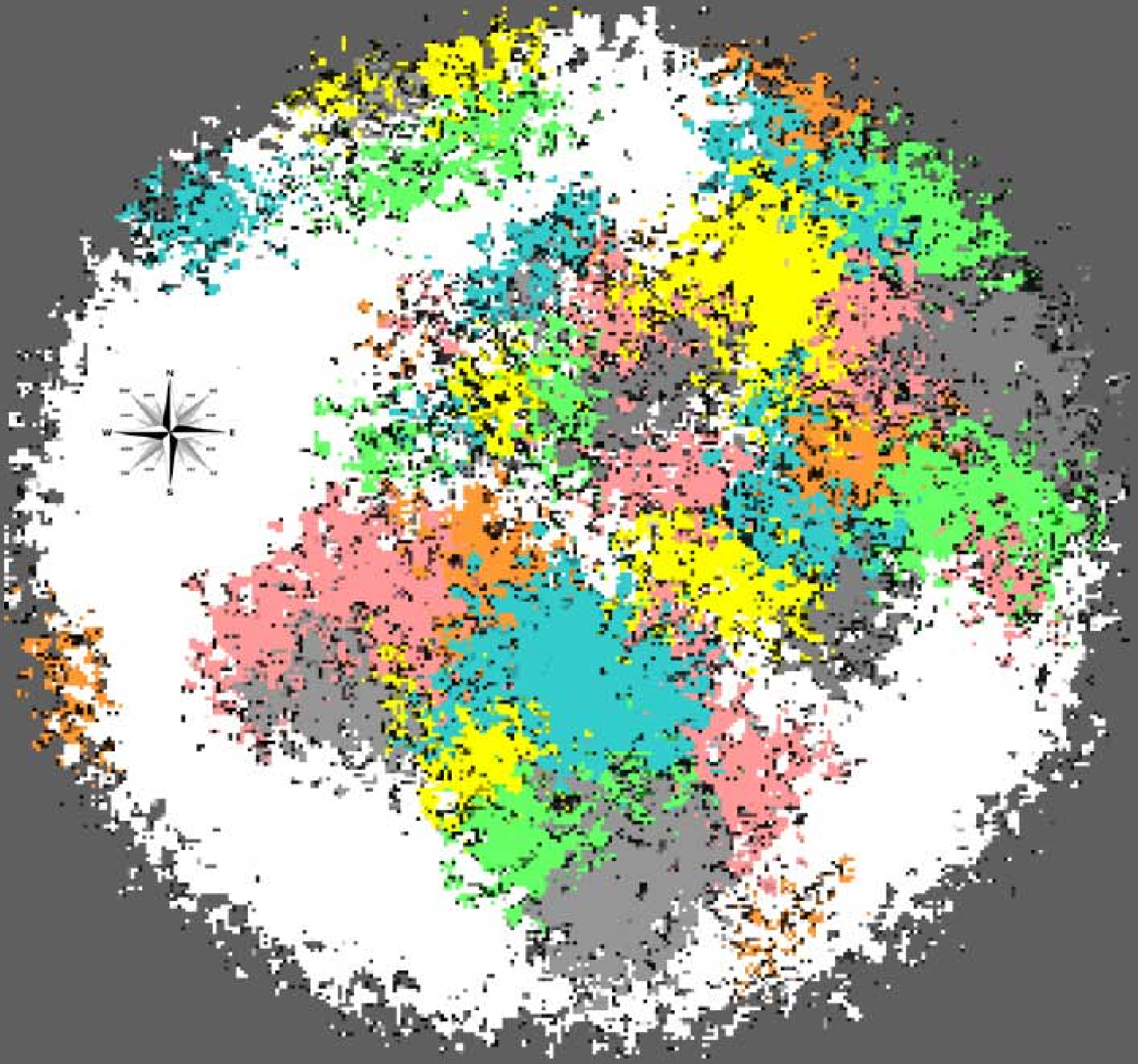

Patrones globales en reproducción y mortalidad del conejo de monte y su impacto en la dinámica de poblaciones

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PATRONES GLOBALES EN REPRODUCCIÓN Y MORTALIDAD DEL CONEJO DE MONTE Y SU IMPACTO EN LA DINÁMICA DE POBLACIONES

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A mi familia.
Pero también,
a todas las personas
que no habría conocido
de no ser por esta tesis

“Uno no sabe lo que se pierde,
hasta que lo encuentra”

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INTRODUCCIÓN GENERAL:

Estudio de la dinámica de poblaciones

Comprender la dinámica poblacional de las especies ha sido siempre uno de los principales objetivos de la Ecología (Turchin 2003, Yoshida 2005). Para ello, es necesario no sólo describir los cambios en la distribución y abundancia de las especies a lo largo del tiempo y del espacio sino también identificar los factores que causan dicha variación (Krebs 1986, Royama 1992, Turchin 2003). Obtener este tipo de información es esencial para la conservación de especies, el control de plagas y la gestión de los recursos naturales, así como para proporcionar datos a estudios en ecología de comunidades o ecosistemas.

El estudio de la dinámica de poblaciones ha estado constituido desde sus orígenes tanto por un componente empírico como por un fuerte componente teórico. Tradicionalmente, la experimentación se llevaba a cabo en el laboratorio (por ejemplo Gause 1932 y Park 1954), sin embargo otros autores (Connell 1961 o Krebs y col. 1995) llevaron este tipo de estudios también al campo. El componente teórico, por su parte, se basa en modelos demográficos cuya finalidad es reproducir la dinámica real de las poblaciones para así poder comprender mejor su funcionamiento y hacer predicciones.

El modelado de las poblaciones ha evolucionado de forma importante desde los primeros modelos matemáticos, como la ecuación la logística (Pearl y Reed 1920), cuya simplicidad permitía soluciones analíticas, hasta los modelos de simulación más recientes, que gracias a los avances en los equipos y software informático, permiten el análisis de sistemas estructuralmente complejos y la inclusión de estocasticidad biológicos y complejidad estructural, la inclusión de (Shanthikumar y Sargent 1983, Humphreys 1990, Williams y col. 2002). En la actualidad existe una gran variedad de modelos que se diferencian, entre otras cosas, en la discretización o no de las unidades temporales, la inclusión o no de variaciones estocásticas, y en el nivel de complejidad del ciclo vital considerado (Uchmański y Grimm 1996).

Un tipo de modelos que ha adquirido mucha importancia en los últimos años son los modelos basados en el individuo (MBIs). Se trata de modelos de simulación que tienen como unidad básica al individuo el cual posee una serie de características (además de la edad) que van cambiando con el tiempo y de la interacción de estas unidades surgen unas propiedades de la población (Grimm 1999). Se trata de modelos que permiten incluir una gran cantidad de detalle y complejidad, y que por lo tanto tienen una mayor dificultad de implementación, requieren un mayor número de parámetros y de tiempo de ejecución

(Fahse y col. 1998). A pesar de lo cual, es una técnica muy utilizada y valiosa para el estudio de la dinámica de poblaciones.

Papel de las variables demográficas y su variabilidad global en el estudio de la dinámica poblacional

El tamaño y viabilidad temporal de las poblaciones depende de sus variables demográficas (nacimientos, muertes, inmigraciones y emigraciones; Krebs 1986, Begon y col. 1996). Estas variables a su vez están determinadas por factores bióticos (e. g. competencia, predación) que suelen actuar de forma dependiente de la densidad y abióticos, como las condiciones meteorológicas o el fotoperiodo, que son independientes de la densidad poblacional (Begon y col. 1996, Williams y col. 2002). Por lo tanto, para poder entender la dinámica de las poblaciones es necesario primero comprender los mecanismos por los cuales dichos factores bióticos y abióticos afectan a los distintos parámetros demográficos (Sutherland y Norris 2002, Oli y Armitage 2004).

Algunas especies dependen enteramente de la disponibilidad de otras para poder sobrevivir y reproducirse y, por lo tanto, su distribución estará restringida a la presencia de este recurso. Estos son los llamados especialistas como por ejemplo el oso panda *(Ailuropoda melanoleuca)* o el lince ibérico *(Lynx pardinus)* (Ferrer y Negro 2004, Shipley y col. 2009). Por otra parte, las especies como el zorro rojo (*Vulpes vulpes)* o el conejo de campo *(Orytolagus cuniculus),* que son más generalistas en sus requerimientos, pueden llegar a tener áreas de distribución muy extensa, siempre que no haya limitaciones fisiológicas, geográficas o históricas (Thompson y King 1994, Dickman 1996).

La gran variabilidad existente en los factores bióticos y abióticos a lo largo del tiempo y del espacio puede generar importantes variaciones interpoblacionales en la demografía de las especies, sobre todo en las que tienen una amplia distribución. Por lo tanto, para poder comprender mejor los mecanismos por lo cuales estos factores influyen la dinámica poblacional de las especies es deseable que los estudios describan y analicen los patrones de variabilidad a escala espacio-temporal lo más amplia posible dentro de la distribución de cada. Esto permitiría además poder predecir el efecto que fenómenos que actúan escala global, como el cambio climático, tienen sobre las distintas poblaciones de cada especie.

Sin embargo, a pesar de que cada vez son más los autores que realzan la importancia de examinar patrones globales (Lester y col. 2007, Moles y col. 2007), la gran mayoría de los estudios sobre dinámica poblacional o variables demográficas, como la supervivencia y la reproducción, se han llevado a cabo a escala local, considerando sólo en el mejor de los caso, la variabilidad temporal (Albon y col. 2002, Gerber y col. 2004, Getz y col. 2006).

El conejo de campo: Historia, distribución y problemática actual

El conejo de campo (*Oryctolagus cuniculus*) es un mamífero lagomorfo de la familia Leporidae. Es el único miembro actual del género Oryctolagus (Robinson y Matthee 2005), que incluiría a los lagomorfos cavadores, como su propio nombre indica: *Orycto* del verbo griego *Orysso* ('excavar') y *lagus* del griego 'liebre' (Corbet 1994, D'Amico 2008). Se trata de una especie nativa del suroeste europeo (Península Ibérica y Sur de Francia), donde, en el pasado, era muy abundante. De hecho, se cree que el nombre de España proviene de *I-Shaphan-Im* ('Tierra de Conejos') que es el nombre que los fenicios le pusieron a la Península Ibérica cuando llegaron a las costas andaluzas en 1100 A.c. (Bochart 1646 citado en D'Amico 2008).

Ya los fenicios, posiblemente también los cartagineses y sobre todo los antiguos romanos contribuyeron en gran medida a la expansión de los conejos por gran parte del Mediterráneo debido a sus cualidades gastronómicas (Flux 1994). Más tarde, se han continuado introduciendo conejos en muchas otras partes del mundo para, por ejemplo, su caza, su carne o su pelaje (Flux y Fullagar 1992). De forma que actualmente el conejo de campo es una de las especies de mamíferos más ampliamente distribuida en el mundo, estando presente en gran parte de Europa, Norte de África, Australia, Nueva Zelanda, Chile, Argentina y más de 800 islas alrededor del mundo (Flux y Fullagar 1992, Alves y Hackländer 2008).

A lo largo de su distribución el conejo de campo presenta una doble problemática. Debido a su potencial reproductor, en muchas de las zonas el conejo se comporta como una especie invasora (Fenner y Fantini 1999, Jaksic y col. 2002), causando importantes daños en la agricultura y los ecosistemas de las áreas invadidas (Williams y col. 1995, Scanlan y col. 2006). En estas regiones se han estado utilizando técnicas para intentar controlar las poblaciones, como por ejemplo el uso de venenos, destrucción de madrigueras, instalación de vallado de exclusión o la utilización de virus letales (Cooke 2008). La introducción deliberada, en el caso del virus de la mixomatosis, o accidental, en le caso de la enfermedad hemorrágica vírica (EHV) ha sido beneficioso para el control de los conejos en lugares como Australia, pero su llegada a Europa ha sido una razón importante de que en muchas áreas exista un segundo problema para esta especie.

En muchas áreas de la Península Ibérica las poblaciones de conejo están en declive desde la aparición de, primero, la mixomatosis y, luego, la EHV (Virgós y col. 2007, Delibes-Mateos et al. 2007). Esto supone un grave problema porque en estas zonas el conejo es una especie clave para el ecosistema, de la que se alimentan un gran número de especies (Delibes y Hiraldo 1981), así como un recurso cinegético importante. De hecho, la no recuperación de algunas poblaciones de conejo, pese a los constantes esfuerzos de repoblación y demás medidas de conservación, ha tenido, entre otras cosas, consecuencias negativas para especies de predadores, como el lince ibérico *(Lynx pardinus)* o el águila imperial *(Aquila adalberti)* que están especializados y dependen del conejo para su subsistencia (Ferrer y Negro 2004).

Estado de conocimiento sobre variables demográficas y dinámica poblacional del conejo

La problemática ecológica y económica del conejo de campo ha promovido, durante décadas, numerosos estudios sobre la biología y la dinámica poblacional de la especie para así poder paliar su declive o sus efectos nocivos (Cooke y Fenner 2002, Cabezas 2005). Estos trabajos han examinado principalmente la biología reproductiva, la supervivencia y las causas de mortalidad del conejo en distintas poblaciones a lo largo de su área de distribución actual (Andersson y col. 1981, Wheeler y King 1985). Los resultados obtenidos en estos estudios muestran que se trata de una especie con una madurez sexual temprana (a los 3 ó 4 meses de edad) y una gestación relativamente corta (sobre 30 días), que junto con la capacidad de tener estros postparto la convierten en una especie muy prolífica (Watson 1957, Soriguer 1981, von Holst y col. 2002).

Por otra parte se trata de una especie con unas tasas de mortalidad elevadas, entre otras razones, debido a su papel en la dieta de los predadores, que en algunas poblaciones pueden llegar a mantener la poblaciones de conejos a bajas densidades (Newsome et al. 1989, Pech 1992), a causas tales como sequías o inundaciones de madrigueras y más recientemente a la introducción de la mixomatosis y la EHV (Reddiex y col. 2002, Moreno y col. 2007). Los distintos estudios también muestran valores de supervivencia, causas de mortalidad y algunos parámetros reproductores (e. g. periodo reproductor o tamaño de camada) muy dispares que sugieren que existe una gran variabilidad, a veces desconcertante, entre poblaciones y años. Sin embargo, este tipo de estudios siempre se han llevado a cabo considerando una única o, a lo sumo, unas pocas poblaciones de conejo, sin comprender los patrones globales de variación a nivel de especie ni los factores que los determinan y por lo tanto sin entender bien como funciona su dinámica poblacional.

Algunos autores han desarrollado también modelos demográficos para abordar el estudio de la dinámica poblacional del conejo (e. g. Calvete 2006a, Calvete 2006b). Estos estudios tienen un valor incalculable no solo para mejorar nuestro entendimiento de la dinámica de las poblaciones de conejos sino también para modelar, y así predecir, la respuesta que las poblaciones pueden tener a distintas medidas de control, gestión o conservación. Desgraciadamente, debido a la gran variabilidad espacio-temporal en las poblaciones de conejo y a la complejidad de los mecanismos que la determinan, estos modelos también se han centrado siempre en escenarios concretos (Angulo y Villafuerte 2003, Scanlan y col. 2006) o en solamente uno o dos determinantes, como la mixomatosis o la EHV (Fa y col. 2001, Aparicio y col. 2006).

Objetivos y Estructura de la tesis

El objetivo de la tesis consiste es llegar a comprender la dinámica poblacional del conejo de campo y los mecanismos por los cuales esta dinámica varia a lo largo del tiempo y del espacio generando los patrones globales de variabilidad existente en los parámetros demográficos de la especie. Para ello se ha utilizado una combinación de datos bibliográficos y modelos de simulación. Concretamente, nos centramos en los parámetros de reproducción y supervivencia. Estas dos variables demográficas son de especial interés, ya que para que una población se encuentre en equilibrio, reclutamiento y mortalidad deben compensarse. Comprender cómo y por qué la dinámica poblacional del conejo varía es necesario para entender las bases de su doble problemática y así optimizar futuros planes de conservación o control de la especie.

En base a la información publicada en anteriores estudios a escala más local, se predijo que: 1) Los factores que han sido descritos anteriormente como importantes para los conejos a dicha escala local, lo serían también para causar las variaciones en la dinámica poblacional del conejo a escala global. Se trata de factores de tres tipos: características individuales (edad y peso), propiedades poblacionales (densidad de conejos y/o de depredadores, presencia de enfermedades endémicas), y variables ambientales (temperatura, fotoperiodo y disponibilidad de alimento). 2) La edad interaccionaría con otros factores, de forma que la magnitud y el efecto de las diferentes variables reproductivas y de mortalidad variarían dependiendo de la edad de los conejos. 3) El cambio climático tendría un efecto importante sobre las poblaciones de conejo de campo, dado que se esperaba que las condiciones ambientales afectasen a las variables demográficas del conejo de campo (e.g. reproducción). 4) Las interacciones entre los distintos factores de mortalidad (e.g. predación y myxomatosis) y reproducción tendrían un papel fundamental en la dinámica poblacional de la especie.

En una primera fase de la tesis (**capítulos 1 y 2**) se revisó la bibliografía existente (artículos científicos, libros e informes) sobre la biología y ecología del conejo. Con estas revisiones se pretendía describir la variabilidad espacio-temporal y rango de valores para los parámetros reproductivos (**capítulo 1**) y de mortalidad (**capítulo 2**) de la especie, así como recopilar e identificar los factores que determinan dichos patrones de variabilidad. Se examinaron un gran número de publicaciones para obtener información de la mayor parte posible de las poblaciones de conejo a lo largo de su distribución mundial.

Se obtuvieron datos de parámetros demográficos y otros factores que podrían influir en la dinámica poblacional del conejo (e.g. edad, densidad, clima) de estudios en diferentes países de Europa, Oceanía, Norte y Sudamérica, desde 56º N a 27º S de latitud y que databan desde 1944 a 2008. Estos datos se completaron con registros climáticos y de fotoperiodo obtenidos de estaciones meteorológicas locales y observatorios astronómicos. Concretamente, en el **capítulo 1** se examinó la variación espacial y temporal en la duración del periodo de gestación, la edad de la madurez sexual y de la primera reproducción, la longitud del periodo reproductor, las tasas de preñez, y el número y tamaño de camada.

La variabilidad global mostrada por algunos parámetros reproductivos se intentó relacionar, mediante modelos lineales generalizados mixtos (GLMMs), con edad y peso, densidad poblacional, temperatura, fotoperiodo y disponibilidad de alimento. Estos GLMMs tienen la ventaja de que permiten el metanálisis del conjunto de datos de diferentes estudios, mediante la inclusión de la variable aleatoria (*estudio*) que controle por la autocorrelación de los datos dentro de cada localidad (Aitkin 1999, Platt y col. 1999). A su vez, esto conlleva un aumento del tamaño muestral que permite aumentar el número de variables examinadas simultáneamente.

En el caso del **capítulo 2** se analizaron, primero, las tasas de supervivencia total del conejo en las distintas poblaciones, para determinar cuales son los factores que las influencian. Más tarde, se examinó también la variabilidad encontrada en los parámetros de las principales causas de mortalidad, como son la mixomatosis, la EHV y la predación, y también en el consumo del conejo de campo por los predadores. En este caso también se realizaron GLMMs en los que se testó el efecto, entre otros, de factores como la edad, densidad de conejos, densidad de predadores, presencia de mixomatosis y/o EHV en la población y las condiciones climáticas (precipitación y temperatura) de las distintas áreas de estudio, aunque estos variaron dependiendo del modelo.

Utilizando la información obtenida en las dos revisiones bibliográficas, se desarrolló un modelo demográfico (**capítulos 3 y 4**) mediante los cuales se simularon diferentes dinámicas poblacionales para intentar reproducir lo que está pasando en las poblaciones naturales de conejo. Esto nos permitió entender mejor los mecanismos que conducen a esas situaciones reales y, por lo tanto, a la doble problemática de la especie. También nos permitió simular escenarios de cambio climático a gran escala para investigar como las poblaciones de conejos van a responder a un fenómeno de impacto global como ese. El modelo consistió en un modelo estocástico basado en el individuo con el tiempo corriendo en días y que incluye el ciclo vital del conejo, periodo reproductor, denso-dependencia en la reproducción y supervivencia.

Debido a la complejidad de la dinámica poblacional del conejo, en una primera fase (**capítulo 3**) nos centramos en examinar la reproducción, la cual es de gran importancia para una especie tan prolífera como el conejo. Se definieron diferentes periodos reproductores en base al modelo predictivo obtenido en el capítulo 1, que relacionaba clima y fotoperiodo con la presencia o ausencia de reproducción en un mes dado. La fecundidad dentro del periodo reproductor estaba representada por una función que incluye los efectos de la densidad y la edad. La supervivencia se simplificó en una única ecuación que, al igual que la reproducción, incorporaba el efecto de la densidad y la edad pero también el efecto de la escasez de alimento en determinados periodos del año. Con este modelo y aprovechando la relación entre el clima y el periodo reproductor del conejo, investigamos el efecto que el cambio climático puede tener sobre las poblaciones de conejo a gran escala (Europa) mediado por alteraciones de su reproducción.

Finalmente, en el **capítulo 4**, se mantuvo le reproducción de la misma forma, pero se desglosó la supervivencia según las principales causas de mortalidad previamente a la llegada de la EHV, es decir, la predación (por especialistas y generalistas), la mixomatosis y un último compartimento que incluye el conjunto de muertes por otras causas como son las sequías, coccidiosis, infanticidio, atropellos, etc. Este modelo se utilizó para evaluar la importancia relativa de las diferentes variables reproductivas y de mortalidad en la dinámica poblacional del conejo. Así como la interacción entre las distintas fuentes de mortalidad y la reproducción y entre la predación debida a especialistas y la mixomatosis. De esta forma se pudo observar cuales son las condiciones que conducen a mayores o menores abundancias poblacionales o a extinciones en poblaciones en las que la EHV no se encuentra presente.

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Capítulo 1

Breeding like rabbits: Global patterns of variability and determinants of European wild rabbit reproduction

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Resumen

La importancia del conejo de campo (*Oryctolagus cuniculus*), tanto por ser una especie invasora en alguna áreas como por ser una presa clave en otros ecosistemas, enfatiza la necesidad de entender que es lo que controla su dinámica poblacional a lo largo del mundo. El objetivo de este estudio es describir la variabilidad existente en los parámetros reproductivos del conejo e identificar los principales factores que gobiernan dicha variabilidad a escala global. A pesar de la amplia distribución de la especie, algunos aspectos reproductivos, como la temprana madurez sexual, la duración del periodo de gestación y la existencia de un estro post-parto, se mantienen constantes en todas las poblaciones confiriendo a la especie un alto potencial reproductivo. Sin embargo, otros parámetros varían substancialmente entre regiones y periodos dando lugar a productividades muy diferentes en las distintas poblaciones y años. Los aspectos que varían son la longitud de la estación reproductora, la proporción de hembras preñadas, la edad de primera reproducción y el número y el tamaño de las camadas. Nuestros resultados muestran que la variabilidad en estos atributos esta principalmente afectada por una combinación de variables ambientales (i.e. temperatura, disponibilidad de alimento y fotoperiodo) y características individuales (edad y peso corporal). Por otro lado, el efecto de factores como la densidad poblacional no pudo ser demostrado en este estudio. Mejorar nuestro conocimiento sobre los factores que controlan los patrones globales de reproducción del conejo de campo nos permitirá comprender su dinámica poblacional y por lo tanto optimizar el manejo y conservación de sus poblaciones.

Abstract:

The importance of European wild rabbits (*Oryctolagus cuniculus*) both as a pest in some areas and as a key prey species in others emphasizes the need to understand what controls its population dynamics worldwide. In this study we aim to describe the variability in rabbit breeding parameters and identify the main factors that govern it at a global scale. Despite the species' wide distribution, some reproductive traits such as short sexual maturity age, duration of gestation period, and existence of post-partum oestrus are similar in all populations conferring the species a high breeding potential. Nevertheless, other aspects vary substantially among regions resulting in highly different population productivities and also across years. These latter parameters are the length of breeding season, proportion of pregnant females, age of first reproduction, and number and size of litters. Our results show that variability in these attributes is mainly affected by a combination of environmental controls (i.e., temperature, resource availability, and photoperiod) and individual properties (age and body weight). On the other hand, the effect of other factors such as population density could not be demonstrated. Knowledge about the factors driving global reproduction patterns of European wild rabbits will improve our understanding about their population dynamics, and thus will help to optimize the management and conservation of their populations.

Introduction:

Although originally the European wild rabbit (*Oryctolagus cuniculus*) was restricted to the Iberian Peninsula and southern France (Lopez-Martinez 1989, Callou 1995), humans have introduced them in numerous countries for thousands of years (Flux and Fullagar 1992). The rabbit is currently present in many places of continental Europe, British Islands, Northern Africa, Australia, New Zealand, Chile, Argentina, and more than 800 islands around the world (Fig. 1, Jaksic and Fuentes 1991, Flux and Fullagar 1992, Rogers et al. 1994).

As a consequence of its extensive distribution, the European wild rabbit shows a wide range of variation in its ecology and demographic status. It has been declared a pest species in several countries and islands where it has been introduced (Fenner and Fantini 1999, Jaksic et al. 2002). On the other hand, within its original distribution, where it is a key prey species for many predators (Delibes and Hiraldo 1981, Rogers et al. 1994), some populations have been in continuous decline or even extirpated since the arrival of myxomatosis and viral haemorrhagic disease (Beltran 1991, Moreno and Villafuerte 1995, Angulo 2003, Virgós et al. 2007).

The need to control some expanding populations and preserve native ones has spurred numerous investigations of the main factors affecting rabbit mortality, such as predation, hunting, and infectious diseases (e.g., Villafuerte 1994, Moriarty et al. 2000, Fa et al. 2001, Calvete et al. 2002, Reddiex et al. 2002). However, a comparatively smaller amount of research has been conducted on the factors that control reproduction in the wild and which may be responsible for variation in breeding success and population dynamics of this prolific species. On a local scale 3 types of factors affecting both domestic and wild animals have been identified (Fig. 1): (1) individual properties such as genetic strains, body condition, social rank, or age effects (Dunsmore 1971, Gibb et al. 1985, von Holst, et al. 2002); (2) population characteristics such as social stress via density (Myers and Poole 1962, Rodel et al. 2004b); and (3) environmental controls associated with temperature (Myers 1971, Gilbert et al. 1987), food availability and quality (Poole 1960, Hughes and Rowley 1966, Myers 1971, Villafuerte et al. 1997), and photoperiod (Boyd 1986, Hudson and Distel 1990). The latter may, at the same time, influence characteristics of individual rabbits. Despite this clear mechanistic understanding associated with local populations we lack a quantitative description of global patterns. Our current knowledge at this scale is that rabbit reproduction shows strong spatial and temporal fluctuations. However, worldwide patterns of variability and their determinants have not yet been clearly identified.

The objectives of this study are to describe patterns of variability in the reproductive parameters of European wild rabbits at a global scale, and to explain those patterns according to the potential effects of individual and population characteristics, and of the environmental controls of rabbit reproduction. Comprehensive quantitative studies that disclose global relationships are necessary to provide a broader understanding of the main processes governing reproduction in rabbits.

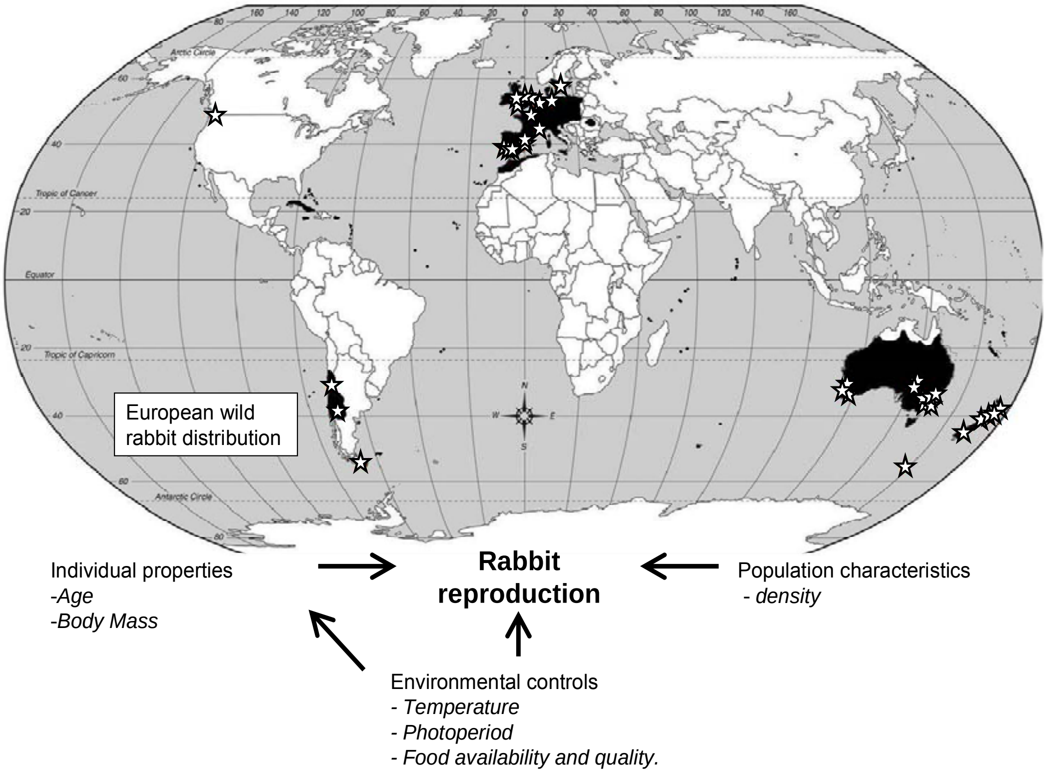

Fig. 1. Map of current distribution of the European wild rabbit (black areas) and locations of the studies reviewed (white stars). The diagram summarizes the factors previously described as important for rabbits at the local level.

Material and Methods:

The following breeding parameters were obtained from available literature (papers and reports, Table 1): gestation period (in days), length of breeding season (in months), pregnancy rates, number and size of litters, age of sexual maturity and first reproduction (in months). Among all the information found, we selected data that were comparable across studies (e.g., we only considered litter sizes measured *in utero*). We also collected information on the environmental variables, population densities, body sizes, and age of rabbits when available. In most cases photoperiod and climate data were supplemented with historical records from the same period of time provided by meteorological stations near the study sites.

Data analyses:

We performed 2 generalized linear mixed models (GLMMs) to investigate the main factors controlling seasonality in reproduction. The dependent variable in both models was presence/absence of reproduction in each month (binomially distributed). Since there might be some residual percentage of females breeding outside the reproductive period in some locations, we did not assign value 1 (presence of reproduction) to a given month until at least 10% of adult females were pregnant. This threshold comprised 88% of the months in which pregnant females were found. When fewer than 10% of females were pregnant we considered reproduction to be absent in that month (value 0). We obtained monthly pregnancy rates from 11 studies (N=261 months) from Europe, South America, and Oceania (Table 1). We treated study site as a random variable to account for autocorrelation. Data from 3 other publications (N=66 months; Delibes and Calderon 1979, Fraser 1988, Villafuerte 1994) were excluded for subsequent model evaluation; the omitted studies were chosen randomly with the only constraint that they included both native and non-native populations.

Table 1. List of publications reviewed for this study. Last column shows the type of analyses in which their data was used.

STUDY	LOCATION	LATITUDE	ANALYSES
Andersson and Meurling (1977)	Southern Sweden	55.7º N	
Andersson et al. (1981)	Southern Sweden	55.7º N	6
Arques (2000)	Eastern Spain	38.0º N	1,3,4,6
Arthur (1980)	Northern France	48.7º N	1,3,4,6
Bell (1977)	North Canterbury (New Zealand)	42.7º S	1,3
Bonino (2006)	Argentina	36.5º- 55.0º S	
Brambell (1944)	Caernarvonshire (UK)	53.0º N	1,3,6
Calvete et al. (2002)	North Eastern Spain	41.7º N	
Calzada (2000)	South Western Spain	37.1º N	6
Delibes and Calderon (1979)	South Western Spain	37.1º N	2,6
Dunsmore (1971)	Eastern Coastal Australia	35.8º S	1,3,5,6
Dunsmore (1974)	Subalpine Australia	36.3º S	6
Fraser (1988)	Central Otago (New Zealand)	45.3º S	2,6
Gibb and Williams (1994)	New Zealand	35.0º - 46.8º S	
Gibb et al. (1985)	Wairarapa (New Zealand)	41.2º S	1,3,6
Gonçalves et al. (2002)	Southern Portugal	38.8º N	6
Jaksic and Fuentes (1991)	Chile	29.0º - 54.0º S	
Lloyd (1970)	Wales (UK)	52.5º N	
	Skokholm (UK)	51.5º N	
	Skerries (UK)	53.3º N	
Myers (1971)	Subtropical Australia	26.3º S	6
	Subalpine Australia	36.3º S	6
	Arid Australia	30.2º S	6
	Mediterranean Australia	35.3º S	6
Parer (1977)	Mediterranean Australia	35.3º S	
Parer and Libke (1991)	South Eastern Australia	35.3º S	1,3,4,6
Phillips et al. (1952)	Wales (UK)	51.9º N	6
Reddiex et al. (2002)	North Canterbury (New Zealand)	42.7º S	
Ribeiro (1983)	Southern Portugal	38.1º N	1,3,4,6
Rodel et al. (2004b)	Bayreuth (Germany)	49.9º N	
Rodel et al. (2005)	Bayreuth (Germany)	49.9º N	
Rogers (1981)	Southern France	43.7º N	6
Rogers et al. (1994)	Continental Europe		
Skira (1978)	Subantartic Australia	54.6º S	1,3,6
Soriguer (1981)	South Western Spain	37.9º N	1,3,4,6
Stevens and Weisbrod (1979)	San Juan Island (USA)	48.5º N	6
Trout and Smith (1998)	Lincolnshire (UK)	53.1º N	
Twigg et al. (1998)	South Western Australia	34.5º S	6
Villafuerte (1994)	South Western Spain	37.1º N	2
von Holst et al. (1999)	Bayreuth (Germany)	49.9º N	
von Holst et al. (2002)	Bayreuth (Germany)	49.9º N	
Wallage-Drees (1983)	Holland	52.5º N	
Watson (1957)	Hawke's Bay (New Zealand)	39.8º S	6
Wheeler and King (1985)	Cape Naturaliste (SW Australia)	33.5º S	5,6
	Chidlow (SW Australia)	31.9º S	5,6
Williams and Robson (1985)	Wanganui district (New Zealand)	39.3º S	6
Wood (1980)	Arid Australia	29.7º S	
Zunino (1987)	Central Chile	33.2º S	1,3
Zunino and Vivar (1985)	Central Chile	33.2º S	6

1 = Breeding season GLMMs, 2 = Breeding season model validation, 3 = Pregnancy rate GLMM, 4 = Pregnancy rate GLMM with data on population change, 5 = Age effect on pregnancy rates, 6 = Litter size regressions.

In a first model we investigated the influence of climate and food resources. The climatic variables tested were total monthly precipitation (*precip*), linear and quadratic effects of mean monthly temperature (*temp*), as well as the interaction between *precip* and *temp*. The lack of pasture data available for all the study sites led us to use an indirect index of vegetation growth (*green_veg*) based on Walter and Lieth (1960) climatic diagrams. This measure takes into account that pasture presence in a month depends on precipitation and temperature (i.e., evaporation) of the previous months. For a given month, *green_veg* was 0 if rainfall in the previous 2 months was insufficient to allow plant growth (*precip* < 2* *temp*) leading to low green pastures availability. Otherwise, *green_veg* equalled 1.

With a second GLMM, we attempted to evaluate if photoperiod also affected the occurrence of reproduction in specific times of the year. The effect of daylight has not been considered important in delimiting breeding season at the local level; however, we want to investigate its relevance when comparing localities across latitudes with highly different photoperiods. Therefore, we added 2 new explanatory variables to the previous model: average daylength (in minutes) in each month (*daylight*) and photoperiod change (*light_change*). The latter was a measure of the magnitude and direction of shifts in the photoperiod and was calculated as the difference between the mean daylength of a specific month and the previous one. Negative values represent a decreasing photoperiod while positive ones mean lengthening days. In this case the study site was also considered as a random variable.

To assess which model (i.e., with or without photoperiod) best predicted the duration of breeding season across years and locations we employed simple matching and phi coefficients. These statistics compare observed values with those predicted by the models and give a measure of the similarity and correlation between them. To evaluate both models, these coefficients were also calculated for the 3 studies excluded from the analyses. Since the importance of photoperiod may change with latitude, and thus also the success of one model over the other, we also computed separate phi and simple matching coefficients for studies below and above 45º latitude in both hemispheres.

With additional GLMMs, we examined the influence of environmental factors, rabbit density, and age on the proportion of pregnancies within the breeding season (defined as above). Using the same 11 studies as above (Table 1), we performed a model in which the response variable was monthly percentage of pregnant does during the breeding period (i.e., months with values > 10%; N = 179 months). A negative binomial distribution was applied to these data due to overdispersion.

We considered the same independent variables, interactions, and random factor as in the second model used to test for presence/absence of breeding, although in this case we also added an index of rabbit density (*dens_month*) to account for possible density-dependent effects. For a given month, *dens_month* is the time passed (in months) since the onset of the reproductive season. This is based on the fact that the number of individuals increases as the breeding season progresses. Thus, the last months of the reproductive period will have larger values of *dens_month*. Five of our sources (Table 1) provided data on population change (monthly rabbit censuses or monthly number of captures). For these studies (N = 90 months) we repeated the model replacing *dens_month* by better approximations of monthly rabbit numbers (*density*). To make data comparable across areas with a priori different carrying capacities, measures of density within each study site were scaled from 0 to 1 $((density - density_{min})/(density_{max} - density_{min}))$.

The effect of rabbit age on fecundity of sexually mature females was tested with a univariate generalized linear mixed model using data of 2 study sites (Dunsmore 1971, Wheeler and King 1985) in which detailed monthly data were available. The proportion of pregnancies in a given month within the reproductive season was used as the response variable (with a negative binomial distribution), and female age was the explanatory. We considered 2 age categories (3 to 12 months vs. >1 year of age), and included the study site and the month of the year as random factors.

Finally, we examined variation in litter sizes among rabbit populations across 24 publications (Table 1). We evaluated the relationship between the mean litter size of a population and the mean adult body weight, length of the breeding season, and climatic variables affecting food availability. Due to the low number of comparable observations, the multicollinearity among variables and the complexity of potential direct and indirect effects, we employed a sequential approach.

First we conducted a multiple regression to assess the relationship of mean body weight and length of breeding season with litter size and then we used simple regressions to relate body size to mean temperature, annual precipitation, and mean length of the vegetation growing season (number of months in which precipitation is greater than twice the temperature according to Walter and Lieth (1960). We also reviewed how other factors such as female age may affect the number of offspring per litter locally.

Results

Worldwide variability in European rabbit reproduction:

We obtained information on reproduction of rabbits from 12 countries of Europe, Oceania, and North and South America (Table 1). These populations were in diverse bioclimatic areas (i.e., from Subalpine to Arid) and at latitudes ranging from 26º 30' to 55º 42'. The years in which they were published varied from 1944 to 2006.

Some reproductive parameters had similar values through its wide area of distribution. Studies from highly separate locations agreed that male and female rabbits may reach sexual maturity at 3 to 4 months (Watson 1957, Soriguer 1981, Zunino and Vivar 1985, Parer and Libke 1991), that gestation period lasts around 28-31 days (Myers and Poole 1962, Dunsmore 1971, Bell 1977, von Holst et al. 1999), and that there is a post-partum oestrus, in which females can be fertilized immediately after giving birth (von Holst et al. 2002, Bonino 2006, Calvete 2006a).

On the other hand, other parameters, such as breeding season, proportion of pregnant females, age of first reproduction, and number and size of litters showed high spatial and temporal variation around the world (Brambell 1944, Myers 1971, Stevens and Weisbrod 1981, Ribeiro 1983, Gilbert et al. 1987).

The breeding period (months with ≥10% of pregnant does) ranged from about 3 months per year in San Juan Island (USA) to approximately year-round in some places of Australia and New Zealand (Table 2). The season in which reproduction occured also changes. In the Iberian Peninsula and central Chile rabbits bred during winter and spring months (Soriguer 1981, Ribeiro 1983, Zunino 1987) while in Sweden and subalpine Australia breeding season was delayed towards the summer months (Brambell 1944, Skira 1978, Andersson et al. 1981, Gilbert et al. 1987 ; Table 2).

Except for San Juan Island where rabbits seem to reproduce consistently from March to May (Stevens and Weisbrod 1981), rabbit populations vary in the duration and timing of the breeding season across years. For example, in Doñana National Park Delibes and Calderon (1979) did not find pregnant females until January, whereas Villafuerte (1994) showed that from 1988 to1990 the reproductive period started in October/November. Arques (2000) also encountered important variations in a rabbit population in Alicante (Spain). In the first year of study, breeders were present from October to February, the second from March to May, and the third breeding season went from December to April.

These differences in the length of the reproductive period were linked to variations in other breeding parameters such as the age of first reproduction and the average annual number of litters per female. Despite reaching maturity as soon as 3 to 4 months old, in populations with short breeding seasons most young rabbits defered until next season to reproduce for the first time. Thus, we can coarsely approach the age of first reproduction as the time between the peak of a reproductive period and the beginning of the next one. This resulted in high variability of this life trait across different climatic regions. In Mediterranean Australia (Myers 1971) and Wairarapa (New Zealand; Gibb et al. 1985), where breeding was practically continuous throughout the year, juvenile rabbits might breed for the first time at 3.5-4 months of age. However, this age increased to 9-10 months in Germany, Sweden, and the United Kingdom, among others (Brambell 1944, Andersson and Meurling 1977, Stevens and Weisbrod 1981, von Holst et al. 2002).

Table 2. Reproductive parameters of wild rabbit populations around the world (all years pooled). Standard deviations (± sd) are included after the mean when available.

Location	**Latitude**	**Length of breeding season**	**Reproduction period**	**Litters per year**	**Litter size (*in uteri*)**	**Monthly pregnancy rate**	**Source**
Arid Australia	30.2º S				4.5		Myers (1971)
Central Chile	33.2º S	6 months	June-November		5.0	66.7% ± 12.6	Zunino (1987)
Wellstead (Australia)	34.5º S					31.0% ± 13.4	Twigg et al. (1998)
Mediterranean Australia	35.3º S	9 months	April/May-January	5.2			Myers (1971)
Subalpine Australia	35.8º S				4.0		Dunsmore (1974)
Subalpine Australia	36.3º S	6 months	August-January	2.9			Myers (1971)
Doñana National Park (SW Spain)	37.1º N				3.9 ± 1.2		Delibes and Calderon (1979)
Sierra Morena (SW Spain)	37.9º N	7 months	November-May	2.3	3.2 ± 1.0		Soriguer (1981)
Alicante (E Spain)	38.0º N				5.3 ± 1.3		Arques (2000)
Southern Portugal	38.1º N	8 months	September-April			38.0% ± 27.1	Ribeiro (1983)
Southern Portugal	38.8º N				3.9 ± 1.6		Goncalves et al. (2002)
Wairarapa (New Zealand)	41.2º S	12 months	All year round	7.0*	5.8 ± 1.9		Gibb et al. (1985)
North Canterbury (New Zealand)	42.7º S	12 months	All year round			56.9% ± 16.0	Bell (1977)
Southern France	43.7º N					53.8% ± 22.0	Rogers et al. (1994)
Central Otago (New Zealand)	45.3º S				6.0 ± 1.8		Fraser (1988)
San Juan Island (USA)	48.5º N	3 months	March-May	3.0	7.3		Stevens and Weisbrod (1981)
Northern France	48.7º N	7 months	February-August	3.5	4.7, 4.8, 4.5 (1977-79)	61.1% ± 20.9	Arthur (1980)
Caernarvonshire (UK)	53.0º N	6 months	January-June		4.9 ± 1.3		Brambell (1944)
Subantartic Australia	54.6º S	7 months	September-March		5.6 ± 1.8		Skira (1978)
Southern Sweden	55.7º N	6 months	March-August			47.8% ± 25.0	Andersson et al. (1981)

*Calculated using Bell's (1977) formula.

The number of litters per adult female and per year increased with the length of the breeding season. In Australia, Myers (1971) found that the mean number of parturitions per year was lower in a subalpine habitat, with shorter reproductive periods, than in a Mediterranean population of the same region (Table 2). Nonetheless, values for some populations (Soriguer 1981, Stevens and Weisbrod 1981; Table 2) did not always reflect this trend.

Finally, the proportion of pregnancies and litter sizes also differed among regions (Table 2). The minimum mean percentage of pregnant does within breeding months (31.0 %) was found by Twigg et al. (1998) in southwestern Australia, while the maximum (66.7 %) was from a Chilean population (Table 2). The size of litters ranged from 3.2 embryos in Spain to 7.3 in the San Juan Island (Table 2), although most populations had a mean litter size between 4 and 6.

Apart from the global-scale differences, the proportions of pregnant females and, to a lesser extent litter sizes also varied locally within the same reproductive period. For the first parameter the coefficients of variation ranged from 0.19 to as large as 0.71 (median and mean CV = 0.41, see Table 2). Several authors have found that in their study areas the values of these 2 parameters changed from month to month tending to peak in the middle of the breeding season (Watson 1957, Myers and Poole 1962, King and Wheeler 1981, Williams and Robson 1985).

Factors affecting breeding parameters of *Oryctolagus cuniculus*:

Both environmental and individual factors have an important role in limiting the duration of the breeding season, controlling the proportion of pregnant females and determining the number of embryos per litter. The probability of finding more than 10% of the females reproducing was higher in months in which vegetation growth was likely (Table 3; Fig. 2). Temperature was also significant, entering models with both a positive linear influence and a negative quadratic influence. The second model revealed that photoperiod also influenced the breeding season. Daylength and photoperiod change appeared to be associated with reproductive events. However, monthly precipitation and the interaction between precipitation and temperature did not enter either model.

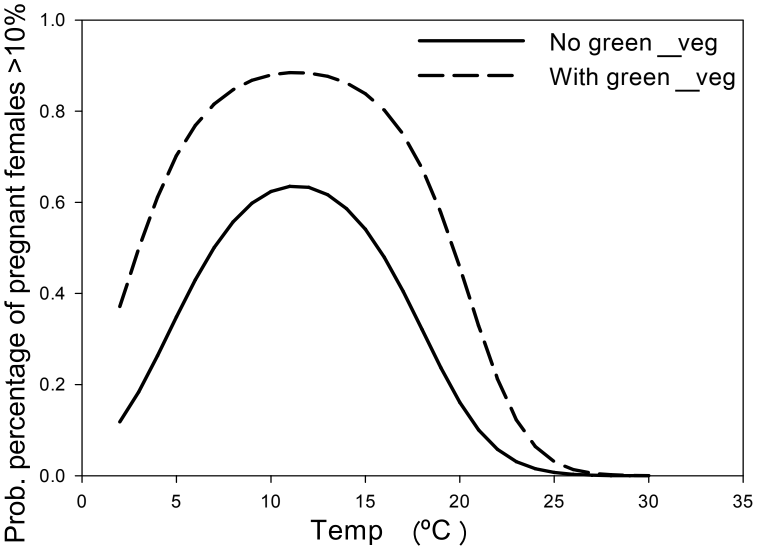

Fig. 2. Effect of temperature and food availability (*green_veg*) on the probability of rabbits to reproduce in a given month according to Model 2 (includes climate, feeding resources, and photoperiod).

Higher values of phi and simple matching coefficients obtained for the second model denote that the correlation and similarity between the values predicted by this model and the observed ones are greater than in the first model (Table 3). The improvement in performance of this second model is emphasized when we compare coefficients across latitudes: at lower latitudes both models have similar values, whereas the efficiency of the first model decreased substantially above 45º in the northern or southern hemispheres.

Thus, the second model predicted more accurately the months in which rabbits will reproduce and should be selected when considering the factors that define the breeding season globally. In any case, the concordance between the coefficients for studies included vs. those that were excluded from the analyses (Table 3) suggests that the results of either model could be extrapolated to populations other than those considered here.

Table 3. Determinants of reproductive seasonality for European rabbits according to general linear mixed models. Lower panel presents model predictability of months with reproduction in studies included and excluded ("Analyzed") from the analyses and in populations at high and low latitudes. Asterisks indicate parameters and statistical results for models without non-significant variables (denoted by ns). Sample size (N) refers to the total number of months within the studies for which data was available.

		Model 1 environmental controls (N = 261)			**Model 2 environmental and individual controls (N = 261)**		
Effects		Parameter (estimate±se)	F	p-value	Parameter (estimate±se)	F	p-value
Intercept		-2.265 ± 1.275			-6.233 ± 1.866		
		-0.837 ± 0.829*			-4.542 ± 1.483*		
precip		ns	2.30	0.1304	ns	2.03	0.1560
temp		0.629 ± 0.160	15.44	0.0001	0.668 ± 0.220	9.22	0.0027
		0.525 ± 0.132*	15.74*	<.0001*	0.605 ± 0.194*	9.72*	0.0020*
*temp*temp*		-0.025 ± 0.005	21.99	<.0001	-0.030 ± 0.007	19.17	<.0001
		-0.023 ± 0.005*	1.35*	<.0001*	-0.029 ± 0.006*	20.06*	<.0001*
*precip*temp*		ns	1.55	0.2150	ns	0.67	0.4148
green_veg	0	-1.327 ± 0.511	6.75	0.0100	-1.436 ± 0.604	5.66	0.0182
		-1.355 ± 0.510*	7.05*	0.0084*	-1.592 ± 0.599*	7.07*	0.0084*
green_veg	1	-			-		
daylight					0.006 ± 0.003	4.40	0.0371
					0.006 ± 0.003*	4.34*	0.0382*
light_change					0.017 ± 0.004	16.48	<.0001
					0.017 ± 0.004*	17.13*	<.0001*

Model Accuracy	Analyzed Yes / No	Latitude <45º / >45º	Analyzed Yes / No	Latitude <45º / >45º
N	261 / 66	229 / 98	261 / 66	229 / 98
Phi coefficient of correlation	0.49 / 0.46	0.57 / 0.30	0.63 / 0.65	0.59 / 0.74
	0.46 / 0.30*	0.58 / 0.03*	0.63 / 0.63*	0.68 / 0.55*
Simple matching coefficient	79% / 76%	83% / 68%	84% / 83%	82% / 88%
	78% / 70%*	83% / 61%*	85% / 83%*	87% / 79%*

As for the factors controlling the percentage of pregnant females, the mixed model built with data from 11 studies suggested that only temperature and photoperiod change have a significant effect. The proportion of pregnancies increased linearly with *temp* and *light_change* (Table 4). The temperature also exhibited a quadratic effect (Table 4), implying that fecundity was favoured by mild temperatures.

Other variables and the interaction between *precip* and *temp* did not seem to affect pregnancy. Neither this analysis nor a second with only the 5 studies containing population change estimations were able to demonstrate the existence of clear signals of density-dependence in reproduction. The latter mixed model confirmed once again the influence of temperature on fecundity, but not the effect of daylength change (Table 4), probably due to the decrease in sample size.

Table 4. Generalized linear mixed models for the factors controlling percentages of pregnant female European rabbits within the breeding season (months with percentages over 10%). On the left, results of the model using all publications available and an indirect index of rabbit density (*dens_month*). On the right, model with only the five sources providing real estimates of population change (*density*). Values indicated by asterisks are parameters and statistical results for models from which non-significant variables (denoted by ns) were removed. Sample size (N) consists of number of months included in the analyses.

		Model with 11 studies (N = 179)			**Model with only 5 studies (N = 90)**		
Effects		parameter estimate(±se)	F	p-value	parameter estimate(±se)	F	p-value
Intercept		3.011 ± 0.381			2.406 ± 0.677		
		2.772 ± 0.198*			2.436 ± 0.329*		
precip		ns	1.60	0.2092	ns	0.91	0.3438
temp		0.149 ± 0.049	8.97	0.0034	0.236 ± 0.072	10.85	0.0015
		0.216 ± 0.033*	43.70*	<.0001*	0.311 ± 0.051*	37.20*	<.0001*
*temp*temp*		-0.007 ± 0.002	15.26	0.0002	-0.011 ± 0.002	26.72	<.0001
		-0.009 ± 0.001*	46.62*	<.0001*	-0.013 ± 0.002*	46.22*	<.0001*
*precip*temp*		ns	2.71	0.1028	ns	1.05	0.3084
green_veg	0	ns	0.97	0.3258	ns	0.06	0.8070
green_veg	1						
daylight		ns	0.35	0.5568	ns	0.64	0.4249
light_change		0.003 ± 0.001	15.29	0.0002	ns	2.11	0.1507
		0.003 ± 0.001*	53.8*	<.0001*			
dens_month		ns	0.63	0.4290			
density					ns	0.16	0.6948

Age also affected the percentage of gestating does (F = 4.83, DF = 50, p = 0.03). Pregnancy rates for sexually mature females younger than 12 months were consistently lower than for older does within the same breeding season (Fig. 3a). A different age classification provided by Watson (1957) revealed how fecundity increases progressively with female age (Fig. 3b).

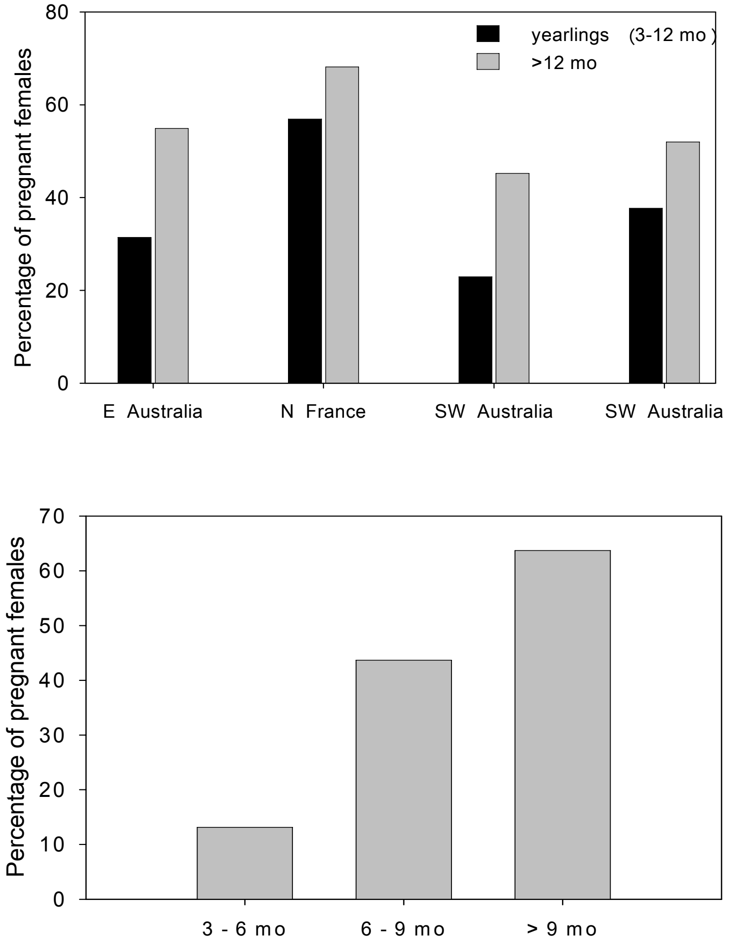

Fig. 3. a) Mean monthly pregnancy rate (within the breeding period) for sexually mature females under and over 12 months (mo) in 4 different locations. Sources were: E Australia (Dunsmore 1971), N France (Arthur 1980), SW Australia (2 different sites from Wheeler and King 1985). b) Increase with age (months) of the within-season percentage of pregnancies in a wild rabbit population in Hawke's Bay, New Zealand (Watson 1957).

Finally, mean litter size was positively correlated with mean adult body weight (F = 6.67, DF= 10, p = 0.03; Fig. 4a) but not with the length of the breeding season. At the same time, simple regressions showed that rabbit size increased in areas with colder mean temperatures (F = 6.44, DF = 14, p = 0.02; Fig. 4b), but is not significantly related to either annual rainfall or growing season length. Individual factors such as female age also appear to affect the number of embryos per litter at a more local scale. Several studies describe an increase of litter size with age (Dunsmore 1971, Myers 1971, Williams and Robson 1985). Some of these even show that the number of embryos may start to decrease again at older ages (Gibb et al. 1985, Fraser 1988; Fig. 4c,d).

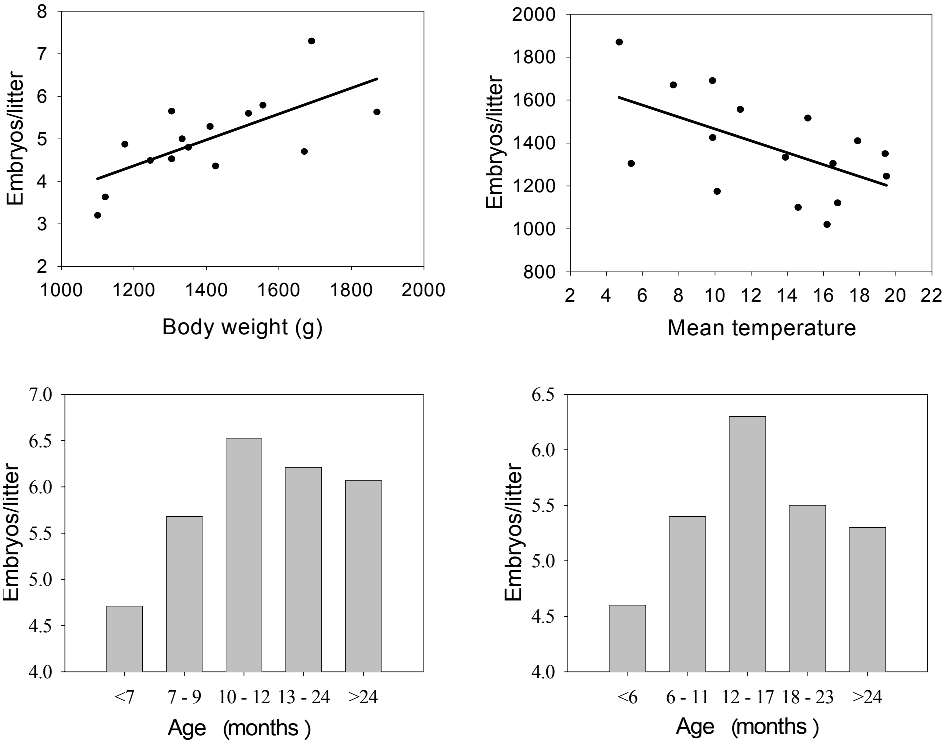

Fig. 4. a) Relationship between litter size and mean body weight of wild rabbit populations. b) Effect of mean temperature on the average body size. c) Age-dependent variability in the number of offspring per parturition in New Zealand rabbits according to Gibb et al. (1985) and d) according to Fraser (1988).

Discussion

The ecological and economic importance of European rabbits in many areas of the world has stimulated numerous studies regarding the biology of the species (Brambell 1944, Delibes and Calderon 1979, Zunino and Vivar 1985, Twigg et al. 1998, Rodel et al. 2004). Unfortunately, data presented by different authors are not always comparable due to different parameter definitions, measurements, and reporting. A more important problem of rabbit literature is that research is extremely localized in time and space and may not represent variation across the entire species' range. These complications create uncertainty around rabbit breeding parameters and emphasize the need to examine them more closely to understand the reproduction of this species.

After reviewing numerous studies, we found that some reproductive traits remain approximately constant in all populations. Moreover, these parameters are the reason why this species “breeds like rabbits.” The ability to reach sexual maturity in a few months, the relatively short gestation period, and the post-partum oestrus confer rabbits a high reproductive potential that will be modified according to parameters such as breeding season duration, pregnancy proportion, and litter sizes.

The duration and timing of the reproductive period varies across regions and also between years. These differences, in turn, generate variability in the age of first reproduction and the annual mean number of parturitions per adult female. However, the dependence of the number of litters on the breeding season is sometimes obscured by confounding factors, such as among-population differences in litter prenatal loss and proportion of first season breeders with lower fecundity (von Holst et al. 2002, Rodel et al. 2004b).

These features might selectively reduce the number of litters per year, and thus eliminate the direct relationship between reproduction duration and litters per year. For example, even though breeding seasons last only three months in San Juan Island, the adult female predisposition to give birth once per month (Stevens and Weisbrod 1981) results in a number of litters per year higher than in places with longer reproductive periods (Table 2).

We also encountered substantial variation in the percentage of pregnant does and the number of embryos per litter. These parameters not only differed among populations but also within them. The importance of breeding season length, proportion of pregnancies, and litter size for the productivity of rabbit populations emphasizes the need to investigate the factors that control their variability.

Many authors have explored the effect of environment and other variables on rabbit reproduction (Myers and Poole 1962, Lloyd 1970, Myers 1971, Rodel et al. 2004b). Nevertheless, the individualized study of these factors together with the local scale of the studies has made it difficult to extrapolate and interpret the results across the species’ range. Recent statistical techniques, such as generalized linear mixed models, have enabled joint analysis of data from different studies and areas (Aitkin 1999, Platt et al. 1999). Therefore, we were able not only to find patterns that operate worldwide but also to augment the number of variables tested simultaneously.

Our mixed models showed that global variability in the duration and timing of the breeding season across very different ecosystems could be explained by the combined effect of climate, both directly and through its effect on vegetation growth, and photoperiod. This agrees with results of other authors that described similar relationships at a more local scale (Poole 1960, Hughes and Rowley 1966, Myers 1971, Rogers 1981, Boyd 1986, Rodel et al. 2005).

Low temperatures are associated both with environmental factors, by reducing food availability (at low mean temperatures vegetation growth and access is reduced), and by increasing thermal stress (Gilbert et al. 1987, Rodel et al. 2004a), resulting in poor body condition and a delay of reproduction (Andersson et al. 1981, Rogers et al. 1994, Bell & Webb 1991, Rodel et al. 2005). On the other hand, high temperatures might prevent spermatogenesis and pregnancy (Poole 1960, Myers 1971, Rogers et al. 1994).

Females depend on availability of quality grazing areas to procreate (Poole 1960, Hughes and Rowley 1966, Wood 1980, Cooke 1981) and reproduction declines when the rainy season ends and green protein-rich pastures become scarce (Rogers 1981, Myers et al. 1994, Arques 2000). Precipitation alone was a bad proxy for food availability since it does not directly affect the length and timing of the breeding period. However, the coarse index of green pasture growth calculated with rainfall and temperature in previous months appeared to be adequate to show the generalized effect of food availability on all populations.

We found that rabbits tend to reproduce in months with longer and preferably increasing photoperiod, although the day lengths required to breed are influenced by other factors, such as temperature and food availability. These findings agree with other authors that have shown the positive association between daylength and rabbit reproduction both in farms and natural populations (Hudson and Distel 1990, Uzcategui and Johnston 1992, Quintela et al. 2001). For example, Theau-Clement et al. (1990) and Mirabito et al. (1994) concluded that increasing light programs in rabbit farming improved female fecundity more than constant photoperiods. The model considering photoperiod appeared to be better at predicting reproductive events (over 80% of the cases) even for studies not included in the analyses. The difference in data fitting for the 2 models (with and without photoperiod) was more evident at high latitudes, suggesting that the effect of photoperiod is stronger above 45º and could have gone unnoticed if we had used only low latitude studies. This highlights the importance of including the maximum variability possible when aiming to elucidate factors that explain global patterns.

Monthly percentages of pregnant does responded to temperature and photoperiod change in a similar way as did reproductive period. Female fecundity is reduced by extreme temperatures (Myers 1971, Rogers et al. 1994, Rodel et al. 2005) and shortening days (Hudson and Distel 1990) and monthly rainfall did not seem to have a direct influence on this parameter. Despite the importance of daylength and the presence of green vegetation in delimiting the breeding season, these parameters did not seem to affect the proportion of pregnant females, possibly because the within-season variation of these 2 variables was too small to show an effect on fecundity. Previous authors have suggested that temporal changes in food abundance could also account for variation in fecundity (Strum and Western 1982, Myers et al. 1994). Unfortunately, we could not investigate this aspect because of the lack of quantitative data on pasture availability.

Population and individual characteristics, such as density and age, also affect wild rabbit reproduction locally. Several studies have shown density-dependence in fecundity (Myers and Poole 1962, Rodel et al. 2004b). For example, in a long-term experimental study in Germany Rodel et al. (2004b) proved that individual female reproductive success decreased with density. Our inability to demonstrate this effect may be due to the poor quality of the density measures available. The populations considered could also be far below carrying capacity, and thus density-dependent processes would not leave a strong signal in the data. The positive influence of age on the percentage of pregnancies is clear in our analyses. Some authors have suggested that the lower breeding success of younger females would be a consequence of their lower social rank and body weight (Garson 1981, von Holst et al. 1999, 2002, Rodel et al. 2004b), thus reflecting the simultaneous effect of population and individual factors.

Variability in litter sizes was correlated with both environmental features and population characteristics. The population mean of adult body mass seems to be directly conditioning the average number of embryos per litter. This agrees with the results of Tuomi (1980) who concluded that contrary to large mammals, in small species the number of young per litter tended to increase with body size. Moreover, temperature would affect litter size indirectly through its negative influence on body weight (Fig.4b; Bergmann 1847 translated in James 1970). We were not able to prove the effect of other variables related to green pasture availability such as length of growing season or annual precipitation. Some authors have suggested that the higher nutritional quality of resources found in climatically harsher areas compensates for the limited abundance of food (White 1983, Albon and Langvatn 1992, Sand et al. 1995). These results, however, should be regarded carefully since the low sample size and the correlative nature of the analyses might impede the detection of further patterns, such as the influence of the breeding season length.

The number of embryos per litter also appears to be controlled by female age at a local scale. Similar to the pregnancy rates, the increase of litter size with female growth might be caused by an improvement of their social rank and body mass (von Holst et al. 1999, 2002, Rodel et al. 2004b). On the other hand, the later decline in embryo numbers could be due to either senescence or adaptive mechanisms for which species with short life expectancy would invest more breeding efforts in the first year of life (Stearns 1976). Variations in mean litter size and proportion of pregnant does through time and across areas could be partially due to differences in the age composition of the populations (Watson 1957, Fraser 1988, von Holst et al. 2002).

Litter sizes could also be density-dependent since *per capita* resources will be lower in dense populations. Unfortunately, we had no data to examine this relationship. Results of previous studies are not conclusive either. Some authors appeared to have associated larger litters with low population densities (Lloyd 1970), while others have not been able to demonstrate significant correlations between the 2 variables (Trout and Smith 1998, Rodel et al. 2004b).

In conclusion, although there may be other effects not considered (e.g., genetic effects) or proven (i.e., density-dependence) in this study, spatial and temporal patterns in rabbit reproduction are controlled mostly by temperature, photoperiod, food availability, body weight, and population age structure. Factors such as age composition will cause local fluctuations in the breeding parameters but should not affect the average values in the long term. However, alterations in the temperature and rainfall patterns might have strong effects on rabbit breeding (i.e., breeding season length, rate of pregnancies, and litter size), both directly and through vegetation growth.

Modifications in the reproductive success of a rabbit population could change its conservation and management status, which results from the interaction between productivity, mortality, and migration rates. All these generate uncertainty about how climate change is going to affect this species across its geographic range. Further studies should investigate the consequences of this environmental shift on the reproduction and future population trends of European wild rabbits.

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Capítulo 2

Dying like rabbits: determinants of the spatio-temporal variability in the survival of European wild rabbits

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Manuscrito en preparación

Resumen

La dinámica poblacional de las especies se ve muy afectada por variaciones de sus variables demográficas como la supervivencia y la reproducción. A pesar de la reconocida necesidad de entender la variabilidad espacio-temporal existente en las tasas de supervivencia, la mayoría de los estudios se han centrado siempre en un número una o pocas poblaciones y también en años o causas de mortalidad concretas. El objetivo de este estudio fue, utilizando el conejo de campo como modelo, investigar como y porqué las tasas de supervivencia varían a lo largo del mundo. Primero, nos centramos en la supervivencia global, describiendo los patrones de variabilidad para diferentes edades y examinando los factores que gobiernan esa variabilidad. Más tarde, realizamos análisis individuales para cada causa de mortalidad para así poder identificar los determinantes de las tasas de predación y la mortalidad por enfermedades. Finalmente, exploramos la mortalidad debida al resto de causas en su conjunto. Los patrones globales mostraron que, al igual que en otros mamíferos, las tasas de supervivencia de los conejos aumenta con la edad mientras que la variabilidad de dichas tasa disminuye. La magnitud de estos incrementos parece estar regulada por procesos denso-dependientes, especialmente entre las clases de edad más jóvenes. Los resultados de nuestros análisis mostraron que factores como el número de enfermedades presentes en una población o la precipitación también afectan a la supervivencia y predación de los conejos, aunque su efecto varía dependiendo de la edad de los conejos. Otras variables que han demostrado ser también determinantes para la predación y consumo de conejos por parte de los predadores fueron la densidad de conejos y predadores en el primer caso y tipo de predadores (generalistas o especialistas) y estación del año en el segundo. En cuanto a las enfermedades, su fenología parece estar gobernada por variables climáticas y por lo avanzada que esté estación reproductora. La letalidad de las enfermedades dependió del grado de virulencia de la cepa y del tiempo pasado desde la llegada de la enfermedad a la población para el caso de los conejos infectados con el virus de la myxomatosis y de la edad de los conejos para los que tenían la enfermad hemorrágica vírica. In conclusión, los patrones espacio-temporales globales de la supervivencia del conejo de campo surgen de una combinación de factores que se interrelacionan tanto directamente como a través de mecanismos denso-dependientes y comprender estas interacciones es crucial para mejorar la estrategias de conservación y manejo.

Abstract

Population dynamics of a species is highly influenced by variations of its demographic variables such as survival and reproduction. However, despite the acknowledged need to understand spatio-temporal variability in survival rates, most studies have focused in only one or a few populations and also in specific years or mortality causes. Here, using the European wild rabbit as a model, we aimed to investigate how and why survival rates vary throughout the world. First, we focused in the overall survival rates, describing the patterns of variability across ages and examining the factors driving that variability. Secondly, we performed cause-specific mortality analyses to identify the determinants of predation rates and disease mortality. Finally, we also explored the overall mortality due to the rest of the causes. Global patterns showed that, like in other mammals, rabbit survival rates increase with age while survival variability decreases. The magnitude of these increases, however, seems to be regulated by density-dependence processes, especially across younger age classes. The results of our analyses showed that factors such as the number of diseases present in a population or precipitation also affect rabbit survival and predation, although their effect changes depending on rabbit age. Other variables demonstrated to be important in determining predation and consumption of rabbits by predators were density of rabbits and predators in the first case and predator type (generalists and specialists) and season of the year in the second one. Regarding diseases, their phenology appeared to be driven by climatic conditions and by number of months passed since the start of the breeding season. Disease case-mortalities, however, depended on strain virulence grade and time since disease arrival in the population for the case of rabbits infected with myxoma virus and on rabbit age for the ones with rabbit haemorrhagic disease. In conclusion, global spatio-temporal patterns of rabbit survival emerge from a combination of factors that interrelate both directly and through density-dependent mechanisms and understanding those interaction is crucial to improve conservation and management actions.

Introduction

Variability in demographic parameters may strongly affect species population dynamics and extinction risks (Mazaris and Matsinos 2006, Ozgul et al. 2006). These parameters change through time and space and understanding which factors are controlling that variation is crucial to conservation biology and management decisions (Rachlow and Berger 1998, Pryde et al. 2005, Berkeley et al. 2007, Nelson et al. 2009). Survival is one of the most investigated population parameters especially in mammals. Numerous studies have previously associated temporal and spatial variability in mammal survival rates to environmental and intrinsic variables (Jorgenson et al. 1997, Coulson et al. 1999, Owen-Smith et al. 2005, Descamps et al. 2008). However, despite the importance of considering as much variability as possible to better understand the system and to avoid casual results, most authors have usually work with only one or a few populations.

This is the case of the European wild rabbit (*Oryctolagus cuniculus*). Their survival has been greatly studied due to the need for both controlling and preserving some of their populations. Factors such as predation and infectious diseases and to a lesser extent other mortality sources (e.g. flooding) have been found to explain survival rates (Villafuerte 1994, Reddiex et al. 2002, Calvete et al. 2002, Rodel et al. 2009). However, despite rabbits being one of the most widely distributed mammals in the world (Flux and Fullagar 1992, Thompson and King 1994), authors have usually focused on specific populations, periods, mortality causes, or age class, without understanding the global variability in wild rabbit survival and how the different survival rates might be interrelated.

Therefore, the objectives of this study were to examine the spatio-temporal variability in rabbit survival and to identify the factors affecting overall and cause-specific survival rates at large scales at the same time as we investigate potential relationships between the different sources of mortality. As in other mammal species (Gaillard et al. 1998, Ozgul et al. 2006), we would expect predict higher and less variable survival probabilities for older than for younger animals. Also, we predict these spatio-temporal patterns found in survival will be determined by age-specific interactions among the mortality factors (predation, infectious diseases, climate, and density dependence). Studies like this which identifying what drives survival changes across space, time and age class will be essential to truly understand population dynamics of these mammal species and predict future trends.

Methods

We obtained information on survival of wild rabbits from 91 publications, between 1953 and 2008, mainly from Spain, France, Germany, UK, Australia, and New Zealand. We gathered data on survival rates, predation, rabbit consumption by predators, disease occurrence, disease mortality and other sources of mortality. Related attributes, such as rabbit age, season, or year, were also collected when possible. Finally, information on climatic conditions in each study area was obtained from nearby meteorological stations. In order to accomplish our objectives, we took a two step approach in which we first examined variability in total survival rates and afterwards performed specific analyses for each cause of mortality.

Overall survival patterns

To investigate temporal and spatial variation in total survival rates, we classified data in three age categories: newborn (less than 1 month), juvenile (from 1 to 4 months) and adults (older than 4 months of age) and compared the survival variability (i.e. coefficient of variation (CV) and standard deviation) of different age classes both across and within studies. We also used survival probabilities from the different studies to perform pairwise correlations between age groups.

Additionally, we performed a generalized linear mixed model (GLMM) using total survival rates as the dependent variable in order to understand which factors are determining those survival variability patterns. Survival records from different study periods (Appendix 1) were standardized by converting them to monthly probabilities (30.4 days), which followed a beta distribution, and the study site was incorporated as random variable to account for the within-study correlation. We then tested for the effect of rabbit age (in months), diseases present in the population, climate, and the interaction between presence of diseases and climate with age. Unfortunately, appropriate data on predation pressure was not available to be tested in the model.

In cases in which rabbit weight was provided instead of age, we used data from other publications of the same or nearby populations to find equivalences between rabbit body mass and the age in months (*age_months*). If rabbit age was expressed as an interval, we used the mean between the extreme values and when the higher limit of the interval was not given (e.g. over 4 month of age), we set a maximum value of 33 months, which is a reasonable life expectancy as shown by Gibb and Fitzgerald (1998) and von Holst et al. (1999).

Regarding diseases, we considered only the two diseases that cause the highest mortalities in rabbit populations: myxomatosis and rabbit haemorrhagic disease (RHD). There were four categories of this variable (*diseases*) depending on the number of diseases that had reached the population by the study period: No diseases, only myxomatosis, only RHD or both diseases. Since high rainfall and low temperatures might be a source of mortality in some areas, we also included mean annual precipitation (*total_p*) and temperature (*mean_t*) as a measure of the climatic conditions in the area and since warren rainfall may affect rabbits differently depending on their age (e.g. warren flooding), we also included the interaction between *total_p* and *age_months*.

The low availability of rabbit density information in the reviewed studies prevented us from including also the effect of density-dependence in the model. However, we were able to apply a second GLMM to a few data provided by Lombardi et al. (2003) and Parer (1977) to test for the association between adult survival rates and density (*rabbit_dens*). In order to make densities comparable across areas, we scaled them from 0 to 1 within each study ((density - density $_{min}$)/(density $_{max}$- density $_{min}$)). In all cases we used the study site as random variable and a beta distribution for the survival data.

Specific Sources of Mortality

Data concerning specific causes of mortality was also compiled and analysed to understand which variables where controlling its spatio-temporal variability. To investigate factors affecting predation upon rabbits, we applied a GLMM to predation rates available within 12 studies (Appendix 1) using the study site as random factor to avoid pseudoreplication. The dependent variable, which was assumed to follow a beta distribution, were predation rates previously standardized to periods of 30.4 days.

Due to the lower sample size we only tested for the effect of age of rabbits (in months) and its interaction with the presence of diseases. Two of these previous studies (Robson 1993, Moriarty et al. 2000) provided data on relative densities of rabbits and their predators along the year. For these studies, we performed an additional model in which predation rate was regressed against *rabbit_dens* and relative predator density (*predator_dens*). Also, including study site as a random factor. For comparison's sake, the latter variable was also standardized from 0 to 1 ((density - density $_{min}$)/(density $_{max}$- density $_{min}$)).

To further explore patterns of predation on wild rabbits, we also performed four GLMMs with information on rabbit consumption by predators (i.e. predator diet; Appendix 1). Study site and predator species were included as random factors in all cases to account for autocorrelation within study and predator species. First, we examined the impact of *season* and *diseases* on the frequency of rabbit occurrence in diet samples. Then, using percentages of rabbit biomass in predator diet, we were able to test for the effect of *predator_type* (generalist or specialist) and the interaction between the latter and *season.* Both response variables (i. e. rabbit occurrence and biomass) were assumed to follow a negative binomial distribution.

In the two last diet models, the response variable was the relative percentage of each rabbit age fed upon by predators, which was assumed to follow a negative binomial distribution. These data allowed us to investigate differences in rabbit age preferred by generalist *vs*. specialist species by including the interaction between *age_class* (newborn, juvenile and adult as defined above) and *predator_type* as the independent term of one of the GLMM. In the other model, we considered instead the interaction between *season* and *age_class* to evaluate if the percentages of each age class consumed by predators changed through the year.

Another important source of mortality in rabbits are infectious diseases, such as myxomatosis and RHD, which became endemic in the populations causing annual or biennial outbreaks (Villafuerte et al. 1995, Fenner and Fantini 1999, Bruce et al. 2004). We analyzed data from studies describing epidemics of these two diseases in different areas and years (Appendix 1) in order to determine which variables control the spatiotemporal variability in disease occurrence and case-mortality in wild rabbit populations. First, presence/absence of disease activity in a given month was regressed against climatic variables and time of the reproductive season. In the GLMMs of both diseases, the dependent variable was binomially distributed and study site was again used as random factor. Data corresponding to the first epidemic outbreak were omitted from the analyses since the absence of antibodies in the population could act as a confounding factor in disease phenology.

Since climate may affect disease transmission (e. g. modifying vector abundance or virus persistence) we evaluated if mean annual precipitation (*total_p*), monthly rainfall *(precip),* and temperature in each month (*temp*) had any effect, either linearly and quadratically, on the probability of observing a disease. Time since the onset of the breeding season (*breed_month*) was also included since reproduction drives the input of susceptible young entering a population, which is necessary for a disease to erupt. This variable was calculated using the model obtained by Tablado et al. (2009). Months outside the breeding season were assigned the value 0. We also examined the quadratic effect of *breed_month*.

Later, we investigated which factors determine disease-induced mortality once rabbits are infected. For both diseases, the response variable of the GLMMs was case-mortality (percentage of infected rabbits dying from the disease), which appeared to follow a beta distribution and the random factor was also the study site. As explanatory variables we used rabbit age (*age_months*) and years since diseases reached the populations (*time*) to account for development of disease resistance. Sometimes data on myxomatosis or RHD arrival period was obtained from publications of nearby areas. In cases in which laboratory rabbits were used, *time was* assigned the value 1 simulating a population first contact with the diseases. Since there are several strains of myxoma virus with different *a priori* grade of virulence, we also added this variable (*Virulence*) to the independent term of the model. *Virulence* of a given strain is determined using domestic rabbits without resistance and goes from 1 to 5 as in Fenner and Marshall (1957).

Finally, we briefly described the variability in the rest of the mortality, which is due other sources such as flooding or warren collapse and which have not received much attention in literature, but might be also important in explaining the differences in survival rates among wild rabbit populations.

Results

Patterns and variability in total survival

Examining age-specific survival in detail, we observed that, as predicted, survival rates increase in magnitude and decreased in variability with, both spatially and temporally (Table 1). We also found, through pairwise correlations between age-specific rates, that newborn and juvenile survivals tended to be negatively associated contrary to adult and juvenile rates whose correlation was positive (Table 1).

The increase of survival with age was confirmed by the GLMM results. However, we found that this increase varied depending on the diseases present in the population (Table 1). This interaction between *diseases* and *age_months* showed that the presence of diseases in a population decreases survival much more in adult animals than in the younger ones whose survival probabilities appear to remain similar to populations without diseases (Table 1; Fig 1a). In fact, presence of diseases *per se* did not reduce survival significantly. Rabbit age in months also interacted positively with the amount of rainfall in the area, although standard significance levels were not reached. That is, the overall negative effect of annual precipitation on rabbit survival decreases in importance in older rabbits (Table 1; Fig. 1b, c). Other variables, such as mean temperature did not seem to be significantly affecting survival. Using data from Parer (1977) and Lombardi et al. (2003) we were not able to find either a significant effect of population density on adult survival (n = 6).

Table 1. Determinants of wild rabbit survival according to general linear mixed models. Non-significant variables are denoted by ns and sample size is given by n. Lower panel presents mean and variability values of survival for rabbits classified in three age groups, as well as the pairwise correlation coefficient between age-specific survival rates.

Effects	parameter estimate(±se) (n = 61)	F	p-value
Intercept	1.5220 ± 0.7007		
age_months	0.1555 ± 0.0560	9.40	0.0053
diseases	-	-	ns
*age_months*diseases*		3.50	0.0465
No diseases	0		
Myxo	-0.0543 ± 0.0472		
Myxo + RHD	-0.1141 ± 0.0504		
total_p	-0.0020 ± 0.0007	8.76	0.0068
*age_months*total_p*	0.0001 ± 0.00004	3.31	(0.0813)[ρ]
mean_t	-	-	ns

Age class	Mean monthly survival	Std. Deviation	CV	Correlation coeff.
Newborn (<1 month)	0.33 (8.4 – 52.8)	0.15[a] 0.17[b]	0.45[a] 0.27[b]	-0.787 (p=0.11; n=5)
Juvenile (1 - 4 months)	0.62 (32.8 – 78.3)	0.12[a] 0.10[b]	0.20[a] 0.20[b]	0.582 (p=0.08; n=10)
Adults (> 4 months)	0.89 (63.6 – 95.7)	0.08[a] 0.06[b]	0.09[a] 0.12[b]	

[ρ] p-value greater than standard level 0.05

[a] *Between studies.*

[b] *Mean of the within study std. deviations and CVs.*

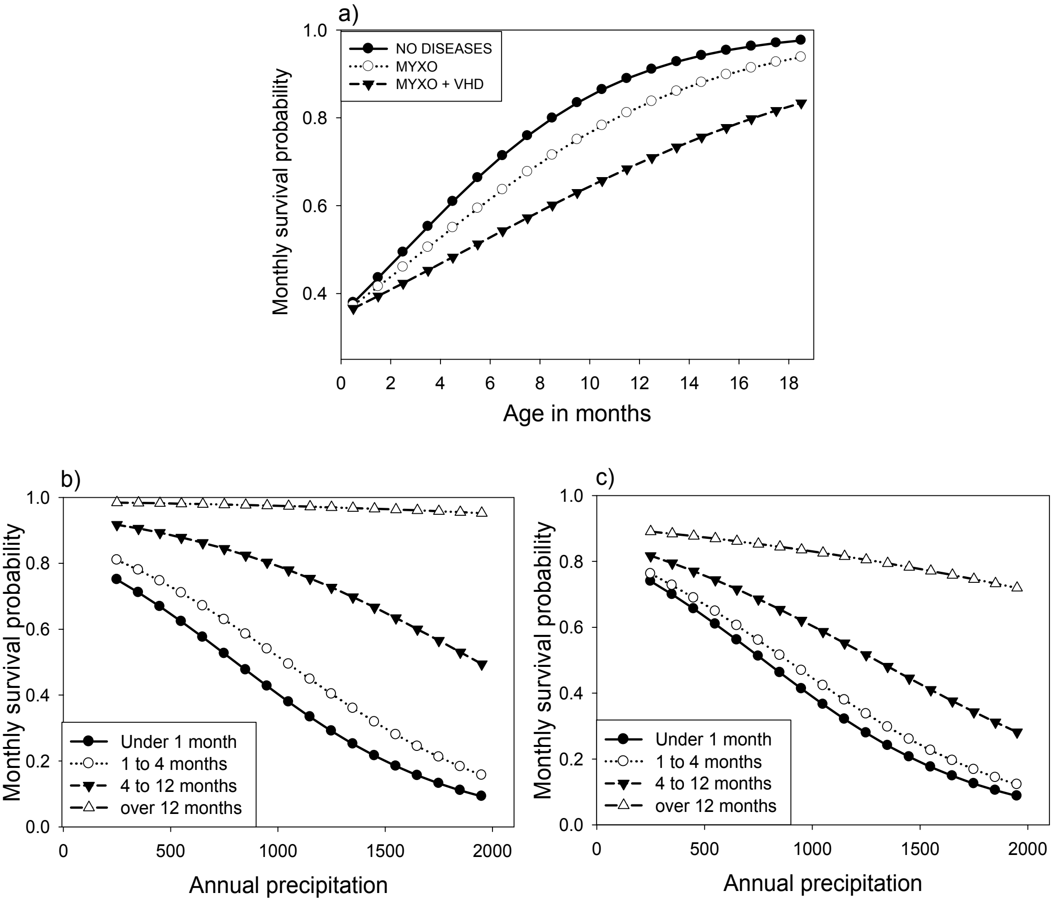

Fig.1. Factors determining wild rabbit survival. Interaction between rabbit age and diseases (a). Varying effect of precipitation on survival as age increases (populations with only RHD were not represented due to the lack of data for this disease category) (b) in a population without diseases and (c) in a population with myxomatosis and RHD.

Causes of mortality

Rabbit age and its interaction with diseases also appear to be important in determining predation rates. Overall predation risk decreases as rabbits grow older (Table 2); however, the trend is shaper in populations without myxomatosis and RHD than in populations where diseases are present. That is, infectious diseases increase predation probability more in juveniles and adults (especially less than 12 months old) than in newborn rabbits (Table 2; Fig 2a). With a different model, we also found that, along the year, predation may vary positively with rabbit and predator density (Table 2).

Table 2. Generalized linear mixed models for the factors controlling rabbit predation (between and within year) and predator food habits (measured as rabbit occurrence and biomass). Sample size (n) consists of the number of predation rates or diet data available in the studies reviewed. Non-significant variables are denoted by ns.

	Predation rate (n = 21)			**Predation rate (along the year) (n = 8)**		
Effects	parameter estimate(±se)	F	p-value	parameter estimate(±se)	F	p-value
Intercept	0.106 ± 0.529					
age_months	-3.474 ± 1.823	5.90	0.0381			
*age_months*diseases*		4.08	(0.0547)$^{\rho}$			
No diseases	0					
Myxo	2.124 ± 1.717					
Myxo + RHD	3.322 ± 1.808					
Intercept				-3.277 ± 1.455		
rabbit_dens				1.526 ± 0.531	8.27	0.0452
predator_dens				1.943 ± 0.490	15.74	0.0166
	Rabbit occurrence in predator diet (n = 32)			**Rabbit biomass in predator diet (n = 53)**		
Effects	parameter estimate(±se)	F	p-value	parameter estimate(±se)	F	p-value
Intercept	3.188 ± 0.245					
Season		3.38	0.0365			
Spring	0.517 ± 0.182					
Summer	0.239 ± 0.183					
Autumn	0.021 ± 0.198					
Winter	0					
diseases		4.37	0.0252			
No diseases	0					
Myxo	0.409 ± 0.214					
Myxo + RHD	0.737 ± 0.251					
Intercept				4.458 ± 0.135		
predator_type					36.08	<.0001
generalist				-0.169 ± 0.150		
specialist				0		
*predator_type*season*				*(fig. 2b)*	6.27	0.0001

$^{\rho}$ p-value greater than standard level 0.05

As for rabbit occurrence in predator food habits, we observed significant intra-annual variations depending on the season of the year and also higher rabbit frequency in predator diet when diseases where present in the population (Table 2). When using percentage of rabbit biomass in diet, we found a significant interaction between *season* and *predator_type*. Specialists consume a similar amount of rabbit in every season, whereas generalist predators include a much higher percentage of rabbit biomass in winter and spring than in autumn (Fig. 2b). In any case, rabbit consumption by specialist predators was always higher than by generalists (Table 2).

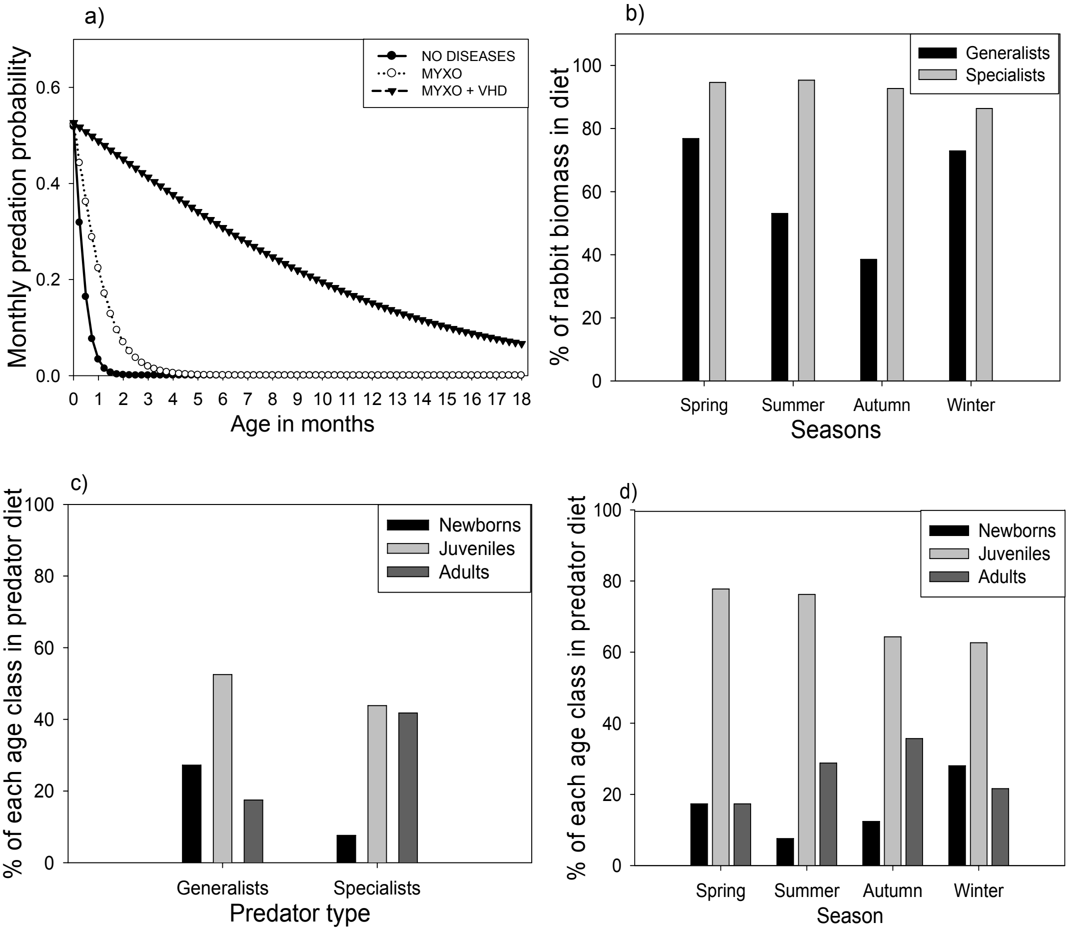

Fig.2. Determinants of rabbit predation risk and predator diet. Effect of rabbit age on predation probability in population differing in disease presence (without diseases and with both diseases simultaneously) (a). Seasonal patterns in rabbit consumption by specialists and generalists predators (b). Representation of each age class in the food habits of specialist and generalist predators (c). Seasonal changes in the percentage of each rabbit age class in predator diet (d).

The results of the last two diet GLMMs showed how *predator_ type* and *season* affect the relative fraction of each rabbit age class present in predator diet. Generalist species made a greater use of juveniles and newborn rabbits while specialists preferred the two older age classes (F = 3.45; df = 44; p = 0.01; Fig 2c;). Throughout the year, juveniles were the most consumed rabbit age group; however the relative percentage of newborns in predator diet increased during the winter and spring months, as opposed to adult rabbits whose relative importance was higher in summer and autumn (F = 8.94; df = 81; p = <.0001; Fig 2d).

As for infectious diseases, we found that the factors associated to myxomatosis activity in rabbit populations are breeding month and annual precipitation, both linearly and quadratically, but not monthly climatic variables (Table 3). This probability decreases during the first months of the breeding season but increases again as the season progresses and may still be relatively high after the end of the reproductive period (i.e. *breed_month* = 0) or in the first months of the next one (Fig. 3a). Myxomatosis outbreaks will be also more common in areas with moderately high mean annual precipitation; however, their probability will decline again in highly wet locations (Fig. 3b).

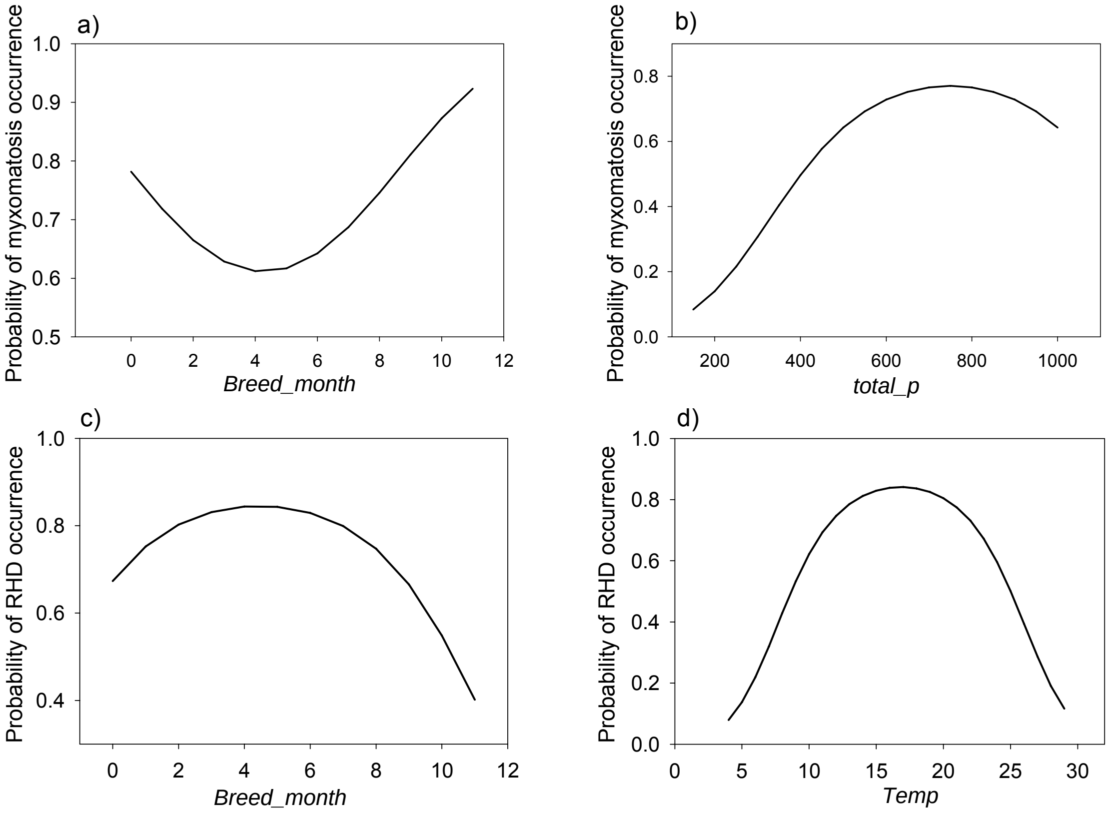

Fig.3. Factors affecting disease phenology, case-mortality and survival times. Effect of month within the breeding season on the probability of myxomatosis (a) and RHD (c) actively present. Occurrence probability of myxomatosis depending on annual precipitation (b) and of RHD with monthly temperature (d).

The phenology of the RHD, on the other hand, appeared to be related linearly and quadratically to monthly temperature. According to these results, it will be more likely to find RHD in months with milder temperatures and the probability declines towards extreme temperatures (Table 3; Fig. 3d). Mean annual precipitation or monthly rainfall did not prove to be significant either linearly or quadratically for this disease. Although standard significance levels were not reached (Table 3), we found that RHD could be also related to the breeding period but in an opposite way with respect to myxomatosis. That is, the probability of encountering rabbits with RHD would increase towards the middle of the reproductive season of a population and not in the end or beginning of it (Fig. 3c).

Regarding disease-related mortality, case-mortality of sick rabbits during a myxomatosis outbreak will decrease as time since the disease was first seen in the population and the virulence grade of the strain increases (Table 3). We were not able to find a significant effect of rabbit age. In the case of RHD; however, lethality does not seem to be influenced by time since disease arrival in the population but increases importantly with the age of sick rabbits (Table 3).

Table 3. Factors affecting disease phenology and mortality according to our analyses. Non-significant variables are designated by ns and sample sizes by n, which in the case of phenology represent number of months with and without disease activity available.

	Myxomatosis phenology (n = 556)			**RHD phenology (n = 165)**		
Effects	parameter estimate(±se)	F	p-value	parameter estimate(±se)	F	p-value
Intercept	-3.724 ± 1.318			-6.282 ± 3.612		
total_p	0.015 ± 0.005	9.25	0.0025	-	-	ns
total_p total_p*	-1E-5 ± 4.4E-6	7.15	0.0077	-	-	ns
Precip	-	-	ns	-	-	ns
precip precip*	-	-	ns	-	-	ns
Temp.	-	-	ns	0.842 ± 0.320	6.92	0.0094
*temp*Temp.*	-	-	ns	-0.025 ± 0.009	8.16	0.0049
breed_month	-0.385 ± 0.112	11.87	0.0006	(0.437 ± 0.242)$^{\rho}$	3.27	0.0726
*breed_month*breed_mont*	0.045 ± 0.013	11.90	0.0006	(-0.049 ± 0.028)$^{\rho}$	3.15	0.0780
	Myxomatosis case-mortality (n = 61)			**RHD case-mortality (n = 26)**		
Effects	parameter estimate(±se)	F	p-value	parameter estimate(±se)	F	p-value
Intercept	3.535± 0.643			-2.286 ± 1.217		
age_months	-	-	ns	1.988 ± 0.376	27.96	<.0001
time	-0.055 ± 0.015	13.21	0.0009	-	-	ns
virulence	-0.875 ± 0.146	36.07	<.0001			

$^{\rho}$ p-value greater than standard level 0.05

Finally, there are other sources of death which have been suggested to be, at least locally, important. These are for example flooding or warren collapse (Copson et al. 1981, Palomares 2003), infanticide (Rodel et al. 2008, Rodel et al. 2009), and coccidiosis (Tyndale-Biscoe and Williams. 1955, Mykytowycz 1962) among other. The mortality due to these causes may greatly vary among areas and affect mainly newborn, with these mortalities ranging from 25 to 75 % (Appendix 2).

Discussion

The global patterns observed confirmed our prediction that survival increases with rabbit age while spatio-temporal variability in age-specific survival rates decreases with age, both within and among studies. Newborn and juvenile rabbits not only had lower but also more variable survival probabilities than adults. This is most likely due to young rabbits being more affected by environmental variability as shown by the interaction between rabbit age and rainfall. A similar pattern was observed by Gaillard et al. (1998) for large herbivores who suggested that higher survival variability in younger classes was due to their greater sensitivity to mortality factors independently of whether they are density-dependent or stochastic and of the taxa involved.

Pairwise correlations between age-specific survival rates, although not significant probably due to small sample sizes, seem to show a positive association between juvenile and adult survival rates implying that both ages are usually affected by similar causes of death (Reed and Slade 2006, Baker and Thompson 2007). On the other hand, the negative apparent correlation between newborn and juvenile survival might suggest that, regardless of the proximate mortality sources, younger age classes are more sensitive to density-dependence, as suggested by Gaillard et al. (1998).Thus, low newborn survival leads to relatively high juvenile survival and *vice versa.*

According to the results of our GLMM, the increase of survival with age appears to have been attenuated with the arrival of myxomatosis and RHD to populations by decreasing survival of older rabbits while overall mortality rates of the youngest ones remain similar. This agrees with results of Henning et al. (2008) who found that predation was much more important than diseases for young rabbits as opposed to older ones. Therefore, the well-known negative influence of these diseases on rabbit population trends (Angulo and Cooke 2002, Henning et al. 2008) may be a consequence of their impact on the oldest ages, both directly and possibly also through increased vulnerability to predation (Fig. 4).

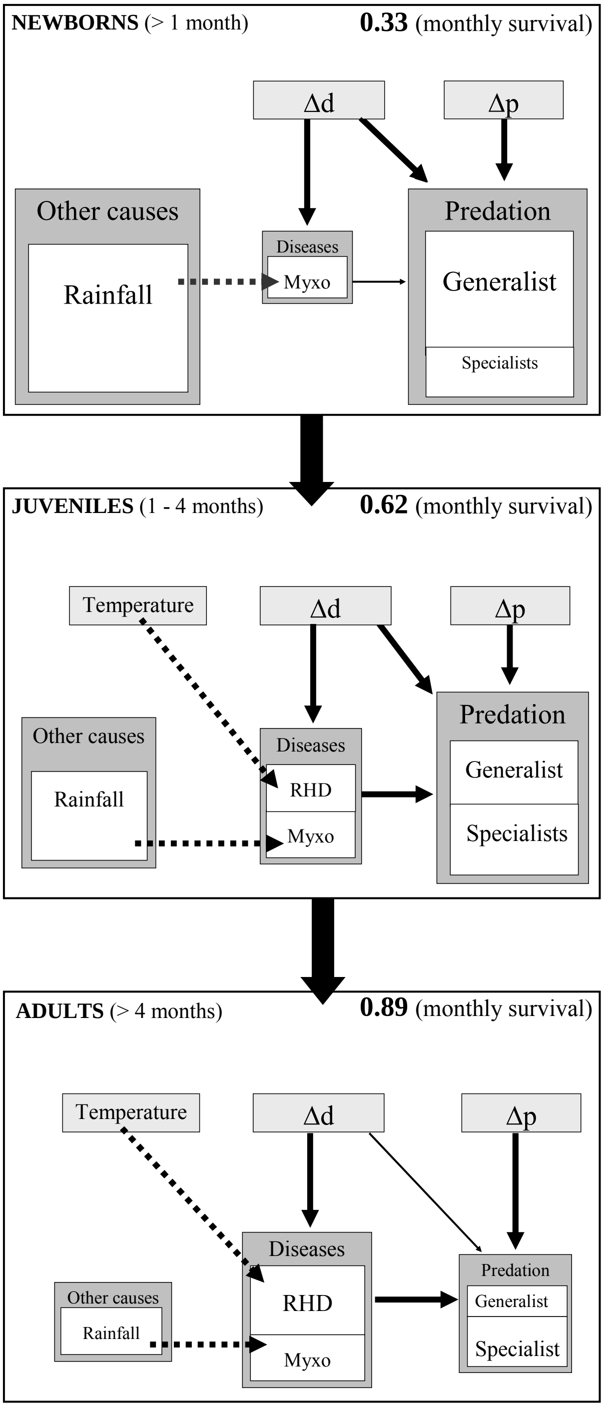

Fig. 4. Schematic view of the factors and variables affecting rabbit survival at different ages. The size of the objects and arrows represents the strength of the effects. Direct influences of climatic variables on specific diseases is expressed with dashed arrows while continuous lines symbolize effects generalized to both diseases or predator types. Δd corresponds to intra-annual variations in rabbit density (breeding season) and Δp refers to intra-annual variations in predator pressure.

Our results also show that annual rainfall has a negative influence on rabbit survival. High precipitation areas are detrimental for rabbits due to warren flooding, hypothermia and collapse (Robson 1993, Palomares 2003). The latter may be the reason for the greater impact of precipitation on younger rabbits with respect to older age groups. Improved pasture growth in regions with abundant rainfall may also lead to dense vegetation that is less digestible for rabbits and thus their body condition may worsen (Williams et al. 1995, Dekker 2007). The positive relationship between myxomatosis and annual precipitation could also be partially responsible for this decrease in rabbit survival with increased rainfall (Fig. 4). This is also consistent with the lower effect of rainfall on older rabbits, which may have antibodies from a previous myxomatosis epidemic. Although some authors have shown an association between low survival rates and cold temperature (Marshall 1959, Rodel et al. 2004), we were not able to demonstrate these effects in our study. This could be due to not having enough variation in temperatures so as to obtain a significant relationship.

We did not find either statistical significance for the influence of density on rabbit survival, probably because of the low sample size. However, the apparent negative trends observed in Lombardi et al. (2003) and Parer (1977) agree with the results of Rodel et al. (2004) who found a decrease in subadult survival as population density increased. Also, as we will see later, density appeared to have a direct effect on specific mortality causes, such as predation rates or disease activity (Fig.4).

As for individual causes of mortality, predation rates also seemed to be affected significantly by age with older rabbits being less predated than younger ones. Disease presence had also an effect on predation through its interaction rabbit age. That is, predation decreased more abruptly with age in populations without infectious diseases than in populations where myxomatosis and RHD were present. Probably because older animals that usually would escape predation might become easy targets when weakened by diseases (Fig. 4). This effect is especially noticeable in adult rabbits less than 12 months of age, since beyond that age animals are more likely to have been previously exposed and immunized against the diseases (Fenner and Fantini 1999; Calvete et al. 2002).

Unfortunately, we cannot distinguish how much of this extra predation corresponds indeed to rabbits eaten as carrion after dying from disease. This pattern could be in part responsible of the similar trends observed in overall survival. Seasonal increases in predator numbers, on the other hand, were found to be positively associated with predation rates in separate analyses. Predation also increased with rabbit density (fig. 4), agreeing with previous studies indicating that predation is density dependent (Erlinge et al. 1984, Sinclair and Pech 1996).

Food habit analyses showed that rabbits are fed upon more often in spring and summer months, which coincides with density peaks at the end of the breeding season in most regions (Fig. 4; Myers et al. 1994, Tablado et al. 2009). Higher disease activity during these seasons could also contribute to this pattern. Indeed, the greater probability of sick rabbit to be predated or eaten as carrion (Rogers et al. 1994, Cabezas 2005) is reflected by the increased rabbit frequency in diet samples of populations with myxomatosis and RHD outbreaks (Fig. 4).

With the data on rabbit biomass in diet, we found that those seasonal variations are due to mainly generalist predators. Specialists, on the other hand, depend on rabbits and consume it in higher proportions without important temporal variations, as shown by the interaction between predator type and season. These findings agree with those obtained by Calzada (2000) and Revilla and Palomares (2002) when examining the diet of single predator species separately.

With further dietary analyses we observed that rabbit age groups are also differently preyed upon depending on the season, and thus on their relative availability. The proportion of juveniles in diet is high throughout the year, but newborns are consumed mainly in winter and spring, which in general corresponds to main breeding season (Myers et al. 1994, Tablado et al. 2009). During the rest of the year, when newborn availability is lower, the relative importance of adult rabbits in diet increases. This coincides with the decrease in rabbit consumption by generalists, who feed mainly on younger classes, and thus specialist species account for most adult predation (Fig. 2b, c, d; Fig. 4). In any case we should be careful when interpreting predator food habits. They help us to understand the system, but the actual impact of predation on rabbit populations cannot be derived from diet data without additional information on predator abundance, rabbit density and attack rates.

Apart from predation, the other main sources of mortality in rabbits are infectious diseases (Appendix 3). This is the case of myxomatosis and RHD in wild rabbits (Fig. 4; Ross et al. 1989, Calvete 2006). These became enzootic lingering, for example, in remnant susceptible rabbits not immunized during epidemics or in infected vectors (Chapple and Lewis 1965, Ross 1972) and breaking out annually or biennially as a result of the input of new susceptible hosts during reproductive pulses (Altizer et al. 2006, Begon et al. 2009). The mortality due to myxomatosis or RHD will depend on, first, the occurrence of an outbreak in the population which infects rabbits and, secondly, on the probability of dying of those sick rabbits.

Our phenological analyses showed that the period of disease activity varies between Myxomatosis and RHD. The period in which myxomatosis outbreaks are more likely goes from the end of the breeding season to the beginning of the next one, that is, from spring to autumn in most locations. These are months when high numbers of susceptible rabbits (Fig. 4) coincide with abundant insects, which are the main vector of myxomatosis transmission, even though direct contact might also be possible (Parer and Korn 1989, Merchant et al 2003). The specific timing of the greatest myxomatosis activity, may then be modified by the type of insects transmitting the disease in each area, since fleas are more active and numerous during rabbit breeding peaks and mosquito number are greater in late spring and early autumn (King and Wheeler 1981, Arthur and Louzis 1988, Merchant et al 2003). Unfortunately, we did not have appropriate data on specific insect vectors in order to further examine this question.

We were not able to demonstrate the influence of monthly temperature and rainfall on myxomatosis phenology but we found a negative quadratic effect of annual precipitation (Fig. 4). That is, wet areas will have higher abundance and activity of insect vectors and thus greater myxomatosis incidence than drier areas (Soriguer 1981, Parer and Korn 1989, Ross et al. 1989, Simon et al. 1998). However, in location with extremely high annual precipitations the occurrence of myxomatosis decreases again. Greater mortalities caused by warren flooding in these populations (Copson et al. 1981) may reduce the availability of susceptible rabbits necessary to sustain myxomatosis outbreaks.

In the case of RHD, precipitation neither monthly nor annual showed a significant effect on disease phenology. The probability of finding sick rabbits in the field is higher in months within rabbit breeding season, even though standard significance levels were not reached (Fig. 4). This may be partially due to greater numbers of sick-to-susceptible contacts during the reproductive period (Cooke 1999, Calvete et al. 2002, Mutze et al. 2002). Temperature also affects RHD occurrence which is more likely in milder months (Fig. 4). High temperatures decrease virus survival (e.g. in infected carcasses), and thus, RHD transmission and activity during hot months (Xu and Chen 1989, McColl et al. 2002). Additionally, extreme temperatures, both hot and cold, may prevent RHD outbreaks by reducing reproduction, and thus, direct contacts and by decreasing vector abundance (e.g. blowflies), which despite not being as important as direct transmission might also participate in spreading the disease, mainly between locations (Asgari et al. 1998, Cooke and Berman2000).

For both diseases, phenology might be also modified by mechanisms which limit the number of sick animals in the population, such as the presence of maternal antibodies transmitted from recovered does to their offspring which protect rabbits for about two months after birth (Fenner and Marshall 1954, Lenghaus et al. 1994; Appendix 3). In some areas, the phenology of the diseases could also be affected by the 'ecological interference' (Rohani et al. 2003) between myxomatosis and RHD. That is, in populations were both diseases are present, density reductions caused by one population could delay the outbreak of the other disease until the number of susceptible rabbits recovers, as suggested by Mutze et al. (2002) in a population in South Australia.

In this study, we also show differences in case-mortality between diseases (Appendix 3). According to our findings, the high case-fatality of RHD is modified by rabbit age. This effect was already showed by Robinson et al. (2002), who found that rabbits under four weeks of age might get infected but usually do not die from RHD, this survival tends to decrease importantly with age especially if maternal antibodies are not present, and by 3 months of age the disease kills around 90% of sick rabbits. Some authors have suggested that genetic resistance to RHD could develop in wild rabbits (Villafuerte et al. 1995, Cooke 1999, White et al. 2001); however, more time might be necessary for this resistance to appear, since we did not encounter any significant effect of time since disease arrival on case-mortalities.

Myxomatosis case-fatalities, on the other hand, have showed a considerable decrease since the introduction of the disease. Shortly after the release of the virus, new strains with lower virulence but enhanced transmission started to establish in rabbit populations (Fenner 1983, Kerr and Best 1998). This attenuation allowed for the selection of genetically resistant rabbits (Marshall and Douglas 1961, Fenner 1983), which in turn might have promoted the selection again of strains slightly more virurent (Fenner and Fantini 1999, Aparicio et al. 2006). In any case, attenuated strains together with genetic resistance have led to the relatively low mortalities directly caused by myxomatosis in current rabbit populations (i.e. average 33%; Table 4).

Although several authors have shown an increase in survival to myxomatosis infection with age (Fenner and Ratcliffe 1965, Parer et al. 1994), we were not able to demonstrate this trend when pooling data from different authors. This may be due to factors increasing young survival which could not be controlled for in this study, such as genetic resistance or sire effect. The latter is a mechanism not well understood yet but which seems to protect kittens born within nine months of paternal infection with myxoma virus (Sobey and Conolly 1986, Williams and Moore 1991, Parer et al. 1995). Maternal antibodies, however, could be ruled out since rabbits used in all survival experiments were previously tested for antibody presence and excluded if positive.

Another reason for the lack of significant correlation between rabbit age and myxomatosis case-fatality could be the low variability in age data, since rabbits used in most studies were older than 3-4 months. It has also been suggested that Grade I strains could behave in an opposite way to the other strains (Sobey et al. 1970, Parer et al. 1994) thus, contributing to obscure the overall influence of age on myxomatosis mortality. Unfortunately, available data did not allowed for the examination of this interaction.

Apart from time since arrival, virulence grade and possibly age, myxomatosis case-mortality appears also to decrease with environmental temperature. Although we could not test the effect of this variable in our analyses, its influence has been already shown by Mykytowycz (1956) and Marshall (1959) and could explain the higher case-fatalities of winter epidemics with respect to summer ones (Fenner 1959, Arques 2000).

Finally, rabbits might be affected by other causes of mortality (e.g. malnutrition, flooding, collapse, coccidiosis or infanticide) which are not generally considered relevant at a global scale but which may strongly influence local survival patterns (Copson et al. 1981, Palomares 2003, Rodel et al. 2008). These sources of death are especially important for newborn rabbits in the nest and juveniles (Tyndale-Biscoe and Williams 1955, Gibb and Fitzgerald 1998, Rodel et al. 2009), as shown, for example, for the interaction between rainfall and rabbit age in our survival analyses (Fig. 4). Sometimes this type of mortalities may be underestimated through its assignment to predation or infectious diseases (e.g. dead rabbits eaten as carrion; Tyndale-Biscoe and Williams 1955, Webb 1993). However, there are studies, such as Rodel et al. (2009), which highlight their importance, since they found that around 50% of litters were still lost after eliminating myxomatosis, RHD and most predation from their enclosed population. Thus, the similarly low survival probabilities found in younger rabbits even in populations without epidemic diseases or predation suggests that to some extent causes of mortality might be compensatory at those ages.

In conclusion, the general pattern of increased survival rates and decreased variability found in European wild rabbits appears to result from the combination of different factors (predation, myxomatosis, RHD, and climate) which interplay with density-dependence and compensatory effects. Future studies should focus on further investigating the potential interactions and compensation between the different sources of mortality, as well as examining the reproductive response of populations exposed to those mortalities. Only then will we be able to understand population dynamics of this species and optimize efforts for controlling or preserving it.

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Appendix 1. Publications reviewed for this study and type of analyses in which they where used.

STUDY	LOCATION	LATITUDE	ANALYSES
Arques 2000	Alicante (E Spain)	38º20'N, 0º28'W	7, 8
Arthur 1980	Auffargis (N France)	48º39'N, 1º50'E	1, 2, 3, 7
Asgari et al. 1998	Australia		
Best and Kerr 2000	Canberra (SE Australia)	35°13'S, 149°08'E	
Bruce and Twigg 2005	Kojaneerup (SW Australia)	34°32'S, 118°21'E	10
Calvete et al. 2002	Zaragoza (N Spain)	41°39'N, 0°53'W	1, 3, 7
Calvete et al. 2004	Zaragoza (N Spain)	41°39'N, 0°53'W	1, 2, 3
Calzada 2000	Donana National Park (S Spain)	37º09'N, 6º26'W	5, 6
Catling 1988	Yathong Nature Reserve (SE Australia)	33º45'S, 145º30'E	4, 6
Chapple and Lewis 1965			
Chapuis et al. 1994	Kerguelen Islands (Indian Ocean)	49°20'S, 69°20'E	
Cooke 1999	Australia		
Cooke et al. 2000	Gum Creek (S Australia)	31º25'S, 138º45'E	
Cowan and Roman 1985	Oxfordshire (S UK)	51º53'N, 1º19'W	1, 2
Delibes and Hiraldo 1981	Spain		6
Donazar 1989	Navarra (N Spain)	42º42'N, 1º40'W	6
Dunnet 1957	Canberra (SE Australia)	35°13'S, 149°08'E	6
Dwyer et al. 1990	Laboratory Rabbits		
Fedriani et al. 1999	Donana National Park (S Spain)	37º09'N, 6º26'W	5, 4, 6
Fenner 1959	Laboratory Rabbits		
Fenner 1983	Gippsland (SE Australia)	37º50'S, 147º37'E	9
	Mallee (SE Australia)	34º10'S, 142º08'E	9
Fenner and Fantini 1999			
Fenner and Marshall 1954	Laboratory Rabbits		
Fenner and Woodroofe 1953	Laboratory Rabbits		
Fenner et al. 1953	Australia		
Fouchet et al. 2008			
Fullagar 1977	Canberra (SE Australia)	35°13'S, 149°08'E	
Gibb and Fitzgerald 1998	Orongorongo Valley (New Zealand)	41º18'S, 174º46'E	1, 2, 3, 4, 6
Gibb et al. 1985	Wairarapa (New Zealand)	41º10'S, 175º20'E	1
Gilbert et al. 1987	Canberra (SE Australia)	35°13'S, 149°08'E	1
	Chidlow (SW Australia)	31°57'S, 116º19'E	1
	Snowy plains (SE Australia)	36°20'S, 148º20'E	1
	Tero creek (SE Australia)	30°14'S, 142º48'E	1
	Urana (SE Australia)	35º18'S, 146º11'E	1
	Wairarapa (New Zealand)	41º10'S, 175º20'E	1
Gilbert and Myers 1981	Snowy plains (SE Australia)	36°20'S, 148º20'E	1
	Urana (SE Australia)	35º18'S, 146º11'E	1
Gil-Sanchez et al. 1999	Sierra de Huetor (S Spain)	37º17'N, 3º39'E	4, 5
Gregg et al.1991	Mexico		
Henning et al. 2006	Himatangi (New Zealand)	40º25'S, 175º18'E	8
Kerr 1997	Australia		
Kerr et al. 2003	Canberra (SE Australia)	35°13'S, 149°08'E	9
King and Wheeler 1981	Cape naturaliste (SW Australia)	33º34'S, 115º02'E	1, 2
	Chidlow (SW Australia)	31°57'S, 116º19'E	1
Lenghaus et al. 1994	Geelong (SE Australia)	38º06'S, 144º17'E	10
	Laboratory Rabbits		
Lombardi et al. 2003	Donana National Park (S Spain)	37º09'N, 6º26'W	1, 3
Marchandau et al. 1998	Ile de France (N France)	48º40'N, 1º60'E	1, 2
Marchandeau and Boucraut-Baralon 1999	Massereau (France)	47º14N, 1º55E	7
Marshall 1959	Laboratory Rabbits		

Marshall and Douglas 1961	Laboratory Rabbits		
	Maryvale (SE Australia)	36º43'S, 142º10'E	9
	Ouyen (SE Australia)	35º08'S, 142º16'E	9
	Urana (SE Australia)	35º18'S, 146º11'E	9
Marshall and Fenner 1958	Albury (SE Australia)	36º03'S, 146º54'E	9
	Barrenbox (SE Australia)	34º15'S, 146º03'E	9
	Laboratory Rabbits		
	Maryvale (SE Australia)	36º43'S, 142º10'E	9
	Noorong (SE Australia)	35º19'S, 143º54'E	9
	Urana (SE Australia)	35º18'S, 146º11'E	9
	Yarram (SE Australia)	38º31'S, 146º39'E	9
McColl et al. 2002	Laboratory Rabbits		
Merchant et al. 2003	Cooma (SE Australia)	36º14'S, 149º07'E	7
Moreno et al. 2004	Donana National Park (S Spain)	37º09'N, 6º26'W	1
Moriarty et al. 2000	Oaky creek (SE Australia)	33°24'S, 149°22'E	1, 3, 7, 8
Morisse et al. 1991	Laboratory Rabbits		10
Mutze et al. 1998	Gum Creek (S Australia)	31º25'S, 138º45'E	10
Mutze et al. 2002	Gum Creek (S Australia)	31º25'S, 138º45'E	7, 8
	Coorong National Park (S Australia)	36º12'S, 139º20'E	7, 8
Myers 1971	Tero creek (SE Australia)	30°14'S, 142º48'E	1
	Urana (SE Australia)	35º18'S, 146º11'E	1
Palomares et al. 1995	Donana National Park (S Spain)	37º09'N, 6º26'W	5, 6
Parer 1977	Urana (SE Australia)	35º18'S, 146º11'E	1, 2, 3, 9
Parer and Fullagar 1986	Mitchell (E Australia)	26º32'S,148º01E	1, 7
Parer et al. 1994	Alice Springs (Central Australia)	23º42'S, 133º52'E	9
	Calindary (Australia)	30º15'S, 142º29'E	9
	Cape naturaliste (SW Australia)	33º34'S, 115º02'E	9
	Pine Plains (SE Australia)	35º26'S, 141º56'E	9
	Urana (SE Australia)	35º20'S, 146º16'E	9
	Yathong Nature Reserve (SE Australia)	32º51'S, 145º53'E	9
Parer et al. 1995	Alice Springs (Central Australia)	23º42'S, 133º52'E	9
	Calindary (Australia)	30º15'S, 142º29'E	9
	Christchurch (New Zealand)	43º33'S, 172º40'E	9
	Pine Plains (SE Australia)	35º26'S, 141º56'E	9
	Urana (SE Australia)	35º20'S, 146º16'E	9
	Yathong Nature Reserve (SE Australia)	32º51'S, 145º53'E	9
Parkes et al. 2002	Earnscleugh (New Zealand)	45º10'S, 169º20'E	10
Reddiex et al. 2002	North Canterbury (New Zealand)	42º52'S, 172º50'E	1, 3, 8
Revilla and Palomares 2002	Donana National Park (S Spain)	37º09'N, 6º26'W	5, 6
Richardson and Wood 1982	Canberra (SE Australia)	35°13'S, 149°08'E	1, 3
Robinson et al. 2002	Canberra (SE Australia)	35°13'S, 149°08'E	10
Robson 1993	North Canterbury (New Zealand)	43º02'S, 172º59'E	1, 2, 3
Rodel et al. 2008	Bayreuth (E Germany)	49º32'N, 11º21'E	1
Rodel et al. 2009	Bayreuth (E Germany)	49º32'N, 11º21'E	1
Ross 1972			
Ross and Sanders 1977	Downham Market (E UK)	52º37'N, 0º23'E	9
	Laboratory Rabbits		
Ross and Sanders 1984	Glen esk, Angus (Scotland)	56º48'N, 2º56'W	9
	Hants, Micheldever (S UK)	51º08'N, 1º16'W	9
	Laboratory Rabbits		
	Salisbury, Wiltshire (S UK)	51º04'N, 1º48'W	9
Ross et al. 1989	Bow hill, Chichester (S UK)	50º56'N, 0º49'W	7, 9
	Bridgets Farm, Winchester (S UK)	51º08'N, 1º14'W	7, 9
	Bylchau Farm, Llanwrtyd wells (Wales)	52º05'N, 3º39'W	7, 9
Saurat et al. 1980	Laboratory Rabbits		
Simon et al. 1998	Navarra (N Spain)	42º42'N, 1º40'W	
Smid et al. 1991	Laboratory Rabbits		
Sobey and Conolly 1986	Laboratory Rabbits		

Sobey et al. 1970	Urana (SE Australia)	35º20'S, 146º16'E	9
	Laboratory Rabbits		
	Natimuk (SE Australia)	36º43'S, 141º54'E	9
	Seaspray (SE Australia)	38º22'S, 147º12'E	9
Soriguer 1981	Sierra de Caravales (S Spain)	37º54'N, 6º27'W	7
Trout et al. 1992	Bridgets Farm, Winchester (S UK)	51º08'N, 1º14'W	9
Twigg et al. 1998	Wellstead (SW Australia)	34º31'S, 118º35'E	7
Tyndale-Biscoe and Williams 1955	Hawkes bay (New Zealand)	39º31'S, 176º53'E	1, 2, 6
Villafuerte 1994	Donana National Park (S Spain)	37º09'N, 6º26'W	1, 2, 3, 6
Villafuerte et al. 1995	Zaragoza (N Spain)	41°39'N, 0°53'W	6
Webb 1993	Norwich (E UK)	52º38'N, 1º19'E	1, 2
Westbury 1996	Australia		
White et al. 2004	Exminster, Devon (SW UK)	50º39'N, 3º29'W	
	Frensham, Surrey (S UK)	51º10'N, 0º46'W	
	Logiealmond, Perthshire (Scotland)	56º26'N, 3º37'W	
Williams and Moore 1991	Quinyambie (Australia)	30º40'S, 140º55'E	9
	Snowy plains (SE Australia)	36°14'S, 148°33'E	9
	Urana (SE Australia)	35º16'S, 146º09'E	9
Williams and Parer 1972	Urana (SE Australia)	35º20'S, 146º16'E	7, 9
Williams et al. 1972	Canberra (SE Australia)	35°13'S, 149°08'E	
Williams et al. 1973	Canberra (SE Australia)	35°13'S, 149°08'E	
Williams et al. 1990	Quinyambie (Australia)	30º40'S, 140º55'E	9
	Snowy plains (SE Australia)	36°14'S, 148°33'E	9
	Urana (SE Australia)	35º16'S, 146º09'E	9
Williams et al. 2007	Canberra (SE Australia)	35°13'S, 149°08'E	1, 2
Wood 1980	Calindary (Australia)	30º15'S, 142º29'E	1, 2, 3
Xu and Chen 1989			

1 = Survival GLMM and varibility, 2 = Correlations between age-specific rabbit survivals , 3 = Predation rate GLMMs, 4 = Analysis on rabbit occurrence in predator diet, 5 = Model on rabbit biomass consumed by predators, 6 = Examination of the percentages of each rabbit age class present in predator diet, 7 = Myxomatosis phenology, 8 = RHD phenology GLMM, 9 = Factors affecting myxomatosis case-mortality, and 10 = Analysis of RHD case-fatality.

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Appendix 2. Mortality rates due to causes other than predation, myxomatosis and RHD.

Study	Location	Age Class	Monthly Mortality (%)
Arthur 1980	Auffargis (N France)	Newborn	0.245
Calvete et al. 2002	Zaragoza (N Spain)	Adult	0.001
Gibb and Fitzgerald	Orongorongo Valley (New Zealand)	Newborn	0.745
Reddiex et al. 2002	North Canterbury (New Zealand)	Newborn	0.590
Robson 1993	North Canterbury (New Zealand)	Newborn	0.290
Rodel et al. 2008	Bayreuth (E Germany)	Newborn	0.580
Rodel et al. 2009	Bayreuth (E Germany)	Newborn	0.450
Villafuerte 1994	Donana National Park (S Spain)	Newborn	0.704

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Appendix 3. Epidemiological parameter of myxomatosis and RHD.

Parameter	Myxomatosis	Rhd	Source
Epidemic period (Months/year)	6.1 (2.5 - 10.9)	3.7 (1 - 7.6)	See Appendix 1 (disease phenology)
Morbidity (%)			
Prevalence during outbreaks	41 (25 – 84)	85 (77 – 98)^{a}	Williams and Parer 1972; Williams et al.1972; Mutze et al. 1998; Marchandeau and Boucraut-Baralon 1999; Parkes et al. 2002; Bruce and Twigg 2005
Annual Incidence	18, 24	-	Simon et al. 1998; Marchandeau and Boucraut-Baralon 1999
Spread rate (days to given prevalence)	42 – 77	56	Williams and Parer 1972; Bruce and Twigg 2005
Main route of transmission	Insect vectors	Direct contact	Xu and Chen 1989; Chapuis et al. 1994; Asgari et al. 1998; Fouchet et al. 2008
Infective virus persistence (days)	At least 100^{f}	At least 20 - 25^{g}, 30^{h}	Chapple and Lewis 1965; Gregg et al. 1991; Lenghaus et al. 1994; Westbury 1996; McColl et al. 2002
Failure to infection after challenge (%)	26.4 (3.8 -87.5)	25^{b}	Fenner and Marshall 1954; Robinson et al. 2002; Kerr et al. 2003
Severe clinical signs			
Day of appearance	10 (5 - 16)	0.75	Fenner and Woodroofe 1953; Ross et al. 1989; Lenghaus et al. 1994; Kerr 1997; Fenner and Fantini 1999; Best and Kerr 2000; Kerr et al. 2003
Duration	25 (13 - 35)	1.25 (0.1 - 2.3)	Williams and Parer 1972; Ross et al. 1989; Lenghaus et al. 1994; Best and Kerr 2000; Cooke and Berman 2000; Robinson et al. 2002; Kerr et al. 2003
Survival time (days)	28 (19 - 36)^{c}	1.9 (0.83 - 3.00)	Lenghaus et al. 1994; Cooke and Berman 2000; Robinson et al. 2002 and See Appendix 1 (Myx)
Case-fatality in wild rabbits	33 (0 - 62)^{c}	3, 54, 86, > 90^{d}	See Appendix 1 (Myx, VHD)
Antibody persistence			
Post-recovery (months)	7- 19	6 - 18	Fenner et al 1953; Fenner and Marshall 1954; Lenghaus et al. 1994; Kerr 1997; Arques 2000
Maternal (weeks)	6 – 8	8 (5 - 11)	Fenner and Marshall 1954; Ross 1972; Lenghaus et al. 1994; Kerr 1997; Cooke 1999; Cooke et al. 2000
Post-recovery antibody protection	Usually complete^{e}	Usually complete^{e}	Fenner et al. 1953; Saurat et al. 1980; Cooke et al. 2000; Fenner and Fantini 1999
Maternal antibody effect			
Additional infection failure (%)	36	-	Fenner and Marshall 1954
Additional reduction of lethality (%)	25 - complete^{e}	complete, 43, 26, Na^{d}	Fenner and Marshall 1954; Ross 1972; Robinson et al. 2002
Sire effect resistance			
Months from sire infection to offspring birth	up to 6 - 9	Na	Williams and Moore 1991; Parer et al. 1995
Additional reduction of lethality (%)	21 - 36	Na	Williams and Moore 1991; Parer et al. 1995

a Refering to first epizootics of rhd, currently the values might be lower.
b For animals aged between 5 - 8 weeks
c Since it depends on many factors (see table 3), here we only consedered values after 1970 for the most common field strains (i.e.Virulence from 2-4; according to Fenner and Fantini 1999)
d Values correspond to age classes: <1, 1-2, 2-3, >3 months respectively
e They might still get infected and have milder symptoms and antibody titres would be boosted
f In infected fleas
g Depends on temperature and substrate, we show the case of rabbit carcasses and warrens at about 22°C
h Rabbit that have recovered from the disease
Na Not aplicable in those cases

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Capítulo 3

Contrasting effects of climate change on rabbit populations through reproduction

Tablado, Z., E. Revilla & F. Palomares

Manuscrito en preparación

Resumen

El cambio climático está afectando a muchos procesos físicos y biológicos en todo el mundo y anticipar sus efectos en las poblaciones es una de las prioridades de los científicos, especialmente en el caso de especies que están en peligro o son invasoras. Los primeros esfuerzos se centraron en predecir las futuras distribuciones y probabilidades de extinción de las especies basándose directamente en las condiciones climáticas existentes en las áreas de distribución actuales. Sin embargo, la relación entre las variables climáticas y los parámetros poblacionales puede ser tan compleja que para poder hacer predicciones primero deberíamos entender cuales son y como van a estar afectados los procesos biológicos individuales que subyacen a la distribución de las especies. En este estudio nosotros utilizamos un modelo mecanístico basado en la fisiología reproductiva del conejo de campo para mostrar como el cambio climático va a alterar profundamente la longitud y variabilidad interanual de la longitud del periodo reproductor de esta especie a lo largo de Europa y evaluar como esos cambios pueden afectar además a su dinámica poblacional. En gran parte del actual área de distribución del conejo los periodos reproductores se acortaran y se harán más variables, lo que se traducirá en declives poblacionales y menor capacidad de respuesta ante perturbaciones. Aunque esto puede ser ligeramente beneficial en áreas donde los conejos son considerados como una peste, las mayores disminuciones poblacionales y aumentos en la probabilidad de extinción ocurrirán en el SO de Europa, donde los conejos son una especie nativa y clave. En estas zonas, por lo tanto, el declive de los conejos tendrá consecuencias muy negativas para la biodiversidad de los ecosistemas mediterráneos.

Por otra parte, en las regiones del note y este del área de distribución de la especie, la abundancia de conejos aumentará debido a un incremento en la longitud y estabilidad de las estaciones reproductoras, reduciendo las limitaciones que este parámetro reproductivo puede imponer en la expansión del conejo hacia nuevas áreas o en el aumento de la amenaza en lugares donde ya esta presente. Nuestro estudio destaca como el cambio climático puede inducir cambios opuestos en un único proceso biológico, el cual al mismo tiempo llevará a alteraciones de la dinámica poblacional a lo largo del espacio. Esto nos obliga a investigar el control y/o conservación de las especies en un contexto más dinámico, considerando las alteraciones, debidas al cambio climático, de los mecanismos que gobiernan el crecimiento y declive de las poblaciones.

Abstract

Climate change is affecting many physical and biological processes worldwide and anticipating its effects at the population level is a research priority, especially for species of conservation or management concern. First efforts focused on directly predicting future species distributions and extinction probabilities based on climatic conditions within their current ranges. However, relationships between climatic variables and population parameters may be so complex that in order to make predictions we should first understand the individual biological processes underlying distribution patterns. Here we use a mechanistic model based on the physiology of European wild rabbit reproduction to show how climate change will deeply modify the length and inter-annual variability of the breeding season of this species across Europe and evaluate how those changes may affect population dynamics. Within most of rabbit current area of distribution, reproductive periods will shorten and become more variable, which will result in population declines and lower resilience to perturbations. Although this may be slightly beneficial in areas where rabbits are now considered as a pest, the stronger population decreases and increased extinction risks will occur in SW Europe, where rabbits are a native keystone species, thus having highly negative consequences for Mediterranean biodiversity. Contrarily, towards northern and eastern regions, rabbit numbers will increase through longer and more stable breeding seasons, reducing the constraints that breeding season length and variability may impose to the invasion or threatening of new areas. Our study highlights how climate can induce contrasting changes on single biological processes, which in turn will lead to rearrangements in species population dynamics across the space. This forces us to investigate management and/or conservation of species in a more dynamic context by considering the alterations, due to climate change, of mechanisms driving population growth and decline.

Introduction to rabbit breeding and distribution

European wild rabbits (*Oryctolagus cuniculus*) are native to SW Europe where they have a high ecological as ecosystem engineer (Ferrer and Negro 2004, Delibes-Mateos et al. 2007) and keystone prey for predator communities and also plays an important role as game species (Angulo and Villafuerte 2003). However, with human help, they have expanded in recent historic times invading multiple territories worldwide (Thompson and King 1994) with thriving populations which are managed as pests due to their damage to agriculture and their impact on local (Lees and Bell 2008).

This is a species for their breeding capacity and the onset and duration of their breeding season are well-known to be controlled by environmental factors (i.e. photoperiod, temperature, and food availability and quality (Poole 1960, Hudson and Distel 1990). A model including average daylength and photoperiod change in each month, a simple and quadratic effect of monthly temperature, and an index of green pastures (defined as available when, in at least one of the previous two months, precipitation (mm) > 2*temperature (ºC)) classifies correctly 84% of the breeding season months anywhere within the current rabbit range (Tablado et al. 2009).

Effect of climate change on rabbit breeding season

Thus, applying this mechanistic model (Tablado et al. 2009) across Europe for a control (1961-1990) and future (2071-2100) climatic period we can examine the effect that climate change will have on the length and inter-annual variability (CV) of rabbit breeding season. Although there are some variations due to the boundary conditions set by the two different general circulation models (GCM) and to the two emission scenarios used in the regional climate model (Déqué et al. 2007, Lenderink et al. 2007), the overall predicted trends are consistent. For 1961-1990 we observed a non-trivial pattern in which breeding seasons are shorter in SW Europe (i.e. Southern Iberian Peninsula) and increase towards the north and east until Eastern Europe and the South of the Scandinavian Peninsula. Beyond these regions as well as in high altitude areas such as the Alps, colder climates reduce again the duration of the reproductive period (Fig. 1; Supplementary Fig. 1).

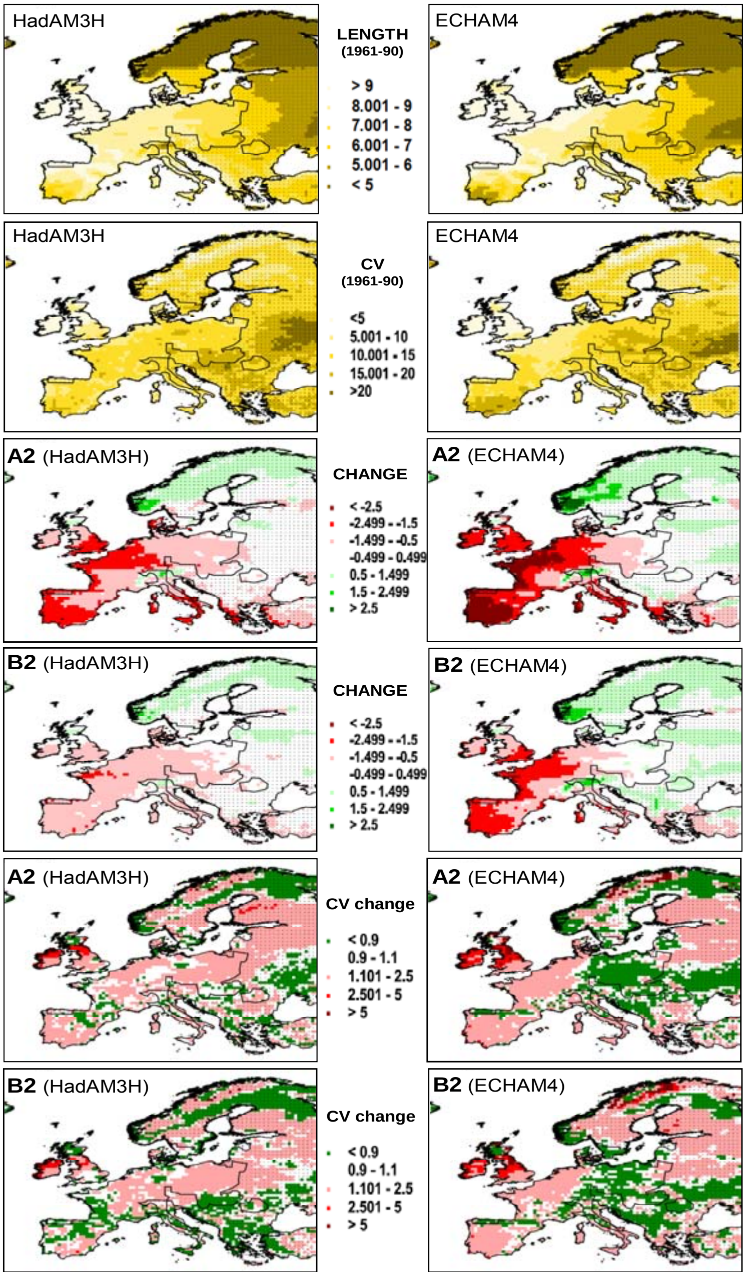


Figure 1. The top four figures show the mean length (months) and CV (%) for the control period. Lower figures represent difference (in months) and changes in inter-annual variability ($CV_{future}/CV_{control}$) from control to future climate. We applied the model in ref Tablado et al. (2009) to monthly temperatures and precipitation predicted for 1961-1990 and 2071-2100 by the Rossby Centre Regional Atmosphere-Ocean model at a 50 km resolution (Döscher et al. 2002). Photoperiod records were provided by the US Naval Observatory. Since rabbits do not breed below 0ºC, reproduction was directly assumed to be absent from months with those temperatures. We considered two scenarios of greenhouse gas emissions (IPCC 2000): A2 (high) and B2 (moderate), each driven by data from two different GCM (Christensen 2005):HadAM3H and ECHAM4. Areas outside current rabbit distribution are marked with dots.

We found that inter-annual variability in the breeding season length also differs greatly from higher values in Mediterranean and continental regions, such as Southern Iberian Peninsula, the Balkans, and Eastern Europe, to less variable seasons in UK, Ireland and mainland areas under a strong Atlantic influence (Fig. 1; Supplementary Fig. 1). These control period results agree greatly with literature data for European populations (Supplementary Table 1).

When comparing with 2071-2100 predictions we observed that climate change will decrease the duration of the reproductive period all over the current range of rabbits in Europe, and these reductions will be especially concerning in the Iberian Peninsula, where seasons were already moderately short in 1961-1990 (Fig. 1; Supplementary Fig. 1). In fact, predicted past trends for Lisbon (West of the Iberian Peninsula) show that this phenomenon could have been already occurring (Supplementary Fig. 2). This would partially explain the described conservation paradox (Lees and Bell 2008) by which the wild rabbit that behave as a successful colonizer in many countries is failing to recover in many areas of the Iberian Peninsula.

Contrarily, towards higher latitudes (i.e. Scandinavian Peninsula and Northern UK), altitudes (e.g. the Alps), and to a lesser extent Eastern limits of rabbit distribution, breeding seasons will increase. Reproductive periods are also predicted to become more variable within current rabbit distribution, especially in the South and West of Europe, while in Northern and Eastern areas the inter-annual variability will decrease with climate change. This will be particularly true in mountain ranges such as the Balkans, and Carpathians, but not in the plains around the Gulf of Finland where climatic alterations will lead to more variable seasons (Fig. 1; Supplementary Fig. 1).

Consequences for population dynamics of the climate-induced changes in reproduction

In order to investigate the consequences at the population level of these breeding season changes we used a stochastic individual-based population model (Supplementary information: Description of the demographic model) to simulate rabbit populations under different 30-year scenarios of breeding season length and CV (Supplementary Table 4). Using generalized linear models (GLMs), we then tested for the impact of those breeding season variables on population dynamics relative to the most important survival and density-dependence parameters as defined by the sensitivity analyses (Supplementary Information: Sensitivity analysis of the population model, Supplementary Table 7).

We found that breeding season variability was the main factor driving extinction probabilities, followed by its duration and the food availability factor (Table 1). To a lesser extent reproductive period was also important in determining mean population size, although in this case the density-dependence parameter and the intercept of the survival function showed a slightly higher influence (Table 1). Note that populations vary along the year, and therefore, their overall size may change dramatically without modifying carrying capacity due to the overshooting produced by the strong seasonality.

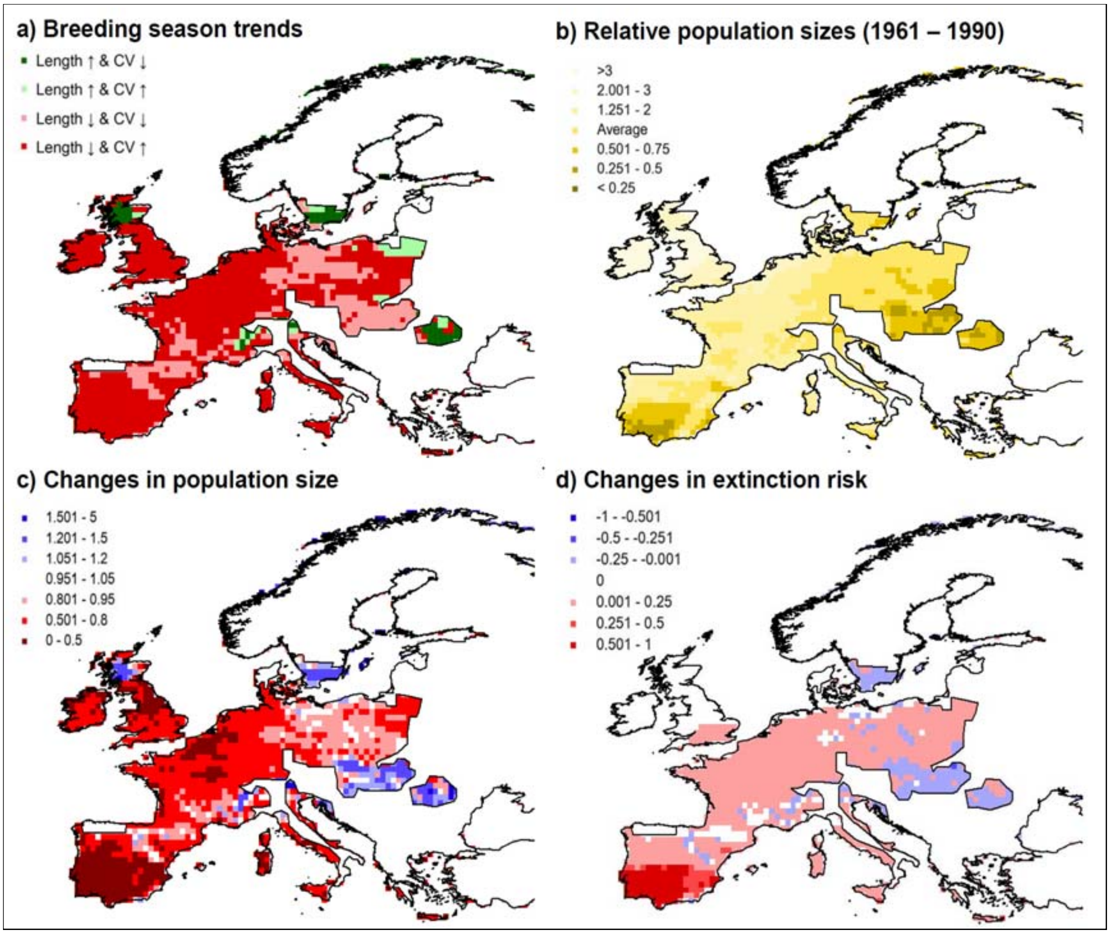
Table 1. Generalised linear models testing the influence of breeding season and other model parameters on extinction probability (binomially distributed) and population mean size (negative binomial distribution) at the end of a 30-year period. The magnitude of the standardized coefficients (Std. Coef.) represents the relative influence of each explanatory variable. Their order of importance in each case is shown in the rank column. As in the case of the sensitivity analyses (Supplementary information), we applied latin hypercube sampling with lattice sampling technique in order to select the 5*1000 combinations of parameters for the simulations, each of which was replicated 50 times and its results averaged before performing the GLMs.

	Probability of extinction		**Mean population size**	
Effect	Std.Coef	Rank	Std.Coef	Rank
Reproductive period				
Mean duration	-273.12***	2	73.38***	4
Coefficient of Variation	475.20***	1	-83.90***	3
Density-dependence in fecundity and survival	112.39***	5	-105.72***	1
Newborn probability of mortality	57.60***	7	-13.92***	6
Daily survival probability over 30 days of age				
Function intercept	-145.88***	4	98.58***	2
Age parameter (from 1 - 4 months)	102.89***	6	-39.68***	5
Food availability factor	-183.35***	3	13.25***	7

*** $p < 0.0001$

As breeding season becomes shorter and more variable rabbit populations get smaller and more prone to extinction. Lower values of the food availability parameter (i.e. greater negative impact of food scarcity on survival) also lead to higher extinction probabilities whereas population sizes also decrease with smaller values of the survival intercept and higher density-dependence. The high importance of the reproductive period in rabbit population dynamics is in agreement with results showing that in small mammals, with early sexual maturation and large litter size, reproductive parameters have relatively high impact on population growth (Heppell et al. 2000, Oli and Dobson 2003).

By applying the outcome of these GLMs to previous predictions of breeding season change across current rabbit distribution in Europe, we were able to examine the potential effect of climate change on rabbit populations at a spatial level (Fig. 2). We observed that, mirroring alterations in reproductive periods, rabbit numbers will decrease in most of the rabbit range especially in areas where not only the length of the reproductive period will increase but also become more variable. The strongest declines will occur in the South of the Iberian Peninsula where, in addition, predicted population sizes are already low in the control period. All these will thus result in important increases of extinction probabilities in areas where rabbits are native.


a) Breeding season trends

b) Relative population sizes (1961 – 1990)

c) Changes in population size

d) Changes in extinction risk

Figure 2. Climate change influence on population dynamics across current rabbit distribution. a) Future trends in breeding seasons calculated using ensembles of both GCM and gas emission scenarios. Results of the GLMs testing the effect of breeding season and other variables on populations dynamics were then applied to those ensemble breeding seasons to obtain b) Pattern of relative population sizes (population size in each cell / overall mean population size) for the control period, c) variations in population numbers with climate change ($N_{future}/N_{control}$), and d) future changes in extinction probabilities of populations ($Prob_{future}-Prob_{control}$). Density-dependence and survival parameter terms of the GLM were average in all cases to clearly show the consequences of breeding season changes.

On the other hand, towards the eastern and northern borders of the species current distribution, population numbers are expected to increase and extinction risks to decrease, principally in regions were breeding season will both increase and stabilize. The scale mismatching prevent us from inferring the dynamics of specific populations directly from our regional predictions, since there may be factors, such as water bodies, crops or altitudinal gradients, locally determining breeding season length. However, this does not invalidate general patterns observed in rabbit population dynamics.

Effects of reproductive changes on population resilience

Despite the relevance of the reproductive period duration and variability when considering the range of values observed at large scales, from a local perspective, rabbit demography will still be mainly driven by variations in survival as shown by our population model when keeping breeding season length and variability constant (Supplementary Information: Sensitivity analysis of the population model, Supplementary Table 6). One of the most common patterns is the collapse of populations after recurrent epidemics (Moleón et al. 2008) or extreme weather events (Williams et al. 1995, Palomares 2003). For all this, we also investigate the influence of length and variability of the reproductive period on population recovery (i.e. time to reach carrying capacity) after these detrimental perturbations.

In order to do so, we run the stochastic individual-based population model again for a range of breeding seasons (Supplementary Table 4) under reduced initial density, moderately low density-dependence, and two different levels of carrying capacity (Supplementary Table 7). Using GLMs, we observed that in situation such as this, where carrying capacity is not limiting, populations increase significantly faster if they have longer reproductive periods (Fig. 3) regardless of the variation in the other parameters of the model. Inter-annual variability, although less strongly, also correlates with the response rate; however, its effect is negative (Fig. 3). Thus, climate change, through its impact on the reproductive period, can seriously affect the capacity of populations to recover after catastrophes.

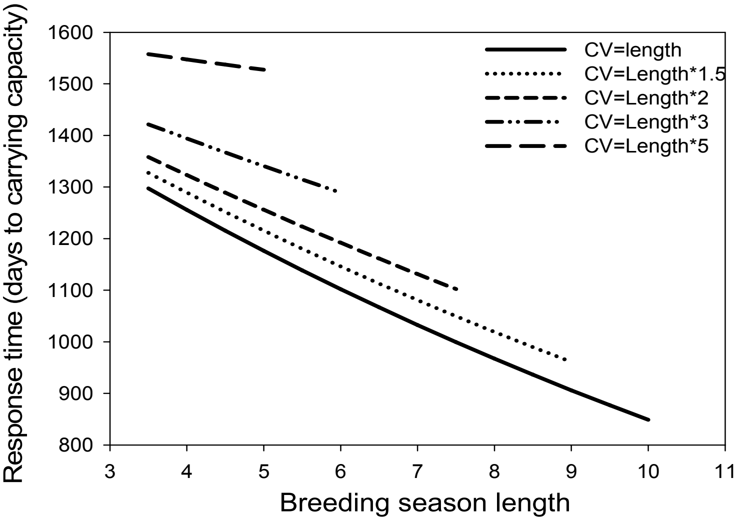


Figure 3. Variation in recovery capacity of rabbit populations according to breeding season length and CV. GLM results with response time as dependent variable (negative binomial distribution) and carrying capacity as random factor: Breeding season length (F= 165.52, p <0.0001) and CV (F= 30.91, p = 0.0001).

Potential role of those changes for rabbit distribution

The clear relationship found between current rabbit occupancy in Europe and breeding seasons predicted for 1961-1990 suggests that rabbit distribution is also likely to be altered by future changes in the reproductive period. In fact, the length of the breeding season alone can correctly classify the presence/absence of rabbits in over 80% of the map cells. (Supplementary material: Association between distribution and European wild rabbit breeding season).

The consequences for rabbit distribution of this climate induced changes in the breeding season, however, are still uncertain since we lack a clear picture of how climate change will alter survival patterns by relaxing harsh cold winters, changing carrying capacities and modifying the impact and phenology of infectious diseases. What we can say is that all the other parameters remaining similar, future patterns in breeding season will lead to shifts in rabbit distribution towards more northern latitudes (Scandinavia), eastern regions (the Balkans), and higher altitudes (the Alps). This does not necessarily mean that rabbit native populations (SW Europe) will disappear, since they contain the highest genetic diversity (Branco et al. 2000) and thus the greater potential for local adaptation to environmental changes, but their situation will worsen.

Conclusions

In conclusion, wild rabbit populations will respond to climate change differently across space emphasizing the conservation-pest dualism. The desertification of SW Europe will negatively affect rabbit populations within their native range, where they are a keystone species already in decline (Virgós et al. 2007, Delibes-Mateos et al. 2008), with important cascading effects on Mediterranean communities and predators relaying on them. Contrarily, in the north and east of Europe, populations will be enhanced and new adjacent areas might be colonized by rabbits with negative consequences for native biota and potential invasional meltdown. The latter, has been already demonstrated in Chile where exotic rabbits facilitated plant invasions (Holmgren et al. 2000).

In the rest of their European distribution wild rabbit populations will also decrease due to breeding season changes, although the consequences of these declines will be less dramatic since these are currently thriving introduced populations. Rabbit reductions in those areas may be beneficial due to alleviating the pressure of exotic rabbits on local biodiversity and agriculture but may be also negative if they disrupt a new balance reached by the system (Lees and Bell 2008).

This diversity of population responses to climate change within the same species and continent highlights that in the context of fast environmental change we will be forced to abandon the static snapshot given by distribution patterns and adopt a more dynamic view which focuses on the biological processes driving population dynamics. This mechanistic approach will allow us to make more reliable predictions and to identify the population parameters upon which we can focus in order to mitigate the effects of climate change.

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Supplementary Information

Control and future breeding season trends in Europe

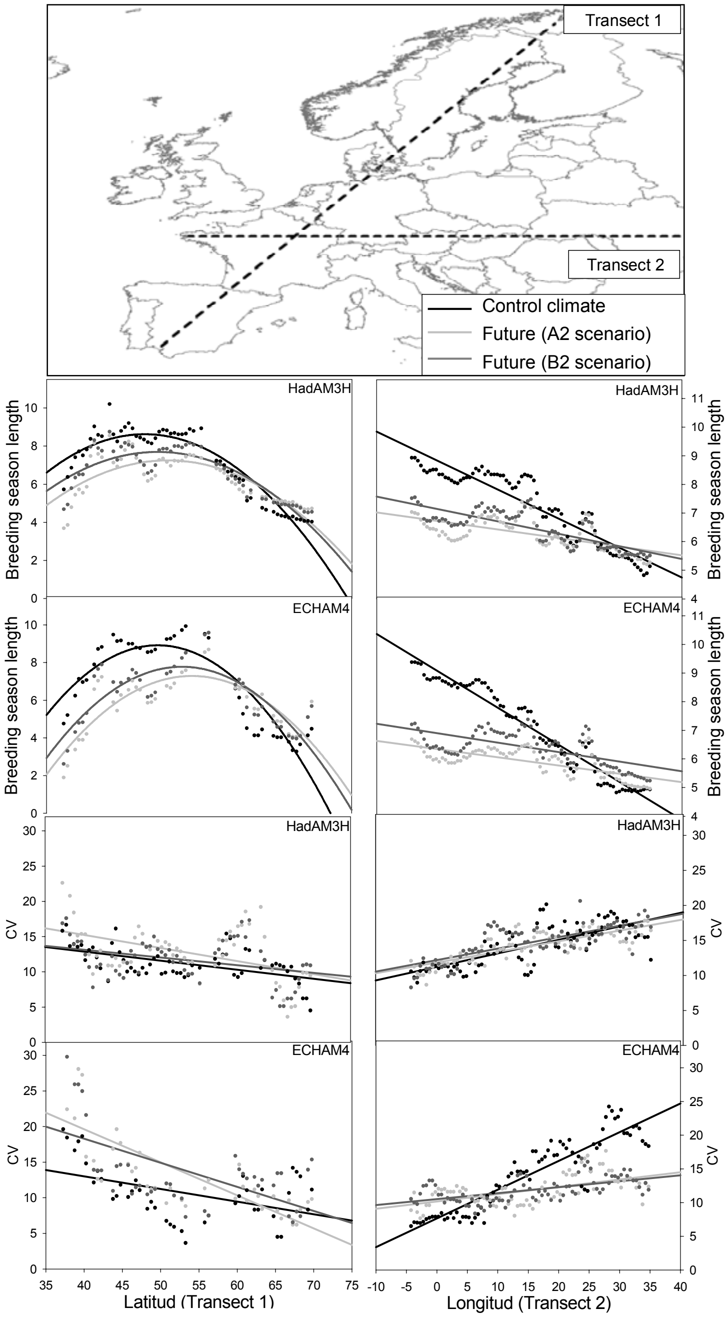

Figure S1. Latitudinal and longitudinal trends in length and CV of rabbit reproductive period following two different transects across Europe for 1961-1990 (Control climate) and 2071-2100 (Future). Future breeding conditions were projected using two general circulation models (HadAM3H and ECHAM4) and a high (A2 scenario) and a moderate (B2 scenario) greenhouse gas emission scenarios.

Comparison of observed and predicted breeding season lengths

Table S1. Duration (months/year) of the reproductive period found in the literature (Observed) and predicted (mean ± standard deviation) using two general circulation models (HadAM3H and ECHAM4) for the period 1961-1990.

Location	**Latitud**	**Longitud**	**Year**	**Breeding Seaton**			**Source**
				Observed	**HadAM3H**	**ECHAM4**	
Beja	38.02	-7.87	1976	8	6.54 ± 0.95	5.29 ± 0.89	Ribeiro 1983
Alicante	38.34	-0.48	1994-97	7*	7.14 ± 1.17	5.79 ± 1.13	Arques 2000
Sierra Morena	37.90	-6.38	1976-77	7	6.83 ± 1.02	5.57 ± 0.96	Soriguer 1981
Auffargis	48.65	1.83	1977-79	7	8.18 ± 0.97	8.67 ± 0.69	Arthur 1980
Caernarvonshire	53.30	-4.50	1941-42	6*	9.79 ± 0.48	9.97 ± 0.18	Brambell 1944
Doñana	37.10	-6.44	1974-75	5	5.7 ± 0.88	4.85 ± 0.9	Delibes and Calderon 1979
Camargue	43.70	4.10	1975-77	4	8.84 ± 0.98	8.53 ± 0.86	Rogers (1979) in Rogers et al. 1994
Scania	55.85	13.41	1972-76	6	8.26 ± 0.96	8.31 ± 1.06	Andersson et al. 1981
Kent	51.19	0.74	1958-60	8*	8.93 ± 0.94	9.45 ± 0.67	Mead and Briggs (1977) in Thompson 1994
Navarra	42.62	-1.61		8*	9.44 ± 0.92	8.86 ± 1.04	Ceballos unpub. in Rogers et al. 1994

* years of study are outside the control climate period (1961-1990)

Past breeding season trends in SW Europe (Lisbon)

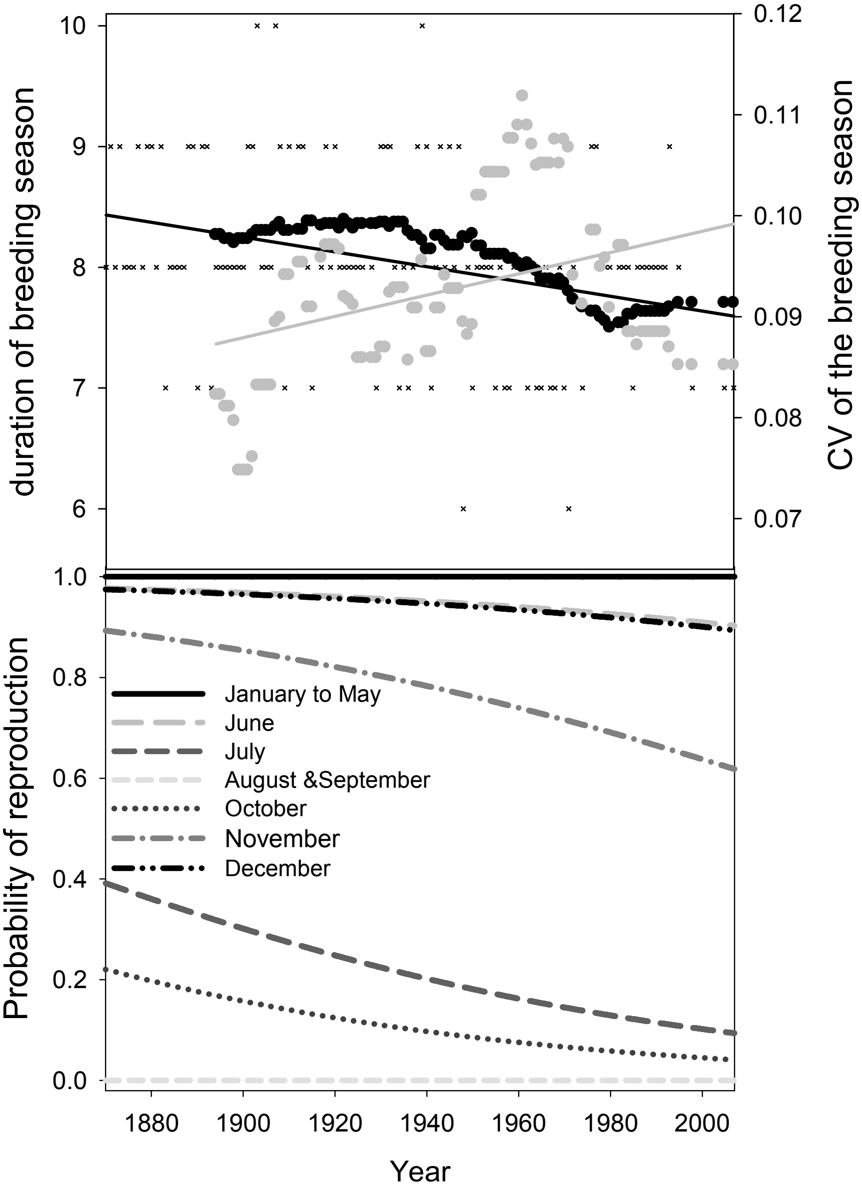

Figure S2. The top figure represents predicted breeding season trends by applying mechanistic model in Tablado et al. (2009) to Lisbon climatic data from 1900-2007. Small X-marks correspond to annual breeding season lengths while larger black and grey dots are mobile estimations (in 30 year intervals) of duration and inter-annual variability of this parameter, respectively. The bottom image shows the phenological changes in rabbit breeding season in Lisbon along this period, with reductions in probability of reproduction being more pronounced around summer months (July, October, and November).

Description of the model for rabbit population dynamics

It is a non-spatial stochastic individual-based model which represents a wild rabbit population in an area of 5 hectares (Fig. S3). Model includes rabbit basic life cycle in which the gestation period lasts 30 days (Dunsmore 1971, von Holst et al. 2002), newborn rabbits stay in their warrens and depend on their mother up to day 30 when they are weaned, Juvenile rabbits reach sexual maturity when they are 4 months old (Soriguer 1981, Fraser 1988) and rabbit longevity is 6.8 years (von Holst et al. 1999). Individual rabbit state are defined by characteristics (Table S2) which are updated in each model step (daily):

Table S2. Individual properties of rabbits.

State variables	
Age	0 - 2479 (days)
Newborn	0 – 30
Juvenile	31 – 122
Adult (Mature)	123 – 2479
Sex	Randomly attributed (Male, Female)
Female reproductive status	
Non-pregnant	-1
Pregnant	0 - 30 (days since fecundation)
Female lactation	
Non-suckling female	-1
Days until offspring weaning	0 - 30 (days since parturition)
Female litter size	
Non-suckling females	0
Suckling females	Mean litter size (L) ± sd

Populations are started by N rabbits with: 1) random gender, 2) age randomly selected within a Gaussian distribution (Mean = 515; SD = 162) truncated at three standard deviations, and 3) if female, absence of pregnancy, lactation or offspring.

1. *Reproduction (*Table S3; Fig. S3)*:*

Rabbit are only allowed to breed in months within the reproductive period which is delimited by climate, food availability and photoperiod according to the following equation (From Tablado et al. 2009).

$$P_B = \frac{1}{1 + e^{(4.542 - 0.605\,T + 0.029\,T^2 - 0.006\,D - 0.017\Delta - W)}} \qquad \text{(Eq. 1)}$$

where T is the mean monthly temperature, D is the average daylength in each month, Δ is the difference between the D of a month and the D of the previous month and W represents food availability (W = 0 if previous two months were dry, that is, precipitation < 2*temperature according to Walter & Lieth (1960) and W = - 1.592 if precipitation was higher than twice the temperature in at least one of the two previous months). Reproduction will occur in months in which *PB* is ≥ 0.5.

Within the breeding season, sexually mature female rabbits (over 122 days) not already gestating will have a probability of becoming pregnant (P_R) that will depend on their age (Dunsmore 1971, Gibb et al. 1985) and population density (Myers and Poole 1962, Rodel et al. 2004) as shown by Equation 2:

$$P_R = \frac{e^{(a + r_A - dr\frac{\eta}{K})}}{1 + e^{(a + r_A - dr\frac{\eta}{K})}} \qquad \text{(Eq. 2)}$$

where a is a constant, rA is a parameter whose value increases with age class (4 - 6 months, 6-9 months and over 9 months (Tablado et al. 2009) and $\left(dr\frac{\eta}{K}\right)$ is the factor representing density dependence in reproduction (with d being a constant, η the population density and K the carrying capacity).

If pregnancy occurs, gestation lasts 30 days (Dunsmore 1971, von Holst et al. 2002). Females then give birth to a number of kittens chosen randomly within a Gaussian distribution with mean equal to the average population litter size (L) and the extremes truncated at two standard deviations. This standard deviation is set to one according to similar literature values (Brambell 1944, Soriguer 1981, Gonçalves et al. 2002). If they get infected with myxomatosis or RHD during pregnancy, gestation will stop losing their litters.

Monthly proportion of pregnant females ($B_{(A)}$) of each mature age class (A; 4-6 months, 6-9 months and over 9 months) is calculated as

$$B_{(A)} = \frac{\text{pregnant females of age class A in a month}}{\text{Total of females of age class A in a month}} \qquad \text{(Eq. 3)}$$

After parturition, females enter the lactation period (30 days; Hudson and Distel 1990, von Holst et al. 2002) in which newborns depend on them. Due to post-partum oestrus females might become pregnant the day after giving birth (Bonino 2006, Calvete 2006) with a probability (P_R). Newborn will be recruited into the population with an age of 0 days and random gender. If they are females they will never be pregnant, lactating, have a litter size or previous pregnancies.

2. *Mortality (*Table S3; Fig. S3)*:*

European wild rabbits have high mortality rates (von Holst et al. 2002) which decrease with age (Arthur 1980, Wood 1980). Main causes of death are predation and endemic diseases, that is, myxomatosis and viral haemorrhagic disease (Villafuerte et al. 1997, Henning 2003). Burrow flooding and collapse, road kills, hunting and other diseases (e.g. such as coccidiosis) might also contribute to population regulation (Myers 1971, Angulo 2003).

Newborn rabbits (less than one month old) which are highly associated to breeding stops and warrens present the higher mortality rates (e.g. Arthur 1980, Wood 1980). The daily probability of survival of young rabbits less than one month of age is

$$P_{S\,N} = \sqrt[30.4]{(1 - \mathrm{M_N})} \qquad \text{(Eq. 4)}$$

where $\mathrm{M_N}$ is the monthly mortality rates for newborn in wild rabbit populations and 30.4 is the average month length in days. In addition, death of suckling females will imply the loss of their offspring increasing even more the mortality figures ($\mathrm{M_N}$) reported by the authors.

Since juvenile and adult rabbit survival compete for food resources, refuge and warrens, the daily probability of survival ($\mathrm{P_S}$) will decrease as population density (Rodel et al. 2004) and the number of months with reduced food resources increase (Wirsing et al. 2002, Rodel et al. 2004 winter) based on the equation

$$P_S = \left(\frac{\mathrm{e}^{\left(\mathrm{b-}\,\delta_\mathrm{A}\ \mathrm{-\,ds}\,\frac{\eta}{\mathrm{K}}\right)}}{1\ +\ \mathrm{e}^{\left(\mathrm{b-}\,\delta_\mathrm{A}\ \mathrm{-\,ds}\,\frac{\eta}{\mathrm{K}}\right)}} \right) \left(1 - \mathrm{e}^{\left(\frac{-\nu}{\mathrm{F_m}}\right)} \right) \qquad \text{(Eq. 5)}$$

where b is a constant, δ_A is a parameter which varies with age class (juveniles: from 1- 4 months and adults: over 4 months), $\left(\frac{-\nu}{F_m}\right)$ is a term representing food scarcity (with ν as a constant and F_m as the number of consecutive dry months (precipitation < 2*temperature) until month *m* and $\left(d_s \frac{\eta}{K}\right)$ accounts for the density-dependence in survival (where d_s is a constant, η is the population density and K the carrying capacity). The daily survival rates for the simulated population are then given by

$$S_{(A)} = 1 - \left(\textit{Deaths in age class } \mathrm{A} \,/\, \textit{Rabbit days in age class } \mathrm{A}\right) \qquad \text{(Eq. 6)}$$

where age (A) is classified as newborn, juveniles and adults.

Table S3. Parameters of the rabbit population model.

Parameter Description	**Symbol**	**Values**
Population density	η	
Carrying capacity	K	
Rabbit age (in days)	A	
Reproduction		
Probability of being within the a breeding season	P_B	(Eq. 1)
Mean monthly temperature (ºC)	T	Meteorological station data
Average daylength in a month (light minutes/day)	D	Meteorological station data
Photoperiod change between 2 consecutive months	Δ	Meteorological station data
Availability of green pastures in a given month	W	= 0 if in both previous months precipitation < 2*Temperature = -1.592 otherwise
Breeding probability of mature females	P_R	(Eq. 2)
Reproduction function intercept	A	
Age effect on female fecundity	r_A	= 0 if female age = 4 – 6 months > 0 if female age = 6 – 9 months > > 0 if female age > 9 months
Factor of density-dependence in reproduction	d_r	
Average litter size	L	3.2 - 7.3 rabbits/ litter (Soriguer
Monthly proportion of pregnant females of age *(A)*	$B_{(A)}$	(Eq. 3)
Survival		
Daily survival of newborns (up to 30 days of age)	P_{SN}	(Eq. 4)
Monthly newborn mortality	M_N	0.4 – 0.9 (Tyndale-Biscoe and Williams 1955, Robson 1993, Villafuerte 1994)
Daily survival of rabbits older than 30 days	P_S	(Eq. 5)
Survival function intercept	b	
Age effect on survival	δ_A	> 0 if rabbit age = 1 - 4 months = 0 if rabbit age > 4 months
Factor of density-dependence in survival	d_s	
Effect of food availability on survival	ν	
Number of consecutive dry months	F_m	
Monthly survival for rabbits of Age *(A)*	$S_{(A)}$	(Eq. 6)

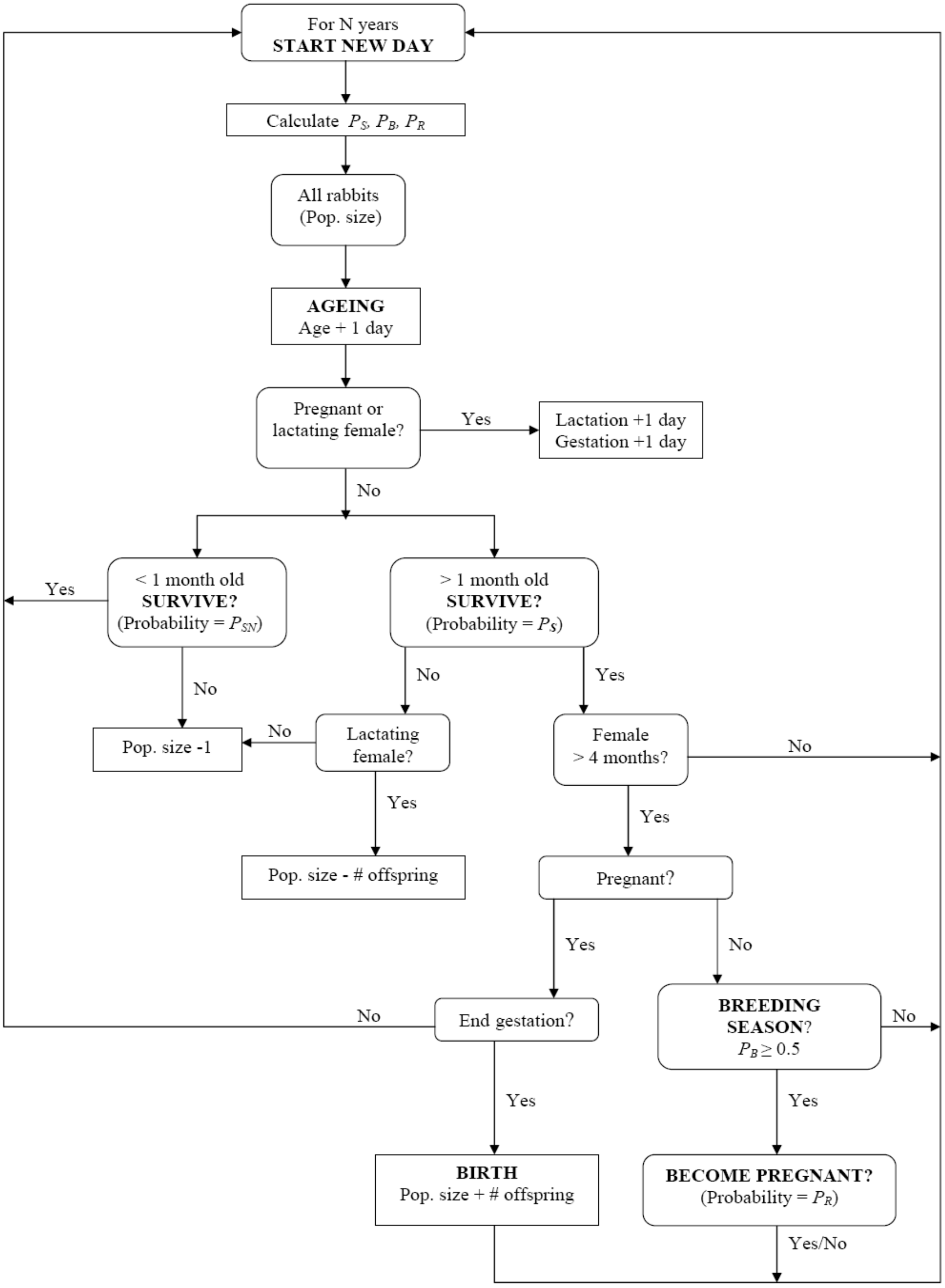

Figure S3. Diagram showing the structure of the population dynamics model for European wild rabbits.

Rabbit breeding season scenarios

Table S4. Mean and inter-annual variability (over a 30-year period) of breeding season length for the scenarios used to examine effect of the reproductive period on extinction risk and size of rabbit populations. Scenarios marked with an asterisk (*) are the ones used to investigate population response time after perturbations.

Scenarios1	Mean	CV
1*	5.45	16
2 *	3.55	24.5
3 *	9.72	14.5
4 *	8.17	8.7
5 *	6.90	14.7
6 *	8.38	8.1
7 *	4.14	8.5
8 *	5.48	13.5
9	8.31	11.4
10	6.90	12.8
11	8.38	7.9
12	9.55	8.5

Sensitivity analysis of rabbit population dynamics model

We performed sensitivity analyses to investigate the response of the population dynamics model to variations in the different input parameters (Hamby 1994, McCarthy et al. 1995). The breeding season was fixed according to typical climate of Southern Spain. We applied Latin hypercube sampling (LHSMcKay et al. 1979) in order to select sets of input values from the ranges of the different parameters in the model (Table S5). In LHS the range of all parameters is divided into *n* non-overlapping equiprobable intervals. A random number is used to choose one of the intervals and the centered value is taken following the lattice sampling technique which is a special case of LHS (Owen 1994, Zhang and Pinder 2003). Each interval is used only once to guarantee representative coverage of the parameter space (McKay et al. 1979).

This results in *n*-sized samples for each parameter which are then randomly arranged to generate a set *n* parameter combinations (in this study $n = 5$). We repeated this process a total of 1000 times. We then ran the simulation model for each of these parameter combinations (*n**1000) to produce a suite of output observations. Each simulation was also replicated 50 times and later replicate results were averaged before the analyses. In every case the model started with a carrying capacity and initial population density (in 5 hectares) of 14 rabbits/ha and was run for ten years. We restricted the analyses to simulations whose parameter combinations resulted in daily survival and pregnancy rates which increase with age as occurs in real wild rabbit populations (Tablado et al. 2009, Wood 1980).

We finally applied generalized linear models (GLMs) to examine the effect of the input parameters (Table S5) on the final population. We used probability of extinction and mean population size after ten simulated years as the dependent variables with binomial and log-normal distribution respectively. The standardized coefficients estimated in this way were then ranked in order to determine relative importance of each model parameter on the simulated population dynamics.

We performed additional analyses to investigate the sensitivity of the model to life history traits usually described for wild rabbit populations in the field. To do so, we repeated the previous GLMs. However, in this case the explanatory variables consisted of the input litter sizes (L; Table S5) together with the output survival and pregnancy rates for the different age classes obtained from the same simulated populations.

Table S5. Input parameter ranges used in the sensitivity analyses (Latin hypercube sampling).

Parameters	Description	Range	Source
Reproduction			
P_R (Eq. 2)	Daily probability of fecundation		
a	Reproduction function intercept	(-3) – 2	
	Age effect on female fecundity		
r_A	r_1 (for rabbits from 4 to 6 months)	0	
	r_2 (for rabbits from 6 to 9 months)	2 – 4	
	r_3 (for rabbits over 9 months)	4.5 – 7	
d_r	Factor of density-dependence in reproduction	0.2 – 10	
L	Mean litter size	3.0 - 7.4	Soriguer 1981, Stevens and Weisbrod 1981
Survival			
M_N	Monthly mortality up to 30 days old	0.4 - 0.9	Tyndale-Biscoe and Williams 1955, Robson 1993
P_S (Eq. 5)	Daily probability of survival for rabbits over 30 days		
b	Survival function intercept	5 – 10	
	Age effect on survival		
δ_A	δ_1 (for rabbits from 1 - 4 months)	2 – 4	
	δ_2 (for rabbits over 4 months)	0	
v	Effect of food availability on survival	10 – 50	
d_s	Factor of density-dependence in survival	0.2 – 10	

The results of the GLMs indicated that the probability of extinction seems to be associated only to changes in survival parameters, especially to the survival function intercept and food availability factor (Table S6). Final population size was also mainly sensitive to survival parameters and to a lesser extent to reproductive parameters (Table S6), with higher standardized coefficients being shown by the density-dependence factor and intercept of survival function, followed by food shortage and density dependence in the fecundity function.

In a second analysis we were able to test the impact of the demographic rates (i.e. of productivity and survival) on extinction risk and population size (Table S6). Extinction risk appeared to be only sensitive to variations in adult survival rates and newborn survival and mean litter size. Adult survival caused the higher population size sensitivities, followed by the percentage of pregnant females over 9 months and newborn survival. The latter two being involved in population recruitment. The least important variables appear to be pregnancy percentages of the younger age classes.

Table S6. Results of the sensitivity analysis. Generalized linear models for the effect of (i) model parameters and (ii) rabbit life history traits on mean population size (lognormal distribution) and extinction probability (binomial distribution) after 10 years. The magnitude of the standardized coefficients (Std.Coef) represents the relative influence of each explanatory variable. Their order of importance in each case is shown in the rank column.

Effect	**Probability of extinction**		**Mean population size**	
i. Model input parameters	Std.Coef	Rank	Std. Coef	Rank
Daily probability of fecundation (Eq. 2)				
Function intercept	ns		5.59***	8
Age parameter (from 6 to 9 months old)	ns		ns	
Age parameter (over 9 months)	ns		2.29**	9
Density-dependence in fecundity	ns		-14.73***	4
Mean litter size	ns		6.02***	7
Newborn probability of mortality	37.20***	4	-13.71***	5
Daily survival probability over 30 days of age (Eq. 5)				
Function intercept	-100.60***	2	38.25***	2
Age parameter (from 1 - 4 months)	36.34***	5	-12.04***	6
Food availability factor	-161.05***	1	24.86***	3
Density-dependence in survival	75.51***	3	-49.64***	1
ii. Rabbit life history traits				
Mean litter size	-38.50***	3	29.72***	4
% of pregnant females (4 - 6 months)	ns		3.30*	7
% of pregnant females (6 - 9 months)	ns		-8.81***	6
% of pregnant females (over 9 months)	ns		69.50***	2
Newborn survival rates	-60.69***	2	45.43***	3
Juvenile survival rates	ns		28.71***	5
Adult survival rates	-117.10***	1	80.85***	1

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Parameter values used in the population dynamics model

Table S7. *Population dynamics* values were used for testing the effect of length and variability of breeding season on population size and extinction probability while *Response time* ones for obtaining the potential rate of increase of rabbit populations under different breeding scenarios.

Model input parameters	**Population dynamics**	**Response time**
Daily probability of fecundation (Eq. 2)		
Function intercept	0	0
Age parameter (from 6 to 9 months old)	3	3
Age parameter (over 9 months)	5.5	5.5
Density-dependence in fecundity	1.5, 5	2
Mean litter size	5	5
Newborn probability of mortality	0.4 - 0.8	0.4 - 0.8
Daily survival probability over 30 days of age (Eq. 5)		
Function intercept	5 – 10	5 – 10
Age parameter (from 1 - 4 months)	2, 4	2, 4
Food availability factor	15, 40	15, 40
Density-dependence in survival	1.5, 5	2
Carrying capacity	14	14, 28
Initial population density	14*	1

*Initial density was set at carrying capacity to increase population stability

Association between distribution and European wild rabbit breeding season

We performed generalized linear models to relate the distribution of the wild rabbit in Europe to predicted breeding seasons for 1961-1990. As the dependent variable we used the presence or absence of rabbits (binomially distributed). According to the data on rabbit distribution provided by ref. Mitchell-Jones 1999, we assigned the value one (occurrence of rabbits) or zero (absence of rabbits) to every point in a grid of 50km resolution over Europe.

We then tested if the predicted mean length and inter-annual variability (CV) in the reproductive period and the interaction between both variables could explain to some extent that distribution. Breeding seasons used were the average between the results of applying the model in ref. Tablado et al. 2009 to climate data from the two different GCM (Christensen 2005): i.e. HadAM3H and ECHAM4.

Although the CV or its interaction with duration were not found to be significant, breeding season length showed a strong positive correlation with rabbit distribution ($F = 922.43$; $p < 0.0001$). In fact, this variable alone explains more than 40 % of the deviance in rabbit distribution.

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Capítulo 4

Factors driving rabbit survival and population dynamics before the arrival of the rabbit haemorrhagic disease

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Manuscrito en preparación

Resumen

Numerosos estudios han examinado la supervivencia y reproducción del conejo de campo *(Oryctolagus cuniculus)* para poder entender su dinámica poblacional. Sin embargo, a pesar de que el conejo es una de las especias de mamífero más ampliamente distribuida y posee tendencias poblacionales muy dispares a lo largo del mundo, los autores normalmente se han centrado en poblaciones concretas o en factores individuales (e.g. predación o enfermedades). El objetivo de este estudio consistió en integrar todos los componentes de la demografía del conejo en un modelo poblacional, con el objetivo de evaluar la importancia relativa de cada uno de ellos para determinar la supervivencia y la dinámica poblacional de los conejos antes de la llegada de la enfermedad hemorrágica vírica. La parametrización del modelo se realizó en base a los rangos de valores de reproducción, supervivencia y causas de mortalidad encontrados en estudios previos de poblaciones reales. De este modo, se reprodujeron poblaciones donde la mixomatosis y la predación por especialistas podían o no estar presentes y donde se cubrió todo el rango, descrito en la literatura, de mortalidades por generalistas, especialistas, mixomatosis, y otras causas. Encontramos que la dinámica poblacional de los conejos fue principalmente sensible a cambios en las tasas de predación por especialistas y por generalistas, seguido de cerca por la myxomatosis y por el resto de causas de mortalidad. El efecto de los especialistas, junto al de los generalistas, es la principal fuente de variación en la supervivencia de los adultos, mientras que en el caso de gazapos y juveniles los factores más influyentes son la mortalidad debida a otras causas y la predación por generalistas. La mixomatosis, por otra parte, a pesar de no mostrar un impacto relativo muy importante en la supervivencia de los conejos, apareció como uno de los principales determinantes de la probabilidad de extinción de las poblaciones, principalmente a través de su interacción con el periodo reproductor y la predación por generalistas. Finalmente, los periodos reproductores más largos tendían a disminuir ligeramente la supervivencia de los conejos por denso-dependencia pero al mismo tiempo favorecían la abundancia de conejos a través de un relajamiento del efecto de los predadores especialistas y de evitar la caída de las poblaciones bajo el control de los predadores generalistas. Estos resultados son importantes para ayudar a comprender mejor la dinámica poblacional del conejo y los procesos a través de los cuales sus poblaciones pueden ser controladas o aumentadas.

Abstract

Many studies have examined survival and reproduction of wild rabbits *(Oryctolagus cuniculus)* in order to understand their population dynamics. However, despite rabbits being one of the most widespread mammals, with highly different population trends across its distribution, authors have usually focused on single populations or specific factors of interest (e.g. predation or diseases). In this study, through the use of a population model, we aimed to integrate all the different components of rabbit demography to asses the relative importance of each of them in determining survival and population dynamics of rabbits before to the emergence of rabbit haemorrhagic disease (RHD). The parameterization of the model was based on ranges of values for reproduction, survival and mortality causes found in previous studies of real populations. In this way, we reproduced populations where myxomatosis and predation by specialists could be present or absent and which covered all the range of mortalities due to generalists, specialists, myxomatosis and “other causes” described in literature. We found that rabbit population dynamics was mostly sensitive to changes in predation rates due to specialists and generalists, closely followed by myxomatosis and by other sources of mortality. The effect of specialist predators, together with that of generalists, is the main source of variation in adult rabbit survival, while in the case of newborns and juveniles, the most influential factors are mortality due to “other causes” and predation by generalists. Myxomatosis, on the other hand, despite not showing a relatively important impact on rabbit survival, appeared to be one of the major determinants of probability of population extinction, especially through its interaction with predation by generalists. Finally, longer reproductive periods tended to slightly decrease rabbit survival through density-dependence, but at the same time favoured rabbit numbers by relaxing specialist predation and by preventing populations from falling under generalist predator regulation. These results will help us to better understand rabbit population dynamics and the processes through which their populations can be controlled or enhanced.

Introduction

Understanding how and why populations vary in abundance and distribution across time and space is one of the main objectives in ecology (Turchin 2003, Yoshida 2005). One of the species whose population dynamics has received more attention from researchers has been the European wild rabbit. This is partially due to the need of recovering rabbit populations within its native range (i.e. Iberian Peninsula), where they are a keystone species (Delibes-Mateos et al. 2008, Bravo et al. 2009) and are in decline (Moreno et al. 2007, Virgos et al. 2007), and to having to control them in many areas in which the species has been introduced and behaves as an invasive pest (Fenner and Fantini 1999, Jaksic et al. 2002).

As a result, there have been many empirical studies about rabbit survival and population dynamics. Rabbit populations are known to be importantly affected by climate, which controls, for example, food availability and warren flooding (Myers et al. 1994, Villafuerte et al. 1997, Palomares 2003), by predation due to generalist and specialists (Villafuerte 1994, Reddiex et al. 2002) and by infectious diseases, such as myxomatosis and RHD (Calvete et al. 2002, Merchant et al. 2003 Bruce et al. 2004). However, owing to the complexity of rabbit ecology, this type of information has been traditionally obtained focusing on one or few populations of interest, on the effect of unique factors or on specific age classes (Ross 1972, Moriarty et al. 2000, White et al. 2004).

The recent development of highly powerful population models (Uchmanski and Grimm 1996, Williams et al. 2002) are an ideal tool to investigate jointly the different components of rabbit population dynamics, because they constitute a simplification of the real world that allow us to understand complex systems, to experiment with them and to make predictions (Drechsler et al. 2007, Lloyd-Smith et al. 2009). Some authors have already modelled rabbit populations. These studies have also been aimed to test control, harvest or conservation strategies on specific areas (Angulo and Villafuerte 2003, Scanlan et al. 2006), or to understand the influence of particular factors, especially RHD, on rabbit populations (Fa et al. 2001, Story 2004, Calvete 2006). However, to our understanding, no previous research has examined rabbit survival and population dynamics at the species level, that is, considering the global variability of survival, mortality and reproductive parameters observed in wild rabbit populations.

The objective of this study was to integrate in a single mathematical model, the main demographic processes underlying rabbit population dynamics and their variability in order to determine the relative importance of each one of them in driving survival and dynamics in the different rabbit populations around the world. Given the complexity of rabbit population dynamics and the fact that RHD dynamics has already been modelled in several occasions, in this study we decided to focus on the functioning of populations before the arrival of the RHD. These were rabbit populations whose mortality, as mentioned before, was due to generalist predators, to “other causes” (e.g. warren collapse, road kills or droughts), to predation by specialists and to myxomatosis, which could be either present or absent.

Based on the results obtained previously in more local studies, we expected, first, that the effect of predation by specialists on rabbit population dynamics would differ from that of generalists since their functional responses vary substantially and each type of predation may affect a different rabbit age class (Chapter 2). Second, that myxomatosis would have a relatively important negative effect on rabbit dynamics, which, at the same time, would magnify the impact of generalist predators on populations where disease was present. Finally, we also expected an interaction between rabbit reproduction and predation and myxomatosis, in which populations with higher productivities would be less strongly affected by increases in mortality rates due to these causes.

Studies like this are necessary to improve our understanding of the main mechanisms and interactions between processes (e.g. between mortality sources or between those and reproduction) leading to the duality in rabbit dynamics that includes both declining and thriving populations. Only obtaining this type of information, will we be able to improve the conservation of endangered species, the control of pests and the efficient management of natural resources.

Material and Methods

Population dynamics model

We used a stochastic individual-based model (IBM) running in days which included a basic rabbit life cycle, where gestation lasted 30 days (Dunsmore 1971, von Holst et al. 2002), newborns stayed in their warrens and have maternal dependence up to day 30. After weaning young rabbits became juveniles until 4 months old when sexual maturity occurred (Soriguer 1981, Fraser 1988) and they entered adulthood where they could live up to 6.8 years old (von Holst et al. 1999). Reproduction was modelled as described in Chapter 3 (i.e. considering monthly detailed breeding season and fecundity varying with age and density). In this case, survival was implemented as a function of the different sources of mortality in pre-RHD times (see Appendix 1 for a complete model description, including RHD dynamics). Thus, the monthly probability of survival was given by the equation:

$$P_S = (1 - P_p)(1 - P_M)(1 - P_\theta) \qquad \text{(Eq. 1)}$$

Where (P_p) is the probability of being predated, (P_M) is the mortality risk due to myxomatosis and (P_θ) is the probability of dying due to other reasons.

At the same time, predation was divided into specialist (ρ_s) and generalist (ρ_g) predators as follows:

$$P_p = 1 - (1 - \rho_s)(1 - \rho_g) = \rho_s + \rho_g - \rho_s \rho_g \qquad \text{(Eq. 2)}$$

Predation by specialists was simplified as an exponential decay function, which decreases with rabbit density (Fig. 1):

$$S_p = \mathrm{s}\, e^{-\left(\mathrm{a}\,\frac{\eta}{\mathrm{K}}\right)} \qquad \text{(Eq. 3)}$$

Where s represents predator numbers, $\left(\mathrm{a}\,\frac{\eta}{\mathrm{K}}\right)$ is the density-dependence term with a constant (a), the population density (η) and the carrying capacity (K).

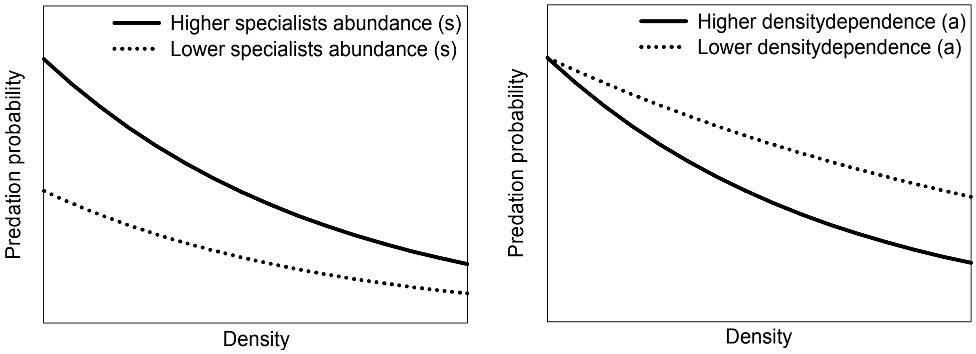

Figure 1. Variation with density of the probability of being killed by specialist predators.

This predation rate was, then, transformed into a probability by

$$\rho_S = 1 - e^{-\left(S_p\right)} \qquad \text{(Eq. 4)}$$

This probability was divided by 5 (i.e. $\frac{\rho_S}{5}$) in the case of newborn rabbits (younger than 30 days) since specialists predators consume mostly older rabbits, in a proportion 5 to 1 with respect to newborns (see fig 2.c. in Chapter 2).

Generalist predation was represented by a log-normal function (Fig. 2) including predator density (g), rabbit density ($\frac{\eta}{K}$), rabbit age (bA; b being a constant and A being rabbit age in days), a shape parameter (c) which modifies the response of generalist predators to rabbit density and the increased vulnerability of myxomatous rabbits (M):

$$G_p = \frac{g}{\left(\frac{\eta}{K}\right)} e^{-\left(\left(\frac{ln\left(\frac{\eta}{K}\right)}{c}\right)^2 + \left(bA - M\right)\right)} \qquad \text{(Eq. 5)}$$

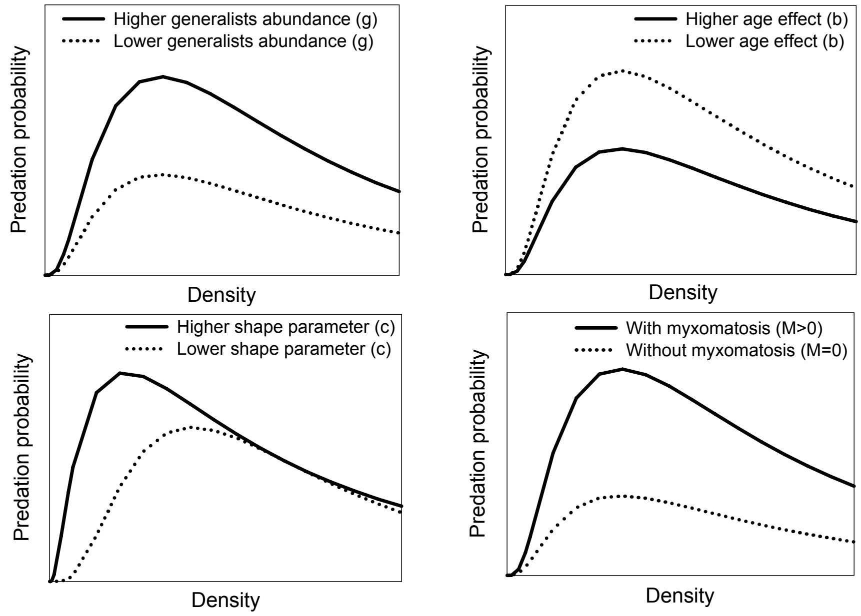

Figure 2. Density-dependence of the probability of being killed by generalists.

Being the risk of predation by generalist as

$$\rho_g = 1 - e^{-\left(G_p\right)} \qquad \text{(Eq. 6)}$$

The impact of myxomatosis was the product of the probability of being infected by the myxoma virus (T_M) and the probability of myxomatous rabbits of dying (i.e. lethality of the virus; D_M). Since the persistence of myxoma virus in infected vectors, carriers or warrens may be long (Chapple and Lewis 1965), we made possible for the virus to be always present in the population. To do so, in every month in which the disease was not present we randomly selected a number of individuals (from 0 to a maximum of 10% of the population) to be actively infected with myxomatosis to allow an outbreak when the conditions were appropriate.

In the case of newborn rabbits, since they remain in the warrens for 30 days after birth, we established that they only could be infected directly by their mothers. For juveniles and adults, we assumed a frequency-dependent probability of infection since myxomatosis is mainly a vector-born disease (McCallum et al. 2001, de Castro and Bolker 2005). Disease transmission also varied depending on precipitation (see Chapter 2 of this thesis). Thus, the probability of being infected by myxomatosis was given by:

$T_M = 1 - e^{-f_M}$, being the force of infection is $f_M = \mathrm{b}_\mathrm{M} \frac{\mathrm{I}_\mathrm{M}}{\mathrm{N}}$ (Eq. 7)

Where b_M is the transmission parameter which differs between wet and dry periods, I_M is the number of infectious individuals in the population shedding the virus and N the total number of rabbits in the population.

Rabbits that were infected with myxomatosis, after the infection period (approx. 31 days; Chapter 2), had a probability of dying represented by the following logistic function (Fig. 3):

$$D_M = \ell_\mathrm{M} + \frac{\mathrm{h}_\mathrm{M}}{1 + \left(\frac{\mathrm{A}}{\mathrm{i}_\mathrm{M}}\right)^{\mathrm{u}}} \qquad \text{(Eq. 8)}$$

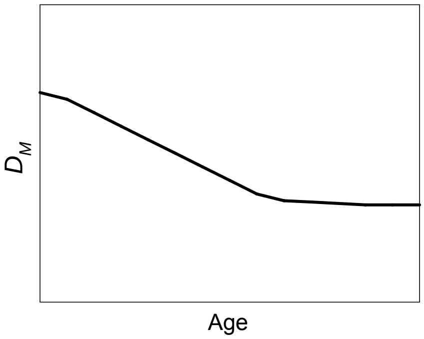

Figure 3. Change in myxomatosis lethality with age.

This probability decreased with rabbit age (A) and was comprise between a maximum ($h_M + \ell_M$) and a minimum (ℓ_M) lethality value, being i_M the age at the inflexion point of the curve and u the curvature parameter.

All this generated a pattern of annual or biennial myxomatosis outbreaks (Fig. 4) similar to those observed in the field:

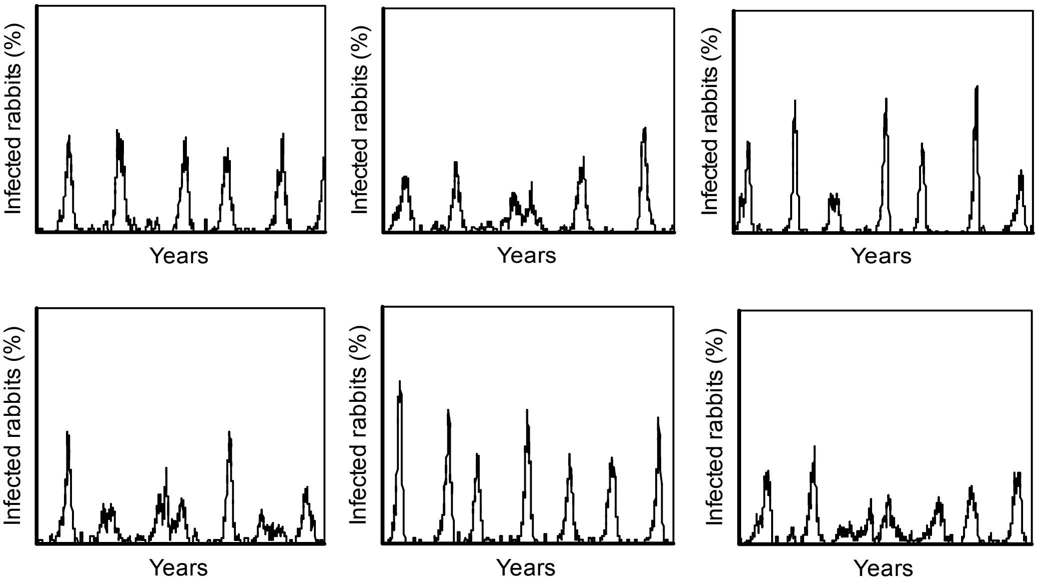

Figure 4. Examples of series of myxomatosis outbreaks through time simulated with our population model.

Rabbits that survive to myxomatosis became recovered rabbits with immunity that lasted a year after which they are susceptible again. If immune females reproduce, kittens will be born with immunity which will last for 49 days (Fenner and Marshall 1954, Ross 1972). Immune rabbits can still become infected but they will develop a milder form of the disease, without dying or infecting other individuals, and their immunity will be reinforced (Ross 1972, Fenner and Fantini 1999).

Finally, we also implemented the mortality due to "other causes" (e.g. infanticide, flooding, road kills or droughts; Fig. 5) which will decrease with age (A):

$$P_{\theta} = 1 - \left[\left(\frac{e^{(\mathrm{j+zA})}}{1 + e^{(\mathrm{j+zA})}} \right) \left(1 - e^{\left(\frac{-\mathrm{q}}{\mathrm{F}} \right)} \right) \right] \qquad \text{(Eq. 9)}$$

Where j is an intercept, z parameterises the effect of age (A) and $\left(\frac{-\mathrm{q}}{\mathrm{F}} \right)$ is a term representing the effect of food scarcity, with a constant parameter (q) and the number (F) of consecutive dry months where precipitation < 2*temperature (Walter and Lieth 1960, Tablado et al. 2009).

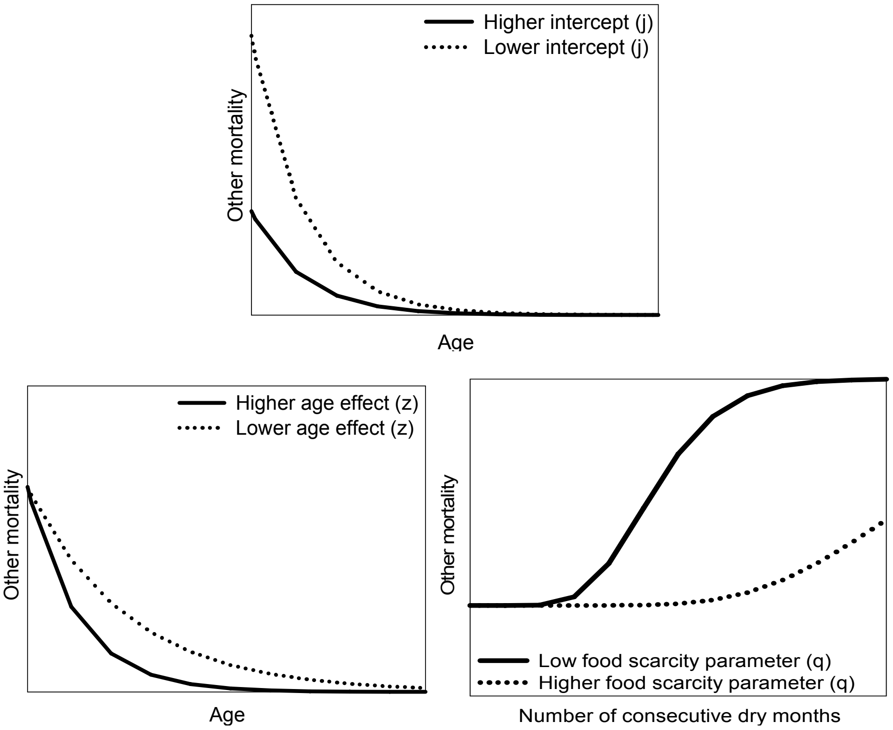

Figure 5. Effect of age and number of dry months on mortality due to other causes.

Model parameterization was done using the ranges of values obtained from literature (Table 1; Chapter 1 and 2) for life-history variables of real wild rabbit population. Myxomatosis could be either absent (as in pre-myxomatosis times) or present in the population. In the latter case, the disease was endemic with recurrent outbreaks and moderate lethality levels as those found in populations a few decades after the introduction of the myxoma virus. Predation by specialist could also be absent from a population representing populations outside the native range of rabbits (i.e. Iberian Peninsula) where no predator species is truly specialized in rabbits. We also considered several types of generalist predators according to their response at low rabbit densities, which depended on the importance of rabbits in their diet. This was done by modifying the shape parameter in the generalist predation function (Fig. 2; Eq. 5).

Sensitivity analysis of the population model

First of all, we performed a sensitivity analysis (Hamby 1994, McCarthy et al. 1995) to examine how rabbit population dynamics responded to the variation of input model parameters (Table 1). We used a latin hypercube sampling (LHS; McKay et al. 1979) to choose combinations of parameter values. In this LHS the range of possible values of a parameter is divided into *n* non-overlapping intervals. Then, an interval is selected randomly for each parameter and the centered value is taken as the input value, according to a lattice sampling technique which is a special case of LHS (Owen 1994, Zhang and Pinder 2003). Each interval (centred value) of each parameter is used only once to guarantee a representative coverage of the parameter space (McKay et al. 1979) and arranged to generate *n* different combinations of parameter values (*n* = 4 in this study).

We repeated this process a total of 1000 times and ran the model for each of these combinations (*n**1000). Each simulation was also replicated 50 times but its results were averaged before analyzing them. Simulated populations run during 29 years and had an initial size and a carrying capacity of 70 rabbits which reproduces an idealized local population with potential to become locally extinct.

Table 1. Range of values of input parameters used in the sensitivity analyses and of output monthly reproduction and survival rates generated with them. These latter were restricted to values reported for real populations (Chapter 1 and 2).

Parameter description	Symbol	Range of Input parameter values	Constrained output rates
Reproduction			
Breeding season (Length in months)		5.7 -12.0	
Probability of becoming pregnant			0.31 - 0.67
Age effect on female fecundity	r_A		
4 – 6 months old		0.50 - 3.00	
6 – 9 months old		3.10 - 5.05	
over 9 months old		5.75 - 8.00	
Factor of density-dependence in reproduction	d	3.00 - 10.0	
Average litter size	L	3.00 - 7.40	
Survival			
Probability of predation by specialists			0 - 0.10
Specialists predator abundance	s	0.000 - 0.015	
Density-dependence constant	a	0.80 - 2.00	
Probability of predation by generalists			0.05 – 0.42
Generalist predator abundance	g	0.04 - 0.10	
Age effect on generalist predation	b	0.002 - 0.001	
Shape parameter	c	1.20 - 2.00	
Parameter of vulnerability to predation	M		
healthy rabbits		0	
Myxomatous ones		0.10 - 3.00	
Probability of dying from myxomatosis			0 – 0.05*
Myxomatosis transmission term	b_M		
dry areas		0.10 - 1.00	
humid areas		1.10 - 5.00	
Lower limit of the curve	ℓ_M		
Myxo absent		0	
Myxo present		0.05 - 0.20	
Higher limit parameter	h_M		
Myxo absent		0	
Myxo present		0.21 - 0.40	
X-value at the inflexion point	i_M	20 - 150	
Curvature parameter	u	0.40 - 1.00	
Probability of dying of "other causes"			0.02 – 0.57
Intercept of the other-causes function	j	3.00 - 7.00	
Age parameter of the mortality function	z	0.01 - 0.15	
Effect of food scarcity	q	10 - 100	

** Morbidity =0 – 0.7; Lethality = 0 – 0.6*

Finally, with the results of these simulations we performed generalized linear models (GLMs) to test for the effect on populations of input parameters (Table 1). We considered only simulations producing survival and pregnancy rates within the range of values found for real populations (Table 1 and 3; Chapter 1 and 2). As dependent variables, we used, the extinction probability (out of 50 replicates; binomially distributed), the mean population size in the 29th simulated year including extinct populations (with a negative binomial distribution), and the change of phase of non-extinct populations. The latter is the drop in mean population size from the first half of the simulated period (year 1 to 14) to the second (15 to 29th) and was used to asses that life-history variables would be able to regulate populations at low densities. Since the variable was not normally distributed we transformed it as $X+X_{min}$ to eliminate negative values and adjust data to a negative binomial distribution. We then ranked the standardized coefficients obtained with all these GLMs so as to determine the relative importance of each model parameter on the simulated population dynamics.

Determinants of rabbit survival and population dynamics in pre-RHD times

To understand what was driving survival and dynamics in rabbit populations before the arrival of the RHD, we applied GLMs to regress survival rates and variables describing population dynamics against the different life history traits usually measured in the field. We used data from the previous simulations, in which we had also calculated realized rates, both age-specific and total, for survival, pregnancy and cause-specific mortalities resulting from each combination of input parameters (Table 1).

First, we assessed the role of cause-specific mortalities, that is, predation by specialists and generalist, mortality due to myxomatosis both directly and indirectly (i.e. predation of vulnerable sick rabbits) and deaths caused by other reasons, in determining the observed survival rates. We performed a different GLM for each age class (newborns, juveniles and adults) where the dependent variable consisted of age-specific rates of monthly survival, which followed a beta distribution. Mortality rates whose effect was tested were always specific of each age class, except for the extra predation of myxomatous rabbits which was calculated for all ages combined.

We also incorporated breeding season length, average percentage of pregnant females and littersize as independent variables in order to test for the possible indirect effect of these reproductive aspects on rabbit survival through density-dependence. These reproductive traits were chosen because they were the most variable (Tablado et al. 2009), and thus, potentially influential breeding aspects.

Finally, we performed GLMs to investigate which were the main traits governing rabbit population dynamics. We used the same explanatory variables as in the survival models. However, here, rates were not age specific, but global, and we examined potential interactions between the length of the breeding season and the mortality due to predators and myxomatosis. We also included the interaction between predation by generalists and myxomatosis, since increased mortality due to myxomatosis could lower rabbit numbers to densities where generalist predation may control populations. As in the case of the sensitivity analyses, the measures of population dynamics that we used as dependent variables of these models were extinction risk, final mean population size and population change.

For each model, output standardized coefficients were ranked so as to determine the relative importance of each demographic variable on rabbit survival and population dynamics. Also, when possible, these results were applied to scenarios typical of pre-RHD times, that is, populations varying in the presence of specialist predators, in breeding season length and in rates of mortality due to myxomatosis and to “other causes” (e.g. flooding or droughts), in order to explore differences in the dynamics of the various rabbit populations.

Results

Our analyses showed that dynamics of rabbit populations are mostly sensitive to variations in predation parameters and density-dependence in reproduction. More specifically, mean population size was most sensitive to high abundances of specialist predators, followed by increases in density-dependence in fecundity and in the parameter shaping predation by generalists (Table 2). To some extent, other predation parameters and the influence of age in mortality due to “other causes” were also affecting population size. Myxomatosis parameters, on the other hand, did not seem to have a relatively significant effect, except for the disease transmission term, which seemed to positively affect rabbit numbers.

Similar results were found for the probability of extinction, with specialist predators and density-dependence in reproduction being some of the main parameters. However, in this case, myxomatosis increased in importance at the same time as generalist predation decreased. When examining the change of phase occurred in non-extinct populations, we observed that populations that showed greater decreases in mean population size from the first to the second half of the simulated period were those with high values of the density-dependent parameter of reproduction. A lower relative effect was also found for length of the breeding season, the density-dependence in predation by specialist predators and the effect of food scarcity (Table 2).

Table 2. Results of the sensitivity analysis results to asses the effect of model parameters on population dynamics. Standardized coefficients (Std. Coef.) and the rank show the relative magnitude and order of importance of each parameter respectively.

Model parameters	**Population size**		**Extinction risk**		**Phase change**	
Reproduction	Std.Coef.	*Rank*	Std.Coef.	*Rank*	Std.Coef.	*Rank*
Breeding season length (months)	ns		ns		0.385*	*2*
Fecundation probability						
Age parameter (from 4 to 6 months old)	ns		ns		ns	
Age parameter (from 6 to 9 months old)	ns		ns		ns	
Age parameter (over 9 months)	ns		ns		ns	
Density-dependence in reproduction	-24.40***	*2*	12.11***	*3*	0.393**	*1*
Average litter size	ns		ns		ns	
Survival						
Probability of predation by specialists						
Specialists predator abundance	-37.98***	*1*	45.35***	*1*	ns	
Density-dependence in predation by specialist	ns		ns		0.270§	*4*
Probability of predation by generalists						
Generalist predator abundance	ns		ns		ns	
Age effect on generalist predation	10.73*	*6*	ns		ns	
Shape parameter	-15.23**	*3*	7.51*	*7*	ns	
Parameter of vulnerability to predation	-10.81*	*5*	ns		ns	
Probability of dying from myxomatosis						
Myxomatosis transmission term	10.26*	*7*	-7.58*	*6*	ns	
Lower limit of the curve	ns		ns		ns	
Higher limit parameter	ns		16.28*	*2*	ns	
X-value at the inflexion point	ns		ns		ns	
Curvature parameter	ns		ns		ns	
Probability of dying of “other causes”						
Intercept of the other causes function	ns		ns		ns	
Age parameter of the mortality function	14.79***	*4*	-11.26**	*5*	ns	
Effect of food scarcity	6.18§	*8*	-12.10***	*4*	-0.303§	*3*

§ = p < 0.08; * = p < 0.05; ** = p < 0.01; *** = p < 0.001

As for the effect of vital rates and life history traits on overall rabbit survival, we observed that the pattern varied among age classes. Newborn and juvenile survival appears to be mostly negatively affected by the mortality due to “other causes” and by generalist predation (Table 3). For both age classes, we found also a negative effect of the breeding variables, but their importance was comparatively low.

Myxomatosis had also a relatively small impact on rabbit survival, both directly and through increased predation. The sign of the relationship between myxomatosis and juvenile survival was always negative; however, newborns, which were not allowed to die from myxomatosis in the model because they reached the juvenile class first, presented a slightly positive association between survival and the indirect effect of myxomatosis.

The relative role of mortality and reproductive variables changed substantially in adult survival with respect to younger ages (Table 3). Here, myxomatosis continues to have a small relative effect, both negative in a direct way and positive through predation of myxomatous rabbits. However, specialist predation increased in importance and became one of the main factors, together with generalists, explaining low adult survival rates. “Other mortality causes” had a lower but also relevant effect on adult survival. Among the reproductive variables, only the length of the breeding season appeared to have a relatively significant influence in this case.

Table 3. Relative effect of cause-specific mortalities and reproductive characteristics on adult survival. The relative importance of each variable is given by the magnitude and rank of its standardized coefficient. Values between brackets are ranges of monthly survival (%) found in literature for each class (Chapter 2).

Survival determinants	**Newborns**		**Juveniles**		**Adults**	
Reproduction	Std.Coef	*Rank*	Std.Coef	*Rank*	Std.Coef	*Rank*
Breeding season length (months)	-0.62***	*7*	-0.38***	*5*	-0.30**	*6*
% of pregnant females	-1.26***	*3*	-0.35***	*6*	ns	
Mean litter size	-0.84***	*6*	ns	*8*	ns	
Survival	*(8.4-52.8)*		*(32.8-78.3)*		*(63.6-95.7)*	
Predation by specialists	-0.93***	*5*	-2.79***	*3*	-7.08***	*2*
Predation by generalists	-7.14***	*2*	-11.08***	*2*	-9.35***	*1*
Predation of myxomatous rabbits	1.19***	*4*	-0.24**	*7*	0.55***	*5*
Mortality due to myxomatosis	-		-1.51***	*4*	-1.77***	*4*
Mortality due to “other causes”	-14.57***	*1*	-15.85***	*1*	-6.10***	*3*

§ = p < 0.08; * = p < 0.05; ** = p < 0.01; *** = p < 0.001

By applying these results to types of populations without RHD, we observed that the worst scenario were areas in which specialist predators co-occur with high mortalities due to “other reasons” (Fig. 6d). These populations presented in average lower survivals in all age classes, a situation that would be aggravated by the arrival of myxomatosis as shown by the decrease of survival experimented by the older age classes as mortality due to myxomatosis increased. The best scenario, on the other hand, corresponded to populations where neither specialist predators exist nor is mortality by other causes elevated. These populations maintained the highest survival rates at all ages even in regions where myxomatosis has the strongest incidence (Fig. 6a?).

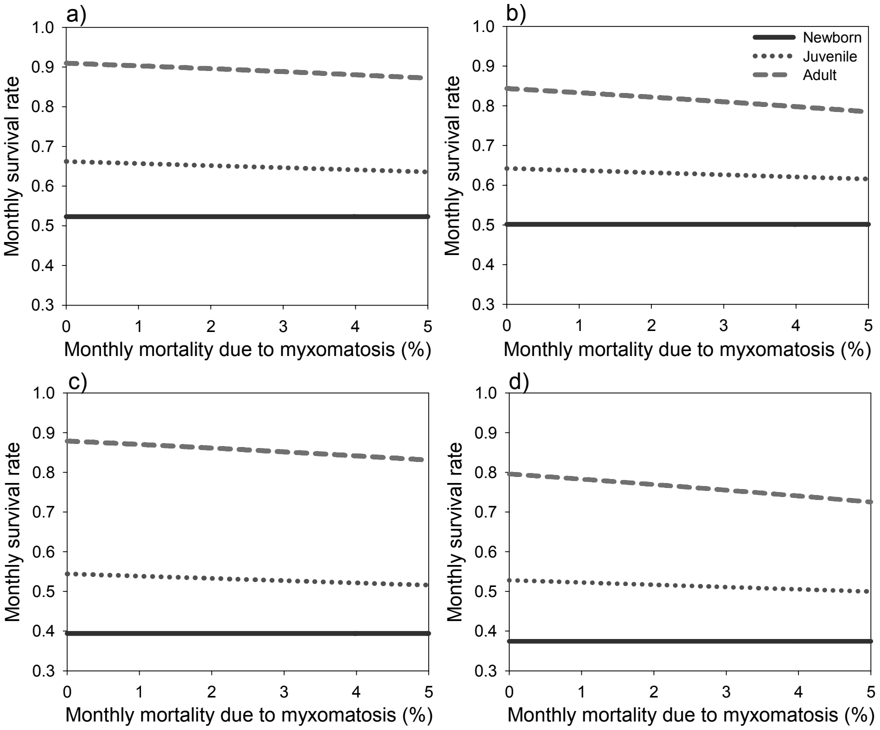

Figure 6. Variation in survival with increasing myxomatosis rates under different population scenarios. The top two graphs represent populations where the mortality due to “other causes” is small and specialist predators are either absent (a) or present (b). The lower ones correspond to populations where reasons, such as droughts, cause higher mortalities, also without (c) or with (d) specialists.

Regarding the impact of mortality rates and breeding traits on population dynamics, we found that, confirming the pattern found in the sensitivity analyses, predation by specialists and generalist appeared as the main causes explaining small rabbit numbers (Table 4), although the effect of both types of predation was less strong in populations with longer breeding seasons as shown by the significant interaction between both variables (Fig. 7.a, b). To a lower extent, mortality due to “other causes” was also found to be important for population size. In fact, when we examined how population numbers varied with breeding season under different population scenarios (combining levels of mortality for “other causes” and specialist predation; Fig. 7.c), we observed that all populations increased towards longer reproductive periods but the trend was much more pronounced in populations without specialist predators and low mortality due to other reasons than when specialist were present and “other-causes” mortality was high.

Table 4. Results of GLMs testing the influence of the main causes of mortality and reproductive aspects on rabbit population dynamics. The magnitude and rank of the standardized coefficient reflect the relative role of each variable.

Effects (STD.COEF)	**Population size**		**Extinction risk**		**Phase change**	
Reproduction	Std.Coef	*Rank*	Std.Coef	*Rank*	Std.Coef	*Rank*
Breeding season length *(BS)*	ns		ns		1.30**	*3*
% of pregnant females	ns		8.28*	*6*	0.63***	*5*
Mean litter size	13.78***	*6*	ns		ns	
Survival						
Predation by specialists	-80.95***	*1*	29.40*	*3*	ns	
Predation by generalists	-62.80***	*2*	ns		1.82**	*2*
Predation of myxomatous rabbits	ns		ns		ns	
Mortality due to myxomatosis	ns		-26.58§	*4*	ns	
Mortality due to “other causes”	-43.19***	*3*	30.00***	*2*	0.52§	*6*
*BS * Predation by specialists*	33.86*	*4*	ns		ns	
*BS * Predation by generalists*	29.39§	*5*	ns		-2.01**	*1*
*BS * Mortality due to myxomatosis*	ns		-34.22*	*1*	ns	
*BS * Predation of myxomatous rabbits*	ns		ns		ns	
*Generalist predation * Myxomatosis*	ns		18.07*	*5*	1.21**	*4*

§ = p < 0.08; * = p < 0.05; ** = p < 0.01; *** = p < 0.001

We found that extinction risk was also sensitive to variations in specialist predation and mortality for reasons other than predation (Table 4). However in this case, myxomatosis became one of the main factors increasing the probability of extinction of rabbit populations, especially in populations with shorter breeding season (Fig. 7.d). The effect of myxomatosis was also noticeable when interacting with mortality by generalist predators, which seemed to increase significantly extinction risk only when the disease was present in the populations (Fig. 7.e). As for population phase changes, predation by generalists was shown to be the main rate leading to decreases in the size of non-extinct populations from the first to the second 15-year periods simulated (Table 4). The effect of generalist predation on population change appeared to vary with the length of the breeding season (Fig. 7.f) and presence of myxomatosis in the population (Fig. 7.g). Thus, the combination of high predation with short reproductive periods led to higher reductions of mean population size than in the case of longer breeding season. In the same way, populations with myxomatosis tend to experiment larger phase changes than areas where myxomatosis is not present. Finally, apart from the mentioned interactions between breeding season and predation, the relative role of the other reproductive characteristics was found to be much smaller, with littersize affecting rabbit numbers and the percentage of breeding season influencing extinction risk and phase change (Table 4).

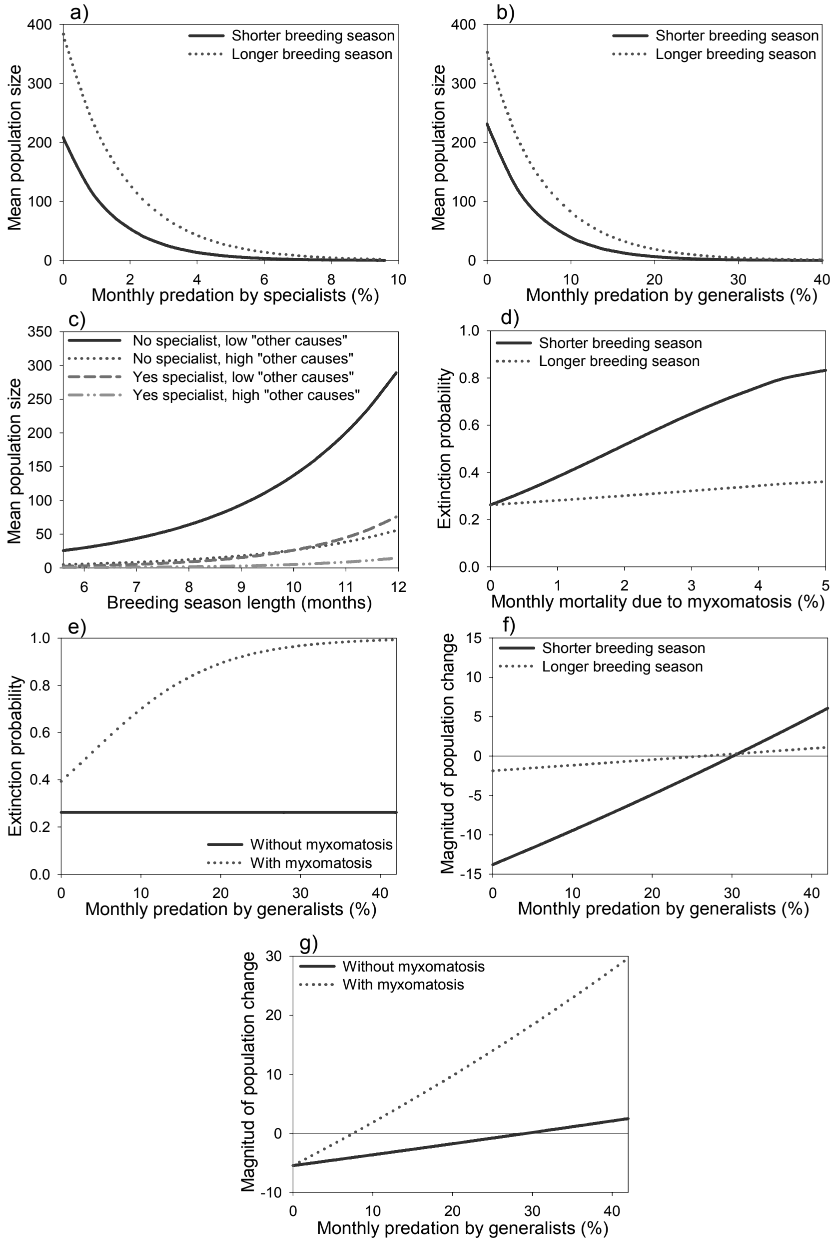

Figure 7. Effect of mortality rates and breeding season on rabbit population dynamics. (a) and (b) interaction between the effect of breeding season and of predation by specialist or generalist, respectively, on population size. Shorter breeding seasons correspond to 6.5 months/year approximately while longer ones were set to around 10 months/year. (c) Influence of breeding season on rabbit numbers in four different population scenarios. (d) Increase of extinction probability with myxomatosis for two breeding season scenarios. (e) Interaction between generalist predation and myxomatosis. (f) Season-dependent effect of predation by generalists on population phase change. (g) Variation in the influence of generalists on non-extinct population phase change according to the presence or absence of myxomatosis. The higher the values of phase change, the stronger is the drop in mean population size between the first and the second part of the simulated period.

Discussion

The contrasting population dynamics presented by European wild rabbits around the world, especially after the establishment of infectious diseases such as myxomatosis, have motivated numerous studies to understand rabbit reproduction and survival (e.g. Moriarty et al. 2000, Gonçalves et al. 2002). However, previous authors have always focused on single locations or on the impact of individual components of rabbit population dynamics. In this study, through the development of an individual-based model, we were able to examine jointly all the reproductive and mortality processes affecting rabbit populations before the arrival of RHD and asses the relative importance of each of them when considering the range of their global variability.

Our population model showed that rabbit population dynamics is mainly sensitive to variation in specialist predator abundance and density dependence in fecundity, but also in the parameters of the generalist predation function and myxomatosis lethality. To a lower extent the effect of age and food scarcity in the "other mortality" function were also important. This is in agreement with studies that suggested that specialized predators may cause substantial population declines when population growth, and thus recovery, are being reduced by stronger breeding density dependence, limited availability of food resources or generalist predation (Hanski et al. 2001, Turchin and Hanski 2001, Huitu et al. 2003).

Despite specialist potential to decrease rabbit abundance, they will only rarely be able to cause the extinction of their prey (Ryall and Fahrig 2006, Holt and Barfield 2009). That is, since specialists depend on rabbits to survive and reproduce, decreases in this prey species are expected to lead to predator declines, as shown for small mammals in northern Europe (Korpimaeki and Krebs 1996), which in turn release predation pressure on rabbits. Therefore, the observed high impact of specialists on rabbit extinction is likely due to not including the predator numerical response (Andersson and Erlinge 1977, Hanski et al. 1991, 2001) in our model. In our case we simulated small local populations, which may be marginal or a fragment of greater populations, and thus whose decline or extinction will not necessarily have an effect on predator numbers. However, numerical response of specialist predators should always be considered in studies considering larger scale populations.

Density-dependence in reproduction also seemed to have a high effect on driving abundance decreases in non-extinct rabbit populations. It was found to be the most relatively important parameter for this phase change variable. This could mean that the slowed recruitment of populations with higher breeding density dependence will prevent rabbits from easily escaping low density phases, such as the "predator pit" described in

Pech (1992) and Pech et al. (1995) in which rabbit populations may be maintained at low densities by generalist predators after a population collapse.

Population phase change (i.e. decline of rabbit abundance) showed also a positive association with breeding season length and the density dependence in the specialist predation function. These findings were surprising since rabbit numbers were expected to be enhanced by increases in specialist density-dependence (Table 2; Fig. 1) and breeding season (Chapter 3). We argue that these results could be the consequence of an inappropriate measurement of phase change since short reproductive seasons and low density-dependence in specialist predation would produce small-sized populations since the beginning of the simulated period. Thus, mean population size in the first 14 years could not be much larger than that of the remaining years and no change from a higher to a lower density phase would happen.

Within predation by generalists, the most influential parameter appeared to be the shape of the functional response curve. Increasing numbers of this parameter result in higher predation rates at low rabbit densities (Fig. 2). This would resemble the case of locations where rabbits are not the primary prey for generalists and instead predators, which are sustained by other food resources, prey marginally on rabbits even when they are scarce (Pech et al. 1995, Sinclair 2003). This may cause significant population decreases and even extinction of rabbit populations.

As for myxomatosis, parameters were set to reproduce disease dynamics similar to those found in populations where myxomatosis had been already established for some time, and thus, less virulent strains had been selected together with some rabbit genetic resistance (Williams et al. 1990, Aparicio et al. 2006, Chapter 2). Despite this disease attenuation, the higher limit of the lethality function showed an important negative effect on the probability of extinction of populations, confirming that myxomatosis may still have a relevant role on rabbit population dynamics.

Interestingly, higher myxomatosis transmission terms appear to be beneficial for rabbit populations. Increased spread rates has been suggested, both for myxomatosis (Fouchet et al. 2008) and RHD (Calvete 2006), to lead to early infections of young rabbits when they are still protected by maternal antibodies, thus, enhancing even further overall population immunity and decreasing mortality due to the disease. In the case of myxomatosis, the positive relationship between disease spread and rabbit populations could also be partially due to greater transmission rates being associated with relatively wet regions where vector abundance is higher (Parer and Korn 1989, Fenner and Fantini 1999) but also there is more food availability and rabbit productivity (Myers et al. 1994, Tablado et al. 2009).

Realized rates obtained from these model parameters were used together with some reproductive traits to examine the effect on rabbit survival of the different aspects usually measured in field studies. The pattern reproduced by the model was consistent with literature data (Chapter 3) and showed how the relative effects of variables tested varied with rabbit age. Survival of newborn and juvenile rabbits was mainly affected by mortality due "other causes" and generalist predators. In real populations, sources of mortality such as malnutrition, warren flooding or collapse, coccidiosis or infanticide are known to reduce substantially young rabbit survival (Tyndale-Biscoe and Williams 1955, Copson et al. 1981, Rodel et al. 2008) even in areas without diseases and low predation rates (Rodel et al. 2009). Generalist predators also tend to feed on more vulnerable young rabbits increasing their mortality importantly (Villafuerte 1994, Fedriani et al. 1999, Calzada 2000).

Reproductive characteristics considered (i.e. breeding season length, percentage of pregnancies and mean littersize) had also a low but negative effect on survival of mainly the two younger age classes. This finding suggests that increases in these breeding traits, which are the ones varying the most across space and time and determining differences in population productivities (Tablado et al. 2009), will lead to higher population densities, and thus, to larger mortalities through density dependence, whose influence is usually greater for young individuals (Gaillard et al. 1998, Rodel et al. 2004).

Density-dependent mechanisms could also explain the slightly beneficial effect of predation upon myxomatous rabbits on newborn and adult survival. In our model this extra predation rate was calculated by pooling all ages together. Therefore, its positive association with survival of the youngest and oldest age classes might imply that this indirect impact of myxomatosis is negatively affecting mainly to juveniles and this increased mortality, although not relatively important for juveniles, is reducing to some extent the density-dependent stress on the other age classes.

The direct influence of myxomatosis on survival also seemed to be comparatively small. This could be due, as mentioned above, to the implementation of lethalities according to moderately virulent strains, rabbit resistance and acquired natural immunization in wild populations (Williams et al. 1990, Kerr 1997, Aparicio et al. 2006, Chapter 2). The concentration of myxomatosis on specific moments of the year (Fenner and Fantini 1999, Mutze et al. 2002) might also contribute to the relatively small role of this mortality in overall rabbit survival.

The importance of predation by specialists as a source of mortality became apparent when examining adult survival. This relative higher effect on adults is probably due to specialist predators usually preying on oldest age classes, as opposed to generalists (Delibes and Hiraldo 1981, Villafuerte 1994, Palomares et al. 1995). It is, thus, through predation of adults, and to lower extent of juveniles, that specialists may reduce rabbit population sizes. This is observed in the analyses relating survival and reproductive factors to population dynamics, where predation by specialists showed one of the highest influences.

Results of these last analyses assessing the effect of life-history variables on rabbit populations confirmed our hypotheses as well as the findings of the sensitivity analyses. Predation by specialists and generalists appeared as the main causes of variation in rabbit dynamics, but their relative importance changed according to the population variable examined. Specialists were found to be the major factor affecting driving population sizes, which is in concordance with results of previous studies that highlight the potential of specialist predators to influence prey abundance (Andersson and Erlinge 1977, Hanski et al. 1991). However, we should be careful when interpreting this finding, since the real effect of specialist on wild rabbit populations will be modified by the predator numerical response (Hanski et al. 2001) not considered in our model.

The relative role of generalist predation, although important for mean population size, was highest in the case of population phase change. This mortality cause, which affects substantially survival of all age classes, has already been suggested as capable of suppressing rabbit populations and maintaining them at low densities (i.e. “Predator pit” of Pech 1992), especially after population collapses caused by other reasons (Trout and Tittensor 1989, Newsome et al. 1989, Banks 2000). In this case, the interaction found between generalists and myxomatosis indicates, as we predicted, that myxomatosis mortality may be one of the reasons that favour regulation by generalist predator through its detrimental effect on rabbit numbers.

Our results also show that the effect of generalists on producing phase changes in non-extinct rabbit populations, that is, suppressing them at lower densities, depended on the length of the breeding season. This means that in areas with shorter breeding seasons, generalist predators will more easily control rabbit numbers leading to larger phase changes and lower population size, while in regions where rabbits have higher productivities, populations will be able to escape those “predator pits” even with strong predation levels, as suggested by Pech (1992), and reach higher abundances. Breeding season also interacted with specialist predation by smoothing their effect. This may be due to longer prey reproductive periods producing greater population growth which make it more difficult for specialists to catch up with their prey numbers (Hanski et al. 1991, Hudson and Bjornstad 2003, Huitu 2003). All these findings supported our expectations about the interaction between predation and reproduction and they imply that, since, breeding seasons depends on food availability among other reasons (Tablado et al. 2009), improving habitat quality could be a possible way to alleviate predation pressure and to enhance rabbit populations.

The other breeding variables had a relatively smaller impact on rabbit populations, which may be a consequence of a balance between its positive effect increasing productivity and its negative association with juvenile and newborn survival through density-dependence. The apparently detrimental influence of percentage of pregnant females on population dynamics, increasing extinction risk and phase decrease, could also result from confusing cause and consequence. That is, relaxed density dependence in populations going extinct or trapped in low-density phases will lead to higher fecundity and pregnancy rates, and not the other way around. Mortality attributable to “other causes”, which were the main determinants of young rabbit survival, was also found to be relatively important for the population dynamics variables. This agrees with results of previous authors that related mortality caused by prolonged droughts, high precipitation, or harsh winter conditions to population declines and even local extinctions (Myers and Parker 1975, Williams et al. 1995, Angulo and Villafuerte 2003, Palomares 2003, Rodel et al. 2004).

Finally, our predictions about the importance of myxomatosis mortality for rabbit populations were also corroborated by the relatively high influence showed by myxomatosis on rabbit extinction risk. Moreover, the effect of this disease on populations appears to interact, on the one hand, with level of predation by generalist suffered by the population and, on the other hand, with the length of the breeding season. The former interaction refers, as mentioned for the case of population phase change, to the magnification of the negative impact of generalist predation on populations where myxomatosis had arrived and established *versus* populations before the arrival of this disease. The second case means that the effect of myxomatosis mortality is much worse in populations with short reproductive periods than in regions where rabbits breed more months per year and thus the higher recruitment may balance the mortality due to myxomatosis. This could, at least, partially explain why in some areas rabbit numbers were able to recover after few decades of myxomatosis arrival (Crawley 1989, Chapman and Flux 1990, Poole et al. 2003).

Although we need to further explore potential compensations among sources of mortality and investigate the predator numerical response, we can conclude that predation, both by generalists and by specialists, could be at least as important as mortality due to myxomatosis and other causes, for explaining differences among rabbit populations in pre-RHD times. We also realized that interactions between mortality causes and reproductive traits, that may go unnoticed in conventional studies examining factors individually, have a high influence on population dynamics. Therefore, future studies should explicitly considered the various causes of mortality and interactions in order to better understand dynamics of rabbit populations around the world and being able to improve control and conservation strategies for this species.

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Appendix 1: Complete model for rabbit population dynamics

It is a non-spatial stochastic individual-based model which represents a wild rabbit population in an area of 5 hectares. Model includes rabbit basic life cycle in which the gestation period lasts 30 days (Dunsmore 1971, von Holst et al. 2002), newborn rabbits stay in their warrens and depend on their mother up to day 30 when they are weaned, Juvenile rabbits reach sexual maturity when they are 4 months old (Soriguer 1981, Fraser 1988) and rabbit longevity is 6.8 years (von Holst et al. 1999). The model also incorporates a number of parameters that control reproduction, predation and the two endemic infectious diseases (myxomatosis and viral hemorrhagic disease (VHD)). Individual rabbit state are defined by characteristics (Table 1) which are updated in each model step (daily):

Table 1. Individual properties of rabbits.

State variables	Values
Age	0 - 2479 (days)
Sex	Randomly attributed (Male, Female)
Female reproductive status	
Non-pregnant	-1
Pregnant	0 - 30 (days since fecundation)
Female lactation	
Non-suckling female	-1
Days until offspring weaning	0 - 30 (days since parturition)
Female litter size	
Non-suckling females	0
Suckling females	Mean litter size (L) ± sd
Myxomatosis status	
Susceptible	-1
Infected but not infectious	0 - 9 (days since infection)
Infected and infectious	10 - 30 (days since infection)
Recovered and immune	31 - 365 (days since infection)
Susceptible	-1 (> 365 days since infection)
Myxomatosis maternal antibodies	
Rabbits born to immune does	0 - 49 (days since birth)
Otherwise susceptible	-1
RHD status	
Susceptible	-1
Infected and infectious	0 - 1 (days since infection)
Recovered, immune and infectious	2 - 30 (days since infection)
Recovered, immune but not infectious	31 - 365 (days since infection)
Susceptible	-1 (> 365 days since infection)
RHD maternal antibodies	
Rabbits born to immune does	0 - 56 (days since birth)
Otherwise susceptible	-1

Populations are started by 70 rabbits with: 1) random gender, 2) age randomly selected within a Gaussian distribution (Mean = 515; SD = 162) truncated at three standard deviations, 3) susceptibility to diseases and 4) if female, absence of pregnancy, lactation or offspring.

1) **Reproduction** (Table 2):

Rabbit are only allowed to breed in months within the reproductive period which is delimited by climate, food availability and photoperiod according to the following equation (From Tablado et al. 2009).

$$P_B = \frac{1}{1 + \mathrm{e}^{(4.542 - 0.605\,\mathrm{T} + 0.029\,\mathrm{T}^2 - 0.006\,\mathrm{D} - 0.017\Delta - \mathrm{W})}} \qquad \text{(Eq. 1)}$$

where T is the mean monthly temperature, D is the average daylength in each month, Δ is the difference between the D of a month and the D of the previous month and W represents food availability (W = 0 if previous two months were dry, that is, precipitation in mm < 2*temperature in ºC according to Walter & Lieth (1960) and W = - 1.592 if precipitation was higher than twice the temperature in at least one of the two previous months). Reproduction will occur in months in which P_B is ≥ 0.5.

Within the breeding season, sexually mature female rabbits (over 122 days) that are healthy (non-infected) and not already gestating will have a probability of becoming pregnant (P_R) that will depend on their age (Dunsmore 1971, Gibb et al. 1985) and population density (Myers and Poole 1962, Rodel et al. 2004) as shown by Equation 2:

$$P_R = \frac{e^{(\mathrm{r_A} - \mathrm{d}\frac{\eta}{\mathrm{K}})}}{1 + e^{(\mathrm{r_A} - \mathrm{d}\frac{\eta}{\mathrm{K}})}} \qquad \text{(Eq. 2)}$$

where $\mathrm{r_A}$ is a parameter whose value increases with age class (4-6 months, 6-9 months and over 9 months (Tablado et al. 2009) and $\mathrm{d}\frac{\eta}{\mathrm{K}}$ is factor representing density dependence in reproduction (with d being a constant, η the population density and K the carrying capacity).

If pregnancy occurs, gestation lasts 30 days (Dunsmore 1971, von Holst et al.

2002). Female, if healthy, then give birth to a number of kittens chosen randomly within a Gaussian distribution with mean equal to the average population litter size (*L*) and the extremes truncated at two standard deviations. This standard deviation is set to one according to similar literature values (Brambell 1944, Soriguer 1981, Gonçalves et al. 2002). If they get infected with myxomatosis or RHD during pregnancy, gestation will stop losing their litters.

Monthly proportion of pregnant females ($B_{(A)}$) of each mature age class (A; 4-6 months, 6-9 months and over 9 months) is calculated as

$$B_{(A)} = \frac{\text{pregnant females of age class A in a month}}{\text{Total of females of age class A in a month}} \qquad \text{(Eq. 3)}$$

After parturition, females enter the lactation period (30 days; Hudson and Distel 1990, von Holst et al. 2002) in which newborns depend on them. Due to post-partum oestrus females might become pregnant the day after giving birth (Bonino 2006, Calvete 2006) with a probability (P_R). Newborn will be recruited into the population with an age of 0 days and random gender. If they are females they will never be pregnant, lactating, have a litter size or previous pregnancies. Young rabbits are also free of diseases, but might have inherited maternal antibodies if born to immune females.

2) **Survival** (Table 2):

The probability of survival will depend on the probability of being predated (P_p), of dying from myxomatosis (P_M) and VHD (P_H) and of being killed by other causes of mortality (P_θ). That is, overall probability of survival will be:

$$P_S = (1 - P_p)(1 - P_M)(1 - P_H)(1 - P_\theta) \qquad \text{(Eq. 4)}$$

1. *Predation:*

Since rabbits are born they have a risk of being predated by specialist predators and by generalist predators:

$$P_p = 1-(1-\rho_s)(1-\rho_g) = \rho_s + \rho_g - \rho_s\rho_g \tag{Eq. 5}$$

Where ρ_s and ρ_g, which are the probability of being predated by specialists and generalists respectively, are represented by the following functions:

By specialists (Fig. 1S):

$$\rho_S = 1 - e^{-\left(S_p\right)} \tag{Eq. 6}$$

Being

$$S_p = \mathrm{s}\,e^{-\left(\mathrm{a}\,\frac{\eta}{\mathrm{K}}\right)} \tag{Eq. 7}$$

Where $\left(\mathrm{a}\,\frac{\eta}{\mathrm{K}}\right)$ is the density dependence term (with a being a constant, η the population density and K the carrying capacity) and s represents the amount of predators.

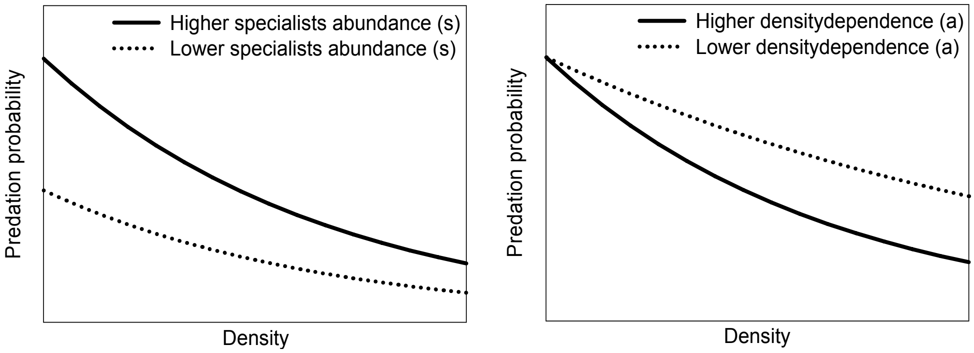

Figure 1S. Variation with density of the probability of being killed by specialist predators.

Since specialists predators focus on consuming mainly juvenile and adult rabbits (see Chapter 2 of this thesis), we consider that for newborn rabbits (below 30 days of age) the risk of being predated by specialist is a fifth of the total (i.e. $\frac{\rho_S}{5}$).

By generalists (Fig. 2S):

$$\rho_g = 1 - e^{-\left(G_p\right)} \qquad \text{(Eq. 8)}$$

Being

$$G_p = \frac{g}{\left(\frac{\eta}{K}\right)}\, e^{-\left(\left(\frac{ln\left(\frac{\eta}{K}\right)}{c}\right)^2 + \left(b\,A - M\right)\right)} \qquad \text{(Eq. 9)}$$

Where g is predator load, $\left(\frac{\eta}{K}\right)$ is factor representing density dependence (with η as the population density and K the carrying capacity). M is presence (>0) or absence (=0) of the effect of myxomatosis favouring predation, c is the shape parameter, b is a constant and A is rabbit age (in days).

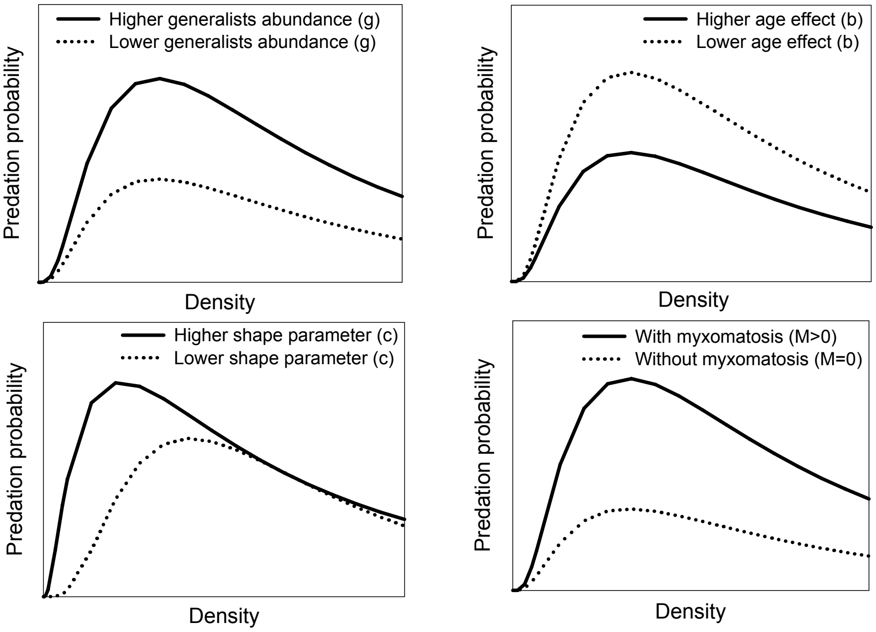

Figure 2S. Density-dependence of the probability of being killed by generalists.

2. *Diseases:*

There are two main diseases to which rabbits might be exposed: Myxomatosis and RHD. Since both myxoma and RHD virus may persist for long periods in warrens, vectors or carriers (Chapple and Lewis 1965, Lenghaus et al. 1994, Westbury 1996, McColl et al. 2002), we established that these diseases could appear any month in the population. To do this, we actively infected some individuals every month (except those in which there were already infectious rabbits, that is, individuals shedding infective virus). The amount of rabbits actively infected was a random number going from zero to 1+ (0.01*population size). Initial infected rabbits were always older than 30 days because younger rabbits will only be infected through their mothers since they stay in their warrens or breeding stops with a reduced contact rate with disease sources. Thus, newborn will only became infected when their mother gets infected. For the same reason, these young rabbits will not enter the pool of infectious animals until they reach one month of age and start interacting with other individual.

Myxomatosis:

Since the main mode of myxomatosis transmission is through insect vectors, the risk of infection of susceptible rabbits will depend on the frequency of infectious rabbits in the population (McCallum et al. 2001, de Castro and Bolker 2005). It will also vary from wet to dry areas (see Chapter 2 of this thesis). Thus, the probability of infection is:

$T_M = 1 - e^{-f_M}$, being the force of infection is $f_M = \mathrm{b_M} \frac{\mathrm{I_M}}{\mathrm{N}}$ (Eq. 10)

$\mathrm{b_M}$ is the transmission parameter which varies from wet locations ($\mathrm{b_M}$ >>0) to dry areas ($\mathrm{b_M}$ >0). Wet areas are those with more than six wet months per year (i. e. precipitation in mm > 2*temperature in ºC) according to Walter & Lieth (1960). Otherwise the location is considered dry. $\mathrm{I_M}$ is the total number of infectious individuals over 30 days old and N the total number of rabbits over 30 days old. Rabbit with myxomatosis are infectious only while they have the injuries suppurating (see above).

Once rabbit are infected with myxomatosis they either recover or die (i.e. 31 days after infection approximately) with a probability (D_M) that is going to be a function of age

(Fenner and Ratcliffe 1965, Parer et al. 1994; Eq. 11; Fig. 3S).

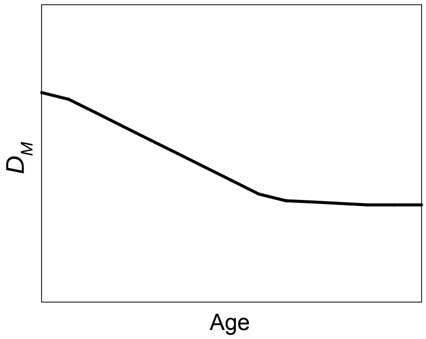

Figure 3S. Change in myxomatosis lethality with age.

$$D_M = \ell_M + \frac{h_M}{1+\left(\frac{A}{i_M}\right)^u} \qquad \text{(Eq. 11)}$$

D_M = Lethality of myxomatosis (from 0 to 1). A is rabbit age (in days) and ℓ_M is the lower plateau, i_M is the value of A at the curve inflexion point and $h_M + \ell_M$ determines the higher plateau and u is the curvature parameter.

Thus, the probability of dying from myxomatosis is

$$P_M = T_M * D_M \qquad \text{(Eq. 12)}$$

Rabbits that survive to myxomatosis become recovered rabbits with immunity. They will loose immunity after a year when they become susceptible again. If female rabbits breed while having immunity, this immunity will be transferred vertically (i.e. maternal antibodies) to their kittens and will last for 49 days after birth (Fenner and Marshall 1954, Ross 1972). While being immune rabbits can still become infected but not infectious because they develop a milder form of the disease. They do not die and reinforce their immune system (Ross 1972, Fenner and Fantini 1999).

RHD:

Since transmission route for the RHD is mainly direct contact, although vectors might also contribute to the spread of the disease, we assumed a density-dependence transmission rate for simplicity sake (Begon et al. 1999, Smith et al. 2009). This function also varied with temperature throughout the year (see Chapter two of this thesis). Thus, the probability of infection is:

$T_H = 1 - e^{-f_H}$ given that the force of infection is $f_H = \mathrm{b_H}\,\mathrm{I_H}$ (Eq. 13)

where $\mathrm{b_H}$ is the transmission parameter which changes temperature and I_H is the total number of infectious individuals over 30 days old shedding virus, which refer to rabbits infected with the disease and those recovered (i.e. up to 30 days since infection).

According to the results obtained in Chapter 2 of this thesis, we considered that $\mathrm{b_H} = 0$ at extreme temperatures (i.e. lower than 3.9 ºC and higher than 29.7 ºC). While at milder temperatures (Temp), the transmission parameter varied quadratically as shown by the following equation (adjusted to the results of Chapter 2) with a parameter (δ) which modifies the magnitude of curve:

$\mathrm{b_H} = \delta * (-0.5913 + 0.1717 * \mathrm{Temp} - 0.0051 * \mathrm{Temp}^2)$ (Eq. 14)

When rabbits are infected with RHD, after approximately two days, they have a probability D_H of dying from this disease. Contrarily to myxomatosis, this probability increases as rabbits grow old (age resilience). According to some data given by Robinson et al. (2002) and Calvete (2006) lethality of RHD would be represented by the following curve (Fig. 4S) and equation:

Figure 4S. Change in myxomatosis lethality with age.

$$D_H = \ell_H + \frac{h_H}{1+\left(\frac{A}{i_H}\right)^v} \qquad \text{(Eq. 15)}$$

D_H = Lethality of myxomatosis (from 0 to 1). A is rabbit age (in days) and ℓ_H is the lower plateau, i_H is the value of A at the curve inflexion point and $h_H + \ell_H$ determines the higher plateau and v is the curvature parameter. Thus, the probability of dying from myxomatosis is

$$P_H = T_H * D_H \qquad \text{(Eq. 16)}$$

Rabbits that survive to RHD infection recover and get immunity for a certain period after which they become susceptible again. If females reproduce while being immune, their offspring will be born with maternal antibodies that protect them against the disease for 56 days (Lenghaus et al. 1994, Cooke 1999). Post-recovery or maternal immunity protects rabbits against death but they can still get infected and have its antibody titres would be boosted (Cooke et al. 2000).

3. *Other causes (Fig. 5S):*

Mortality (P_θ) caused by sources other done predation or diseases, such as flooding or collapse, decrease with rabbit age according to the following equation:

$$P_\theta = 1 - \left[\left(\frac{e^{(\mathrm{j+zA})}}{1+e^{(\mathrm{j+zA})}}\right)\left(1-e^{\left(\frac{-\mathrm{q}}{\mathrm{F}}\right)}\right)\right] \tag{Eq. 17}$$

Where j and z are constants, A is rabbit age and $\left(\frac{-\mathrm{q}}{\mathrm{F}}\right)$ is a term representing food scarcity (with q as a constant and F as the number of consecutive dry months (precipitation < 2*temperature).

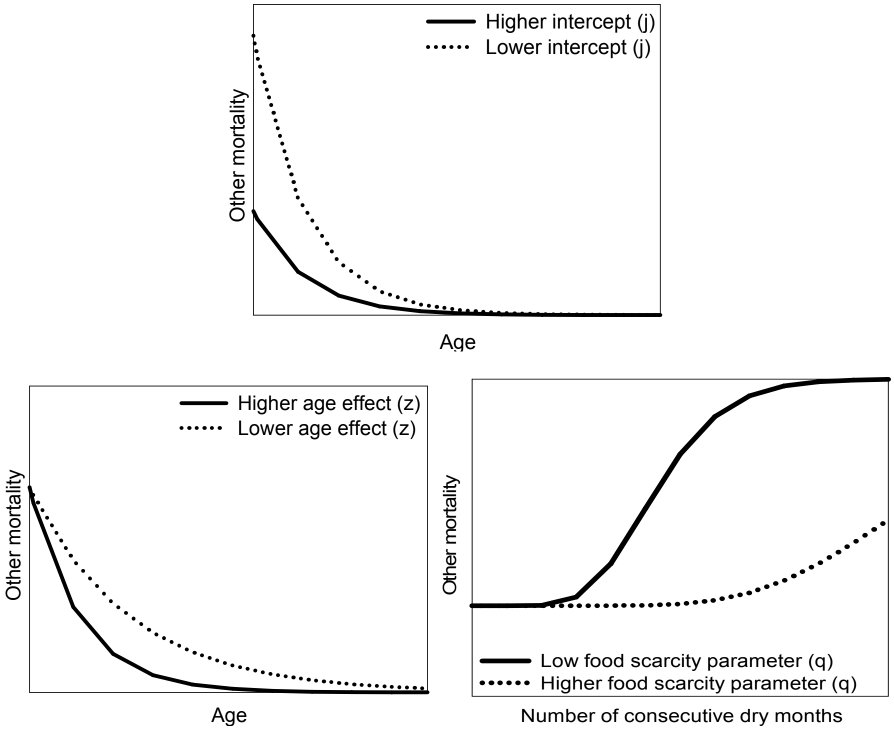

Figure 5S. Effect of age and number of dry months on mortality due to other causes.

Output monthly survival ($S_{(A)}$**)** of each age class (A; <1 months, 1- 4 months, and > 4 months) will be then calculated by the model as

$$S_{(A)} = 1 - \left(\frac{\text{dead rabbits of age class A in a month}}{\text{Total rabbits of age class A in a month}}\right) \tag{Eq. 18}$$

Table 2. Parameters of the rabbit population model.

Parameter description	**Symbol**	**Values**
Population density	η	
Carrying capacity	K	
Rabbit age (in days)	A	
Reproduction		
Probability of being in a breeding season month	P_B	(Eq. 1)
Mean monthly temperature (ºC)	T	Meteorological station data
Average daylength in a month (light minutes/day)	D	Meteorological station data
Photoperiod change between 2 consecutive months	Δ	Meteorological station data
Availability of green pastures in a given month	W	= 0 if precip < 2*Temp in the previous two months. = -1.592 otherwise
Breeding probability of mature females	P_R	(Eq. 2)
Age effect on female fecundity	r_A	= 0 from 4 – 6 months old > 0 from 6 – 9 months old > > 0 over 9 months old
Factor of density-dependence in reproduction	d	
Average litter size	L	3.2 - 7.3 rabbits/ litter (Soriguer 1981, Stevens and Weisbrod 1981)
Monthly realized proportion of pregnancies	$B_{(A)}$	(Eq. 3)
Survival	$\boldsymbol{P_S}$	**(Eq. 4)**
Predation probability	P_P	(Eq. 5)
Probability of predation by specialists	ρ_s	(Eq. 6)
Rabbits consumed by specialist predators	S_p	(Eq. 7)
Specialists predator abundance	s	
Density-dependence constant	a	
Probability of predation by generalists	ρ_g	(Eq. 8)
Rabbits consumed by generalist predators	G_p	(Eq. 9)
Generalist predator abundance	g	
Constant of the predation function	b	
Shape parameter	c	
Parameter for vulnerability of myxomatous rabbits	M	> 0 if infected with myxoma virus = 0 otherwise
Probability of dying of myxomatosis	P_M	(Eq. 12)
Probability of being infected with myxoma virus	T_M	(Eq. 10)
Force of infection of the myxoma virus	f_M	
Myxomatosis transmission term	b_M	>>0 when more than 6 wet months per year >0 otherwise, in dry areas
Number of myxomatous rabbits	I_M	
Total number of rabbits over 30 days old	N	
Myxomatosis case-mortality	D_M	(Eq. 11) $0 \leq D_M \leq 1$
Lower limit of the curve	ℓ_M	
X-value at the inflexion point	i_M	
Higher limit of the curve	$h_M + \ell_M$	
Curvature parameter	u	

Parameter description	**Symbol**	**Values**
Probability of dying of RHD	P_H	(Eq. 16)
Probability of being infected with RHD virus	T_H	(Eq. 13)
Force of infection of the RHD virus	f_{H}	
RHD transmission term	$\mathrm{b_H}$	(Eq. 14)
Number of infectious rabbits (with RHD)	$\mathrm{I_H}$	
Magnitude of the transmission curve	δ	
RHD case-mortality	D_H	(Eq. 15) $0 \le D_H \le 1$
Lower limit of the curve	ℓ_{H}	
X-value at the inflexion point	$\mathrm{i_H}$	
Higher limit of the curve	$\mathrm{h_H} + \ell_{\mathrm{H}}$	
Curvature parameter	v	
Probability of dying of other causes	P_θ	(Eq. 17)
Intercept of the mortalities mortality	j	
Age parameter of the mortality function	z	
Effect of food scarcity	q	
Number of consecutive dry months	F	
Monthly age-specific realized survival	$S_{(A)}$	(Eq. 18)

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CONCLUSIONES GENERALES:

1. En este estudio observamos que tras la gran variabilidad espacio-temporal de los parámetros reproductivos y de supervivencia de una especie globalmente distribuida como el conejo, existen determinados patrones que pueden ser explicados a través de características individuales, poblacionales y ambientales, siendo estas últimas el resultado de la adaptación de la especie a las condiciones de cada localidad.

2. La revisión bibliográfica de la reproducción del conejo mostró que a pesar de su amplia distribución geográfica, existen parámetros que poseen valores similares en todas las poblaciones, como la duración de la gestación, la temprana madurez sexual y los estros post-parto, y que son los que confieren a la especie su alto potencial reproductivo.

3. El alto potencial reproductivo de la especie se ve modificado a nivel poblacional por la variación existente en otros parámetros que son la longitud del periodo reproductor, el porcentaje de hembras preñadas, la edad de primera reproducción y el tamaño y número de camadas. Los factores que, según este estudio, determinan los patrones de variabilidad global encontrados en dichos parámetros son la edad y el peso de los conejos, y las variables ambientales. De hecho, se obtuvo un modelo que predice con gran fiabilidad la longitud de la estación reproductora de los conejos a partir de la temperatura, precipitación y fotoperiodo de cada mes.

4. Mediante la revisión de la mortalidad, encontramos que el aumento en magnitud y disminución en variabilidad de las tasas de supervivencia a medida que los conejos envejecen es el resultado de una combinación de factores como la predación, enfermedades y otras causas adicionales que afectan de forma diferente a cada clase de edad del conejo. El efecto negativo de las abundantes precipitaciones y de la predación afecta principalmente a las clases más jóvenes, es decir gazapos y juveniles, mientras que la presencia de enfermedades en la población disminuye las tasas de supervivencia principalmente de juveniles y adultos, y no de gazapos.

5. Las tasas de predación están correlacionadas, a parte de con la edad, con la densidad poblacional y de predadores de forma positiva y con la presencia de

myxomatosis y la enfermedad hemorrágica vírica (EHV) en las poblaciones, que aumentan la vulnerabilidad de los individuos. La actividad de dichas enfermedades a lo largo del año depende tanto de las variables climáticas como del periodo reproductor, debido a que la temperatura y la precipitación condicionan la transmisión por vectores y la persistencia del virus y a que la reproducción es el medio a través del cual se reclutan nuevos individuos susceptibles en la población. La letalidad de las enfermedades, sin embargo, varía según el grado de virulencia de la cepa y la resistencia genética de la población en el caso de la mixomatosis y según la edad del conejo en el caso de la EHV.

6. Utilizando un modelo demográfico basado en el individuo para examinar el efecto de las variaciones de la reproducción en la dinámica poblacional del conejo, observamos que la duración y la variabilidad de la estación reproductora tienen mucho peso en el tamaño y la probabilidad de extinción de las poblaciones. Así mismo, dado que la estación reproductora está determinada por el clima y el fotoperiodo, las alteraciones climáticas que se están produciendo a nivel global tendrán consecuencias importantes para las poblaciones de conejo a lo largo de su área de distribución.

7. En gran parte del área de distribución actual del conejo, y especialmente en la Península Ibérica donde los conejos son una especie clave, el cambio climático producirá declives poblacionales, aumentará el riesgo de extinción y disminuirá la capacidad de recuperación de las poblaciones tras un colapso. Mientras que por el contrario, hacia los límites norte y este de su distribución, la abundancia de conejos aumentará, la probabilidad de extinción disminuirá y las poblaciones se recuperarán más fácilmente tras una perturbación, lo que aumentará el potencial invasor de la especia en esas zonas.

8. Implementando los diferentes componentes de la supervivencia, excepto la EHV, y la reproducción de los conejos de forma conjunta en el modelo basado en el individuo, encontramos que la dinámica poblacional de los conejos se ve principalmente afectada por variaciones en los niveles de predación, tanto por especialistas como por generalistas, seguido de cambios en la mortalidad debido a myxomatosis y a otras causas como la sequía o los atropellos.

9. La mortalidad debida a predación y myxomatosis interacciona de forma significativa con las variables reproductivas de la población. Es decir, poblaciones con tasas de reproducción más bajas sufren en mayor medida el impacto de la myxomatosis y la predación y caen con más facilidad bajo la regulación por predadores generalistas que las mantienen a bajas densidades. Asimismo, el efecto de los generalistas también se ve potenciado por la presencia de myxomatosis en las poblaciones.

10. El conejo de campo es una especie que presenta dinámicas poblacionales muy complejas y dispares a lo largo de su distribución, estando en declive en algunas regiones y comportándose como especie invasora en otras. Por lo tanto, estudios como éste son necesarios para poder llegar a entender mejor la dinámica poblacional del conejo y los procesos a través de los cuales podemos actuar para mejorar su conservación o su control.

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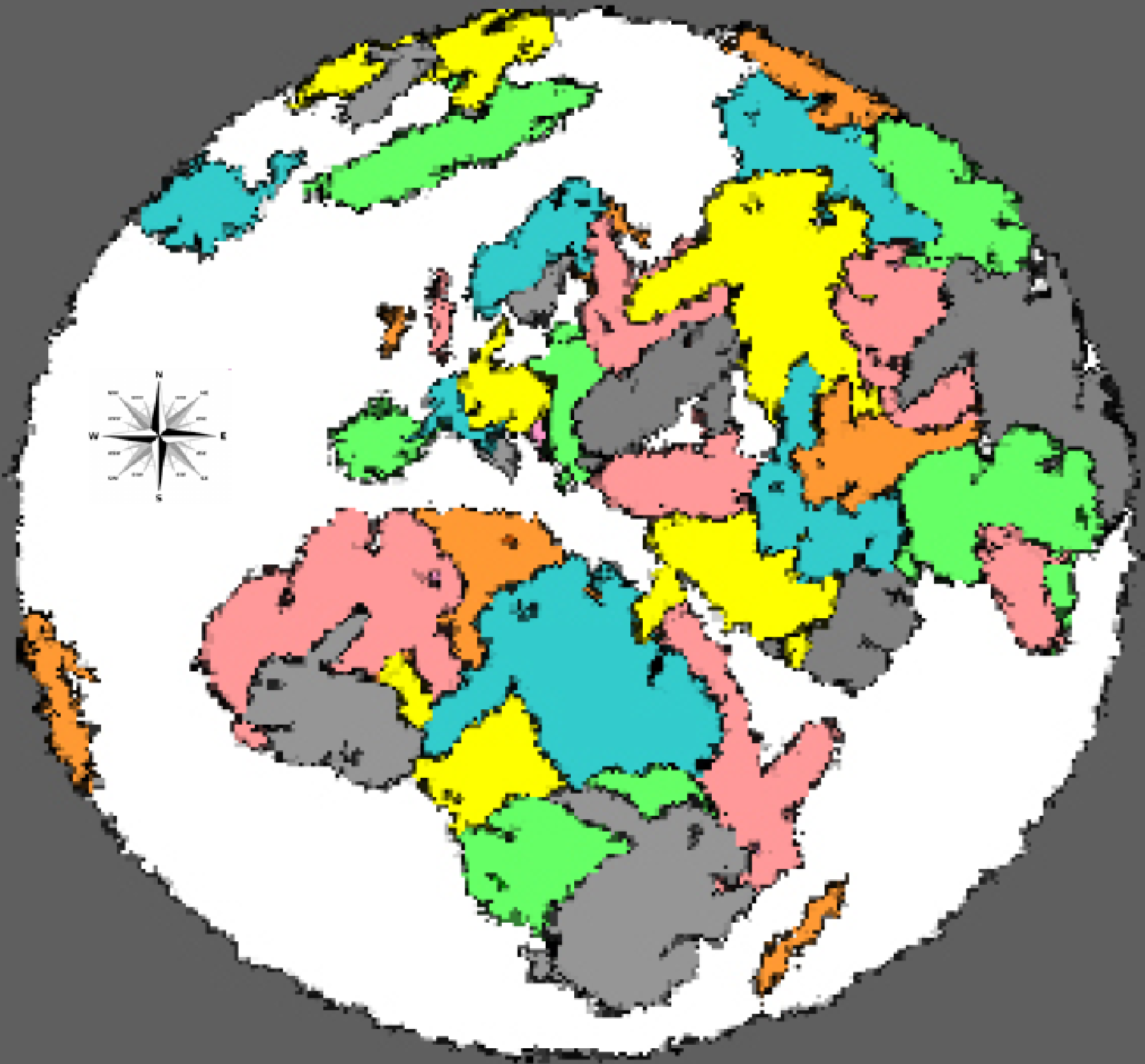

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