusk (Burthe et al. 2006).

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CHAPTER II

Inference on fine temporal variation in demographic parameters from sparse capture-mark-recapture data

1 | INTRODUCTION

Capture-recapture models have been a turning point for estimating population parameters. Their ability to consider the imperfect detection of all their individuals has made it possible to estimate demographic parameters more robustly. However, as with any model, their usefulness is limited when data is sparse due to parameter non-identifiability (Viallefont et al. 1998, Morris et al. 2006) and because estimates are too unstable to be useful due to their large uncertainty (McKelvey and Perason 2001, Schaub et al. 2001, Getz et al. 2006, Goldberg et al. 2015).

We consider sparse data an amount of data relatively small in relation to the variance of the parameters or the complexity of the model needed to answer the desired question. Sparse data is the result of logistical and financial constraints as well as of low recapture/resighting/recovery rates (Mace et al. 1994, Schaub et al. 2001, Spehar et al. 2015). Consequently, it is challenging to study in detail the population dynamics of elusive species (Mace et al. 1994, Goldberg et al. 2015), species living in hard-to-sample habitats (Da Silva et al. 2000, Calambokidis and Barlow 2004), species with ephemeral biological processes (Schaub et al. 2001, Morris et al. 2006), species with temporal low density phases (Haukisalmi et al. 1988, Boonstra et al. 1998), or species with constant small population abundance such as threatened species (Hoyle et al. 2001, Danancher et al. 2004, Mollet et al. 2015). Given the wide range of species populations that may not be able to be analyzed in the desired detail, and that some of them are a priority for understanding the ecosystems or planning conservation strategies, to overcome the analytical limitations imposed by sparse data is urgent.

The main approach to reduce non-identifiability and improve precision of estimates have been to pool data from multiple spatial and temporal samples (e.g. Hargrove and Borland 1994, Schaub et al. 2001, Hoyle et al. 2001, Schaub and Jenni 2001, Morris et al. 2006, Tersago et al. 2012, Mollet et al. 2015). However, data pooling prevents us from knowing changes in the demographic parameters during the spatial and temporal pooling interval (Schaub et al. 2001, Danancher et al. 2004, Fletcher and Boonstra 2006), and, therefore, from knowing in detail the mechanisms underlying their population fluctuations (Yoccoz et al. 1998, Schaub et al. 2001, Tersago et al. 2012).

To overcome this issue, we propose here a capture-recapture model in which parameters are penalized using smoothing priors and shrunk to a value, biased into some tolerable degree, in exchange for reducing the variance of the parameter estimates (Efron and Morris 1975, Efron and

Hastie 2006, Greenland 2000, Greenland 2012, Cole et al. 2013, Bolker 2015). We hypothesized that the improvement could be large enough to understand hitherto inaccessible details of the demographic mechanisms at fine temporal resolution driving population fluctuations.

We evaluated the advantages of our approach by comparing its performance to estimate parameters and, if so, their precision and accuracy, with the performance of a traditional capture-mark-recapture model (hereafter, non-smoothed model). In particular, we used two simulated scenarios: (1) simulated populations with a relative high abundance of individuals: (2) simulated populations with a relative low abundance of individuals. We used scenario 1 to assess the reliability of our methodology, i.e. whether our approach can retrieve known parameters similarly to the non-smoothed models. We expected that both smoothed and non-smoothed models provide similar estimates, but that those of our smoothed models may be less accurate because the bias but more precise (i.e. known trade-off bias-variance). We used the scenario 2 to assess whether our smoothed model can mitigate estimation issues associated to sparse data, i.e. non-identifiability and estimates with poor accuracy and precision. We expected the smoothed model to identify more estimates and be more precise and accurate. Complementary to these two simulated scenarios, we evaluated the performance of the smoothed and non-smoothed models in a real capture-recapture data of a vole population with relatively sparse data. We used this case study to show the real contribution of our approach in unraveling the drivers of population fluctuations.

2 | MATERIAL AND METHODS

2.1 | Simulation of the populations: structure, dynamics and CMR sampling

We focused our simulations on real population of microtine populations because they are model species for understanding different aspects of population dynamics (Norrdahl and Korpimäki 2002, Tallmon and Mills 2004, Korpimäki et al. 2004, Ophir et al. 2008). Their breeding rates have drastic and high intra-annual variations that allow most adult individuals to move in short time from breeding to non-breeding reproductive status, and vice versa (Nakata 1989, Pinot et al., 2014). Whereas the intra- and inter- annual fluctuations of their survival rates often are soft (Krebs et al. 1969, Crespin et al. 2002). The population structure of voles can be classified into several categories using the reproductive states of the individuals – e.g. juveniles, non-breeding adults, and breeding adults (see below). Since the time that individuals spend at each stage varies from very short to relatively long, this also allows identifying parameters related to ephemeral and non-ephemera states. In general, the use of vole populations as a case study allows the performance of capture-mark-recapture models to be evaluated on a wide range of parameters present in populations of many species (e.g. Testa et al. 1991, Duellman 1995, Coronado and Hilborn 1998, Hakkarainen et al. 2002, van Bruggen et al. 2006).

We simulated a type of population for each scenario. For scenario 1, we simulated populations with relatively high abundance due to relatively high constant recruitment. We called these populations as "high recruitment populations", hereafter HR populations. Whereas for scenario 2, we simulated populations with relatively low abundance due to a relatively low constant recruitment. We called these populations as "low recruitment populations", hereafter LR populations. The HR and LR populations differed in population abundance, but had the same population structure and demographic rates (see below). In both HR and LR populations, we allowed for three transitions between reproductive states representing: (i) maturation, for the transition from juvenile to non-breeding (Ψ_{JNB}), (ii) breeding, for the transition from non-breeding to breeding (Ψ_{NBB}), and (iii) pause of reproduction, for transition from breeding to non-breeding (Ψ_{BNB}).

To obtain reliable results, we simulated and analyzed 30 capture-recapture histories from HR populations and other 30 from LR populations, for a total of 60 capture-recapture histories datasets. In each capture-recapture history, we simulated 48 sampling occasions, emulating two years of biweekly sampling. For the 60 capture-recapture histories datasets, we allowed transition parameters with relatively large and abrupt temporal variations in one-time periods ($\Phi_{\{t\}}$) (see values below), survival parameters with relative small rates of change in one-time period ($\Psi_{\{t\}}$), and constant recapture parameters to decrease computational time ($p_{\{.\}}$). We also simulated seasonal variation –i.e. breeding or non-breeding season— for the survival and transition probabilities of three reproductive states. See Appendix A for details on parameters used in simulations and script "sc_simulations.R" found in the supplementary material for full details on programming.

2.2 | Real vole population

We used capture-mark-recapture data of a vole population of *Microtus ochrogaster* collected by Charles Krebs and his students from May 1967 to April 1970 in Indiana, USA (see Appendix B for details). To estimate demographic parameters, we used the same biological model as that employed in the simulations. We classified the individuals into juveniles, non-breeders, and breeders based on their weight and the reproductive status of their sexual organs (see Appendix B for details). We only analyzed females. In total, the dataset contained information on 93 individuals, including 13 juveniles, on 78 sampling occasions. The range of captures per sampling occasion was 0 to 15 and the median three, to estimate nine parameters (i.e. three recapture, three survival, and three transition parameters). Thus, this dataset provides a good opportunity to test the contribution of our approach to the study of population dynamics under very limited data conditions.

2.3 | Models

A difficulty in dealing with sparse data is finding an optimal compromise between pooling data too much, i.e. relative low temporal resolution, so that valuable information on demographic variations at fine temporal resolution are lost, and pooling too little, so that estimates are non-informative. To overcome it, we propose imposing a high temporal resolution on the parameter time series, while regularizing the estimates by penalizing variation away from the (constant) average.

We assumed that changes in demographic parameters are likely to be temporally autocorrelated, i.e. that values close in time tend to be more similar than values at more distant time points, which leads to the expectation of a certain level of smoothness in the time series of estimates. Enforcing the smoothness of the parameter time series effectively amounts to applying a soft pooling of the data locally, around any given time point. The smoothness of the parameter time series (or rather its wiggliness: how much the parameter values are allowed to depart from a constant) ultimately determines the effective temporal resolution of the inference.

By letting the level of smoothness/wiggliness to be estimated from the data, it is possible to let the effective temporal resolution of the inference adjust to the amount of information present in the data.

2.3.1 | Non-smoothed multistate capture-recapture model

Although we focus here on multistate capture-mark-recapture models, our approach can be implemented in any one. Multistate capture-mark-recapture models are a generalization of the Jolly-Seber model that includes a transition parameter to consider the movement of individuals between sites or status between sampling occasions, in our case between reproductive status (Jolly 1965; Seber 1965; Lebreton and Pradel 2002). See Pradel (2005), and Lebreton et al. (2009) for further details about multistate models. We used the non-smoothed multistate capture-mark-recapture model provided by MARK (White and Burnham 1999; see details below).

2.3.2 | Smoothed multistate capture-recapture model

2.3.2.1 | State-space model

To develop our smoothing capture-mark-recapture model, we used a state-space modelling framework (Gimenez et al., 2007, Royle 2008) because of it allows implementing smoothly time-varying parameters. See Appendix C for details about the state-space modelling framework. The state-space models are defined by two matrices: a state-transition matrix (Ω), where the probability of transition between states are specified mathematically; and an observational matrix (Θ), where the observation process (i.e., the capture of individuals) is mathematically specified. We defined the model following Kéry and Schaub (2011, pages 263-313). The state-transition matrix has four dimensions $\Omega_{n,\, m,\, i,\, t.}$ representing that the reproductive states individual *i* is transitioning from *n* to *m* states in time *t* (i.e. in state *n* at time *t,* and in state *m* at $t + 1$). The observational matrix also has four dimensions $\Theta_{n,\, m,\, i,\, t}$ representing the probability that individual *i*, which is in state *n* at time *t,* is observed in state *m* at time *t*. The state-transition model is then defined with equations 1 and 2.

$$z_{i,f_i} = fs_i \tag{1}$$

$$z_{i,t+1} \mid z_{i,t} \sim categorical\ (\Omega_{z_{i,t},1\ldots S,i,t}) \tag{2}$$

While equation 1 defines the state at the first capture, assuming no error, equation 2 defines the transitions between reproductive states over time (Kéry and Schaub, 2011). The first parameter of the categorical distribution, $z_{i,t}$, is the reproductive state of the individual *i* at time *t*, the second argument, *1…S*, is a vector with the same length that the number of reproductive status in the population, *1…3* in our case, the third argument, *i,* is the individual, and the fourth argument, *t*, is the sampling occasion. Similarly, the observational equation defines the probability of observing an individual in state X given its previous state Y (equation 3). See details provided by Kéry and Schaub (2011).

$$y_{i,t} \mid Z_{i,t} \sim categorical\ (\Theta_{z_{i,t},1\ldots O,i,t}) \qquad (3)$$

In that observational equation, the argument *y* represents the observed multistate capture-recapture data. The categorical distribution is similar to the one explained in the state-transition (equation 2), but changing the second argument (i.e. "1…*O*") by a vector with the same length than the potential observed states (see Tables 1 and 2 for the definition of the state-space and observational matrices, respectively).

		True state at time *t* + 1			
		Juvenile	**Non-breeding**	**Breeding**	**Dead**
True state at time *t*	**Juvenile**	$\Phi_J(1-\Psi_{JNB})$	$\Phi_J\Psi_{JNB}$	0	$1-\Phi_J$
	Non-breeding	0	$\Phi_{NB}(1-\Psi_{NBB})$	$\Phi_{NB}\Psi_{NBB}$	$1-\Phi_{NB}$
	Breeding	0	$\Phi_B(1-\Psi_{BNB})$	$\Phi_B\Psi_{BNB}$	$1-\Phi_B$
	Dead	0	0	0	1

Table 1 | Probabilities to move from a given state at time *t* to another state or remain in the same one at time *t+1*. Φ depicts the survival rates, while the subscripts *J*, *NB*, and *B* indicates that the survival rate belongs to the reproductive status juveniles, non-breeding and breeding, respectively. *Ψ* depicts the transition rates given individual *i* is alive, while the sub-indexes *JNB, NBB,* and *BNB*, indicates that the transition rate belongs to the transition from the juvenile to the non-breeding state, from the non-breeding to the breeding state, and from the breeding to the non-breeding state, respectively.

		Observation at time *t*			
		Seen as juvenile	**Seen as non-breeding**	**Seen as breeding**	**Not seen**
True state at time *t*	**Juvenile**	p_J	0	0	$1-p_J$
	Non-breeding	0	p_{NB}	0	$1-p_{NB}$
	Breeding	0	0	P_B	$1-P_B$
	Dead	0	0	0	1

Table 2 | Detection probability (*p*) of the different reproductive states. See details about subscripts in Table 1.

2.3.2.2 | Parameter estimation and smoothing

We defined the time-varying survival parameter of the three reproductive states as:

$$logit(\Phi_{s_t}) = \Phi_{s.} + \Phi_{s_{var\_t}} \tag{4}$$

where the survival probability of the reproductive state *s* at time t (Φ_{s_t}) depends on the mean survival probability of the reproductive state *s* for the whole study period ($\Phi_{s.}$) plus a time-varying survival probability ($\Phi_{s_{var\_t}}$) with priors given by equations 5 and 6.

$$\Phi_{s.} \sim N\ (\mu_{\Phi_{s.}}, \sigma^2_{\Phi_{s.}}) \tag{5}$$

$$\Phi_{s_{var\_t}} \sim N\ (\mu_{\Phi_{s_{var\_t}}}, \sigma^2_{\Phi_{s_{var\_t}}}) \tag{6}$$

Regularization of the time-varying parameters was achieved by a random walk hyperprior assuming a Normal distribution of the second-order differences in Φ_t (Equation 7).

$$\mu_{s_\delta} = 2 * \Phi_{s_{var\_t}} - \Phi_{s_{var\_t-1}} - \Phi_{s_{var_t+1}} \tag{7}$$

Finally, we constrained the prior for σ^2_δ between a minimum $min.\,\delta$ = 0 (i.e. a constant parameter value) and a maximum $max.\,\delta$ reflecting the maximum rate of change we were prepared to accept as plausible or useful for our purposes (Equations 8 and 9). To define the maximum rates of change, we simulated multiple temporal fluctuations of population growth rates with different degrees of smoothness and observing which ones coincided with our study goals (Appendix D).

$$\mu_{s_\delta} \sim N\ (0, \sigma^2_{s_\delta}) \tag{8}$$

$$\sigma^2_{s_\delta} \sim U\ (min.\,\delta_s, max.\,\delta_s) \tag{9}$$

We defined the time-varying transition parameters as:

$$\Psi_{JNB_t} = \frac{\exp(\varphi_{JNB_t})}{1 + \exp(\varphi_{JNB_t})} \tag{11}$$

$$\Psi_{NBNB_t} = \frac{\exp(\varphi_{NBNB_t})}{1 + \exp(\varphi_{NBNB_t})} \tag{12}$$

$$\Psi_{BB_t} = \frac{\exp(\varphi_{BB_t})}{1 + \exp(\varphi_{BB_t})} \tag{13}$$

The subscripts *J, NB,* and *B* depict the departure and arrival reproductive states, respectively. The mathematical specifications ensured that the sum of the probabilities having the same reproductive state as departure state was 1. For these parameters, we also specified their priors and hyperpriors like those of the survival rates (i.e. equations 5-9). We defined the remaining three transition parameters (i.e. Ψ_{JB_t}, Ψ_{NBB_t}, and Ψ_{BNB_t}) without the need to define priors:

$$\Psi_{JB_t} = \Psi_{JJ_t} - \Psi_{JNB_t} \tag{14}$$

$$\Psi_{NBB_t} = 1 - \Psi_{NBNB_t} \tag{15}$$

$$\Psi_{BNB_t} = 1 - \Psi_{BB_t} \tag{16}$$

2.3.2.3 | Priors

We defined our priors based on previous studies and expert knowledge. We assumed informative priors for the survival and transition probabilities, while little informative priors for the recapture probabilities due to our lack of knowledge about these parameters. We considered that the average biweekly survival of the juveniles was close to 0.6 (i.e. median value of the assumed probability distribution), while the average biweekly survival of the adults was close to 0.8. We also assumed that the variables related to seasonality (time-varying parameters) were basically binomial (i.e. 0 or 1). See details in Table 3, while full technical details of the model, priors, and code to run the capture-mark-recapture model in the R script *sc_smoothed_model.R* found in the supplementary material.

Parameter	Constant	Time-varying
Φ_J	*N(0.5, 0.4)*	*N(0, 0.4)*
Φ_{NB}	*N(1.6, 1)*	*N(0, 0.4)*
Φ_B	*N(1.6, 1)*	*N(0, 0.4)*
Υ_{JJ}	-	*N(0, 0.01)*
Υ_{JNB}	-	*N(0, 0.01)*
Υ_{NBNB}	-	*N(0, 0.04)*
Υ_{BB}	-	*N(0, 0.04)*
p_J	*U*(0,1)	-
p_{NB}	*U*(0,1)	-
p_B	*U*(0,1)	-

Table 3 | Mean and precision of the probability distributions of the different priors. Φ = survival rates; Υ = transition rates; p = recapture rates; The subscripts depict the different reproductive states (J = Juvenile; NB = non-breeding; and B = breeding). The precision is the inverse of the variance.

2.4 | Data analysis

2.4.1 | Specifications for running the models in the simulated populations

We ran the non-smoothed model for the 30 HR and 30 LR populations using the multistate capture-recapture model with only recaptures from MARK software through the R package *RMark* (Laake 2013, R Core Team 2017). We used the default link function *logit* following the section *mstrata* of the RMark manual. We indicated the three reproductive states and constrained the unreal transitions Ψ_{JB}, Ψ_{NBJ}, and Ψ_{BJ} to have probability 0. We specified constant recapture probabilities and time-varying survival and transition probabilities (i.e. occurrence-specific). The estimates could vary between reproductive states. See full details in the R script *sc_RMark_non_smoothed_simul.R* found in the supplementary material.

We ran our smoothed capture-recapture model in WinBUGS with R package *rube* (http://www.stat.cmu.edu/~hseltman/rube/; see full details in the R script called *sc_BUGS_smoothed_simul.R* found in the supplementary material; see Appendix E for further details about the R package *rube*).

2.4.2 | Specifications for running the models in the real population

We analyzed real vole population data using the same programming specifications as for the HR and LR populations, except for one modification to account for the lack of sampling sessions in two periods (Appendix B). We fixed as 0 the recapture probabilities in those sampling occasions. See technical details in the R scripts *sc_RMark_non_smoothed_real.R* and *sc_BUGS_smoothed_real.R* found in the supplementary material.

2.4.3 | Assessment of the performance

2.4.3.1 | Simulated populations

For the simulated populations, we assessed the performance of the smoothed and non-smoothed models using three different aspects: (i) the proportion of identified parameters; (ii) the accuracy of the identified estimates; and (iii) the precision of the identified estimates. We considered that the non-smoothed model did not identify parameters when the confidence intervals at 5% and 95% were 0-1 (i.e. the full range of values), and 0-0 or 1-1 (e.g. issues when estimating at boundary;

Viallefont et al. 1998). Whereas that the smoothed model did not identify parameters when the 5th and 95th percentiles were 0-0, 1-1, or the difference between both 5th and 95th percentiles was greater than or equal to 0.9. We did not used the range 0-1 since Bayesian approach may be less susceptible than MARK to problems related to estimations at boundary (MARK manual; section 4-77). Therefore, we preferred to be more conservative with our approach and considered as unidentified to those estimates whose credibility intervals had a range ≥ 0.9. In any case, we noted that unidentifiable parameters of the simulations were not related with estimations at the boundary, since our simulated values are far from the boundaries (see script *sc_simulations.R* in supplementary material). We measured the accuracy as the difference between the estimated value provided by MARK and the median of the posterior distribution with the real value. Finally, we respectively measured the precision of the estimates as the difference between the values of the confidence intervals at 5% and 95% obtained with the non-smoothed model and the values at 5th and 95th percentiles obtained with the smoothed model.

To assess the quality of the estimates of the real population, we assessed the parameter identifiability and the precision of the estimates. Note we could not assess the accuracy of the estimates due to we did not know the real value. To show the contribution of our approach in order to understand population dynamics, we compared and discussed the information provided by both smoothed and non-smoothed models to explain the observed population fluctuations in this real vole population.

3 | RESULTS

3.1 | Results on the simulated populations

We first compared the results of the non-smooth model of the HR and LR populations to show the impact of sparse data on the estimates. Next, we compared the results of the HR populations when estimated with the smoothed and non-smoothed models to show the reliability of our approach. We finally compared the results of the LR populations to show how our smoothed approach enhanced qualitatively and quantitatively the demographic estimates.

The non-smoothed model identified fewer parameters in the LR populations than in the HR populations, and when it did, these were less accurate and precise. In these simulated populations, the non-smoothed model identified four to 20 times fewer estimates in the LR populations. Moreover, unlike in the HR populations, the non-smoothed models had trouble in the LR populations identifying parameters associated with ephemeral states, even constant ones (i.e. p_J). The accuracy and precision of estimates in HR populations were twice as high than those in LR populations (Fig. 1; Tables S1 and S2; see standard errors). Beyond the specific values that depend on our case study, these results showed the large effect of data availability on the estimation of demographic parameters.

The smoothed model improved the estimates in both scenarios. In the HR populations, unlike the non-smoothed model, the smoothed model identified all parameters (Fig. 1 and Table S1). Although the smoothed model provided estimates with a similar accuracy to the non-smoothed model, its precisions were up to four times higher (e.g. Φ_{NB}, Φ_B, and Ψ_{JNB} Fig. 1; Table S1). In the LR populations, the smoothed model only had problems identifying parameters related to larger and faster temporal changes, i.e. Ψ_{NBB} and Ψ_{BNB}; which contrasted with the problems of the non-smoothed in identifying any type of parameter (Fig. 1; Tables S1 and S2). The smoothed model identified about ten times more parameters, and increased the precision of the estimates from 1.5 to five times (i.e. p_J, Φ_J , Φ_{NB}, Φ_B, and Ψ_{JNB}; Fig. 1 and Table S2). Interestingly, the smoothed model sometimes identified more parameters and with higher precision when data was relatively sparse, than the non-smoothed model when the data was relatively abundant (e.g., Φ_J, Φ_{NB}, Φ_B, and Ψ_{JNB}; Tables S1 and S2).

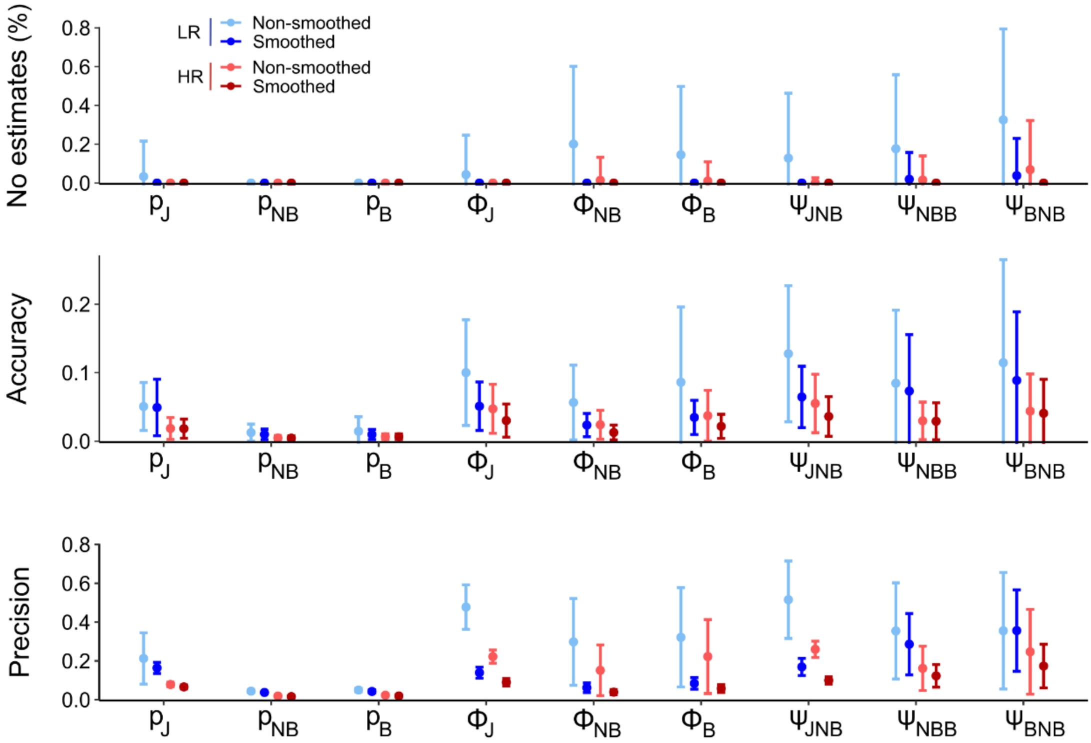

Fig. 1 | Comparison of the proportion of unidentified estimates, accuracy, and precision values across the different parameters. The y-axis means to a range of values of 0-1. The vertical "lines" represent the performance assessed for the non-smoothed and smoothed model (light and dark colors respectively) in the LR and HR populations (blue and red colors, respectively). The dot and whispers represent the mean and standard deviation respectively of these measures across the 48 sampling occasions in the 30 populations.

3.2 | Results about the real population

The non-smoothed model could identify almost no parameters, whereas the smoothed model identified all of them (Fig. 2). Therefore, we only described the temporal variations of the estimates obtained with the smoothed model, to later discuss their usefulness to understanding population dynamics. The precision of estimates related with juveniles mainly ranged between 0-1, being little informative for understanding population dynamics. In contrast, the precision of estimates related to adults was higher and allowed us to detect temporal variations in these parameters. Estimates related to the apparent survival of breeding individuals showed soft temporal fluctuations, whereas estimates related to adult transition rates and survival of non-breeding individuals showed larger temporal fluctuations (Fig. 2).

Along the three studied years (spring 1967 – spring 1970), the estimates of the apparent survival rates of breeding and non-breeding females (i.e. Φ_{NB} and Φ_{B}) showed no clear intra-annual or seasonal fluctuations, excluding those of non-breeding females in the last year (Fig. 2). In the first studied year, the estimates of the apparent survival of both breeding and non-breeding females increased more or less constantly from spring 1967 to winter 1967-68. Later, the estimates of the apparent survival rates decreased more or less constantly until the following winter (1968-69). However, in the third studied year, the apparent survival of non-breeding and breeding females were a bit different. Both apparent survival of non-breeding and breeding females appeared to increase to its maximum for that year in the fall 1969, but that of breeding females later declined during the remainder of the study period (fall-spring), while that of non-breeding females remained more constant (Fig. 2).

The estimates of the transition rates, i.e. Ψ_{NBB} and Ψ_{BNB}, had a lower precision, but showed more intra-annual or seasonal fluctuations. In the first year, there was no clear seasonal fluctuation and both transition rates decreased from spring 1967 to winter 197-68. However, from winter 1968 both transition rates appeared to have an opposite trend. From this latter winter to summer 1968, the transition rate from the breeding to the non-breeding state kept with the previous trend and decreased, while that from the non-breeding to the breeding state increased. From summer-fall 1968, the trends were reverted. That from the non-breeding to the breeding state appeared to decrease until the end of the study period, in spring 1970; while that from the breeding to the non-breeding state appeared to increased. The values at the 2.5th and 50th percentiles of this latter transition rate, appeared to be more or less constant during 1969, however, that at 97.5th percentile appeared to have a seasonal fluctuation, reaching its maximum in winter-spring.

In general, our results showed different intra- and inter- annual variations in the parameters on apparent survival and reproduction processes, i.e. transition parameters, as well as in the parameters on non-breeding and breeding individuals.

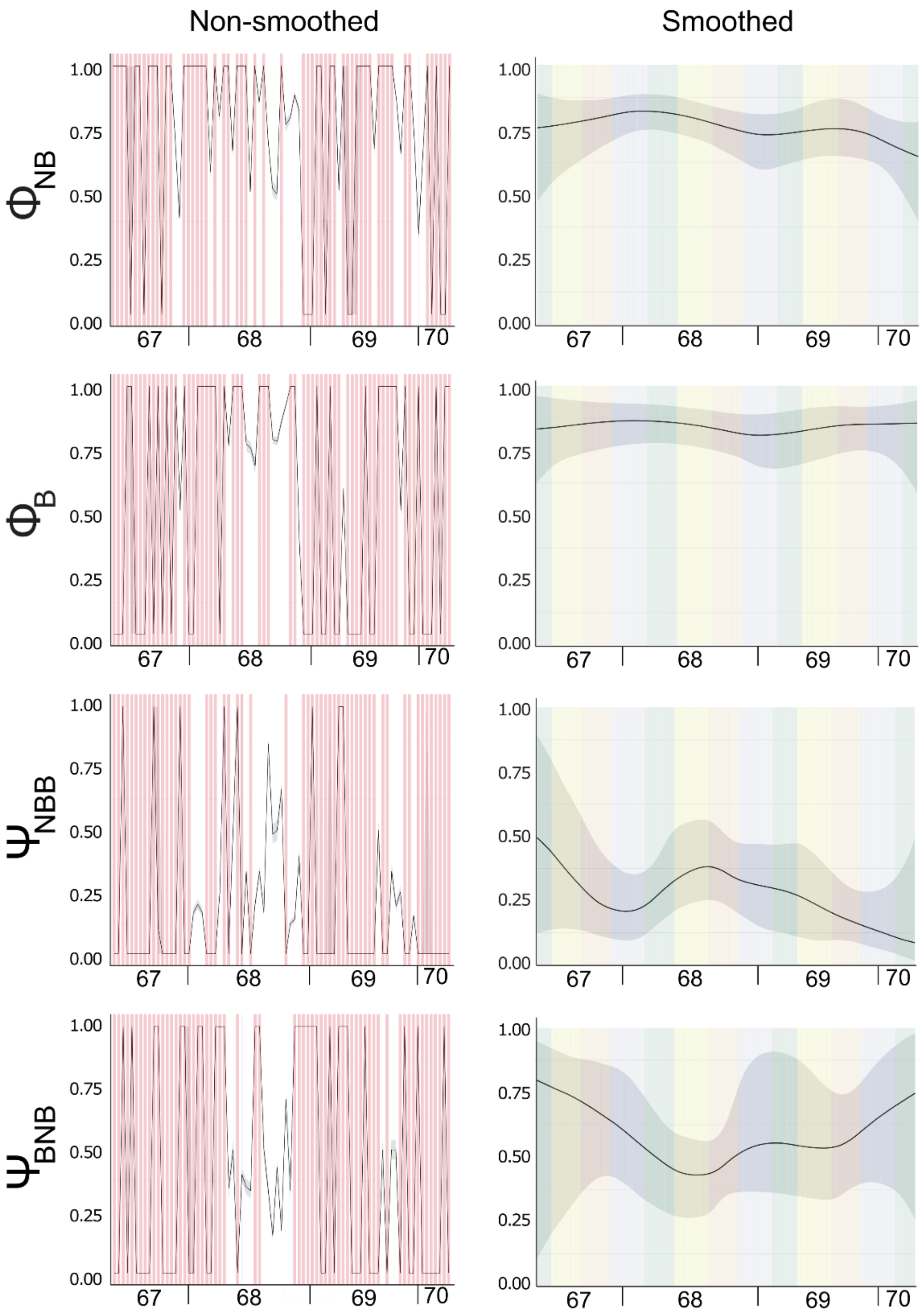

Fig. 2 | Estimates of the vital rates from the non-smoothed and smoothed model. The red background in the plots belonging the non-smoothed model represents the times with unidentified estimates. Blue, green, yellow, and orange background colors in the smoothed plots respectively depict winter, spring, summer, and autumn, while grey shades depict the credibility intervals at 95%. Because visualization problems, we did not represent the confidence intervals of the non-smoothed model. We did not show the estimates about the juveniles because of the were mostly little informative for understanding population fluctuations (Fig. 3).

4 | Discussion

The utility of capture-mark-recapture models can be limited or non-existent when the amount of data is relatively sparse (Viallefont et al. 1998, Schaub et al. 2007, Goldberg et al. 2015, Spehar et al. 2015, Kéry 2018). We propose here a non-parametric extension for capture-mark-recapture models based on regularization or smoothing techniques to reduce non-identifiability issues and increase parameter precision.

The adequate estimates in both HR and LR populations demonstrated the reliability or our specifications as well as its capacity to adapt the level of smoothness to the available data, alleviating potential concerns about unnecessary biases.

The comparison of the estimates from our simulations showed the overall contribution of our approach to the study of population dynamics. Certainly our approach enhanced the estimates even when data were relatively abundant (i.e. higher precision in HR populations). However, its contribution was qualitatively and quantitatively much higher when data was sparser (i.e. more parameters identified and more accurate and precise estimates). In fact, our actual case study perfectly reflects this improvement, as the non-smoothed model was unable to detect most of the estimates, while the smoothed model estimated all of them. Moreover, these estimates were of sufficient quality to show the inter- and intra-annual variations that may allow us to understand the population dynamics of the Townsend's vole (Fig. 3).

For instance, in the actual vole population, female abundance was stable in the fall-winter of 1967-68, a season in which it tends to decline (abundance estimated with a complementary smoothed capture-mark-recapture model; see Chapter III). A visual inspection of our estimates suggest that this phenomenon is more related to survival or immigration processes than to reproductive ones (i.e. apparent survival of non-breeding and breeding females increased in than period (Figs. 2 and 3). In contrast, the increased female abundance in spring-summer 1968 occurred when the apparent survival of both non-breeding and breeding females decreased and the transition rate from non-breeding to breeding state increased (a proxy of the maturation and a synchronized reproduction). Therefore, it is more likely that this seasonal increase was due to reproductive processes than to survival or dispersal ones. On the other hand, the abrupt decline in fall-winter 1968-69 occurred as the apparent survival of both non-breeding and breeding females declined, as well as when the transition rate from the breeding to the non-breeding state increased. Thus, this decline in abundance may be the result of a pause in reproduction as well as increased mortality. Finally, the estimates of female abundance suggested a population outbreak at the end of the study period. However, further exploration of the minimum number of individuals alive and the capture rate of new individuals suggest that it was an artefact. In summary, our approach outperformed the traditional approach and estimated demographic parameters well enough and with fine temporal resolution to shed light on the mechanisms underlying population dynamics.

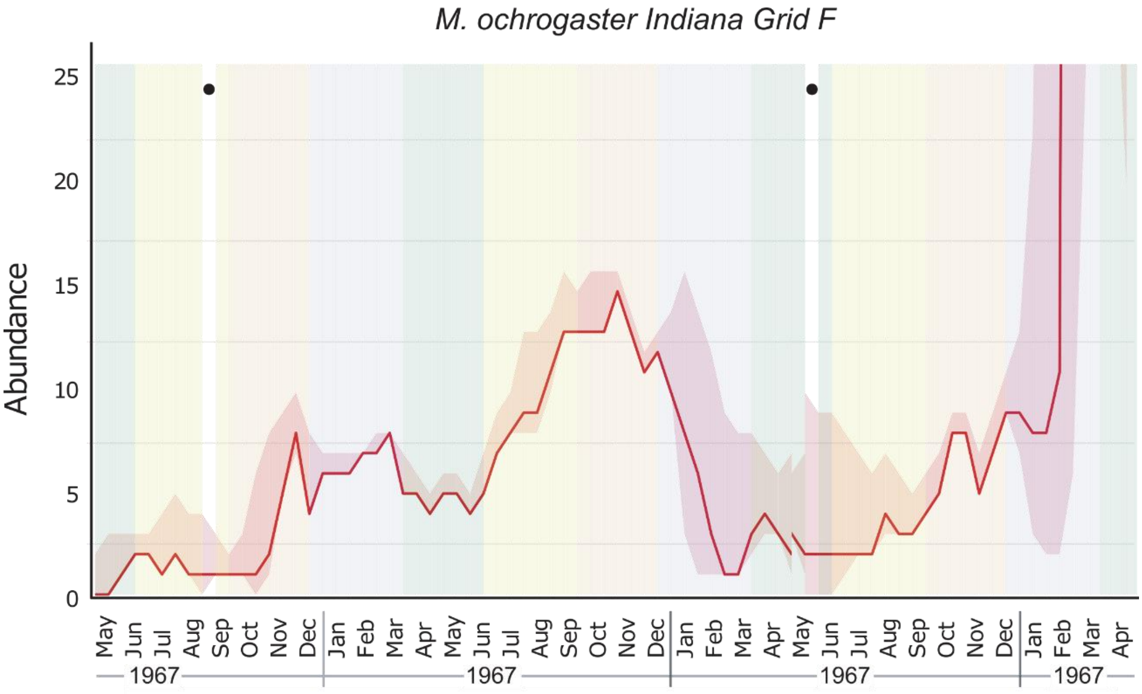

Fig. 3 | Estimated abundance of the adult females. Shades depict the confidence intervals at 95%. Blue, green, yellow, and orange background colors represent winter, spring, summer, and autumn, respectively. The two dots depict the two periods without sampling. Estimated abundance increase abruptly in 1970 suggesting a vole outbreak, but it was an artefact (see discussion).

The smoothed model provided strange abundance estimates at the end of the study period. We indeed expected worse estimates at the boundaries of the series because of the lower amount of information to estimate them (i.e. less closer sampling occasions). However, we expected less accurate estimates, not large population increases or decreases suggesting wrong biological inferences (e.g. vole outbreaks). Based on the results from other populations showed in the following chapter, we observed that it happened twice just when there was very sparse data at the end of the study period. Certainly, more research is needed to provide details on this phenomenon. In the meantime, we recommend to evaluate the similarities between the minimum number alive and the estimates. If there are large differences that cannot be explained because of the capture of dispersal individuals, we recommend to discard those points. Indeed, the loss of this information may be important for answering some questions. However, losing those estimates and using our approach is still better than using traditional approaches, since we can still make fine inferences of the mechanisms causing the population dynamics in the rest of the series.

The implementation of the capture-recapture model in Bayes along with the smoothing of the estimation trigger large computing times comparing to those of commonly used software. For example, the computational time to estimate the parameters of the LR, HR, and real populations was ~3, ~20, and ~5 days, respectively, compared to the minutes when using RMark. Thus, although our approach improves even estimates when there are relatively large amounts of data, these large time requirements may lead to using this approach when more traditional approaches are not useful for answering biological questions (e.g., our case study). However, constant computer and programming advances are drastically reducing analysis times (e.g., NIMBLE) and favouring its use as a first choice in day-to-day practice.

In this stud we show how smoothing efficiently handles data sparseness, being able to provide reliable estimates of six time-varying parameters and three constant ones from a dataset with a median of three captures per sampling occasion. A limitation of the approach is that the complexity of the temporal variation pattern is only known up to the level of information the data hold. A simple functional form may either be a reflection of the reality or of the inability of a particular data set to afford greater temporal resolution unless credible intervals are small.

Non-parametric capture-recapture models can promote a qualitative leap in the study of population dynamics, as they can allow the study of demographic mechanisms at higher spatial-temporal resolutions, hitherto unattainable in some cases. Their flexibility and capacity to be included in any type of capture-recapture model gives them a great potential to be an important tool in many fields such as population, applied, or evolutionary ecology by opening the door to answer new and old questions.

Contributions

Rubén Bernardo-Madrid and Thomas Cornulier conceived the project. TC conceived the statistical approach. TC and RBM developed the capture-recapture models. RBM, TC and José Jiménez written the code to run the models. Xavier Lambin, RBM, and TC conceived the biological model. RBM and Eloy Revilla conceived the simulations. RBM performed the analyses. RBM wrote the first draft. RBM, TC, XL, ER, and JJ commented and discussed the manuscript.

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APPENDIX CHAPTER II

Inference on fine temporal variation in demographic parameters from sparse capture-mark-recapture data

Appendix A | Simulation of the capture-recapture histories

We simulated 60 capture-recapture histories (i.e. 30 HR populations and 30 LR scenarios populations), with 48 simulated sampling occasions emulating two years of biweekly sampling. Each capture-recapture history had information for three types of individuals: juveniles, non-breeding adults, and breeding adults, and three types of transitions simulating the: maturation (Ψ_{JNB}), breeding (Ψ_{NBB}), and pause of the reproduction (Ψ_{BNB}). We also simulated a seasonal variation for survival and transition probabilities by simulating the seasonal reproduction of vole populations.

To simulate the seasonal variation, we categorized each of the 48 sampling occasion of the 60 simulated capture-mark-recapture history (i.e. 30 HR and 30 LR populations) into the breeding and non-breeding season levels. We classified the first sampling occasion of each capture and recapture history at either level using a Bernoulli trial with equal probabilities. We then forced the next 11 sampling occasions to belong to the same breeding season. Once 12 consecutive sampling occasions belonged to the same breeding season, we allowed the next occasion to be any reproductive season using the Bernoulli trial again. We repeated the above process until we categorized all 48 sampling periods.

Once we categorized the 48 sampling occasions of each capture-recapture history into breeding and non-breeding season, we assigned a random value to each combination of "*parameter* x *reproductive state* x *reproductive season*". Those values represent the survival, transition, and recapture parameter of each state at a given time. For the survival and transition parameters, we specified one probability distribution for the non-breeding period and another for the breeding period.

Finally, we simulated 60 capture-recapture histories of HR and LR populations, i.e. 30 and 30, by using the R specifications of Kéry and Schaub (2011, 271f.; R Core Team 2017) along with our biological model, the categorization of each sampling occasion in a reproductive season, and the demographic rates assigned to each combination "*parameter* x *sampling occasion* x *reproductive state*". The code provided by Kéry and Schaub (2011) assumed that all individuals grouped in a reproductive state and occurred at same time had the same demographic rates. For the simulations, we specified that LR populations started with ten juveniles, ten non-breeders, and ten breeders, and assigned a recruitment of ten juveniles per sampling occasion, whereas HR populations started with 50 juveniles, 50 non-breeders, and 50 breeders, and assigned a recruitment of 50 juveniles per sampling occasion. See full details in the R script *sc_simulations.R*.

The simulated seasonality makes that most adult individuals would be in the non-breeding status during the non-breeding season and in the breeding status during the breeding season. The constant recruitment together with the higher number of transitions that end on the non-breeding status (i.e. maturation and pause of the reproduction) comparing to the unique transition that end on the breeding status (i.e. breeding activity) favours that the non-breeding status has more individuals during the breeding season than the breeding status during non-breeding season. Consequently, we expect that capture-recapture models provides more estimates and with more accuracy from those parameters associated to the non-breeding status than with the breeding status.

We are aware that real vole populations have no constant recruitment. Nevertheless, we note that the constant recruitment only affects the amount of individuals in the population and therefore the amount of data to estimate the parameters. But it did not affect the types of parameters we are testing (e.g. parameters about ephemeral states or parameters with drastic temporal changes). Thus, our model specifications do allow estimating the performance of the estimates from both smoothed and non-smoothed models in a wide range of cases (e.g. ephemeral processes and variables with soft and drastic temporal variations). We only included a constant recruitment due to it has no effect on our goals and it simplifies the simulations.

We also recognize that establishing 12 as the minimum number of consecutive sampling occasions that must belong to the same season is arbitrary as a trial to simulate real lengths of the breeding season. Nevertheless, the length of the breeding season has no effect on our inferences.

Appendix B | Real population

We used capture-recapture data of a vole population of *Microtus ochrogaster* collected from May 1967 to April 1970 in Indiana, USA by Charles Krebs and his students. They trapped voles in 0.8-ha grid in grassland 78 sampling occasions, spaced every two weeks (Myers and Krebs 1971, Gaines and Krebs 1971). Along the three years sampled biweekly, two fortnights were not sampled. This dataset has been previously used in scientific studies and was known as grid *F*. The dataset contains information of each capture about the weight of individuals and the reproductive state of their external sex organs. We only used here the capture-recapture histories of females. In total, the dataset contains information about 93 female voles captured during the 78 sampling periods. See further details in Chapter I

We classified individuals into the three reproductive states based on their weight and the reproductive state of their sex organs. We first classified individuals as reproductive and non-reproductive using the sex organ information, classifying females that had large nipples (i.e. lactating), open pubic symphysis (i.e. had recently given birth), or were pregnant as reproductive individuals. We then used the weight of these breeding females to classify individuals as juveniles and non-breeding adults. We considered that all females weighing greater than or equal to the minimum weight observed in breeding females should be capable of breeding (i.e., the minimum weight observed at sexual maturation). We then classified non-breeding females below and above the minimum weight at sexual maturation as juveniles and non-breeding adults, respectively. To be conservative, we defined the minimum weight at sexual maturation to be the 5th percentile of the weight distribution of breeding females.

Appendix C | Frameworks to specify capture-recapture models

Capture-mark-recapture models, included the multistate version, can be specified by using a multinomial likelihood or a state-space modelling framework (Lebreton et al. 1992, Gimenez et al. 2007, Royle 2008). However, both approaches are based on the same sampling design and underlaying models (Kéry and Schaub 2011, 173). The frequentist approach commonly uses the multinomial likelihood. Whereas the Bayesian approach uses both multinomial likelihood and the state-space formulation (Kéry and Schaub 2011, p. 265). Although, both approaches provide similar results when the same model is assessed (Kéry and Schaub 2011), the difference between them reside in that whereas the multinomial likelihood is computationally faster, the state-space formulation provides greater flexibility in modelling (White and Burnham 1999, Kéry and Schaub 2011, 265).

We used the multistate capture-recapture model provided by MARK software (White and Burnham 1999) as our non-smoothed model; which uses a multinomial likelihood formulation. In contrast, we used capture-recapture model similar to the provided by Kéry and Schaub (2011) as our smoothed model; which uses a state-space modelling framework. We used two different frameworks for our smoothed and non-smoothed models because of time limitations. To implement our shrinkage specifications, we used the state-space modelling framework due to we required its flexibility. However, to use a common non-smoothed approach, we used the multinomial likelihood approach provided by MARK because the state-space modelling is quite time consuming and limiting. Nevertheless, the use of two different approaches has no effect on our comparisons since both approaches provide similar results (Kéry and Schaub 2011). We thus assume that differences between both non-smoothed and smoothed models when estimating parameters are because of the smoothness specifications.

Appendix D | Code for assessing ranges of the smoothing

We prepared a code in R to generate a multi-panel graph with as many panels as degrees of smoothness are assessed (R Core Team 2017). Each panel shows the simulation of the seven temporal fluctuations in population growth rates. By visualizing the population growth rates we are able to understand if the smoothing is too high or too low to capture the processes we want to study.

```
# Degrees of smoothness to check
check.smoothness <- c(7, 5, 3, 1, 0.5, 0.25)

# Number of simulations per degree of smoothness
sims<- 7

par(mfrow= c(3, 2))
for (k in 1:length(check.smoothness)){
 sd.var <- check.smoothness [k]
 p <- matrix(0.5, 50, sims) # Initial values of the vector p
 logitp <- log(p/(1-p))
 for(j in 1:sims){
  for (i in 3:50){
    diff.p <- rnorm (1, mean=0, sd=sd.var)
    logitp[i,j] <- 2*logitp[i-1,j] - logitp[i-2,j] - diff.p
    p[i,j] <- plogis(logitp[i,j])
  }
 }
 matplot(p, type="l", lty= 1, ylim= c(0, 1))
}
```

Appendix E | R package *rube*

The R package *rube* was developed by Howard Sheltman and defined as a Really Useful WinBUGS and JAGS Enhancer. The goal of this package is to facilitate the writing and running of Bayesian analyses using WinBUGS or JAGS from R (R Core Team 2017). We used *rube* package because of it provided details about the model and data used before running it, which could be used to detect potential errors such as the adequacy of the initial values. To further information and download the package, please follow the next website (http://www.stat.cmu.edu/~hseltman/rube/). Importantly, at 18/06/2019, Howard Seltman inform us that the package is no longer maintaining due to his retirement.

Supplementary Tables

Parameter	Error	Uncertainty interval	Prop. useless estimates	Model
p_J	0.019 ± 0.016	0.078 ± 0.012	0	Non-smoothed
p_J	0.018 ± 0.014	0.066 ± 0.010	0	Smoothed
p_{NB}	0.005 ± 0.004	0.019 ± 0.003	0	Non-smoothed
p_{NB}	0.004 ± 0.004	0.016 ± 0.003	0	Smoothed
p_B	0.006 ± 0.004	0.023 ± 0.003	0	Non-smoothed
p_B	0.006 ± 0.004	0.019 ± 0.002	0	Smoothed
Φ_J	0.047 ± 0.036	0.222 ± 0.034	0	Non-smoothed
Φ_J	0.030 ± 0.024	0.090 ± 0.019	0	Smoothed
Φ_{NB}	0.024 ± 0.021	0.151 ± 0.131	0.014 ± 0.118	Non-smoothed
Φ_{NB}	0.013 ± 0.011	0.039 ± 0.013	0	Smoothed
Φ_B	0.037 ± 0.037	0.222 ± 0.191	0.010 ± 0.099	Non-smoothed
Φ_B	0.022 ± 0.018	0.058 ± 0.020	0	Smoothed
Ψ_{JNB}	0.055 ± 0.043	0.260 ± 0.042	0.001 ± 0.027	Non-smoothed
Ψ_{JNB}	0.036 ± 0.029	0.099 ± 0.019	0	Smoothed
Ψ_{NBB}	0.030 ± 0.027	0.162 ± 0.114	0.016 ± 0.124	Non-smoothed
Ψ_{NBB}	0.029 ± 0.027	0.123 ± 0.058	0	Smoothed
Ψ_{BNB}	0.044 ± 0.054	0.247 ± 0.219	0.069 ± 0.253	Non-smoothed
Ψ_{BNB}	0.041 ± 0.050	0.173 ± 0.112	0	Smoothed

Table S1 | Comparison of the estimates of the demographic parameters from the HR populations using a non-smoothed and a smoothed multistate capture-recapture method. To calculate the performance of each demographic parameter, we used the 48 occasions of the 30 populations. *Error*: The average and standard deviation of the differences between the real values and the estimates; *Uncertainty interval*: The average and standard deviation of the uncertainty interval; *Prop. useless estimates*: *The a*verage and standard deviation of the proportion of useless estimates.

Parameter	Error	Uncertainty interval	Prop. useless estimates	Model
p_J	0.051 ± 0.035	0.212 ± 0.132	0.033 ± 0.183	Non-smoothed
p_J	0.049 ± 0.041	0.164 ± 0.029	0	Smoothed
p_{NB}	0.013 ± 0.012	0.044 ± 0.007	0	Non-smoothed
p_{NB}	0.010 ± 0.008	0.037 ± 0.006	0	Smoothed
p_B	0.014 ± 0.021	0.050 ± 0.009	0	Non-smoothed
p_B	0.010 ± 0.007	0.042 ± 0.008	0	Smoothed
Φ_J	0.100 ± 0.077	0.477 ± 0.115	0.043 ± 0.204	Non-smoothed
Φ_J	0.051 ± 0.035	0.139 ± 0.029	0	Smoothed
Φ_{NB}	0.056 ± 0.055	0.298 ± 0.224	0.201 ± 0.401	Non-smoothed
Φ_{NB}	0.024 ± 0.017	0.062 ± 0.025	0	Smoothed
Φ_B	0.086 ± 0.110	0.321 ± 0.256	0.145 ± 0.353	Non-smoothed
Φ_B	0.035 ± 0.025	0.084 ± 0.030	0	Smoothed
Ψ_{JNB}	0.128 ± 0.099	0.515 ± 0.200	0.128 ± 0.335	Non-smoothed
Ψ_{JNB}	0.065 ± 0.045	0.169 ± 0.044	0	Smoothed
Ψ_{NBB}	0.085 ± 0.107	0.354 ± 0.248	0.177 ± 0.382	Non-smoothed
Ψ_{NBB}	0.073 ± 0.082	0.286 ± 0.158	0.019 ± 0.138	Smoothed
Ψ_{BNB}	0.115 ± 0.151	0.355 ± 0.300	0.326 ± 0.469	Non-smoothed
Ψ_{BNB}	0.089 ± 0.100	0.356 ± 0.210	0.038 ± 0.192	Smoothed

Table S2 | Comparison of the estimates of the demographic parameters from the LR populations using a non-smoothed and a smoothed multistate capture-recapture method. See legend of Table 1 for details about the variables.

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CHAPTER III

Global determinants of population growth rate anomalies in voles

1 | Introduction

Inter-annual population fluctuations of rodents have been intensively studied since Robert Collet (1895) and Charles S. Elton (1924) described the periodic eruptions of lemmings and voles. Over the last century, more than 1,000 theoretical, laboratory, and field studies, have provided essential information and built a solid scientific basis for understanding population fluctuations. Nevertheless, what mechanisms are responsible and how generally they operate across populations and species, arguably, are amongst the most intriguing Gordian knots in population ecology (Chitty 1967, Krebs et al. 1973, Krebs 1996, Stenseth 1999, Ozgul et al. 2004, Smith et al. 2006, Getz et al. 2007, Krebs 2013, Radchuck et al. 2016).

In the middle of last century, Chitty (1960) suggested that all population dynamics were variations resulting from the same mechanisms. However, over the years, studies supported the existence of different mechanisms for different types of population fluctuations such as cyclic or non-cyclic dynamics. While cyclic fluctuations are those where population abundance fluctuates between years with regular amplitude and periodicity (i.e. commonly every 3-5 years for voles and lemmings), non-cyclic fluctuations occur when population abundance fluctuates little between years, showing mainly seasonal variations, or fluctuate normally seasonally but with high amplitude outbreaks occurring irregularly (Hansson 1984; Turchin et al. 1991; Royama 1992; Stenseth 1996; Ims et al. 2008). Previous studies supported the notion that cyclic fluctuations mostly result from the destabilization effect of delayed density dependent effects, while non-cyclic fluctuations result from the effects of extrinsic density independent factors (e.g. resources pulses) and direct density-dependent factors (Turchin et al. 1991; Royama 1992; Kendall et al. 1999; Murray 2003; but see Goswami et al. 2011). However, the mechanisms causing population dynamics to vary in space and time across populations and species are poorly known (Row et al. 2014). Thus, the strong conceptual dichotomy between cyclic and non-cyclic populations may be artificial, and there could be a continuum in variability, as it is often difficult to decide between the two (Sandell et al. 1991; Turchin 2003). This opens the door for the mechanisms underlying different population interannual fluctuations sharing similarities.

To answer whether there are general demographic mechanisms across species and populations, as well as to know their importance in driving population fluctuations requires, first, to link the relationship between the temporal variation of vital rates and population growth rates (hereafter PGR; Oli and Dobson 1999, 2001; Ozgul et al. 2004). Second, it is necessary to assess whether similar PGR result from the same variations in the demographic rates along the different species and populations (hereafter general demographic patterns), and if such patterns are identified, to quantify their importance in population fluctuations (e.g. proportion of PGR explained by general demographic patterns).

So far many authors have studied the link between vital rates and population abundance (Kalela 1957; Hoffman 1958; Krebs and Myers 1974; Oli and Dobson 2003; Ozgul et al. 2004), discussed the generality of the patterns (e.g. Krebs and Myers 1974; Getz et al. 2000; Oli and Dobson 2003), and identified factors that, alone or in combination, can explain population dynamics, such as predation (Hanski et al. 2001, Korpimäki et al. 2004, Graham and Lambin 2002), food availability and quality (Gilbert and Krebs 1981, Batli 1986, Huitu et al. 2003, Boonstra and Krebs 2012), maternal effects (Ginzburg and Taneyhill 1994, Inchausti and Ginzburg 1998), genetic effects (Chitty 1960; Krebs and Myers 1974; Krebs 1996), and social organization and behaviour (Calhoun 1949; Chitty 1960; Lambin et al. 1992; Lambin et al. 1998).

Although these studies have allowed us to advance in the understanding of population dynamics, part of the knowledge provided is not adequate to unravel all the complexities necessary to understand population dynamics in detail. Our current understanding is often based on indices of abundance rather than formal estimates that might not be suitable for identifying the mechanisms at work (e.g. Esther et al. 2014; Pinot et al. 2014), on studies with a short duration providing only snapshots of demographic processes (e.g. Norrdahl and Korpimäki 2002; Shang et al. 2019), or on data at too coarse temporal resolution to detect processes occurring in relatively in the short periods of time relevant to the fast life histories of rodents (Yoccoz et al. 1998, Stenseth 1999; Aars and Ims 2002; Ozgul et al. 2004). On the other hand, the knowledge on general patterns is formulated in literary rather than analytical terms, lacking global analyses (e.g. Krebs and Myers 1974; Boonstra 1985; Krebs 2013). As a result, despite the enormous advances made so far, it remains unknown whether the general demographic patterns underpinning fluctuations of vole populations and their drivers can have a conceptual generalization across populations and species.

Some of these problems have arisen because of analytical limitations in the unbiased estimation of demographic parameters and the absence of suitable datasets for joint analyses. However, new analytical approaches are emerging that allow estimating demographic parameters at sufficient spatio-temporal resolution and understanding population dynamics in detail (Chapter 2). In addition, many essential field data collected throughout history are currently available and allow evaluating the existence of general demographic patterns (Chapter 1).

Here we compiled capture-mark-recapture data on vole populations in Europe and North America and re-analysed them with modern tools; obtaining standardized estimates of population abundance and vital rates at fine temporal resolution. We then evaluated the existence of common relationships between inter-annual variations in population growth rates and the demographic rates among species and populations. In particular, we modelled the deviations from the expected seasonal pattern of population growth rate (PGR), what we called the population growth rate anomalies (PGRA), with the estimated vital. As described in the introductory chapter, there is a large number of studies supporting the existence of general demographic patterns in animal populations. We therefore expect that some specific vital rates explain a relative high proportion of the PGRA. We tested the predictions of three families of hypotheses associated with the most accepted drivers of population fluctuations: food availability, predation and social interactions (e.g. Batzli 1986; Korpimäki et al. 2004; Lambin et al. 1998). Because these three factors can act in multiple ways, here we only assess the support our results give to the most important predictions of these factors, since their most accepted effects mostly influence different vital rates, sexes and reproductive states in different periods. Thus, our results can provide insights about which drivers are more likely to be the modeller of the general dynamics of voles.

When formulating predictions about predation, we assumed that predator abundance increases as the number of prey increases (i.e. density dependent), and the lag of this response depends in part on whether the predator aggregate where prey availability increases. The density of generalist predators tends to be higher than that of specialist where prey inhabit, since specialist predators tend to move to those areas where vole abundance is high. Thus, we expect generalist predators to influence voles before specialist predators. In particular, generalist predators are expected to affect vole abundance more in the summer peak, whereas specialist predators affect vole abundance more in the autumn, when specialist predators detect this increase in density (Hanski et al. 1993; Turchin and Hanski 1997; Gilg et al. 2006; Therrien et al. 2014; Fauteaux et al. 2015; Mougeot et al. 2019). If predation is a major driver of variation in PGR, we expect to detect negative associations between survival rates and PGRA in summer and autumn, as well as an interaction between survival rates and abundance (i.e. density dependent effect). As there is no a general agreement about the generality of sex-biased predation (e.g., MacLean et al. 1974; Mappes et al. 1993; Klemola et al. 1997; Norrdahl and Korpimäki 1998; Graham and Lambin 2002), we expect that the signal in the survival rates of males and females, and different reproductive stages (e.g. sub-adults and adults), will be similar (but see Getz et al. 1990).

When formulating predictions about food supply, we assumed that the availability and quality of food mostly influence the physiological condition of individuals, hence affecting reproductive activity. So, if food availability is a major general driver of PGR, we expect to detect positive associations between the variables reflecting reproduction and the PGRA. In addition, food availability and quality can affect survival (i.e. starvation), especially in winter (Huitu et al. 2003; Ergon et al. 2014). So, if the main influence of food is starvation, we expect to detect a negative association between survival and PGRA in autumn-winter. As there is no reason to assume a sex or age biased effect of food, we expect that any signal on reproduction or survival will be similar in males and females as well as in different reproductive states or ages.

In the predictions about social interactions, we assumed that they mostly affect recruitment and survival (Lambin 1994; Mappes et al. 1995; Lambin and Yoccoz 1998; Andreassen and Gundersen 2006). When population density increases along the breeding season with the incorporations of the new cohorts, the limitations for juveniles to settle locally increases. However, as in many vole species females are philopatric (e.g., Lambin 1994; McGuire et al. 2002), the pressure of social interactions ought to differ strongly between males and females. While in many *Microtus* vole species, females are allowed to settle in the colony forming kin-clusters, males are pushed to disperse (Madison 1980; Lambin 1994; Gauffre et al. 2009; but see McGuire et al. 1993). Thus, if social pressure is a major general driver, we expect to identify a signal in the reproductive stages associated to the new cohorts (e.g. juveniles and sub-adults) and specially during the middle and end of the breeding season (summer-autumn), when space competition is higher. As males may be more pressured to disperse while females to delay reproduction (Bujalska 1990; Lambin 1994; Gauffre et al. 2009), we expect that signals in males will be detected in the estimates of apparent survival, while those about females in the estimates about the reproduction.

2 | Material and methods

2.1 | Datasets

We compiled capture-mark-recapture datasets on vole populations of the genus *Microtus* from North America and Europe meeting the following criteria: 1) at least 24 months long if there was one trapping site or at least 12 months long if there were two or more trapping sites acting as spatial replicates of local populations (hereafter grid) in order to determine the seasonality of the population; 2) data not aggregated across grids to capture population variability; 3) grids without fences so that dispersal was allowed; 4) capture-mark-recapture data collected with weekly, biweekly or monthly sampling intervals in order to capture demographic processes occurring at high temporal resolution (e.g. sexual maturation).

In total, we collated of capture-mark-recapture data from 17 trapping grids, belonging to five geographical areas (hereafter study areas), and four species cumulatively spanning ca. 67 years. These datasets contain information about *Microtus agrestis* (1 study area / 4 grids / ca. 24 years in total), *M. ochrogaster* (1/4/ca. 10 years), *M. pennsylvanicus* (2/6/ca. 17 years; two grids in one study area and four grids in the other one), and *M. townsendii* (2/4, two grids in one study area and two grids in other one, ca. 16 years in total). We defined each combination of “species” and “study area” as a “population”.

All species inhabit grasslands and have closely similar life histories and maturation schedules. Females and males reach sexual maturity ca. 36 and 42 days respectively. Gestation period lasts 21 days and litter size are ca. 4.4 but as most *Microtus* species, litter size varies depending on diverse factors such as the age of the female and the number of previous gestations. The inter-litter interval is close to 20 days, so females can have 3-4 litters per year (Wootton 1987; Grzimek 1990; Hayssen et al. 1993).

All studied populations experience high amplitude outbreaks but only populations from *Microtus agrestis* in Kielder forest (United Kingdom) have demonstrably cyclic dynamics (Lambin et al. 2000). See further details about populations and grids in Table 1 and Chapter 1.

2.2 | Biological model

We studied demographic patterns by using a biological model with three functional stages: juveniles, non-breeding adults, and breeding adults. Juveniles encompass those individuals physiologically not yet able to breed, while adult stages (i.e. non-breeding and breeding) include those that have the physiological capacity to breed. The non-breeding stage includes the individuals that may have not yet reproduced or that may have previously reproduced, while breeding adults includes the individuals that are breeding at capture time. We used this biological model and not one based on juveniles, subadults, and adults because it is challenging to identify genuine subadults and because it provides more details about the breeding period (see Appendix A for details).

To classify the individuals as juveniles, non-breeding adults and breeding adults, we used their weight and recorded external appearance of their sex organs (see Appendix B for details). Our biological model allows four transitions between reproductive states: (i) transition from juvenile to non-breeding (Ψ_{JNB}), (ii) transition from juvenile to breeding (Ψ_{JB}), (iii) transition of adults from non-breeding to breeding (Ψ_{NBB}), and (iv) transition from breeding adult to non-breeding status (Ψ_{BNB}). Temporal variation in Ψ_{NBB} and Ψ_{BNB} informs about the onset and end of the breeding season, respectively, while, temporal variation in Ψ_{JNB} and Ψ_{JB} can directly inform about the two reproductive strategies that yearlings can follow: to breed in their birth year or wait to breed in the next breeding season (Fairbairn 1977; Boonstra 1989; Lambin 1994; Lambin and Yoccoz 2001).

2.3 | Capture-Mark-Recapture models

For each grid, we ran two types of capture-mark-recapture models (hereafter, CMRs). One CMR to estimate the survival rates and transition rates of the three reproductive states (hereafter, survival and reproductive rates, respectively, or vital rates in general), and another CMR to estimate population abundance (Fig. 1). Temporal dynamics of vital rates and abundances can vary between females and males, requiring models that are too complex for the available number of captures. We thus estimated the vital rates and abundance of females and males separately. In total, we fitted 68 CMRs (17 grids x two sexes x two types of CMRs).

We estimated the vital rates by using the smoothed parameters CMR developed in Chapter 2, but also allowing the transition from the juvenile to the breeder state (i.e. Ψ_{JB}). To estimate population abundance, we included the smoothing specifications of Chapter 2 into a CMR focused on estimating population abundance (Kéry and Schaub 2011, pp. 115 ff.). Because individuals at juvenile stage are difficult to capture, and large temporal variations in their capturability can introduce too much noise for the analyses (see discussion), we used the abundance of adults as a proxy of population abundance. We ran all CMRs in WinBUGS by using the R packages *rube* and *R2WinBUGS* (R Core Team 2017; Sturtz et al. 2005; http://www.stat.cmu.edu/~hseltman/rube/). See Appendix C for details about the modelling and computational limitations.

Differences in the amplitude and frequency of the temporal fluctuations in abundance and vital rates may depict real differences in their variability, but also different abilities of the CMR to estimate them because of dissimilarities in data abundance and the variance of such demographic processes along the individuals of the population. As we used these estimates to model PGRA, i.e. deviations from the expected seasonal pattern of population growth rate, our use of smoothed estimates might have imparted artificially low variability (i.e., high smoothness) and this may mask important relationships affecting our inferences about the potential causal mechanisms (see below). To remove possible doubts, we visually assessed whether apparently very smoothed estimates were estimated with relatively little data. See Fig. S1 for details about the number of juvenile, non-breeding, and breeding females and males captured in each grid and sampling session.

Species	Study area	Grid	Study period	Sampling frequency	Size (ha)	Captures (Total)	Individuals (Total)	Trap
M. agrestis	Kielder Forest (England)	BHP	06/2001 – 03/2007	Monthly	0.3	4,074	1,748	Ugglan
M. agrestis	Kielder Forest (England)	KCS	05/2001 – 03/2007	Monthly	0.3	3,234	1,286	Ugglan
M. agrestis	Kielder Forest (England)	PLJ	05/2001 – 03/2007	Monthly	0.3	2,965	1,398	Ugglan
M. agrestis	Kielder Forest (England)	ROB	06/2001 – 03/2007	Monthly	0.3	3,9	1,582	Ugglan
M. ochrogaster	Indiana (U.S.A)	A	06/1965 – 02/1969	Biweekly	0.8	1,516	401	Longworth
M. ochrogaster	Indiana (U.S.A)	C	03/1969 – 04/1970	Biweekly	0.8	745	185	Longworth
M. ochrogaster	Indiana (U.S.A)	F	05-1967 – 04/1970	Biweekly	0.8	721	211	Longworth
M. ochrogaster	Indiana (U.S.A)	H	07-1967 – 06/1969	Biweekly	0.8	1,353	321	Longworth
M. pennsylvanicus	Indiana (U.S.A)	A	06/1965 – 04/1970	Biweekly	0.8	5,781	1,183	Longworth
M. pennsylvanicus	Indiana (U.S.A)	F	03/1967 – 04/1970	Biweekly	0.8	783	206	Longworth
M. pennsylvanicus	Indiana (U.S.A)	I	06/1967 – 04/1970	Biweekly	0.8	2,255	541	Longworth
M. pennsylvanicus	Toronto (Canada)	A	05/1978 – 12/1981	Biweekly	0.8	11,071	2,922	Longworth
M. pennsylvanicus	Toronto (Canada)	F	05/1978 – 06/1982	Biweekly	0.8	14,183	2,441	Longworth
M. townsendii	Vancouver (Canada)	C	05/1971 – 06/1975	Biweekly	0.8	8,071	1,593	Longworth
M. townsendii	Vancouver (Canada)	E	06/1971 – 08/1976	Biweekly	0.8	9,637	1,545	Longworth
M. townsendii	Vancouver (Canada)	1	02-1988 – 09/1991	Weekly	0.5	15,31	1,395	Longworth
M. townsendii	Vancouver (Canada)	2	12-1988 – 09/1991	Weekly	0.5	10,418	1,533	Longworth

Table 1 | Details about the study areas and grids. Sampling frequency depicts the most frequent sampling frequency of the primary trapping sessions. Size denotes the area covered by the trapping sites with live traps. Captures (totals) depicts the total number of captures in the study period; there can be several captures of the same individual in different periods. Individuals (Total) depicts the number of different individuals captured in the study period. Traps depict the live trap to capture individuals (see Lambin and MacKinnon 1997 for details about their relative efficiencies).

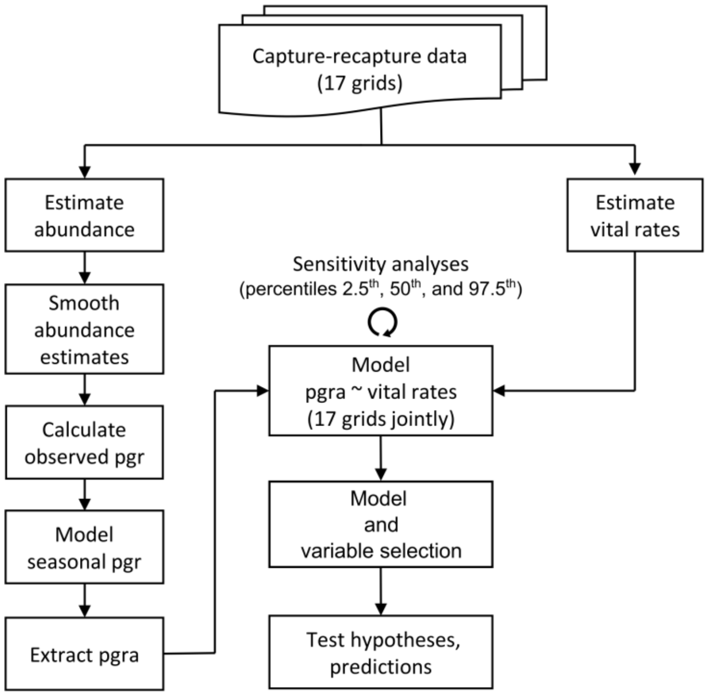


Fig. 1 | Workflow to assess the existence of common demographic patterns among species and populations as well as to shed light on the potential general drivers.

2.4 | Analyses

2.4.1 | Population growth rate anomalies (PGRA)

Population growth rates (PGR) are relative changes in population abundance over a defined time interval. In environments with clear seasonality, such as the ones we are analysing, changes in climatic conditions and resource availability trigger seasonal fluctuations in the reproduction and survival of individuals, and therefore, in the PGR. By evaluating suitably long time series, we can identify an average seasonal PGR describing the typical fluctuations of the population within years. Anomalies or deviations from these seasonal PGR generate the inter-annual population fluctuations, what we call population growth rate anomalies; PGRA. Positive PGRA represent PGR higher than average for that time of year, while negative PGRA represent PGR lower than average. Their demographic meanings vary depending of the baseline population trajectory at that period. In periods when the baseline trajectory is an increasing population abundance (e.g., breeding season), a positive PGRA reflects that the population grew faster than average; while a negative PGRA can depict that the population increases more slowly than average, remains stable, or even decreases. In contrast, in periods when the baseline trajectory is a decreasing population abundance (e.g., non-breeding season), a positive PGRA can depict either that the population decreases more slowly than average, remains stable, or even increases; while a negative PGRA can only reflect that the population decreased faster than average. We identified the demographic significance of PGRA by visually relating them to their context in the time series after performing global analyses (see below).

2.4.2 | Estimation of the PGRA

The PGR are relative changes in population abundance in a given time window. Our abundance estimates might contain stochastic fluctuations more related to capture-mark-recapture analyses than to real biological fluctuations (e.g., variability in trappability and number of capture histories in consecutive trapping periods due to different weather conditions). So before calculating PGR, we mitigated potential stochastic fluctuations in abundance estimates by smoothing them with a five-period moving average window (Fig. 1). As with the smoothing of capture-mark-recapture models (i.e., regularization; Chapter II), this smoothing reduces the temporal variability of the estimates, and can make it even more difficult to detect relationships between PGRA and vital rates.

We calculated the PGR of each grid at each time step as the abundance at time *t* minus the abundance at time *t*-1, dividing the result by the abundance at time *t*; where abundance is the sum of the smoothed estimates abundances of adult males and females and times refers to the different sampling sessions. We refer to this value as observed PGR. We then modelled the average seasonal growth rate of each population to obtain a common seasonal growth rate for all grids of the same species at the same location, regardless of when the samples were taken (e.g. data about *M. townsendii*; Table 1). We called this value seasonal PGR. Specifically, we fitted generalized additive models (GAM) with the observed PGR as the dependent variable, the weeks of the year as the explanatory variable, and the populations as random effects. We finally calculated the PGRA as the difference between the observed PGR in a given year and the estimated seasonal PGR, which are the residuals of the model. To control for the non-independency of our data, we included three random effects indicating the grids, species, and study areas to which the data belong (see Appendix D for details).

2.4.3 | Seasonal blocks

We divided years in in four seasonal blocks reflecting what we viewed as biological distinct seasonal stages of annual population dynamics to study the relationship between vital rates and PGRA for three reasons. First, drivers such as food, predation, or social interactions affect demographic parameters over specific time periods and specifying seasonal blocks facilitates formulating and testing block-specific predictions about different hypotheses. Second, and related to the previous one, some functional groups are frequently absent at certain times. For instance, juveniles and breeding adults are typically absent in winter, the common non-breading season. Therefore, their presence or absence in specific seasonal blocks is informative about unusual but important processes such as winter breeding. Thirdly, the biological meaning of the PGRAs varies along the year, so their assessment in seasonal blocks facilitates the understanding of the demographic processes.

The four seasonal blocks were: (i) the onset of the breeding period, (ii) the middle of the breeding period, (iii) the end of the breeding period and (iv) the non-breeding period (hereafter the onset, middle, end, and non-breeding blocks, respectively). We defined these blocks using the average seasonal fluctuation of the proportion of females that are breeding. We defined the onset block as the week in which the proportion of breeding females increases seasonally and reaches 50% of its relative range, plus/minus 30 days. For example, if the proportion of breeding females of a species ranges from 10 to 80% throughout the year, we set the onset in the week with the closest proportion at 55%, plus/minus 30 days. Similarly, we defined the end of breeding season block as the week in which the proportion of breeding females decreases seasonally and reaches 50% of its relative range, plus/minus 30 days. To estimate these blocks, we fitted the same models as for estimating the average seasonal growth rate of the population but using the proportion of breeding females as an explanatory variable. We later predicted the values over the weeks of the year and identified the onset and end blocks. We finally defined the weeks between the onset and end blocks as the breeding and non-breeding blocks. See Appendix E for details.

2.4.4 | Modelling PGRA

We modelled the block-specific relationship of the PGRA in relation to: (i) survival rates (i.e. survival rates of non-breeding adults and breeding adults; Φ_{NB}, and Φ_{B}, respectively); (ii) reproductive rates (transition rates, from non-breeding to breeding state, and from breeding to non-breeding state; Ψ_{NBB}, Ψ_{BNB}, respectively); and (iii) logarithm of population abundance (Stenseth 1999). We also considered the interactions between the abundance and vital rates since the biological meaning of PGR t-t+1 varies with abundance at t. Although we described the estimates about the transitions from juveniles (i.e. Ψ_{JNB}, Ψ_{JB}), we did not use them in modelling because data manipulation errors when estimating their confidence intervals, a crucial aspect for our sensitive analyses (see below). This human error has no effect on the rest of the estimates. But because of the large computer time limitations, we excluded them from the analyses presented in the Thesis. Thus, we only evaluated here the existence of general demographic patterns associated with adults.

We did not combine the vital rates of different sexes in a same model because those models were too complex for the available data (i.e., risk of model overfitting). Instead, we quantified the role of each sex in explaining variation in PGRA by comparing the outputs of two sets of models, one for each sex. We compared the importance of the processes of each sex by comparing the marginal regression coefficients of the standardized variables as well as the proportion of the variance in PGRA explained (see details below). In total, we ran 7,040 models (880 abundance and demographic models x two sexes x four seasonal blocks). We ran the models with function *lmer* of the R package *lme4* (Bates et al. 2015). We used the R package *tidyverse* to manipulate and plot the data (Wickman 2017).

We included three nested random effects: year, grid and species (i.e. year/grid/species). We could not include the study area because most species were sampled in different study areas and their individual effects were not identifiable. Occasionally, the variance explained for some random effects was zero. In those cases, we assumed that our model was too complex and removed those "null" random effects, even removing all random effects if necessary. See Table S1 for details about the random effects in set of models. We chose the best model of each sex and seasonal block with the corrected Akaike information criterion (Akaike 1973, 1974; Hurvich and Tsai 1993; hereafter AICc). To allow for model comparison, we forced all models in the same seasonal block to have the same random effects as the saturated one (Table S1). If any nested model had problems of convergence or singularity, we discarded it. We discarded 590 models for females and 71 for males.

We performed a visual diagnosis of the most parsimonious models (i.e. models with the lowest AICc; evaluation of the residuals). We observed that models with simplified random effects had more heteroscedasticity problems.

The uncertainty of the estimates of population abundance varied across populations and time. We included such uncertainty in our models by weighting the observations with their uncertainty (i.e. inverse of the range between the percentiles 2.5th and 97.5th through the option "weight" of the function *lmer* of the R package *lme4* (Bates et al. 2015). To also consider the uncertainty of the explanatory variables, we ran sensitivity analyses that consisted of using the values of the vital rates at different percentiles of their estimated probability distribution (i.e. the output of the CMR models). We performed analyses using as explanatory variables the values in the percentiles 2.5th, 50th and 97.5th (Fig. 1). Thus, one sensitivity analysis is a set of models that used the values in the same percentiles as explanatory variable. In total, we performed 21,120 models (880 demographic models x two sexes x four seasonal blocks x three sensitivity analyses).

We observed that some estimates had r-hat > 1.2 (i.e. potential convergence issues). However, we did not remove them from our analyses because bias estimates are overcome by performing our inferences on the three sensitivity analyses (see following section and Appendix F for details).

2.4.5 | Inference

We made our inferences about those variables that had a statistically significant relationship with PGRA ($p<0.05$) and whose regression coefficient had the same sign (i.e., positive or negative) in the three sensitivity analyses. In other words, we only considered that a variable was part of a general demographic pattern when the coefficient values in the percentiles 2.5th, 50th and 97.5th of their probability distribution had a same qualitative and significant relationship with PGRA, when we considered the effect of those variables as consistent. We assumed that a strong real association between two variables should be similar when considering the relationship between any of their values, as the truth value can be within the whole range of the posterior distribution. In addition, we only used for inference those consistent variables that appeared in the model with the lowest AIC_c of each sensitivity analyses and in the models with a $\Delta AIC_c >$ 2 (all Δ_2 models were nested models). We assumed that consistent variables were part of general demographic patterns, and that their detection supported the existence of a strong effect across populations and species. We used the presence/absence of these consistent variables in the analyses of each seasonal block to test different hypothesis about the mechanisms underlying general demographic patterns (i.e. predation, food, and social interaction hypothesis; see introduction for details).

We also expected specific relationships between PGRAs and abundance and vital rates (i.e., positive or negative relationships) as well as relative importance of each variable. Since we standardized the explanatory variables, we compared regression coefficients to find out which variables have the greatest influence in explaining PGRA. As we fitted three sensitivity analyses (i.e., sets of models with the same explanatory variables but whose values reflect different percentiles of the posterior distribution), to compare the coefficients, we used the mean of the regression coefficients of the most parsimonious models of each sensitivity analysis (i.e., AICc = 0).

Additionally, we represented the partial residual plot of each variable (Larsen and McCleary 1972, Cook 1993, Cook and Croos-Dabrera 1998). With this information, we can better know the strength of the pattern (e.g. if the low or high values of our consistent variables are mostly associated with positive or negative PGRA, or if there is a relationship between the consistent variable and the PGRA but the effect is not biologically relevant; Fig. 2; left and centre panels respectively). To represent the partial residual plots, we used the function *Effects* of the R package *effects* (Fox 2003; Fox and Weisberg 2018, 2019).

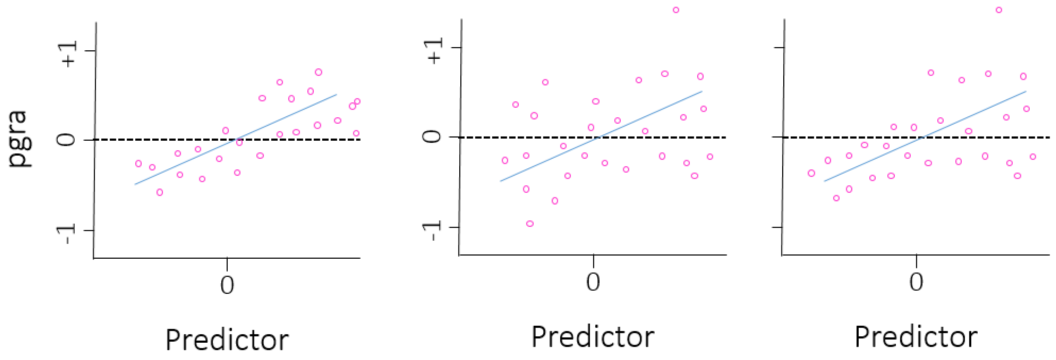


Fig. 2 | Hypothetical partial residual plots of three variables. The three predictors have similar marginal regression coefficients. However, their fit varies and the inference that can be reached based on each plot is different. The left plot shows that values below 0 of the predictor are clearly associated with negative PGRA, while values above 0 are associated with positive PGRA. The central plot shows that the probability of observing negative PGRA is greater as the predictor values decrease whereas the probability of observing positive PGRA is greater as the predictor values increase. However, the residuals at both extremes of the predictor are negative and positive, showing that, although a trend exists, the pattern is much less well described by a linear regression than in the left plot. Finally, in the right plot, there is a clear pattern over negative PGRA, but not for positive PGRA.

With the above information, we know whether there are consistent demographic patterns across species and sites and which variables are defining those patterns, as well as what is the type of relationship and their strength. However, we still cannot know the true demographic meaning of PGRA, which varies from period to period and for some periods its meaning may be ambiguous. For example, a negative PGRA in the breeding season may depict that population abundance increased unusually slowly, remained constant, or even decreased. To understand the demographic meaning of the patterns, we selected the observations representing anomalies (e.g. PGRA <0 and predictor < 0), and explored their location in our time series of estimated abundance. This allowed us to understand the actual demographic meaning and to better discuss the general patterns and factors behind them.

Finally, to know if observed general demographic patterns play an important role in the observed inter-annual population fluctuations, we quantified the coefficient of determination of the models that include only the consistently selected variables. Values close to 1 indicate that most observed variance in PGRA is explained by general demographic patterns, while values close to 0 indicate that there may be general patterns but that they are not very relevant for the understanding of observed PGRA (e.g. other local or delayed processes may be more relevant). The coefficient of determination in mixed models is a proxy for the variance captured by the explanatory variables (i.e. pseudo-R^2 metrics; Nakawaga and Schielzeth 2013). We used the pseudo-$R^2_{marginal}$ as a proxy of the proportion of the total variance captured by the fixed effects (Nakawaga and Schielzeth 2013; Nakawaga et al. 2017).

2.5 | Descriptive analyses

To understand better similarities/differences between population dynamics of different species and populations, and then provide more clues about the biological meaning of the demographic patterns, we also described the estimates obtained as well as the inter-annual variance of (i) density (estimated abundance divided by the size of the grid), (ii) seasonal population growth rate (sPGR), and (iii) population growth rate anomalies (PGRA). We measured the inter-annual variance in abundance as the standard deviation of the (i) log-transformed density, (ii) sPGR, and (iii) PGRA. We called these metrics s-index$_{Density,}$ s-index$_{sPGR,}$ and s-index$_{PGRA}$. This approach has been widely used as a crude proxy for "cyclicity" and compare populations dynamics (e.g. Stenseth and Framstad 1980; Hansson and Henttonen 1985). To compare long term population dynamics, only (log) abundance in autumn is commonly used. But as we are interested on evaluating differences along the whole year, we used the data of all our sampling sessions. Complementarily, we evaluated differences in this metric across species, populations, and seasons by using Kruskal-Wallis test with the R function *kruskal.test* (R Core Team 2020). We considered that statistical differences in this metric reflect differences in the amplitude or magnitude of the fluctuations.

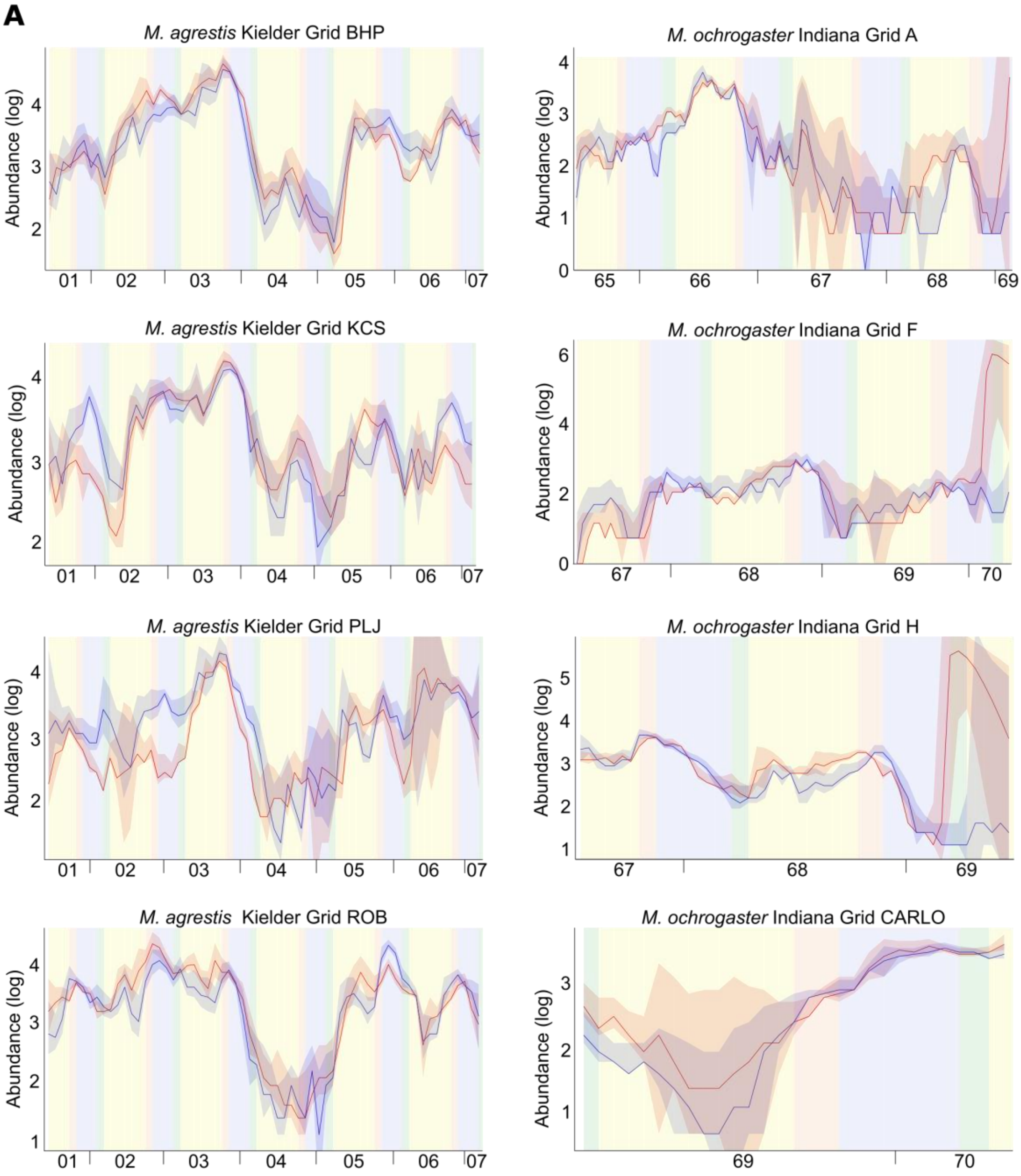
3 | Results

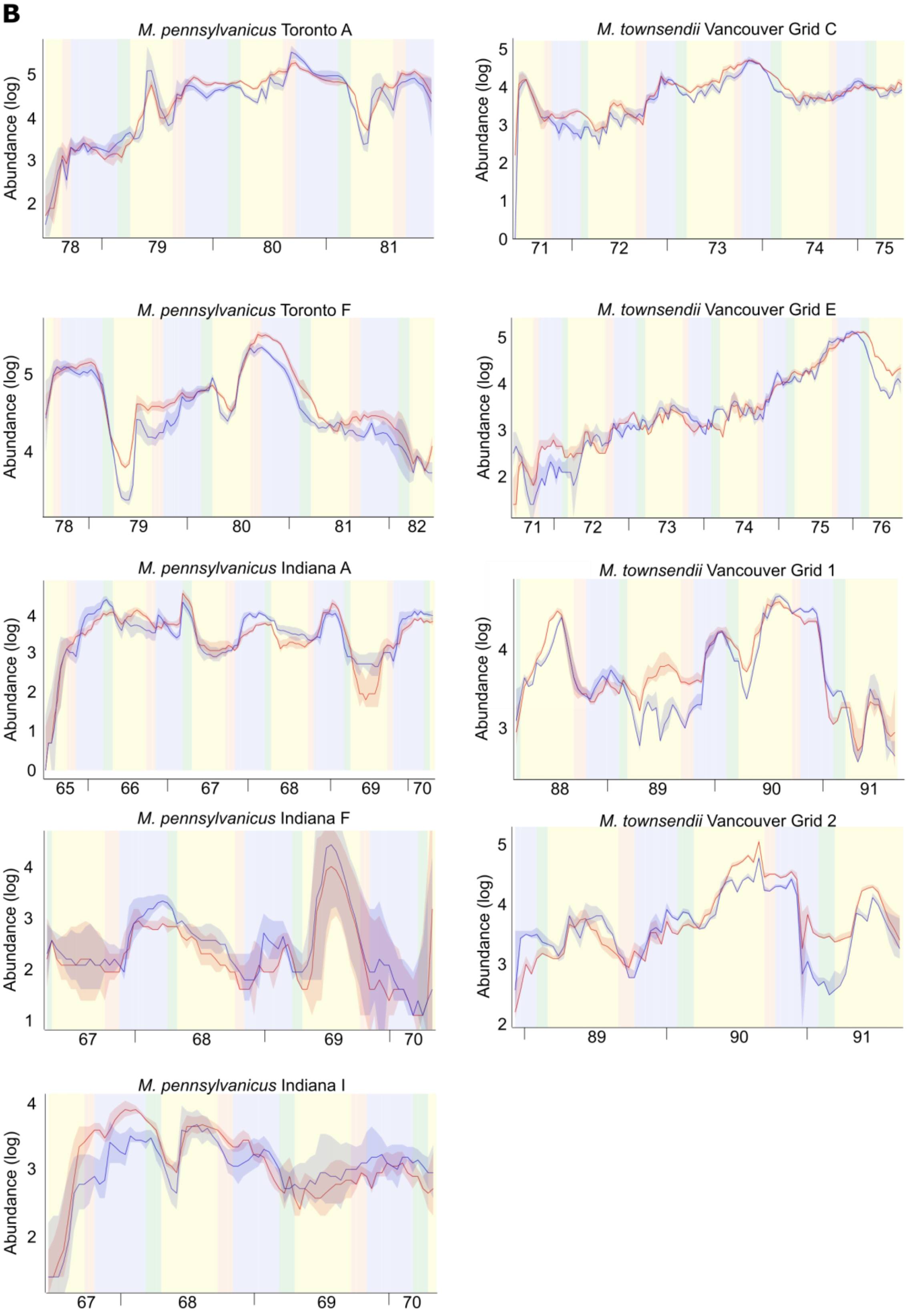
3.1 | Abundance estimates

Our estimates of abundance were similar to those provided by previous studies (Fig. 3; Myers and Krebs 1971a,b; Krebs et al. 1978; Boonstra and Rodd 1984; Lambin 1994; Begon et al. 2009). Nevertheless, some estimates differed, especially when abundance was very low (ca <10 individuals per hectare) at the end of the study period (Figs. 3 and S1; e.g. grid F of *M. pennsylvanicus*, and grids A, F, and H of *M. ochrogaster*; see chapter 2 for further details about these artefacts). We did not use those estimates in subsequent analyses.

The estimated vole densities varied between species, populations, and grids (median, minimum, and maximum densities; estimated abundance divided by trapping grid size). For instance, vole densities in grids BHP and KCS of *M. agrestis* or grids C and E of *M. townsendii* varied more than 50%. The lowest vole densities were observed in Indiana (*M. ochrogaster* and *M. pennsylvanicus*), whereas the highest ones in Toronto (*M. pennsylvanicus*). See Table 2 and Fig. 3 for details.

Figure 3 | Abundance estimates for each species, population and grid (log scale). Each panel contains the estimates of one grid indicated at the top. X-axes indicate the year when the trapping grid was sampled, while y-axes the estimated abundance in a log scale. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different seasonal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See Fig. S1 details about the temporal variation in the number of captures of juvenile, non-breeding, and breeding females and males.




B
M. pennsylvanicus Toronto A
Abundance (log)
2 3 4 5
78 79 80 81
M. townsendii Vancouver Grid C
Abundance (log)
0 1 2 3 4 5
71 72 73 74 75
M. pennsylvanicus Toronto F
Abundance (log)
4 5
78 79 80 81 82
M. townsendii Vancouver Grid E
Abundance (log)
2 3 4 5
71 72 73 74 75 76
M. pennsylvanicus Indiana A
Abundance (log)
0 1 2 3 4
65 66 67 68 69 70
M. townsendii Vancouver Grid 1
Abundance (log)
3 4
88 89 90 91
M. pennsylvanicus Indiana F
Abundance (log)
1 2 3 4
67 68 69 70
M. townsendii Vancouver Grid 2
Abundance (log)
2 3 4 5
89 90 91
M. pennsylvanicus Indiana I
Abundance (log)
2 3 4
67 68 69 70

		Spring			Summer			Autumn			Winter		
Grid	Site / Grid	Median (Ind / ha)	S-index	Range (Ind / ha)	Median (Ind / ha)	S-index	Range (Ind / ha)	Median (Ind / ha)	S-index	Range (Ind / ha)	Median (Ind / ha)	S-index	Range (Ind / ha)
M. agrestis	BHP	143	0.25	37-387	247	0.32	80-513	260	0.4	60-677	190	0.46	53-380
M. agrestis	KCS	103	0.15	63-290	160	0.13	80-350	200	0.14	117-417	147	0.21	67-303
M. agrestis	PLJ	130	0.25	43-373	147	0.47	40-483	173	0.27	50-457	140	0.09	70-180
M. agrestis	ROB	173	0.33	43-337	200	0.59	30-297	273	0.6	27-453	197	0.52	37-373
M. ochrogaster	A	19	0.6	13-197	20	0.75	10-267	19	0.78	7-227	16	0.65	7-140
M. ochrogaster	C	23	0.01	43-223	10	0.05	20-50	38	0.09	57-120	79	0.01	163-223
M. ochrogaster	F	10	0.15	0-963	9	0.26	jul-73	18	0.38	7-103	19	0.17	7-1000
M. ochrogaster	H	60	0.03	53-933	45	0.03	80-163	56	0.06	120-243	26	0.14	17-843
M. pennsylvanicus	A (I)	93	0.27	0-430	50	0.31	7-323	71	0.06	120-320	115	0.02	190-533
M. pennsylvanicus	F (I)	23	0.15	13-230	25	0.03	47-457	16	0.08	30-113	23	0.45	13-147
M. pennsylvanicus	I (I)	39	0.1	20-230	40	0.25	20-250	59	0.03	113-227	58	0.08	110-263
M. pennsylvanicus	A (T)	224	0.15	220-1010	235	0.59	23-1640	330	0.69	157-1610	300	0.63	143-1003
M. pennsylvanicus	F (T)	159	0.13	230-883	208	0.17	317-1503	330	0.17	473-1497	270	0.11	367-1177
M. townsendii	C	114	0.16	27-413	100	0.14	153-550	103	0.3	127-727	143	0.25	133-667
M. townsendii	E	66	0.55	47-780	74	0.74	30-827	53	0.86	27-1013	58	0.88	57-1070
M. townsendii	G1	132	0.17	87-543	142	0.28	103-687	130	0.2	180-573	140	0.1	130-450
M. townsendii	G2	150	0.12	133-533	172	0.27	150-903	138	0.39	67-583	102	0.07	137-297

Table 2 | Summaries of the estimated densities of males and females per trapping session in each grid over the four seasons of the year. Median (Ind/ha) = median estimated density (joint abundance of estimated adult females and males divided by trapping grid size in hectares); Range = Minimum and maximum estimated densities in the whole period for each trapping grid. S-index is the interannual variance in density. Abbreviation in the column Site/Grid depict the sites of the studies: (I) = Indiana and (T) = Toronto.

The amplitude of density fluctuations (s-index$_{Density}$) was similar among seasons and species, but differed among populations (i.e., there were statistical differences evaluating data from the four seasons together, but not when evaluating data from each season; Tables S2-4).

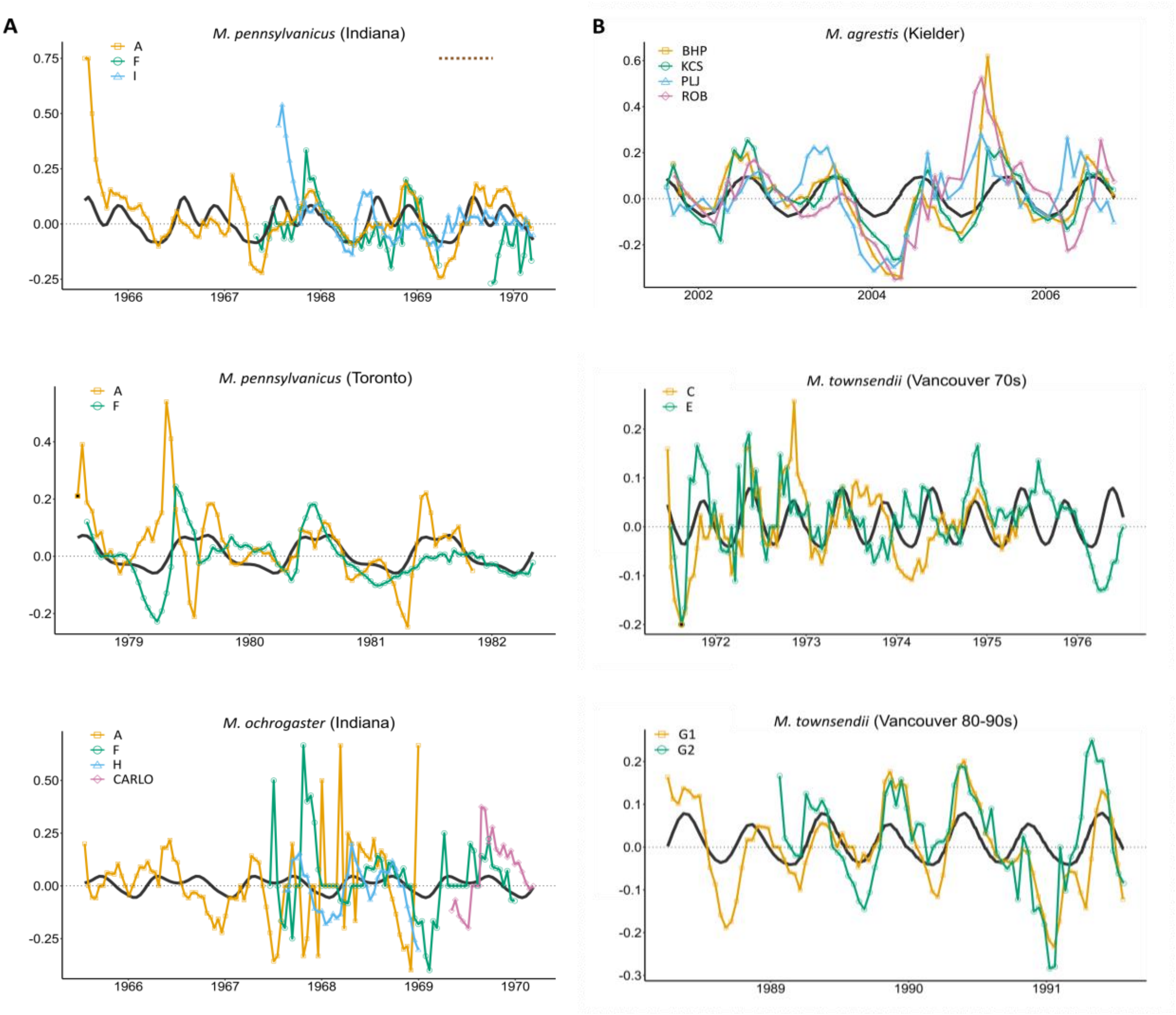
3.2 | Population growth rates, seasonal population growth rates and population growth rates anomalies (PGR, sPGR and PGRA)

The observed seasonal fluctuations varied across species (sPGR ; Fig. 4). The population of *M. agrestis* had an annual population increase (in spring-summer) and an annual population decrease (in autumn-winter). In contrast, populations of *M. ochrogaster, M. pennsylvanicus* in Indiana*,* and *M. townsendii* had two annual population increases (in late spring early summer and early winter) and two annual population decreases (in late summer and late winter; Fig. 4). PGR generally fluctuated similarly to sPGR, in high density populations (i.e. *M. agrestis*, *M. townsendii* and *M. pennsylvanicus* in Toronto). In contrast, PGR fluctuated at times quite differently from sPGR in those grids with very low density and sometimes close to 0 (i.e. *M. ochrogaster* and *M. pennsylvanicus* in Indiana; Figs. 3-4 and S1). In other words, observed population growth rates (PGR) were more different from seasonal population growth rates (sPGR) when the latter was calculated from low abundances; when PGR is very susceptible to small variations.

The amplitude of the observed seasonal fluctuation (s-index$_{sPGR}$) was different among species and seasons (Kruskal-Wallis tests; Tables S5-7). In addition, such differences were higher in spring and summer (i.e. higher s-index$_{sPGR}$).

On the other hand, within populations, the magnitude of the deviations in pgr from the expected seasonal trajectory varied among seasons (s-index$_{PGRA}$; Table S8). In contrast, comparing among species, the magnitude of pgra only differed in summer (Tables S9-10).

Fig. 4 | Plots A and B show the seasonal and observed population growth rates in each grid. To help compare PGR of similar data, each plot shows the PGR of grids of a same species in a given study site and period. The solid black line represent the estimated common seasonal PGR along grids and years. The horizontal dotted line at 0 in the y-axis depicts the absence of change in the population abundance from one sampling period to the next one. Values above the dotted line indicates that the population abundance increased, while values below the dotted line indicates that the population abundance decreased. The brown horizontal dotted lines in the plot about *M. pennsylvanicus* (Indiana, F) depicts that we discarded those data for the subsequent analyses beacause the estimates were missleading (see above). See Figure S8 for a more detailed viasualization of the seasonal and observed PGRs of each grid along the four seasonal blocks.



3.3 | Vital rates

Our estimates differed to those few available in previous studies (e.g. grids A of *M. pennsylvanicus* and *M. ochrogaster* in Indiana; see Tables 6 and 7 provided by Krebs et al. (1969)). See Figs. S2-7 and Tables S11-16 for further details. Visual explorations showed that vital rates of *M. ochrogaster* and *M. pennsylvanicus* individuals in Indiana, i.e., the populations with the lowest observed abundance, had temporal fluctuations with lower relative frequency and amplitude (e.g. ϕ_{NB}, Ψ_{NBB}, $\Psi_{BNB;}$ Figs. S2, S6 and S7). As for sexes, vital rates of males varied over the years by 25-30% more than females' (1.01-1.13 vs 1.31-1.43, respectively; confidence intervals at 95% of the estimated marginal means about the differences in the mean estimates of all vital rates between sexes; complementary lineal model using the CV of all variables as dependent variable and the sex as explanatory variable). Those differences were higher in estimates associated with non-breeding adults (i.e. ϕ_{NB} and Ψ_{NBB}; Figs. S2 and S7). When comparing the vital rates, the survival rates fluctuated up to 10-20 times less than the transition rates, and the transitions whose destiny was the breeding state those with the highest inter-annual variability (Table 3). Within the transition parameters, those associated with adults (i.e. Ψ_{NBB}, Ψ_{BNB}) generally had fluctuations with similar amplitudes and frequency than those associated with juveniles (i.e. Ψ_{JB}, Ψ_{JNB}). But within parameters associated with the apparent survival of adults, those associated with breeding individuals (ϕ_B) expected to be resident tended to have fluctuations with lower frequency and amplitude than those associated with non-breeding individuals (ϕ_{NB}). See Table 3 for further details.

With the aim to understand whether such differences biologically meaningful, we performed complementary explorations. A visual exploration of the abundance of captured individuals showed that the more smoothed fluctuations belonged to populations and reproductive groups with lower relative abundances, but not in the case of sexes, where the relative abundance of non-breeding females was similar or even higher than those of males (Figs. S1-7). Complementarily, an exploration of the number of estimates with convergence issues in each parameter also showed that these more smoothed fluctuations belonged not only to species and reproductive groups but also to sexes and grids with more convergence issues (e.g., grid A of *M. ochrogaster* and *M. pennsylvanicus* in Indiana and grids C and E of *M. townsendii*; Table S17). In fact, female parameters had in general more convergence issues than male parameters (Table S17; Wilcoxon signed rank test: V = 40, p-value = 0.02; analyses performed with function *wilcox.test* of R software (R Core Team 2021). For example, fluctuations of female vital rates on ϕ_{NB}, Ψ_{JB}, and Ψ_{JNB} of *M.townsendii* in grid 2 were more smoothed than those of grid 1, and those parameters in grid 1 had many convergence issues, while those in grid 2 none (Table S17). Thus, differences in the smoothing of the estimates between species and reproductive status were more associated with natural variations in sample size and convergence issues, but those between sexes and grids only with convergence issues.

	Mean	**CV**
φ_{NB}	0.73 – 0.78	0.10 – 0.41
φ_{B}	0.75 – 0.79	-0.24 – 0.11
Ψ_{JNB}	0.59 – 0.65	1.42 – 1.59
Ψ_{JB}	0.15 – 0.19	1.87 – 2.02
Ψ_{NBB}	0.30 – 0.35	1.81 – 1.96
Ψ_{BNB}	0.34 – 0.39	1.71 – 1.86

Table 3 | Confidence intervals at 95% of the estimated marginal means (EMMs). EMMs are the differences obtained from a linear mixed models where the mean and the coefficient of variation (CV) of the estimates of the vital rates across the seasonal blocks seasons was modelled only with the variables "sex" (i.e. female and male) and "vital rate" (i.e. φ_{NB}, φ_{B}, Ψ_{JNB} Ψ_{JB}, Ψ_{BNB}, and Ψ_{NBB}). The confidence intervals of the CV of females and males were 1.01-1.13 and 1.31-1.43, respectively (results not shown in table). We calculated EMMs with the function *emmeans* of the R package *emmeans* (Lenth 2021). To calculate EMMS, we did not include the variable seasonal block since it was not statistically significant ($p>0.70$ and $p>0.20$, mean and CV, respectively). In addition, we did not include the variable population since we had one data per population. Thus, these data describe our populations more than general patterns.

3.4 | Relationship between the PGRA and vital rates

Vole abundance and vital rates explained a large proportion of the variation in PGRA in the four seasonal blocks (pseudo-$R^2_{marginal}$ of the most parsimonious models in each block ranged between ca. 0.45-0.75; Fig. 5). Processes associated with females and males commonly explained PGRA differently (i.e., R^2; Fig. 5). Female variables seemed to explain more PGRA in the onset block, but there was high uncertainty, whereas male variables contributed most in the breeding and end blocks (see details below). In contrast, both female and male vital rates explained PGRA similarly in the non-breeding period.

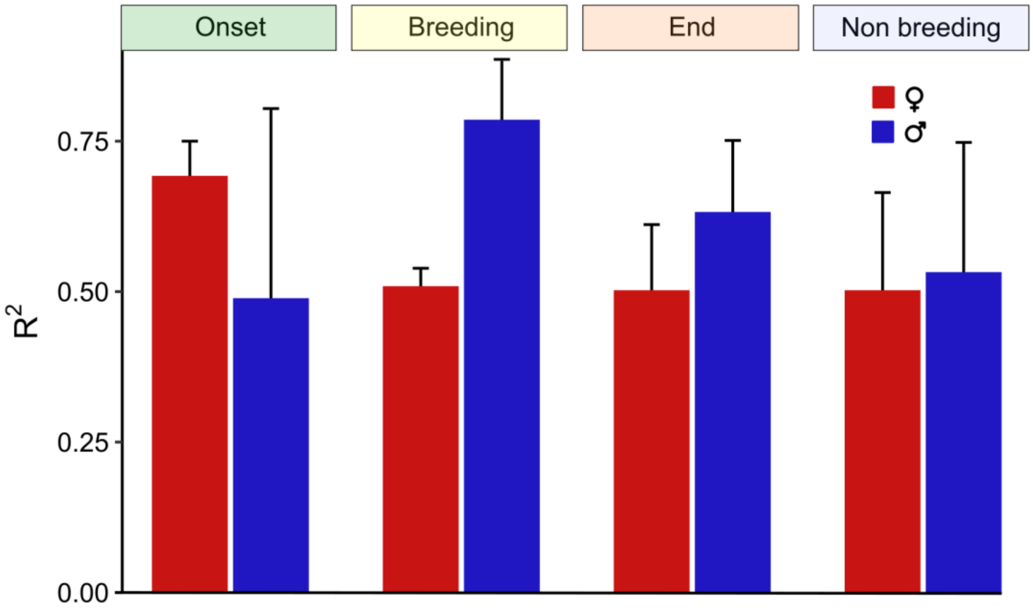


Fig. 5 | Proxy of the variance in PGRA explained by the abundance and vital rates selected in the most parsimonious model (i.e. marginal pseudo-R^2; only variance explained by the fixed effects). The bars depict the mean pseudo-R^2 of the three most parsimonious models (i.e. three sensitivity analyses; Fig. 1). While the error bars depict the standard deviation.

Only the abundance and the survival of the non-breeding individuals were selected as important when explaining variance in PGRA in the four seasonal blocks (i.e. statistically significant and with consistent effects; Fig. 6 and Table S18). The other variables were only selected as important for explaining PGRA in specific seasonal blocks. As for the sexes, both males and females affected PGRA; however, their influence was through different reproductive status in three seasonal blocks (i.e. a variable such as the transition from non-breeding to breeding was never selected in models of males and females for the same seasonal block). Thus, processes associated with general patterns were sex and reproductive state specific (Fig. 6 and Table S18).

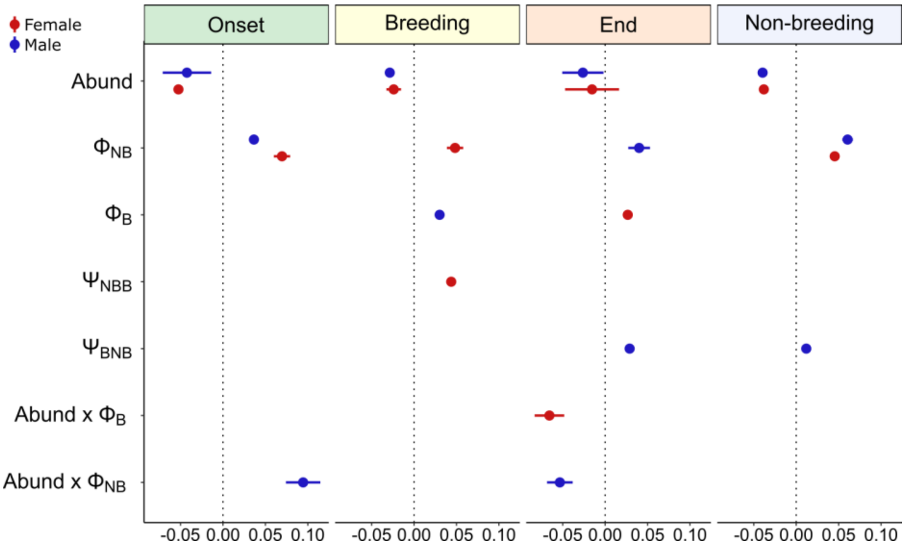


Fig. 11 | Mean and standard error of the regression coefficients of the variables included in the model with the lowest AICc of each sensitive analyses (i.e. models using as explanatory variables the values at the percentiles 2.5%, 50%, and 97.5% of the vital rates and abundance). Abund = Abundance. The symbol "x" represents the interaction between the two variables. See numerical values in Table S18. These standard errors represent the difference among sensitivity analyses, rather than the uncertainty on the central estimate. See those details in Tables S19-26. As for the single effects, points to the right of the dotted vertical bar indicate a positive relationship between that variable and the PGRA, while points to the left indicate a negative relationship. For the interactions the effect should be plotted. The absolute values of each point indicate the relative influence of each variable. Variables with higher absolute values had a higher influence.

In the non-breeding block, the abundance of both females and males correlated negatively with PGRA, while the synchronized maturation rate and the apparent survival correlated positively (Fig. 6 and Table S18). However, the demographic effect of the synchronized maturation rate was relatively minor (Figs. 6 and S9; but see discussion). The partial residual plot of the abundance showed that when population abundance was extremely low, there was no clear pattern (i.e. model fit was poor), but when abundance was relatively high, PGRA was mostly negative (i.e. population mostly decreased faster than average; see Figs. 2 and S10-11 for demographic details). On the other hand, when the apparent survival of the non-breeding males and females was low, PGRA was mostly negative, but when it was high, PGRA was mostly positive (Figs. 2 and S12-13).

Exploration of the raw data showed that observed negative PGRA were population collapses, whereas positive PGRA reflected a lack of typical winter declines. This biological significance of PGRA together with the detected patterns showed that population collapses in winter were associated with relative high abundances and anomalously low apparent survival (e.g., *M. ochrogaster* grid H in 1967/68; *M. townsendii* grids G1 and G2 in 1990/91; *M. agrestis* grids BHP, ROB, PLJ, and KCS in 2003/04; Figs. 3-4). On the other hand, populations that did not experience the common winter decline, independently of population abundance, were associated with anomalously high apparent survival of individuals rather than reproductive activity. Furthermore, despite the slight signal in global analyses (Figs. 6 and S9 and Table S18), complementary analyses suggest that reproduction activity is not important to explain why populations avoided or did not avoid the common winter decline (t-test: t(399)=-0.143, p=0.89; complementary analyses evaluating differences between values with PGRA <0 and PGRA>=0). However, the reproductive strategy of the last cohorts (to breed or not to breed in their year of birth) partially explained whether those populations that avoided the common seasonal decrease remained almost stable or even increased (complementary analyses: t(134.8)=17.49, p<0.001; analyses evaluating statistical differences in the transition rate from non-breeding to breeding states between increasing populations in winter: e.g. *M. pennsylvanic*us "grid A" and *M. ochrogaster* "grid A" in winter 1965/66; and stable populations in winter: e.g. *M. pennsylvanicus* "grid A" "grid F" and "grid I" in winter 1967/68 and *M. ochrogaster* "grid CARLO" in 1969/70; Figs. 3-4). Thus, there were two general patterns in the non-breeding block, winter population collapses were associated with high abundances and low apparent survival, whereas non-declining populations were primary associated with high apparent survival and secondarily with winter reproduction.

In the onset block, PGRA correlated negatively with abundance (Fig. 6 and Table S18). The partial residuals of the female abundance showed that when population abundance was relatively high, PGR was mostly below average (i.e. negative PGRA; population grew slower, remained stable, or even decreased). In contrast, when female abundance was relatively low, there was no clear pattern (i.e. the model did not fit well; see partial residual plots in Figs. S14). Male abundance showed a similar influence when the apparent survival of the non-breeding males was low, but it was reversed when the apparent survival was high (interaction abundance and apparent survival; Fig. S15). The apparent survival of both non-breeding females and males correlated positively with PGRA, except when male abundance was relatively low that correlated negatively (i.e. interaction; Figs. 6; see discussion). High apparent survival rates were associated with positive PGRA. In contrast, low apparent survival of both males and females were associated with negative PGRA. This pattern was clearer in females (see partial residuals and marginal regression coefficients; Figs. 6 and S16-17; Table S18).

A visual exploration of raw data showed that most observed negative PGRA were not anomalous low population increases but continuations of winter population declines that generally occurred when population abundances were high in the winter (hereafter spring declines; e.g. *M. townsendii* "grid C" in 1973 and 1974, *M. townsendii* "grid E" in 1976, *M. agrestis* "grids ROB, KCS, and BHP" in 2004, *M. pennsylvanicus* "grid F" in 1979 and 1981, *M. pennsylvanicus* "grid F" in 1981, and *M. townsendii* "grid

G1" in 1990 and 1991; Fig. 3). This exploration together with the results of the global model showed that spring declines were associated with high abundances (i.e., density-dependent) and low apparent survivals.

On the other hand, the observed positive PGRA were unusually fast population growth rates constituting the beginning of large population increases (e.g., *M. ochrogaster* "grid A" in 1966, *M. pennsylvanicus* "grid Toronto A" in 1979 and 1980 and *M. townsendii* "grid "E" in 1975 and *M. townsendii* "grid 2" in 1990) as well as punctual increases (e.g., *M. townsendii* "grid 1" and "grid 2" in 1989 and 1991, *M. townsendii* "grid "E" in 1973 and 1974 or *M. townsendii* "grid "C" in 1972 and 1975; Fig. 3). These explorations together with the results of the global model showed that the beginning of large population increases were associated with high apparent survivals (of non-breeding individuals) rather than a reproductive process (i.e., higher synchronised spring maturation that would be reflected in high values of Ψ_{NBB} for a time).

In the middle breeding block, PGRA correlated negatively with the abundance of males and females (Fig. 6 and Table S18). When abundance was relatively low, there was no clear pattern. On the contrary, when abundance was relatively high, population growth rate was mostly below average (i.e. negative PGRA; population grew more slowly than average or even declined; Figs. S18-19).

The apparent survival of males and females was positively associated with PGRA (i.e. marginal regression coefficient). The influence of males and females occurred through different reproductive states. Males vital rates influenced more PGR through processes associated with breeding individuals, the most abundant reproductive state in this period, while females did so through processes associated with non-breeding individuals, a state encompassing subadult individuals (Fig. 6 and Table S18). The apparent survival of both non-breeding females and breeding males correlated positively with PGRA. However, although the unusually low population growths occurred mainly when the apparent survival rates were low (i.e. negative PGRA), it was not clear whether relatively high apparent survival rates were associated with positive anomalies (Figs. S20-21).

On the other hand, the synchronized maturation rate of females also correlated positively with PGRA in the middle of the breeding season. When the synchronized maturation rate was relatively high, the probability of detecting positive PGRA was high (i.e. population grew faster than average), but when the synchronized maturation rate was relatively low, negative PGRA was more likely to be observed (i.e. population abundance grew unusually slowly or even declined; Fig. S22).

A visual exploration of raw data showed that observed positive PGRA were anomalous spring increases mostly in February-March. Thus, our results showed that anomalous high increases in late spring - early summer were associated with a higher apparent survival of non-breeding females and breeding males as well as synchronized maturation rate in females. On the other hand, observed negative PGRA were particularly strong declines at the end of the breeding season. Thus, earlier seasonal declines were predominantly associated with a lower synchronized maturation rate.

In the end of breeding season block, abundance of males and females also correlated negatively with PGRA. Although this effect was modulated by the apparent survival of breeding females and non-breeding males (i.e., interaction; Fig. 6). The pattern was most evident when the apparent survival was high. In this case, PGR was below average when abundance and apparent survival of non-breeding males and breeding males were high, while PGR was above average when the abundance and apparent survival were low (Figs. S23-24).

The apparent survival of the non-breeding females and breeding males correlated positively with PGRA when abundance was low, but as abundance increased, the relationship between PGRA and the apparent survival mainly disappeared. Positive PGRA were primarily associated with high apparent survival rates of non-breeding and breeding individuals (i.e. population abundance decreased unusually slowly or even increased), whereas negative PGRA were mostly associated with low apparent survival rates (i.e. population abundance decreased unusually quickly; Figs. S25-26).

The rate representing the end of male reproduction correlated positively with PGRA (Fig. 6). Although there was no clear pattern when this rate was low, positive PGRA were associated with high values of this rate (Fig. S27). Interestingly, this pattern indicates that the presence of an uncommon group, such as breeding individuals, in the non-breeding period is an important predictor of positive PGRA (i.e., population abundance decreased unusually slowly or even increased). However, the relative influence of reproduction seems to be less than that of survival (see marginal regression coefficients in Fig. 6 and Table S18).

A visual exploration showed that negative PGRA were population collapses, while positive PGRA were absences of common seasonal declines. These two events were associated to variations in abundance and apparent survivals of two reproductive groups that vary among sexes. In addition, the absence of common seasonal declines was associated with the stop of the reproduction in males.

4 | Discussion

During several decades, lively discussions have taken place on the existence and origin of common demographic patterns in population fluctuations of voles (Hoffman 1958, Krebs and Myers 1974, Lidicker 1978, Sandell et al. 1991, Norrdahl and Korpimäki 2002, Krebs 2013). Here we qualitatively contribute to this discussion and provide robust empirical evidences of how, despite large differences in temporal fluctuation of abundance and vital rate estimates between species, populations and grids (Figs. 3-4), there are indeed common syndromes of demographic change that coincide with patterns in inter-annual population fluctuations in four *Microtus* vole species at five locations in Europe and North America (Fig. 6). Interestingly, such common syndromes and patterns explain a large proportion of the observed deviations of population growth from the seasonal baseline trajectory (PGRA; Fig. 5). And contribute to the emergence of shape inter-annual population fluctuations, may indeed be the result of ubiquitous similar demographic processes.

The contribution of abundance and vital rates in explaining PGRA varied among phases of the seasonal cycle (Ozgul et al. 2004), suggesting the existence of multiple and time-varying processes (Lidicker 1978, Ozgul et al. 2004, Goswami et al. 2011, Krebs 2013). However, the signals of demographic processes related to abundance and apparent survival of non-breeding individuals were larger and more consistent, which may contrast with the observed minor contribution of adult survival to population dynamics of a population of prairie voles not included in our panel of data (Oli and Dobson 2003). The overall patterns on negative PGRA support that anomalous population declines throughout the year were predominantly associated with relatively high population abundances and low apparent survivals; although in autumn (end block) the relationship is more uncertain due to the interaction between these two factors. Signals in winter and spring (non-breeding and onset blocks) probably reflect survival processes, as those related to space and mate competition use to be more frequent in spring, summer and autumn (Boonstra 1989, Lambin and Krebs 1991, Lambin 1994). Whereas signals in spring, summer and autumn may reflect more social and survival processes (Krebs and Boonstra 1978, Beacham 1980, 1981, Taitt and Krebs 1973, McGuire et al. 1993). Likely, autumn declines do not reflect early cessations of reproduction (Krebs 1964b, Gliwicz 1996, Keller and Krebs 1970, Krebs and Myers 1974) as higher synchronized cessations of male reproduction were associated with positive PGRA instead of negative ones (Figs. 5 and S23). As there is no agreement about the general predation bias by sex and reproductive states (e.g., Mappes et al. 1993, Norrdahl and Korpimäki 1998, Graham and Lambin 2002), and we detected a signal in non-breeding males and breeding females in autumn, the two reproductive states expected to be affected by social interactions in populations with female philopatry (i.e., non-breeding males disperse more whereas breeding females compete for space; Boonstra 1989; Lambin 1994a,b), autumn declines are more likely due to social processes. In contrast, signals in summer are more uncertain. While, the associated lower synchronized maturation of females suggest that summer declines are partly associated with social interactions (Lambin 1993), the signal on the apparent survivals of non-breeding females and breeding females do not support expectations of natal female philopatry, and may suggest the existence of less intuitive social process or even the unlikely survival bias to sex and reproductive stage. Alternatively, our analytical approach was not able to capture the relationship of some variable. If so, the already observed signals associated with reproduction and the survival of breeding males and non-breeding females, suggest that general patterns in summer may be associated with reproductive, survival, and social processes.

Positive PGRA reflect the absence of normal seasonal population declines, as well as anomalously large population increases, depending on time specific effects of the apparent survival and reproductive activity. In winter, anomalous high population increases were primarily explained by survival (Aars and Ims 2002, Johnsen et al. 2017) and secondarily by reproduction activity. At the beginning of the breeding season, i.e., onset block, the most important process in explaining common PGRA surprisingly were not associated with our proxy of reproduction (Krebs and Myers 1974, Tkadlec and Zejda 1995, Ergon and Lambin 2001, Ergon et al. 2010), but with survival and/or social interactions of overwintered individuals (Krebs and Boonstra 1978, Taitt and Krebs 1983, Boonstra and Boag 1992); which we argued were probably mediated by food availability and quality because the timing (see predictions above). In contrast, anomalous population increases in late spring (mid-breeding season block), appeared to be less associated with a higher survival (Figs. S20-21) than with a greater synchrony in female reproductive activity (i.e., Ψ_{NBB}; Fig. S22); a process more related to condition of female individuals than to female territoriality and relatedness (Lambin 1993). In autumn, i.e. end block, both reproduction and apparent survival were important. The signals involving the apparent survival of non-breeding males and breeding females may support more the role of social interactions; a hypothesis supported by the strong density-dependent signal in this period (i.e. interaction between apparent survival and abundance). In addition, our results support that breeding cessation may be an important factor. The unique reproductive signal in males may *a priori* support the existence of factors that caused bias breeding cessation (e.g., Nelson et al. 1989). However, the large number of parameters on the reproductive cessation of females with convergence problems (Table S17) open the door to the possibility that the lack of signal in females is artefactual, and that breeding suppression of both sexes is important. Under such scenario, these demographic patterns may also support, that in addition to the potential effect of social interactions (breeding cessation), indirect effects of predators (mortality on both sexes) may be behind these anomalies (Ylönen and Ronkainen 1994, Koskela et al. 1996, Klemola et al. 1997, Fuelling and Halle 2003; but see Hansson 1995, Lambin et al. 1995, Korpimäki and Krebs 1996, Mappes et al. 1998).

In summary, anomalous low and high population abundances in all four seasons are often caused by the same demographic syndromes across populations, but causal factors may vary along the year according to the predictions tested here, with factors associated with mortality being most supported in winter and spring while with social interactions in summer and autumn.

Our descriptive results provide important clues that can help to advance in the understanding of general population dynamics. The similar amplitude of observed density fluctuations in our vole populations (s-index$_{\text{Density}}$) may contrast with previous literature supporting the important role of extrinsic variables such as the weather as a major factor explaining differences in the amplitude and frequency in cyclic fluctuations across geographical areas (e.g. Hansson and Henttonen 1988, Ergon and Lambin 2001, Cornulier et al. 2013). This result may be explained because of time series were relatively short and did not contain such variations, despite we studied close to 70 years of capture-mark-recapture data. On the other hand, the higher magnitude of seasonal fluctuations (s-index$_{\text{sPGR}}$) in summer (results not shown) along with the difference in s-index$_{\text{PGRA}}$ among species only in that season (Table S9), may suggest that processes acting in summer prompt the highest common differences among species in seasonal and observed fluctuations (Ims and Andreassen 2000).

To ensure the robustness of our inferences, we explored whether small sample sizes may have affected to the smoothness in temporal fluctuations of abundance and vital rates (capture-mark-recapture models), and then have masked some relationships between PGRA and our demographic variables. Some differences in smoothness can be explained from a biological point of view (e.g. some reproductive groups are not present or in low abundances in some periods). However, other ones are less intuitive. For instance, the degree of smoothing of vital rates appears to correlate with the number of estimates with convergence issues (Figs. S2-7 and Table S17) despite there were no large differences in the number of data used to estimate some parameters (Fig. S1). Potentially, these different smoothing may reflect real dissimilarities in the variance of the vital rates of males and females that affect to parameter estimation in CMR. As for concrete cases, beyond the already discussed potential bias in the breeding cessation of females, we did not observe a clear effect. In fact, some parameters estimated from relative scarce data were selected as important in explaining PGRA (e.g. the detected signals on breeding females non-breeding males in the end block). If artificial smoothness would have been an important source of bias, we would expect to detect larger fluctuations in apparent survival of non-breeding females and breeding males rather than in breeding females and non-breeding females, the parameters most selected in models. In contrast, the apparent survival of non-breeding males had fluctuations with higher frequencies and amplitudes than those of females, whereas those about breeding males and females were similar (Fig. S2-7). Thus, potentially, artificial smoothness may have had a quantitative effect rather than qualitative (i.e. reduced regression coefficients rather than removed variables from the model). In summary, the analyses being based on estimates of vital rates using novel methods (Chapter 2) yielded some unexpected and maybe odd patterns for some species grids, that may reflect sampling frequency sample size and true variation sometimes in unknown proportions. These patterns would require further analyses to know the extent of their influence on our inferences. Although our higher or lower support to diverse causal mechanisms should be taken carefully because the potential lack of other demographic syndromes, the current explorations support that differences in fluctuating vital rates mostly describe demographic processes adequately and that the absence of any signal in global models can be real.

Given the methodological limitations including both dependent and predictor variables measured with error, our analyses can be viewed as conservation in the extent to which they reveal common cross site cross species syndrome of PGR variation. Indeed, the number and strength of the common patterns, at least for our studied populations, are probably greater than those described here. We consider it due to, first, the different sampling methodologies of the datasets introduce to some extent noise into de the analyses (e.g., different sampling frequencies and protocols, as well as weather conditions affecting sampling). Second, we evaluated nearly 70 years of capture-mark-recapture data. But the time period of each grid may be relatively short to fully capture the fluctuations of each population. In other words, we may have looked for patterns in snapshots of population dynamics that reflect different demographic events (e.g., different population phases) or that do not adequately describe the processes we desire to capture. For example, the temporal asynchrony between PGR and sPGR in the Indiana populations of *M. ochrogaster* and *M. pennsylvanicus* probably reflects that we calculated the sPGR when population abundances were very low and variations in PGR are likely stochastic due to the large effect of small variations in abundance (Figs. 3-4 and S1). Consequently, some sPGR and PGRA estimates may be wrong and introduced more noise in the global analyses. Finally, because it was the only solution to study general patterns in time series with relative scarce data, we artificially minimized temporal variations by smoothing estimates of abundance and vital rates with the CMR models (abundance and vital rates) and a moving average window (abundance; Fig. 1). Altogether these factors reduce our chances to detect relationships between PGRA and our demographic variables and suggest that our results are even conservative.

We observed an importance role of direct density dependent and density independent factors when explaining PGRA (Goswami et al. 2011). However, due to the relative short length of our time series, we were not able to explore the influence of delayed density dependent effects, one of the most accepted aspects to explain some population dynamics (Hörnfeldt 1994, Stenseth 1999, Smith et al. 2006, Ergon et al. 2011). Previously it has been suggested that the relative influence of delayed and non-delayed density dependent effects caused the different population dynamics (e.g. differences between cyclic and non-cyclic populations; May 1981, Murray 2003). However, the high common variance already explained by direct density dependent and density independent factors in the present cyclic and non-cyclic populations suggest that such dichotomy is not so strong (Sandell 1991); what may “re-open” an interesting debate about the relative importance of each type of factor in population dynamics.

Similarly, the high variance in PGRA explained when exploring population dynamics of multiple species located in Europe and North America, may question the relative importance of local and general factors in observed population dynamics. We acknowledge that in both cases our results are limited to make such inferences because of the relative small number of species populations evaluated (i.e. five). However, our results can form the basis of these discussions, which will become more robust as more studies provide new insights.

Here we overcame a great challenge in the study of population dynamics of many species beyond small mammals, such as the estimation of demographic variables at fine scale when population abundance is relatively low. We also related for the first time variance in vital rates at fine scale with population dynamics of multiple vole species (but see Ozgul et al. 2004), and provided empirical evidences about the existence of common demographic patterns in species populations worldwide distributed and with cyclic and non-cyclic behaviours (Sandell 1991). Such common inter-specific patterns support the idea that population dynamics of small mammals have similar explanations (Krebs 1996, Myers 2018). In addition, the identification of the relative influence of demographic parameters on population dynamics from an empirical point of view rather than a theoretical one (Cole 1954; Lewonting 1965; Oli and Dobson 1999, 2003) will help unravel the mechanisms behind them. Overall, our study contributes new empirical pieces that should help to discern the small mammals’ population dynamics puzzle, aiding also as the baseline of future studies on population ecology.

Contributions

Eloy Revilla conceived the project. Xavier Lambin proposed to use old capture-mark-recapture data to answer the questions. XL and Rubén Bernardo Madrid contacted to researchers to collaborate. RBM depured the data. XL, TC, and RBM conceived the biological model for capture-mark-recapture models. Thomas Cornulier and RBM developed the smoothed capture-mark-recapture models. RBM, TC, and José Jiménez wrote the R code to run the capture-mark-recapture models. Rubén Bernardo-Madrid proposed the first analytical approach to search for general demographic patterns. RBM, EL, and XL discussed and proposed improvements for studying general demographic patterns. RBM wrote the first draft of the manuscript. RBM, XL, and ER discussed and comment the manuscript.

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APPENDIX CHAPTER III

Global determinants of population growth rate anomalies
in voles

Appendix A | Biological model

To study the demographic processes within vole populations, previous studies have assumed a biological model with three functional categories: 'juvenile', 'sub-adults', and 'adults' (Haukisalmi et al. 1988; Prévot-Julliard et al. 1999; Eccard & Herde 2013). In that biological model, juveniles are those individuals without breeding capacity; subadults are those individuals with the potential of breeding, but that their growth (beyond a certain weight) and do not breed until the onset of the following breeding season; and adults are non-juveniles individuals that breed in their year of birth (Kalela 1957; Myllymäki 1977a,b; Prévot-Julliard et al. 1999). This biological model assumes the existence of a trade-off between reproduction and survival (i.e. delaying reproduction increases the survival of individuals; Mappes & Ylönen 1997; Komdeur 2006; but see Kaitala et al. 1997; Ricklefs & Cadena 2007). Although this biological model is realistic because it considers the potential different roles of adults with breeding capacity, it is limited to inform about the onset and cease of the reproduction; important processes affecting one of the main drivers of population fluctuations such as the length of the breeding period (Krebs & Myers 1974; Stenseth et al. 1985; Smith et al. 2006).

To study the cease of the reproduction, studies commonly assess the first and last breeding activities of individuals in the raw data or assess the proportion of adults breeding in the population (e.g. Krebs 1966; Norrdahl & Korpimäki 2002). However, by assessing the raw data, we cannot consider the detectability of individuals, whereas by assessing the proportion of the adults breeding, we cannot differentiate whether this proportion decrease because the amount of subadults increase, because the breeders stop their reproduction, or because breeders die (Pelikan 1982). In summary, we preferred using an approach that combine to some tolerable degree the combination of individuals with different roles in the population (i.e. "subadults" and "adults" in the non-breeder state during the non-breeding season), in exchange for obtaining detailed information about mechanisms related with the onset and cease of the breeding period as well as for estimating biological processes while controlling for detectability of individuals.

Our biological model has three functional categories that explicitly inform about the reproductive capacity and activity of individuals. The three functional categories are: 'juveniles', 'non-breeder adults', and 'breeder adults'. Juveniles encompasses to those individuals without breeding potential, while adult states (i.e. breeder and non-breeder) encompass to those individuals that have physiological potential to breed. The non-breeder state includes to those individuals that have not yet reproduced or that have previously reproduced and but stopped. Whereas the breeder state includes the individuals that are breeding at that time. As in the traditional biological model, the subadults and adults will be grouped in different categories during the breeding season (i.e. non-breeder and breeder states, respectively). However, both "subadults" and "adults" can be mixed during the non-breeding season in a same reproductive state in our biological model (i.e. non-breeder). Nevertheless, our analyses about survival showed unimodal distributions for the posterior distributions, supporting that our biological model does not violate any assumption of capture-recapture models. However, unlike the traditional model, ours provide more details about the cease of the reproduction better because of a new transition parameter from the breeder to the non-breeder states. In contrast, traditional model assumes that individuals that started breeding does not stop.

Appendix B | Classification of individuals into reproductive states

To classify the individuals as juveniles, non-breeder adults, and breeder adults, we used their weight and the reproductive state of their sex organs. We first classified the individuals as breeders and non-breeders by using the information about the sex organs. We classified females with large nipples (i.e. lactating), open pubis (i.e. have recently given birth), or pregnant classified, as well as males with testes in a scrotal position as breeding adults. We later classified the non-breeding individuals as juveniles and non-breeding adults. We considered that individuals with a weight equal or higher than the minimum one observed in the breeding individuals have the potential to breed. We thus calculated the minimum observed weight in breeding individuals for each species and sex, hereafter minimum weight at sexual maturation. Then, we classified non-breeding individuals with a lower and higher weight than the minimum weight at sexual maturation as juveniles and non-breeding adults, respectively. To be conservative and consider that some individuals can start breeding unusually fast, we defined the minimum weight at sexual maturation as the percentile 5th of the distribution of the breeder weight.

We excluded those observations without information about sex organs and weight as well as about those individuals with information for both female and male sex organs along its whole capture history. We also excluded the observations of individuals that were captured two years after its first capture since vole life span is lower (Getz 1960; Weigl 2005; Booner & Schwarz 2006; Rose & Kratimenos 2006). Due to the low number of removed observations (<0.5%), we expected that their elimination would not affect our conclusions.

Appendix C | Specification of the capture-recapture analyses

For each CRM, we run four chains with a number of iterations ranging between 500,000 and 2,000,000, and burnt the first 10,000 iterations. Due to space limitations, we thinned the outputs by 10-50 times (Link & Eaton 2012).

When running the CRMs in a computer with 32 GB RAM and a processor Intel® Xeon® E5-2698 v3, the median computational time of the 76 CRMs was ~30 days, but ranged between 12 and 120 days depending on the length of the time series and the amount of captures. Due to the Bayesian approach, we could not use computer clusters, but rather multiple computers to run chains independently. In total, analysing our CRMs in a unique computer would have lasted about a year.

Appendix D | Generalized additive mixed models to estimate the seasonal growth rate

We ran the generalized additive mixed model by using the *gam* function of the R package *mgcv* (R Core Team 2017; Wood 2011, 2017). We used the family beta in the models because breeding rate ranged between 0 and 1. We converted all 0 values as 0.00001 while 1 values as 0.99999 since family beta does not accept values at 0 and 1. We included the random effects of the study area by specifying group-specific smoothers for each study area, which Pedersen et al. (2019) called the I-model. By this way, we can obtain different seasonal trends per study area if they exist. On the other hand, we included the random effects of the grid, nested to the effect "study area", by using penalized regression terms through the term 's(Grid, Study area, bs="re")' of the function "gam". We followed the specifications provided in the R documentation of the package *mgcv*, section *random.effects* (https://stat.ethz.ch/R-manual/R-devel/library/mgcv/html/random.effects.html, accessed in September 2019). We thus assumed that the seasonal dynamics of grids located in the same study area were the same. Similarly, we included the random effects of the species and nested to study area, by using penalized regression terms but including a "by-variable" smooth ('s(Study area, bs="re", by=Specie)'. Because of we used the term "by", we were able to detect different seasonal patterns for each combination of "species" x "study area" if they exist. We obtained the pgra by using the function *residuals* of the R package *mgcv* with the specification *type* as *response*.

Appendix E | Definition of the temporal blocks

We classified the study period in four temporal blocks: (i) the onset of the breeding period, (ii) the middle of the breeding period, (iii) the end of the breeding period and (iv) the non-breeding period, by using the output of the additive mixed model.

We followed the same approach than in Appendix D but using the proportion of females breeding as dependent variable. To reduce noise, we only used time steps with more than 10 females. The output was a seasonal average trend with the proportion of adult females breeding in each population, where we can observe the centered average proportion of adult females breeding in each week of the year.

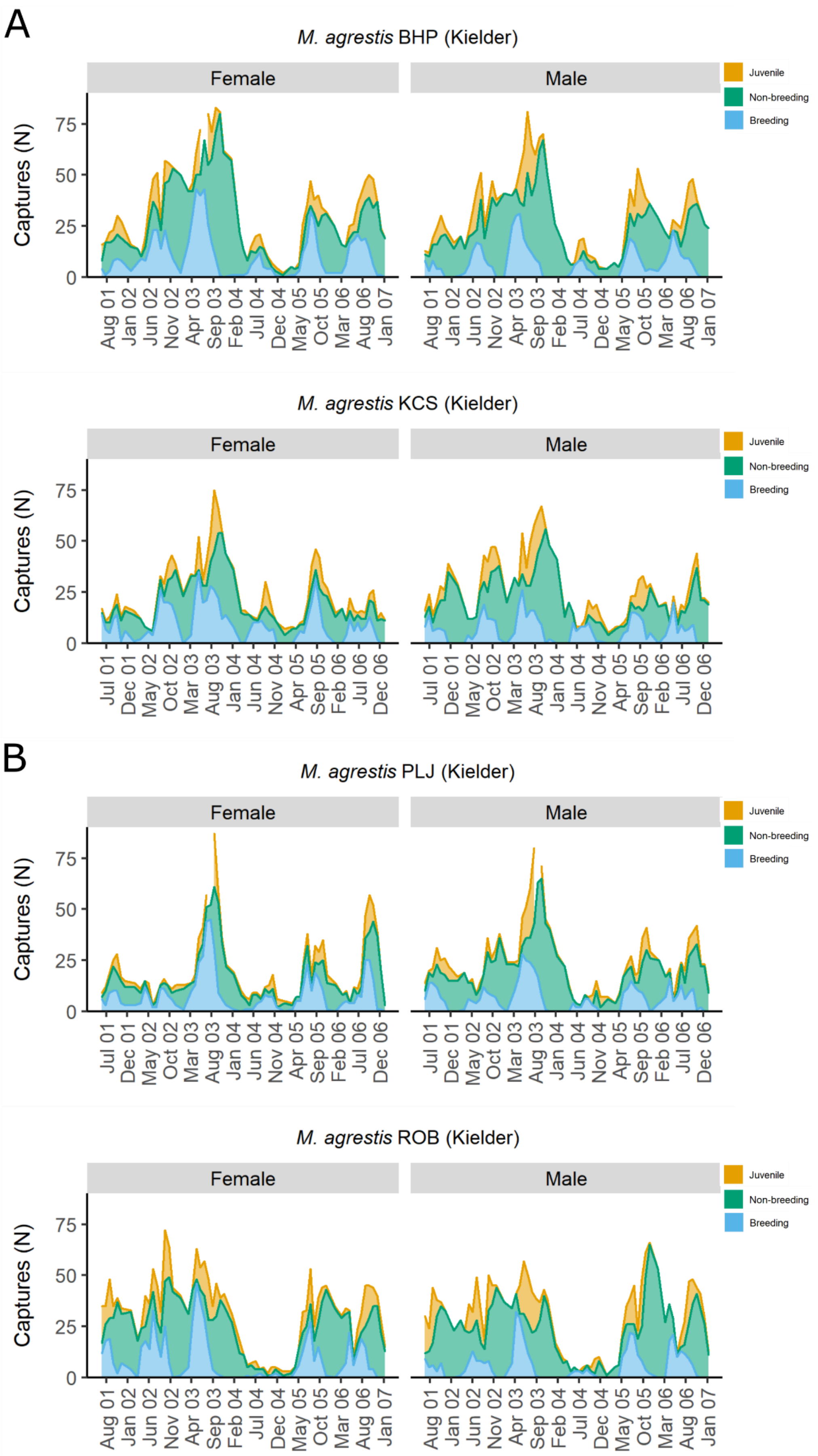
We assumed the first week of the breeding season to the week of the year with the closest value to 0 during the seasonal increase of the proportion of female adults breeding, while the last week of the breeding season to the week of the year with the closest value to 0 during the seasonal decrease of the proportion of female adults breeding. Subsequently, we used the estimated first and last weeks of the breeding period of each population to define the temporal blocks. We defined the "onset of the breeding period" as the weeks encompassing the four previous and subsequent weeks of the estimated first week of the breeding period. Similarly, we defined the "end of the breeding period" as the weeks encompassing the four previous and subsequent weeks of the estimated last week of the breeding period. We later defined the "middle of the breeding period" and "non-breeding period" as the weeks between the temporal blocks "onset and end of the breeding season".

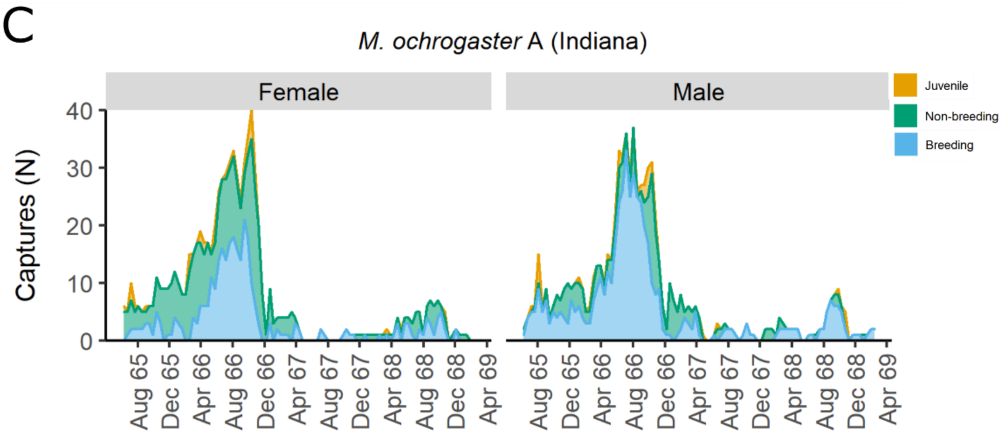
Appendix F | Lack of convergence of some estimates

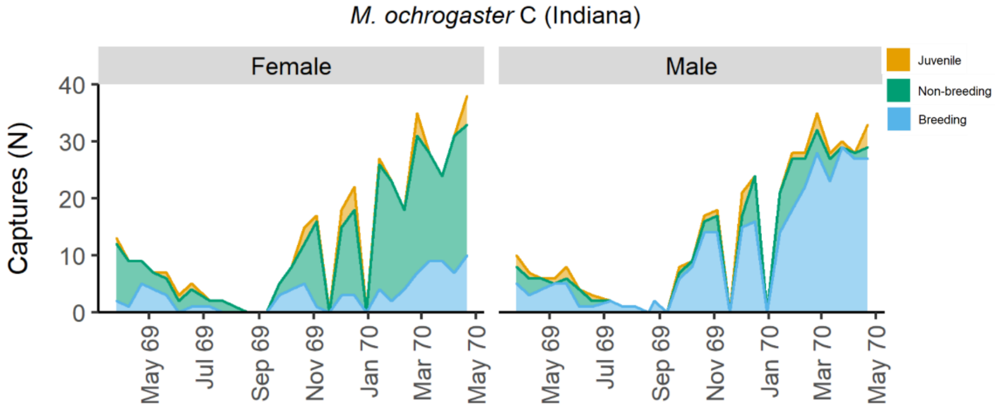
Some of the estimates about abundance and vital rates had some convergence issues (r-hat > 1.2) that were not overcome by increasing the number of iterations in reasonable analysis time (>15 days). Convergence issues indicate that the chains have not sampled from the stationary distribution and that our posterior distribution may not be representative. The literature recommends discarding these values. But if we do it, our sample size was too low to answer some questions (i.e. lack of degrees of freedom). We therefore decided to keep them since our approach of using only the consistent variables prevent us to make wrong inferences. Note that if a vital rate has huge convergence issues, its temporal trends will be different when we focus on their values at different percentiles. But because we only made inferences on thus consistent variables, any artificial pattern resulted from convergence issues will be discarded.

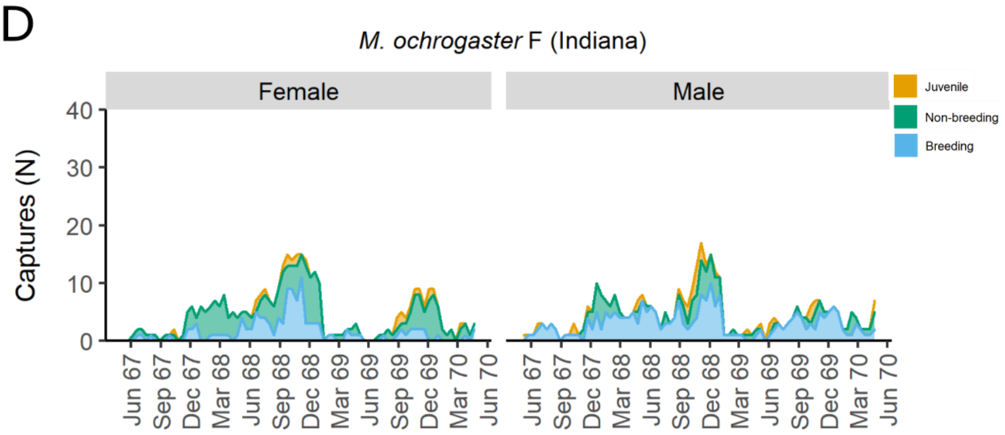
Suplementary Figures

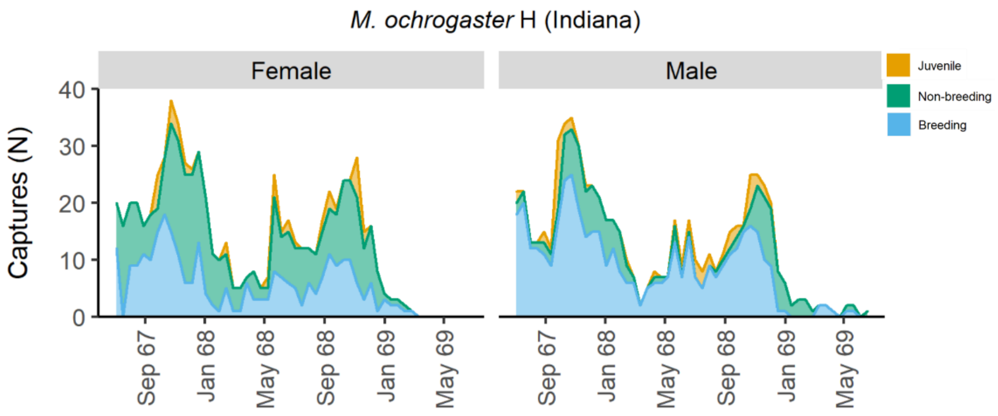
Fig. S1 | Temporal variation in the number of juvenile, non-breeding and breeding males and females captured. The x-axis scale can vary between grids of the same population depending on their sampling period. The the y-axis scale vary between populations, being defined by the grid with the highest number of captures in each population. The number of females and males captured was similar within the same grid. However, the relative abundance of the reproductive states varied between sexes in some populations. While the relative abundance of juveniles was mostly similar in all populations, the relative abundance of non-breeding and breeding individuals varied. In populations of *M. pennsylvanicus, M. ochrogaster,* and *M. townsendii* (grids C and E), the relative number of non-breeding females captured was higher than that of males while the relative number of breeding males captured was higher than that of females. In contrast, in populations of *M. agrestis* and *M. townsendii* (grids G1 and G2) the number of non-breeding and breeding individuals captured was more balanced between sexes.

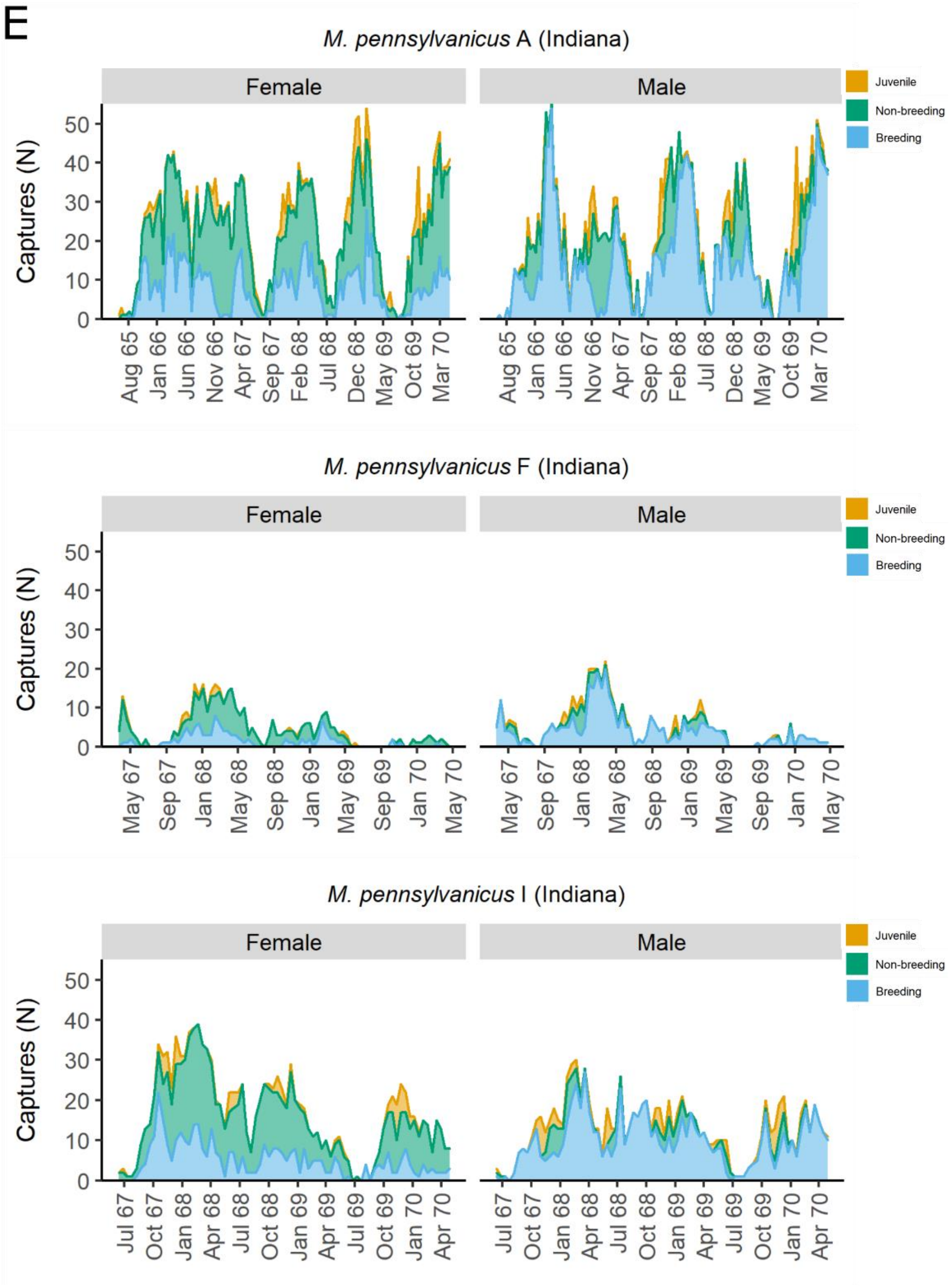

A
M. agrestis BHP (Kielder)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
0
25
50
75
Aug 01
Jan 02
Jun 02
Nov 02
Apr 03
Sep 03
Feb 04
Jul 04
Dec 04
May 05
Oct 05
Mar 06
Aug 06
Jan 07
M. agrestis KCS (Kielder)
Jul 01
Dec 01
May 02
Oct 02
Mar 03
Aug 03
Jan 04
Jun 04
Nov 04
Apr 05
Sep 05
Feb 06
Jul 06
Dec 06
B
M. agrestis PLJ (Kielder)
M. agrestis ROB (Kielder)


C
M. ochrogaster A (Indiana)
Female
Male
Captures (N)
0
10
20
30
40
Aug 65
Dec 65
Apr 66
Aug 66
Dec 66
Apr 67
Aug 67
Dec 67
Apr 68
Aug 68
Dec 68
Apr 69
Juvenile
Non-breeding
Breeding

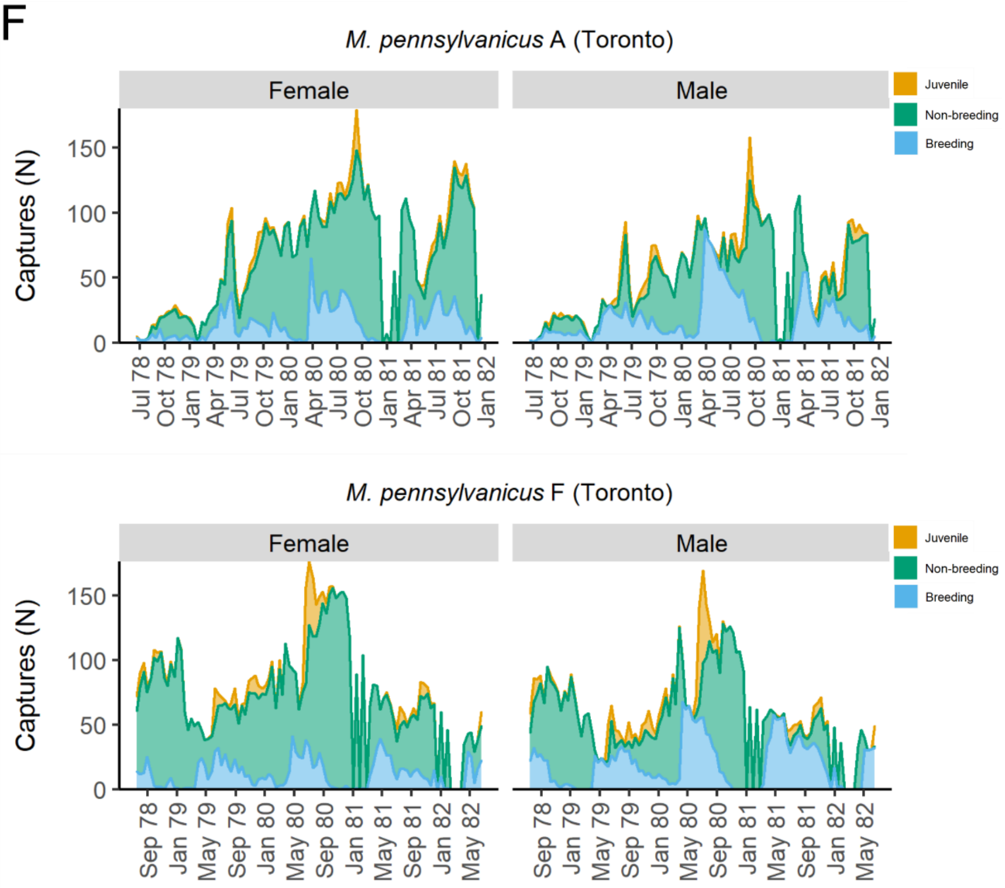

M. ochrogaster C (Indiana)
Female
Male
Captures (N)
0
10
20
30
40
May 69
Jul 69
Sep 69
Nov 69
Jan 70
Mar 70
May 70
Juvenile
Non-breeding
Breeding


D
M. ochrogaster F (Indiana)
Female
Male
Captures (N)
0
10
20
30
40
Jun 67
Sep 67
Dec 67
Mar 68
Jun 68
Sep 68
Dec 68
Mar 69
Jun 69
Sep 69
Dec 69
Mar 70
Jun 70
Juvenile
Non-breeding
Breeding

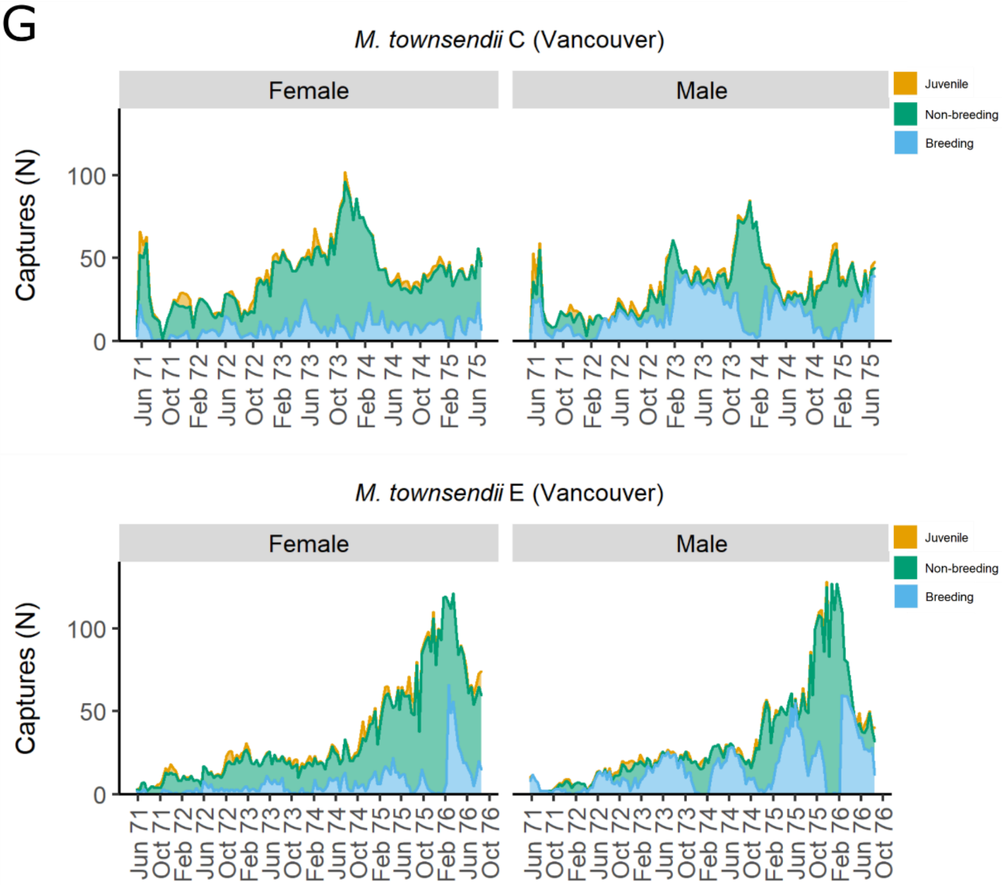

M. ochrogaster H (Indiana)
Female
Male
Captures (N)
0
10
20
30
40
Sep 67
Jan 68
May 68
Sep 68
Jan 69
May 69
Juvenile
Non-breeding
Breeding


E
M. pennsylvanicus A (Indiana)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
50
40
30
20
10
0
Aug 65
Jan 66
Jun 66
Nov 66
Apr 67
Sep 67
Feb 68
Jul 68
Dec 68
May 69
Oct 69
Mar 70
M. pennsylvanicus F (Indiana)
May 67
Sep 67
Jan 68
May 68
Sep 68
Jan 69
May 69
Sep 69
Jan 70
May 70
M. pennsylvanicus I (Indiana)
Jul 67
Oct 67
Jan 68
Apr 68
Jul 68
Oct 68
Jan 69
Apr 69
Jul 69
Oct 69
Jan 70
Apr 70

F


M. pennsylvanicus A (Toronto)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
0
50
100
150
Jul 78
Oct 78
Jan 79
Apr 79
Jul 79
Oct 79
Jan 80
Apr 80
Jul 80
Oct 80
Jan 81
Apr 81
Jul 81
Oct 81
Jan 82
M. pennsylvanicus F (Toronto)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
0
50
100
150
Sep 78
Jan 79
May 79
Sep 79
Jan 80
May 80
Sep 80
Jan 81
May 81
Sep 81
Jan 82
May 82

G


M. townsendii C (Vancouver)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
0
50
100
Jun 71
Oct 71
Feb 72
Jun 72
Oct 72
Feb 73
Jun 73
Oct 73
Feb 74
Jun 74
Oct 74
Feb 75
Jun 75
M. townsendii E (Vancouver)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
0
50
100
Jun 71
Oct 71
Feb 72
Jun 72
Oct 72
Feb 73
Jun 73
Oct 73
Feb 74
Jun 74
Oct 74
Feb 75
Jun 75
Oct 75
Feb 76
Jun 76
Oct 76

H

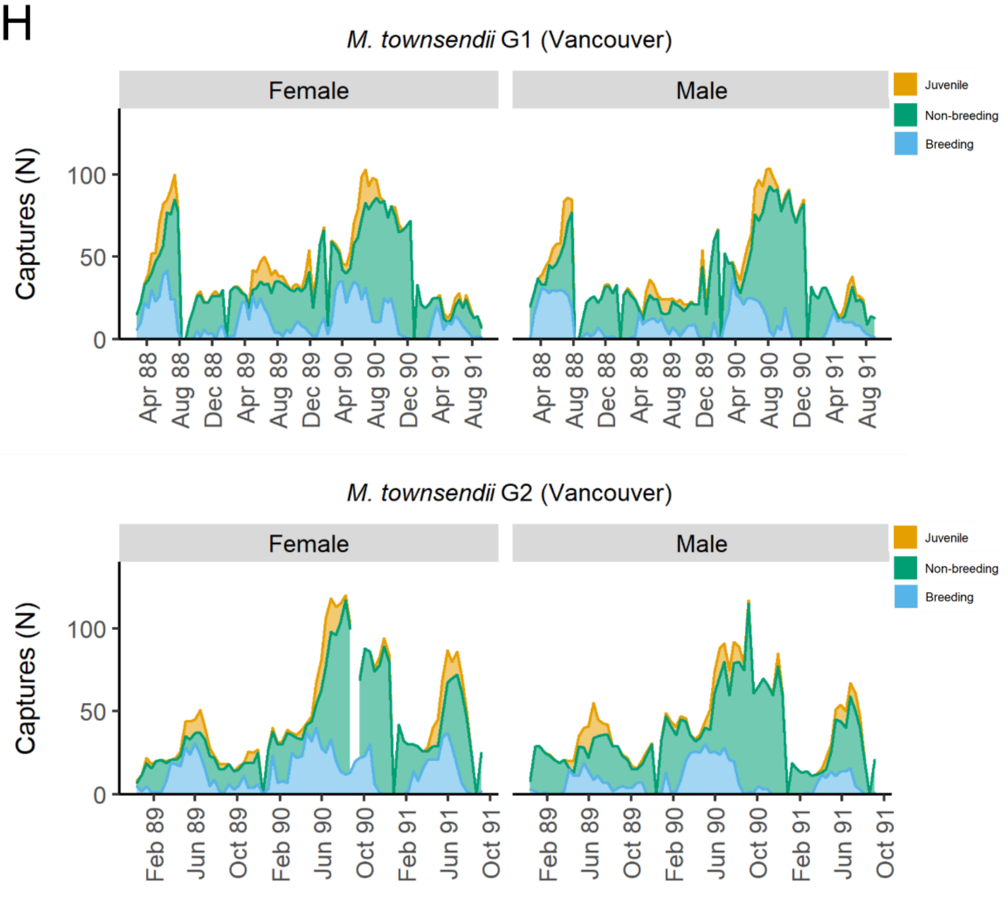
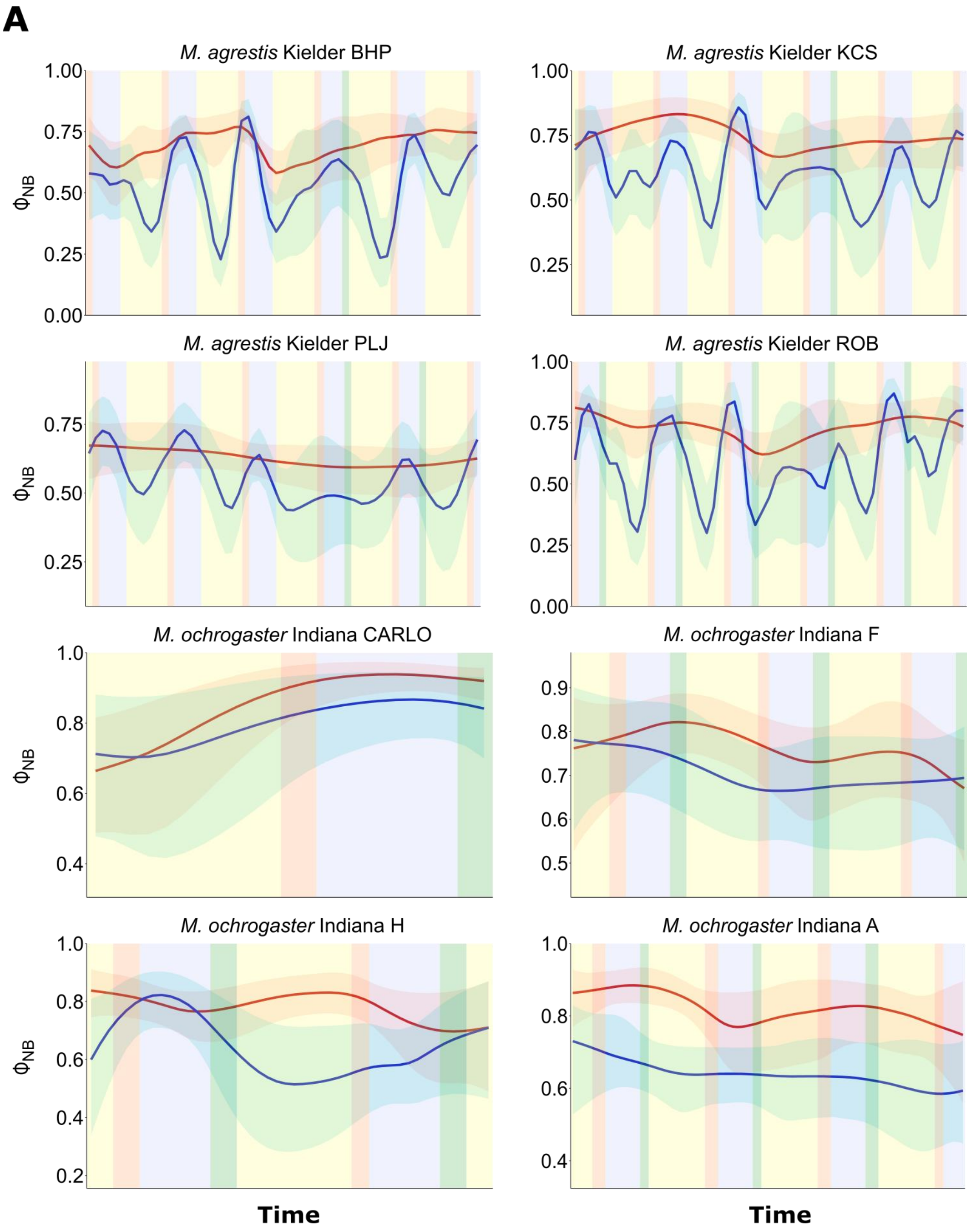

M. townsendii G1 (Vancouver)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
100
50
0
Apr 88
Aug 88
Dec 88
Apr 89
Aug 89
Dec 89
Apr 90
Aug 90
Dec 90
Apr 91
Aug 91
M. townsendii G2 (Vancouver)
Female
Male
Juvenile
Non-breeding
Breeding
Captures (N)
100
50
0
Feb 89
Jun 89
Oct 89
Feb 90
Jun 90
Oct 90
Feb 91
Jun 91
Oct 91

Fig. S2 | Estimates of the apparent survival of non-breeding individuals. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S11.



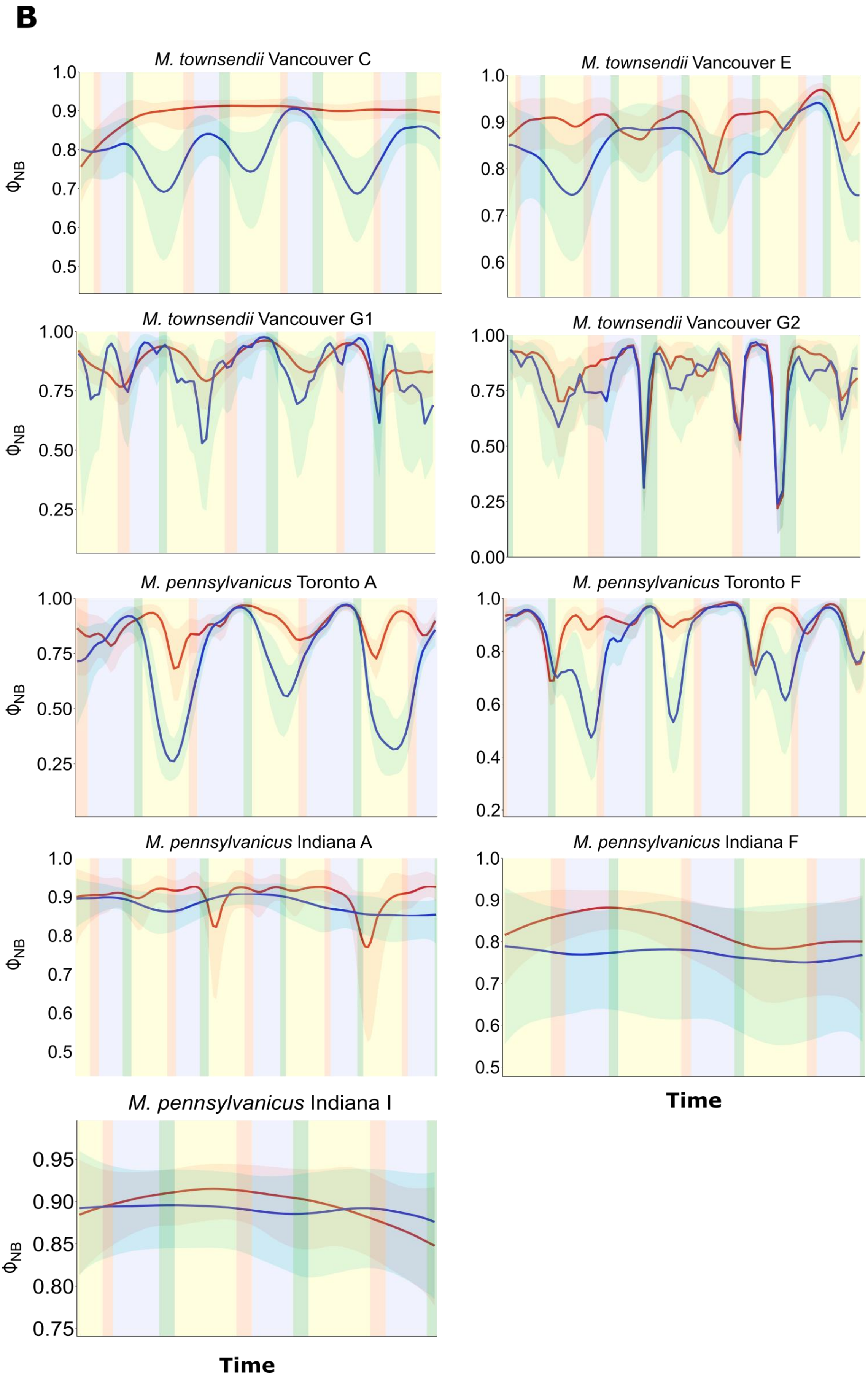
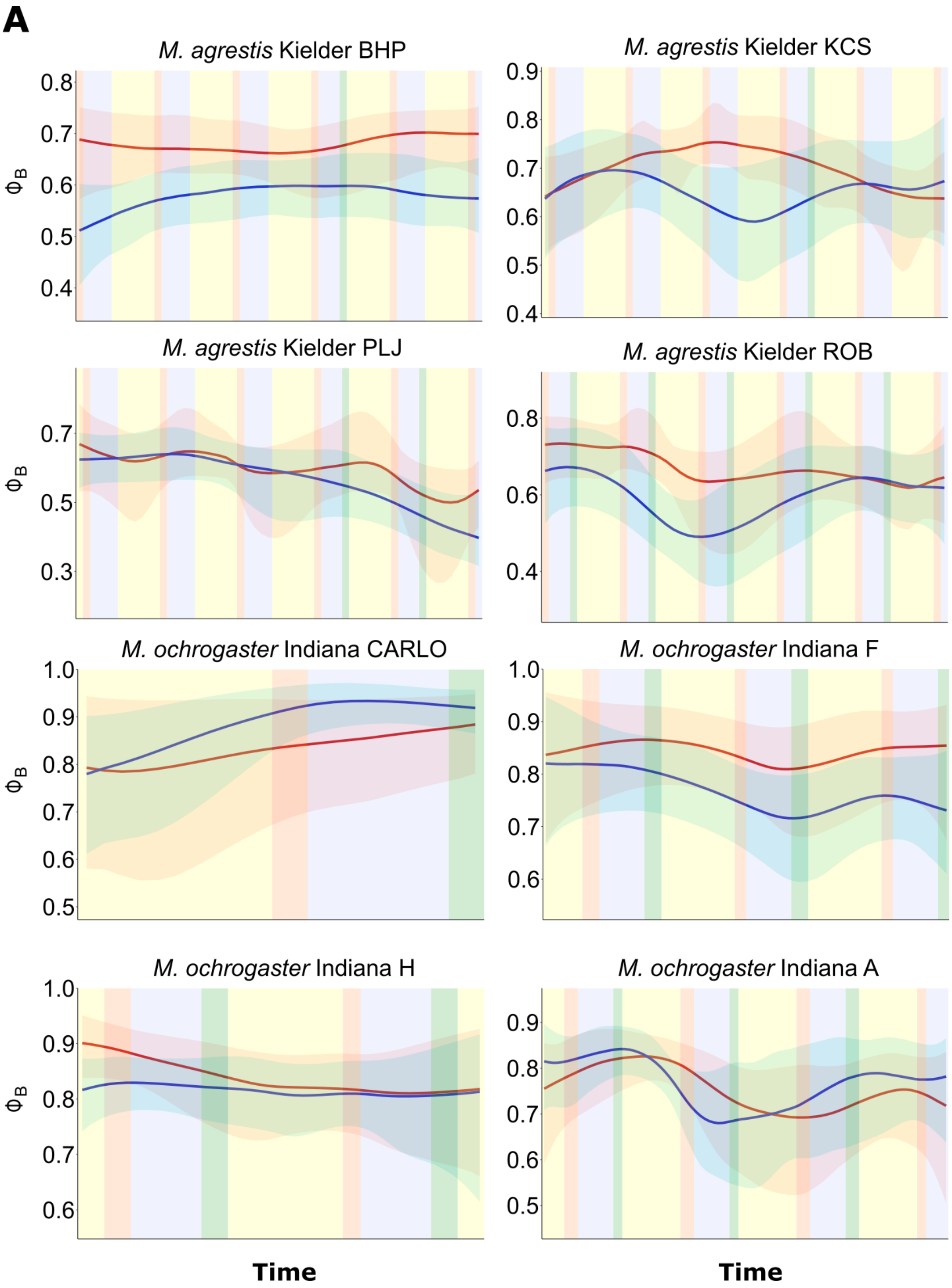

B
M. townsendii Vancouver C
M. townsendii Vancouver E
M. townsendii Vancouver G1
M. townsendii Vancouver G2
M. pennsylvanicus Toronto A
M. pennsylvanicus Toronto F
M. pennsylvanicus Indiana A
M. pennsylvanicus Indiana F
M. pennsylvanicus Indiana I
Φ_{NB}
1.0
0.9
0.8
0.7
0.6
0.5
1.00
0.75
0.50
0.25
0.00
0.4
0.2
0.95
0.90
0.85
0.80
Time
Time

Fig. S3 | Estimates of the apparent survival of breeding individuals. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S12.



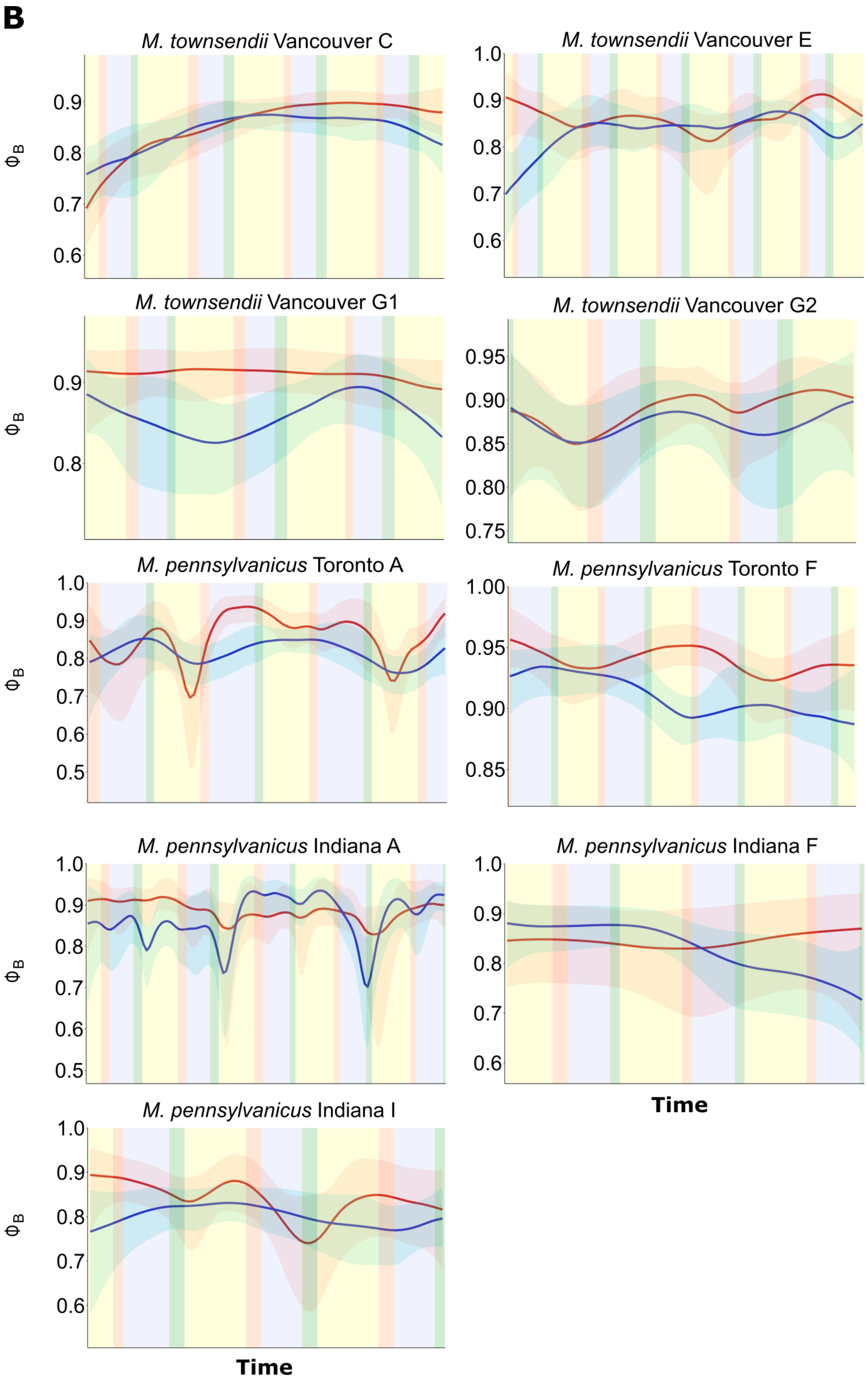
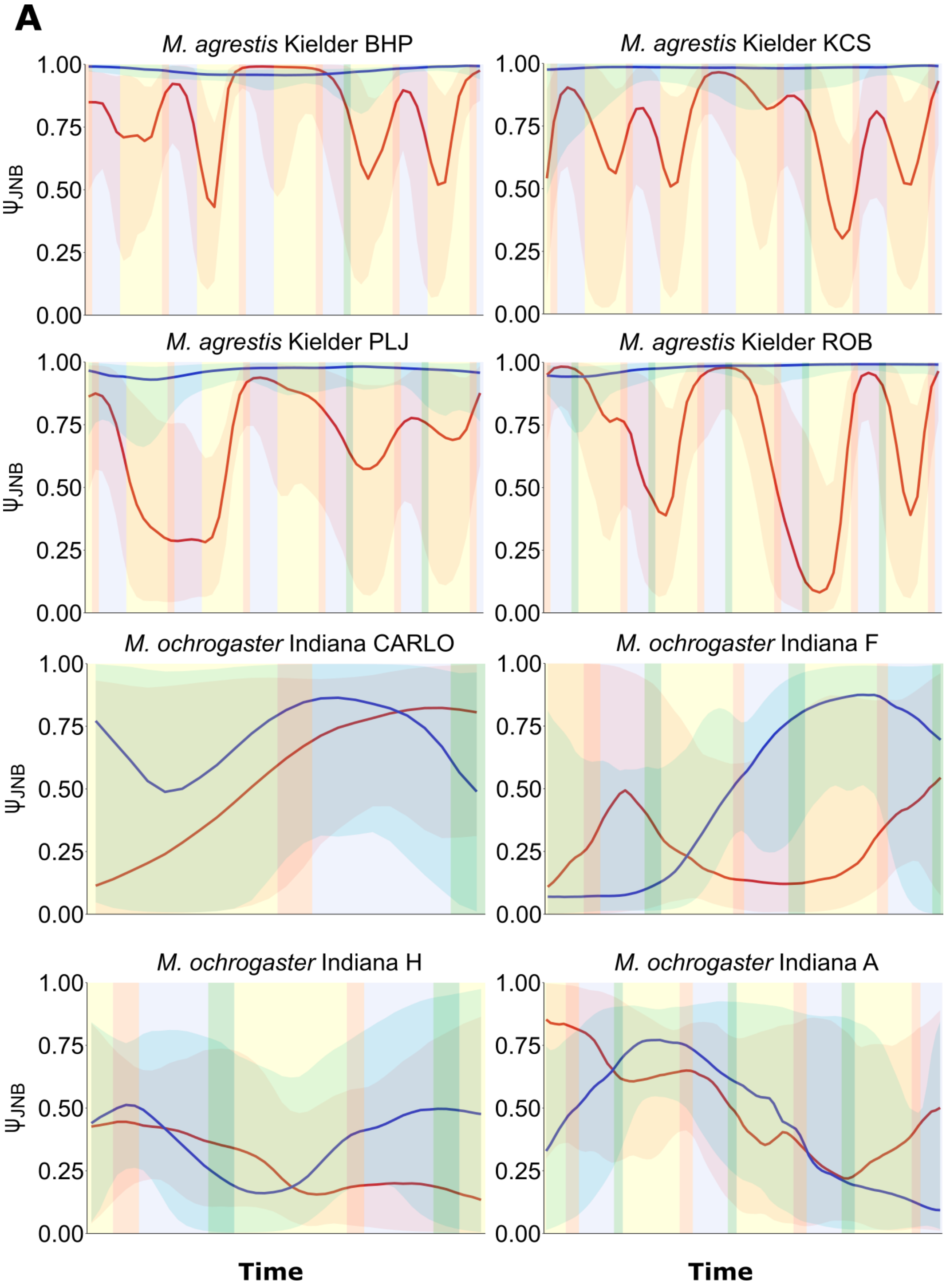

B
M. townsendii Vancouver C
0.9
0.8
0.7
0.6
ΦB
M. townsendii Vancouver E
1.0
0.9
0.8
0.7
0.6
M. townsendii Vancouver G1
0.9
0.8
ΦB
M. townsendii Vancouver G2
0.95
0.90
0.85
0.80
0.75
M. pennsylvanicus Toronto A
1.0
0.9
0.8
0.7
0.6
0.5
ΦB
M. pennsylvanicus Toronto F
1.00
0.95
0.90
0.85
M. pennsylvanicus Indiana A
1.0
0.9
0.8
0.7
0.6
0.5
ΦB
M. pennsylvanicus Indiana F
1.0
0.9
0.8
0.7
0.6
Time
M. pennsylvanicus Indiana I
1.0
0.9
0.8
0.7
0.6
ΦB
Time

Fig. S4 | Estimates of the transition from juvenile to non-breeding reproductive states. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S13.



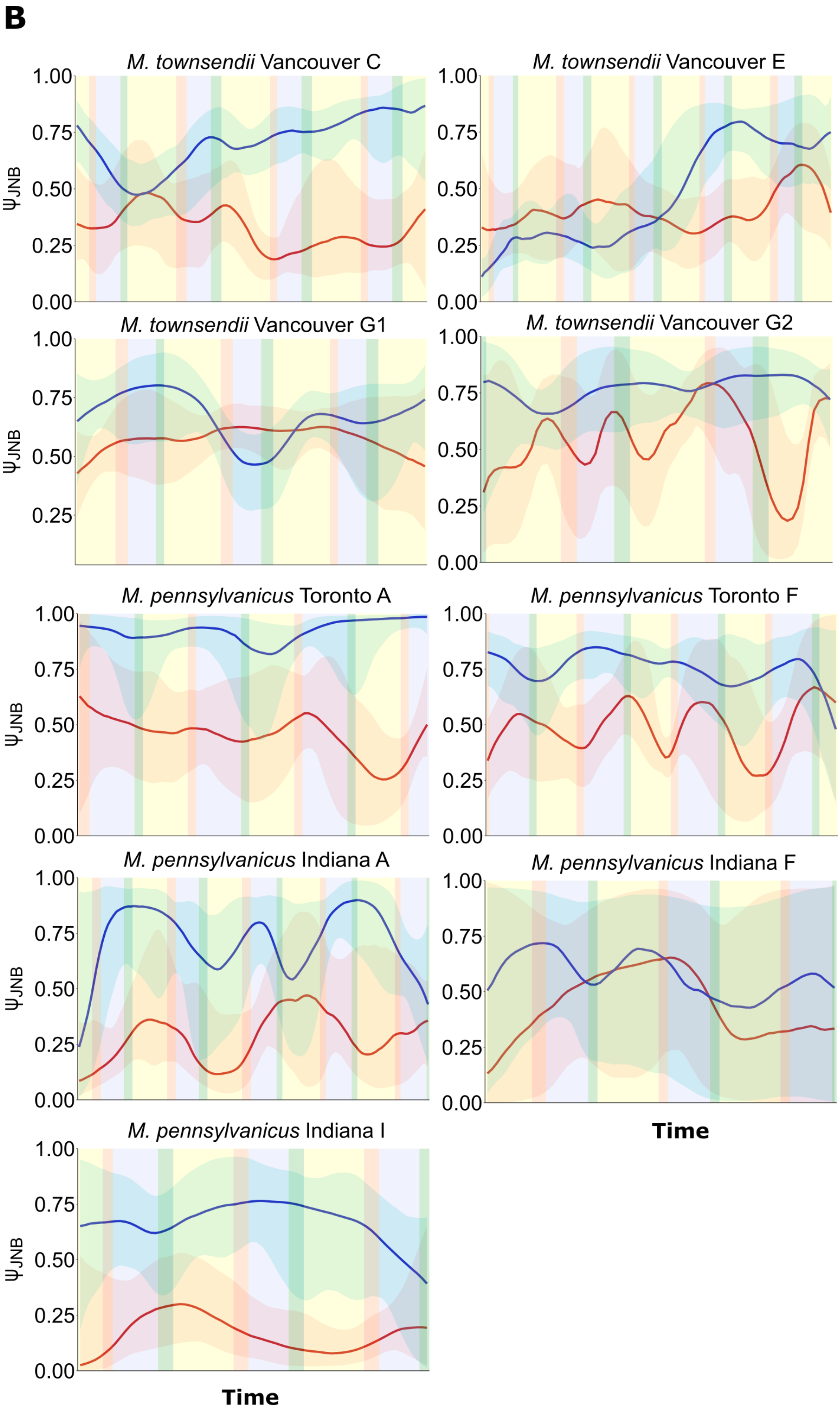
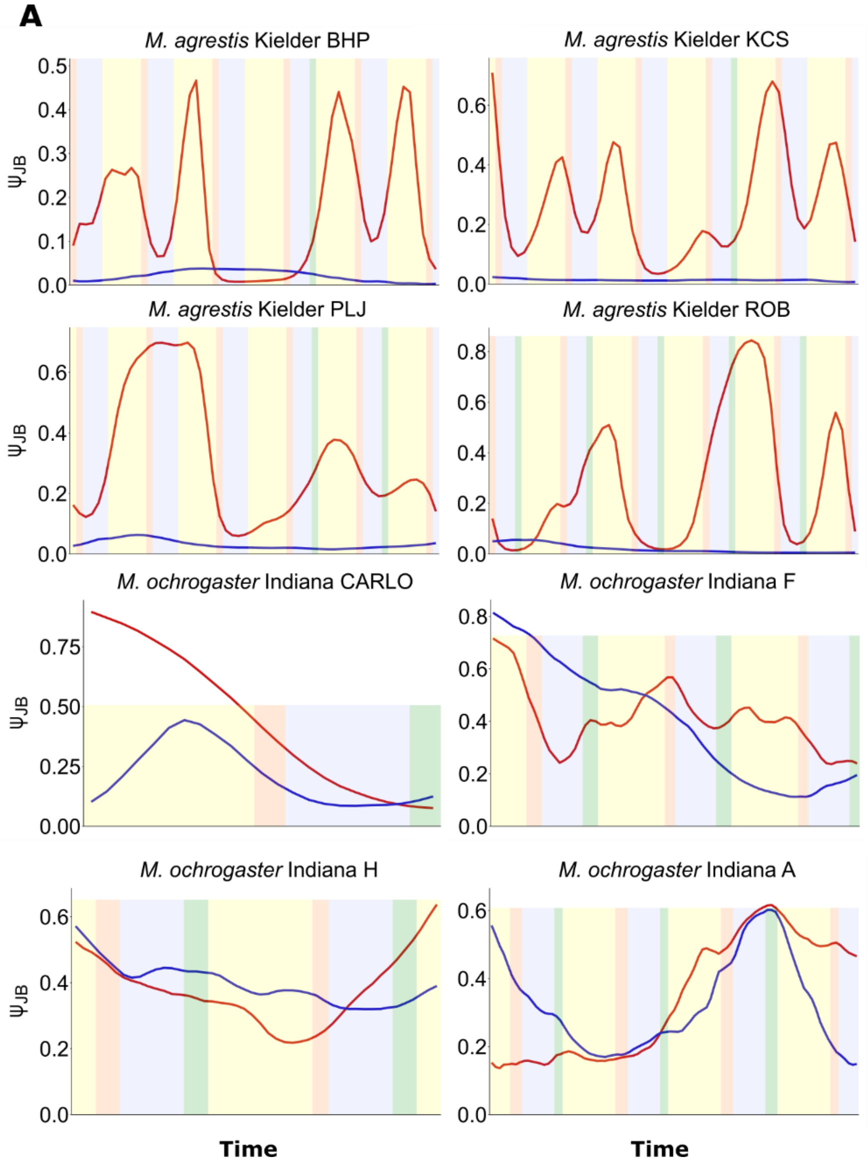

B
M. townsendii Vancouver C
M. townsendii Vancouver E
M. townsendii Vancouver G1
M. townsendii Vancouver G2
M. pennsylvanicus Toronto A
M. pennsylvanicus Toronto F
M. pennsylvanicus Indiana A
M. pennsylvanicus Indiana F
M. pennsylvanicus Indiana I
Ψ_{JNB}
1.00
0.75
0.50
0.25
0.00
Time

Fig. S5 | Estimates of the transition from juvenile to breeding reproductive states. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males. This figure does not contain the credibility interval (percentiles 5th and 95th) because an error in data manipulation. The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S14.



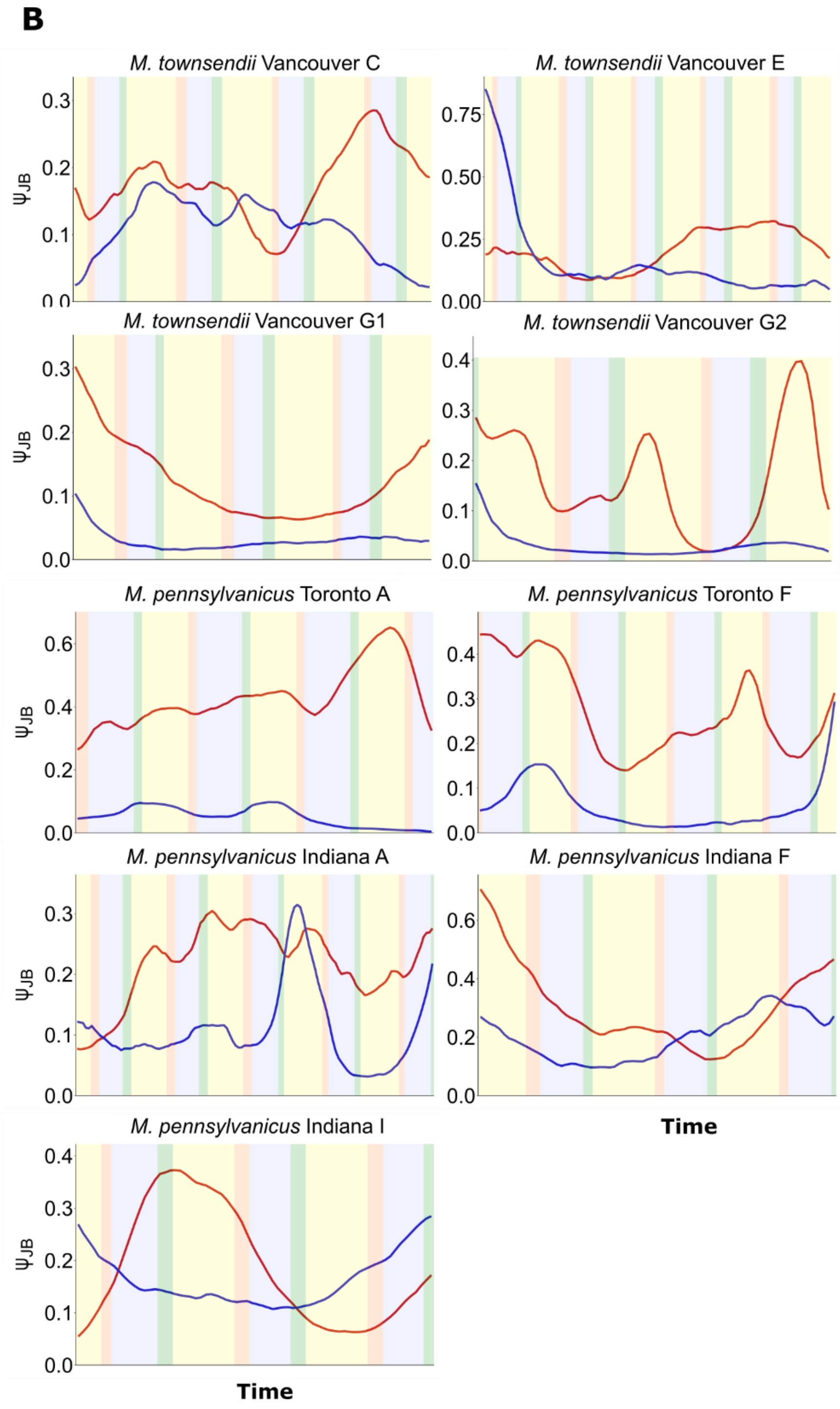
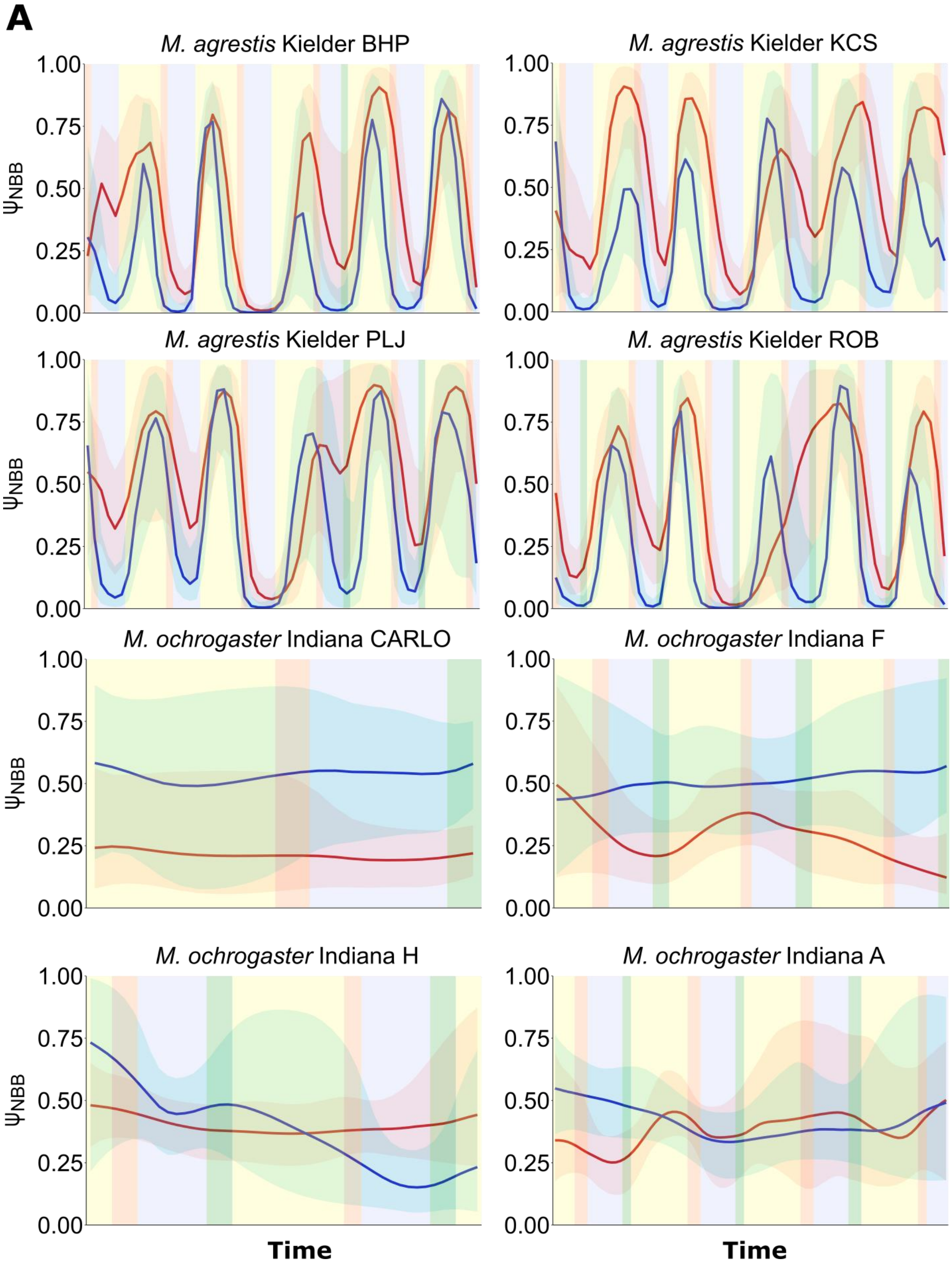

B
M. townsendii Vancouver C
ψJB
0.3
0.2
0.1
0.0
M. townsendii Vancouver E
0.75
0.50
0.25
0.00
M. townsendii Vancouver G1
ψJB
0.3
0.2
0.1
0.0
M. townsendii Vancouver G2
0.4
0.3
0.2
0.1
0.0
M. pennsylvanicus Toronto A
ψJB
0.6
0.4
0.2
0.0
M. pennsylvanicus Toronto F
0.4
0.3
0.2
0.1
0.0
M. pennsylvanicus Indiana A
ψJB
0.3
0.2
0.1
0.0
M. pennsylvanicus Indiana F
0.6
0.4
0.2
0.0
Time
M. pennsylvanicus Indiana I
ψJB
0.4
0.3
0.2
0.1
0.0
Time

Fig. S6 | Estimates of the transition from non-breeding to breeding reproductive states. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S15.



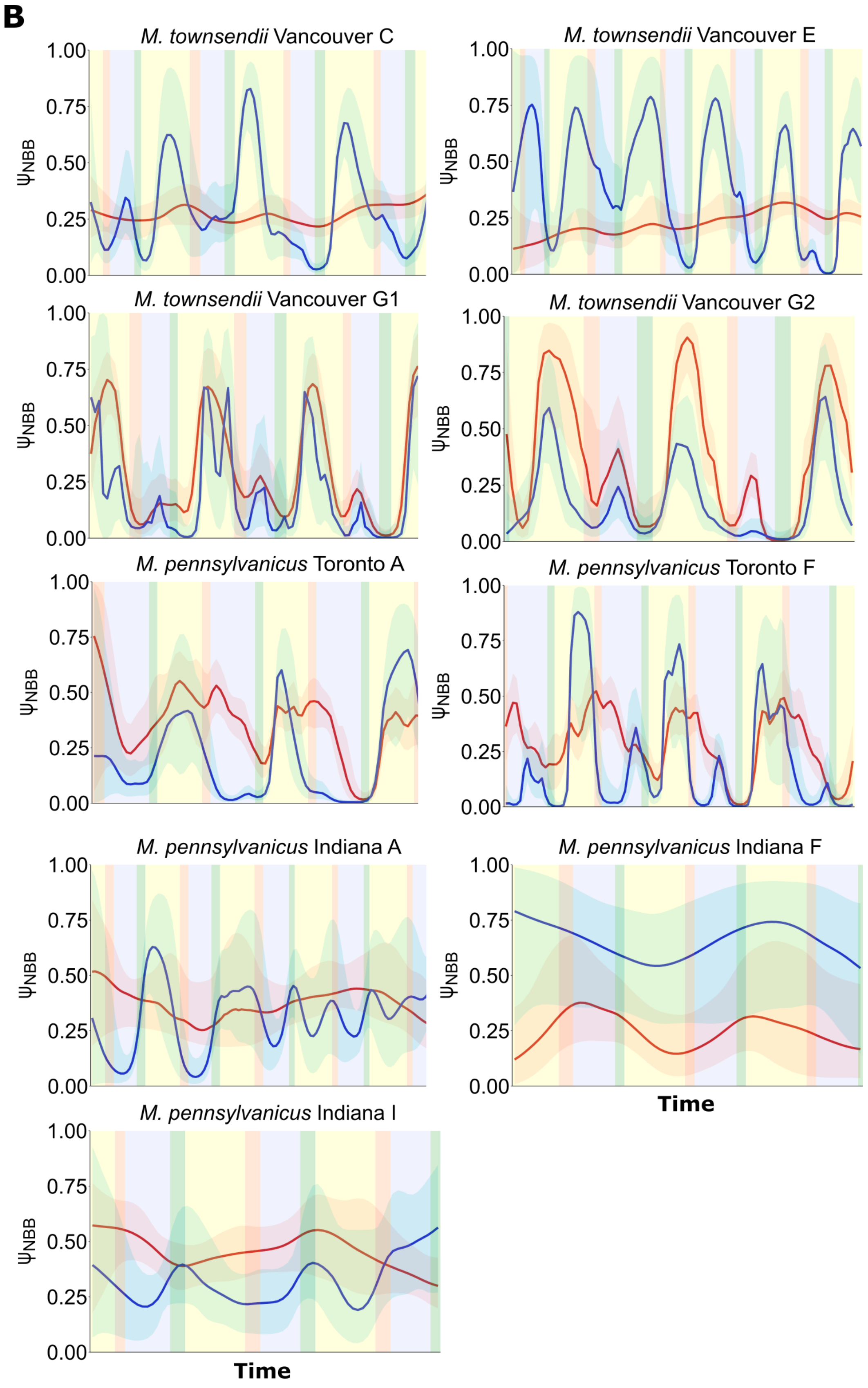
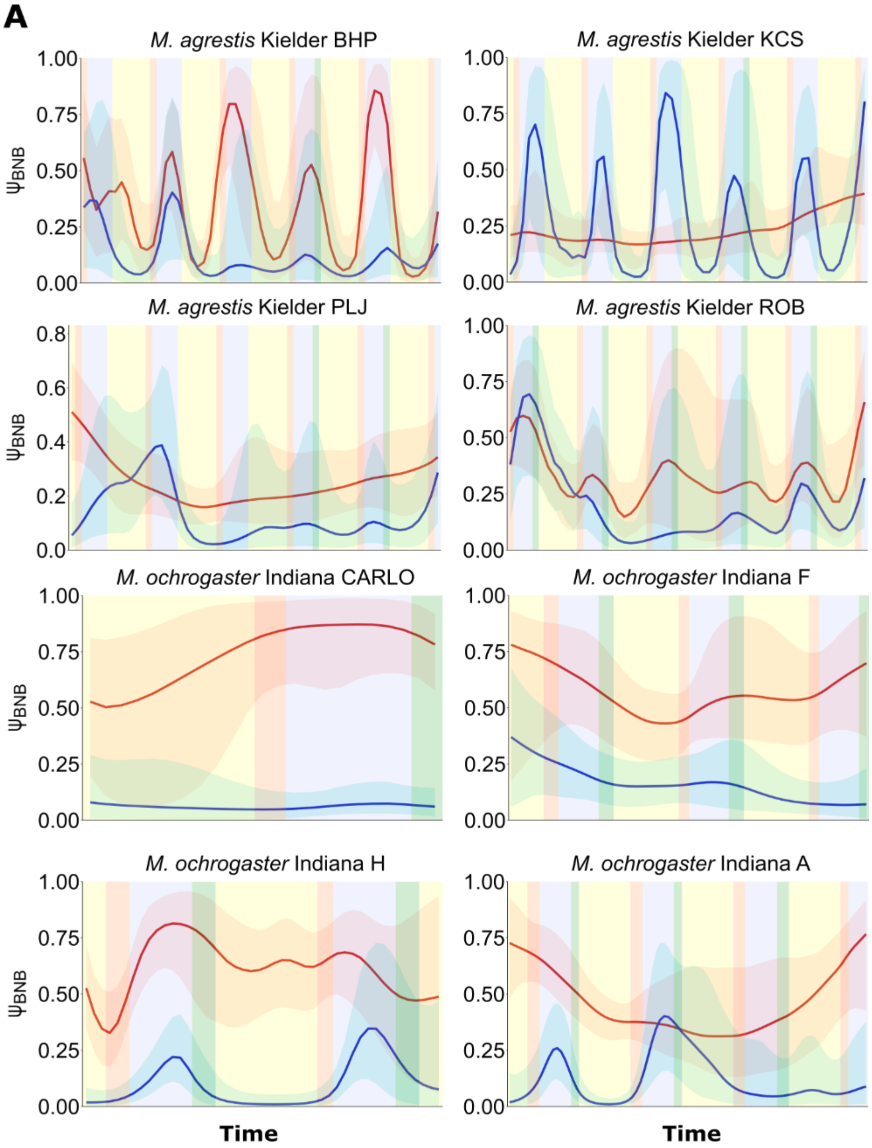

B
M. townsendii Vancouver C
M. townsendii Vancouver E
M. townsendii Vancouver G1
M. townsendii Vancouver G2
M. pennsylvanicus Toronto A
M. pennsylvanicus Toronto F
M. pennsylvanicus Indiana A
M. pennsylvanicus Indiana F
M. pennsylvanicus Indiana I
ψNBB
1.00
0.75
0.50
0.25
0.00
Time

Fig. S7 | Estimates of the transition from breeding to non-breeding reproductive states. Each panel contains the estimates of one grid indicated at the top. The red and blue lines respectively represent the mean estimates of females and males, while the shaded areas surrounding the lines depict the credibility interval (percentiles 5th and 95th). The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. See details about the mean and coefficient of variation of the estimates in Table S16.

A



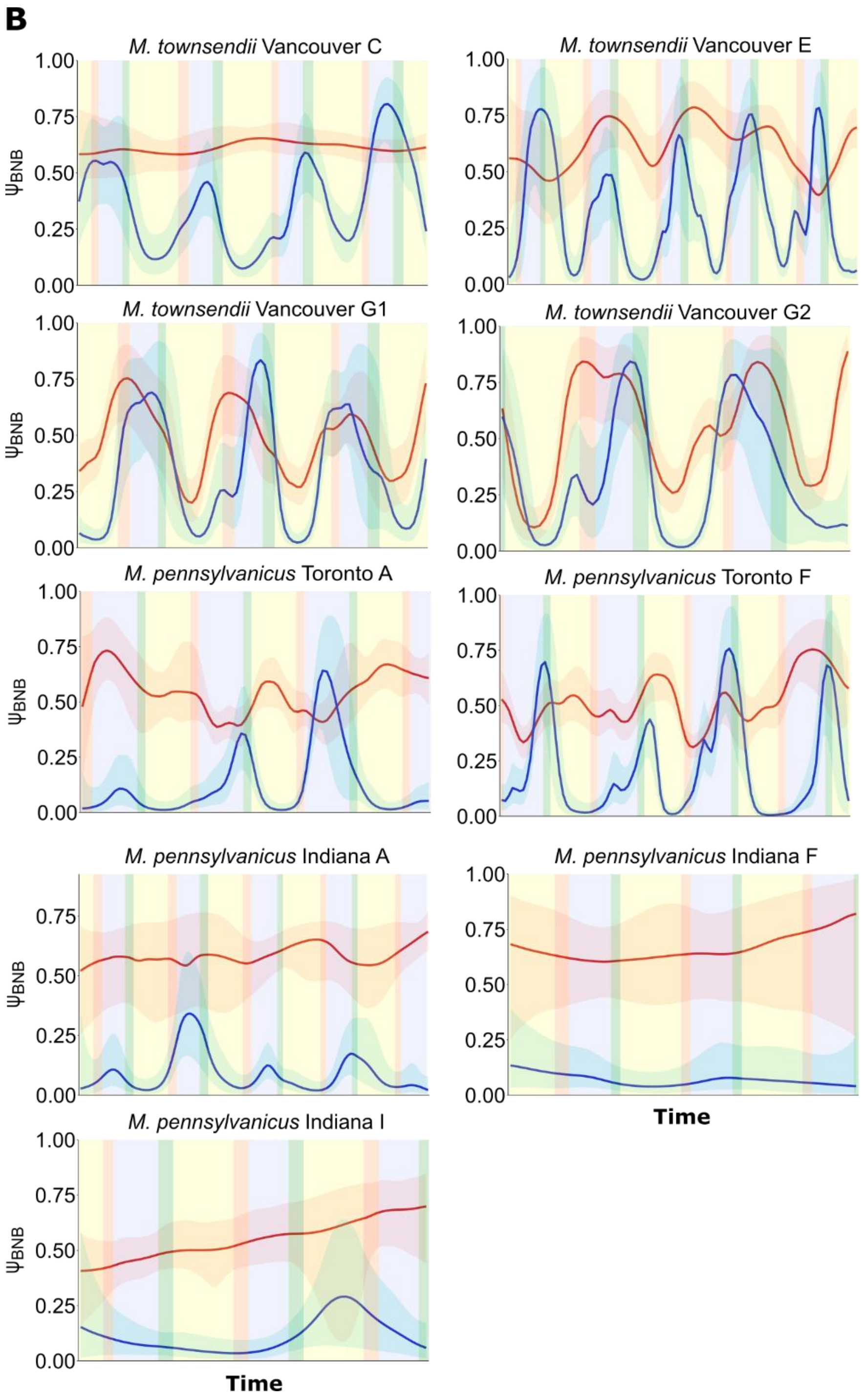
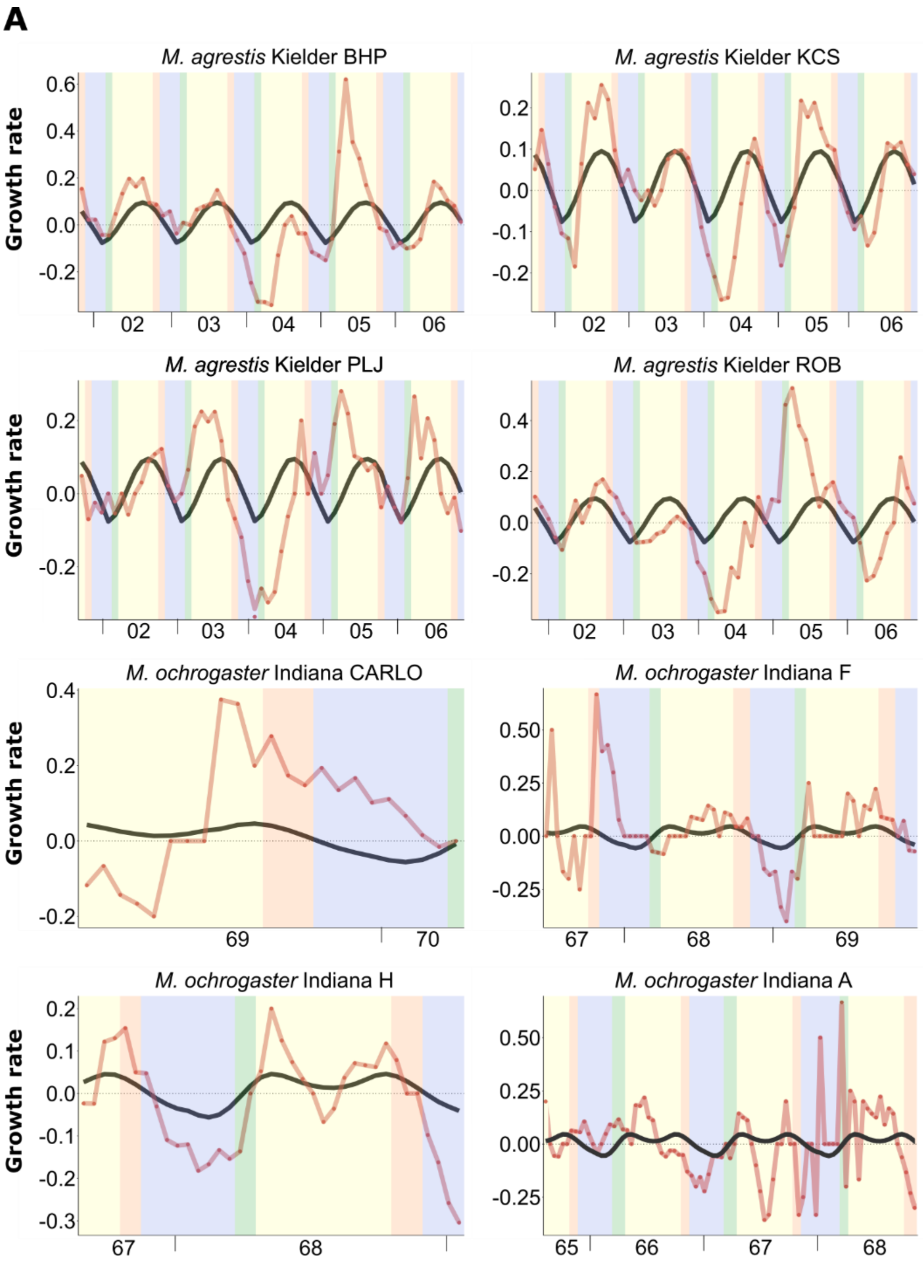

B
M. townsendii Vancouver C
M. townsendii Vancouver E
M. townsendii Vancouver G1
M. townsendii Vancouver G2
M. pennsylvanicus Toronto A
M. pennsylvanicus Toronto F
M. pennsylvanicus Indiana A
M. pennsylvanicus Indiana F
M. pennsylvanicus Indiana I
ΨBNB
1.00
0.75
0.50
0.25
0.00
Time
Time

Fig. S8 | Observed and seasonal population growth rate (black and red lines, respectively). The red dots in the red line represent the specific value. The colors of the background represent the different temporal blocks: green = onset of the breeding season; yellow = middle of the breeding season; orange = end of the breeding season; and blue = non-breeding season. The x-axis indicate the abbreviated years when sampling occurred.



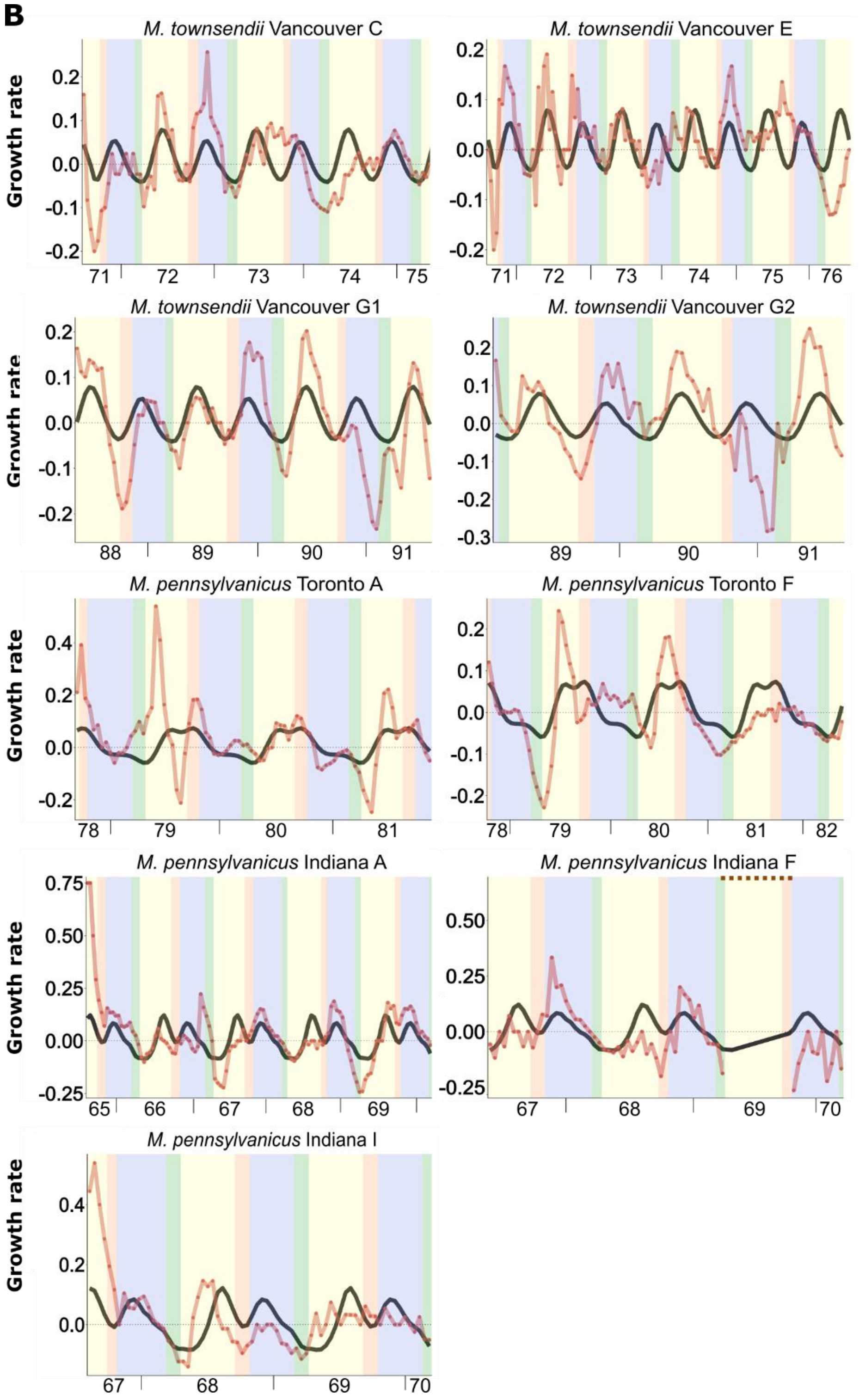

B
M. townsendii Vancouver C
Growth rate
0.2
0.1
0.0
-0.1
-0.2
71
72
73
74
75
M. townsendii Vancouver E
0.2
0.1
0.0
-0.1
-0.2
71
72
73
74
75
76
M. townsendii Vancouver G1
Growth rate
0.2
0.1
0.0
-0.1
-0.2
88
89
90
91
M. townsendii Vancouver G2
0.2
0.1
0.0
-0.1
-0.2
-0.3
89
90
91
M. pennsylvanicus Toronto A
Growth rate
0.4
0.2
0.0
-0.2
78
79
80
81
M. pennsylvanicus Toronto F
0.2
0.1
0.0
-0.1
-0.2
78
79
80
81
82
M. pennsylvanicus Indiana A
Growth rate
0.75
0.50
0.25
0.00
-0.25
65
66
67
68
69
M. pennsylvanicus Indiana F
0.50
0.25
0.00
-0.25
67
68
69
70
M. pennsylvanicus Indiana I
Growth rate
0.4
0.2
0.0
67
68
69
70

Fig. S9 | Display of the marginal effect of maturation rate of males in the non-breeding block (y-axis = pgra; x-axis = standardized maturation rate. The blue line represents the fitted model, with a point-wise 95-percent confidence band shown around the fitted effect. The magenta circles depict the observations. We performed the plot with the R package *Effects* (Fox & Weisberg 2018). The vertical dotted line depicts the medium observed value of the predictor in the whole study period, in this case the maturation rate of males. The values on the left and right represent lower and higher abundances than the observed mean. The units of the x-axis represent the number of standard deviations an observed value has from the observed mean. The horizontal dotted line at the value 0 of the y-axis indicates that the observed pgr is equal than the expected seasonal pgr. Values above and below 0 indicate that pgr were higher or lower than average (i.e. positive and negative pgra). See Fig. 2 for details about the demographic meaning.

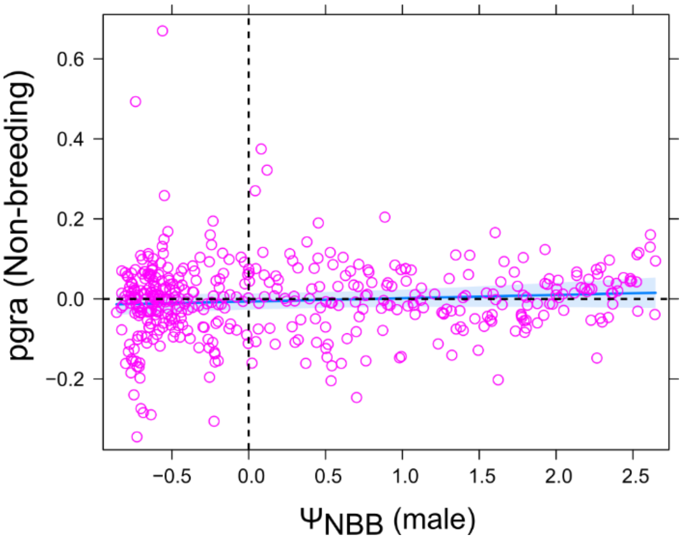


Fig. S10 | Display of the marginal effect of female abundance in the non-breeding block (y-axis = pgra; x-axis = standardized female abundance in logarithmic scale). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

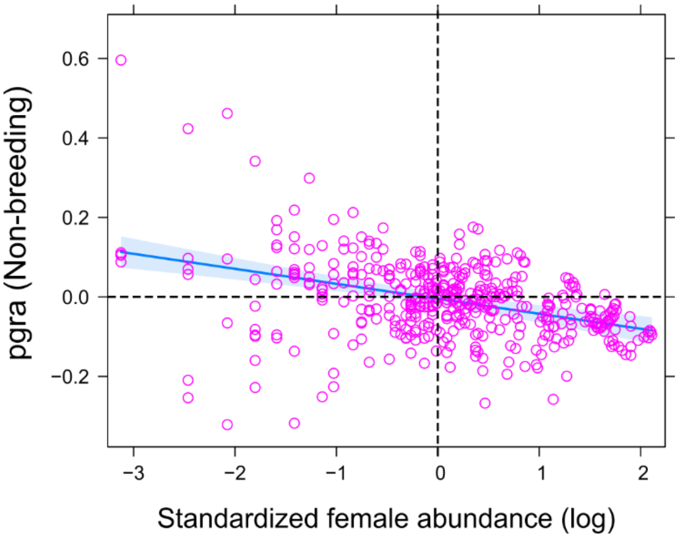


Fig. S11 | Display of the marginal effect of male abundance in the non-breeding block (y-axis = pgra; x-axis = standardized male abundance in log scale). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

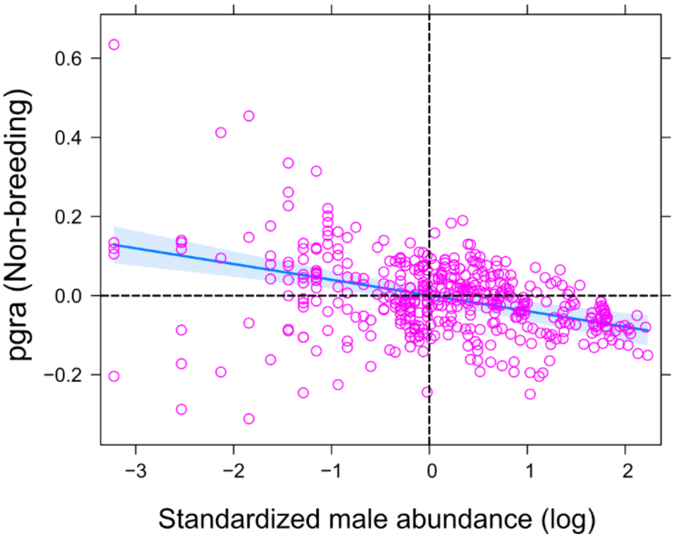


Fig. S12 | Display of the marginal effect of the apparent survival of females in the non-breeding block (y-axis = pgra; x-axis = standardized apparent survival of females). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

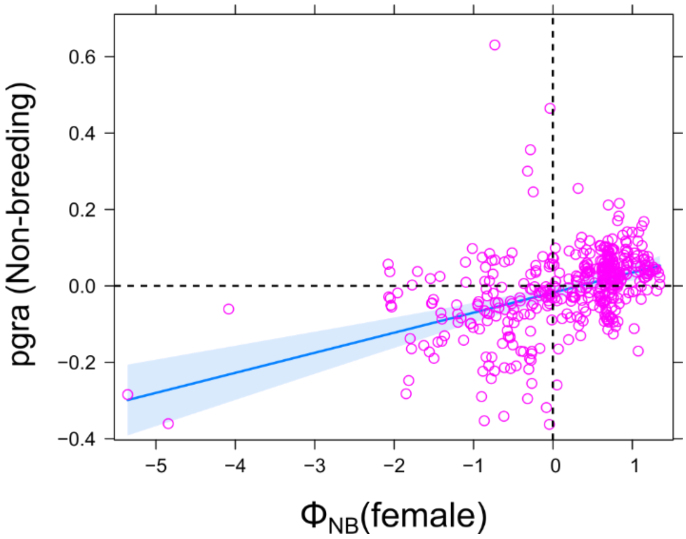


Fig. S13 | Display of the marginal effect of the apparent survival of males in the non-breeding block (y-axis = pgra; x-axis = standardized apparent survival of males). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

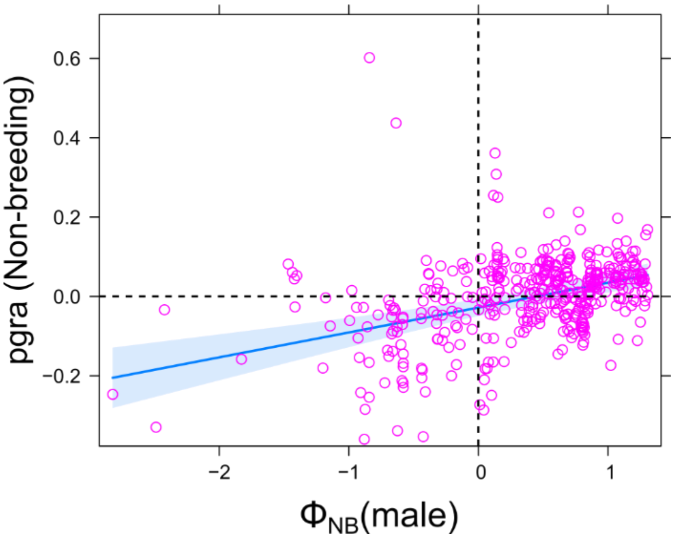


Fig. S14 | Display of the marginal effect of female abundance in the onset block (y-axis = pgra; x-axis = standardized female abundance in logarithmic scale). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

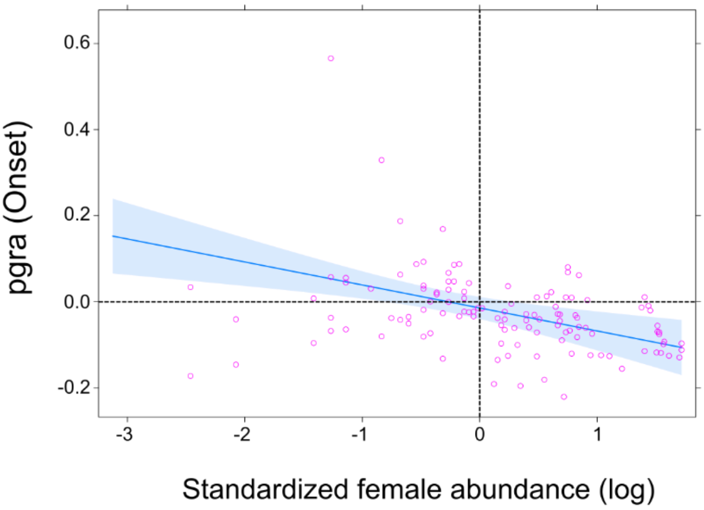


Fig. S15 | Display of the interactive effects of male abundance and the apparent survival of non-breeding males in the onset block (y-axis = pgra; x-axis = standardized male abundance in logarithmic scale). The five panels depict the relationships between the abundance and pgra at different values of the apparent survival rate. The vertical green line in the strip at the top of each panel depicts the conditionally fixed values of survival rates. It indicates that the survival rate increases from left to right across its range. In each panel, the blue line represents the fitted model, with a point-wise 95-percent confidence band shown around the fitted effect. This figure shows that the relationship between male abundance and pgra was negative when survival was low, and changed to a positive relationship as the survival rate increased. When the survival of non-breeding males was relatively high (i.e. right panel), pgra and abundance correlated positively. As the survival of non-breeding males was lower, the relationship between pgra and abundance varied to negative.

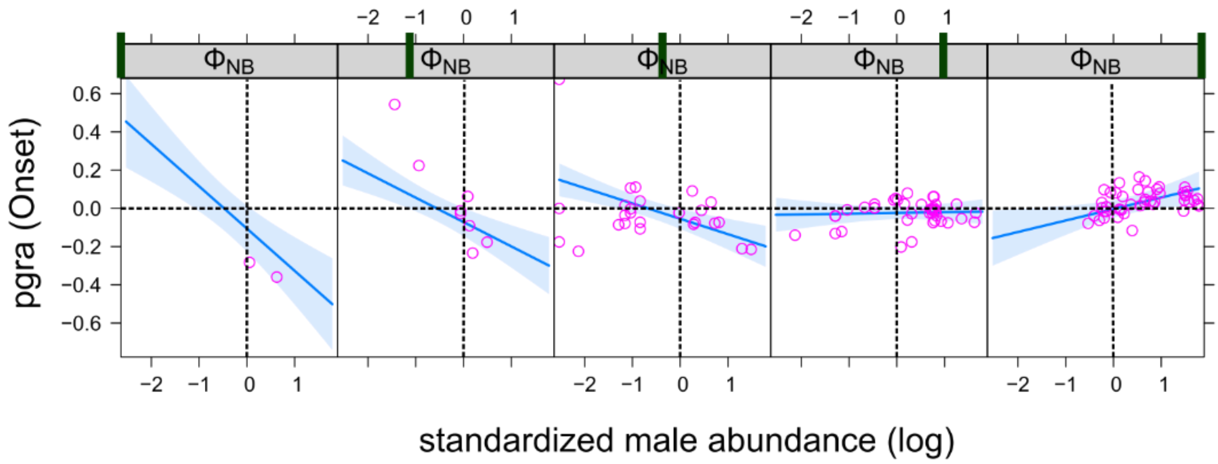


Fig. S16 | Display of the marginal effect of the apparent survival of females in the onset block (y-axis = pgra; x-axis = standardized apparent survival of females). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

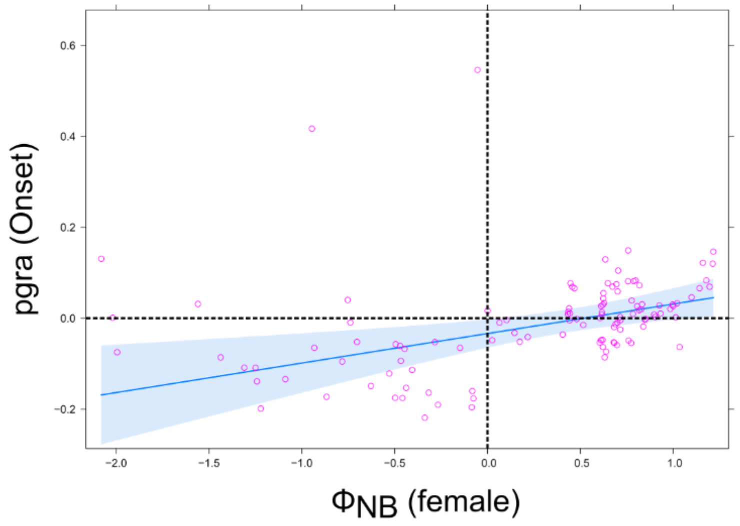


Fig. S17 | Display of the marginal effect of the interaction between the apparent survival of males and their abundance in the onset block (y-axis = pgra; x-axis = standardized apparent survival of males). See caption from Fig. S14 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

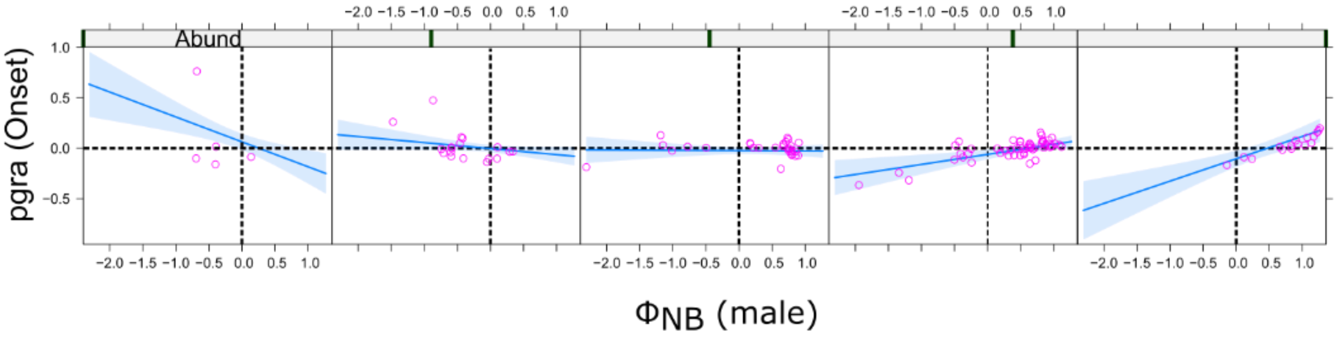


Fig. S18 | Display of the marginal effect of female abundance in the middle of the breeding season (i.e. breeding block; y-axis = pgra; x-axis = standardized female abundance in logarithmic scale). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

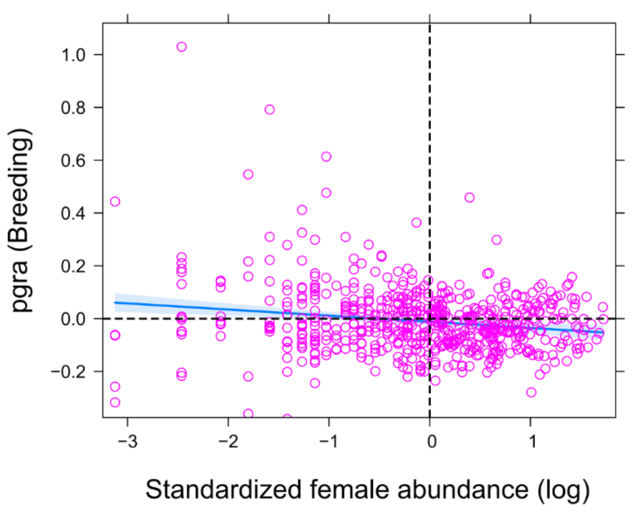


Fig. S19 | Display of the marginal effect of male abundance in the middle of the breeding season (i.e. breeding block; y-axis = pgra; x-axis = standardized male abundance in logarithmic scale). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

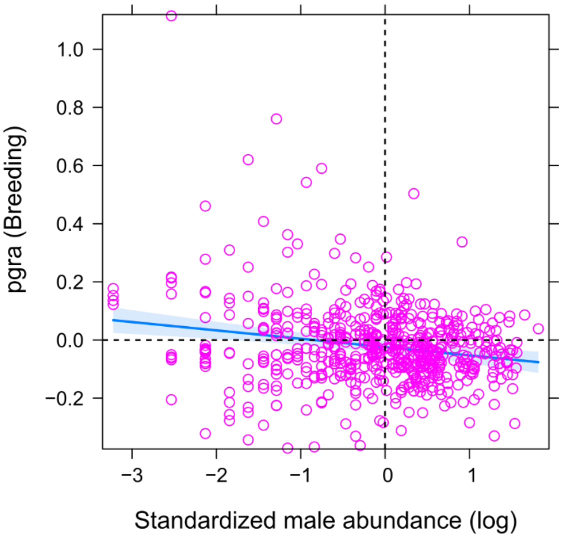


Fig. S20 | Display of the marginal effect of the apparent survival of breeding males in the middle of the breeding season (i.e. breeding block; y-axis = pgra; x-axis = standardized apparent survival of breeding males). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

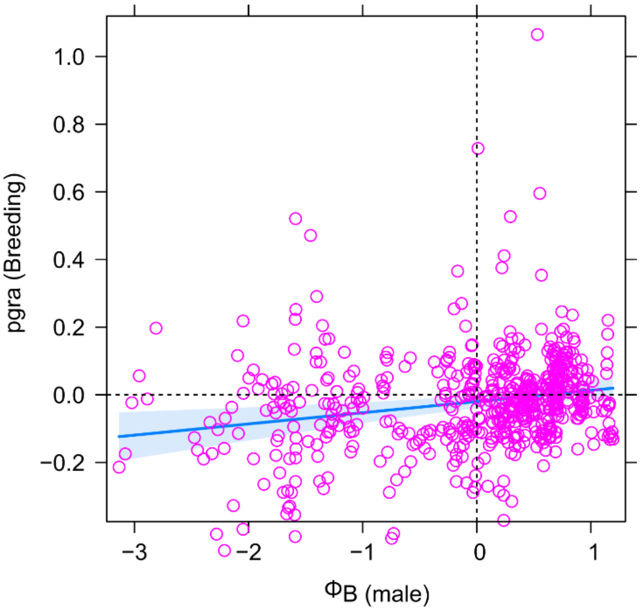


Fig. S21 | Display of the marginal effect of the apparent survival of non-breeding females in the middle of the breeding season (i.e. breeding block; y-axis = pgra; x-axis = standardized apparent survival of non-breeding females). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

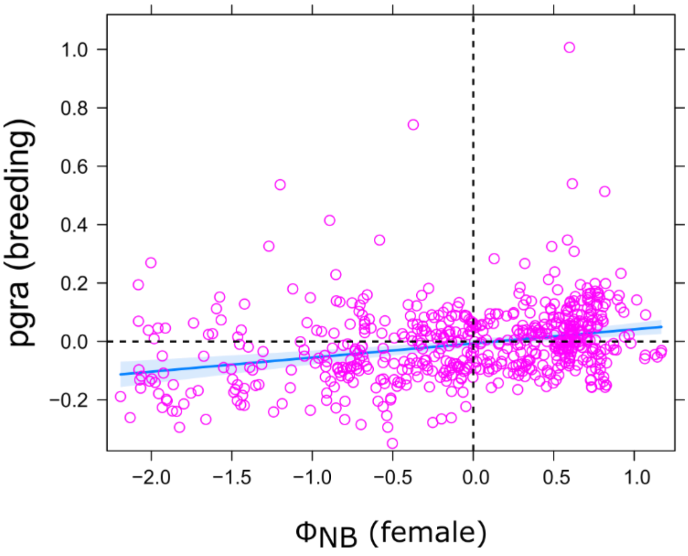


Fig. S22 | Display of the marginal effect of the transition rates from non-breeding to breeding state (i.e. maturation rate) in the middle of the breeding season (i.e. breeding block; y-axis = pgra; x-axis = standardized maturation rate of females). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

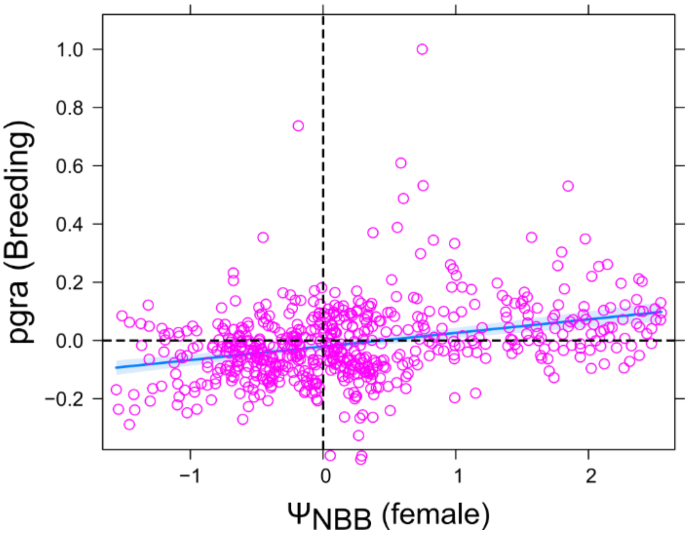


Fig. S23 | Display of the marginal effect of male abundance along different values of the apparent survival of females in the end block (i.e. interaction; y-axis = pgra; x-axis = standardized female abundance). See caption from Fig. S14 for details about the elements of the plots. See Fig. 2 for details 16about the demographic meaning.

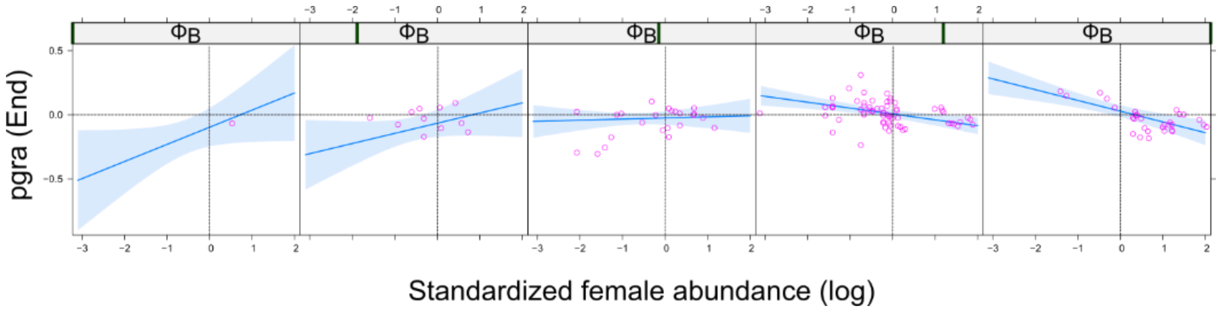


Fig. S24 | Display of the marginal effect of male abundance along different values of the apparent survival of males in the end block (i.e. interaction; y-axis = pgra; x-axis = standardized male abundance). See caption from Fig. S14 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

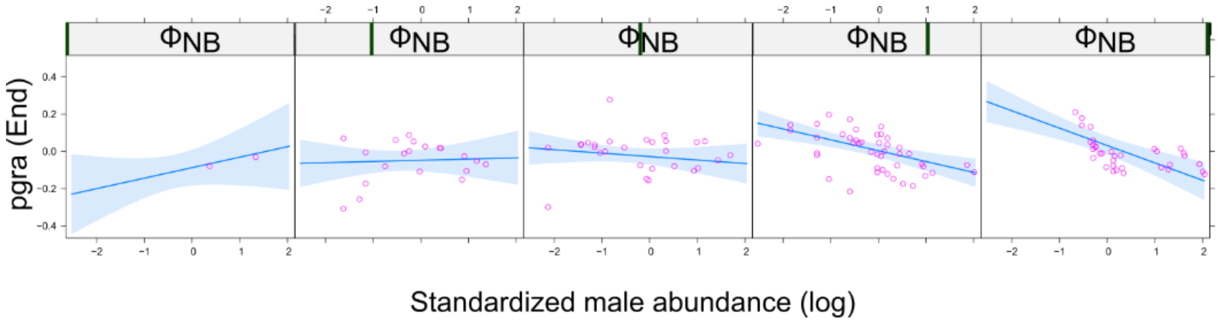


Fig. S25 | Display of the marginal effect of the apparent survival of non-breeding males along different male abundances in the end block (i.e. interaction; y-axis = pgra; x-axis = standardized apparent survival of non-breeding males). See caption from Fig. S14 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

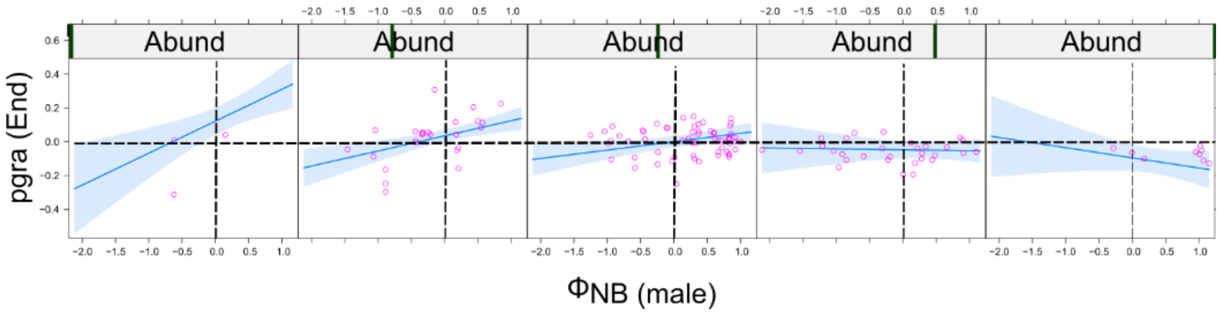


Fig. S26 | Display of the marginal effect of the apparent survival of breeding females along different female abundances in the end block (i.e. interaction; y-axis = pgra; x-axis = standardized apparent survival of breeding females). See caption from Fig. S14 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.

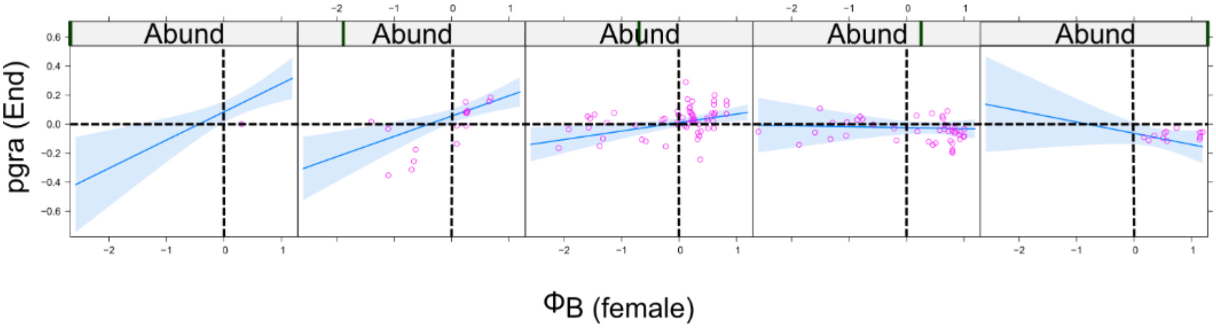
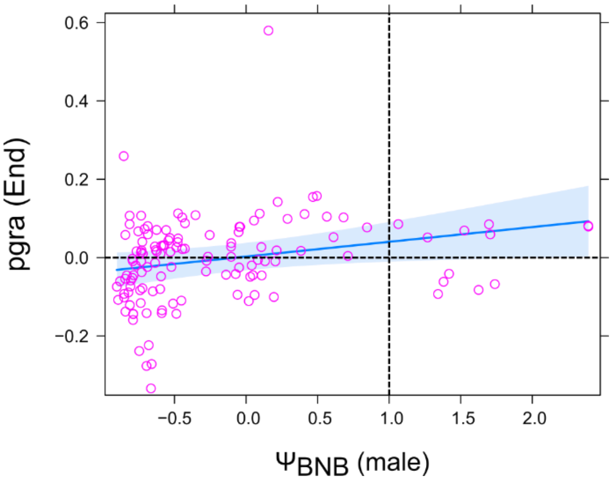


Fig. S27 | Display of the marginal effect of the transition rates from breeding to non-breeding state (i.e. stop of maturation) in the end of the breeding season (i.e. end block; y-axis = pgra; x-axis = standardized rate of the reproduction stop). See caption from Fig. S9 for details about the elements of the plots. See Fig. 2 for details about the demographic meaning.



Supplementary Tables

Table S1 | Random effects included in the models of each temporal block. The random effects were nested and depended on the saturated model of each temporal block.

Temporal block	**Sex**	**Random effects**
Onset	Female	Species
Onset	Male	Population/Species
Middle	Female	Year/Population/Species
Middle	Male	Population/Species
End	Female	Year/Population/Species
End	Male	Population/Species
Non-breeding	Female	Population/Species
Non-breeding	Male	Year/Population/Species

Table S2 | Kruskal-Wallis test evaluating differences in s-index$_{\text{Density}}$ between pairs of seasons. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Spring	Summer	Autumn	Winter
Spring	-	0.13	0.24	0.92
Summer	2.25	-	0.89	0.42
Autumn	1.37	0.02	-	0.67
Winter	0.01	0.66	0.19	-

Table S3 | Kruskal-Wallist test for evaluating whether the species and locations had different s-index$_{\text{Density}}$ (inter-annual variability in density). We tested the differences in each season and in all seasons together (All). These results suggest that s-index$_{\text{Density}}$ differed among populations when analyzing data from the four seasons together (p-value = 0.04), but not when analyzing the differences in each season (p-values > 0.25). There was a similar pattern when evaluating the differences between species (All: p-value = 0.11; each season: p-values > 0.35). See Table 2 for raw data.

	Seasons	Chi-squared	df	p-value
Species	Spring	2.45	3	0.48
	Summer	1.39	3	0.71
	Autumn	3.22	3	0.36
	Winter	0.65	3	0.89
	All	6.04	3	0.11
Population	Spring	2.61	3	0.46
	Summer	1.90	3	0.59
	Autumn	3.89	3	0.27
	Winter	1.29	3	0.73
	All	8.22	3	0.04

Table S4 | Results of t-test evaluating the differences in s-index$_{\text{Density}}$ in grids of diverse species. We tested whether species located in the rows had values lower s-index$_{\text{Density}}$ than species located in the columns. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Agr	Pen	Och	Tow
Agr	-	0.04	0.15	0.64
Pen	4.42	-	0.92	0.08
Och	2.11	0.01	-	0.15
Tow	0.22	3.07	2.11	-

Table S5 | Kruskal-Wallis test evaluating differences in s-index$_{\text{spgr}}$ between pairs of seasons. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Spring	Summer	Autumn	Winter
Spring	-	0.13	0.24	0.92
Summer	2.25	-	0.89	0.42
Autumn	1.37	0.02	-	0.67
Winter	0.01	0.66	0.19	-

Table S6 | Kruskal-Wallist test for evaluating whether the species and locations had different s-index$_{\text{spgr}}$. We tested the differences in each season and in all seasons together (All).

	Seasons	Chi-squared	df	p-value
Species	Spring	10.14	3	0.017
	Summer	8.74	3	0.033
	Autumn	11.66	3	0.009
	Winter	8.75	3	0.032
	All	13.85	3	0.003
Population	Spring	14.508	3	0.003
	Summer	11.18	3	0.002
	Autumn	3.30	3	0.011
	Winter	11.20	3	0.348
	All	4.27	3	0.011

Table S7 | Results of t-test evaluating the differences in index$_{\mathrm{spgr}}$ among species. We tested whether species located in the rows had values lower s-index$_{\mathrm{spgr}}$ than species located in the columns. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Agr	Pen	Och	Tow
Agr	-	0.04	0.65	0.23
Pen	4.28	-	0.01	0.8
Och	0.20	6.98	-	0
Tow	1.46	0.06	17.19	-

Table S8 | Kruskal-Wallis test evaluating differences in s-index$_{\mathrm{pgra}}$ between pairs of seasons. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Spring	Summer	Autumn	Winter
Spring	-	0.69	0.1	0.38
Summer	0.16	-	0.11	0.36
Autumn	2.68	2.57	-	0.5
Winter	0.77	0.83	0.45	-

Table S9 | Kruskal-Wallist test for evaluating whether the species and locations had different s-index$_{\mathrm{pgra}}$. We tested the differences in each season and in all seasons together (All).

	Seasons	Chi-squared	df	p-value
Species	Spring	4.62	3	0.20
	Summer	9.71	3	0.02
	Autumn	3.12	3	0.37
	Winter	2.68	3	0.44
	All	5.11	3	0.16
Population	Spring	4.61	3	0.20
	Summer	9.18	3	0.02
	Autumn	3.50	3	0.32
	Winter	5.51	3	0.14
	All	4.19	3	0.24

Table S10 | Results of t-test evaluating the differences in index$_{pgra}$ among species. We tested whether species located in the rows had values lower s-index$_{pgra}$ than species located in the columns. Upper triangular matrix indicates the p-values, whereas lower triangular matrix indicates the t-values. All degrees of freedom were 1.

	Agr	Pen	Och	Tow
Agr	-	0.21	0.68	0.04
Pen	1.54	-	0.48	0.44
Och	0.17	0.49	-	0.13
Tow	4.30	0.58	2.27	-

φ_{NB}	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.67±0.17	0.57±0.27	0.69±0.15	0.45±0.4	0.71±0.14	0.58±0.32	0.69±0.13	0.65±0.21
M. agrestis (KCS)	0.74±0.13	0.6±0.22	0.74±0.13	0.54±0.32	0.74±0.13	0.66±0.26	0.74±0.12	0.7±0.18
M. agrestis (PLJ)	0.62±0.13	0.56±0.23	0.62±0.12	0.5±0.31	0.63±0.12	0.6±0.23	0.62±0.12	0.63±0.21
M. agrestis (ROB)	0.73±0.14	0.58±0.31	0.72±0.13	0.52±0.39	0.74±0.12	0.68±0.27	0.74±0.12	0.71±0.26
M. ochrogaster (CARLO)	0.91±0.05	0.82±0.14	0.75±0.2	0.7±0.25	0.9±0.07	0.81±0.15	0.93±0.04	0.85±0.1
M. ochrogaster (A)	0.82±0.11	0.64±0.12	0.81±0.1	0.63±0.16	0.8±0.11	0.63±0.17	0.81±0.12	0.64±0.14
M. ochrogaster (F)	0.77±0.12	0.7±0.16	0.76±0.12	0.7±0.16	0.76±0.11	0.69±0.15	0.76±0.11	0.71±0.15
M. ochrogaster (H)	0.76±0.11	0.63±0.25	0.82±0.08	0.56±0.32	0.81±0.08	0.65±0.25	0.76±0.1	0.71±0.19
M. pennsylvanicus (A.T)	0.92±0.06	0.88±0.09	0.85±0.12	0.49±0.41	0.84±0.09	0.65±0.21	0.88±0.09	0.87±0.1
M. pennsylvanicus (F.T)	0.85±0.14	0.85±0.13	0.89±0.09	0.7±0.23	0.93±0.04	0.8±0.18	0.93±0.06	0.92±0.06
M. pennsylvanicus (A.I)	0.88±0.09	0.88±0.04	0.88±0.1	0.88±0.05	0.91±0.04	0.88±0.05	0.91±0.04	0.87±0.05
M. pennsylvanicus (F.I)	0.82±0.11	0.75±0.16	0.85±0.08	0.76±0.16	0.84±0.08	0.76±0.16	0.82±0.1	0.75±0.15
M. pennsylvanicus (I.I)	0.89±0.05	0.88±0.06	0.9±0.04	0.89±0.05	0.9±0.04	0.89±0.05	0.89±0.05	0.88±0.05
M. townsendii (C)	0.9±0.03	0.81±0.07	0.89±0.05	0.75±0.13	0.88±0.05	0.81±0.09	0.89±0.04	0.84±0.06
M. townsendii (E)	0.91±0.05	0.85±0.07	0.87±0.06	0.81±0.11	0.9±0.05	0.84±0.1	0.92±0.05	0.86±0.07
M. townsendii (G1)	0.88±0.09	0.87±0.11	0.84±0.09	0.76±0.26	0.87±0.09	0.83±0.17	0.9±0.08	0.9±0.13
M. townsendii (G2)	0.91±0.07	0.87±0.11	0.82±0.16	0.77±0.2	0.79±0.21	0.72±0.22	0.78±0.33	0.77±0.32

Table S11 | Mean and coefficient of variation of the apparent survival of the non-breeding females and males in each grid along the four temporal blocks.

φ_B	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.67±0.08	0.58±0.1	0.67±0.08	0.58±0.09	0.67±0.09	0.57±0.12	0.67±0.08	0.58±0.11
M. agrestis (KCS)	0.7±0.11	0.65±0.14	0.69±0.11	0.65±0.13	0.69±0.11	0.65±0.14	0.7±0.11	0.65±0.13
M. agrestis (PLJ)	0.59±0.21	0.57±0.17	0.58±0.2	0.56±0.18	0.6±0.16	0.56±0.19	0.59±0.17	0.57±0.17
M. agrestis (ROB)	0.67±0.15	0.59±0.18	0.66±0.14	0.59±0.18	0.67±0.15	0.6±0.19	0.67±0.15	0.6±0.18
M. ochrogaster (CARLO)	0.87±0.1	0.91±0.05	0.78±0.19	0.82±0.13	0.82±0.13	0.91±0.05	0.85±0.1	0.93±0.04
M. ochrogaster (A)	0.75±0.13	0.76±0.15	0.75±0.13	0.76±0.12	0.74±0.13	0.76±0.11	0.74±0.14	0.75±0.13
M. ochrogaster (F)	0.83±0.1	0.75±0.12	0.83±0.1	0.77±0.11	0.84±0.09	0.76±0.1	0.83±0.09	0.76±0.11
M. ochrogaster (H)	0.83±0.08	0.82±0.07	0.83±0.08	0.81±0.06	0.84±0.08	0.82±0.06	0.84±0.08	0.82±0.06
M. pennsylvanicus (A.T)	0.88±0.08	0.83±0.06	0.82±0.12	0.8±0.07	0.84±0.08	0.8±0.07	0.87±0.1	0.83±0.06
M. pennsylvanicus (F.T)	0.94±0.02	0.91±0.03	0.93±0.03	0.91±0.03	0.94±0.02	0.91±0.03	0.94±0.02	0.91±0.03
M. pennsylvanicus (A.I)	0.87±0.08	0.83±0.12	0.86±0.11	0.86±0.1	0.9±0.05	0.88±0.07	0.89±0.05	0.87±0.09
M. pennsylvanicus (F.I)	0.83±0.11	0.81±0.1	0.83±0.09	0.86±0.06	0.83±0.09	0.85±0.07	0.83±0.1	0.81±0.09
M. pennsylvanicus (I.I)	0.79±0.13	0.8±0.06	0.84±0.1	0.79±0.09	0.86±0.07	0.79±0.08	0.83±0.09	0.8±0.07
M. townsendii (C)	0.87±0.05	0.85±0.05	0.85±0.08	0.84±0.06	0.84±0.08	0.84±0.06	0.85±0.06	0.84±0.06
M. townsendii (E)	0.86±0.06	0.84±0.06	0.85±0.06	0.83±0.06	0.86±0.06	0.83±0.07	0.87±0.06	0.83±0.07
M. townsendii (G1)	0.91±0.03	0.86±0.05	0.91±0.03	0.86±0.06	0.91±0.03	0.85±0.06	0.91±0.03	0.86±0.06
M. townsendii (G2)	0.9±0.05	0.87±0.06	0.88±0.05	0.87±0.05	0.86±0.06	0.85±0.06	0.88±0.05	0.86±0.06

Table S12 | Mean and coefficient of variation of the apparent survival of the breeding females and males in each grid along the four temporal blocks.

Ψ_{JNB}	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.69±0.46	0.96±0.04	0.69±0.41	0.96±0.04	0.87±0.18	0.97±0.03	0.83±0.23	0.97±0.03
M. agrestis (KCS)	0.73±0.38	0.95±0.08	0.59±0.56	0.95±0.08	0.73±0.33	0.94±0.11	0.8±0.25	0.95±0.09
M. agrestis (PLJ)	0.6±0.55	0.93±0.09	0.58±0.55	0.93±0.09	0.7±0.39	0.93±0.08	0.68±0.42	0.94±0.08
M. agrestis (ROB)	0.67±0.54	0.96±0.07	0.6±0.56	0.97±0.05	0.77±0.33	0.97±0.04	0.75±0.41	0.96±0.05
M. ochrogaster (CARLO)	0.7±0.5	0.49±0.98	0.42±0.95	0.55±0.74	0.6±0.55	0.7±0.47	0.71±0.37	0.66±0.52
M. ochrogaster (A)	0.49±0.62	0.55±0.57	0.5±0.62	0.5±0.65	0.53±0.61	0.43±0.76	0.52±0.62	0.49±0.69
M. ochrogaster (F)	0.37±1.02	0.47±0.76	0.35±1.01	0.5±0.69	0.37±0.91	0.54±0.59	0.4±0.89	0.45±0.77
M. ochrogaster (H)	0.4±0.71	0.32±1.07	0.32±0.77	0.35±0.8	0.33±0.73	0.48±0.51	0.38±0.65	0.44±0.68
M. pennsylvanicus (A.T)	0.43±0.55	0.82±0.23	0.41±0.54	0.87±0.17	0.47±0.44	0.93±0.07	0.5±0.42	0.9±0.13
M. pennsylvanicus (F.T)	0.58±0.44	0.71±0.25	0.46±0.52	0.71±0.25	0.38±0.39	0.78±0.14	0.53±0.39	0.77±0.16
M. pennsylvanicus (A.I)	0.33±0.63	0.69±0.37	0.33±0.79	0.66±0.41	0.3±0.77	0.67±0.36	0.32±0.57	0.71±0.29
M. pennsylvanicus (F.I)	0.47±0.72	0.5±0.71	0.48±0.78	0.57±0.59	0.48±0.76	0.6±0.54	0.49±0.69	0.55±0.61
M. pennsylvanicus (I.I)	0.23±0.83	0.56±0.47	0.2±0.86	0.66±0.33	0.17±0.82	0.67±0.31	0.2±0.69	0.62±0.35
M. townsendii (C)	0.37±0.48	0.7±0.24	0.35±0.52	0.68±0.23	0.3±0.52	0.68±0.22	0.32±0.49	0.69±0.23
M. townsendii (E)	0.43±0.41	0.5±0.51	0.4±0.47	0.48±0.54	0.38±0.43	0.43±0.57	0.41±0.38	0.47±0.52
M. townsendii (G1)	0.56±0.28	0.59±0.35	0.55±0.25	0.68±0.2	0.6±0.18	0.63±0.27	0.59±0.23	0.6±0.34
M. townsendii (G2)	0.45±0.69	0.77±0.25	0.54±0.45	0.74±0.18	0.58±0.5	0.74±0.2	0.57±0.48	0.77±0.21

Table S13 | Mean and coefficient of variation of the transition between the juvenile and non-breeding reproductive states of females and males in each grid along the four temporal blocks.

Ψ_{JB}	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.26±1.01	0.02±0.89	0.25±0.9	0.02±0.77	0.11±1.18	0.02±0.81	0.14±1.19	0.02±0.87
M. agrestis (KCS)	0.24±1.01	0.01±0.7	0.37±0.78	0.01±0.88	0.24±0.87	0.02±1.1	0.18±0.99	0.01±0.98
M. agrestis (PLJ)	0.32±0.78	0.04±1.01	0.33±0.74	0.04±1.11	0.22±1	0.04±1.04	0.25±0.93	0.04±0.92
M. agrestis (ROB)	0.24±1.12	0.03±1.77	0.28±0.83	0.03±1.51	0.15±1.16	0.02±1.14	0.17±1.26	0.03±1.45
M. ochrogaster (CARLO)	0.05±0.81	0.11±0.69	0.35±0.71	0.21±0.71	0.21±0.59	0.1±0.81	0.09±0.72	0.09±0.72
M. ochrogaster (A)	0.22±0.64	0.24±0.61	0.24±0.66	0.23±0.53	0.25±0.68	0.22±0.55	0.24±0.7	0.24±0.67
M. ochrogaster (F)	0.21±0.74	0.28±0.68	0.23±0.84	0.29±0.68	0.21±0.77	0.29±0.66	0.18±0.73	0.29±0.71
M. ochrogaster (H)	0.25±0.3	0.24±0.68	0.26±0.43	0.3±0.43	0.31±0.24	0.31±0.3	0.3±0.24	0.27±0.45
M. pennsylvanicus (A.T)	0.39±0.42	0.1±1.21	0.4±0.38	0.07±1.02	0.34±0.34	0.04±0.88	0.32±0.43	0.06±1.33
M. pennsylvanicus (F.T)	0.22±0.65	0.09±0.93	0.26±0.47	0.09±1.14	0.23±0.29	0.04±0.66	0.22±0.56	0.05±0.8
M. pennsylvanicus (A.I)	0.18±0.46	0.12±0.76	0.17±0.56	0.11±0.83	0.17±0.6	0.08±0.45	0.18±0.43	0.1±0.61
M. pennsylvanicus (F.I)	0.14±0.77	0.1±0.85	0.16±1.02	0.11±0.62	0.18±0.73	0.13±0.58	0.16±0.8	0.13±0.67
M. pennsylvanicus (I.I)	0.21±0.63	0.15±0.47	0.17±0.75	0.13±0.47	0.14±0.64	0.13±0.5	0.19±0.48	0.15±0.43
M. townsendii (C)	0.19±0.29	0.1±0.54	0.18±0.39	0.11±0.49	0.16±0.44	0.1±0.43	0.16±0.35	0.09±0.45
M. townsendii (E)	0.21±0.42	0.1±0.61	0.2±0.44	0.12±1.16	0.19±0.5	0.15±1.17	0.2±0.43	0.13±0.92
M. townsendii (G1)	0.1±0.29	0.03±0.56	0.13±0.46	0.03±0.41	0.11±0.46	0.03±0.38	0.1±0.35	0.03±0.62
M. townsendii (G2)	0.19±0.4	0.03±0.84	0.14±0.69	0.02±0.5	0.06±0.68	0.02±0.24	0.09±0.62	0.02±0.76

Table S14 | Mean and coefficient of variation of the transition between the juvenile and breeding reproductive states of females and males in each grid along the four temporal blocks.

Ψ_{NBB}	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.28±0.84	0.21±1.04	0.57±0.49	0.39±0.83	0.29±0.88	0.08±1.68	0.21±1.09	0.05±1.5
M. agrestis (KCS)	0.27±0.72	0.12±0.95	0.65±0.39	0.42±0.71	0.53±0.5	0.17±1.07	0.3±0.72	0.06±1.3
M. agrestis (PLJ)	0.43±0.69	0.22±0.91	0.65±0.43	0.56±0.57	0.48±0.56	0.22±1.12	0.33±0.81	0.12±1.35
M. agrestis (ROB)	0.31±0.88	0.1±1.12	0.55±0.51	0.43±0.75	0.32±0.73	0.09±1.69	0.23±1.08	0.04±2.03
M. ochrogaster (CARLO)	0.25±0.41	0.64±0.33	0.28±0.72	0.5±0.61	0.23±0.63	0.55±0.47	0.21±0.45	0.55±0.34
M. ochrogaster (A)	0.38±0.47	0.42±0.36	0.43±0.45	0.45±0.42	0.4±0.5	0.46±0.48	0.38±0.55	0.43±0.41
M. ochrogaster (F)	0.27±0.49	0.52±0.34	0.33±0.53	0.53±0.41	0.29±0.51	0.53±0.41	0.26±0.5	0.53±0.36
M. ochrogaster (H)	0.37±0.28	0.51±0.51	0.4±0.28	0.48±0.62	0.41±0.23	0.36±0.62	0.39±0.26	0.38±0.52
M. pennsylvanicus (A.T)	0.25±0.67	0.2±0.78	0.44±0.3	0.41±0.63	0.46±0.33	0.14±1.19	0.27±0.56	0.06±1.4
M. pennsylvanicus (F.T)	0.12±0.81	0.03±1.33	0.39±0.34	0.45±0.71	0.41±0.27	0.08±1.54	0.22±0.59	0.11±1.15
M. pennsylvanicus (A.I)	0.38±0.35	0.48±0.36	0.41±0.38	0.4±0.63	0.39±0.37	0.27±0.89	0.36±0.33	0.27±0.69
M. pennsylvanicus (F.I)	0.31±0.56	0.58±0.44	0.25±0.69	0.61±0.39	0.31±0.68	0.62±0.38	0.29±0.6	0.59±0.41
M. pennsylvanicus (I.I)	0.42±0.36	0.47±0.5	0.47±0.31	0.31±0.65	0.47±0.27	0.32±0.61	0.44±0.28	0.36±0.56
M. townsendii (C)	0.27±0.24	0.38±0.67	0.3±0.23	0.4±0.63	0.27±0.23	0.21±0.51	0.25±0.23	0.17±0.8
M. townsendii (E)	0.23±0.28	0.33±0.59	0.25±0.3	0.54±0.52	0.21±0.36	0.38±0.74	0.21±0.33	0.19±1.12
M. townsendii (G1)	0.22±0.66	0.11±1.33	0.45±0.55	0.33±0.95	0.18±0.55	0.15±0.97	0.13±0.79	0.1±1.33
M. townsendii (G2)	0.24±0.81	0.17±0.79	0.51±0.59	0.26±0.9	0.3±0.48	0.11±0.89	0.13±1.19	0.08±1.27

Table S15 | Mean and coefficient of variation of the transition between the non-breeding and breeding reproductive states of females and males in each grid along the four temporal blocks.

Ψ_{BNB}	Onset		Breeding		End		Non breeding	
Pop	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
M. agrestis (BHP)	0.52±0.59	0.3±0.99	0.22±0.97	0.12±1.18	0.38±0.68	0.16±1.11	0.55±0.51	0.27±0.98
M. agrestis (KCS)	0.27±0.54	0.46±0.79	0.24±0.53	0.17±1.29	0.24±0.5	0.25±0.89	0.25±0.48	0.54±0.57
M. agrestis (PLJ)	0.26±0.49	0.21±0.95	0.25±0.51	0.15±1.04	0.29±0.52	0.16±0.97	0.28±0.49	0.21±0.92
M. agrestis (ROB)	0.42±0.61	0.35±0.94	0.3±0.7	0.2±1.06	0.38±0.56	0.23±0.82	0.44±0.55	0.36±0.83
M. ochrogaster (CARLO)	0.76±0.23	0.07±0.87	0.56±0.57	0.1±1.03	0.8±0.21	0.06±0.86	0.82±0.19	0.08±0.67
M. ochrogaster (A)	0.44±0.39	0.2±1.01	0.46±0.42	0.12±1.32	0.53±0.39	0.11±0.93	0.49±0.42	0.22±0.88
M. ochrogaster (F)	0.58±0.36	0.18±0.64	0.54±0.4	0.19±0.79	0.54±0.33	0.17±0.75	0.6±0.31	0.18±0.65
M. ochrogaster (H)	0.69±0.35	0.09±0.97	0.57±0.34	0.03±1.08	0.56±0.32	0.06±0.86	0.71±0.25	0.21±0.75
M. pennsylvanicus (A.T)	0.52±0.25	0.19±0.91	0.58±0.21	0.04±1.14	0.56±0.25	0.07±0.93	0.53±0.3	0.23±1.03
M. pennsylvanicus (F.T)	0.56±0.26	0.54±0.49	0.54±0.22	0.13±1.49	0.47±0.3	0.05±1.03	0.51±0.32	0.26±0.89
M. pennsylvanicus (A.I)	0.58±0.23	0.14±0.92	0.56±0.26	0.08±1.07	0.56±0.25	0.07±0.96	0.58±0.21	0.14±0.98
M. pennsylvanicus (F.I)	0.63±0.32	0.09±0.91	0.62±0.31	0.1±1	0.64±0.31	0.1±0.85	0.64±0.31	0.1±0.82
M. pennsylvanicus (I.I)	0.57±0.24	0.09±0.69	0.49±0.39	0.17±1.07	0.53±0.31	0.15±1.05	0.56±0.25	0.1±0.86
M. townsendii (C)	0.62±0.1	0.43±0.52	0.62±0.11	0.25±0.67	0.61±0.13	0.38±0.48	0.61±0.12	0.53±0.39
M. townsendii (E)	0.64±0.26	0.46±0.53	0.61±0.23	0.17±0.99	0.59±0.23	0.31±0.56	0.6±0.28	0.56±0.43
M. townsendii (G1)	0.4±0.4	0.4±0.69	0.43±0.42	0.18±1.04	0.66±0.23	0.47±0.52	0.58±0.29	0.6±0.42
M. townsendii (G2)	0.47±0.42	0.4±0.73	0.42±0.56	0.18±1.1	0.7±0.25	0.45±0.69	0.73±0.23	0.61±0.46

Table S16 | Mean and coefficient of variation of the transition between the breeding and non-breeding reproductive states of females and males in each grid along the four temporal blocks.

	Female							Male						
Population	**phi J**	**phi NB**	**phi B**	**psi JJ**	**psi JNB**	**psi NBB**	**psi BNB**	**phi J**	**phi NB**	**phi B**	**psi JJ**	**psi JNB**	**psi NBB**	**psi BNB**
M. agrestis (BHP)	7	0	0	0	9	0	0	0	0	0	5	24	0	0
M. agrestis (KCS)	8	0	6	0	7	0	0	7	0	4	12	21	0	0
M. agrestis (PLJ)	0	43	0	0	18	0	0	3	0	17	2	3	0	0
M. agrestis (ROB)	24	0	0	5	47	0	2	0	0	0	4	29	0	0
M. ochrogaster (A)	0	32	11	97	66	74	28	9	44	46	96	85	64	0
M. ochrogaster (Carlo)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. ochrogaster (F)	0	8	8	73	70	18	20	17	11	7	45	33	56	0
M. ochrogaster (H)	0	0	0	15	0	19	0	0	0	0	0	17	0	0
M. pennsylvanicus (A Indiana)	52	36	41	85	102	122	113	71	115	0	70	85	0	0
M. pennsylvanicus (F Indiana)	0	50	26	41	48	9	62	3	6	24	78	72	43	15
M. pennsylvanicus (I Indiana)	0	10	0	21	30	41	59	8	26	12	18	53	10	0
M. pennsylvanicus (A Toronto)	46	0	0	47	88	0	0	24	0	0	53	56	0	0
M. pennsylvanicus (F Toronto)	40	0	65	29	30	0	0	71	0	31	35	40	0	0
M. townsendii (C)	102	67	106	88	57	46	83	88	0	82	83	105	0	0
M. townsendii (E)	107	0	64	113	130	86	0	68	0	59	132	131	0	0
M. townsendii (G1)	3	0	92	39	67	0	0	0	0	6	40	34	0	0
M. townsendii (G2)	16	0	0	0	0	0	0	2	0	0	31	30	0	0

Table S17 | Number of estimates with a r-hat > 1.4 (Gelman-Rubin convergence statistic).

Table S18 | Mean and standard error of the regression coefficients of the variables included in the model with the lowest AICc of each sensitive analyses (i.e. models using as explanatory variables the values at the percentiles 2.5%, 50%, and 97.5% of the vital rates and abundance). Abund = Abundance. The symbol “x” represents the interaction between the two variables. The symbol “-“ represents the variables without significant or consistent effect across sensitve models. The symbol “x” represents the interaction between the two variables. We used these values to represent Figure 6. Thus, these error values does not represent the uncertainty on the central estimate. See those details in Tables S19-26.

	Onset		**Breeding**		**End**		**Non-breeding**	
Variables	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Abundance	-0.05±0.01	-0.04±0.03	-0.02±-0.01	-0.03±0	-0.02±-0.03	-0.03±-0.02	-0.04±0	-0.04±0
φ_{NB}	0.07±0.01	0.04±0.00	0.05±0.01	-	-	0.04±0.01	0.05±0	0.06±0.01
φ_{B}	-	-	-	0.03±0	0.03±0	-	-	-
Ψ_{NBB}	-	-	0.04±0.01	-	-	-	-	-
Ψ_{BNB}	-	-	-	-	-	0.03±0	-	0.01±0
Abundance x φ_{B}	-	-	-	-	-0.07±0.02	-	-	-
Abundance x φ_{NB}	-	0.09±0.02	-	-	-	-0.05±0.02	-	-

Table S19 | Coefficients of the most parsimonious model of females at the onset block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. We did not include neither the values of the consistent variables in the Δ_2 models nor the other sensitivity analyses (see main text). We used these estimates together with the estimates of the most parsimonious models of the two other sensitivity models to represent Fig. 6 and Table S18. The goal of Tables S19-26 is to show some clues about the error of the estimates.

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-0.07	0.03	-2.14
Abund	0.08	0.03	2.87
phiNB	0.06	0.01	4.6
psiJNB	0.05	0.02	2.95
psiJB	0.1	0.02	4.33
psiNBB	0.05	0.02	2.46
psiBNB	0.02	0.01	1.62
Abund x psiJB	-0.13	0.02	-6.2

Table S20 | Coefficients of the most parsimonious model of males at the onset block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	0.04	0.03	1.26
Abund	-0.08	0.02	-4.76
phiNB	0.07	0.02	3.7
psiJNB	0.01	0.02	0.74
psiNBB	0.06	0.03	2.27
psiBNB	0.03	0.01	2.48
Abund x phiNB	0.07	0.02	3.67
Abund x psiJNB	-0.1	0.01	-7.13

Table S21 | Coefficients of the most parsimonious model of females at the middle breeding block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	0.03	0.03	1.06
Abund	-0.06	0.01	-4.46
phiNB	0.08	0.02	4.58
phiB	-0.01	0.02	-0.26
psiJNB	0	0.02	0.09
psiJB	-0.06	0.03	-2.16
psiNBB	0.03	0.01	2.66
psiBNB	-0.04	0.01	-3.95
Abund x phiB	0.04	0.02	2.08
Abund x psiJNB	0.06	0.01	4.27

Table S22 | Coefficients of the most parsimonious model of males at the middle breeding block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value	Random_structure
Intercept	-0.01	0.07	-0.11	(1|Pop_uo/Spp_uo)
Abund	-0.23	0.08	-2.92	(1|Pop_uo/Spp_uo)
phiNB	0.02	0.03	0.64	(1|Pop_uo/Spp_uo)
phiB	0.05	0.03	1.77	(1|Pop_uo/Spp_uo)
psiJB	0.01	0.04	0.33	(1|Pop_uo/Spp_uo)
psiNBB	0	0.05	0	(1|Pop_uo/Spp_uo)
Abund x phiNB	-0.07	0.02	-3.95	(1|Pop_uo/Spp_uo)
Abund x psiJB	0.07	0.03	2.53	(1|Pop_uo/Spp_uo)
Abund x psiNBB	-0.18	0.07	-2.76	(1|Pop_uo/Spp_uo)

Table S23 | Coefficients of the most parsimonious model of females at the end block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	0.05	0.05	1
Abund	0.05	0.05	0.88
phiNB	0.04	0.03	1.33
phiB	0.04	0.04	0.9
psiJNB	0.02	0.03	0.68
psiJB	-0.07	0.05	-1.58
psiBNB	-0.06	0.03	-2.07
Abund x phiB	-0.09	0.03	-3.37
Abund x psiJNB	-0.07	0.03	-2.31
Abund x psiJB	-0.12	0.04	-3.16

Table S24 | Coefficients of the most parsimonious model of males at the end block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	-0.01	0.07	-0.11
Abund	-0.23	0.08	-2.92
phiNB	0.02	0.03	0.64
phiB	0.05	0.03	1.77
psiJB	0.01	0.04	0.33
psiNBB	0	0.05	0
Abund x phiNB	-0.07	0.02	-3.95
Abund x psiJB	0.07	0.03	2.53
Abund x psiNBB	-0.18	0.07	-2.76

Table S25 | Coefficients of the most parsimonious model of females at the non-breeding block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	0.17	0.07	2.46
Abund	-0.05	0.03	-1.47
phiB	0.01	0.05	0.21
psiJNB	-0.05	0.04	-1.26
psiJB	-0.29	0.06	-4.46
psiBNB	-0.01	0.03	-0.22
Abund x phiB	0.11	0.04	3.03
Abund x psiJNB	-0.11	0.03	-3.38
Abund x psiBNB	-0.07	0.03	-2.09

Table S26 | Coefficients of the most parsimonious model of males at the non-breeding block when the values of the probability distribution of the abundance and vital rates at the percentile 50th. See Table S2 caption for further details about the goal of this information.

Variable	Estimate	Std. Error	t value
Intercept	-0.03	0.01	-2.82
Abund	-0.04	0.01	-3.16
phiNB	0.06	0.02	4.15
psiJNB	0.03	0.01	2.47
Abund x psiJNB	0.03	0.01	3.2

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CHAPTER IV

A recommendation to detect and report predictors for management decision-making: an example with vole outbreaks in Mediterranean farmlands

1 | Introduction

Animal population and disease outbreaks can generate enormous health, economical, and ecological damages (Karesh et al. 2005, West et al. 2008). These outbreak impacts can be reduced to tolerable levels when managers apply preventive managements before the populations are too large or diseases too widespread (a component of the ecologically based management paradigm; Douangboupha et al. 2010). Nevertheless, managers are often unable to apply preventive management constantly because of economic or ecological limitations, and therefore require predictions to assist them in their decision-making. However, not all predictive models are useful in deciding whether to apply preventive outbreak management.

The usefulness of predictions in assisting decision-making hinge first on their timing, and second, on their profitability. Timing is essential since only predictions issued before time window for intervention are useful for outbreak managements. On the other hand, profitability is essential since erroneous predictions lead to losses, and users will only use predictions in decision-making if in the long term the associated benefits with correct predictions outweigh the associated costs with erroneous ones (Murphy 1989, Davis et al. 2004, Brown et al. 2007). Although both timing and profitability issues are paramount in applied ecology, some research studies look for the best predictors against biological outbreaks without regard to management deadlines (Wu et al. 2007, Sullivan and Sullivan 2010, Tian et al. 2015), or evaluate model performance statistically, such as with R2 or AUC, without considering the costs and benefits associated with erroneous and correct predictions that also affect to the decision-making (Leirs et al. 1996, Khalil et al. 2014, Haredasht et al. 2015). As a result, those studies cannot guarantee the usefulness of their predictive models for assisting in decision-making.

The timing issue can be intuitively addressed by searching for warning signals ahead management deadlines. However, our knowledge about predictors is generally limited, while the number of potential predictors is large; making the chances of using a wrong or sub-optimal predictor high. Wrong time windows make it difficult to understand the mechanisms underlying the phenomenon under study, as they can give us the false sense that there is no relationship between the biological outbreaks and the explanatory variable. While sub-optimal predictors lead to unnecessary erroneous predictions, and, therefore, losses that could be saved.

Addressing profitability is also a challenge, as the model prediction has four possible outcomes: an outbreak is predicted and occurs (true-positive), an outbreak is predicted but does not occur (false-positive), no outbreak is predicted but occurs (false-negative), no outbreak is predicted and does not occur (false-positive). And each outcome has different benefits and costs associated with it. For instance, in a true-positive there is neither expenses of control nor losses because an outbreak, whereas in a false-negative there is no expenses of control but the losses because an outbreak are maximum since there is no preventive management to mitigate them (Equation 1).

$$Model\ profitability = TP * Benefits_{TP} + TN * Benefits_{TN} - FP * Costs_{FP} - FN * Costs_{FN} \tag{1}$$

Where TP, TN, FP, and FN represent the true-positive, true-negative, false-positive, and false-negative rates, respectively, while the benefits and costs with the different subscripts represent the benefits and costs resulting from each type of prediction. Thus, model profitability depends on equally important statistical and management aspects, and a given predictive model can be useful for one subset of users but not another depending on the management to be applied or the predicted risk used to start applying preventive treatments, hereafter risk threshold (Davis et al. 2004, Vickers and Elkin 2006).

Here we propose a dual and nested approach to detect timing warning signals against biological outbreaks as well as to report its profitability and best practice for any potential manager. First, we propose to systematically search for the best warning signal in periods that allow known and effective preventive managements (e.g. van de Pol et al. 2016). Second, we propose to evaluate model usefulness to aid decision-making with a metric that considers both statistical and management aspects (Vickers and Elkin 2006, Vickers et al. 2008, 2016) and to report the profitability and a user guide of the model to any potential users (an extension proposed here). We illustrated the contribution of our approach by detecting a warning signal of rodent outbreaks and providing specific indications on its target user and its use.

Rodent outbreaks occur worldwide and trigger a wide range of ecological, public-health, economic, and socio-political impacts (Altieri and Nicholls 2004, Oerke 2006, Singleton 2010, Luque-Larena et al. 2017). We focused on detecting warning signals of common vole (*Microtus arvalis*, Pallas, 1778) outbreaks in NW Spain. This is one of the most problematic vertebrate pests affecting plant production in Europe (Jacob and Tkadlec 2010). The Mediterranean farmlands of NW Spain were colonised by common voles in the late 1970s and ever since, large-scale recurrent outbreaks have occurred where voles thrive in alfalfa crops (Luque-Larena et al. 2015). As the use of anticoagulant rodenticides is being banned in the EU, there is a need to refine ecologically-based management (EBM) of vole outbreaks, which often takes time to implement. Therefore, the identification and correct use of early warning signals is more important than ever.

To identify warning signals of impending outbreaks, i.e. predictors, we considered the potential mechanisms triggering such outbreaks. Pulses of food availability can drive rodent outbreaks in arid and semi-arid environments, which have similarities with our study area (Pech et al. 1999, Jaksic 2001, Lima et al. 2002, Leirs 2003, Stenseth et al. 2003, Zhang et al. 2003). We assessed whether proxies of food availability in our study area predicted vole outbreaks during periods that allow performing preventive management measures. The relationship between proxies of food and vole outbreaks may be complex, with varying lags and duration. Therefore, we searched systematically for the best warning signal of vole outbreaks amongst all potential combinations of periods of time. Next, we conducted an analysis to learn and inform for which potential managers the use of our new warning signal is the best option to employ in decision-making as well as the way in which they should use it in each case.

2 | Material and Methods

2.1 | Study species and area

Common voles are small herbivorous mammals widely distributed across the Palearctic, ranging from Northern Spain to Central Russia and the Middle East. Populations can be strongly unstable, and while some show cyclic fluctuations in abundance every 3-5 years (Jędrzejewski and

Jędrzejewska 1996, Lambin et al. 2006), others seem to outbreak more irregularly (Jacob and Tkadlec 2010). In particular, vole populations in Castilla y León seem to show periodic outbreaks every 3-5 years (Luque-Larena et al. 2013). In Castilla y León region (a political administration of NW Spain with an extension of 94.193km2), during outbreaks, voles invade and damage all crops, while during non-outbreak years, voles persist in field margins road, verges, and permanent alfalfa crops; being these latter ones especially important since offer food with a high nutritional value and long-term stable habitats because are left unploughed for 3-10 years (Jareño et al. 2015, Rodríguez-Pastor et al. 2016).

We focused on the district of Tierra de Campos as voles reach the highest densities there during outbreaks (Luque-Larena et al. 2013, Rodríguez-Pastor et al. 2016). Tierra de Campos, as most of Castilla y León, is part of a high elevation plateau with a continental-Mediterranean climate characterized by cold winters and dry summers, when water availability is limiting. Our study area is an intensive agricultural area of ca. 5.000 km2, mainly dedicated to the growth of winter cereal crops, but where most of the regional cultivation of alfalfa occurs (see http://atlas.itacyl.es; Jareño et al. 2015 for details about the farming landscape).

2.2 | Vole outbreaks

In the absence of a continuous and standardised long-term data set on common vole abundance in our study area, we used two complementary data sources to reconstruct the occurrence of past regional outbreaks. We first used the historical reconstruction by Luque-Larena et al. (2013) that covered the period 1967-2010. Luque-Larena et al. (2013) collected data reporting vole outbreaks in governmental documents and local newspapers. The highest spatio-temporal resolution of the historical reconstruction was the annual presence or absence of vole outbreaks in each of the nine administrative provinces of Castilla y León. Luque-Larena et al. (2013) identified 11 years with vole outbreaks (i.e. 1979, 1983, 1984, 1988, 1989, 1993, 1994, 1997, 1998, 2007, and 2008). To provide more conservative results, we only used data from 1985 onwards, as the vole colonisation process of the agricultural areas of Castilla y León was not complete until 1983-84 (Luque-Larena et al. 2013, Jareño et al. 2015). Our second source of data consisted of vole density indices derived from live-trapping conducted in the provinces of Palencia, Valladolid and Zamora (in Tierra de Campos) during 2009-2016 (Rodríguez-Pastor et al. 2016). This monitoring program identified 2011 and 2014 with marked increases in vole density. In 2011, vole abundance increased mostly in field margins, alfalfas and fallows, but invasion of the main crops was limited and did not translate into a region-wide outbreak that would qualify as such in Luque-Larena et al. (2013) (Rodríguez-Pastor et al. 2016). In contrast, in 2014, vole density increased in all crops, invading cereal fields, which triggered complaints by farmers in media and reactive management actions by the regional government (Rodríguez-Pastor et al. 2016; BOCYL-D-14072014-12, BOCYL-D-27032007-14). We thus considered that between 1985 and 2016 vole outbreaks occurred in 1988, 1989, 1993, 1994, 1997, 1998, 2007, 2008 and 2014.

As the spatial resolution of the first dataset does not allow ascertaining if consecutive vole outbreaks represent independent outbreaks or the spatial extension of an outbreak of the previous year, we performed two sensitivity analyses: one excluding the first year, and another excluding the second year in cases of two consecutive outbreak years. Complementarily, we assessed whether classifying 2011 as a vole outbreak year altered results.

2.3 | Climatic and vegetation variables

Vegetation providing vole food and cover is influenced by local to large-scale climatic factors (Stige et al. 2006, Wen et al. 2012). We assessed the predictive power of six proxies of vegetation availability that ranged from general to specific. As general proxies, we selected the following: (i) cumulative rainfall; (ii) mean temperature; and (iii) North Atlantic Oscillation (NAO) index. As more specific proxies, we selected the following: (iv) Normalized Difference Vegetation Index (NDVI); (v) agronomic Turc index to estimate the yield of crops (Turc and Lecerf 1972); and (vi) alfalfa Growing Degree Days index (GDD).

Cumulative rainfall — We used cumulative rainfall as a proxy of water availability, which is a prime determinant of vegetation growth and quality, especially in water limited areas, such as Mediterranean habitats (Yahdjian and Sala 2006). For each month, we calculated the cumulative rainfall using data from all weather stations within Tierra de Campos, using their average as proxy (Appendix A).

Temperature — Temperature also is a prime determinant of vegetative development (Ritchie et al. 1998). We used two indices based on temperature: mean temperature and GDD. We calculated the monthly mean temperature using daily mean temperature and the average across the available weather stations, as we did with rainfall. The GDD is a good proxy of the initial growth stages of crops, and it has been used to estimate the optimal time for first alfalfa harvest (Sanderson et al. 1994). We calculated the daily GDD following method 1 of McMaster and Wilhelm (1997; Appendix A). The monthly GDD was the cumulative sum of the GDD within a month. Finally, we used as our proxy the average monthly GDD values calculated using data from all weather stations. Unlike previous studies that used a unique start day to calculate the cumulative GDD (Sharratt et al. 1989), we calculated the cumulative monthly GDD for each potential predictive time window.

NAO index —Large-scale climate indices such as the NAO index simultaneously capture variation in many weather variables (Stenseth and Mysterud 2005). We downloaded daily NAO index values from the Climate Predictor Centre of the National Weather Service (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml) and calculated monthly mean values (Appendix A).

Vegetation growth index—NDVI is a satellite-derived index that indirectly reflects primary production. Because no single source had data for the whole study period, we used two complementary sources to calculate monthly NDVI values (NOAA data for 1980-2013 and MODIS data for 2014-2016; Appendix A).

Agronomic index —The Turc index reflects agricultural potential for dry and irrigated crops (Méndez et al. 2003) particularly relevant in Mediterranean environments (Milla et al. 2010).

Higher values indicate more favourable conditions for vegetation growth. We calculated the variant for irrigated crops, using information about rainfall and temperature, maximum insolation, extra-terrestrial radiation, solar radiation at soil level, duration of the daylight period and relative humidity (Appendix A).

2.4 | Detection of outbreak warning signals

We searched for (i) a warning signal based on conditions in the year preceding a potential vole outbreak, and (ii) a complementary warning signal after that initial time period but before the maximum population density of the potential outbreak. While the first warning signal can be useful in decision-making, the second warning signal can be useful to know better outbreak drivers and therefore to apply the best management. When there is a vole outbreak, damages to crops are apparent in summer (Rodríguez-Pastor et al. 2016). We thus used July as the latest time when warning signal must be apparent to allow farmers to adjust their management (i.e. the latest month for the secondary warning signal). As most seasonal crops are winter cereal in our study area, a critical time in terms of decision-making for preventive measures (some of which include deep ploughing) is the sowing of winter cereal. We therefore started searching for early warning signals preceding the sowing of winter cereals, i.e. nine months before July. In summary, we searched an early warning signal between 20 and nine months before July (hereafter early period), that could be used in decision-making. We also searched a complementary late warning signal between nine and zero months before July of the focal year (hereafter second or late period), that could be used to understand better outbreak drivers.

To identify the best early warning signal across our six variables, we conducted a systematic search assessing how each variable predicted vole outbreaks in all potential time windows of the early period (Fig. S1; van de Pol et al. 2016). We performed logistic models, using the values of predictors within each potential time window as explanatory variables, with the function *slidingwin* of the R package *climwin* (van de Pol et al. 2016). We subsequently selected the best time window for each of our six variables (hereafter best predictor of each variable) comparing AICc. Our baseline model was a logistic model with only the intercept, assuming a constant risk.

Later, we calculated the probability that the best predictor of each variable was a random signal by randomizing the monthly values of the explanatory variable (e.g. monthly mean temperatures) and performing a new logistic model using the same time window. We repeated this procedure 1,000 times and assessed the probability of obtaining an AICc lower or equal to the one obtained with the real data in the randomized data (hereafter Psim), using the function *randwin* of the R package *climwin* (van de Pol et al. 2016). Finally, we selected the best predictor between the six proxies as our early warning signal by using the Nagelkerke pseudo R-squared values of the logistic models (Nagelkerke 1991), calculated with the function *NagelkerkeR2* of the R package *fmsb* (Nakazawa 2018). We repeated the same search procedure to identify warning signals in the second period. See Appendix B for details.

2.5 | Model profitability

To assess model profitability, we adapted the widely accepted *decision curve analyses* (hereafter DCA; Vickers and Elkin 2006, Vickers et al. 2008, 2016). To facilitate the understanding of our approach, we first explained the theory behind DCA and later the extension proposed here.

2.5.1 | Decision curve analyses (DCA)

DCA is a methodology to compare predictive models based on the concept of net benefit (Vickers and Elkin 2006, Vickers et al. 2008, 2016). For each predictive model or strategies that can be used for assisting in decision-making (e.g., the new one and other existing alternatives), DCA calculate a metric called net benefit and used them in model selection, similarly to other metrics for model comparison such as AICs or BICs, where the model or strategy with the highest net benefit would be the one that should be used in decision-making (Vickers and Elkin 2006). DCA calculates the net benefit as the difference between the rate of true-positives (TP) and the rate of false-positives (FP):

$$Net\ benefit\ = TP - FP \tag{2}$$

Unlike the conceptual and intuitive Equation 1 about model profitability, DCA only consider true-positives and false-positives (but see later our extension). DCA also does not require explicit prior information on the benefits and costs associated with a true-positive and false-positive. This type of approaches is commonly employed in fields such as medicine where it is not appropriate or possible to value the success or failure of a treatment or prediction (e.g. to value human lives). Nonetheless, we cannot simply subtract TP and FP since they depict things. Equation 2 is an algebraic equation with the terms TP and FP whose coefficients are 1. Thus, to solve the algebraic equation, we must indicate the relationship between the two terms. DCA do it by using an exchange rate that convert the true-positives into false-positives (Equation 3).

$$Net\ benefit\ = TP * Exchange.Rate - FP \tag{3}$$

Conceptually, the exchange rate depicts how many times a true-positive is better than a false-negative for the person in charge of the evaluation (i.e. the ratio TP/FP). Vickers and Elkin (2006) proposed a particular exchange rate that increases exponentially with the risk threshold used. Their aim was to further penalise models that fail when their expected risk is higher. Although this penalty may make sense in some cases, it may not in others, limiting its usefulness. To overcome it, we propose an alternative to provide results useful in any case.

2.5.2 | Extension of the DCA

We firstly show the relationship between the exchange rate and specific preventive treatments. Next, we detailed our mathematical expression to calculate the net benefit. The exchange rate used to transform true-positives into false-positives can be defined as the number of times the benefits associated with the timely implementation of preventive managements are greater than costs associated with implementing unnecessary preventive managements (Equation 4; Benefits_{TP} and Costs_{FP} terms, respectively). In other words, the exchange rate is the number of years a manager can invest in preventive treatments and still make a profit, as long as there is only one outbreak in those years.

$$Net\ benefit\ = TP * \frac{Benefits_{TP}}{Costs_{FP}} - FP \tag{4}$$

As Benefits_{TP} and Costs_{FP} depends on the effectiveness and expenses of the treatments (Equation 4; Fig. 1), different exchange rates represent different treatments or the same treatments with different effectiveness because it was applied at different periods. So to inform about the usefulness of new warning signals to any potential user, we can estimate the net benefit with the exchange rates representing all potential treatments that can be applied based on it. Then, our first modification of the DCA was to calculate the net benefit under a wide range of exchange rates that cover any potential real treatment (see section 2.5.3 for details).

In our second modification of the DCA, we included the false-negatives in the calculation of the net benefit. False-negatives also have important consequences that can influence manager decisions since they affect to model profitability and user confidence on the methods (Equation 1; Petticrew et al. 2000, Davis et al. 2004). To include the rate of false-negatives, we identified the benefits or costs are associated with them conceptually, and included them algebraically in Equation 4. When there is a true-positive, users will apply a preventive management and will reduce more or less the damage, or in other words obtain gains, depending on the management effectiveness. Then, the associated benefit with true-positives can be quantified as the avoided damages because of the effectiveness of the management (e.g. saved crop harvest arising from a management intervention) minus the expenses of applying a management (e.g. expenses of deploying management action; Fig. 1). When there is a true-negative, users will not apply a preventive management and there will be no damage because outbreaks. Therefore, there is no associated expenses nor avoided damage, and that term is excluded from the calculation of the net benefit. When there is a false-positive, users will apply a preventive management but there will not be any outbreak damage to avoid. Then, the associated cost with false-positives are the expenses of applying the management. Lastly, when there is a false-negative, users will not apply a preventive management but there will be damages because outbreaks. Then, the associated cost with false-negatives is the damage that could be saved by applying a necessary management minus the expenses of applying that necessary management (Fig. 1). As true-positives save the salvageable costs of a false-negative (Fig. 1b), we can consider true-positive and false-negatives as the same algebraic term but with different coefficients (positive and negative, respectively) and include it in the calculation of the net benefit (Equation 5).

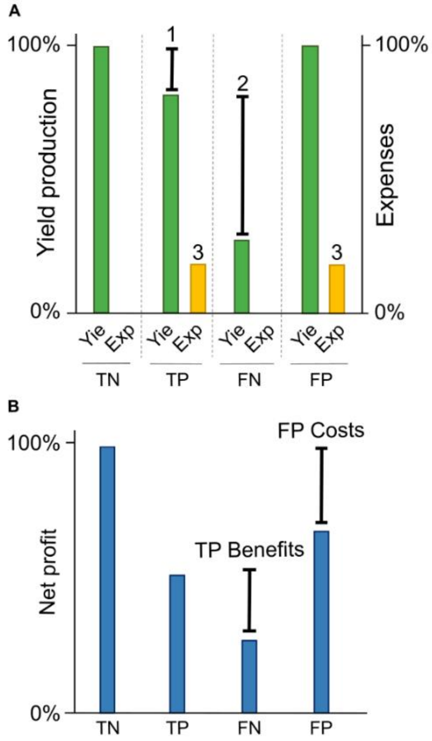

Fig. 1 | Hypothetical crop yield, preventive treatment expenditures, and net profit in four scenarios: true negative (TN), false negative (FN), true positive (TP), and false positive (FP). Plot A represents the hypothetical proportion of the crop yield the farmer can use or sell (Yie; green bars) and the hypothetical expenses on a given preventive treatment as the proportion of the crop yield the farmer has (Exp; yellow bar). In the TN and FP scenarios, the crop yield is maximum because there are no vole outbreaks. However, when there are vole outbreaks, the crop yield is lower and depends on whether a preventive treatment has been applied. When farmers apply preventive treatments (TP), the yield will only decrease if the treatment is not 100% effective (whisker line 1), an economic loss independent of model performance, but there are also expenses because the treatment (3; yellow bar). Conversely, when farmers have not applied preventive treatments, yield will decrease more (whisker line 2). Plot B represents the result of resting the proportion of the crop yield available minus the proportional loss of the expenses of preventive treatment. The net loss is the difference between the net profit in the correct prediction and the incorrect prediction (i.e., TN-FP and TP-FN). We call the difference in net profits between the TP and FN scenario as $\text{Benefits}_{\text{TP}}$, while that between TN and FP as Costs_{FP}. The ratio between these $\text{Benefits}_{\text{TP}}$ and Costs_{FP} represents alternative treatments with different associated expenses and efficacy.

$$Net\ benefit\ = (TP - FN) * \frac{Benefits_{TP}}{Costs_{FP}} - FP \tag{5}$$

We exclude the true-negatives since their cost/benefit is 0 (Davis et al. 2004). To avoid misunderstandings, because of TP and FN depict the same algebraic term, we specified the ratio as prediction benefits divided by prediction costs (Equation 6):

$$Net\ benefit = (TP - FN) * \frac{Prediction\ Benefits}{Prediction\ Costs} - FP \tag{6}$$

We note that our methodological approach only uses theoretical ratios. It is later and outside our approach when each user of the predictive model (e.g. farmers, manager and policy-makers) must calculate the prediction benefits and costs of their preventive treatments, and then search which of our results are the valid for them. We anticipate that although it is far from our goal, we discussed ways to measure prediction benefits and costs to facilitate the use of our approach.

2.5.3 | Calculation of the rates of true-positives, false-positives and false-negatives

The net benefit of a predictive model varies with (i) the treatment that will be applied to mitigate vole outbreaks and (ii) the minimum predicted risk that managers use to start applying their preventive managements (i.e. risk threshold). While the former one affects to the exchange rate, the latter one affects to the rate of true positives, false-negatives, and false-positives. Thus, for each model, we calculated the net benefit of using that model under an array of combinations of multiples exchange rates and risk thresholds. In particular, we calculated the net benefit in the combination of 11 management thresholds (0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 and 0.99) and ten ratios of the prediction benefits and costs (i.e. 1.5, 2, 3, 4, 5, 6, 7, 8, 9, and 10).

To calculate the net benefits under a given risk threshold, we followed Vickers and Elkin (2006), but including the false-negatives:

$$Net\ benefit\ = \left(\frac{N_{True\ positive}}{N_{Total\_sup}} - \frac{N_{False\ negative}}{N_{Total\_inf}}\right) * \left(\frac{Prediction\ benefits}{Prediction\ costs}\right) - \frac{N_{False\ positive}}{N_{Total\_sup}} \tag{7}$$

where N_{Total_sup} is the number of years, from our empirical data, with a predicted outbreak risk equal or higher than the given probability threshold, while N_{Total_inf} the number with a lower predicted risk. To make the calculations, we considered the years grouped in N_{Total_sup} as outbreaks, while the years grouped in N_{Total_inf} as non-outbreaks. We then counted the number of true-positives (i.e. $N_{True\ positive}$) and false-positives (i.e. $N_{False\ positive}$) in N_{Total_sup}, as well as the number of false-positives (i.e. $N_{False\ negative}$) in N_{Total_inf}.

2.6 | Model comparison

We compared the net benefit of using our warning signal in those previous conditions to the net benefits of other existing approaches in the same circumstances. To our knowledge, there is no other predictive model for our study but some regular monitoring performed by the government to estimate an abundance index. However, we do not know the data and criteria used by the government to start applying some management measures such as burning field margins. We thus could not compare the net benefit of our predictive model with that of another predictive models. Nevertheless, we compared the net benefit of our model with those derived from two alternative strategies that managers can use: to apply always or never a preventive management (Davis et al. 2004, Vickers and Elkin 2006, Vickers et al. 2016). The strategy of never applying preventive managements would apply in cases where managers have no clues about biological outbreaks until they happen, a common situation with rodent outbreaks (Davis et al. 2004). In contrast, the strategy of always applying preventive managements would depict cases where the benefits of a treatment are much higher than the costs. Although this second strategy is not common for managing rodent outbreaks, it is used to mitigate other biological damages such as spray herbicides or vaccines.

Our case study had only 32 points. Thus, we tested whether our sample size could affect our inference by incorporating uncertainty in the data. One way of incorporating uncertainty is to bootstrap the data (Vickers et al. 2008). We then bootstrapped 1,000 times the dataset for each threshold value, recalculated the hit-and-error rates of our warning signal and those of the two alternative strategies, and later recalculated their net benefit. For each bootstrapping, we assessed which strategy (i.e. our warning signal or the two null strategies) obtained the highest net benefit in each ratio (i.e. potential real treatment), independently of the risk threshold. This result indicates which strategy should be followed in each potential treatment. If the best strategy was to use our predictive model, we identified the risk threshold that provide the maximum net benefit in each treatment.

The output is one matrix per strategy assessed, one for our warning signal and two for the null strategies, indicating the relative amount of times that a particular combinations of risk thresholds and ratios triggered the highest net benefit. In our case study, our warning signal always provided the highest net benefit. Therefore, we only provided one matrix as a heat map indicating the proportional frequency of the risk managements that trigger the maximum net benefit for each ratio of prediction benefits and costs. This result explicitly suggests the minimum risk that each manager should use to obtain the greatest long-term profits when using our model predictions to begin implementing management against vole outbreaks.

2.7 | Additional analyses about model performance

To allow comparison of our model with other studies, we also assessed (i) the adjusted R-square of the predictive model based on the early warning signal; (ii) its calibration; and (iii) its discrimination capacity (see Appendix C for details).

3 | Results

3.1 | Warning signals

We found that the combination of early and late warning signals correctly classified all years with and without vole outbreaks between 1985 and 2016. While in the early period there was a single best warning signal, in the late period we found four similarly performing warning signals.

The best early warning signal was the cumulative precipitation between July and October of the previous year (Table 1), which was positively associated with vole outbreak probability, and captured 65% of the variance (Fig. 2 and Table 1). Amongst the other variables, low values of the Turc index, mean temperature, and GDD were also associated with vole outbreak probability (Table 1). The best temporal window of these latter three variables was 13 months before our focal month (July), capturing between 35% and 38% of the variance (pseudo-R2). Unlike cumulative rainfall, the best predictors of the Turc index, mean precipitation, and GDD were however only marginally better than random (Table 1). The best predictors of NAO index and NDVI were positively and negatively associated with vole outbreaks, respectively, but weakly captured variance in vole outbreak occurrence (pseudo-R2 = 0.18 and 0.11, respectively). Thus, the cumulative rainfall in the previous summer-autumn explained the occurrence of most vole outbreaks, accounting for twice as much variance as any other variable.

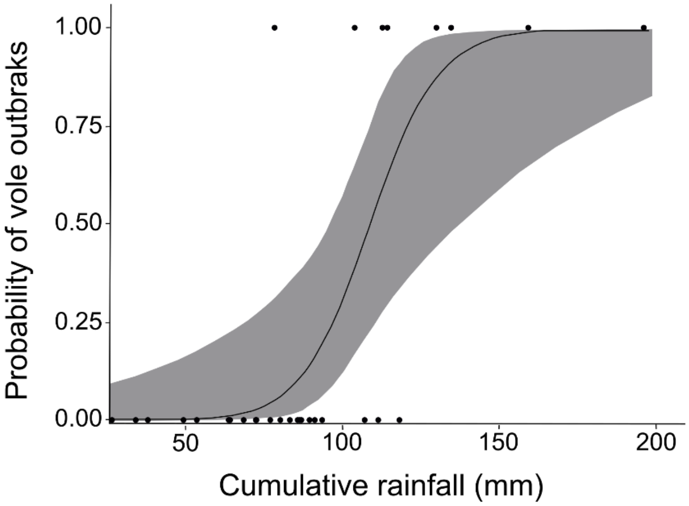

Figure 2 | Predicted vole outbreak probability (± 95% confidence interval) based on the cumulative rainfall between 13 and ten months before July of the focal year (July-October). Dots represent the observations (occurrence or absence of vole outbreak, 1 and 0 respectively, and their associated cumulative rainfall in the x-axis).

In the late period, we found that the cumulative precipitation, mean temperature, GDD, and NDVI between May to July predicted similarly well (Table 2). These late warning signals together with the early one correctly classified all occurrences/absences of vole outbreaks. Precipitation had a positive association with vole outbreak occurrence, as in the earlier period, while mean temperature, GDD, and NDVI had a negative association. Low values of Turc index also captured a high proportion in variance of vole outbreaks (pseudo R2 = 0.91). We detected no significant signal with the NAO index.

We found the same qualitative results when considering the year 2011 as a year with vole outbreaks (Table S1), as well as when considering the first year of the double outbreak years as non-outbreak (Table S2). In contrast, we found no statistically significant warning signals when excluding the second year of the double years (Table S3).

Variable	Window Open	Window Close	Psim	Parameter	Estimate	Std. Error	Z-score	P-value	pseudo-R^2
Cumulative rainfall	13	10	0.002	Intercept	-10.00	3.67	-2.72	0.006	0.646
				Signal 1	0.01	0.01	2.61	0.009	
Turc index	13	13	0.060	Intercept	30.77	12.77	2.41	0.016	0.384
				Signal 1	-4.57	1.84	-2.47	0.013	
Mean temperature	13	13	0.088	Intercept	16.69	7.22	2.31	0.021	0.357
				Signal 1	-0.96	0.40	-2.42	0.015	
Mean NAO index	10	9	0.557	Intercept	-1.45	0.53	-2.71	0.007	0.182
				Signal 1	-1.24	0.64	-1.92	0.054	
GDD	13	13	0.083	Intercept	12.81	5.67	2.25	0.024	0.365
				Signal 1	-0.02	0.01	-2.40	0.016	
NDVI	11	10	0.286	Intercept	-23.19	11.10	-2.09	0.036	0.113
				Signal 1	61.96	30.59	2.02	0.043	

Table 1 | Results of the logistic model for the time window with the best predictor of each variable in the earlier period. The columns “window close” and “window open” indicate the range of the time window in months from July used as predictor of the vole outbreaks. Psim is the probability of the signal of that time window to be a random signal.

Variable	Window Open	Window Close	Psim	Parameter	Estimate	Std. Error	Z-score	Chisq	P-value	pseudo-R^2
Cumulative rainfall	1	0	0.066	Intercept	-18.377	8.66	-	27.86	<0.001	-
				EWS	0.014	0	-	19.45	<0.001	
				Signal 2	0.007	0	-	7.18	0.007	
Turc index	1	1	0.39	Intercept	74.32	44.26	1.68	-	0.930	0.912
				EWS	0.02	0.01	1.76	-	0.079	
				Signal 2	-14.21	8.03	-1.77	-	0.077	
Mean temperature	1	1	0.014	Intercept	39.04	21.68	-	5.78	0.016	-
				EWS	0.02	0.01	-	21.90	<0.001	
				Signal 2	-3.15	1.636	-	11.19	0.001	
Mean NAO index	3	1	0.349	Intercept	-17.55	7.93	-2.21	-	0.027	0.781
				EWS	0.02	0.01	2.20	-	0.028	
				Signal 2	-4.90	2.73	-1.79	-	0.073	
GDD	1	1	0.056	Intercept	17.393	10.33	-	3.45	0.063	-
				EWS	0.014	0.01	-	20.85	<0.001	
				Signal 2	-0.038	0.02	-	10.04	0.002	
NDVI	2	2	0.005	Intercept	19.37	12.48	-	3.41	0.065	-
				EWS	0.02	0.01	-	25.06	<0.001	
				Signal 2	-70.92	36.16	-	10.38	0.001	

Table 2 | Results of the logistic model for the time window with the best predictor of each variable in the later period with our early warning signal. See Table 1 for details on the columns. The parameter estimates for cumulative rainfall, mean temperature, GDD, and NDVI were calculated with Firth's correction (Firth 1993).

3.2 | Performance of the predictive model

Statistical assessments of the early warning signal show a high overall discrimination performance (area under the ROC curve = 0.92; Fig. S2) and calibration (GiViTI test p = 0.717; Fig. S3). Our modified decision curve analysis shows, that independently of the ratio of prediction benefits and costs tested, using our warning signal is always better than applying always or never preventive treatments. According the ratio of prediction benefits and costs is higher, the most profitable use of our warning signal happens when the probability threshold is lower (Fig. 3).

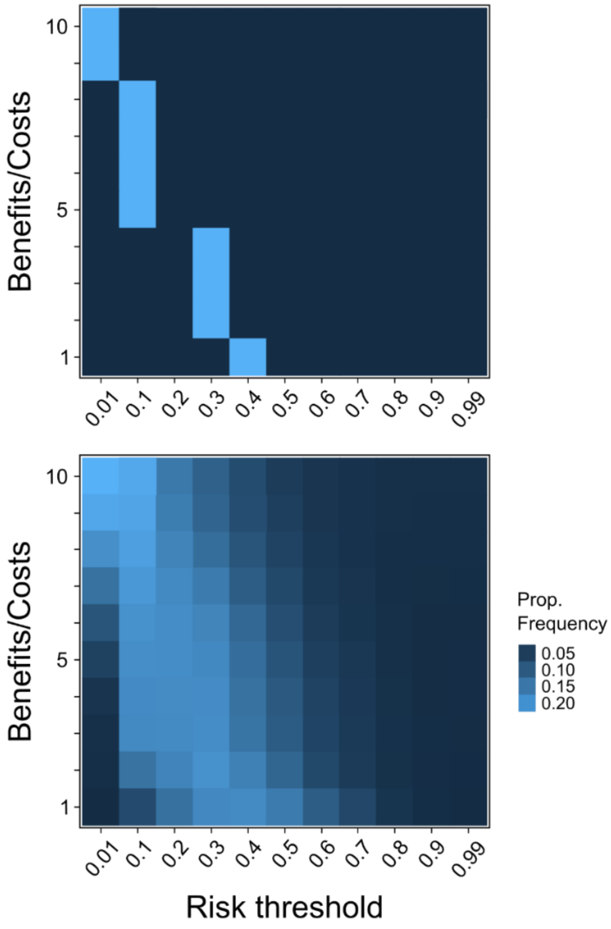

Figure 3 | Heat map indicating the risk threshold that managers should use to obtain the highest profitability when using each theoretical treatment (i.e. ratio of prediction benefits and costs). We only represented the values about our warning signal since it provided the highest net benefit in all randomizations. Plot A**.** The blue light colour indicates the probability thresholds triggering more frequently the highest net benefit along the 1,000 randomizations. Plot B. Representation of the total proportion of frequencies to show the uncertainty for defining the best probability threshold. The different shades of blue indicate the proportion of frequencies.

4 | Discussion

The high socioeconomic, public health and ecological consequences of biological outbreaks call for provisioning timely warning signals. Moreover, since the usefulness of predictive models depends on the treatment to be applied based on their predictions, scientific studies providing predictive models should report their profitability to assist in the decision-making of implementing any management as well as facilitate their correct use by managers. By combining two widely accepted methodologies (Vickers and Elkin 2006, van de Pol et al. 2016), we propose a conceptual framework that fulfils both requirements and favours a higher and better use of theoretic research in real decision-making.

We showcased our approach by identifying an early warning signal that predicts vole outbreaks in a Mediterranean environment almost one year in advance. This anticipated information could allow farmers to perform preventive management of their crops and fields in order to reduce damages and economic losses during the next crop season. Our results are consistent with a link between vole outbreaks in Mediterranean environments and summer - early autumn rainfall (Mutze et al. 1990, Leirs et al. 1996, Jaksic 2001, Lima et al. 2002, Kenney et al. 2003, Zhang et al. 2003, Davis et al. et al. 2004; but see Jacob 2003). While our correlative analyses cannot identify the causative mechanism, they point towards a pulse of primary productivity in summer and autumn being triggered by rainfall between July and October in normally dry Mediterranean areas (Mutze et al. 1990, Boonstra and Krebs 2012). The growth of vegetation with high protein content during and at the end of the summer may extend the breeding period as well as increase vole survival and recruitment rates, as found in other species (Mutze et al. 1990, Kenney et al. 2003, Tkadlec et al. 2006, Ergon et al. 2011, Pinot et al. 2014). Relief from drought limitation to plants is undistinguishable from lower soil hardness and greater excavatability of burrows (Goszczynska and Goszczynski 1977, Blank et al. 2011) that may also facilitate the establishment of new colonies across the farming landscape, such that both mechanisms are plausibly involved.

Our failure to detect early signals related to the NDVI may be explained by the dominance of crops in shaping this index and that voles are not there but in the edges (Pinot et al. 2014, Rodríguez-Pastor et al. 2016). The absence of a relationship between the NAO index and vole outbreaks may reflect the fact that NAO captures processes operating at larger spatial scales, which looking at the rest of our analyses do not seem to be correlated with productivity in our area of study. We found negative associations between vole outbreaks and mean temperature, Turc index, and GDD. The negative association of these metrics in summer with temperature is consistent with a role for increased primary productivity, as lower temperatures in Mediterranean summers allow for a longer period of vegetative growth (Mooney et al. 1974). This fact along with that GDD is mainly correlated with the alfalfa growth before its first cut (i.e. May-June) suggest that the GDD and Turc index in July-October reflect temperature more than vegetative growth in that period. In any case, our results show that the best predictors of outbreaks are the rainfall conditions during the previous summer and early autumn, hinting that longer breeding periods precede vole and other herbivorous mammal outbreaks as this allows the individuals born early in the same season to breed (Tablado et al. 2009, Ergon et al. 2011, Ims et al. 2011).

Our early warning signal together with a complementary later signal explained all occurrences and absences of vole outbreaks in our data set. Although our second signal is useless for decision-making due to its timing, it helps unravelling outbreak drivers and could be used to increase or refine managements. The sign of the relationships between vole outbreaks and proxies of food availability in the second period was similar to those obtained in the first period, except for NDVI. The negative association with NDVI may suggest that during years with vole outbreaks, crops might mature earlier, consistent with conditions allowing an earlier onset of vole breeding; what can be also supported by the positive association with the GDD. Altogether, the detection of warning signals in the early and late periods suggest the conjunction of two sets of circumstances leading to an overabundance of voles in this Mediterranean environment.

Regarding our complementary analyses about outbreaks spanning two years, the lack of signal when removing the second year together with the total explanation of the vole occurrences when removing the first years suggest that neither the first years were peak phases of vole population fluctuations nor the second years were the spatial spread of the outbreak occurred in the first year (Tables 2 and 3; Roos et al. 2018). Nevertheless, due to the resolution of the data and our limited sample size, these latter conclusions must be taken with caution. Potentially, the first years might be the increase phases while the second one the peak phases. Undoubtedly, long-term projects, such as the live-trapping carried out in our area of study since 2009 and whose data have been partially used in this study will help to respond to this in the future.

Although some clues were available about in what time windows process that facilitate outbreak might operate (Leirs et al. 1996, Lima et al. 2002), without performing a systematic search, we could have not been certain whether we detected the best predictor, the main goal for assisting in decision-making. Using systematic searches that flexibly evaluate cumulative effects, here cumulative rainfall between July and October, yielder a higher predictive power that using a fixed time windows (e.g., Lima et al. 2002); such as lagged influence of rainfall in given months. For instance, our best rainfall predictor with a time window of one month was June of the previous year; which had a R2 of 0.25, a value much lower than our predictor considering the cumulative rainfall between July and October (R2=0.65). The availability of tools like the R package climwin that facilitates and make systematic searches flexible (van de Pol et al. 2016), together with the need of detecting the best predictor against biological outbreaks, encourage to search predictive models by using this approach.

We acknowledge that our binomial categorization of the years into outbreak and non-outbreak years is a simplification of the reality and does not consider local variations in population increases. Thus, our predictive model may be more useful for a regional perspective than for a local one because of the resolution of our data. For example, the regional government of our study area performs continuous monitoring that experts use to perform their recommendations. Potentially, our warning signal can serve to advice about the need of increasing the frequency and intensity of samplings, provide some recommendations to farmers, or even to start applying some preventive management.

Outputs like the resulted proposed heat map are much more explicit and easy to understand than outputs based on statistical performance such as R2, AUC, or calibration tests (Fig. 3). Nonetheless, farmers, managers, or policy-makers may still have little or no knowledge about how to interpret statistical results such as risk thresholds. We therefore recommend, when it is possible, to transform the risk threshold into the explanatory variable. For instance, in our case, we also included a table indicating the threshold of cumulative rainfall between July and October to start applying for each potential preventive managements (Table 3). All these steps will facilitate the understanding and application of the results by a wider range of users.

$\mathbf{Prediction}_{\mathbf{Benefits}}$ / $\mathbf{Prediction}_{\mathbf{Costs}}$	**Risk threshold**	**Cumulative rainfall threshold (mm)**
1.5	0.4	1047
2	0.3	998
3	0.3	998
4	0.3	998
5	0.1	851
6	0.1	851
7	0.1	851
8	0.1	851
9	0.01	590
10	0.01	590

Table 3 | Probability threshold and cumulative rainfall thresholds that should be used to start applying preventive managements in each kind of management (i.e. ratio of prediction benefits and costs).

We are aware that there is at least one similar methodology for estimating model profitability in literature on rodent outbreaks (Davis et al. 2004; a methodological convergence for answering similar problems in two different fields of science). However, we used DCA because the approach proposed by Davis et al. (2004) (i) estimates the utility of the predictive model with the same data used to build it, making it difficult to know whether the model is overfitted and thus overly optimistic; and (ii) does not consider any uncertainty around model predictions (Vickers et al. 2008). Nevertheless, note that both aspects could also be implemented in a manner similar to that proposed by Vickers et al. (2008).

Our extension took into account that multiple managers can be interested on implementing alternative preventive treatments, due to subjective, economic or logistical factors. We thus overcome a major shortcoming of existing approaches, which left the assessment of the utility of the model for applying treatments other than those explored in the scientific study in the hands of managers, such as farmers that may not know how to make such calculations (e.g., Davis et al. 2004, Vickers and Elkin 2006, Vickers et al. 2016).

Research using our approach do not need to know a priori the benefits and costs associated with each potential treatment against biological outbreaks because of it uses a range of theoretical ratios depicting them. Nevertheless, farmers, managers, or policy-makers do need to estimate benefits and costs to know what results to look at. Although this task it is far from our goal, it is essential to use our approach in real decision-making. We therefore also suggest here approaches to estimate benefits and costs associated with each treatment. Before explaining it, we briefly indicated some challenges in order to understand our choice for this task. Calculating prediction benefits and costs requires that managers (i) anticipate the damage of a biological outbreak, the effectiveness of a treatment and its costs, (ii) estimate damages on elements such as environment and wildlife that are difficult to quantify comparing to economic (e.g. on agriculture) and social (e.g. on health) impacts which are more easily perceived and more reported by stakeholders (Vila et al. 2010, Guerry et al. 2012); (iii) estimate elements that can be outside their interests (e.g., environment and wildlife; Rawn et al. 2001, Brakes and Smith 2005, Sánchez-Barbudo et al. 2012), making them less important or even unimportant when considering the impacts (Ellison and Daily 2003); and (iv) consider that biological outbreaks and the treatments against them may directly and indirectly impact on multiple aspects and social groups, and that such impacts can be positive or negative as well as measured with different units (Liu et al. 2011). To anticipate the expenses, damages, and effectiveness, managers can assess the impacts and costs of past outbreaks and treatments as well as studying similar research (Davis et al. 2004, Larsson 2005, Brown et al. 2007); but to overcome the other issues are more challenging. We can partially estimate the costs and benefits associated with treatments on hard-to-quantify elements such as biodiversity by using its relevance as ecosystem services (Guerry et al. 2012, Daily et al. 2000, Chaplin-Kramer et al. 2019). Although the previous tasks can be complex and require the intervention of experts, maybe the greatest challenge is to measure and average costs and benefits in aspects measured with different units and which may have very different importance for diverse groups in society. We suggest to do this task with methodologies such as Deliberative Multi Criteria Evaluation (hereafter DMCE).

DMCE provide the advantages of multi-criteria decision analysis by allowing evaluating multiple aspects with the same or different units (e.g. reduction in crop damage and damage to water quality when applying a pesticide in rice crops; Kiker et al. 2005, Dodgson et al. 2009), together with the benefits of incorporating diverse view in the decision-making (e.g., scientist, politicians, NGOs, and stakeholders; Proctor and Drechsler 2006, Stirling 2006, Rauschmayer and Wittmer 2006, Liu et al. 2011, Huang et al. 2011). By accepting views from different social sectors, managers can favour consensus, transparency, and social learning; and then, increase the acceptance of the results, reduce conflicts between stakeholders, and finally favour the use of scientific findings in applied ecology (Redpath et al. 2004, Stirling 2006, Liu et al. 2011, Lauret et al. 2019). In addition, DMCE also allows including uncertainty in decision-making, which makes it easier for any social sector to understand the limitations of predictions as well as to reduce overconfident decisions and mistrust of scientific predictions (Shea et al. 2002, Liu et al. 2011). In fact, it is common for a group of experts to assist policy-makers. For instance, in Spain there are co-management boards composed by different social sectors to assist management in the prevention of impacts of the common vole in our study area, as well as of other invasive species such as the apple snail (*Pomacea canaliculata*) and the blue crab (*Callinectes sapidus*) in the Ebro Delta in NW Spain. Therefore, DMCE or similar approaches are realistic tools for estimating the costs and benefits of different treatments in a robust and holistic manner; making the assessment of the model's contribution more robust.

Although our recommendations to consider prediction benefits and costs cannot recognise the whole complexity that managers weigh up when making financial decisions (e.g., variable prizes of the crops along time, opportunity costs, discount rates; Norton and Mumford 1993), this approach suppose a qualitative advance when evaluating the profitability of predictive models in decision-making.

Here we propose a generalizable framework to detect early warning signals of biological outbreaks that allow performing preventive management and to inform about their usefulness with explicit and non-technical recommendations. Under the current prospect of increase of the frequency of extreme climatic events, coupled with land-use changes, the amount of phenomena affecting human and ecosystem well-being can increase (Easterlin et al. 2000, Rosenzweig et al. 2001). Thus, methodological approaches such as ours to facilitate the understanding of scientific findings and promote the correct use of predictive models in management decision-making will be indispensable.

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Contributions

Rubén Bernardo-Madrid, François Mougeot and Eloy Revilla conceived the project; RBM conceived the methodological approach. RBM, FM and Juan José Luque-Larena collected and prepared the data. RBM performed the analyses. RBM wrote the first version of the manuscript. RBM, FM, JJLL, Xavier Lambin, Beatriz Arroyo, and ER discussed and wrote the final manuscript.

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APPENDIX CHAPTER IV

A recommendation to detect and report predictors for management decision-making: an example with vole outbreaks in Mediterranean farmlands

Appendix A | Environmental data

Cumulative rainfall — We used cumulative rainfall as a proxy of water availability, which, in water limited areas such as Mediterranean habitats, is a prime determinant of vegetation growth and quality (Yahdjian and Sala 2006). For each month, we calculated the cumulative rainfall using data from all weather stations within Tierra de Campos, using their average as proxy. In particular, we calculated the monthly cumulative rainfall using daily rainfall data from 88 official weather stations distributed throughout our study area. Daily rainfall below 0.1mm was not registered in the weather stations. To calculate monthly values, we summed the daily rainfall for each combination weather station and month, obtaining the monthly cumulative rainfall of each weather station. For this and the remaining variables, we discarded the monthly values of those weather stations lacking data in at least one day of the month. Consequently, the number of weather stations used to calculate each monthly value varied between 17 and 48 according to the availability of information. Finally, we averaged the values of all weather stations to calculate the average monthly cumulative rainfall of our study area.

Temperature — Temperature also affects vegetative development (Ritchie et al. 1998). We used two indices based on temperature: mean temperature and GDD. We calculated the monthly mean temperature using daily mean temperature and the average across the available weather stations, as we did with rainfall.

The *GDD* is a good proxy of the initial growth stages of crops, and it has been used to estimate the optimal time for first alfalfa harvest (Sanderson et al. 1994). We calculated the daily GDD following method 1 of McMaster and Wilhelm (1997). The monthly GDD was the cumulative sum of the GDD within a month. Finally, we used as our proxy the average monthly GDD values calculated using data from all weather stations. Unlike previous studies that used a unique start day to calculate the cumulative GDD (Sharratt et al. 1989), we calculated the cumulative monthly GDD for each potential predictive time window.

In particular, we calculated monthly GDD using the daily minimum and maximum air temperature from the same weather stations as for the cumulative precipitation. Specifically, we calculated the daily GDD as:

$$GDD_{daily} = \left[\frac{(T_{max} + T_{min})}{2}\right] - T_{base} \tag{S1}$$

where if $[(T_{max} + T_{min})/2] < T_{base}$, then $[(T_{max} + T_{min})/2] = T_{base}$. Where T_{max} was the daily maximum temperature, T_{min} was the daily minimum temperature, and T_{base} was the base temperature for alfalfa growth (9°C). To calculate the monthly value for our study area, we first calculated the cumulative GDD for each month and weather station (n=88) –i.e., we summed the daily GDD values from the first day of the month to the last one. We then averaged the values of all weather stations with available information (between 17 and 48 weather stations) to calculate the monthly GDD of the study area.

NAO index —Large-scale climate indices such as the NAO index simultaneously capture variation in many weather variables (Stenseth and Mysterud 2005). We downloaded daily NAO index values from the Climate Predictor Centre of the National Weather Service (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml) and calculated monthly mean values. The Climate Predictor Center of the National Weather Service provided daily information about the NAO index, so we calculated the monthly mean values as our explanatory variable. We found no data on 26th of October 2006 and 26th of January 2007, so we excluded those days.

Vegetation growth index—NDVI is a satellite-derived index that indirectly reflects primary production. Because no single source had data for the whole study period, we used two complementary sources to calculate monthly NDVI values (NOAA data for 1980-2013 and MODIS data for 2014-2016). To model the NDVI data from NOAA through the data from MODIS, we performed a linear model using the function "lm" of the package "stats" of R (Team 2013) to predict the NOAA data using the MODIS data as predictor using the years with data for both sources of information (February 2000 – December 2013) (adjusted R2 = 0.86; F1, 165=1014). Finally, we predicted the NOAA values from January 2014 to July 2016 using the previous model, and the data for that period provided by MODIS.

Agronomic index —The Turc index reflects agricultural potential for dry and irrigated crops (Méndez et al., 2003) particularly relevant in Mediterranean environments (Milla et al. 2010). Higher values indicate more favourable conditions for vegetation growth. We calculated the variant for irrigated crops, using information about rainfall and temperature, maximum insolation, extra-terrestrial radiation, solar radiation at soil level, duration of the daylight period and relative humidity. We calculated the monthly cumulative rainfall, temperature, sun hours and relative humidity using data from weather stations within our study area. We obtained the maximum number of sun hours for our study area from a website of the "Universidad Politécnica de Madrid" (http://ocw.upm.es/ingenieriaagroforestal/climatologia-aplicada-a-la-ingenieria-y-medioambiente/contenidos/tema-3/TABLA-NUMERO-DE-HORAS-DE-SOL-MAXIMAS.pdf). In particular, we used the information about the latitudes 41 and 42. We obtained the extra-terrestrial solar radiation from the website http://www.soda-pro.com/es/web-services/radiation/extraterrestrial-irradiance-and-toa.

Appendix B | Warning signal of the later period

To identify warning signals in the second period, we repeated the search procedure performed for the earlier period (see main text). To ensure that the signals detected in the second period complemented the early warning signal, we added the explanatory variables included in the early warning signal to the baseline model (van de Pol et al. 2016). For some of our variables, the GLMs considering the additive effect of the early warning signal and the predictor of the later period classified the years with and without vole outbreaks perfectly. In those cases, we calculated the estimates by applying Firth's likelihood correction (Firth 1993) using the function logistf of the R package *logistf* (Heinze et al. 2013).

Appendix C | Model performance

1 | *Strength of association*

We measured the strength of the relationship between our early warning signal and vole outbreaks as the percentage of variance that our early warning signal collectively explained. In particular, we calculated the pseudo R-squared of Nagelkerke, which is a logarithmic scoring rule for generalised linear models (Steyerberg et al. 2010), using the R function "NagelkerkeR2" of the R package "*fmsb*" (Nakazawa 2014).

2 | *Calibration*

We also explored whether our early warning signal explained vole outbreaks along with the whole range of potential values by using the GiViTI calibration test and belt (Finazzi et al. 2011, Nattino et al. 2014, 2016). The GiViTI calibration test consists of a polynomial logistic regression that relates the observed values to the logit transformation of the estimated probabilities along with the whole range of values. The GiViTI calibration belt illustrates the confidence interval of the test in order to show under which range of values the predictor is good, informing on the credibility of the early warning signal to predict vole outbreaks as a whole and around each range of potential values. In particular, we used the function givitiCalibrationBelt from the R package *givitiR* (Nattino et al. 2017).

3 | *Model discrimination*

We assessed the model discrimination by measuring the area under the ROC curve through the function roc of the R package *pROC* (Robin et al. 2011).

Supplementary Figures

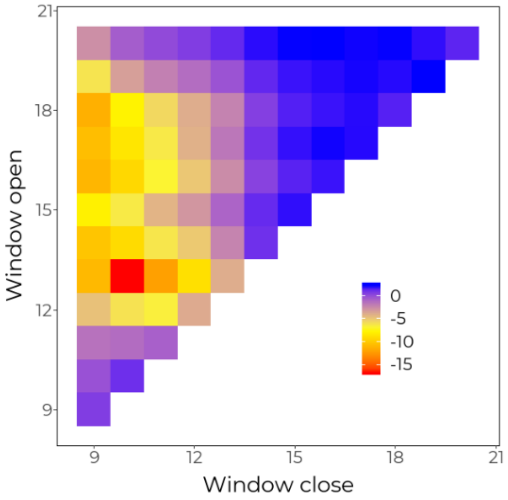

Figure S1 | AIC of models using the cumulative rainfall of each time window as the explanatory variable. The open window and the closed window (y and x axes) indicate the time window as the number of months prior to July. For example, the lowest AIC indicated with a red square, approx. -15, belonged to the model with the accumulated precipitation between 13 and 10 months before July (June-October).

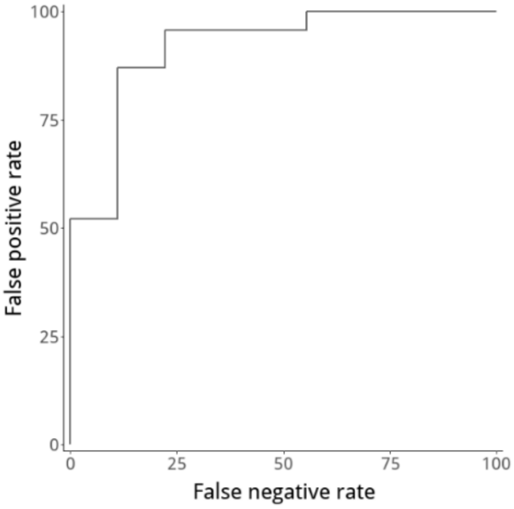

Figure S2 | The area under the ROC curve for the model based on the early warning signal.

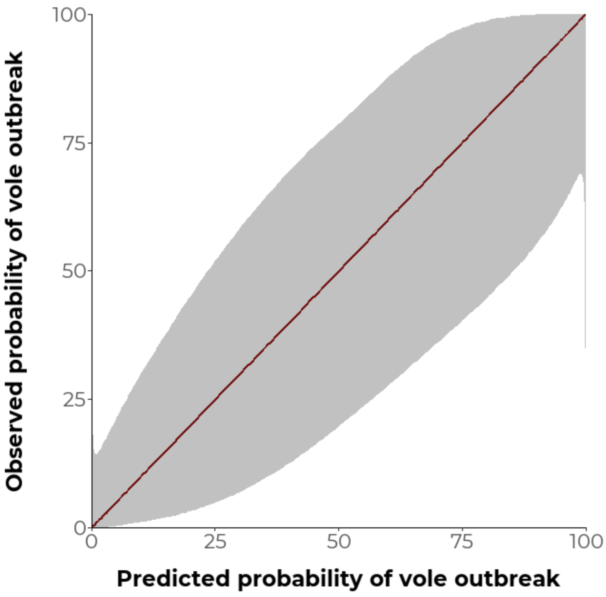

Figure S3 | Calibration test and belt. The p-value indicates the value of the calibration test, while the plot represents under which risk of vole outbreak the predicted and observed values match. The shaded area that covers the diagonal red line indicates that our predictor is good across the whole range of values.

Supplementary Tables

Variable	Window Open	Window Close	P_{sim}	Parameter	Estimate	Std. Error	Z_{score}	P_{value}	$_{pseudo}R^2$
Cumulative r	13	10	<0.001	Intercept	-8.844	3.144	-2.813	0.005	0.616
				Signal 1	0.008	0.003	2.691	0.007	
Turc index	13	13	0.118	Intercept	27.543	11.77	2.34	0.019	0.337
				Signal 1	-4.072	1.694	-2.403	0.016	
Mean temper	13	13	0.079	Intercept	17.527	7.397	2.369	0.018	0.372
				Signal 1	-0.999	0.406	-2.463	0.014	
Mean NAO	10	9	0.448	Intercept	-1.351	0.526	-2.568	0.010	0.223
				Signal 1	-1.393	0.654	-2.129	0.033	
GDD	13	13	0.100	Intercept	12.93	5.662	2.284	0.022	0.362
				Signal 1	-0.06	0.007	-2.414	0.016	
NDVI	11	11	0.179	Intercept	-23.81	10.622	-2.242	0.025	0.256
				Signal 1	62.44	28.583	2.184	0.029	

Table S1 | Results of the logistic model for the time window with the best predictor of each variable in the earlier period when considering the occurrence of a vole outbreak year in 2011. The columns “window close” and “window open” indicate the range of the time window in months from July used as predictor of the vole outbreaks. P_{sim} is the probability of the signal of that time window to be a random signal.

Variable	Window Open	Window Close	P_{sim}	Signal	Estimate	Std. Error	Z_{score}	Chisq	P_{value}	$_{pseudo}R^2$
Cumulative rainfall	16	9	<0.001	Intercept	-22	10.065	-	24.933	<0.001	1
				EWS	0.006	0.003	-	18.76	<0.001	
Turc index	13	12	0.042	Intercept	59.594	24.127	2.470	-	0.014	0.475
				EWS	-4.330	1.720	-2.518	-	0.012	
Mean temperature	13	12	0.030	Intercept	45.139	19.299	2.339	-	0.019	0.555
				EWS	-2.406	1.006	-2.392	-	0.017	
Mean NAO index	11	11	0.930	Intercept	-1.782	0.541	-3.291	-	0.001	0.102
				EWS	0.902	0.699	1.291	-	0.197	
GDD	13	12	0.032	Intercept	31.745	13.830	2.295	-	0.022	0.528
				EWS	-0.018	0.008	-2.384	-	0.017	
NDVI	12	9	0.022	Intercept	-54.002	22.110	-2.442	-	0.015	0.545
				EWS	142.370	59.232	2.404	-	0.016	

Table S2 | Results of the logistic model for the time window with the best predictor of each variable in the earlier period when excluding the years 1988, 1993, 1997, 2007, i.e. the former years of the consecutive years with vole outbreaks. The columns “window close” and “window open” indicate the range of the time window in months from July used as predictor of the vole outbreaks. Psim is the probability of the signal of that time window to be a random signal.

Variable	Window Open	Window Close	Signal	Estimate	Std. Error	Z_{score}	Chisq	P_{value}	${}_{pseudo}R^2$
Cumulative rainfall	16	16	Intercept	-2,619	0,811	-3,228	-	0,001	0,154
			EWS	0,003	0,002	1,695	-	0,09	
Turc index	17	17	Intercept	-1,386	0,5	-2,773	-	0,006	0,14
			EWS	-129,821	13276,53	-0,01	-	0,992	
Mean temperature	17	17	Intercept	1,07	1,91	0,56	-	0,576	0,122
			EWS	-0,564	0,405	-1,394	-	0,163	
Mean NAO index	15	12	Intercept	-2,333	0,809	-2,884	-	0,004	0,408
			EWS	3,39	1,571	2,158	-	0,031	
GDD	17	17	Intercept	-1,469	0,506	-2,902	-	0,004	0,121
			EWS	-0,01	0,007	-1,387	-	0,165	
NDVI	15	15	Intercept	-8,809	5,903	-1,492	-	0,136	0,099
			EWS	12,226	9,829	1,244	-	0,214	

Table S3 | Results of the binomial GLM for the time window with the best predictor of each variable in the earlier period when excluding the years 1989, 1994, 1998, 2008, i.e. the latter years of the consecutive years with vole outbreaks. The columns "window close" and "window open" indicate the range of the time window in months from July used as predictor of the vole outbreaks.

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GENERAL DISCUSSION

Discussion

Vole population fluctuations are one of the most studied phenomena in ecology because of its importance in ecosystems and human welfare (Mougeot et al. 2019, Rodríguez-Pastor et al. 2019, Jacob et al. 2020). This dissertation covers most of the important aspects for its understanding and management, starting with the essential tasks of data collection (**Chapter I**), following with the development of statistical models for their analyses (**Chapter II**), the study and discussion of general patterns in demographic parameters (**Chapter III**), the identification of early warning signals against vole outbreaks for use in decision making (**Chapter IV**), and ending with the proposal of frameworks to promote the correct use of predictive models in applied ecology (**Chapter IV**). This final section represents a synthetic effort to integrate its main challenges, findings and contributions into a broader theoretical and applied ecological context.

Data collection

This dissertation has modestly addressed one of the biggest problems in science: the loss of irreplaceable historical data (Vines et al. 2014, Baker 2017, Tessarolo et al. 2017). In **Chapter I**, we compiled capture-recapture data from 17 sampling areas located in four geographic areas and belonging to five populations of four vole species. We then standardised their metadata. Although the information from these datasets used in **Chapter III** covers about 67 years of capture-recapture and already has an enormous value, it is only about 50% of what has actually been collected during the PhD (some of them also reflected in the metadata; **Chapter I**). Beyond the use that we gave to the data here, and its higher potential use, I would like to emphasize its immense value. These datasets are in part the result of what we now consider the beginning of the field of Ecology (Collet 1912, Crowcroft 1991, Pond et al. 2015), and they cement much of our knowledge on population dynamics, especially of small mammals (e.g. Keller and Krebs 1970, Boonstra 1989, Lambin 1994). Therefore, its future preservation in appropriate repositories will be an important heritage (Michener et al. 2015, Baker 2017).

One of the main objectives of the dissertation was to offer all these data so that they are not lost and can be the basis of future studies (e.g., reanalysis, global analysis). Although due to lack of time we have not been able to publish them before the defence of the present dissertation, this is one of the most important future tasks to be carried out. Encouraging the use of doctoral theses as a tool for carrying out this type of task can be a great opportunity with benefits for the doctoral student and science. On the one hand, doctoral students benefit from the possibility of answering some questions from new perspectives (Zimmerman 2008). And on the other hand, science benefits from the preservation of the original data and the discoveries made (e.g. **Chapter III**).

Estimation of demographic parameters

Once we compiled and curated the capture-recapture data (**Chapter I**), we estimated abundance and vital rates with the aim of finding general demographic patterns across populations and species with a mechanistic perspective on population fluctuations (**Chapter III**). But due to the characteristics of vole populations, obtaining this information was a big challenge. The low number of captures in some periods, as well as the complexity of biological models to adequately describe the mechanisms underlying population fluctuations, make the number of parameters to be estimated too large for the available data (i.e. number of captures of a given reproductive state per sampling session; e.g. Getz et al. 2006). Therefore, we could not estimate the parameters needed to answer our questions with the capture-mark-recapture methods available in the literature (e.g. White and Burnham 1999, Kéry and Schaub 2011). This issue has been generally overcome by pooling data at the cost of a reduction in the temporal or spatial resolution (e.g. Desy and Batzli 1989). However, it did not allow us to analyse the key processes that occur at fine resolutions such as the fast maturation of individuals (Yoccoz et al. 1998, Stenseth et al. 1999). We therefore developed a non-parametric extension of capture-mark-recapture models based on widely accepted and used concepts about regularization to estimate demographic parameters at desired temporal resolutions (**Chapter II**). We regularized the time-varying parameters using a random hyper prior assuming a normal distribution of second-order differences. We defined the priors, and then constrained the degrees of smoothness, performing exploratory simulations and selecting those values that provided fluctuations most similar to reality (expert knowledge).

In **Chapter II**, we demonstrated its correct functioning by comparing the estimates of a classical capture-recapture model and our approach when estimating the parameters of simulated populations, whose real values we knew. We first simulated a scenario with relatively high abundant populations to assess if our extension estimates parameter values similar to those obtained with traditional capture-recapture methods, adapting the degree of smoothing to data availability. The similar, or even better, quality of the estimates provided by the smoothed capture-mark-recapture models strongly supported that our method can be used in situations where traditional capture-recapture model is used without fear of a negative effect of the smoothing; an important aspect to alleviate concerns about when to use one approximation or another.

Secondly, we simulated a scenario with low abundant populations to assess that our approach actually overcomes limitations of traditional capture-recapture models. Our results showed a clear improvement in the number of estimated parameters, as well as in their precision and accuracy, confirming the usefulness of our method in the study of population dynamics. Finally, we demonstrated its contribution in a real example by comparing the demographic estimates of traditional and smoothed capture-recapture models in a real vole population. Our results reveals that while the traditional capture-recapture model was unable to estimate most parameters at fine temporal resolution, our model not only estimated them but also allowed identifying the temporal fluctuations necessary to disentangle the drivers underlying population dynamics that otherwise were difficult or impossible to answer (e.g. **Chapter III**).

The contribution of capture-recapture models using regularizations like the one proposed in **Chapter II** goes beyond the study of population dynamics of voles and small mammals and can be a point of inflection in the study of multiple population dynamics for which we have a limited amount of information, an issue that affects a wide range of species such as elusive species (Mace et al. 1994, Goldberg et al. 2015), species living in hard-to-sample habitats (Da Silva et al. 2000, Calambokidis and Barlow 2004), species with temporal low density phases (Haukisalmi et al. 1988, Boonstra et al. 1998) or species with constant small population abundances such as threatened ones (Hoyle et al. 2001, Danancher et al. 2004, Mollet et al. 2015). Thus, statistical approaches like ours can be the starting point of new methodologies that will play a key role to better understand theoretical, population and conservation ecology.

General demographic patterns

Population fluctuations, and in particular in rodents, is one of the most studied ecological phenomena due to their influence on ecosystem as well as evolutionary and community structure (Lidicker 1978, Ozgul et al. 2004, Krebs 2013). A plethora of studies have discussed during the last decades on the existence of general demographic patterns in population fluctuations of voles and on the mechanisms originating them (Hoffman 1958, Krebs and Myers 1974, Lidicker 1978, Sandell et al. 1991, Krebs 2013). However, despite the body of knowledge acquired in the last 100 years there is no analytical evidence of the general patterns nor their importance in observed population fluctuations across populations and species.

In **Chapter III**, we showed that a large proportion of population growth rate anomalies, i.e., pgra; deviations of the expected seasonal population growth rate, were the result of the same demographic mechanisms in cyclic and non-cyclic population fluctuations of four *Microtus* species located in Europe and North America. Although our study provides interesting information on pgra, elements of inter-annual population fluctuation, it is a small piece of a huge and complex puzzle. Therefore, I will not speculate on the importance of the general patterns detected in the different inter-annual population fluctuations observed in nature. However, I do consider that **Chapter III** contributes qualitatively to this lively discussion on population fluctuations and can "re-open" a debate on the relative importance of local and general factors, and on the different mechanisms driving cyclic and non-cyclic population fluctuations (e.g. Turchin et al. 1991, Royama 1992, Kendall et al. 1999, Murray 2003, Sandell et al. 1991, Turchin 2003).

Abundance and vital rates explained population growth rate anomalies differently along the year in non-trivial ways, supporting the existence of multiple and time-dependent processes (Lidicker 1978, Ozgul et al. 2004, Goswami et al. 2011, Krebs 2013). Anomalous population declines in winter and spring were likely more associated with lower than usual survival of overwintered individuals, whereas anomalous declines in summer and autumn were more likely associated with social interactions. The absence of expected seasonal declines in winter as well as the anomalously large population increases in early spring also were more associated with survival of overwintered individuals than with reproductive activity (winter: Aars and Ims 2002, Johnsen et al. 2017; spring: Krebs and Boonstra 1978, Taitt and Krebs 1983, Boonstra and Boag 1992). These results may be surprising because of the expected high importance of winter breeding (Krebs and Myers 1974, Ergon et al. 2001, Lambin 2001, Ergon et al. 2011) as well as of reproductive processes in a period when breeding is the key (i.e., onset of the breeding season; Krebs and Myers 1974, Tkadlec and Zejda 1995, Ergon et al. 2001, Ergon et al. 2011). In contrast, anomalously large population increases in late spring and autumn were associated with reproductive and social processes. In general, reproductive, survival and social processes are behind the common demographic patterns observed. However, survival and social processes are probably involved in a larger number.

Based on the timing of the observed signals and of the most probable effect of some accepted causal factors in driving population dynamics (e.g., Batzli 1986, Korpimäki et al. 2004, Lambin and Yoccoz 1998), predictions on direct or relative direct effects of food and social interactions may match better with the observed common demographic patterns. However, these conclusions should be taken with caution, since we did not perform any specific test but evaluated the predictions of the most discussed hypotheses.

Overall, **Chapter III** demonstrated the existence of common demographic patterns across species and populations; evidenced their high relevance in observed inter-annual population fluctuations; identified some of the demographic mechanisms; and provided some clues about the causal factors behind those changes. Thus, **Chapter III** not only sheds light on one of the oldest topics in ecology, but also provides fundamental material for the discussion and planning of future studies.

Detection of early warning signals

One of the important tasks of science is to apply scientific knowledge to solve or mitigate everyday problems. Rodent pests are a major problem for humans because of the diseases they cause (Luque-Larena et al. 2015) or because of economic and supply losses (Stenseth et al. 2003). In **Chapter IV**, we show how basic ecological knowledge of the species and new scientific advances make it possible to detect predictive models of biological outbreaks to be useful in management decision-making.

In **Chapter IV**, we looked for early warning signals to predict vole outbreaks of *Microtus arvalis* in a Mediterranean region located in Spain. We focused on this objective, on the one hand, because of the significant socioeconomic and health damages caused by vole outbreaks in the region, and on the other hand, because vole outbreaks have been partially managed with poison, a controversial control that causes significant environmental impacts (Sánchez-Barbudo et al. 2012), and social conflicts in the region (pers. comm.). Thus, the identification of early warning signals of vole outbreaks in this region may allow applying alternative preventive managements in advance to reduce vole damages, alleviating both environmental and social issues.

In **Chapter IV**, we detected an alert one year in advance based on cumulative rainfall in July-October that support the link in Mediterranean environments between vole outbreaks and summer – early autumn rainfall (Leirs et al. 1996, Lima et al. 2002, Kenney et al., 2003, Zhang et al. 2003), and point towards that pulses of primary productivity in those periods may extend the breeding season as well as increase vole survival and recruitment preparing the base for the vole outbreak in the following year (Mutze et al. 1990, Boonstra and Krebs 2012). Its timing allows applying preventive management against vole damages from the point of view of the farmer (e.g., growing less vulnerable plants) and the administration (e.g., plowing the edges in winter or considering the possibility of subsidizing the plowing of old alfalfa fields). Thus, **Chapter IV** provides an early warning signal that enhances our knowledge about vole outbreaks in Mediterranean regions and that may be of immediate use in advising management decision-making on one important human-wildlife conflict.

Translating statistical models to the broad public

An important challenge of theoretical ecology, and specifically of modellers, is to offer predictive models that have a proven benefit for use in applied ecology. However, the contribution of predictive models is often evaluated exclusively from a statistical point of view (e.g., R^2, AUC, calibration tests; Leirs et al. 1996, Khalil et al. 2014, Haredasht et al. 2015), forgetting that in applied science their usefulness also depends on the costs and benefits associated with actions taken based on their predictions (Davis et al. 2004, Vickers and Elkin 2006, Vickers et al. 2016). Another challenge is that the predictive models are used correctly in decision-making. However, to our knowledge, it is not common to point out that the benefit of using a predictive model for decision-making depends on the threshold chosen by the user to start applying measures to prevent the predicted event, and that this threshold cannot be random, but depends on the costs and effectiveness of the measures to be applied based on that prediction (i.e., specific to the user; Davis et al. 2004; Vickers and Elkin 2006).

In **Chapter IV**, we proposed a conceptual and methodological framework that addresses these issues. In particular, we proposed a methodological approach widely used in Medicine to evaluate the profitability of new warning signals without the need for prior information on the costs and effectiveness of the treatments to be applied based on its predictions (Vickers and Elkin 2006; Vickers et al. 2008, 2016). Subsequently, we proposed an approach to inform each potential user on how to use the model prediction to obtain the greatest benefits when using it in decision making. We exemplify it by showing how the new one-year alert against vole pests is better than existing alternatives from a management perspective (i.e., comparing net benefits; Vickers and Elkin 2006; Vickers et al. 2016). We then provided a simple and intuitive table for each user to get a rough idea of whether to apply preventive management based on the accumulated rainfall in July-October and the effectiveness and costs of their particular preventive treatment.

Chapter IV brings to light a topic little discussed in the ecological modelling field, such as the user-specific profitability of using model predictions in decision-making (but see Davis et al. 2004). Furthermore, we proposed a framework to inform how to use model predictions, not only in vole outbreaks, but also in any event that is of interest to prevent damage because predictive events; facilitating a better use of predictive models in any applied science.

Where from here?

Here I briefly and modestly state some of the questions about the general demographic patterns in vole population fluctuations that may be raised or encouraged by this dissertation.

1) *How general are the detected demographic patterns?*

This thesis provides novel analytical evidences for the existence of common demographic patterns in vole population fluctuations. However, although the number of species and populations analyzed here can be considered large, due to the enormous effort to obtain them, they are relatively few to answer this question. To achieve this, it is necessary to collect and analyze a larger number of species and populations distributed throughout the world. It would even be interesting to evaluate the existence of these patterns beyond voles. Certainly, this is hard work that will require new projects and funding in the medium and long term to collect and analyze the information. Nonetheless, the detection of general patterns for a set of species and populations distributed in North America and Europe may be a good incentive to solve a question that has been hanging over ecology for more than 100 years.

2) *Which factors are behind the common changes in vital rates?*

This thesis provides specific variations in abundance and vital rates useful for testing experiments to answer (i) what are the factors behind these changes (e.g. intrinsic or extrinsic factors), (ii) whether these factors have a direct or delayed influence; or (iii) whether these factors are common in different geographical areas and ecosystems (e.g. Scandinavian and Mediterranean ecosystems). Certainly these questions have been part of the scientific discussion during the last century, but for the first time there is some analytical that can help to test the different hypotheses.

3) *How important are these common mechanisms in driving inter-annual population fluctuations?*

The large proportion of population growth rate anomalies that are explained by common demographic mechanisms (i.e., a large R^2; **Chapter III**) supports that the inter-annual population fluctuations observed in our five study populations are largely caused by general processes.

However, pgra is only one side of a many-sided polyhedron, and different perspectives would be necessary to understand the full picture. Moreover, as discussed in Chapter III, our data sets are relatively sparse and short to answer this question robustly. Therefore, as well as to answer about the generality of these patterns, a larger amount of data is needed. Thus, future studies with new data and with this and other analytical approaches may provide new information on the relevance of local and general factors in the different inter-annual population fluctuations.

Summary

This dissertation has focused on the population dynamics of voles from the point of view of basic, theoretical and applied ecology. The data, statistical approaches, and results provided open the door to deepen the knowledge of the generalization of vole population dynamics. Moreover, the breadth of the contributions, and their multidisciplinary nature, can make this dissertation the cornerstone of many and diverse works that will help not only to understand and manage the population dynamics of voles, but also that of other species.

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GENERAL CONCLUSIONS

1. This dissertation compiled capture-recapture data at weekly, biweekly, and monthly resolution for five populations of four *Microtus* species in 17 sampling areas located in four geographical areas from North America and Europe; being the most comprehensive dataset on small mammal capture-recapture data to date.

2. The regularization implemented in the capture-mark-recapture model adapts adequately the smoothing to the available data, alleviating any concerns about unnecessary biased estimates. In fact, in conditions when traditional models are able to estimate demographic parameters, the smoothed model can provide even better estimates.

3. The smoothed capture-recapture model opens the door to estimating demographic parameters when traditional capture-mark-recapture models are unable to do so due to relative data sparsity, offering new opportunities to understand demographic details that were not possible to date.

4. There are general demographic patterns in the vole populations studied. In particular, population growth rate anomalies, i.e., deviations from expected seasonal population growth rates and proxies for the elements we detect as inter-annual population fluctuations, were largely the result of common demographic mechanisms.

5. The mechanisms of these common demographic patterns were type specific. Anomalous low population growth rates were associated with survival and social processes, whereas anomalous high population growth rates were associated with survival, social, and reproductive processes.

6. The mechanisms of these common demographic patterns were also season-specific. Reproductive processes were most influential in spring and summer, while social and survival processes were important throughout the year, but with variable relevance.

7. Of the set of hypotheses considered, our results were most supportive of the predictions of those related to food and social interactions.

8. An alert one year in advance based on cumulative rainfall in summer-fall largely predicts vole outbreaks of *Microtus agrestis* in a Mediterranean environment; allowing on the one hand applying some preventive managements and on the other hand supporting the role of food in rodent outbreaks in arid and semi-arid environments.

9. The two nested methodological approach allowed to ensure the most optimal and timing predictive model, to evaluate their profitability for any potential user, as well as to provide guides for its use; favouring the use of predictive models in real management decision-making.

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Esta bonita etapa, y sobre todo su producto, no habría sido tampoco posible sin mis directores, Eloy y Xavier. Eloy, gracias por haber confiado en mí desde el primer momento, y por seguir haciéndolo con el paso de los años. Me has dicho muchas veces halagos y no siempre he reaccionado quizás como debiera por la vergüenza, pero te agradezco todos y cada uno de ellos. Pero ahora me toca a mí. Eres uno de los investigadores más brillantes que conozco, en serio, no para de impresionarme tu capacidad para saber y aprender de todo. Ha sido un privilegio saber que cualquier duda demográfica, biogeográfica, informática, estadística, y laboral iba a ser contestada. ¡Eres un fenómeno! Y no olvidemos que tienes más mano izquierda que un pelotari zurdo, algo que sin duda me ha ayudado a lidiar con muchos problemas. Pero sobre todo quisiera agradecer tu predisposición para que volara con proyectos personales, aunque supieras que no iban a llegar a puerto. Dicho de otra manera, gracias por dejarme buscar mi hueco. Xavier, sin duda esta tesis no hubiera sido la misma sin ti. ¡Eres el **** amo de los topillos! Gracias por tu eterna implicación pese a todas las dificultades y mis distracciones con proyectos paralelos; por recibirme

en Aberdeen con los brazos abiertos; por darme la oportunidad de conocer a algunos de los mejores (y mayores) ecólogos del mundo; por tener siempre tiempo para una reunión o videollamada; por revisar infinitamente los trabajos. Sin tu ayuda hubiera acabado un poco más loco si cabe, y quien sabe si hubiera terminado la tesis. Pero sobre todo me quedo con que eres un ejemplo de muchos valores de la ciencia. Serás duro, pero también un mentor excepcional.

Joaquín, ese compañero de estudios, batallitas, y ciencia. Permíteme que no ponga aquí ninguna de las hazañas/historietas vividas durante los casi 15 años que llevamos "de relación", ya que todavía están a tiempo de leer estas líneas y no permitirme defender. Pero sí que quiero resaltar que tu motivación, que sin duda roza el frikismo científico, ha sido un generador de pajas mentales que me ha hecho gozar al máximo la ciencia. ¡Qué de horas de teléfono!, ¡qué de mañanas, tardes, y noches soñando y riendo con las bioregiones, los roles, los corpúsculos, los paisajes de soluciones! ....No hay nada mejor que el subidote de una nueva idea con un colega de risas, ¡¡¡un brindis por las pajas mentales!!! Pero más allá de las colaboraciones, permíteme que copie a cierto huraño de la serranía madrileña, eres mi acicate. Sutil palabra para describir a un co-autor o colega tocapelotas que te discute todo hasta la saciedad. Creo que el resto de cosas ya te las diré en persona con un buen entrecot y una paletilla. Mientras tanto voy preparándome para la preguntita. ¡Vamos RAFA!

Manuela, mi codirectora de esa segunda y frustrada tesis (que en nada retomaré). ¡Qué suerte haber podido aprender de ti durante los primeros años!, sin duda los más bonitos en cuanto a ciencia se refiere. El verte marchar de la EBD fue una de las mayores tristezas. ¡Lo que hubiera pagado por haber seguido teniéndote allí! Aunque no tanto como la uni de Reading..... Quiero agradecerte todo lo que me enseñaste y todo el apoyo para sacar cualquier proyecto personal. Por ahora, los intentos de volver a currar juntos (y cerca) no han salido bien, pero quién sabe en un futuro. ¡Quién no quiere estar cerca de una pedasho investigadora como tú! Así que nada, estaré cerquita, aunque sea telemáticamente, para ver si se me pega algo.

Antes de seguir con toda la gente que me ha acompañado durante la tesis, quería hacer una mención especial a Junoy, o como se le conoce en mi casa, "el del pulpo". Hace 10 años di contigo los primeros pasos en investigación, y debieron de ser buenos y divertidos porque me lancé de lleno. Gracias por darme la oportunidad de meter la cabeza en la ciencia y encima por hacerlo de una manera divertida. Esta tesis también es por tu culpa.

Los TRIANEROS que nos acogieron en Sevilla cuando aterrizamos (aunque solo fuera porque no tenían cine). Miguel, Gemma, Elena, Manolo, Xuso, Laurita, Alvarito, Ester....gracias por aceptarnos en vuestro núcleo, así como por enseñarnos Sevilla desde dentro. Quién diría que a mi primera feria quería ir con un delantal por delante y por detrás, y que tras un lustro iría con traje, pin y os colaría en una caseta. Se me acumulan las anécdotas en los dedos, los miércoles de cerveza, el coche de Gemma para cambiar una tarjeta de fotos de boda en modo 007, ser testigo de una boda, el valor seguro de Elena, las "aspiraciones" de Manolo, Montpellier y su braga, el jirafazo, el diluvio en Les Cévennes, la paella de resaca, las tardes de elecciones y pizza, las cañas de Semana Santa, los rebujitos de la feria, Conil, los ceviches caseros, las copas de tardeo made in Triana, el parapente jamás realizado, obviaré el cumpleaños maldito.... pero sin duda lo que más siento es que cuento con vosotros para lo que sea. ¿Es eso lo que es una familia?

Continuar por Alamillo/Weekend. Eneko, Marina, Irene, Victor, Jorge, Sarai, Ale, Rosa, Grego, Joan, Laura..., y como han sido muuuuchos años llegaron los "infiniti" Javi, Lina, Juan, Nicola, y claro ya era feo no esperar a Pedro, Elena, Enrico, Berni, Manu, Wouter.... Joder, con vosotros me lo he pasado también muy, pero que muy bien: los viernes de Alamillo, las noches en el urbano, los duelos de baile en el Fun Club, la fiesta de las mallas (digo de mi fin de contrato), la fiesta del tutu, Grazalema, su pinpong y su futbolín, los viajes por Extremadura, las cortijadas..... Pasarse tantos años con una tesis tiene una carga emocional y psicológica grande, peeeeero también permite conocer a mucha más gente maravillosa.

Una mención más que especial al jipunki de Sevilla. Quién me hubiera dicho a mí cierta noche en el *Lola por Dios* que aceptar tu propuesta de vivir juntos iba a ser una de las mejores decisiones de mi vida. Por mi cabeza sólo se pasaba que a tu lado iba a tener risas y pedradas a partes iguales.....y acojonaba. ¡Pero qué aciertazo! No se nos da nada mal eso de vivir juntos. Podemos decir que hemos pasado un apocalipsis "light" de risas: nuestras paraolimpiadas caseras, las partidas de cartas infinitas, los sábados de "*Pichilín*", nuestro paso de semana santa....pero lo mejor es que me llevo un colega para toda la vida!

Y tras el apocalipsis "light", cuánto daño nos ha hecho Hollywood, decidimos aventurarnos a vivir en la sierra y ampliar la familia. Fue una decisión difícil elegir el niño y la edad, pero acertamos con uno ya crecidito. ¡Y así llegó Wouter a nuestras vidas! El mejor pajarero de estos lares. Tu motivación, y la de Peter, me han hecho frikear más de lo que hubiera imaginado. Ya cumplía de sobradas maneras el primer criterio para ser pajarero, pero con vuestra ayuda me veo capaz de cumplir el segundo. Pero más allá de las charlas científicas, menuda vida nos estamos pegando. ¡Estos pocos meses a vuestro lado están siendo de lo más reparador para el alma! La verdad que estamos jugando duro en la Sierra-Sevilla, pero es que se nos da muy bien. Empezando por una entrada memorable en la Sierra, y continuando con bbq ibéricas, noches de chimeneíta y whisky, partidas de dardos caseras....que siga la buena vida!

Continuing with flatmates, another special mention for THE AFRICAN FAMILY, one of the greatest experiences of my life has been sharing a small period of time with you. Wilbard, Emma T, Emma G, you welcomed me with open arms and changed my way of thinking about life. Surprisingly, by your side, some of the quietest people I know, the most surreal things have happened to me. I still freak out thinking about the whole soap opera with the fourth musketeer... And how could I not remember the trip to the Highlands and the tick crisis? I just wish we could watch again as soon as possible. A big hug.

María y Fernan, lejos quedan nuestros intentos de ponernos super-mazaos y nuestras compensaciones con los helados (inciso para indicar que *Créeme* es la mejor heladería de Sevilla y me ha dado tantos buenos momentos como calorías). María te gano cuando quieras en un duelo de baile, y Fernan, sorprendentemente, eres el orgullo de *CoreStudio* y, merecidamente, el médico de la EBD hipocondriaca. Aunque estáis en todos los grupos, nunca sobra mención individual.

Y no va a ser menos SAGUNTO, empezando por Marta y Javi que fueron el primer apoyo en Sevilla cuando estaba más solo que un vegano en un asado. Y continuando con Marta, que gracias a su baile de casas cayó en Sagunto, y nosotros con ella. De esta manera tuvimos la suerte de conocer a gente muy dispar y cachonda: Lydie, Jovhanna, Nasta, Jose, Koldo, Chiara, Olivia, Luis...., y ¡¡¡de disfrutar esas pedazo de fiestas, amigos invisibles, cumpleaños y conciertos en Sagunto !!! Aunque todavía no entiendo por qué hay que partir el queso de una determinada manera para luego fundirlo.....(quizás por eso llevo tanto tiempo con la tesis). ¡Y cómo olvidar esos Carnavales y los viajecitos a Marruecos y Tenerife! Porque soy buena persona, pero ahora podría tener unos cuantos camellos en casa, o incluso haber podido dormir bajo una lona en el desierto. Esos momentos de desconexión fueron 100% necesarios para seguir cuerdo y tener la sensación de felicidad al recordar esos años. Por lo que vosotros también habéis sido parte indirecta de esta tesis.

CARNIVOROS, qué suerte de haber caído en un grupo con tan buen rollo y tanto arte. Sofi y su totipotencia, Carlos y su buen rollo, Miguel y sus mil y una historias, Jacinto y sus chistes, Miguelito y su arte, Carlines y su kayak de travesía, Paco y su Jabugo, Néstor y su Inés Rosales.......y todos aquellos que habéis pasado y estáis en el grupo, habéis hecho que fuese con ganas a trabajar. Tampoco me olvido de los “linces acoplados”, Godo, Elena, María, Dani, Enrico, Maritxu..., que hacéis que las quedadas y comidas suban de nivel. Ha sido un lujazo disfrutar con vosotros todo este tiempo.

XIXIROOM, la verdad que a veces me doy asco al pensar en la suerte que he tenido de estar a diario en un despacho tan molón! En primer lugar, gracias a Andrea que estuvo pringando conmigo como una condenada sacando datos de topis durante casi un año, a Bego que es una fuente de buen rollo y alegría constante, a Pablo Lucas (he dudado en darte las gracias por matarme de frío y no invitarme al café de bienvenida) que es una persona de las que siempre hace piña, a Flor que fue esa hermanita pequeña en mi primer año de tesis, a Estrella y su predisposición para cualquier actividad de riesgo, y a todas las personas que en algún momento u otro formaron parte de ese grupo tan cojonudo.

Más reciente, pero no menos importante, el gran despacho del edificio verde. Era difícil pensar que juntar a especímenes tan raros y dispares iba a salir algo tan bueno. Nos juntaron porque todos estábamos en la fase final de nuestras tesis (a alguno se nos ha hecho más largo que a otros), pero creo que lo que nos unió fue el compañerismo. Marina, Eneko, Paula, Lau, Joan, Ana, Erika, mi alumna predilecta Clara……qué buen rollo se respiraba.

Y ya sí que sí, mi último despacho antes de leer (o eso espero). El 5.6. Una mención especial para Montse y Belinda por darme la oportunidad de trabajar con ella pese a las circunstancias que me rodeaban, y por hacerme sentir siempre muy cómodo e integrado. Y como no a ese despachito pre-covid: Ale, Javi, Berni, Rocío, ha sido poco tiempo y para otros fines, pero también os habéis comido algún día gracioso de tesis.

De otros de los que no me puedo olvidar ni en broma es de LOS INFORMÁTICOS. ¡Esta tesis de se ha llevado a cabo 100% gracias a vosotros! Gracias por haberme solucionado los problemas superurgentes y todas las pijotadas necesarias para correr los análisis. Todavía recuerdo la cara que me pusisteis al pedir un servidor con 300GB de RAM, o pedir 80 cores para no tardar 4 años en correr mis análisis. Y lo mejor es que siempre lo habéis hecho con un cachondeo que se agradece y da envidia. Qué buen rollito se palpa en esa zona, sobre todo los viernes a última hora. Os lo habrán dicho mil y una vez, pero no está mal que estas cosas queden reflejadas siempre que se pueda. La EBD es lo que es en gran parte gracias a vosotros. ¡La próxima vez que vaya os prometo que será con unas cervecitas y un picoteo!

Hablando de informáticos y cañas, cómo no hablar del trío calavera Juanele, Carlitos y Quini. Esos partiditos de padel con su cañita güena. Sin duda estáis entre los tíos más personajes de la EBD, y eso es digno. A ver si retomamos esas tardecitas de risas. Y siguiendo con el deporte e intentando cerrar agradecimientos y ciclo, debo volver a los orígenes y el FUTBITO. Echando la vista atrás he vivido desde momentos de gloria, jugar la liguilla y pelearme por entrar en la lista del seleccionador, al decaimiento en el que no dábamos ni para un equipo propio. Pero bueno, todos los grandes imperios caen. Quisiera agradecer en especial al gran Marcello, il Ronaldo, il predatore della zona, el apadrinarme en el futbito y descubrirme otro de los grandes momentos de la EBD, por supuesto que hablo de las cañas. La verdad que el futbol se nos podría dar mejor o peor, pero el postpartido……qué postpartidos echábamos. Pues no han caído historietas y risas con Xim, Nestor, Grego, Duarte, Dani, Ricardo… yo soy personaje, pero es que menuda tropa. Esos miércoles eran el bálsamo perfecto a mitad de semana.

También agradecer su ayuda indispensable a todo el personal de la EBD, administración, LAST… que sin ellos nada funcionaría en la EBD. Con mención especial a los conserjes y personal de limpieza: Elvira, Emilio, Reyes, Santi…, ¡Qué arte tenéis!. Gracias por recibirme con una sonrisa cada día, y por dar vidilla a ese edificio.

Y por último a toda la gente que de una u otra manera también habéis estado ahí, Pinchos, Uni, Lope, Aberdeen….a todos os agradezco vuestras charlas y buenos momentos.