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FACTORES QUE AFECTAN A LA DISTRIBUCIÓN Y ABUNDANCIA DEL CONEJO EN ANDALUCÍA

MEMORIA PRESENTADA PARA OPTAR AL GRADO DE DOCTOR POR

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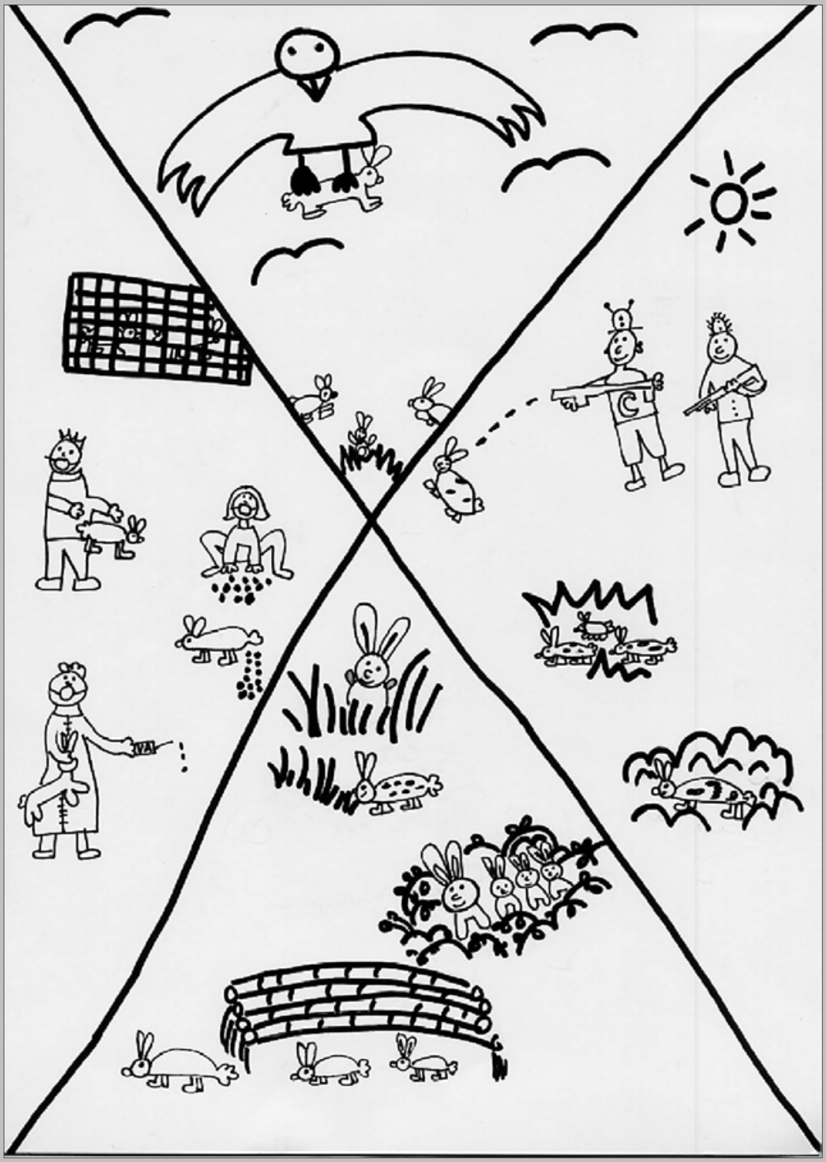

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Memoria presentada por
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para optar al grado de Doctor en Ciencias Biológicas
Programa de Ecología y Medio Ambiente

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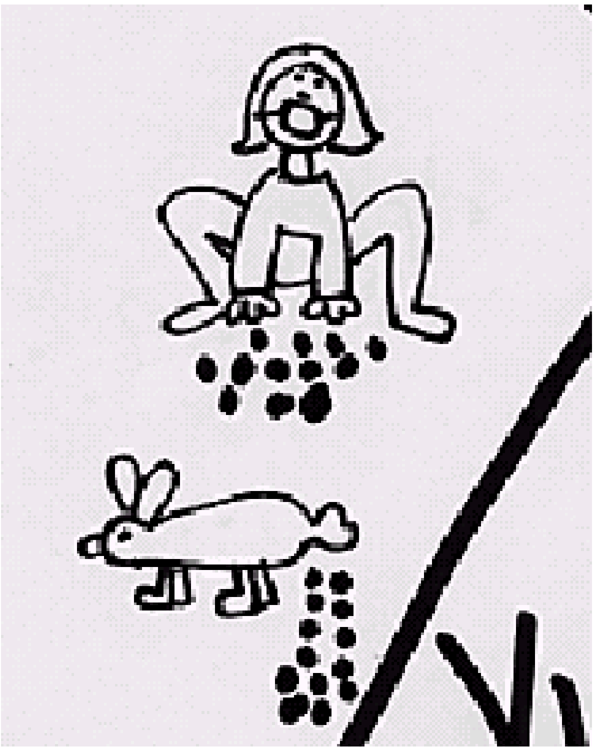
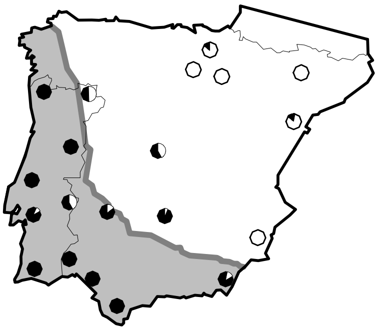


INTRODUCCIÓN

INTRODUCCIÓN

Origen del conejo europeo

El conejo europeo, *Oryctolagus cuniculus*, se originó en la Península Ibérica a partir de la especie *O. laynensis*. Durante las glaciaciones del cuaternario, se refugió en dos núcleos: uno en el Sur peninsular y otro en el Noreste de España o en el Sudeste de Francia (Biju-Duval et al. 1991; Monnerot et al. 1994). Como resultado de esta separación geográfica actualmente se distinguen dos subespecies: *O.c.algirus* y *O.c.cuniculus*, respectivamente. Durante el período postglacial, las dos subespecies se dispersaron y volvieron a encontrarse en una franja que divide a España en dos mitades desde Galicia a Almería.



Distribución geográfica de las subespecies *O.c.cuniculus* y *O.c.algirus*. La linea gruesa indica la separación sugerida por Ferrand en 1995. Los diagramas de sectores indican la distribución de ADN mitocondrial característico de cada una de las subespecies (negro para *O.c.algirus* y blanco para *O.c.cuniculus*). Modificado de Branco et al.(2000) y Ferrand (1995).

O. c. cuniculus se extendió de manera natural por el resto de Europa, también fue transportada por el hombre al resto del mundo y, a partir de ella, se crearon las razas domésticas. Esta alta manipulación provocó la pérdida de la diversidad genética heredada de la especie predecesora. Sin embargo, la subespecie del Sur, menos manipulada, mantiene actualmente una alta diversidad genética. Esta alta diversidad se ha mantenido a pesar de las glaciaciones, de los depredadores, de los efectos del hombre y de las enfermedades, que no han conseguido producir un cuello de botella en sus poblaciones (Biju-Duval et al. 1991; Branco et al. 1999). Por estos motivos, las poblaciones de conejo de la Península Ibérica representan las poblaciones de conejo originales y deben ser conservadas.

El conejo, una especie prolífica

Las altas abundancias de conejo que han favorecido esta conservación de su diversidad genética, se deben a unas características biológicas subyacentes en un modelo de vida que le hace ser muy adaptable a diferentes condiciones ecológicas. Entre otras cabe destacar que es una especie muy prolífica. Su alta productividad se debe a que alcanza la madurez sexual a los cuatro meses, la hembra es receptiva todo el año, tiene un período de celo tras el parto y produce una numerosa camada (Soriguer 1981).

Sin duda constituye el mamífero más extendido a lo largo de la Península Ibérica. Su elevada productividad está compensada por una alta mortalidad. Tan sólo en España se han citado 39 especies de vertebrados, además del hombre, que depredan sobre el conejo. Pocas especies son capaces de presentar de forma natural tan elevadas densidades con tan gran número de depredadores. El conejo debe superar el impacto de la depredación, su principal causa natural de mortalidad, a través de su modo de vida, gracias a una serie de caracteres morfológicos y ecológicos. El conejo está preparado para evitar a los depredadores: su actividad es fundamentalmente crepuscular, para evitar a las rapaces durante el día y a los carnívoros que cazan de noche; su fisonomía le hace críptico con el medio que le rodea; su pelaje es pardo; su oído capta las frecuencias bajas que emiten los depredadores cuando acechan; sus ojos enfrentados le dan una visión completa de su entorno y están adaptados a la visión en las horas crepusculares. Su comportamiento social (se alimentan en grupos y colaboran en la vigilancia) causa un efecto de dilución frente a los depredadores. Por último, el conejo ha desarrollado numerosas y variadas estrategias ecológicas para evitar al depredador y minimizar el riesgo de depredación. En función de los depredadores existentes, del momento del día y de las características de la vegetación que le rodea, usa preferentemente los ecotonos entre el refugio y las zonas de alimentación; usa las madrigueras cuando el refugio es escaso y la abundancia de conejos es alta (así se reparten los costos del mantenimiento de madrigueras), y usa el hábitat a lo largo del día de forma variable y dependiente de los depredadores (un refugio efectivo ante un depredador puede ser vulnerable ante otro) (Burnett y Hosey 1987; Villafuerte 1994; Moreno et al. 1996; Cox et al. 1997; Villafuerte y Moreno 1997; Banks et al. 1999).

Importancia ecológica en su área de distribución original: el conejo como presa clave

La importancia numérica de las poblaciones de conejo le ha convertido en una especie clave desde el punto de vista ecológico en el ecosistema mediterráneo del Sur de Europa. El conejo constituye una de las especies presa más consumida, soportando, como se dijo más arriba, casi 40 especies de depredadores diferentes. De éstas, una veintena prefieren al conejo antes que cualquier otra presa y una decena prácticamente sólo consumen conejo (Gortázar et al. 2000). Probablemente el conejo ha sido el causante de la diferenciación de dos depredadores endémicos de la “tierra de los conejos”: el águila imperial Ibérica, la rapaz más amenazada de Europa, y el lince ibérico, el felino más amenazado del mundo. Estos depredadores se diferencian de sus homólogos europeos en su tamaño, que fue variando al especializarse en consumir una presa muy abundante y de un tamaño intermedio entre los ungulados y los roedores.

Además, la alta disponibilidad de gazapos durante la primavera, su menor tamaño y su mayor vulnerabilidad, hace que sean una fuente extra de recursos para la cría de rapaces de menor tamaño o de carnívoros más generalistas. En este sentido, mientras los depredadores más dependientes del conejo provocan un impacto moderado sobre las poblaciones de conejo, los depredadores oportunistas producen pérdidas mayores en el potencial reproductivo de las poblaciones (Villafuerte 1994).

Sin embargo, las poblaciones de conejo siguen siendo localmente abundantes y es importante que sigan manteniendo sus densidades altas para la conservación de la comunidad de depredadores mediterráneos y, en concreto, para los ya citados más dependientes del conejo y en grave peligro de extinción, algo muy importante en Andalucía, ya que, debido a la gran variedad de climas y ambientes que contiene, a su situación geográfica privilegiada al sur de Europa, a su baja densidad humana y a su escaso desarrollo industrial, esta región ha mantenido el patrimonio natural en muy buen estado de conservación.

Importancia ecológica fuera de su área de distribución original: el conejo como especie invasora

Durante su evolución de miles de años, ese modelo de vida que le hace ser tan prolífico, ha permitido al conejo colonizar paisajes muy diversos. Ya en la historia reciente y, ayudado por el hombre, el conejo se ha enfrentado a ecosistemas de continentes lejanos a los de su área de distribución original. En muchos de estos lugares cuando el clima es adecuado, compite con gran éxito frente a las especies autóctonas y, a falta de una comunidad de depredadores que regulen sus poblaciones, se ha convertido en una plaga de gran impacto económico y ambiental. El control del conejo cuesta cada año 170 y 310 millones de dólares en Gran Bretaña y Australia respectivamente. Los daños no van exclusivamente dirigidos a la agricultura; el conejo es una de las principales causas de la rarefacción y extinción de animales y plantas australianas. (Robinson et al. 1997; Fenner y Fantini 1999).

Caricatura de la propuesta de Pasteur para el control de conejos a través del bacilo del cólera del pollo. Obtenido de Fener y Fantini 1999.

La abundante literatura científica que existe sobre el conejo se debe fundamentalmente a los estudios que se han realizado en aquellos lugares en donde actúa como una especie invasora. Actualmente el flujo de información es recíproco entre las investigaciones realizadas para la conservación del conejo y para su control. Numerosos métodos de control se han ensayado, desde la destrucción de las madrigueras, el uso de venenos o el control de la fertilidad, hasta los métodos de control biológico como el uso de virus o sus vectores. En este sentido, una gran parte de la problemática actual del conejo en el Sudoeste de Europa se debe a las formas de control que se han ido sugiriendo y utilizando en aquellas partes del mundo y que han ido llegando al área de distribución original de la especie (Boag, 1987; Sheail, 1991; Thompson y King 1994; Holland, 1999; Twigg et al. 2000).

La problemática actual: el descenso de las abundancias de conejo

Es un hecho que en las últimas décadas el conejo está experimentando un grave declive en sus poblaciones (Moreno y Villafuerte 1995; Villafuerte et al. 1998). Pero, ¿cómo se ha llegado a la situación actual de declive en una especie tan prolífica?. Según la teoría de ecología de poblaciones, la dinámica de una especie depende de tres parámetros fundamentales: la reproducción, la supervivencia y la migración (Johnson 1996). Examinando los factores que afectan a estos parámetros, especialmente a la reproducción y la supervivencia de los conejos, se pueden establecer ciertas hipótesis para intentar resolver esta pregunta.

Por un lado, la reproducción en los conejos está en función directa de la calidad del alimento, calidad que depende del tipo de hábitat y de las condiciones climáticas. La disminución o desaparición del hábitat adecuado puede ser una de las causas que expliquen esta disminución del conejo (Wallage-Drees 1983; Bell y Webb 1991; Moreno y Villafuerte 1995; Villafuerte et al. 1997; Palma et al. 1999).

Por otro lado, la supervivencia depende de los factores de mortalidad a los cuales la especie se ve sometida. En el caso del conejo esta mortalidad se puede clasificar en 3 tipos: la depredación, la caza y las enfermedades. Estas causas de mortalidad podrían haber provocado la situación actual en que se encuentran las poblaciones de conejo. La depredación ha sido extensamente estudiada por diversos autores (Rogers 1974; Kufner 1986; Villafuerte et al. 1994; Calzada 2000). Como se ha mencionado anteriormente, el conejo ha existido desde siempre con esa alta diversidad de depredadores y ha sido capaz de mantener abundancias altas a pesar del impacto de la depredación, sin que dicho impacto repercutiera en la viabilidad de sus poblaciones. Recientemente, Trout y Tittensor (1989) han mostrado que la depredación puede ser un factor limitante en los casos en que la abundancia poblacional de conejo sea muy baja. Es lo que se conoce como la “trampa del predador”. Sin embargo, en este caso la presión de depredación no es el origen del declive de la especie, sino el factor que impide que sus abundancias aumenten o se recuperen. En otros casos, los depredadores especialistas pueden estar protegiendo a las poblaciones de sus presas, al expulsar del territorio o incluso matar a otras especies de depredadores competidores. Es lo que se conoce con el nombre de “intraguild predation” o “interespecific killing” (Palomares et al. 1995; Palomares et al. 1996; Fedriani et al. 1999).

Por último, la gestión cinegética trata de modificar los parámetros de la población con el fin último de recuperar la poblaciones. Tanto la reproducción como la supervivencia de los individuos tienden a ser incentivadas a través de diferentes estrategias de manejo. Por este motivo la gestión cinegética es otro factor a analizar para ver su efecto sobre el estado actual de las poblaciones de conejo.

Asumiendo que la depredación no ha afectado de manera importante el estado actual de las poblaciones de conejo en la Península Ibérica, a continuación se desarrollan los cuatro factores restantes que pueden haber afectado: los cambios en el paisaje, las enfermedades, la actividad cinegética y la gestión de las especies cinegéticas.

La distribución actual del conejo: el paisaje y la carga histórica

Durante el siglo XX el hombre ha provocado la degradación del medio y la fragmentación del hábitat. El paisaje mediterráneo se ha mantenido sin cambios significativos en los últimos dos mil años con unos usos del territorio relativamente sostenibles. Sin embargo, en la última mitad del siglo XX ha sufrido mayores trastornos, como resultado de la deforestación, el pastoreo, la intensificación de la agricultura y el fuego. Como en todo ecosistema, existe un mecanismo de retroalimentación (o “feed-back”) que liga estos cambios del paisaje a la dinámica de las poblaciones, de manera que la alteración del paisaje mediterráneo afectaría a la distribución de las especies que en él habitan (Rundel 1998). Esta hipótesis sería válida para el caso del conejo, cuyo declive ha sido más acusado a partir de mediados del siglo XX, por lo que se hace necesario explorar si la distribución actual del conejo está relacionada con el paisaje resultante de estos cambios.

Los estudios de distribución de especies se basan en la elaboración de modelos que relacionan dichas especies con distintos factores de su entorno, normalmente del paisaje en el que habitan. Estos modelos se realizan con tres fines fundamentales: para formalizar o describir el conocimiento actual de la especie; para conocer y poder predecir los factores que afectan a la distribución o abundancias de las especies, y para generar hipótesis sobre la especie de interés (Morrison et al. 1998). Por otro lado, una de las presunciones básicas de los modelos de distribución de especies es que la probabilidad de detección de una especie debe ser mayor en sus hábitat óptimos. No obstante, esa presunción puede ser falsa cuando la distribución actual de una especie está reflejando situaciones pasadas, porque hayan existido cambios en las abundancias o en la distribución de la especie (Seoane y Bustamante 2001). Éste es el caso de las poblaciones ibéricas de conejo silvestre, que han sufrido extinciones locales que han producido una reducción en su área de distribución (Villafuerte et al. 1995).

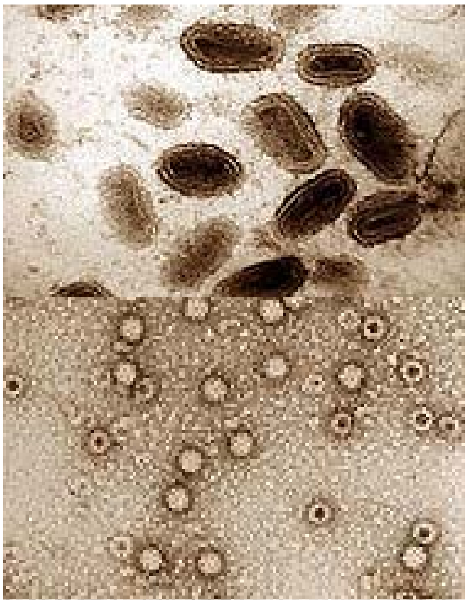
Aunque estas extinciones parecen haber ocurrido en los hábitats menos preferidos por el conejo, es necesario tener en cuenta la posibilidad de que la distribución actual del conejo no responda únicamente a características paisajísticas (entendiendo como tales a los tipos de hábitat, la geología, topografía, hidrología y climatología del lugar), sino que en mayor medida sea un reflejo de causas históricas, como por ejemplo, el efecto de las enfermedades, de la caza o del manejo de las poblaciones para su recuperación.

La distinción entre variables ecológicas, definidas como las relacionadas con los requerimientos ecológicos a los que se adecúan las especies, y variables históricas, definidas como los eventos no frecuentes y posiblemente irrepetibles, han sido sugeridas por otros autores como Lobo y Hortal (2003) para predecir la diversidad de especies en un ecosistema. A menudo los cambios en el paisaje han sido examinados a través de la historia que ese paisaje ha sufrido, tanto de forma natural (p.e. el efecto de los fuegos) como provocada por el hombre con los cambios políticos o sociales (Moreira et al. 2001; de Blois et al. 2002). Algunos estudios han relacionado estas variables históricas, sobre todo aquellas relacionadas con la presión cinegética, con la evolución de la especie, cuando había datos disponibles sobre su dinámica poblacional a lo largo del tiempo (Little et al. 1996; Riley et al. 1998; Smedshaug 2001). Sin embargo, son escasos los estudios en los que se analizan variables históricas cuando esos datos no están disponibles.

En el caso del conejo, los estudios más recientes han descrito el conocimiento actual de la especie mediante modelos de distribución (Fa et al.1999; Trout et al. 2000; Virgós et al, en prensa). La formulación de estos modelos se basó en el extenso conocimiento que ya existía sobre la especie: efectos climáticos de la temperatura y de la precipitación (sobre la duración e intensidad del período reproductor a través de la disponibilidad de alimento), efectos de la dureza del suelo (que impide excavar madrigueras que sirvan de refugio y para la cría); o efectos de los tipos de hábitat preferidos o de las estructuras del hábitat seleccionadas (que influyen en una reducción más o menos efectiva del impacto de depredación) (Hayward 1961; Jaksic et al., 1979; Rogers y Myers 1979; Simonetti y Fuentes, 1982; Wallage-Drees 1983; Parer y Libke 1985; Kolb 1985; Kufner 1986; Bell y Webb 1991; Kolb 1991; Kolb 1994; Trout y Smith 1995; Moreno et al. 1996; Villafuerte et al. 1997; Villafuerte et al. 1997; Trout y Smith 1998).

Los modelos de Trout et al. (2000), Fa et al. (1999) y Virgós et al. (en prensa) formalizan las relaciones que se encuentran en aquellos trabajos, estableciendo relaciones claras entre el conejo y el paisaje. Esto indicaría que la distribución y abundancia de conejo siguen siendo moduladas por el paisaje. El modelo de Fa et al. (1999) incorpora las abundancias de conejo 3 años después de la entrada de la EHV, comprobando que la abundancia de conejo sigue respondiendo a las características del hábitat. Resultados similares se están obteniendo en los modelos actualmente en curso, como el que desarrolla Carlos Calvete (comunicación personal) para las poblaciones de conejo en un paisaje agrícola de Zaragoza. Sin embargo, los modelos desarrollados por Néstor Fernández (comunicación personal) para el área de Doñana, ponen de manifiesto que las poblaciones de conejo a bajas abundancias no parecen estar respondiendo a las variables de paisaje, por lo se hace necesario investigar los posibles efectos de otras variables. Estos resultados apoyan las sugerencias de los trabajos mencionados anteriormente, y que apuntan la necesidad de valorar los efectos de las enfermedades, de la presión cinegética y la gestión de las poblaciones.

Las enfermedades


Fotografías al microscopio electrónico del virus de la mixomatosis (arriba) y del virus de la EHV (abajo).

Sin duda, los efectos negativos de origen humano sobre las poblaciones de conejo silvestre no han hecho más que sumarse a los posibles efectos negativos de las enfermedades del conejo. Hay dos enfermedades, ya endozoóticas en las poblaciones silvestres, que han hecho disminuir drásticamente las abundancias de conejo en las últimas décadas: la mixomatosis y la enfermedad hemorrágica (Muñoz-Goyanes 1960; Villafuerte et al. 1995; Fenner y Fantini 1999). El primer declive importante de las poblaciones ibéricas fue causado por la aparición de la mixomatosis, enfermedad causada por un virus procedente de conejos americanos del género *Sylvilagus* (a los que no produce la muerte). Desde su descubrimiento, a finales del siglo XIX, el virus de la mixomatosis se ensayó como método de control biológico del conejo. Fue introducido en los años 50 en Australia, causando una mortalidad de hasta el 99%. En 1953 un propietario francés liberó el virus porque los conejos le producían daños en sus cultivos, iniciando de ese modo su diseminación por toda Europa. Más recientemente, en 1984, aparece la enfermedad hemorrágica (EHV). A través del conejo doméstico llega desde China a Europa y entra en las poblaciones naturales ibéricas de conejo silvestre en 1989, produciendo mortalidades del 50% al 80%. Posteriormente, la EHV se ha utilizado como método de control en Australia, Nueva Zelanda, Argentina y Chile.

El papel de ambas enfermedades ha sido claro en el aumento de la mortalidad de las poblaciones de conejo silvestre. Sin embargo, aun queda mucho por investigar sobre el efecto de las enfermedades en relación con la densidad poblacional, la recuperación de las poblaciones o su persistencia en las poblaciones de un año a otro (Cooke 2002; Calvete et al. 1999).

El conejo como especie cinegética

El conejo es una de las especies de caza más importantes en la Península Ibérica. Históricamente, la gran abundancia de conejos ha sido aprovechada por el hombre como recurso alimenticio y por sus pieles. Hoy en día, la caza es un deporte que genera una actividad económica de gran relevancia. Alrededor del 70% de la superficie de nuestro país son áreas cinegéticas. Hay más de un millón de cazadores que salen a cazar cada temporada, obteniendo unos cuatro millones de conejos al año. Más aún, el número de cazadores en los años 60 era menor a medio millón por lo que dicho número ha tenido un crecimiento exponencial en los últimos 50 años (REGHAB 2002).

Andalucía es la comunidad autónoma con mayor número de licencias de caza y esta actividad se lleva a cabo en más del 80% del territorio. El sector agrario, que engloba al agrícola, ganadero y forestal, ha sido históricamente el fundamento de la economía andaluza. Dichos sectores son comúnmente percibidos en estrecha relación con la naturaleza. Sin embargo, la revolución de la agricultura y los duros procesos de adaptación a las normativas comunitarias han potenciado otros sectores económicos antes no tan importantes como el turismo o la actividad cinegética. La caza es uno de los recursos renovables más importantes con los que cuenta Andalucía y una de las formas de explotación más recomendables para los ecosistemas mediterráneos. Además el turismo cinegético es un sector en plena expansión en las últimas décadas gracias al desarrollo de las nuevas redes de comunicación, de manera que la caza se vende a cazadores extranjeros que valoran y costean este recurso.

Analizando esta información, se podrían plantear las siguientes preguntas: ¿cuál es el efecto de la caza sobre las poblaciones de conejo en declive? ¿Podría ser el aumento de la actividad cinegética una de las causas que han producido su declive?.

Efecto de la caza sobre las poblaciones de conejo

Históricamente, el hombre disfrutaba de la caza de forma libre, sin que existiera ningún tipo de regulación, porque era la base de su supervivencia. Sin embargo en la historia reciente ante el incremento poblacional humano y el desarrollo de armas cada vez más eficaces, se hizo necesario regular la caza para preservarla a largo plazo. Fue Leopold en 1933 quien estableció que la sobreexplotación por la caza era el principal problema de las especies cinegéticas. La caza se estableció como un derecho de las clases dominantes y se protegieron los períodos de reproducción durante los cuales las especies eran más vulnerables. A partir de ese momento, la caza ha sido considerada como un recurso natural que puede llegar a agotarse. Uno de los principios fundamentales de la teoría de la caza se basa en que únicamente las poblaciones que evolucionan de manera creciente pueden ser explotadas puesto que la caza implica una reducción de la abundancia poblacional. Por otro lado, las poblaciones a baja densidad sufren más frecuentemente fenómenos estocásticos y cuando están sujetas a la caza, ésta provoca la reducción de la estabilidad de la población, por lo que la caza no es aconsejable si no se supera un determinado umbral de densidad (Caughley y Sinclair 1994; Caughley y Gunn 1996; Lande et al. 1997; Bennet y Robinson 2000b; Sutherland 2001).

La actividad cinegética debe estar, por tanto, regulada por las legislaciones nacionales (Strickland et al. 1996). En España actualmente es la Administración del estado quien regula la temporada cinegética, pero los cazadores son quienes establecen los cupos de caza dentro de los márgenes impuestos por la Administración. Para cada temporada de caza, la autoridad competente de cada Comunidad Autónoma establece las especies susceptibles de ser cazadas, los métodos de caza, la temporada de caza y los días de la semana en que se puede cazar dentro de esa temporada. La reducción de las temporadas o de los días de caza se suele basar en las observaciones de la evolución de las abundancias de cada especie (por desgracia en pocos casos se basan en conocimientos científicos, sino que responden más bien a la experiencia acumulada a través de la historia). De hecho, las temporadas de caza para el conejo no han cambiado significativamente durante el siglo XX, siendo similares la actuales a las establecidas en la Ley de Caza de 1902 y más tarde recogidas en la actual Ley de caza de 1970 (RegHab 2002).

Una gestión adecuada del recurso cinegético requiere un conocimiento básico del comportamiento de la población, de los métodos actuales de extracción cinegética y de los efectos de su regulación sobre la sostenibilidad de las poblaciones (Sutherland 2001). Sin embargo, el estudio experimental de los efectos de la actividad cinegética es difícil de llevar a cabo, ya que requiere seguimientos a largo plazo. Una aproximación para analizar los efectos de la caza sobre una población, es a través de la modelización de su dinámica poblacional, de manera que se puedan examinar los cambios en la evolución de la población al aplicar diferentes escenarios de caza (Johnson 1996). Mediante modelos de dinámica poblacional se ha estudiado el efecto de diferentes herramientas de control para las poblaciones de conejo. Estas herramientas pueden no ser específicas, de manera que se elimine un porcentaje de la población sin determinar el método que se utiliza, como en los modelos desarrollados por Darwin y Williams (1964), Smith y Trout (1994) y Smith (1997), o pueden ser métodos de control específicos como los modelos más recientes de Pech and Hood (1998) o Hood et al. (2000), en los que las enfermedades son el método de control. Puesto que el conejo es una especie invasora, uno de los métodos tradicionales para su control es la caza. Incluso en la

Península Ibérica, la caza ha sido un método de control necesario para evitar los daños en los cultivos; por ello los trabajos mencionados analizan los métodos para llevar a cabo un control efectivo de las poblaciones de conejo. Hasta la fecha ningún estudio ha valorado los efectos de la caza para la conservación de las poblaciones de conejo, aunque en la literatura científica abundan referencias sobre otras especies (Ginsberg y Milner-Gulland, 1994; Pascual y Hilborn 1995; Mattson et al. 1996; Alvard et al. 1997; Barbosa 2001).

Los modelos de Darwin y Williams (1964) y Smith y Trout (1994) se desarrollaron fundamentalmente para determinar cual es la mejor época para llevar a cabo el control del conejo en Nueva Zelanda e Inglaterra respectivamente, y para analizar los efectos sobre la población al aplicar diferentes presiones de control. Los resultados de ambos trabajos sugieren que el mejor período de control debe aplicarse cuando la población está en su mínimo anual, es decir justo antes de iniciarse el período reproductor, de manera que cada hembra cazada reduce el potencial reproductor de la población durante la siguiente temporada. Aplicando estos resultados a la Península Ibérica, se podría decir que el actual período de caza del conejo coincide con el mejor período para llevar a cabo un control de la población, y por tanto, es el peor período para llevar a cabo una caza sostenible.

Teniendo como base estos estudios generales realizados para otras poblaciones de conejo, se plantea la necesidad de una evaluación de la bondad de las actuales temporadas de caza para el mantenimiento de las poblaciones ibéricas de conejo silvestre. En la actual situación de declive de las mismas, se hace necesario explorar, no sólo el efecto de las temporadas cinegéticas, sino el de la propia presión de caza. Para modelizar la caza con una aproximación realista es necesario, por un lado, conocer la presión cinegética que aplican los cazadores en sus cotos, y, por otro lado, modelizar dichas presiones en poblaciones de conejo de diferente calidad, es decir en poblaciones que evolucionan de manera creciente a diferentes niveles.

El recurso cinegético : La gestión de las poblaciones de conejo

Como se ha mencionado antes, para que la actividad cinegética pueda llevarse a cabo es fundamental que las poblaciones mantengan una alta calidad (determinada por unas altas abundancias y un crecimiento positivo) que soporte la extracción cinegética, (Caughley y Sinclair 1994; Caughley y Gunn 1995; Lande et al. 1997; Sutherland 2001). Caughley en 1977 estableció los tres problemas con los que los gestores de especies cinegéticas se tenían que enfrentar: el control de las poblaciones cuando la abundancia es alta o la población tiene un crecimiento exponencial; la conservación de las mismas cuando la abundancia es baja o la población decrece, y la búsqueda del nivel de explotación adecuado para mantener la población en equilibrio (a partir de Strickland 1996).

En el caso de las poblaciones de conejo se dan los tres problemas a escala mundial, pero se pueden limitar a los dos últimos en las poblaciones ibéricas de conejo. Para resolver ambos problemas se llevan a cabo por un lado estrategias que gestionan las especies cinegéticas o los factores del medio que las limitan y, por otro, estrategias de gestión que regulan directamente la extracción cinegética. En general, la gestión cinegética se puede agrupar en las siguientes categorías: manejo de hábitat, control de depredadores, manejo de enfermedades, translocaciones de individuos y reducción de la caza.

La efectividad de las estrategias de gestión está siendo estudiada actualmente, estableciéndose las medidas oportunas para optimizar su uso. Por ejemplo, Calvete et al. (1997) pusieron de manifiesto que la supervivencia de los ejemplares translocados sería más efectiva si se reducía el tamaño del grupo de ejemplares liberados y se realizaban previamente mejoras del hábitat y reducción de depredadores. Los manejos de hábitat como los desbroces de matorral o la creación de pastizales han sido evaluados por Moreno & Villafuerte (1995), y parecen efectivos para incrementar las abundancias de conejo, ya que la intensidad de reproducción está asociada a la disponibilidad de alimento de alta calidad (Wallage-Drees y Michielsen, 1989; Villafuerte et al. 1997). Por otro lado, Trout et al. (1992) manipularon con éxito los vectores de la mixomatosis en Gran Bretaña de forma que redujeron los efectos de la enfermedad en la población; sin embargo Osácar et al. (1996) no consiguieron los mismos efectos en España, probablemente por la diversidad de vectores en nuestro país. La efectividad de otras medidas, como el control de depredadores, están también bajo discusión. Trout y Tittensor (1989), Smedshaug et al. (1999), y Banks (2000) mostraron como esta estrategia de manejo puede tener éxito para incrementar las poblaciones de conejo, aunque su efectividad en un ecosistema mediterráneo (con mayor número de depredadores) no ha sido evaluada en profundidad y supone problemas asociados como el control ilegal de otros depredadores (Ruiz-Olmo 1986; Villafuerte et al. 1998; Duarte y Vargas 2001).

Existe un amplio desconocimiento sobre las estrategias de gestión que se utilizan en la Península Ibérica, su frecuencia de uso y su evolución durante las últimas décadas. Es el gestor el que debe decidir las estrategias a utilizar y en la mayoría de los casos utiliza más de una. Mientras que los estudios que se han revisado en el párrafo anterior intentan valorar la efectividad de cada una de estas estrategias por separado, no hay estudios que, de una manera global, relacionen las estrategias de manejo con el incremento de la abundancia de las poblaciones. Por tanto, por un lado es necesario recabar información sobre las estrategias de gestión que se utilizan para recuperar o conservar las poblaciones de conejo y, por otro lado, es necesario analizar los efectos de esas estrategias múltiples sobre las poblaciones.

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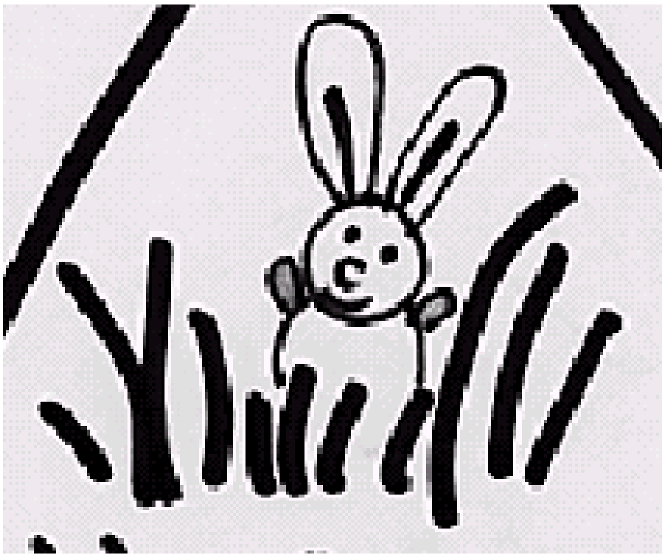


ESTRUCTURA Y OBJETIVOS DE LA TESIS

ESTRUCTURA DE LA TESIS

La presente Tesis Doctoral está estructurada en Introducción, Objetivos, una serie de capítulos (Capítulos 1-4), una Discusión General y las Conclusiones. En la Introducción, en castellano, se revisan los antecedentes y el contexto teórico del tema. A continuación se exponen los objetivos de la Tesis, a desarrollar en los siguientes capítulos. Cada uno de estos capítulos reproduce el texto íntegro, en inglés, de manuscritos enviados para su publicación en revistas científicas internacionales (indicándose si es un manuscrito enviado, aceptado o ya publicado y su referencia). Previamente a dicho texto en inglés, en cada capítulo se presenta un Resumen en castellano. Finalmente, en la Discusión General, también en castellano, se discuten e integran los resultados más relevantes de cada uno de los capítulos. Acaba la Tesis con las Conclusiones, en castellano.

OBJETIVOS

Como se ha comentado en la Introducción, donde se ha querido mostrar la importancia del conejo silvestre en Andalucía y su problemática actual, el conejo es una especie muy prolífica, que ha sido muy abundante en su área original de distribución, ha conservado el patrimonio genético de la especie original, ha permitido el desarrollo y sostenibilidad de una comunidad de depredadores de alto valor ecológico y también de una actividad cinegética de gran valor económico. La pregunta de fondo es cómo una especie tan prolífica y ecológicamente "asentada" (por decirlo de alguna manera) ha podido pasar a ser tan escasa, hasta estar en declive en su área de distribución original. En un intento de responder a dicha pregunta, el objetivo general de esta tesis es analizar los principales factores (históricos, ecológicos o de gestión) que afectan o limitan la distribución y abundancia de las poblaciones de conejo en Andalucía. Este objetivo general puede desglosarse en una serie de objetivos particulares que quieren responder a las siguientes preguntas:

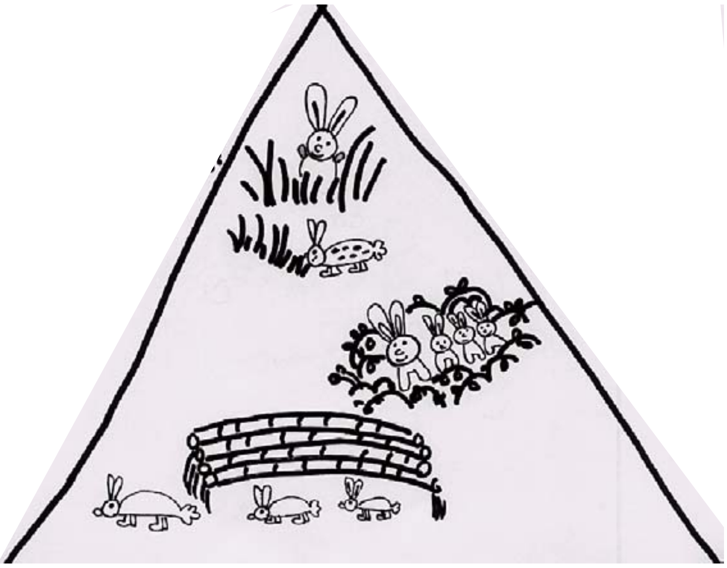
- ¿Es la distribución y abundancia del conejo modelada por el paisaje o es consecuencia de unos efectos históricos previos? Mediante un análisis global de la distribución y abundancia del conejo en Andalucía se pretende elucidar si el estado de las poblaciones de conejo es consecuencia de características actuales del hábitat o de hechos históricos (entendiendo como tales la gestión cinegética, la caza, las enfermedades y otros factores humanos). Este objetivo se desarrolla en el Capítulo 1.

- ¿Cuáles son las medidas de gestión del conejo que se utilizan en Andalucía? Mediante un estudio descriptivo se analizan las estrategias de manejo, su intensidad de uso y su evolución en las últimas décadas, relacionándolo con la tendencia de las poblaciones de conejo en los últimos años y con su abundancia local. Puesto que los tipos de gestión de la caza menor, incluyen de manera conjunta al conejo y a la perdiz, este capítulo considera a ambas especies en conjunto. Este objetivo se desarrolla en el Capítulo 2.

- ¿Cómo afectan las poblaciones de conejo y su gestión al grado de conservación de la naturaleza? Se estudian las relaciones entre la aplicación de las estrategias de gestión de la caza menor y la conservación de especies de fauna silvestre. Mediante un caso práctico con el águila azor perdicera (*Hieraaetus fasciatus*), se analiza cómo las poblaciones de conejo pueden afectar a los depredadores. Al igual que en el objetivo anterior, puesto que el caso práctico se basa en una especie de depredador que consume de forma habitual conejo y perdiz, se considera a ambas en conjunto. Este objetivo también se desarrolla en el Capítulo 2.

- ¿Cuál es el efecto de la actividad cinegética sobre las poblaciones de conejo? Se trata de evaluar, en función de la calidad de las poblaciones de conejo, los efectos sobre las mismas de la diferente presión cinegética y de las fechas de la temporada de caza. Este objetivo se desarrolla en el Capítulo 3.

- ¿Qué efecto tienen, a escala mundial, sobre las poblaciones de conejo las enfermedades y sus tratamientos? Mediante un estudio bibliográfico se analiza, en primer lugar los efectos que las enfermedades han tenido sobre las poblaciones de conejo y, en segundo lugar, el posible impacto de las nuevas herramientas para el control y la conservación del conejo basadas en virus genéticamente modificados. Este objetivo se aborda en el Capítulo 4.



CAPÍTULO 1

Distribution and abundance of wild rabbitt populations: accounting the effects of historical variables versus traditional GIS variables

Influencia de las variables históricas y de las variables de paisaje sobre la distribución y abundancia de las poblaciones de conejo en Andalucía

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Resumen

El conejo, ampliamente distribuido por el Sudoeste de Europa, ha tenido una tendencia negativa en las últimas décadas, tanto en su distribución como en sus abundancias. Sería de esperar, por tanto, que la distribución actual reflejara el efecto de acontecimientos que ocurrieron en el pasado. El objetivo de este Capítulo es comprobar dicha cuestión y cuantificar si las poblaciones de conejos responden a estas características y propiedades del paisaje o, por el contrario responden a otros factores históricos que pudieran haber forzado su distribución o abundancias en el pasado. Para la consecución de dicho objetivo se han desarrollado modelos de regresión (modelos lineales generalizados) tomando como variable dependiente la presencia, en unos casos, y la abundancia, en otros, de conejo en 307 áreas andaluzas, y siendo las variables independientes, bien variables de paisaje (procedentes de sistemas de información geográfica, SIG), bien variables históricas (obtenidas mediante encuestas). Así mismo, también se evaluó el uso de diferentes fuentes de información de las variables explicativas.

Las variables de SIG permitieron comprobar la influencia del paisaje (hábitat, clima, topografía, geología, efectos humanos y patrones espaciales) sobre la presencia y abundancia de conejo. La presencia de conejo presentó un patrón espacial, relacionado probablemente con las extinciones de conejo que ocurrieron en los hábitat menos adecuados para dicha especie. Las variables de paisaje seleccionadas en los modelos de presencia de conejo fueron: los suelos más duros y pedregosos (que están relacionados con una menor probabilidad de encontrar una población de conejos), los climas más benignos para el conejo y la superficie cubierta por cultivos mixtos de secano (ambas aumentan la probabilidad de encontrar una población de conejos). Las variables de SIG seleccionadas en los modelos de abundancia mostraban que los climas benignos y la superficie cubierta por cultivos mixtos de secano también se asocian a mayores abundancias de conejo. Además la abundancia de conejo

también se relacionó positivamente con una mayor superficie de ecotono, de cultivos mixtos en regadío y de cultivos homogéneos de secano, así como con la cantidad de superficie cubierta por vegetación natural.

Los mejores modelos de presencia de conejos se obtuvieron con las variables históricas, que parecen haber forzado su distribución o abundancias en el pasado: las enfermedades y los manejos. La presencia de conejos y su abundancia fueron explicadas en mayor grado por la intensidad de la recuperación de las poblaciones después de la entrada de la enfermedad hemorrágica durante la década de los 90 y en menor grado por la intensidad de la recuperación de las poblaciones después de la entrada de la mixomatosis durante los años 50. La presencia de la mixomatosis estuvo positivamente relacionada con la presencia de conejo pero negativamente relacionada con su abundancia. Esto se puede explicar, por un lado, por la relación existente entre la detección de la enfermedad y la densidad poblacional y, por otro lado, por el efecto obvio de la enfermedad en el incremento de la mortalidad en las poblaciones.

La presencia de conejo estuvo también relacionada con la intensidad de las estrategias de gestión desarrolladas a lo largo de los últimos 30 años. La presencia de conejos mostró una relación negativa con la intensidad de uso de las translocaciones y de las estrategias de prevención de enfermedades y parásitos. Esto se puede explicar porque dichas estrategias normalmente se aplican cuando la abundancia de conejo es muy baja.

Por último, el abandono del campo resultó inversamente relacionado con la presencia y la abundancia de conejo. Es más difícil encontrar una población de conejos en los lugares donde ha habido abandono del campo, y en el caso de encontrarla su abundancia es baja. Esta variable parece tener un componente espacial importante, posiblemente porque está asociada a un determinado tipo de paisaje.

Este Capítulo pone en evidencia la necesidad del uso de múltiples fuentes de información cuando se modela la distribución o abundancia de una especie silvestre. Esta aproximación es especialmente útil cuando las especies han sufrido cambios en cualquiera de estos dos parámetros, por lo que su distribución y abundancia puede venir influida por acontecimientos ocurridos en el pasado.

Distribution and abundance of wild-rabbit populations: accounting for the effects of historical variables versus traditional GIS variables

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ABSTRACT

Wild rabbit (*Oryctolagus cuniculus*) is widely distributed in southwestern Europe; however their population has declined over the past century both in terms of distribution and abundance, been expected that the current distribution reflects the effects of past factors. The aim of the present study was to test whether rabbits are responding to suitable and available landscape features, or to other factors that may have constrained their distribution or abundance in the past. To achieve this aim, we evaluated different sources of information to understand the present distribution and abundance of wild-rabbit populations.

We used GIS techniques to test the effects of landscape: habitat features, climate, topography, geology, hydrology, human presence, and spatial patterns. Rabbit presence was spatially segregated, which was probably related to population extinctions occurring in the least-preferred landscapes for rabbit, with these landscapes exhibiting an inherent spatial structure. Rabbit presence was explained to a high degree by variables related to the effects of past factors. However, rabbits avoided hard soils, preferring mixed non-irrigated cultures, their abundance being associated with the amount of the surface covered by these cultures. Rabbit abundance correlated also with the amount of ecotone, and with mixed irrigated cultures, homogeneous non-irrigated cultures, and other natural-vegetation habitats.

The best models for rabbit presence were those with factors that may have constrained rabbit populations in the past: rabbit diseases and historical management. Rabbit presence and abundance was related to the degree of recovery of the rabbit population after the first outbreaks of rabbit hemorrhagic disease and myxomatosis. The presence of myxomatosis was positively selected for rabbit presence, indicating the relationship between their detection and population density, and negatively selected for rabbit abundance, indicating the negative impact on rabbit populations. Rabbit presence was negatively related to the management strategies of rabbit translocations and the prevention of diseases and parasites, since these are normally applied when rabbit abundance is low.

Our paper provides new evidence that multiple information sources are required when modeling the distribution and abundance of wildlife species; especially historical information could be useful when the species is suspected to have suffered from changes in any of these two parameters and when the current distribution is the result of past situation effects.

INTRODUCTION

Most research into the factors affecting the distribution or abundance of wildlife populations and species has focused on the effects of habitat, microhabitat, or landscape structure (Mills and Gorman 1997; Henderson and Eason 2000). Recently, new GIS techniques have offered a wide variety of variables, such as those related to climate, human presence, or topography, for use in the study of the distribution and abundance of wild populations when habitat features provide insufficient information to answer a particular ecological question. For example, topographic characteristics have a strong influence on the selection of nesting and hunting areas by raptors (Bustamante et al. 1997; Martínez et al. 2003); climatic features and seasons regulate population growth of small birds (Bellamy et al. 1998); and human presence or activity limits species distribution (Smith et al. 1997; Harcourt et al. 2001).

The models of wildlife species abundance developed to date search for the optimal habitat of a species without considering the effects of past events on the current abundance (Seoane and Bustamante 2001; Seoane 2002). Some authors have attempted to resolve this problem by combining information on population dynamics (when available) with GIS data or studying historical changes in the habitat (i.e., using satellite photographs) in order to explain historical trends (Silander 1983; Rushton et al. 1997; Kujawa 2002). However, in many cases habitat is not the main factor determining such trends since it remains available. There is considerable information, mostly derived from studies of endangered and pest species, showing that a wide variety of historical factors cause changes in wildlife abundance or distribution. For example, Milner-Gulland and Lhagvasuren (1998) showed the importance of historical hunting data in explaining the declines in numbers and distribution of the Mongolian gazelle *Procapra gutturosa*, an endangered ungulate. Swenson et al. (1995) showed the importance of political policies to the conservation of brown bear; and Hudson et al. 1992, Scott (1988), and Tompkins et al. (1999) showed the importance of infectious diseases and parasites to changes in wildlife abundance. However, such features – the effects of hunting or predator pressures, historical or current data on the management of wild populations, and historical information on diseases – have not been incorporated into global studies of the distribution of wild species. This may be attributable to the difficulty of making predictions based on such data as it is showed in the Figure 1. This

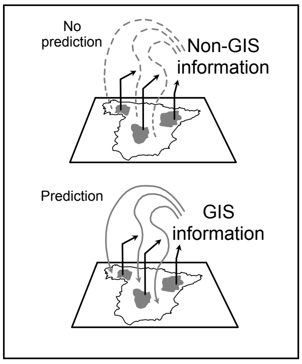

Figure 1. Schemes of two classes of wildlife model according to source of data and utility of the model. GIS information can be obtained for the whole area, and, once analyzed for the sample areas, abundance can be predicted for the whole area. Non-GIS information is not suitable for obtaining the whole surface because of the trade-off between costs and rate of change of the information produced; this can be obtained and analyzed for the sample area but is not suitable for a prediction covering the whole area

difficulty has led to low interest in applying conservation measures over wide regions and the allocation of scant resources to the collection of such information.

There is therefore a need to evaluate whether historical and recent data on diseases, management strategies, predator pressure, and hunting pressure could be included in global studies when describing factors affecting the distribution of wild species, and whether their use could improve studies involving mainly habitat-availability models based on GIS techniques. We have studied these questions using the wild rabbit (*Oryctolagus cuniculus*) as an example. We selected this species because it is an important prey species and small-game species in Mediterranean ecosystems, it is widely distributed, there is considerable information on the factors affecting its abundance and distribution, and the species has suffered a steady decline in southwestern Europe since the 1950s (Delibes and Hiraldo 1981; Villafuerte et al. 1998; Angulo and Cooke 2002).

Wild rabbits originated in southwestern Europe and have been dispersed worldwide for food or hunting (Monnerot et al. 1994). In many of the areas where it was introduced, such as Australasia and UK , it is a pest species. The need to control wild-rabbit populations meant that initial research on the distribution and abundance of wild rabbit focused on determining the factors limiting wild-rabbit populations. Experimental studies have shown how soil hardness, climate, and habitat can limit rabbit abundance. Soil hardness limits the abundance of rabbits by limiting their ability to dig warrens that are used for breeding (Kolb 1985; Trout and Smith 1995, 1998), as well as for refuge against predators (Kolb 1991, 1994) and refuge against extreme climate (Hayward 1961; Parer and Libke 1985). Climate regulates the breeding season by limiting the quality and quantity of food, and thus it regulates the potential for population growth (Wallage-Drees 1983; Bell and Webb 1991; Villafuerte et al. 1997). Many studies worldwide have shown that habitat structure plays a role in rabbit distribution (Jaksic et al., 1979; Soriguer and Rogers, 1979; Simonetti and Fuentes, 1982), with rabbits preferring to use an ecotone of scrub and pasture where they can optimise the relation between feeding and refuge (Rogers and Myers 1979; Kufner 1986; Moreno et al. 1996; Villafuerte et al. 1997).

In southwestern Europe, the climate, topography, and habitat are excellent for wild rabbit because it was in this region that they originally evolved. The main difference between the situation in this original range and that in countries where wild rabbit constitutes a pest is that population growth rates in southwestern Europe seem to have been limited historically by predator pressure (there are more than 29 different predators of rabbits) and hunting activity (almost 1.3 millions of hunters in Spain alone) (REGHAB 2002). However, the sharp decrease in wild rabbit numbers in southwestern Europe has been an important issue for national scientific, environmental, and hunting agencies. The main causes of this decrease are habitat loss and diseases (most importantly the arrival of myxomatosis in the 1950s and rabbit haemorrhagic disease (RHD) in the 1990s), which may be exacerbated by hunting and predator pressures (Villafuerte et al. 1997; see also Chapter 3). Management of wild rabbit populations has increased to conserve their populations, and the associated strategies are being continuously improved and optimised (Trout et al. 1992; Moreno and Villfuerte 1995; Calvete et al. 1997).

The most recent studies have investigated the decline of wild-rabbit populations, in particular the factors affecting fragmented populations. Some studies have focused on landscape analysis and habitat characteristics (Fa et al. 1999; Virgós et al. in press), while others have combined habitat information with climate and topography using GIS information (Trout et al. 2000; Calvete et al. in prep.). An attempt to introduce predator effects and the management of predators can be found in Trout et al. (2000). The results of these studies have brought to light the importance of other factors (not considered by these authors) that could provide an important source of variation, such as diseases, predator or hunting pressures, and direct management of rabbit populations, which are difficult to investigate in GIS or environmental studies. Some of these factors, such as diseases, definitely limit rabbit densities (Trout et al. 1992; Villafuerte et al. 1995; Trout et al. 1997; Marchandeau et al. 1998; Calvete et al. 2002). Diseases are one of the main control measures in areas in which rabbits constitute a pest (Kovaliski 1998; Fenner and Fantini 1999; O'Keefe et al. 1999).

In this paper we evaluate different sources of information in order to understand the present distribution and abundance of wild-rabbit populations in southwestern Europe. Two models were developed and tested. In the first one, GIS techniques were used to test the effects of habitat features, climate, topography, geology, hydrology, human presence, and spatial patterns on the distribution and abundance of wild rabbit in southern Spain. In the second model, we obtained historical and recent information on the management strategies applied to rabbit populations, on the presence and effects of diseases in these populations, and on hunting activity and related socioeconomic activities, and tested their effects on the distribution and abundance of wild rabbit in southern Spain. Both models were tested at two different levels: firstly, to analyse the variables related to the current distribution of the species; and secondly, to analyse the variables that are related to high or low wild-rabbit abundance in the areas where rabbit populations are present.

METHODS

Study area and sampling

To carry out the study we selected 307 locations in southern Spain (Fig. 2). The geographic coordinates of the survey points were selected using GIS via the software IDRISI (Clark University, USA).

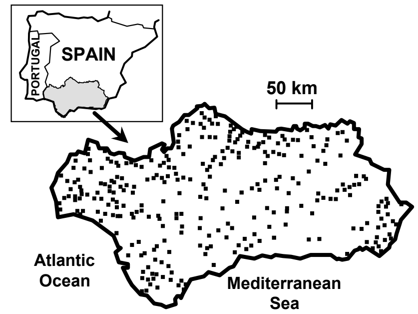

Figure 2. Study area. Sampled areas are represented by black squares.

Survey points were selected based on a step-random sample design based on altitude and topography: areas lower than 1200 m in altitude and with slopes of less than 30% were favoured in the selection of study areas, in order to exclude mountain areas that are not suitable for wild rabbits. In addition, the locations were separated by at least 2 km.

Table 1. Final variables used in the model. a) Raw variables. b–f) Principal-component analysis (PCA) performed with groups of related raw variables. Factors of principal components extracted from original variables are in italics. Variables with the highest factor loading are indicated using boldface. Numbers in brackets are the PCA variances.
Sources: Mapa Digital de Elevaciones (MDT-20, Modelo Digital del Terreno, Consejería de Medio Ambiente de la Junta de Andalucía), Mapa Geológico Andaluz (SINAMBA, Consejería de Medio Ambiente de la Junta de Andalucía y SCIT, Universidad de Córdoba), Mapa Territorial de Andalucía, Mapa Hidrológico de Andalucía, y LandCover (SINAMBA, Consejería de Medio Ambiente de la Junta de Andalucía). We used southern Spain LandCover data for 1995 with a resolution of 50×50 m.

a) Raw variables

GIS variable	***Non-GIS variable***
Geographical coordinates, climate types	Hunting property and activities:
Land cover:	Hunting regime
Urban	Type of property
Non-irrigated homogenous herbaceous cultures	Free access
Non-irrigated homogenous cultures of trees	Rural abandonment
Irrigated homogenous cultures	Presence of livestock
Non-irrigated mixed cultures	Rabbit translocations in 1999
Irrigated mixed cultures	Reduction of hunting pressure in 1999
Mixed cultures and natural vegetation	Diseases:
Dense oak forest	Presence of RHD in 1999
Other dense forests	Presence of myxomatosis in 1999
Sparse scrub	Intensity of myxomatosis outbreaks
Dense scrub	Recovery degree after RH
Oak savanna (dehesa)	Recovery degree after myxomatosis
Pastures	

b) Topography PCA (95.59%)	***Altitude***	***Slope***
Mean slope	0.23	**0.95**
SD slope	0.09	**0.94**
Mean altitude	**0.97**	0.21
SD altitude	0.29	**0.90**
Maximum altitude	**0.95**	0.31
Minimum altitude	**0.99**	0.11

c) Hydrology PCA (71.32%)	***Water***	***River veg.***
Longitude of water	**0.69**	0.35
Surface of water	**0.79**	–0.25
River vegetation	–0.01	**0.92**

c) Soil hardness cover PCA (79.26%)	***Hard soil***	***Soft soil***	***Sandy soil***
Sandy soils	0.02	0.00	**0.99**
Soft soils	0.08	**0.97**	–0.12
Compact soils	**0.82**	–0.53	–0.18
Stony soils	–0.00	0.14	0.02
Rocky soils	–**0.93**	–0.33	–0.15

d) Human effects PCA (87.54%)	***Road***	***Ecotone***	***Population***
Density of villages	–0.00	–0.03	**0.90**
Distance to nearest village	–0.19	–0.11	–**0.85**
Road density	**0.96**	0.05	0.13
Road length	**0.97**	0.05	0.06
Ecotone density	0.03	**0.94**	–0.01
Ecotone length	0.06	**0.93**	0.08

f) Hunting management intensity PCA(69.99%)	***Predator control***	***Habitat manag.***	***Disease manag.***
Current habitat management	0.16	**0.76**	0.14
Current predator control	**0.89**	0.07	0.09
Current disease management	0.18	–0.07	0.67
Habitat management 10 years ago	0.07	**0.90**	0.10
Predator control 10 years ago	**0.92**	0.13	0.09
Disease management 10 years ago	0.10	0.09	**0.80**
Habitat management 30 years ago	0.08	**0.82**	–0.00
Predator control 30 years ago	**0.87**	0.12	0.06
Disease management 30 years ago	–0.08	0.20	0.69

GIS variables

We quantify landscape composition within a 1-km^2 square centered on each sample point. In each of these squares we obtain a complete description of the area in terms of climatic, topographic, and habitat characteristics, and information on geological and hydrological data and human influences using available georeferenced data. We used ARC/INFO software (ESRI 1998) to analyse the data by assigning a spatial component, to obtain the variables of each sample square (Table 1). The initial 64 categories of soil were grouped into five types on the basis of soil hardness. The type of land cover was categorised into 16 groups on the basis of similarity of habitat characteristics for rabbits.

Interviews and field survey

People trained in wildlife surveys carried out interviews and rabbit surveys at the 307 selected points during June and July of 1998 and 1999. At each survey point, the interviewer identified the land and the hunting property in the area, and located an appropriate person to interview: a hunter, a landowner, or a conservation manager who knew management history of hunting in the area.

At each survey point, we conducted a census of rabbit abundance in June and July 1999. Rabbit abundance was estimated from faecal pellet counts. Such counts have been widely used and are particularly useful in areas where the rabbits themselves or other signs are difficult to detect, or where detection may be influenced by other factors such as soil or habitat type (Moreno and Villafuerte 1995; Palma et al. 1999). The counts were carried out at each survey point in 50 circular sampling units (0.5 m^2 per unit) randomly distributed over a 2-ha area selected as habitat being representative of the surrounding area. The rabbit abundance index at each survey point was computed on the basis of the mean number of faecal pellets in 0.5 m^2; a logarithmic transformation was necessary to prepare the data for statistical analysis.

Non-GIS variables used in the model

In each personal interview with the local hunter, landowner, or conservation manager, we wanted to obtain information on the main characteristics of the hunting area, including current and past rabbit management strategies, the effects of diseases on rabbit populations, and the history of diseases in the area (Table 1).

In the interview we asked about the type of property (private or public land), the hunting regime (private hunting area or social hunting area), access to the area (public or reserved), and information related to other socioeconomic activities: participants were asked whether there was livestock in the area and whether previously cultivated areas had been abandoned.

In regard to the effects of diseases on wild-rabbit populations, participants were asked to indicate the intensity of myxomatosis in the area, the degree of recovery of the rabbit population after the first epizootic of myxomatosis during the 1950s and after the first epizootic of RHD during the 1990s, and whether myxomatosis and RHD were detected in the area in 1999.

In regard to small-game management, participants were asked to indicate the intensity of use of a number of management strategies both at present as well as 10 and 30 years ago. The latter two of these historical periods correspond to the declines in rabbit abundance due to RHD and myxomatosis, respectively (Angulo and Cooke 2002). We distinguished nine management strategies that were grouped into habitat, predator control, and prevention of diseases and parasites (for more information on single management strategies, see chapter 2 entitled “Multiple strategies for the management of small game: implications for wildlife conservation”). We calculated a management intensity index based on the number of management strategies applied and the intensity of application of each one, for habitat, disease, and predation management strategies, and distinguished them into three periods: currently, and 10 and 30 years ago. We calculated the same index for the reduction in hunting pressure and for current translocations applied in the area during 1998-1999 hunting season.

Analytical procedures

There were many raw variables, and so we used exploratory correlation matrices to test the correlations between them. The correlation between pairs of continuous variables were determined using the Pearson correlation test; correlations between a continuous and a categorical variable were determined using ANOVA; and correlations between pairs of categorical variables were determined using cross-tabulation tables. Pairs of variables with Pearson *r* values, multiple *R* values, or phi-squared values higher than 0.4 were considered to be too highly correlated to both be used in regression analysis. In these cases, principal-component analyses (with a varimax rotated solution) were used and the original raw data set was reduced. To facilitate interpretation, principal-component analyses were performed within groups of related raw variables (i.e., topography, historical management, geology, human influence and fragmentation, and hydrology). The principal components obtained and the explained variance and final row variables are recorded in Table 1. Exploratory analyses were performed using STATISTICA software (STATISTICA 5.5, StatSoft, USA, 1999).

We built a generalised linear model (GLM) using the GENMOD procedure of the SAS package (SAS 1997) to fit explanatory variables to the observed data. GLMs allow the appropriate use of distribution errors and links for the dependent variable (Martínez et al. 2003). We constructed two separate models which used different explanatory variables: one using those obtained from GIS, the other using those obtained from interviews. Within each type of model we distinguished between a model for rabbit distribution (presence/absence) and a model for rabbit abundance (considering only areas where rabbits were present). We built a GLM for the presence/absence of rabbits in each sample area with binomial distribution errors and the logit link function. We decided to build a GLM for rabbit abundance [log(transformed pellets)/0.5 m^2] with normal distribution errors and an identity link, which minimized the deviance of the model, after considering other data distributions and links (gamma and negative binomial error distributions) (Herrera 2000). We started from a complete model on which we applied a backward elimination procedure to obtain the final model, using statistical criteria: the variable with the maximum non-significant probability was excluded in each step. The final model was attained when all variables retained were statistically significant ($P<0.005$). We corrected for overdispersion in the models of rabbit abundance. Finally, in order to account for spatial autocorrelation, we introduced spatial structures into the models that took the form of a second-degree polynomial of the X and Y geographic coordinates of the sampled sites (Legendre 1993).

Once we had finalised each model, we tested that the sign of the estimated coefficient for each independent variable retained in the final model was determined by the true correlation with independent variables and not by the sign of the coefficient of the other variables retained. We achieved this by exploring the relationship between every variable retained in the final model and the rabbit presence by fitting a new GLM (with the same error distribution and link) only with the variable under test. In addition, we used these models to obtain the percentage of deviance explained by each variable when compared to the null model (Martínez et al. 2003).

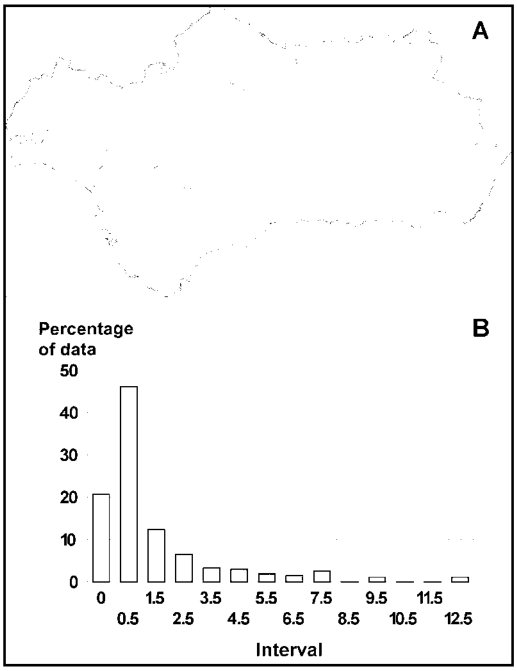

Figure 3. Rabbit abundance in the study area. (A) Map of rabbit abundance in southern Spain; each sampled point is represented by a circle whose size is directly related to rabbit abundance. (B) Histogram of the frequency of rabbit abundance. Number of cases is represented as a percentage of the total data (N=275), while intervals are based on the ranges of the values.

RESULTS

Study areas and rabbit abundance

Pellet counts could not be performed in some areas, thus resulting in a reduction in the sample number (to N=275). The data from some other areas were totally or partly invalidated because the interviewer could not find a suitable person to interview or the interviewed person did not answer all the questions. For this reason, the sample size of different analyses varied from 120 to 275.

Absence of rabbits was recorded in 57 areas, with rabbits present in 218. Rabbit abundance varied greatly, both spatially and numerically, with low abundance predominating (with 50% of data sampling units being under 0.5 pellets/0.5 m^2) (Fig. 3). The mean rabbit abundance was 1.37 pellets/0.5 m^2 (with an SD of 2.25 pellets/0.5 m^2) when including the absence areas, and 1.74 pellets/0.5 m^2 (SD 2.40 pellets/0.5 m^2) when considering only areas where rabbits were present. The maximum rabbit abundance in any sampled area was 12.2 pellets/0.5 m^2.

The sampled areas varied greatly in size, type of property, hunting regime, primary habitat type, level of wildlife conservation, and management strategies applied. Collectively, the sampled areas were representative of the whole of southern Spain, where the ecosystems predominately cover highly variable landscapes.

Table 2. Generalised linear model (GLM) for the probability of presence and abundance of wild rabbits in southern Spain using GIS information. The percentages of deviance explained by each variable are shown (%). The sign of the single relationship is indicated in brackets when the sign in the whole model does not correspond to the sign of each single variable against the dependent variable. SP: spatial pattern considered.

Variable	*Parameter*	*Standard error*	X^2	*P*	*%*
PRESENCE without SP					
Intercept	25.4675	0.2690			
Climate iii	24.0774	0.0000	4.54	0.0331	16.0
Climate 44	–0.9364	0.3356	7.97	0.0047	31.5
Irrigated mixed cultures	–0.0037	0.0016	4.73	0.0297	1.9
Mixed cultures and natural vegetation	–0.0022	0.0007	10.25	0.0014	18.1
Oak savanna (dehesa)	–0.0017	0.0005	10.82	0.0010	32.6
PRESENCE with SP					
Intercept	–2300.11	788.2802			
Climate iii	26.9889	0.0000	15.36	<0.0001	11.5
Climate 43	(–)1.9444	0.7103	9.01	0.0027	0.3
Non-irrigated mixed cultures	0.0138	0.0116	4.07	0.0436	8.1
Irrigated mixed cultures	–0.0045	0.0018	5.92	0.0150	1.4
Hard-soil factor	–0.5039	0.1921	7.28	0.0070	1.1
Spatial pattern:					
X	–0.5168	0.1556	11.61	0.0007	4.2
Y	(–)1.1766	0.3857	8.98	0.0027	34.1
$X \times Y$	(–)1.2356	0.3729	11.56	0.0007	5.1
$Y \times Y$	–14.8093	4.7180	9.58	0.0020	34.3
ABUNDANCE with SP					
Intercept	–877.806	331.8696			
Climate iii	–1.0487	0.3796	7.63	0.0057	11.7
Climate 41	–0.8212	0.3582	5.25	0.0219	6.2
Climate 44	–0.5750	0.2100	7.50	0.0062	16.2
Non-irrigated homogenous herbaceous cultures	0.0014	0.0005	6.74	0.0095	10.2
Non-irrigated homogenous cultures of trees	0.0016	0.0005	8.21	0.0042	2.4
Non-irrigated mixed cultures	0.0035	0.0010	12.33	0.0004	1.4
Irrigated mixed cultures	0.0026	0.0010	6.80	0.0091	2.6
Mixed cultures and natural vegetation	0.0018	0.0007	7.08	0.0078	3.1
Dense oak forest	0.0023	0.0006	14.32	0.0002	15.2
Dense scrub	0.0019	0.0006	11.15	0.0008	0.5
Sparse scrub	0.0021	0.0005	15.55	<0.0001	0.2
Oak savanna (dehesa)	0.0020	0.0006	11.52	0.0007	2.3
Pastures	0.0021	0.0007	9.47	0.0021	0.7
Ecotone factor	0.1873	0.0858	4.76	0.0290	27.0
Spatial pattern:					
Y	(–)0.4209	0.1602	6.90	0.0086	0.02
$Y \times Y$	–5.0675	1.9332	6.87	0.0088	0.02

Models with variables obtained by GIS

The model for rabbit distribution (presence/absence) explained 13.5% of the original deviance (Fig. 4a). This model showed that the probability of finding a wild-rabbit population in a random area of southern Spain decreased with the amount of oak savanna cover (dehesa), with the amount of mosaics of natural vegetation and cultures, and with the amount of surface covered by mixed irrigated crops (Table 2).

When geographic coordinates are introduced into the model, four variables of the polynomial performed with the geographic coordinates were selected (Table 2), indicating a spatial pattern in the rabbit distribution (Fig. 4a) . When the spatial autocorrelation is accounted for, some modification of the previous model appears: the probability of finding a wild-rabbit population in a random area increases with the amount of cover of non-irrigated mixed cultures, whereas it decreases with the amount of hard-soil cover and with the amount of cover of irrigated mixed cultures (Table 2). The amount of dehesa cover and mixed cultures of natural vegetation is substituted by the amount of non-irrigated mixed cultures and soil hardness when accounting for the spatial pattern.

The two models for rabbit abundance produced similar results: the one excluding spatial autocorrelation explained 18.6% of the original deviation, while the one including spatial autocorrelation explained 22.6% of it. Therefore, we only show the results of the latter (Fig. 4a). The spatial pattern accounted for a small proportion of the total deviance explained by the model (Table 2). In areas where rabbit populations are present, many land-use variables modulate their abundance (Table 2). Rabbit abundance mainly increases with the amount of ecotone between different uses of land, the amount of natural vegetation, and the amount of non-irrigated cultures or irrigated mixed cultures.

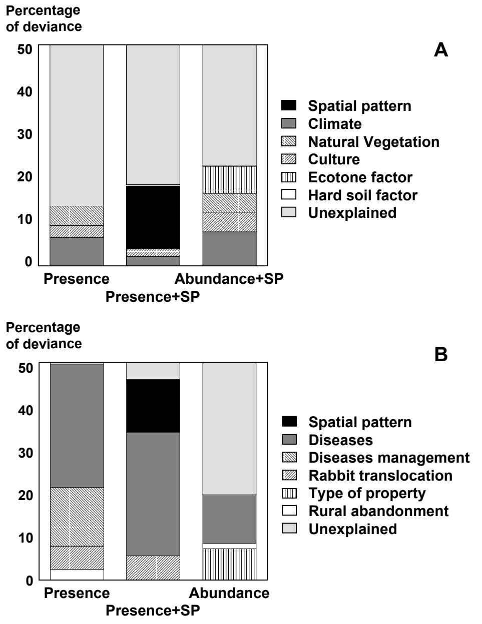

Figure 4. Percentage of deviance explained in models for rabbit presence and abundance, and when accounting for spatial pattern (SP). Independent variables have been grouped. (A) Models based on GIS variables. (B) Models based on historical variables.

Models with variables obtained by interviews

The model of rabbit distribution (presence/absence) accounted for 49.6% of the original deviance (Fig. 4b). Diseases and their management accounted for most of this deviance. The probability of finding a wild-rabbit population increases with a high degree of recovery after the first RHD outbreaks and when myxomatosis is present in the area, and decreases with the intensity of rabbit translocation and the intensity of disease management. Finally, the probability of finding a wild-rabbit population in a random area of southern Spain decreased when there is free access to the area or where there is rural abandonment.

When introducing spatial autocorrelation, the model obtained explained a lower percentage of the deviance (46.06%; Table 3). The spatial pattern accounted for almost 25% of the deviance explained by the model (Fig. 4b). The following variables were not selected when accounting for the spatial pattern: intensity of disease management, presence of myxomatosis in the area, and rural abandonment. Three explanatory variables obtained from the interviews had a significant effect on this model, predicting again high probabilities of presence of wild-rabbit populations with a high degree of recovery after the first RHD outbreaks and decreasing with a high intensity of rabbit translocations. A new variable is selected in this model, predicting high probabilities of finding rabbit populations with high recovery after the arrival of myxomatosis.

Table 3. Generalised linear model (GLM) for the probability of the presence and abundance of wild rabbits in southern Spain using non-GIS information. The percentages of deviance explained by each variable are shown (%). The sign of the single relationship is indicated in brackets when the sign in the whole model does not correspond to the sign of each single variable against the dependent variable. SP: spatial pattern considered.

Variable	*Parameter*	*Standard error*	X^2	*P*	%
PRESENCE without SP					
Intercept	0.1846	0.8285			
Free access	–1.3611	0.7260	4.01	0.0453	<0.01
Rural abandonment	–1.26.3	0.6085	4.56	0.0327	5.0
Rabbit translocations in 1999	–0.7434	0.3115	6.24	0.0125	10.7
Disease management factor	–0.6300	0.2878	4.39	0.0362	27.2
Presence of myxomatosis in 1999	1.5284	0.6334	5.93	0.0149	7.1
Recovery degree after RHD	1.7805	0.5933	15.11	0.0001	50.0
PRESENCE with SP					
Intercept	238.784	116.2153			
Rabbit translocations in 1999	–0.7288	0.3758	4.74	0.0295	12.1
Recovery degree after RHD	1.5671	0.5403	14.07	0.0002	56.2
Recovery degree after myxomatosis	–0.9520	0.4107	5.40	0.0201	5.5
Spatial pattern:					
X	–0.6692	0.3284	5.07	0.0243	5.6
Y	–0.0542	0.0274	4.91	0.0268	10.8
$X \times Y$	(–)1.4477	0.7673	4.19	0.0407	5.9
$X \times X$	(–)0.0838	0.0308	10.14	0.0014	4.0
ABUNDANCE without SP					
Intercept	–0.7233	0.2625			
Type of property	0.9312	0.2868	10.54	0.0012	36.7
Rural abandonment	–0.5617	0.2381	5.57	0.0183	6.4
Presence of myxomatosis in 1999	–0.7813	0.3190	6.00	0.0143	7.8
Recovery degree after RHD	0.2626	0.1136	5.35	0.0208	49.0

Models analysed to explain rabbit abundance in the areas where rabbit populations are present lead to identical results whether or not the spatial autocorrelation is accounted for. Any of the variables describing spatial structures were selected, while three variables from the interviews had a significant effect on the model (Table 3). In summary, the model for rabbit abundance explained 19.6% of the original deviance (Fig. 4b). Rabbit abundance increases with a higher degree of recovery after the first RHD outbreaks and decreases when myxomatosis was present in the area and with rural abandonment. Rabbit abundance was higher on public land than on private properties.

DISCUSSION

Wild rabbit has been an abundant species in the past, to the extent of being considered a pest species in many countries. It is widely distributed throughout southwestern Europe, where it originated from, occupying all landscapes at different abundance levels. However, in this region the populations of wild rabbits are currently the lowest recorded for centuries, in terms of both population abundance and species distribution (Villafuerte et al. 1995). This situation is reflected in our study area, where we observed that rabbit abundance was depleted, and is in agreement with previous studies (e.g., Fa et al. 1999).

Given the steady decline in rabbit numbers, it is expected that areas in which rabbits currently exist have special characteristics. In our paper, we have attempt to detect these characteristics by fitting models to rabbit presence. Although we have used a random sampling design, we show that spatial autocorrelation affects rabbit presence. This effect could be explained by the history of rabbit abundance, with local extinctions recorded in the last few decades occurring in the least-preferred landscapes for rabbits (Villafuerte et al. 1995; Palma et al. 1999). As most landscape structures are themselves spatially structured by their own generating processes (Legendre et al. 2002), rabbit preferences for particular landscapes may be the source of the spatial pattern detected in the current rabbit distribution.

The spatial pattern of rabbit presence was independent of the set of variables analysed, as it appears in the two models of rabbit distribution. However, the spatial pattern is much less important for modelling rabbit abundance than for modelling rabbit distribution. The rabbit distribution was explained to a lower degree by variables related to landscape availability, as obtained by GIS techniques, than by variables obtained from interviews related to the effects of past situations. However, landscape variables retained in the model are consistent with previous studies that found climatic, topographic, and habitat effects on wild-rabbit distribution (Fa et al. 1999; Trout et al. 2000; Virgós et al. in press; Calvete et al. in prep.). Our results showed that soil hardness limits rabbit distribution, which is in agreement with previous works stating that soft soils are needed for the digging of warrens in order for the animals to reproduce and protect themselves from predators (Parer and Libke 1985; Trout and Smith 1995). However, although soil hardness is a significant variable in our model, habitat features remain more important.

Mediterranean landscapes mainly comprise a mosaic of cultures, situated in valleys where the most productive soils are located, and natural vegetation areas, situated in areas difficult to cultivate due to unfavorable orography. In the past 50 years, agricultural intensification has led to a reduction of natural vegetation, to an increase in the size of cultures, and to an increase in irrigated culture surfaces (Nadal et al. 1996; Tella et al. 1998). Our results show that rabbit populations are more likely to be found in mixed non-irrigated cultures, and that this type of culture is correlated with higher rabbit abundance. Studies on the diet and food habits of rabbits in agricultural landscapes have shown that cultivated Gramineas (e.g., wheat and barley) are positively selected, especially during the growing season, which coincides with the rabbit breeding period (Homolka 1988; Chapuis and Gaudin 1995). In fact, irrigated cultures are only positively related to rabbit abundance when different crops are mixed, which may represent an optimal food resource for rabbits. This idea is confirmed by the observation that the amount of ecotone is positively correlated with rabbit abundance: as cultures become more mixed, ecotone should increase. Ecotone between other types of landscape features has been shown to be essential for wild rabbits (Rogers and Myers 1979; Moreno et al. 1996). As a prey species, the wild rabbit is expected to optimise the time spent between refuge patches and food patches (Villafuerte and Moreno 1997).

Models analysed with variables not related to landscape availability remained those that most explained the current distribution of rabbit populations. However, information obtained from interviews reflects the perceptions of people regarding the evolution of rabbit abundance in the area. This is an assumption of the methods used in this paper, and should be taken into consideration in future studies. Variables selected in models analysed with interview information are related mainly to the evolution of rabbit populations in relation to diseases, to the pattern of rabbit diseases, and to historical management of rabbit populations. In addition, rural abandonment was negatively associated with rabbit presence. The probability of finding rabbit populations is higher in the absence of rural abandonment. Moreover, when a rabbit population is present, rabbit abundance is lower if rural abandonment has occurred. The variable of rural abandonment has an important spatial component, because it is not selected in models that account for spatial autocorrelation, which is probably explained by rural abandonment being associated with specific landscapes (Etienne et al. 1998; Schröder 1998).

Our results show that rabbit populations are most likely to be found – and at higher abundance – when the degree of recovery of the population after the first RHD outbreak was higher. This result corroborates previous studies which showed that the intensity of RHD recovery could be related to rabbit abundance: those areas with higher rabbit abundance were the ones that had recovered the most (Villafuerte et al. 1995). The same relationship appears to be present with myxomatosis, that is, in our model the intensity of recovery from myxomatosis is related to higher rabbit abundance. In fact, our results show also the importance of the detection of myxomatosis for wild-rabbit populations and its relationship with rabbit density. It is more likely to find rabbits in areas where myxomatosis is detected, but the presence of myxomatosis is related to lower rabbit abundance. The probability of encountering a sick rabbit in the field increases with the rabbit population density, because young myxomatous rabbits are easily seen . Thus, myxomatosis becomes a factor explaining rabbit distribution. However, it has an inherent negative effect on the population (Trout et al. 1992; Angulo and Cooke 2002), an effect reflected in our study by the negative relationship between myxomatosis detection and rabbit abundance. Both myxomatosis and RHD have been exposed as the main causes of the decline of wild-rabbit populations (Angulo and Cooke 2002). Firstly, the arrival of myxomatosis reduced the number of rabbits during the 1950s, and their populations – which could not recover to previous levels – were further reduced by the arrival of RHD during the 1990s; RHD had devastating effects on both wild-rabbit populations and on the populations of their predators, many of which are now endangered (Fernández 1993; Angulo 2001; Martínez and Calvo 2001; Martínez et al. 2003).

The decline in rabbit populations (and those of their predators) has led to management strategies in recent decades aimed at recovering their populations. Hunters, landowners, and conservation agencies are managing this process with different intensities, characterised by both the number of different strategies applied and by the frequency of their use. For example, the management of small game in an area is usually performed using multiple strategies (i.e. habitat and predator control, hunting reduction, translocations, and the prevention of parasites and diseases). Our data on the intensity of management strategies in southern Spain indicate that management intensity has increased during the past 30 years, with strategies related to wild-rabbit disease and parasite prevention (which are the most costly to implement) having increased in importance (see chapter 2 entitled “Multiple strategies for the management of small game: implications for wildlife conservation”). This paper shows that rabbit populations are found with a higher probability when the intensity of management applied to disease and parasite prevention is lower. This relationship may indicate either that disease management is mostly carried out when the populations are very low, or that the use of this type of management leads to the extinction of the populations. Although the effects of multiple strategies applied to wild-rabbit populations are not well understood, the effectiveness of individual measures has been assessed. In relation to disease and parasite management, some authors have successfully manipulated vectors of myxomatosis in the UK in order to reduce effects on populations, but Osácar et al. (1996) were unable to apply this procedure to Spain, probably because of the wider vector range present. However, no negative effects on population have been recorded when applying these measures. We can thus accept that disease management is mostly carried out when the populations are very low. In addition, if we distinguish between the three measures considered here – medication supply, disease vaccination, and deparasitations – the latter two are associated with rabbit translocations, as such animals should follow a sanitary protocol that includes vaccinations against myxomatosis and RHD, and deparasitation (Calvete et al. 1997). Our results show that rabbit translocations are also negatively related to rabbit presence; this indicates, as stated above, that these measures are applied when rabbit populations are scarce. C. Calvete (pers. comm.) maintain that rabbit translocations are carried out in Spain for hunting and conservation purposes in order to enhance rabbit populations when their abundance is low. This agrees well with our finding that rabbit populations are mostly absent when both measures – rabbit translocations and disease management – are carried out.

CONCLUSION

In this paper, we show that the current rabbit distribution is associated not only with the available landscape features, but also with factors that may have constrained their populations in the past: diseases and the management of their populations. This constitutes a good example of how research on factors affecting the current distribution of a wildlife species should include historical variables that might have previously constrained the distribution or abundance of the species.

When factors affecting wild species can be obtained by remote sensors, the information can be used to create easily updatable prediction maps (Seoane and Bustamante 2001; Seoane 2002). However, GIS data continue to be expensive and difficult to obtain. When it is necessary to obtain information through field surveys (which is not possible to obtain from any other sources), such as habitat features or land uses, it would be interesting to record information on historical, social, and disease events, as we have done in this paper for the wild rabbit. Models resulting from these factors would be useless as predictive models, because of the lack of information covering the whole area. However, these models are important for wildlife conservation when the goal is to identify the risk factors of endangered species, the variables that need to be improved, and the areas that need immediate attention (Seoane 2002). Moreover, they become very useful when the species population has decreased due to the effects of past situations. In these cases, which apply to most endangered species, suitable landscape features are available, and it is other factors that constrain their distribution.

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NOTES

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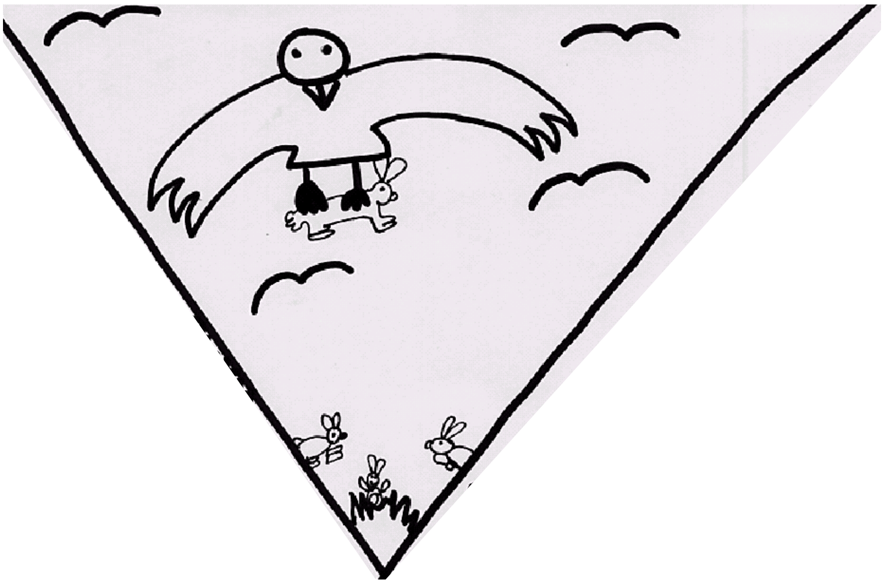

CAPÍTULO 2

Multiple strategies for the management of small game: implications for wildlife conservation

El uso de las estrategias múltiples para la gestión de la caza menor: implicaciones en la conservación natural

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Resumen

El conejo y la perdiz son las especies reina de la caza menor en España, y también son especies básicas para la comunidad de depredadores de los ecosistemas mediterráneos. Dado que las poblaciones de ambas especies se encuentran en declive en la Península Ibérica, la gestión de las poblaciones se ha convertido en una herramienta imprescindible. Sin embargo, poco se conoce sobre las medidas de gestión que se aplican, la intensidad de las mismas y su evolución en los últimos años. Tampoco hay estudios globales que cuantifiquen el efecto de dichas medidas sobre las poblaciones diana a las que van directamente dirigidas o sobre las poblaciones de depredadores a las que van indirectamente dirigidas.

El Capítulo se plantea en formato de dos publicaciones. La primera aborda, desde una perspectiva regional, la descripción de la gestión cinegética de caza menor, su intensidad y evolución temporal y su relación con las especies diana de la gestión y con el resto de fauna silvestre. En la segunda publicación se expone un caso práctico representativo de la importancia de los conejos (y las perdices) en la ecología de los depredadores del ecosistema mediterráneo, en este caso, del águila azor perdicera (*Hieraaetus fasciatus*).

En la primera publicación realizamos una valoración cuantitativa de la efectividad de las estrategias de gestión analizando las estrategias múltiples de manejo, a través de encuestas y censos en 307 áreas andaluzas. Más del 95% de las áreas usan estrategias para recuperar las poblaciones de conejo y perdiz. El uso de dichas estrategias ha aumentado en las últimas tres décadas significativamente. El manejo de hábitat, la reducción de la caza y el control de depredadores fueron estrategias más usadas que las translocaciones o la prevención de parásitos y enfermedades. No se ha podido mostrar que las estrategias de manejo estén relacionadas con un incremento significativo en la abundancia poblacional a corto plazo; sin embargo, este incremento está directamente relacionado con el nivel de abundancia inicial. Es

decir el incremento poblacional es mayor en las áreas en las que la abundancia es mayor. En los lugares en que las poblaciones de perdiz se han considerado en declive en los últimos diez años, la intensidad de manejo es significativamente más alta que en las áreas en las que dichas poblaciones se han considerado estables. Sin embargo, esta relación no se ha observado para el caso del conejo.

Se estimaron los gastos medios que supone cada estrategia de manejo, con el objeto de analizar la intensidad de manejo en cada área. Los resultados indican que la media de gastos para la gestión de la caza menor en un área de 2 000 ha. varía entre 4 500 y 8 800 euros al año. Los gastos más altos corresponden a las áreas donde la abundancia de ambas especies es mayor, probablemente debido a que los cazadores están más interesados en la actividad cinegética de la que obtienen un beneficio económico. La intensidad de manejo está relacionada con un mayor nivel de conservación natural de las áreas, estimado éste a través de la cantidad de especies de fauna que se encuentran en el área y del valor ambiental de dichas especies .

En conclusión, los resultados que se exponen en la primera publicación de este Capítulo, indican que la gestión de la caza menor es utilizada muy frecuentemente y con gran intensidad en Andalucía y que puede tener un papel muy importante en la conservación de las especies silvestres. Sin embargo, se requieren nuevos estudios que evalúen con mayor detalle los beneficios que la gestión cinegética tiene, no sólo para las especies diana de dicha gestión sino también para los depredadores que de ellas dependen.

La segunda publicación de este Capítulo, analiza los factores que pueden afectar a la duración del período comprendido entre el primer vuelo del joven de águila azor perdicera y el comienzo de la dispersión. Este período, denominado de post-emplumamiento, es un período de aprendizaje de las jóvenes águilas. Además de los posibles efectos de la disponibilidad de alimento (abundancia y evolución temporal de las especies que consume, conejos y perdices), se analizaron otros factores como la fecha de puesta, la fecha de eclosión, la condición corporal y el estado nutricional de los individuos. Para determinar los cambios temporales en la disponibilidad de conejos durante el período de post-emplumamiento se muestrearon, mediante censos mensuales, las abundancias de conejo y perdiz en el área de estudio. A partir de un índice de abundancia media mensual, a cada joven águila se le asignó una disponibilidad de presas en función de los meses que duró su período de post-emplumamiento.

La mayor duración del período post-emplumamiento estuvo directamente relacionada con una más temprana fecha de eclosión del huevo. Por otro lado, una menor duración de dicho período se correlacionó positivamente con una mayor abundancia de conejos y con una menor abundancia de perdices. Estos resultados se explican por la fenología de las abundancias de las dos especies presa consideradas. Por un lado, la reproducción de los conejos acaba de empezar cuando las águilas ponen los huevos y, como consecuencia, se observa un incremento en las abundancias de conejo hasta alcanzar el máximo en junio y julio. Con la llegada del verano, la reproducción de los conejos finaliza y su abundancia va decreciendo hasta los mínimos poblacionales, en octubre y noviembre. En el caso de la perdiz, la reproducción es más tardía, comienza en marzo, y los máximos poblacionales se observan al final del verano.

Por tanto, las águilas que se emplumaron y volaron más pronto (a partir del 15 de mayo) pudieron disfrutar de una mayor abundancia de conejos, lo que explicaría que completasen más rápidamente el post-emplumamiento. Las águilas que volaron más tarde dispusieron de menor abundancia de conejos y necesitaron más tiempo para adquirir una condición física adecuada para dispersarse. Estas águilas “tardías”, con acceso a una mayor abundancia de perdices, podrían haberse alimentado preferentemente de perdices en lugar de conejos, resultando en la misma duración del período de post-emplumamiento que los jóvenes que se emplumaron antes. El conejo parece ser una presa preferente (aparece en mayor proporción en la dieta del águila azor perdicera) y de mayor calidad (tiene más biomasa), lo cual podría explicar las diferencias observadas. En conclusión, se observa la importancia de la disponibilidad del conejo en la duración del período de post-emplumamiento del águila perdicera.

Multiple strategies for the management of small game: implications for wildlife conservation

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Abstract

Declines in the populations of wild rabbit and red-legged partridge have made their management necessary since they are the most important small-game species in southwestern Europe and they sustain a great number of predators in Mediterranean ecosystems. Here we provide a quantitative assessment of small-game management effectiveness using a large sample of areas in southern Spain in which multiple strategies were applied. These strategies are used to improve both rabbit and partridge populations in more than 95% of the areas sampled, and their use has increased significantly during the past 3 decades. Among the strategies employed, habitat management, reduction in hunting, and predator removal have been more common than translocations and the prevention of diseases and parasites. Most strategies were significantly associated to a second strategy. The observed data fitted significantly to the combination of next associations: predator control and habitat management, predator control and reduction in hunting, prevention of diseases and parasites and rabbit translocations, rabbit and partridge translocations, and predator control and high rabbit abundance. Annual growth rate of rabbit and partridge between 1998 and 1999 were not associated to any management. We have calculated that the mean annual expenditure on managing small game in an area of 2000 ha is 4500–8800 euros. High management intensity is associated with high abundance of both species, which probably reflects the large hunter interest in small game. When partridge populations are declining the intensity of management is significantly higher than when the population is stable, but this is not the case for rabbits. Areas with higher expenditure on management and that have high rabbit abundance have higher levels of wildlife conservation; in addition, wildlife conservation is enhanced by habitat management and the reduction of hunting. Our findings illustrate that small-game management is employed in most areas of southern Spain, and may have a role to play in wildlife conservation. There is a need to evaluate the long-term benefits of small-game management not only to improving small-game populations but also to wildlife conservation.

Keywords: wild rabbit, red-legged partridge, *Oryctolagus cuniculus*, *Alectoris rufa*, conservation, small game.

INTRODUCTION

The management of game species is necessary to maintain the desired level of population abundance, and the proportions of sex and age classes. The populations of wild rabbit (*Oryctolagus cuniculus*) and red-legged partridge (*Alectoris rufa*) in Europe, the most important small-game species in Spain, have been declining for many areas; hence, management of their populations has become necessary for their recovery. The primary goal of small-game management remains recreational hunting. More than 70% of the national territory is covered by hunting areas, and hunters kill more than four million rabbits and almost four million partridges annually (Ministry of Agriculture, Fisheries and Food, 1996; Millán et al. 2001). Moreover, rabbits and partridges are the most important vertebrate prey species in Mediterranean ecosystems, being preyed upon by more than 30 predator species. The biodiversity of Mediterranean ecosystems is usually associated with large numbers of these species (Delibes & Hiraldo, 1981). Moreover, rabbits are the main prey of two of the most endangered predators in the world: the Iberian lynx: (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*).

Management strategies are carried out in hunting areas by hunters or landowners, and in protected areas by government agencies responsible for environmental protection in order to increase the prey available to endangered predators. Several scientific studies have proposed small-game management as the best method to conserve endangered predators (Palomares et al. 1991; Castro & Palma, 1996; Real & Mañosa, 1997). Moreover, the Spanish government has provided considerable funding to projects over the last few decades, the main goal of which was to improve rabbit and partridge populations in order to conserve the Imperial Eagle and Iberian lynx. Thus, the effectiveness of the management of rabbit and partridge populations should be measured not only by increases in their populations, the main goal of hunters, but also by improvements in the conservation of wildlife, the ultimate goal for conservation purposes.

Different factors have contributed to the decline of rabbit and partridge populations, including fragmentation of habitat, habitat loss, excessive hunting, diseases, and excessive predation pressure by generalist predators. In particular, rabbit haemorrhagic disease (RHD) has caused a sharp decline in rabbit populations over the last decade. RHD became enzootic in wild populations (Calvete et al. 2002), and many populations continued decreasing and eventually became extinct (Villafuerte et al. 1995). Numerous management strategies have been implemented in an attempt to restore rabbit and partridge numbers. These strategies can be classified into five groups: directly increasing abundance by translocation, improving habitat, reducing hunting pressure, preventing diseases and parasites, and reducing predation pressure.

The effectiveness of some management strategies has already been evaluated, and where necessary new measures have been proposed. For example, Calvete et al. (1997), Gortázar et al. (2000), and Putaala & Hissa (2000) have evaluated the effectiveness of translocation. The traditional method of management involves releasing large numbers of animals without any habitat management or reduction in predators, but this is ineffective, costly, and results in high mortality rates in the animals released. Trout et al. (1992) successfully manipulated vectors of myxomatosis (a rabbit disease) in the UK, to reduce their effects on populations, but an attempt by Osácar et al. (1996) to apply a similar procedure in Spain failed, probably because of the presence of a wider vector range. Habitat management such as scrub and pasture management have been evaluated by Moreno and Villafuerte (1995), who found that such measures improve rabbit populations. Hoodless et al. 1999) showed that supplementary feeding does not increase the abundance of small game birds. However, the supplementary feeding of partridges may improve the general condition of populations (Blanco-Aguiar et al. 2001), while reproduction in wild rabbits is associated with the availability of high quality food (Wallage-Drees & Michielsen, 1989; Villafuerte et al. 1997).

Other measures used for small-game management have been considered, not only in terms of their effect on small-game populations but also their effects on non-target species. For example, Trout and Tittensor (1989), Smedshaug et al. (1999), and Banks (2000) showed that removing predators improves small-game numbers, while Côte and Sutherland (1996) concluded that predator removal is not very effective for conservation. The effectiveness of these techniques in a Mediterranean ecosystem with a high number of predators has not been fully evaluated. For example, the conservation problems caused by the illegal control of non-target predator species is currently under investigation. The lack of selectivity of predator control measures has been demonstrated, as has their potential negative effects on the conservation of non-target species (Ruiz-Olmo 1986; Duarte & Vargas 2001). Moreover, Villafuerte et al. (1998) showed that a decline in the number of rabbits was followed by the illegal control of predators leading to the decline of a species of raptor.

The usual situation in Spain is that the management of small game within an area involves multiple strategies. However, there is little information available on the frequency of use of management strategies, on the expenditure in managing small game, or in which situations management is applied. For example, two goals that could be set by managers applying small-game management are (1) to recover the populations when their abundance is low or (2) to produce higher economic benefits when their abundance is high. Past studies on management effectiveness have focused on one management strategy at a time, with none having assessed quantitatively the effectiveness of using a large sample of areas where multiple strategies are applied. In addition, a full evaluation of the effects of general small-game management is needed, not only on rabbit and partridge populations, but also on other wildlife species.

Our study assessed the intensity of small-game management in southern Spain, with the aim of determining whether this intensity is related to the abundance (or trends therein) of small-game populations, and discovering the relationship between small-game management and wildlife conservation. Thus, we explored the importance of the management of small game in rabbits and partridges, the frequency of different management strategies, and the changes in their use over the past three decades. We hypothesised firstly that small-game management would be used most intensively in areas where rabbit and partridge population abundance were low or declining, and secondly that the areas managed most intensively would exhibit a better level of wildlife conservation. We also evaluated the short-term effect of different management strategies on rabbit and partridge populations.

METHODS

Interviews and field survey

More than 35 people trained in wildlife surveys carried out 307 interviews and rabbit surveys in southern Spain during June and July of 1998 and 1999 (Figure 1). Survey points were based on a step-random sample based on altitude and topography, with areas lower than 1200 meters in altitude and with slopes of less than 30% were favoured in the selection of study areas. At each survey point, we conducted a census of rabbit and partridge abundance, identified the land ownership of the area, and personally interviewed a local hunter, landowner, or conservation manager.

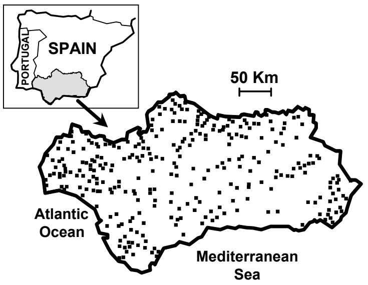

Figure 1. Study area. Sampled areas are represented by black squares.

The first interviews were carried out in June 1998. We asked about which game species was the focus of game management in each area. We used a questionnaire involving nine management strategies that favoured small game (Table 1). Participants were asked to indicate whether these management practices were usually applied in the area currently, and 10 and 30 years ago.

A second interview was conducted at the same survey points in June 1999 – involving the management strategies favouring small game applied during the 1998–1999 hunting season – using a more complete questionnaire. The participants were asked to indicate whether or not management practices designed to favour the increase of small-game numbers were applied in their area. Those practices that hunters or landowners may have applied voluntarily each year are listed in Table 1.

In the 1998 interview the participants were asked to indicate whether the following wildlife species were present in the area: predators such as Egyptian mongoose (*Herpestes ichneumon*), genet (*Genetta genetta*), polecat (*Mustela putorius*), stone marten (*Martes foina*), badger (*Meles meles*), wild cat (*Felis silvestris*), Iberian lynx, wolf (*Canis lupus*), and large and small eagles; big-game species such as feral pig (*Sus scrofa*), roe-deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and Spanish ibex (*Capra pyrenaica*); and finally small-game species such as hare (*Lepus granatensis*), quail (*Coturnix coturnix*), turtledove (*Streptopelia turtur*), wood pigeon (*Columba palumbus*), thrush (*Turdus turdus*), rabbit, and red-legged partridge. In the case of rabbit and red-legged partridge, participants were also asked to indicate the levels of abundance 10 years ago and the trends in their populations during the previous decade in the area (allowed answers were no change, increasing, and decreasing).

Table 1. Management strategies for improving small game in southern Spain as used in the 1999 questionnaire. Strategies marked with an asterisk were used in the 1998 questionnaire. The mean annual expenditure on applying each managing strategy in a 2000-ha area is shown (in euros). Percentage of areas where such management are applied (1) and percentage of areas where each management is the only one applied (2) are also indicated.

GROUP OF MANAGAMENT STRATEGIES	MANAGEMENT STRATEGY	Expen-diture (euros)	% AREAS (1)	% AREAS (2)
Habitat improvement	Creation of pastures*	2300	64.0	13.2
	Scrub management*	755		
	Food supply*	2000		
	Water supply*	800		
	Management of rabbit warrens*	11000		
Predator and pest control*	Foxes control	11000	45.6	2.4
	Dogs and cats control			
	Corvids control			
	Rats control			
Prevention of diseases and parasites	Medication supply*	240	15.8	0
	Vaccination*	2150		
	Prevention of rabbit-disease vectors*	2400		
Translocations	Translocation of rabbits	900	12.5	0
	Translocation of red-legged partridges	600	21.7	1.7
Hunting strategies	Area of hunting reserve		61.0	10.8
	Reduction in hunting days			
	Reduction in hunters per day			
	Reduction in number of hunted animals			
	Reduction in number of hunting hours per day			

During June 1998 and June 1999, rabbit and red-legged partridge abundances were estimated along a 4-km route, checking for evidence of rabbits and partridges in each survey point. Each transect was walked along and sightings of rabbits and partridges were recorded, as well as evidence of three typical rabbit signs: faecal pellets, scrapes, and latrines. Such signs have been widely used in previous studies (Trout et al. 2000; Virgós et al. in press), with faecal pellets being particularly appropriate where the rabbits themselves are difficult to detect or the detection of certain signs may be influenced by other factors such as soil or habitat type (Moreno and Villafuerte 1995; Palma et al. 1999). Partridge abundance was computed on the basis of the number of partridges seen per 4-km transect. To assess rabbit abundance, we used principal component analysis (PCA) to express the four correlated variables of rabbit abundance using a single factor. The factor of rabbit abundance explains 75.99% of the original variance. A logarithmic transformation of the variables was necessary before applying PCA.

Hypothesis tested and statistical analyses

We used the frequency of management strategies to built a multidimensional table in order to determine associations among management strategies in southern Spain in the 1998-1999 hunting season. We analysed associations between the five groups of management strategies, but separating translocations by species (Table 1). In addition, we determined possible associations among those strategies and the annual growth rates of partridges and rabbits between 1998 and 1999, and their abundance during 1999. Partridge annual growth rate was based on the number of red-legged partridges seen per transect. Rabbit annual growth rate was based on the factor of rabbit abundance, which was converted to positive numbers by addition of the lowest negative number prior to the calculation of the annual growth rate. Abundance of both species was categorized in two groups: below and above mean; while annual growth rate was categorized in two groups: increasing and decreasing. Data analysis was done using BMDP–4F (Dixon 1983); associations among variables were tested using G-tests and differences between percentages using Fisher exact tests.

To determine whether the frequency of use and the possible associations described in the previous analysis explained the observed situation in southern Spain, a log-linear model was built considering only the significant associations between strategies. We searched for the most simple model with no significant differences with the observed data, beginning with the complete model (with all the significant associations) and eliminating the association with the lowest G^2 at each step. The expected values generated by the final model (lambda) were compared with the table of observed values by a G-test (Heisey 1985). Standardized values of the log-linear parameters of the model were used to test the deviations of predicted frequencies from randomness (Edwards 1989).

We used generalised linear models to analyse for differences in the use of the nine types of management strategy (1998 questionnaire, Table 1), for differences between the current use and the uses 10 and 30 years ago, and for differences in the change of use of different types of management strategy. We analysed a generalised linear model in which the dependent variable was the use of each management strategy (used or not used; a binomial variable); the independent variables were the historical period (with three levels: currently, and 10 and 30 years ago) and the type of management strategy (with nine levels corresponding to the management strategies of the 1998 questionnaire, Table 1). To test the goodness-of-fit statistics of each model, aggregating data before the computation of the test solved problems caused by sparseness of the binomial variable.

We performed a second analysis to determine whether differences in the use of different types of management strategy and differences in their current use with respect to their use during the previous decade were affected by the level of abundance of rabbit and partridge in each historical period. We grouped management strategies into three categories (habitat management, predator control, and prevention of diseases and parasites) in order to reduce the analysis levels. The types of management strategy considered were different for rabbit and red-legged partridge. All strategies were considered for rabbits. For red-legged partridge, in the prevention of diseases and parasites category, vaccinations and prevention of rabbit disease vectors were not used, while in the habitat management category, warren management was not used (Table 1). We analysed two generalised linear models (one for each species) in which the dependent variable was binomial (the use of each group of management strategies) and the independent factors were the type of management strategy (habitat, predator control, or prevention of diseases), level of abundance of each species (low or high), and historical period (currently and 10 years ago). Goodness-of-fit statistics of each model considered sparseness of the binomial variable.

Currently two opposing goals potentially motivate managers or hunters to apply management strategies for the improvement of small game: (1) to increase the population in an area where it is declining, and (2) to encourage small-game hunting, which is an economically important activity. We wanted to test both hypotheses. We performed two ANOVA tests, one for each species, to test for differences in the expenditure on management strategies in relation to the abundance and its trend of each species. We calculated the mean yearly expenditure for each management strategy when applied to a 2000-ha area from information provided by specialist managers; we consider that management will cover 500 ha each year (Table 1). Strategies for the reduction of hunting pressure were not considered. Since we knew which management strategies were usually applied in each area (see Table 1, from the 1998 interviews), we calculated the mean annual expenditure. As some management strategies are aimed at improving rabbit populations, such as management of warrens or vaccinations, the costs of rabbit management were different from those of partridge management. We related this amount to the level of abundance of both species in the area (low and high) and the trends of the rabbit and partridge populations over the last decade (no change, increasing, or decreasing) in each area.

To test the possible effects of small-game management strategies on environmental conservation, we related an environmental value of each area to the intensity of management. We used data on the presence of wildlife species in the area: carnivores, eagles, and large- and small-game species. We obtained the environmental value of each species for the whole study area that was dependent on the number of areas in which the species was present. Thus, the environmental value of each species in southern Spain was calculated as 100 minus the percentage of areas in which the species was present. We then calculated the environmental value of each area as the summation of the environmental values of all the species present in that area (Hiraldo & Alonso 1985).

We used the environmental value of each area as the dependent variable in a generalised linear model in which the independent variables were related to the intensity of management using the mean annual expenditure on small-game management in each area (from the 1998 interviews, see Table 1). To control for the effects of rabbit and partridge abundance, we included their abundance (low or high, as assessed in the 1999 field survey; number of partridges seen in the 4-km transect and PCA obtained from the indirect variables of rabbit abundance) in the analysis. This was done firstly because these two species are the most important prey in Mediterranean ecosystems (Delibes & Hiraldo, 1979) and their abundance could affect the presence of other wildlife species such as predators, thereby enhancing the level of conservation of an area, and secondly because the intensity of management could be related to their abundance. We tested the effects of the interactions between the intensity of management and rabbit and partridge abundance. We added five further independent variables in relation to the use of each group of management strategies (habitat management, predator control, prevention of diseases and parasites, reduction of hunting, and translocations) to test whether each group of management strategies could affect wildlife conservation.

All statistical analyses were performed using STATISTICA software (StatSoft, USA, 1999) except of multidimensional log-linear analysis that was done using BMDP–4F (Dixon 1983).

RESULTS

The areas selected in the sample varied greatly in size, type of ownership, hunting regime, primary habitat type, level of wildlife conservation, and management strategies applied. However, hunting areas represented more than 95% of the areas considered, with the remainder being environmentally protected areas. More than 25% of the questionnaires were either totally or partly invalid, and hence the number of cases included in each analysis varies with the number of valid answers. In most areas small-game species were the target species of the management strategies (84.45%), with rabbits and red-legged partridges being the species favoured in 81.82% of the surveyed areas (*N*=165).

The management strategies for improving small-game populations were applied in most of the surveyed areas during the 1998–1999 hunting season (94.5%, *N*=272). Regarding types of management strategy, we showed the percentages of use of each strategy in Table 1. Habitat management and reduction of hunting were the most applied while translocations and prevention of diseases and parasites were the less applied. It is interesting to note that individual measures are not very frequently applied alone in the same area, this indicating that multiple strategies are the most frequently management situation in southern Spain. For example, rabbit translocations and prevention of diseases and parasites are never applied alone in the same area.

We did not find any third order association among the use of management strategies during the 1998-1999 hunting season. As stated before, we found that most of the strategies are used associated to a second management (Table 2A), but the relationship between strategies in each pair is not always symmetrical (Table 2B). For example, considering the total number of areas where habitat management occurs, the percentage of which predator control is also applied is similar that when considering the percentage of areas where habitat management is applied from the total number of areas where predator control occurs; but for example, these percentages are significantly different when considering the association between habitat management and prevention of diseases and parasites: only 19.5% of the areas where habitat management occurs, prevention of diseases is also applied, while 79.1% of the areas where prevention of diseases occurs, habitat management is applied.

Table 2. Associations among pairs of managements strategies. (A) Percentage of areas occurring both estrategies; in brackets, G2-values and significance levels of G-test, ***p<0.001, **p<0.01, *p<0.05, *n.s* .non-significant. (B) Percentages of areas where a management strategy is used within the total areas where a second strategy occurs; the first value is when row management co-occurs within column management (e.g. % of areas that perform habitat improvement over the total of areas with predator control), and the second value is when column management co-occurs within row management (e.g. % of areas that perform predator control over the total of areas with habitat improvement). Significance level obtained by Fisher ‘s exact tests when comparing both percentages; significance levels as in (A). Degree of freedom are 1 in all cases.

A) G^2-test

	Habitat improvement	Predator and pest control	Prevention of diseases	Rabbitt translocations	Partridge translocations
Predator and pest control	36.0 % (7.16 **)				
Prevention of diseases	12.5 % (0.00 *n.s.*)	12.1 % (5.17*)			
Rabbitt translocations	9.6 % (0.61 *n.s.*)	8.8 % (0.43 *n.s.*)	7.0 % (15.15 ***)		
Partridge translocations	18.4 % (2.25 *n.s.*)	15.1 % (1.70 *n.s.*)	8.1 % (1.58 *n.s.*)	9.9 % (37.57 ***)	
Hunting strategies	45.2 % (4.16 *)	35.7 % (11.69 ***)	13.6 % (1.04 *n.s.*)	9.6 % (0.80 *n.s.*)	18.0 % (2.95 *n.s.*)

B) Fisher’s exact test

	Habitat improvement	Predator and pest control	Prevention of diseases	Rabbitt translocations	Partridge translocations
Predator and pest control	56.3 / 79.0 *n.s.*				
Prevention of diseases	19.5 / 79.1 ***	26.6 / 76.7 **			
Rabbitt translocations	14.9 / 76.5 ***	19.3 / 70.6 **	44.2 / 55.9 *n.s.*		
Partridge translocations	28.7 / 84.7 ***	33.1 / 69.5 *	51.2 / 37.3 *n.s.*	79.4 / 45.8 *n.s.*	
Hunting strategies	70.7 / 74.1 *n.s.*	78.2 / 58.4 n.s	86.0 / 22.3 ***	76.5 / 15.7 ***	83.0 / 29.5 ***

We explored whether rabbit or partridge abundance and their annual growth rate between 1998 and 1999 were associated to any management strategies. We found that only high rabbit abundance was significantly associated to the use of predator control, and prevention of diseases and parasites (G^2 = 7.27, P =0.007 , and G^2 = 4.47, P = 0.035 respectively). The resulting most simple model with no significant differences with the observed data, was formed by the associations: habitat management and predator control, predator control and hunting reduction, prevention of diseases and parasites and rabbit translocations, rabbit and partridge translocations, and rabbit abundance and predator control (X^2 = 102.6, P = 0.79, d.f.= 115). Neither partridge abundance, nor rabbit and partridge annual growth rate appeared in the model.

We found significant differences in the use of the nine types of management strategy and in the historical changes in their use, but not in their interactions (Table 3, A). Differences are displayed in Figure 2, in which we show the frequency of use of each management strategy during different historical periods (between the use in the 1970s, the 1990s, and the current use as at 1998). The nine management strategies exhibit different patterns of use. In general, the most frequently used strategies are related to the improvement of habitat, such as pasture and scrub management, and to water and food supplies. The control of predators occupies a middle position, and the less-used strategies are those related to the prevention of diseases and parasites, such as vaccination, deparasitation, and the supply of medication.

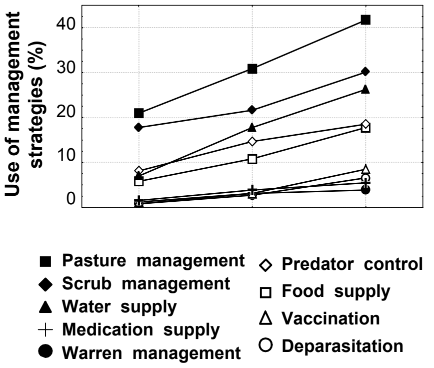

Figure 2. Frequency of use of management strategies during three historical periods.

The overall use of all management strategies has increased from the 1970s to the present day. Although differences in the interactions between historical changes and type of management are not significant, the use of some strategies has increased more than others. We can distinguish between more modern management techniques, such as the strategies related to the prevention of diseases and parasites and the supply of food and water, which have increased since the 1970s, and more traditional management techniques such as scrub management, pasture management, and predator control that are as common today as they were in the 1970s.

In Table 3 (B, C) we show the results on the influence of the levels of abundance of rabbit and partridge (low or high) on the differences in the use of different types of management strategy (habitat, predator control, or prevention of diseases and parasites) and in historical period (currently and 10 years ago). Results for both species confirm previous results showing statistical differences in the use of management strategies between historical periods, with management strategies more common today than 10 years ago. We also confirm previous results showing significant differences in the use of different types of management strategy, with habitat management and predator control strategies being more common than the prevention of diseases and parasites. The use of management strategies is greater in areas where rabbit or partridge abundance is higher. Interactions between rabbit and partridge abundance and historical periods or types of management strategy, and between the latter two, were not significant. We found that the goodness-of-fit statistics of both models did not exhibit overdispersion.

Table 3. Generalised linear model (binomial error and logit link function) to test for differences between (A) the use of nine small-game management strategies*, historical changes in their use**, and the interaction between both factors; (B) the use of groups of management strategies, historical periods, and rabbit abundance; and (C) the use of groups of management strategies, historical periods, and red-legged partridge abundance.

A	Wald stat.	*df*	*P*
Intercept	1537.31	1	<0.001
Type of management strategy	78.85	8	<0.001
Historical period	383.26	2	<0.001
Interaction	16.18	16	0.44
B	Wald stat.	*df*	*P*
Intercept	595.97	1	<0.001
1. Rabbit abundance	31.09	1	<0.001
2. Type of management strategy	123.34	2	<0.001
3. Historical period	31.32	1	<0.001
1*2	3.38	2	0.18
1*3	0.01	1	0.91
2*3	2.40	2	0.30
C	Wald stat.	*df*	*P*
Intercept	225.80	1	<0.001
1. Partridge abundance	17.47	1	0.003
2. Type of management strategy	45.33	2	<0.001
3. Historical period	8.92	1	<0.001
1*2	3.91	2	0.14
1*3	0.94	1	0.33
2*3	0.79	2	0.67

* For more details, see Table 1.
** Use of management strategies in 1970s, 1990s, and 1998.

To test whether small game species were being managed because their populations were declining or because their high abundance brings economic benefits, we performed two ANOVA tests, one for each species. We looked for mean differences in the expenditure on management strategies with two levels of abundance (low and high) and three trends in each

Table 4. Analysis of variance of the expenditure on rabbit and red-legged partridge management for different trends in their populations and for different rabbit and partridge abundances. Independent variables obtained through interviews.

	Rabbit management			Partridge management		
	F	d*f*	*P*	*F*	d*f*	*P*
Population trend	2.78	1	0.064	3.82	1	0.023
Population abundance	5.86	2	0.016	12.51	2	<0.001
Interaction	1.57	2	0.21	0.91	2	0.40

	Rabbit management			Partridge management		
Population abundance	Mean	SD	Tukey testψ	Mean	SD	Tukey testψ
Low	3449.78	5498.16	a	2866.89	4568.90	a
High	6523.37	6805.45	b	4544.53	5564.32	b

	Partridge management		
Population trend	Mean	SD	Tukey testψ
No change	2771.54	4303.50	a
Increase	4648.10	5381.79	ab
Decrease	4288.31	5691.67	b

species (no change, and increase or decrease during the past 10 years). There were significant differences in both species when considering the level of abundance, and in the case of red-legged partridges also when considering the population trend (Table 4). We did not find a significant interaction between the two factors, neither in rabbits nor in partridges. Using the Tukey HSD test to explore these differences, we found that the expenditure was higher in areas with a higher rabbit or partridge abundance. We also found that the expenditure was higher when partridge populations were declining than when populations had not changed (Table 4). The relationships between variables are displayed in Figure 3. The mean expenditures on managing small game in southern Spain during the 1998–1999 hunting season were 6880 and 8800 euros for partridge and rabbit, respectively. These amounts were lower when calculated for the strategies more frequently applied in each area, at 3800 and 4500 euros, respectively.

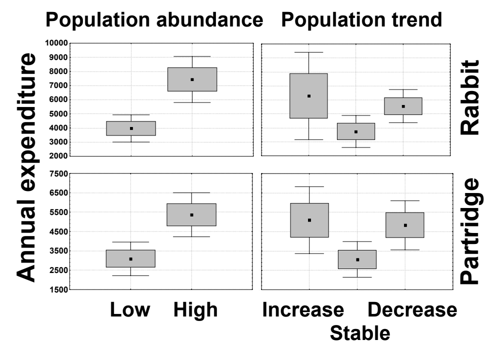

Figure 3. Annual expenses of small-game management for different levels of population abundance and for different trends in their populations. Central black square is the mean, the box limits indicate SE, and vertical lines indicate 1.96×SE.

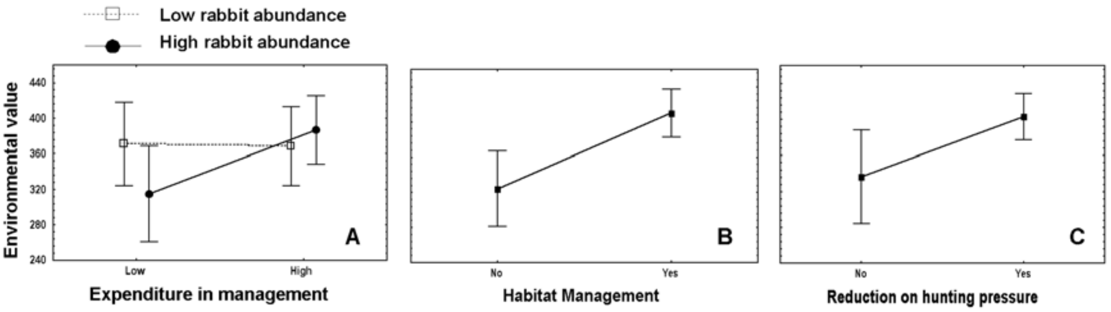

Figure 4. Relationship between the mean environmental value with: (A) High and low rabbit abundance and when expenditure are high or low. Categories of rabbit abundance: low, ≤ –0.3; high, > –0.3. Expenditure categories: ≤1000 or >1000. (B) Habitat management (C) Hunting reduction.

To test the possible effects of small-game management strategies on environmental conservation, we related the environmental value of each area to the intensity of management using a generalised linear model, in which we tested the effects of rabbit and partridge abundances and the use of each group of management strategies (habitat management, predator control, prevention of diseases and parasites, reduction of hunting, and translocations). Rabbit abundance and its interaction with the intensity of management were related to the environmental value of an area (Figure 4), while the relationship with the intensity of management was marginally significant (Table 5). In relation to the management strategies applied in the area, only habitat management and reduction of hunting were related to the environmental value of an area (Figure 4). The environmental value was higher in areas where habitat management or reduction of hunting were applied.

Table 5. Generalised linear model of the factors affecting environmental value of an area: rabbit and partridge abundance, intensity of management, and the use of different management strategies.

Variables	Parameter	SE	F	df	P
Intercept	294.30	21.51	187.26	1	<0.001
1. Rabbit abundance	–35.45	17.10	4.30	1	0.04
2. Partridge abundance	3.16	2.80	1.27	1	0.26
3. Expenditure on management	0.004	0.002	3.70	1	0.05
1*3	0.006	0.002	5.50	1	0.02
2*3	–0.0003	0.0002	1.33	1	0.24
Habitat management	–50.67	12.20	17.24	1	<0.001
Predator control	17.99	12.13	2.19	1	0.14
Prevention of diseases/parasites	20.29	16.84	1.45	1	0.23
Hunting reduction	–37.53	12.22	9.42	1	0.002
Translocations	–6.25	13.75	0.21	1	0.65

DISCUSSION

Towards the end of the 20th century there was a decline in the range and numbers of wild rabbits and red-legged partridges, to the extent that they required intensive management. In this paper, we have shown that in 85% of the areas surveyed in southern Spain, game management has focused on rabbits or partridges. Both species were favoured through management strategies in 95% of the areas during the 1998–1999 hunting season. We have calculated that the annual mean expenditure on managing small game in an area of 2000 ha ranged between 4500 and 8800 euros, with the maximum reaching 33500 euros. Management is applied more intensely through strategies related to habitat management, reduction of hunting pressure, and control of predators than through those related to translocations and the prevention of diseases and parasites. These strategy preferences could be attributed to the former strategies being easier and cheaper to apply. The intensity of management has increased in recent decades, showing that both hunters and landowners are aware of the decline of both species. It is interesting to note that the prevention of diseases and parasites has experienced a large increase in recent decades, showing that managers perceive diseases as one of the main causes of the decline of small-game populations.

Multiple strategies were the most frequently management situation in southern Spain during the 1998-1999 hunting season, been most strategies significantly associated to a second management. Associations of pairs of variables were not symmetrical been frequent that the management strategies less used were mostly associated to the management strategies more used. The observed data fitted significantly to the combination of associations: translocations of rabbit and partridges were usually applied in the same areas; predator control was usually associated to habitat management and to reduction in hunting; rabbit translocations were associated to prevention of diseases and parasites; and high rabbit abundance to the use of predator control. We have showed that in general, intensity of management was related to high rabbit and partridge abundance areas. The association we found between high rabbit abundance and the use of individual strategies, can not be considered as a causality relationship but simply that when rabbit abundance is high these management strategies are more used than when rabbit abundance is low.

Rabbits and partridges are important game species, and are also the main prey species in Mediterranean ecosystems. Thus, if we are to conserve Mediterranean biodiversity, the declines in rabbit and partridge numbers must be arrested and measures put in place to increase their abundances to past levels. For this reason it is important to consider the high intensity of management carried out by hunters or landowners, focusing especially on these species. The efficiency of this management should be fully evaluated. The effectiveness of most management strategies has already been evaluated by other authors (Newsome et al. 1989; Trout y Tittensor 1989; Trout et al. 1992; Moreno & Villafuerte 1995, Calvete et al. 1997; Gortázar et al. 2000). These studies covered monitoring over an extended period during which the management strategy evaluated was maintained. We have shown in this paper that increases or decreases on rabbit and partridge numbers between 1998 and 1999 are not associated to any applied management strategy. The lack of associations could be explained because we have only analysed the annual growth rate over 1 year and the effects may be only detectable over a more extended period. However, management strategies used in each area can change each year (depending on the hunter or manager agreements which are normally based on their perception of small-game populations), been difficult to assess management effects over a more extended period. As stated by Strickland et al. (1996), management goals should be implemented through the development of specific management objectives than have to be established for a period of several years, in order that effectiveness can be measurable. Moreover, these same authors do not recommend changing objectives based on year-to-year fluctuations in estimates of population numbers or establishing objectives for subpopulations. The same recommendations should be applied when managing for hunting purposes or for wildlife conservation.

We have shown that the level of wildlife conservation in an area is related to the use of habitat management and the reduction of hunting pressure. Habitat management has previously been shown to successfully increase small-game populations (Moreno & Villafuerte, 1995; Blanco-Aguiar et al. 2001). The level of conservation in an area was also related to the interaction between rabbit abundance and the intensity of management. This relationship shows that in areas where rabbit abundance is high, the level of conservation is higher only when there is also a high expenditure on management. This suggests the corollary that when rabbit abundance is high but the intensity of management is low, the conservation level of the area is low, and even lower than in areas with lower rabbit abundance. The reduction of hunting pressure and habitat management are the two management strategies commonly used by hunters and landowners, with the latter used also by environmental agencies when the main goal is the conservation of habitat and species. Our results suggest that habitat management for small game favours the conservation of all wildlife. Habitat suitability is essential for the conservation of endangered predators in Mediterranean ecosystems (Ferrer & Harte, 1997; Palma et al.1999), and habitat management and reduction of hunting have been suggested as measures for enhancing predator numbers (Castro & Palma, 1996; Real & Mañosa 1997).

The annual growth rates of rabbit and partridge populations are dependent on the level of abundance of each population, with the population growth rate being higher when the abundance is higher. This result is very important when trying to improve areas with a low abundance of rabbits or partridges, because management in such areas is expected to produce a lower population increase than is achieved by management in areas with a high abundance. Moreno and Villafuerte (1995) arrived at the same conclusion when studying the effectiveness of scrub and pasture management on the improvement of wild-rabbit populations.

This result leads to the conclusion that conservation should be applied more in areas of low rabbit and partridge abundance. We have shown that low-abundance areas are less favoured by hunting managers. Hunters are more interested in spending money when the abundance of small game is high and thus hunting is more likely to produce a higher financial return and satisfaction. However, we have also shown in this paper that hunters and landowners applied more intensive management when partridge populations were declining than when they were stable. This relation was not seen in the case of wild rabbit. Thus, when planning the conservation of rabbit and partridge populations in a large territory, such as nationally, a trade-off appears: on the one hand, high-abundance populations could be enhanced with an expected high improvement, but these areas are more managed by hunters and landowners; while on the other hand, low-abundance populations could be enhanced with a lower expected improvement, and these are less managed by hunters and landowners. Low-abundance areas are normally at the edges of the species distribution and hence are of higher interest for conservation purposes.

MANAGEMENT IMPLICATIONS

Small-game management is initiated to improve rabbit and red-legged partridge populations, but a by-product of their management is an effect on wildlife conservation. Small-game management may have a role to play in wildlife conservation, but this role requires qualification. The need to evaluate the long-term benefits of small-game management to wildlife conservation should continue to be the focus of political and scientific studies. In our study the level of conservation in an area is dependent on the rabbit or partridge abundance (the most important prey species in Mediterranean ecosystems), and on the intensity of management; in addition, the level of conservation is related to the application of habitat management or reduction of hunting pressure.

Where small game numbers are too low to make hunting and management economically viable, integrated programs should be implemented to enhance the numbers of these species and the economic cost of such programs should be included in conservation goals . Alternatively, where small-game management is economic, because the abundance of small-game species is higher, wildlife conservation might best be achieved by hunters and landowners through a guided management plan. Efforts should be made to maintain small game management in areas with large rabbit and partridge populations, and to enhance and guide small-game management in areas with low population densities. In this sense, hunters, managers, conservation agencies and policy makers should favour the development of specific management goals, that should be based on the application during several years of the specific strategies, in order to assess effectiveness of management through monitoring along the management period.

The management plans of hunters and landowners should be guided and improved with the optimisations resulting from scientific evaluations of management plans. Understanding the effectiveness of small-game management in improving their populations and in conserving wildlife biodiversity is of critical importance to policy and funding decisions. Much of the existing Mediterranean biodiversity is unlikely to survive without effective strategies for small-game management.

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NOTE:

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FACTORS INFLUENCING LENGTH OF THE POST-FLEDGING PERIOD AND TIMING OF DISPERSAL IN BONELLI'S EAGLE (*HIERAAETUS FASCIATUS*) IN SOUTHWESTERN SPAIN

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ABSTRACT.—We studied factors influencing the length of the post-fledging period (from fledging to the start of dispersal) of Bonelli's Eagle (*Hieraaetus fasciatus*) nestlings in southwestern Spain, using 13 nestlings equipped with radiotransmitters. The age at fledging was negatively correlated with hatching date, but the duration of the post-fledging period was directly related to hatching date. This pattern could be explained by seasonal changes in prey abundance, especially that of wild rabbits (*Oryctolagus cuniculus*). Young increased their mobility throughout the post-fledging period, with a significant increase in the middle of the period. Dispersal began suddenly. The direction of dispersal was random, but most of the areas first used were located <25 km away and at lower altitudes than the nesting area.

KEY WORDS: *Bonelli's Eagle;* Hieraaetus fasciatus; *juvenile dispersal behavior; post-fledging period; Red-legged partridge; wild rabbits;* Oryctolagus cuniculus; Alectoris rufa.

Factores que influyen en el período de post-emplumamiento y el comienzo de la dispersión en jóvenes águilas perdiceras *Hieraaetus fasciatus.*

RESÚMEN.—Estudiamos los factores que influyen en la duración del período de post-emplumamiento, período comprendido entre el primer vuelo del joven hasta el comienzo de la dispersión, del águila perdicera (*Hieraaetus fasciatus*) en el sudoeste de España, mediante el radio-seguimiento de 13 águilas jóvenes. Pese a que hubo una correlación negativa entre la fecha de eclosión y la duración del período de emplumamiento, la duración del período de post-emplumamiento estuvo relacionada directamente con la fecha de eclosión. Este patrón podría ser explicado por los cambios estacionales en la abundancia de presas, especialmente de conejo silvestre (*Oryctolagus cuniculus*). Las jóvenes águilas fueron aumentando su movilidad a lo largo del período de post-emplumamiento, con un incremento drástico hacia la mitad de este período. El comienzo de la dispersión fue repentino. La dirección en la que ocurrió la dispersión fue al azar, pero la mayoría de las áreas utilizadas por vez primera estaban situadas a <25 km y a menores altitudes que las áreas de nidificación.

[Traducción de autores]

In most birds, young are dependent on their parents for some time after leaving the nest. For birds of prey, young usually stay within the natal territory until initiation of juvenile dispersal. Waser (1985) suggested that later dispersing individuals would probably have less competitive abilities. However, the length of the period from fledging to the start of dispersal, referred to as post-fledging period, and factors that influence the onset of dispersal vary considerably (Donázar and Ceballos 1990, Ferrer 1992, Bustamante and Hiraldo 1993).

The length of the post-fledging period might be

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influenced by food availability, be a result of parent-offspring conflict (Trivers 1974), or a decision made by the young themselves. When food is abundant, young may stay longer within the natal territory (Walker 1988, Kennedy and Ward 1995) but, when food is scarce, they may leave earlier (Kenward et al. 1993). Some studies have suggested that when there is abundant food in the territory, young reach dispersal or migration condition sooner and, therefore, leave the natal territory earlier (Bustamante 1994a, Wood et al. 1998).

Factors influencing the timing of dispersal may be either environmental, endogenous, or a combination of both (Howard 1960). Young develop their flying and hunting skills prior to independence (Ferrer 1992, Real et al. 1998) and the endogenous component is reflected in increased exploratory behavior near the time of dispersal (Holekamp 1986).

Here, we evaluate the factors affecting the length of the post-fledging period in the Bonelli's Eagle, especially the influence of food availability, and describe the first movements involved in juvenile dispersal. For Bonelli's Eagles, an Endangered Species (Tucker and Heath 1994), this information is limited to two studies conducted by Morvan and Dobchies (1990) and Real et al. (1998). In order to discriminate whether young Bonelli's Eagles leave the parental territory as soon as possible or whether environmental factors determine the length of the post-fledging period, we related territory quality and temporal food availability with movement patterns of young. If individuals that disperse sooner have greater competitive abilities (Waser 1985), and environmental factors were not involved, we expected that young that fledged later or with good physical condition had a shorter post-fledging period. Likewise, young with good physical condition would move farther from nests at the end of the post-fledging period.

STUDY AREA AND METHODS

We conducted the study in the provinces of Huelva, Cádiz, Málaga, and Sevilla, in southwestern Spain (Fig. 1). The study area is very heterogeneous comprising mountains, lowlands, and plains. The more mountainous areas supported Mediterranean woodlands and scrublands, while agricultural fields were prevalent in the lowlands.

We studied the post-fledging period of Bonelli's Eagle, from fledging to start of dispersion. We analyzed the length of the post-fledging period in relation to food availability, body condition, hatching date, and fledging duration.

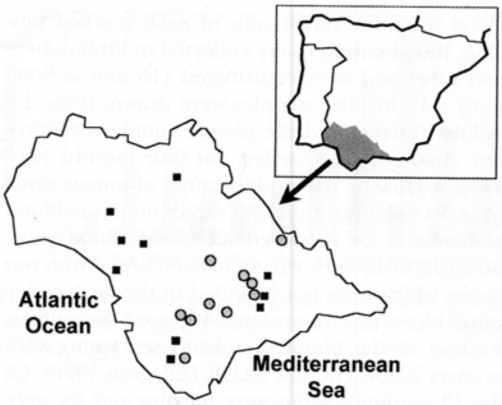


Figure 1. Study area in southwestern Spain, 1998. Grey circles represent territories of Bonelli's Eagles and black squares are the sites of prey availability counts.

During early February 1998, we searched known Bonelli's Eagle territories for accessible nests occupied by incubating adults. All nests were situated on cliffs, usually surrounded by Mediterranean woodlands (*Quercus ilex* and *Quercus suber*). The landscape in breeding areas was a mosaic of cleared woods, Mediterranean scrublands, and olive orchards. After egg laying, nests were checked every 10–20 d to estimate hatching dates. We estimated age of young based on morphometric measurements (Torres et al. 1981). In May–June 1998, when nestlings were 40–50 d old, we instrumented 14 young from 10 broods with solar ($N = 8$) and battery-powered ($N = 6$) transmitters, attached with backpack harness (Kenward 1987). One solar transmitter failed after the young eagle was released and was excluded from the analysis. Five unmarked siblings (three from a brood of two and two from a brood of three) flew from their nests during capture and were observed flying with their marked sibling during the post-fledging period.

When radio-tagging birds (on average 12 d before fledging, range = 1–22 d), measurements and blood extraction were performed to estimate body condition. We assessed body condition as the residuals of a linear regression of body mass against forewing length (Reist 1985, Krebs and Singleton 1993, Jacob et al. 1996). We used the concentration of urea in the blood to evaluate nutritional condition (Ferrer 1990, 1993) by extracting 2 ml of

blood from the radial vein of each marked nestling. Blood samples were collected in lithium-heparin tubes and were centrifuged (15 min at 3000 rpm) <12 hr after samples were drawn. Both the cellular fraction and the plasma samples were frozen. Analyses were carried out four months later using a Hitachi 705 multichannel automatic analyzer. To minimize circadian variations of the blood parameters, we extracted all blood samples between 1300–1800 H, except for one brood with two young which were not included in the analysis because blood was drawn later. We used the cellular fraction of the blood sample to sex young with primers 2945F, cfR and 3224R (Ellegren 1996). Of the 13 nestlings, seven were females and six were males. Therefore, our results were not biased by sex.

We considered marked young to have fledged if they were observed flying or seen on a perch inaccessible from the nest. We searched for young in natal territories once every week using two vehicles equipped with roof-mounted, omnidirectional antennae to detect young and directional antennae to triangulate their location. Although the estimated territory size of Bonelli's Eagles in our study area averaged 3 km around nests (del Junco 1984, Gil et al. 1996, Mínguez unpubl. data), we considered young to have left their natal territories only when they roosted >4.5 km from their nests. This was the greatest distance we recorded young roosting and returning to nests a few days later. Dates of fledging and initiation of dispersal were considered as the middle of the interval between two visits. Because visits were made once a week, we assumed an error of ±4 d.

To determine if seasonal changes of prey availability could affect fledging date and length of post-fledging period, we used data from a study on European rabbits (*Oryctolagus cuniculus*) and Red-legged Partridges (*Alectoris rufa*), the main prey of Bonelli's Eagles (Real 1996, Ontiveros and Pleguezuelos 2000). From January–November 1998, we conducted monthly surveys of rabbits and partridges in six different sites (Fig. 1). Vehicle surveys were conducted along permanent roadside transects (10–14 km long) 1 hr before dusk at 10 km/hr (Villafuerte et al. 1993). Monthly indexes of rabbit and partridge abundance were computed for the entire study area as the mean number of rabbits and partridges seen per kilometer in each area. Prey abundance for each young eagle was considered as the mean of the monthly index of prey abundance for the months of the fledging or post-fledging period. Thus, an average of rabbit and partridge abundance for the months during which fledging or post-fledging occurred corresponded to each young. Although these surveyed sites were not within Bonelli's Eagle territories, we related the post-fledging period with an average of prey abundance of all the surveyed sites, thus representing the general seasonal pattern of prey availability throughout the study area.

For the analyses, we used mean values of the length of fledging and post-fledging period for each brood, except for analyses regarding dispersal movements, when we considered young as independent observations. Because sample sizes were small, we used nonparametric tests (Norusis 1992). Spearman correlation coefficients were used to test the relationship between the length of fledging and post-fledging period with the different factors considered in the study (body condition, hatching date, fledging duration, and prey abundance) and to test the relationship between body condition and dispersal distance. We used comparisons between means for circular statistics to analyze the direction of dispersal from nests to the first known roosts, as defined by Batschelet (1981, cited in Upton and Fingleton 1989). We analyzed differences in the distance moved throughout the post-fledging period (dividing this period in groups of 20 d) with Levene's test for equality of variances, Wilcoxon paired tests and Friedman tests. Statistics were conducted using SPSS software.

RESULTS

Post-fledging Period. Young fledged between 15 May–22 June ($\bar{x} = 27$ May) and were between 44–69 d old at fledging ($\bar{x} = 59 \pm 8.2$ d, ±SD, $N = 10$). The post-fledging period ranged between 43–131 d ($\bar{x} = 90 \pm 23.4$, $N = 10$). Age at fledging correlated negatively with hatching date ($r_s = -0.65$, $P = 0.04$, $N = 10$). However, length of the post-fledging period correlated positively with hatching and fledging dates ($r_s = 0.75$, $P = 0.01$, $N = 10$ and $r_s = 0.79$, $P = 0.006$, $N = 10$, respectively). No statistically significant relationship was found between age of fledging and availability of prey ($r_s = -0.15$, $P = 0.67$, $N = 10$ and $r_s = 0.15$, $P = 0.67$, $N = 10$, for rabbits and Red-legged Partridges, respectively). Length of the post-fledging period correlated negatively with seasonal rabbit abundance and positively with seasonal partridge abundance (Fig. 2). During the year of the study,

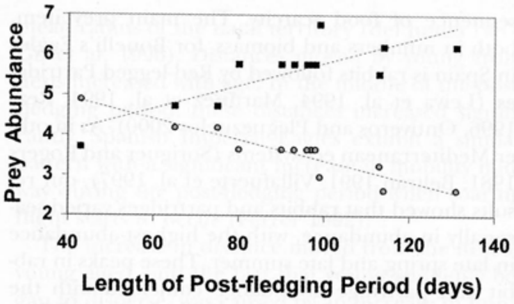


Figure 2. Relationship between prey abundance index (average of monthly prey abundance for the months of the post-fledging period) and length of post-fledging period of Bonelli's Eagles (number of days from fledging to the day that young roosted >4.5 km from the nest) in southwestern Spain, 1998. Grey circles represent rabbit abundance ($r = -0.93$, $P < 0.001$, $N = 13$) while black squares represent partridge abundance ($r = 0.76$, $P = 0.003$, $N = 13$).

rabbit abundance reached its highest level in June and July and declined thereafter, while partridge abundance reached its highest level in late summer. Peaks for maximum and minimum prey availability were in the same months throughout the study area, although the level of abundance was different in each surveyed site (Fig. 3). This strongly suggested that all of the study area had similar patterns of prey availability.

Neither urea concentration in the blood nor size corrected by body mass before fledging, showed a correlation with the length of the post-fledging period (Spearman correlation, $r_s = -0.15$, $P = 0.65$, $N = 11$ and $r_s = -0.04$, $P = 0.89$, $N = 13$, respectively).

During the post-fledging period, movements of young increased until about 80 d after fledging (Fig. 4, Levene's test for equality of variances, $F = 6.6$, $P = 0.001$). The development of mobility increased throughout the post-fledging period (Friedman test, $\chi^2_4 = 14.84$, $P = 0.005$, $N = 5$). Mean distance young moved from their nests increased significantly at about the middle of the post-fledging period (Wilcoxon paired test, 40 vs. 60 d after fledging, $Z = -2.20$, $P = 0.028$, $N = 8$). Distance moved increased gradually prior to the middle of the post-fledging period (Wilcoxon paired test, 20 vs. 40 d after fledging, $Z = -1.63$, $P = 0.10$, $N = 10$) and remained the same thereafter (Friedman test, comparing groups 60, 80, and 100 d after fledging $\chi^2_2 = 1.14$, $P = 0.56$, $N = 7$).

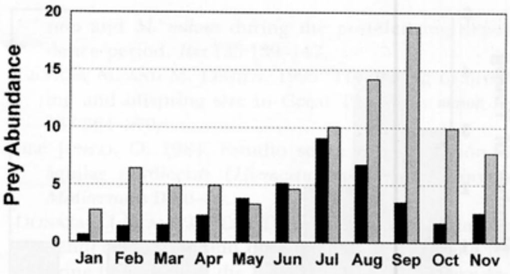


Figure 3. Monthly prey abundance of rabbits (black bars) and Red-legged Partridges (grey bars) for the six sites surveyed during the post-fledging period.

The Onset of Dispersal. All 13 instrumented young survived the post-fledging period, and the onset of dispersal occurred from 27 June–2 October ($\bar{x}$ = 21 August ± 25 d). Young from broods of two young ($N = 3$) did not start dispersal at the same time but with a delay of 16, 16, and 38 d between siblings.

The distance from the nest to the first-known roost site outside the territory averaged 33 km ± 25.7 ($N = 13$). However, the sample differed from a normal distribution and the median distance was 23.8 km (Fig. 5). Distance to the first-known roost outside the territory was not related to condition of young (urea levels or size corrected by body mass; Spearman correlation, $r_s = -0.07$, $P = 0.85$,

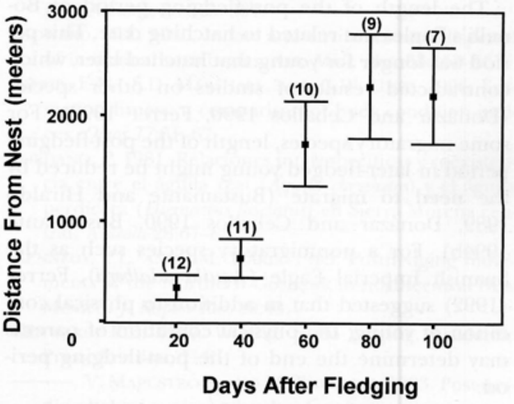


Figure 4. Mean distances to nest (±SE) moved by young Bonelli's Eagles by age during the post-fledging period in southwestern Spain, 1998. Data obtained by direct observations and short distance triangulations. Number of fledglings in parentheses. Sample sizes decrease by days as young started dispersal.

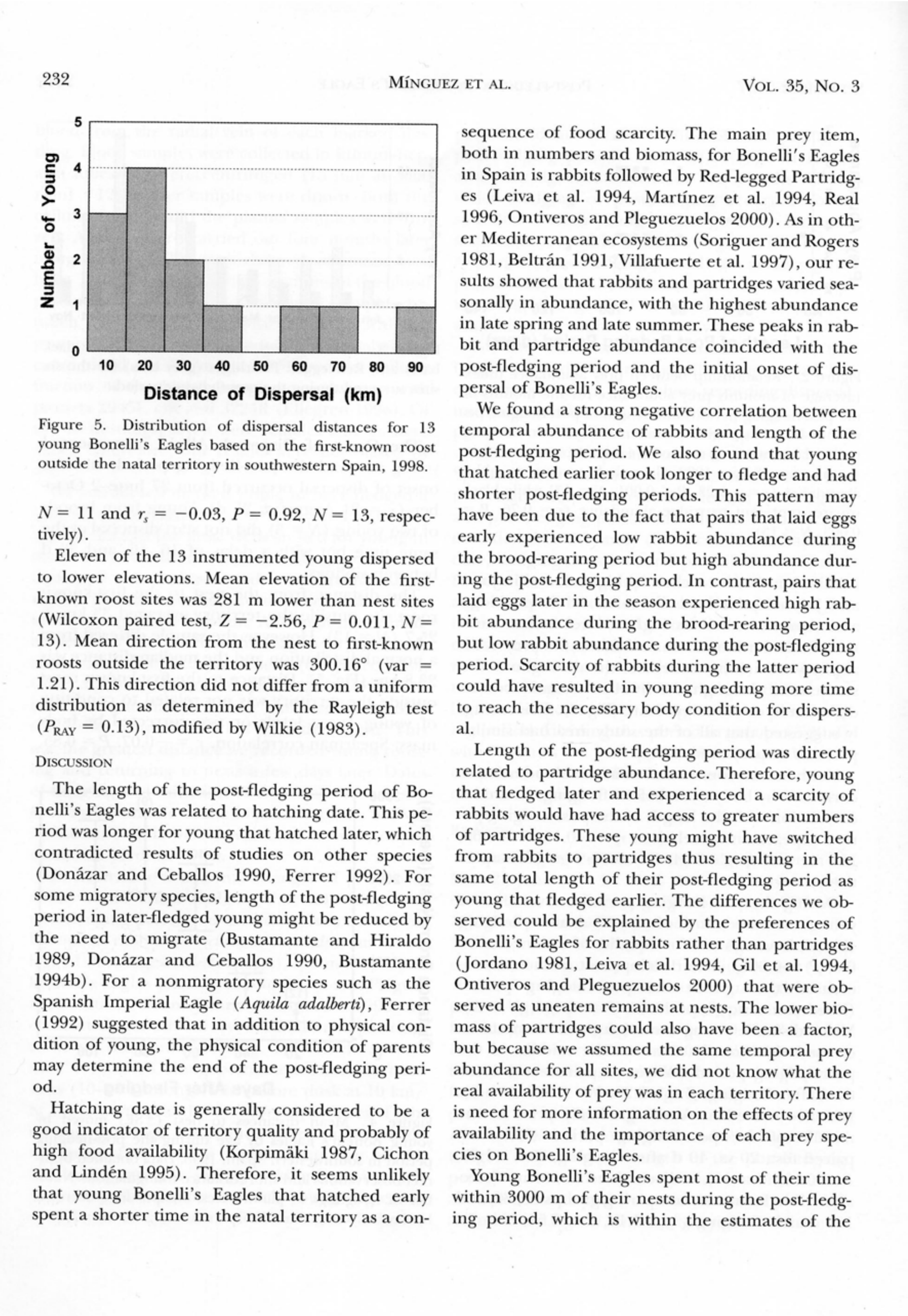


Figure 5. Distribution of dispersal distances for 13 young Bonelli's Eagles based on the first-known roost outside the natal territory in southwestern Spain, 1998.

$N = 11$ and $r_s = -0.03$, $P = 0.92$, $N = 13$, respectively).

Eleven of the 13 instrumented young dispersed to lower elevations. Mean elevation of the first-known roost sites was 281 m lower than nest sites (Wilcoxon paired test, $Z = -2.56$, $P = 0.011$, $N = 13$). Mean direction from the nest to first-known roosts outside the territory was 300.16° (var = 1.21). This direction did not differ from a uniform distribution as determined by the Rayleigh test ($P_{RAY} = 0.13$), modified by Wilkie (1983).

DISCUSSION

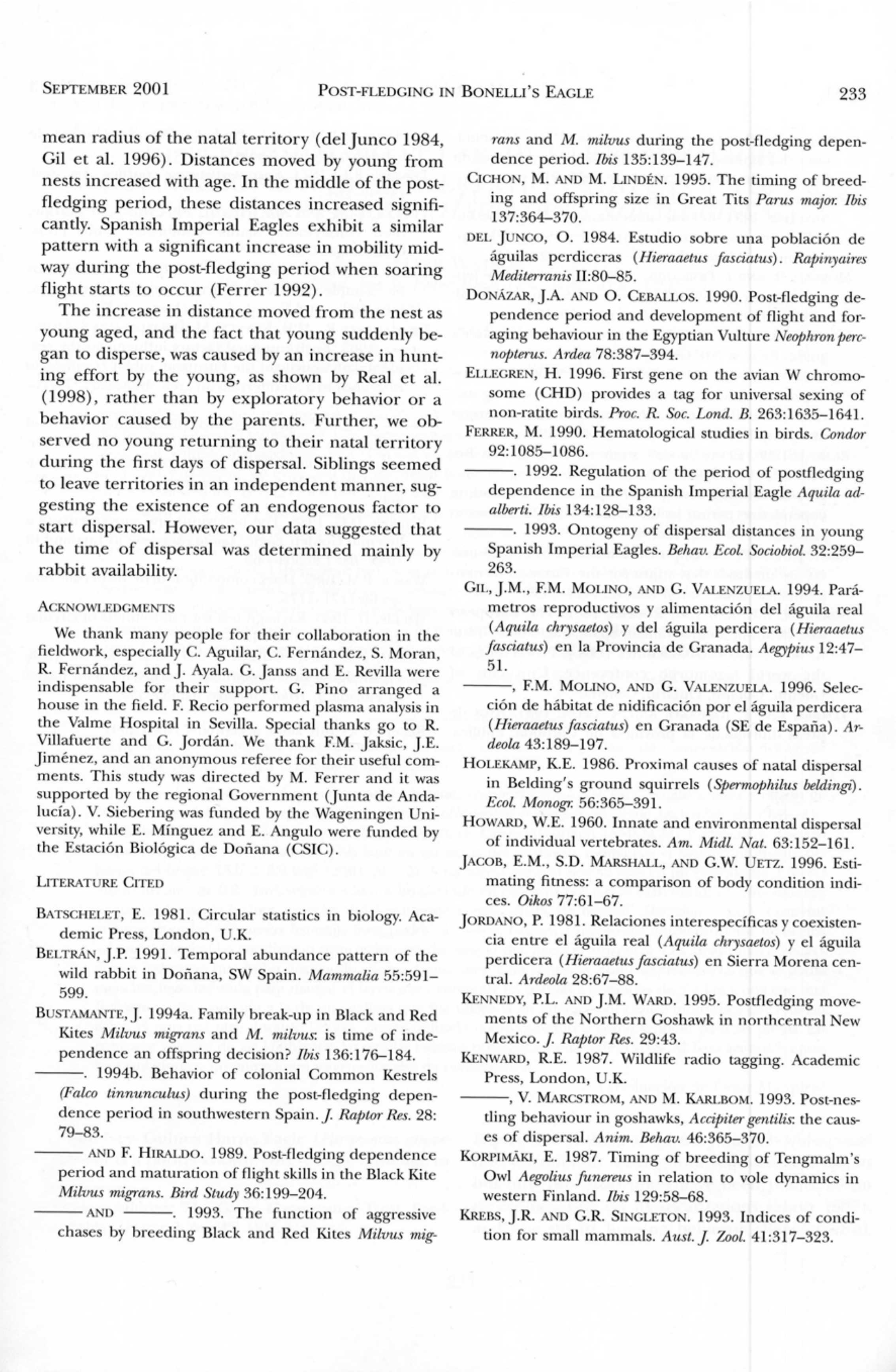
The length of the post-fledging period of Bonelli's Eagles was related to hatching date. This period was longer for young that hatched later, which contradicted results of studies on other species (Donázar and Ceballos 1990, Ferrer 1992). For some migratory species, length of the post-fledging period in later-fledged young might be reduced by the need to migrate (Bustamante and Hiraldo 1989, Donázar and Ceballos 1990, Bustamante 1994b). For a nonmigratory species such as the Spanish Imperial Eagle (*Aquila adalberti*), Ferrer (1992) suggested that in addition to physical condition of young, the physical condition of parents may determine the end of the post-fledging period.

Hatching date is generally considered to be a good indicator of territory quality and probably of high food availability (Korpimäki 1987, Cichon and Lindén 1995). Therefore, it seems unlikely that young Bonelli's Eagles that hatched early spent a shorter time in the natal territory as a consequence of food scarcity. The main prey item, both in numbers and biomass, for Bonelli's Eagles in Spain is rabbits followed by Red-legged Partridges (Leiva et al. 1994, Martínez et al. 1994, Real 1996, Ontiveros and Pleguezuelos 2000). As in other Mediterranean ecosystems (Soriguer and Rogers 1981, Beltrán 1991, Villafuerte et al. 1997), our results showed that rabbits and partridges varied seasonally in abundance, with the highest abundance in late spring and late summer. These peaks in rabbit and partridge abundance coincided with the post-fledging period and the initial onset of dispersal of Bonelli's Eagles.

We found a strong negative correlation between temporal abundance of rabbits and length of the post-fledging period. We also found that young that hatched earlier took longer to fledge and had shorter post-fledging periods. This pattern may have been due to the fact that pairs that laid eggs early experienced low rabbit abundance during the brood-rearing period but high abundance during the post-fledging period. In contrast, pairs that laid eggs later in the season experienced high rabbit abundance during the brood-rearing period, but low rabbit abundance during the post-fledging period. Scarcity of rabbits during the latter period could have resulted in young needing more time to reach the necessary body condition for dispersal.

Length of the post-fledging period was directly related to partridge abundance. Therefore, young that fledged later and experienced a scarcity of rabbits would have had access to greater numbers of partridges. These young might have switched from rabbits to partridges thus resulting in the same total length of their post-fledging period as young that fledged earlier. The differences we observed could be explained by the preferences of Bonelli's Eagles for rabbits rather than partridges (Jordano 1981, Leiva et al. 1994, Gil et al. 1994, Ontiveros and Pleguezuelos 2000) that were observed as uneaten remains at nests. The lower biomass of partridges could also have been a factor, but because we assumed the same temporal prey abundance for all sites, we did not know what the real availability of prey was in each territory. There is need for more information on the effects of prey availability and the importance of each prey species on Bonelli's Eagles.

Young Bonelli's Eagles spent most of their time within 3000 m of their nests during the post-fledging period, which is within the estimates of the



mean radius of the natal territory (del Junco 1984, Gil et al. 1996). Distances moved by young from nests increased with age. In the middle of the post-fledging period, these distances increased significantly. Spanish Imperial Eagles exhibit a similar pattern with a significant increase in mobility midway during the post-fledging period when soaring flight starts to occur (Ferrer 1992).

The increase in distance moved from the nest as young aged, and the fact that young suddenly began to disperse, was caused by an increase in hunting effort by the young, as shown by Real et al. (1998), rather than by exploratory behavior or a behavior caused by the parents. Further, we observed no young returning to their natal territory during the first days of dispersal. Siblings seemed to leave territories in an independent manner, suggesting the existence of an endogenous factor to start dispersal. However, our data suggested that the time of dispersal was determined mainly by rabbit availability.

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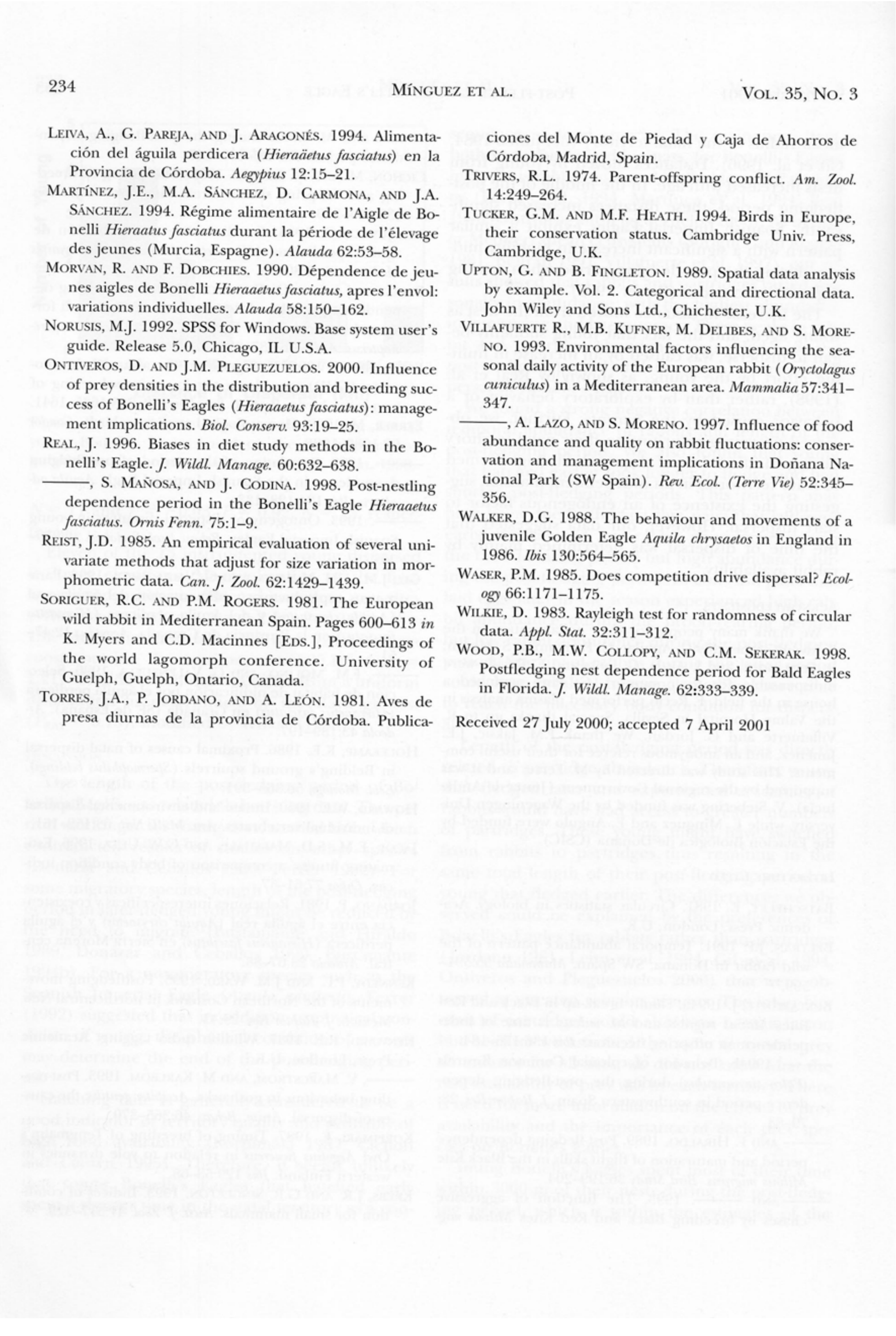

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ERRATUM

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FACTORS INFLUENCING LENGTH OF THE POST-FLEDGING PERIOD AND TIMING OF DISPERSAL IN BONELLI'S EAGLE (*HIERAAETUS FASCIATUS*) IN SOUTHWESTERN SPAIN

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Figures 1 and 3 printed in the article "Factors influencing length of the post-fledging period and timing of dispersal in Bonelli's Eagle (*Hieraaetus fasciatus*) in southwestern Spain," (*Journal of Raptor Research* 35[3]:228–234) were incorrect, draft versions. The correct, revised figures that correspond to this article and that should be substituted for Figure 1 (page 229) and Figure 3 (page 231) are printed below.

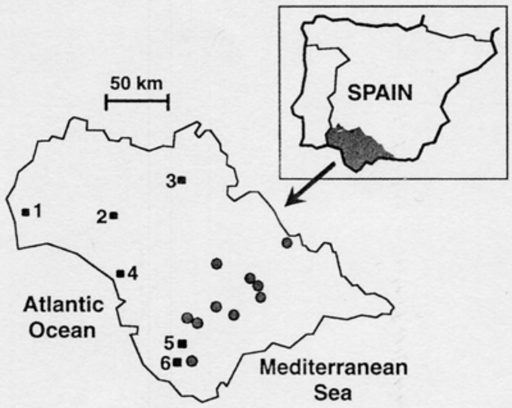

Figure 1. Study area in southwestern Spain, 1998. Grey circles represent the ten territories of Bonelli's Eagles, and numbered black squares are the six sites of prey availability counts.

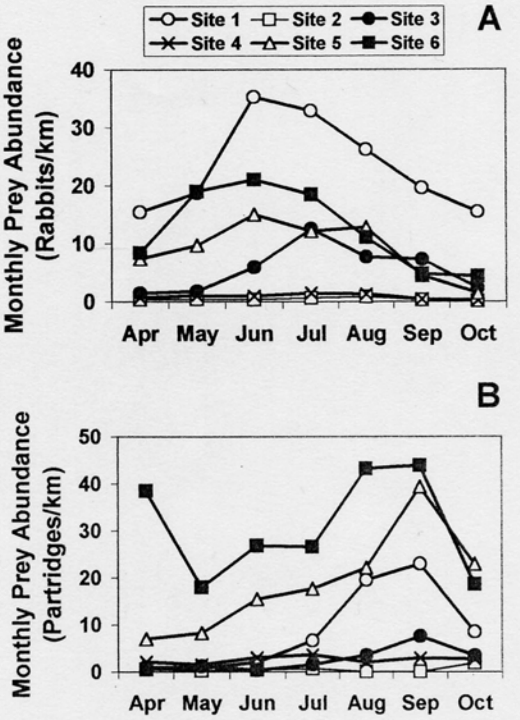

Figure 3. Monthly prey abundance for the six surveyed sites (see Fig. 1 for the geographic locations) during the post-fledging period. (a) European rabbit (*Oryctolagus cuniculus*) abundance. (b) Red-legged Partridge (*Alectoris rufa*) abundance.

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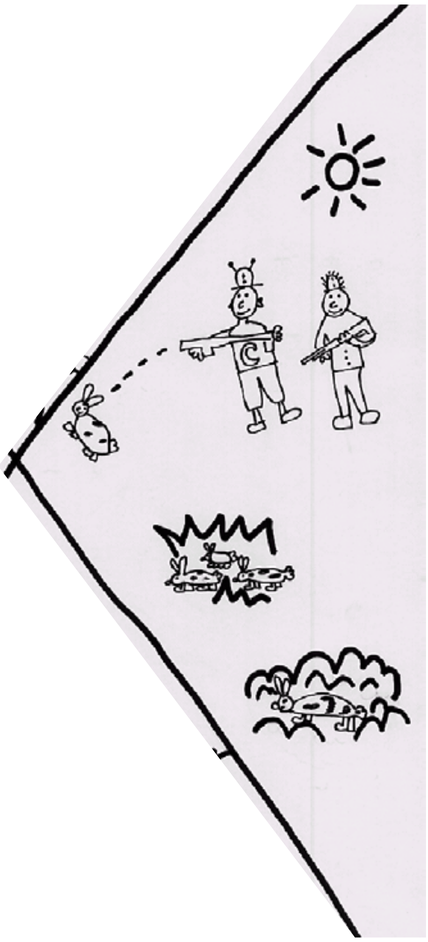

CAPÍTULO 3

Modelling hunting strategies for the conservation of wild rabbitt populations

Efecto de las estrategias de caza sobre las poblaciones de conejo

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Resumen

El conejo está considerado como una especie plaga en muchos lugares de su área de distribución. Incluso en su área de origen, el Sudoeste de Europa, la especie fue muy abundante, actuando la actividad cinegética como una medida de control autosostenible. Sin embargo, actualmente las poblaciones de conejo del Sudoeste de Europa están en declive, por lo que es necesario reconsiderar los efectos de la caza sobre sus poblaciones. Por un lado, es importante evaluar si la temporada de caza, que no ha cambiado durante todo el siglo XX, es adecuada para la conservación de las poblaciones de conejo. Por otro lado, también es necesario analizar cual es la presión cinegética que se aplica y sus efectos sobre estas poblaciones.

En este Capítulo se investigaron los efectos del período de caza sobre la conservación de las poblaciones de conejo, a través de un modelo matemático que simula su dinámica poblacional. Los parámetros utilizados en este modelo fueron recogidos por Rafael Villafuerte durante los años 1989 y 1990 y aparecen publicados en su tesis doctoral. La caza se incluyó en el modelo como una mortalidad aditiva, y se simularon diferentes escenarios de caza. Los escenarios se diferenciaban en la variación de las temporadas cinegéticas, de la presión cinegética y de las estrategias de caza (basadas en la edad de los ejemplares que se cazan). Estos escenarios fueron simulados en tres poblaciones de diferente calidad, que diferían en la mortalidad juvenil aplicada.

Para analizar la aplicabilidad de los resultados del modelo, se realizaron 307 encuestas en diferentes áreas de Andalucía. A través de las encuestas se valoró la actitud de los cazadores hacia la actual temporada de caza y su postura en el caso de que se produjera un cambio en la normativa actual que la regula. Al mismo tiempo, se obtuvo información sobre la presión cinegética que se aplicaba en cada uno de estos lugares y se analizó su relación con la abundancia de conejo.

Los resultados de las simulaciones indicaron que la actual temporada de caza (Octubre a Diciembre) puede estar afectando gravemente a las poblaciones de conejo, porque es el período que tiene mayor impacto sobre la tasa de crecimiento poblacional. Se observa que la caza aplicada al final de la primavera es la situación más adecuada para optimizar la extracción y a la vez conservar las poblaciones. Los beneficios de la caza en este período son más marcados cuanto mejor es la calidad de la población y cuando tanto los adultos como los juveniles son cazados. Cuando la calidad de la población es mala (por ejemplo, a bajas abundancias de conejo), los efectos de la presión cinegética son muy superiores a los efectos de las diferentes temporadas de caza o de las diferentes estrategias de caza relacionadas con la edad de los ejemplares que se cazan.

Casi la mitad de los cazadores entrevistados piensan que el período actual de caza no es adecuado y estarían de acuerdo con un cambio de dicho periodo. En más del 75% de los lugares visitados, los cazadores solían aplicar manejos para conservar las poblaciones de conejo, que se basan en la reducción de la presión cinegética. Estas estrategias fueron más frecuentemente empleadas en lugares de alta abundancia de conejos, lo que muestra que existe una gestión inadecuada de la actividad cinegética en las áreas de baja abundancia.

Los resultados sugieren que la presión cinegética actual podría mantenerse si el período de caza fuera trasladado al final de la primavera. Sin embargo, para la recuperación de las poblaciones en las áreas de baja abundancia de conejo es necesaria una mayor participación de los cazadores en la aplicación de medidas de reducción de la caza. En conclusión, el manejo de las temporadas de caza y el incremento de la participación de los cazadores en zonas de baja abundancia de conejos pueden optimizar tanto la explotación del recurso cinegético, como la conservación de las poblaciones de conejo en el Sudoeste de Europa.

Modelling hunting strategies for the conservation of wild rabbit populations

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Running head: Modelling strategies for conserving rabbits

Abstract

Recently, European wild rabbit (*Oryctolagus cuniculus*) populations have undergone a sharp decline that may be exacerbated by hunting. We investigate the effects of the timing of hunting on the conservation of wild rabbit using a model for rabbit population dynamics. Scenarios with different hunting rates and age strategies were simulated for different population qualities. We interviewed hunters to ascertain the degree to which they would accept a change in the timing of hunting. We also investigated the hunting pressure applied by hunters and its relationship with rabbit abundance. Modelling results indicate that the current hunting season has the greatest impact on rabbit abundance. Hunting in late spring optimises hunting extraction while conserving rabbit populations. When the rabbit population quality is low the effects of age strategies and the timing of hunting are less important than the effect of the hunting rate applied. Almost half the hunters would agree to policy changes. More than 75% of hunters implemented self-imposed hunting restrictions to improve rabbit populations, that were more frequently applied in high rabbit abundance areas. Therefore, changing the timing of hunting and increasing the participation of hunters in low abundance areas could optimise both the exploitation and the conservation of wild rabbit populations in Southwestern Europe.

Keywords: **European wild rabbit; hunting timing; *Oryctolagus cuniculus*; pest management; population dynamics.**

1. Introduction

European wild rabbits *Oryctolagus cuniculus* are native to the Iberian Peninsula in Southwestern Europe (Monnerot et al., 1994). Their range has expanded naturally to most of continental Europe, and humans have introduced them worldwide for food or hunting (Monnerot et al., 1994). In most countries where rabbits are found they are considered pests, and hunting is an environmental and economic necessity to control rabbit populations to avoid crop damage and/or the extinction of native species (Sheail, 1991; Drollette 1997; Hone, 1999; Angulo, 2001).

In the Iberian Peninsula, however, rabbits are regarded as the staple prey of the Mediterranean ecosystem (Valverde, 1967). They sustain a large number of predator species and generate economically important hunting activity, with over 30000 private hunting areas covering more than 70% of the region (Villafuerte et al., 1998). The progressive decline in wild rabbit populations on the Iberian Peninsula is a concern (Beltrán, 1991), and current numbers are the lowest in decades (Villafuerte et al., 1997).

Effective management of hunting resources requires knowledge of the current regulations and the effects of regulations on the sustainability of wild populations. In Spain (Iberian Peninsula), hunting regulations mainly take the form of hunting quotas set by individual hunting associations and the open hunting season set by the Spanish Government (mainly from October to December). In both cases, regulations are not supported by scientific studies and measures are implemented without knowledge regarding their effects on wild rabbit populations.

Hunters are distributed throughout the Spanish territory, and meet in specific hunting areas where they form hunting associations. Each year, the hunters of each association agree on the hunting quota for their hunting area based on their perception of rabbit population quality. Decisions on hunting quotas move between two contrary attitudes: to conserve rabbit population for coming years, limiting hunting activity, or to hunt the greatest number of animals, without any restriction on hunting activity. However, no information is available on the hunting quotas applied by hunting associations.

Governmental policies on the timing of rabbit hunting in Spain have not changed at least since 1902 (B.O.E., 1970). These policies probably were established as rabbit control measures in response to huge economic losses in agriculture due to rabbits. However, since the sharp decrease in rabbit abundance, damage to crops has become sporadic and the timing of the rabbit hunting season in Spain has been maintained more for historical reasons than to protect agricultural assets. This also occurs in other Southwestern European countries such as Portugal and France (Javier Viñuela, comm. pers; REGHAB, 2002). It would be advantageous to be able to predict the level of hunting that current rabbit populations can support, and when hunting should be applied so as to ensure the smallest impact on rabbit populations while maintaining hunting activity.

Rabbit population models have been used to increase knowledge regarding the efficacy of different management strategies aimed primarily at rabbit control. These include general models on unspecific control strategies (Darwin and Williams, 1964; Smith and Trout, 1994; Smith, 1997) and, more recently, models in which disease is the control method (Pech and Hood, 1998; Hood et al., 2000). However, models focusing on rabbit conservation have received little attention (Calvete, 2000; Fa et al., 2001). All rabbit population models developed to date have been based on parameters obtained from populations outside of the original range of rabbits (i.e. Smith and Trout 1994). It is well known that there are ecological differences between rabbits throughout Europe, including a latitudinal trend in reproductive parameters and differences in survival and mortality (Rogers et al., 1994). Additionally, genetic analyses have revealed differences between Southwestern European rabbits and rabbits from other regions (Monnerot et al., 1994).

Use of ecological models developed in other areas to assess the timing of rabbit hunting in a particular area, Southwestern Europe in the present case, should be undertaken with prudence when interpreting model results. Previous rabbit models have explored the optimal timing to carry out population control in wild rabbit populations in New Zealand (Darwin and Williams, 1964) and England (Smith and Trout, 1994; Smith, 1997). These models suggest that control should be applied when the population is naturally declining and each female killed reduces overall reproductive capacity for the next season. Applying these results to Southwestern Europe, and disregarding differences in the demographic parameters, we can hypothesise that the current Spanish hunting period coincides with the best population control period.

Our main goal was to evaluate whether the current timing of hunting in Southwestern Europe maintains current rabbit populations, and to explore which is the optimal quarter of the year to hunt rabbits while conserving their populations. To explore these issues, we present a simple age-structured population dynamics model based on a Spanish free-living rabbit population. This model is used to investigate the effects of hunting strategies, hunting timing and hunting rates on wild rabbit populations of Southwestern Europe. In view of the fact that the modelling results may be used to change the hunting laws in Spain, we additionally ascertained hunters' perceptions regarding Spanish policy on the timing of hunting, and their attitudes toward a change. Finally, we present hunting quotas applied by hunting associations and their relation with the conservation of rabbit populations. If hunters were involved in the conservation of rabbit populations, they would be expected to apply a lower hunting pressure in areas with low rabbit abundance. Thus, the degree to which they restrict their hunting activities should be inversely correlated with the quality of the rabbit population in their hunting area (good quality for hunters meaning high rabbit density). Here, we have ascertained the levels of restriction implemented by hunters and the relationship between the level of restriction and rabbit abundance. This information was then used to evaluate the extent to which hunters take into account the sustainability of rabbit populations when deciding the hunting quotas.

2. Methods

2.1. Database of the model

Most available data on wild rabbit biology and ecology derives from areas in which rabbits are an introduced species (Parer, 1977; Wood, 1980; Gibb, 1993), and there is a general lack of data from Southwestern Europe, the original distribution range of rabbits. Given that rabbits introduced into new areas will have adapted to different environmental conditions, many aspects of their original biology may have changed. Thus, the population parameters used in our model - fecundity, mortality and age structure - were taken from an area in which rabbits are native. All data used in our study were taken from Villafuerte's (1994) study of a free-living rabbit population in Doñana National Park (Southwestern Spain). Below we summarise the methods used by Villafuerte (1994) to obtain the demographic parameters used in our model. Although most parameters are seasonally dependent, in cases where Villafuerte's data were scarce to distinguish differences within the whole year period, those parameters were fixed at the average value of the available data (litter size, litter mortality, and juvenile mortality).

Villafuerte (1994) assessed rabbit fecundity from capture-recaptures every month between October 1988 and September 1990. Considering the resulting average productivity for the years 1989-1990, the proportion of reproductive females in the model was set seasonally for a one-year period (Table 1). Litter size data was obtained from weekly observations conducted along a fixed 6-km-long transect, in which breeding stops were searched and analysed between October 1988 and September 1990 (Villafuerte, 1994). The resulting average litter size was 3.5. This average, which was used in the model presented here, is in accordance with previous studies carried out in Spain in different areas and years (Delibes and Calderón, 1979; Soriguer, 1981).

Table 1 . Percentage of reproductive females (n= 88 females) and adult mortality rate (n = 28 radio-tracked rabbits) used in the model. Data calculated from Villafuerte (1994).

Period	% Reproductive females	Mortality rate
February– May	85	0.025
June	50	0.02
July – September	20	0.02
October– January	50	0.125

The main causes of death in wild rabbits are predation and disease. The high number of predator species that consume rabbits in Southwestern Europe facilitates the predation, not only of low body condition animals, but also of sick rabbits and the consumption of animals dead from disease (Villafuerte et al., 1997). Thus, the causes of mortality from disease and predation may be incorrectly classified in the data of Villafuerte (1994); we considered both causes together in our model.

Villafuerte (1994) monitored litter success through weekly observations conducted along a fixed 6-km-long transect and captures on site between October 1988 and September 1990. We used the resulting mortality rate of new-born in our model, which was fixed at 0.3 throughout the year. To assess juvenile and adult mortality, Villafuerte (1994) captured rabbits, fitted them with radio-collars and located them daily between April 1989 and March 1990 (Villafuerte et al., 1994; Moreno et al., 1996). The resulting adult mortality rates were set seasonally over a one-year period in the model (Table 1), and the resulting yearly averaged juvenile mortality rate was 0.75. Smith and Trout (1994) proposed that variation in juvenile survival greatly affects population quality, where high juvenile survival means a growing population and low juvenile survival means a declining population. We used three juvenile mortality rates to permit an analysis of ‘good’ (juvenile mortality rate = 0.73), ‘medium’ (0.75) and ‘bad’ (0.78) population quality. High and low juvenile mortality rates were established by calibration in the model to obtain an additional growing populations and a stable population with growth rates above and below 0.75 (Fig. 1). We did not simulated a declining population because hunting will lead the population to collapse. The model assumes no migration; this is justified because rabbits extend over the whole area, and emigration balances immigration.

2.2. Structure of the model

Previous models on the effects of timing of rabbit control have been developed using Leslie matrices in which control was applied by varying the survival rates of different age-classes at different months (Darwin and Williams, 1964; Smith and Trout, 1994). We have adapted this approach to the study of rabbit populations in Southwestern Europe. In our model, stochastic components are included into the demographic parameters, hunting mortality of different age classes depends on their proportion in the population, and hunting is applied over three consecutive months.

Models that describe species population dynamics often are based on the same general structure representing the rate of change in a population, using either continuous or discrete time models (Lotka, 1925; Volterra, 1926; Nickolson and Bailey, 1935). Let D, M and N denote population density, mortality and natality, respectively. Population density at time t is represented by the equation:

$$D_{(t)} = D_{(t-1)} + D_{(t-1)} (N-M) * \text{☚} t \qquad \text{eqn 1}$$

We divided the rabbit population into three age-classes: new-born (n), juveniles (j) and adults (a). New-borns are rabbits under one-month old that depend on the mother and live in a breeding stop; juveniles are rabbits between one and four months old (*j1, j2, j3,* and *j4,* respectively); and adults are older rabbits, comprising the reproductive class. On the basis of Boyd (1985) and Smith et al., (1995), we set the rabbit sex-ratio to be 1:1. The number of new-born is a function of the initial number of adult females, the proportion of reproductive females (*R*) and their fecundity (*F*). The model runs on a monthly time step, the transit time among age-classes. The resulting age-class population density is represented by the following discrete time equations:

$Dn_{(t)} = 0.5 * Da_{(t-1)} * F * R * \text{☚}t$ eqn 2
$Dj1_{(t)} = Dn_{(t-1)} * (1-Mn) * \text{☚}t$ eqn 3
$Dj2_{(t)} = Dj1_{(t-1)} * (1-Mj) * \text{☚}t$ eqn 4
$Dj3_{(t)} = Dj2_{(t-1)} * (1-Mj) * \text{☚}t$ eqn 5
$Dj4_{(t)} = Dj3_{(t-1)} * (1-Mj) * \text{☚}t$ eqn 6
$Da_{(t)} = Dj4_{(t-1)} * (1-Mj) * \text{☚}t + Da_{(t-1)} (1-Ma) * \text{☚}t$
eqn 7

The population model (eqn 2-7) was solved using the software Stella II 3.05 (High Performance Systems, 1992). Although the model is deterministic, we added a stochastic component through the introduction of a random range for two population parameters : the proportion of reproductive females and the adult mortality. Each stochastic component was based on the variance of field data recorded by Villafuerte (1994). It corresponded to a random number between cero and the variance of each parameter, that was added to the monthly proportion of reproductive females and adult mortality. This stochastic component was included to simulate the variability of the Mediterranean environments of Southwestern Europe.

Conflicting reports on the effect of density on demographic parameters (Trout and Smith, 1998; Twigg and Williams, 1999; Smith, 1997) led us to simplify the model to assume no density dependence. The assumption that density is relatively unimportant is supported by the steady decline in rabbit populations in Southwestern Europe over the last decades (Rogers et al., 1994; Villafuerte et al., 1998).

Each hunting scenario was modelled for a twelve-year period. The first three years of each simulation run were not used to ensure differentiation between hunting scenarios. We assessed the effects of different scenarios with the averaged growth rate (λ - 1) per year for a nine-year period. The population size is growing when (λ - 1) > 0, stable when (λ - 1) = 0, and declining when (λ - 1) < 0. We ran each hunting scenario 50 times, then averaged all runs. Similar to Villafuerte (1994) all scenarios were started with an initial population structure of $n = 100$, $j = 70$, and $a = 160$.

2.3. Model testing

To evaluate performance, the model was validated using data recorded for the same rabbit population. Data on rabbit abundance was obtained by vehicle surveys along a permanent 13-km transect in Doñana National Park. When possible (i.e. no flooding), monthly data were collected at dusk on three consecutive days over the period of 1991 to 1999 (for more details see Villafuerte et al., 1997). The model was tested without adding hunting, as rabbit population of Doñana National Park is not subject to hunting.

We used the Pearson correlation test to compare the average abundance in each month of field data with the results of 50 runs simulating the population dynamics of a medium quality population. We expected no difference between model and field data.

2.4. Modelling hunting management strategies

Although diseased rabbits may be more vulnerable to hunting (e.g., young myxomatose rabbits are expected to be more easily detected by hunters), additive mortality has been showed to occur in wild rabbits populations (Trout and Tittensor, 1989; Trout et al., 1992). Therefore, we assumed in our model that hunting mortality is additive to natural mortality, so we are both: simplifying the model, and applying the most severe hunting mortality to the modelled populations (Hone, 1999).

The probability of being hunted may be age- and sex-dependent. Rabbit hunters cannot discriminate between the sexes in the field, but, although difficult, they may distinguish among age-classes due to differences in body size. To include this effect in our investigation, we modelled two hunting strategies: (1) age-selective, according to which hunters discriminate rabbit body size and shoot only adults; and (2) non-age-selective, according to which hunters do not discriminate on the basis of size. In the non-age-selective scenario, adults and juveniles are shot according to their proportion in the population.

Current policies in Spain permit rabbit hunting during a 3-month period between autumn and winter, mainly October, November and December. In special cases, hunting permits are issued in summer to control rabbits in specific areas where they cause great crop damage.

First, we analysed the effect of hunting on population growth rate. This analysis was designed to determine the maximum hunting rate needed to keep the population stable over the 3-month hunting period (October to December) under six scenarios: three population qualities (good, medium and bad) in conjunction with two age-selection strategies (age-selective, non age-selective). Hunting rate is represented by the percentage of rabbits hunted each hunting month, and varied from 0 to 90% in 5% steps. Second, we selected three hunting rates (the maximum hunting rate obtained in the first analysis and this rate ± 10%) for each of the six scenarios, to determine the effects of hunting in a different period of three consecutive months of the year in each scenario. Finally, we calculated the maximum percentage and the maximum number of rabbits hunted per year for the 12-year simulation period in a population of good quality. These percentages were then compared to determine the hunting pressures that can be applied for different hunting timings and age-selection strategies. Knowledge of the number of rabbits hunted is necessary to understand the differences in the resulting hunting pressures between scenarios.

2.5. Interviews with hunters

We carried out a survey in 307 areas in Andalusia (Southern Spain) to learn about the attitudes of hunters to a change of hunting timing policy and to gather information on the hunting pressure applied by hunting societies and the relation between hunting pressure and rabbit abundance (Figure 1). Selection of geographic coordinates of survey points was conducted by using the geographic information systems software IDRISI (Clark University, USA). Selection was based on a step-random sample based on altitude and topography, to exclude areas where rabbits were impossible to exists or hunt. Thus, we favoured areas lower than 1200 meters of altitude and slopes lower than 30% (Blanco and Villafuerte, 1993). More than 35 people with at least two years' training in wildlife surveys and interviews conducted interviews and rabbit surveys in each area in June and July 1999.

At each survey point, the interviewer identified the adequate person (a hunter member of the hunting association) to interview in order to adequately answer on the hunting decisions and attitudes on each case. A questionnaire about hunting activity applied in the area in 1998-1999 and attitudes towards hunting policy was used. Participants were asked to indicate if they were satisfied with the permitted hunting period, and whether they would change it. Lastly, they were asked whether the hunting management practices designed to restrict hunting pressure listed in the questionnaire were applied in their area in 1998-1999. These practices, which are voluntary, comprise reducing hunting days, reducing the number of hunters per day, reducing the number of rabbits hunted per day, and reducing hunting hours per day. Only yes/no answers were allowed.

At each survey point rabbit abundance was estimated from faecal pellet counts. Such counts have been widely used and are particularly useful in areas where the rabbits themselves or other signs are difficult to detect, or where detection may be influenced by other factors such as soil or habitat type (i.e. Moreno and Villafuerte, 1995; Palma et al., 1999). Counts were carried out at each survey point in 50 circular sampling units (0.5 m^2 per unit) randomly distributed over a 2 Ha. area carefully selected in order to be representative to the rest of the hunting area. The rabbit abundance index at each survey point was computed on the basis of the average number of pellets in 0.5 m^2; a log-transformation was needed to prepare the data for statistical analysis.

These estimations of rabbit abundance enabled us to assess whether the use of self-imposed restrictions was related to rabbit abundance, and thereby allowed us to test the hypothesis that such hunting restrictions are more frequently employed when rabbits are scarce than when numerous. Each year, the hunters of each association agree on the degree of restrictions to be employed in their hunting area (reducing hunting days, reducing the number of hunters per day, reducing the number of rabbits hunted per day, and/or reducing hunting hours per day). They decide on the basis of their perception of rabbit population quality (good quality for hunters meaning high rabbit abundance). We expected lower rabbit abundance in areas where voluntary hunting restrictions were applied in 1998-99. We performed two analyses to compare differences in mean rabbit abundance: (1) t-test to compare among areas where one specific restriction is employed and areas where that restriction is not employed; and (2) ANOVA test to compare three types of areas: a) with no restrictions; b) with some restriction; and c) with all restrictions, and exploring differences with a post-hoc Tukey HSD test.

3. Results

3.1. Simulations

The average simulated monthly rabbit abundance (for a medium quality population) was correlated with mean field data obtained from vehicle surveys over the period 1991-1999 ($r = 0.93$, $P < 0.01$, $n = 12$). In addition, we represented the yearly averages of field rabbit abundances and the evolution of simulated populations during that period (Fig. 1). As the simulation and field data had different scales, we normalized all values by setting the initial value (first year represented in the figure) to 100. Field data seems to correlate well with the medium quality simulated population, although in some years (1994-95 and 1998-99) the field data is closer to the simulated population with bad quality (Fig. 1).

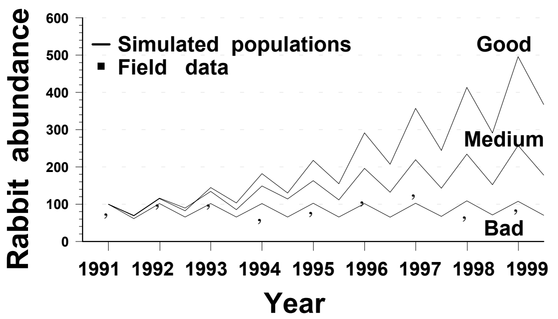

Figure 1. Population size estimates from modelling (black lines) and from vehicle surveys (black squares). Plots show the yearly maximum and minimum number of rabbits from simulations and the yearly average of rabbits seen per kilometre, respectively. Both data sets were normalized by setting the initial value to 100.

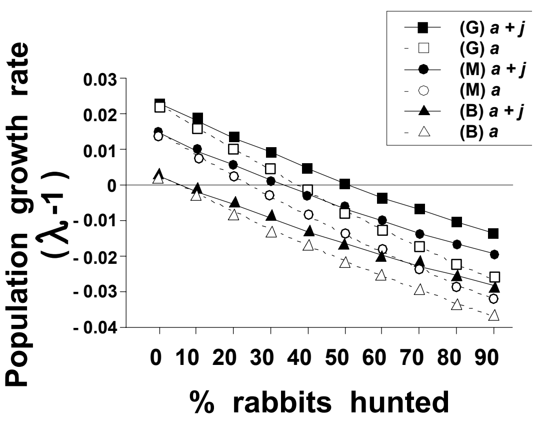

Figure 2. Effect of hunting rate on population growth rate (λ - 1) in good (G), medium (M) and bad (B) rabbit populations when a non-age-selection strategy (*a* + *j* : adults and juveniles hunted) or an age-selection strategy (*a* : only adults hunted) is simulated. Hunting rates are simulated in the hunting period currently in force in Southwestern Europe (October-December).

We simulated the effect of hunting rate on population growth rate applied during the hunting period currently in force in Spain (October-December) (Fig. 2). The maximum hunting rates that could be applied while maintaining stable populations were 5, 35 and 50% for the bad, medium and good quality populations respectively. For the medium and good quality populations, the maximum hunting rate decreases to 25% and 40%, when the age-selection strategy was used (i.e., when only adults are hunted), whereas for the bad quality populations the maximum hunting rate does not change between the two age-selection strategies. Differences in the population growth rate between hunting strategies increase with the percentage of hunted rabbits. When the simulated hunting rate is high (>60%), the population growth rate of a good population hunted indiscriminately (adults and juveniles) is lower than that of a medium population in which only adults are hunted. These results suggest that it could be beneficial to hunt both adults and juveniles instead of only adults.

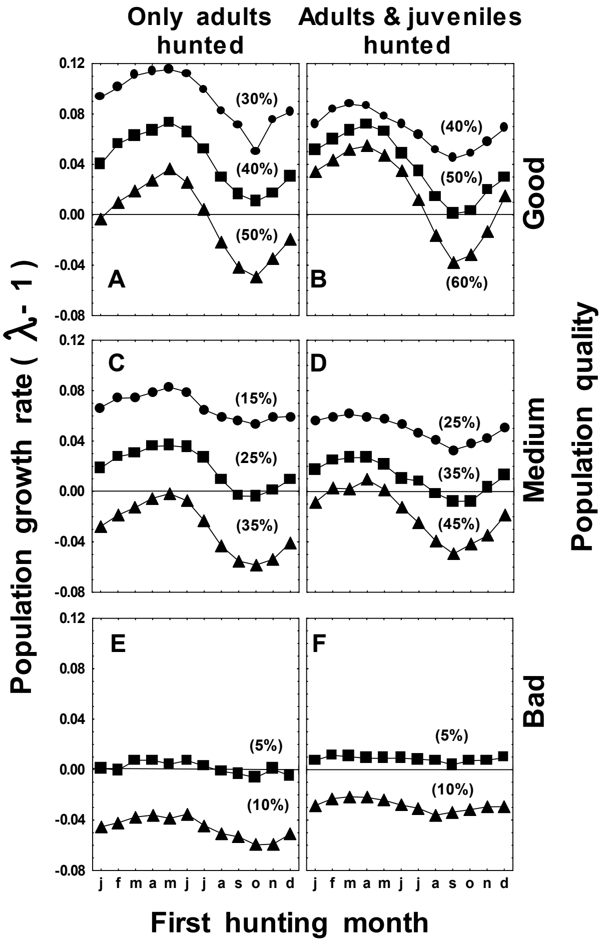

Figure 3. Effect of high (triangles), medium (squares) and low (circles) hunting rates on population growth rate (λ - 1) simulated during a consecutive 3-month period. (A). Good population, only adults hunted. (B) Good population, adults and juveniles hunted. (C) Medium population, only adults hunted, (D) Medium population, adults and juveniles hunted. (E) Bad population, only adults hunted. (F) Bad population, adults and juveniles hunted. Hunting rate applied in each case is shown in parentheses.

We simulated the effects of different hunting rates in all possible periods of three consecutive months of the year under the six different scenarios: three population qualities and two age-selection strategies (Fig. 3). Three different hunting rates were simulated for each scenario: the maximum hunting rate for each scenario (Fig. 2) and this rate ± 10%. The resulting population growth rates for the different hunting periods show greater variation for good quality populations (Figs 3a and b) than for medium quality populations (Figs 3c and d). For bad quality populations, we only simulated a medium hunting rate of 5% and a high hunting rate of 15%. In comparison to the good and medium populations, simulations of the bad population yield the lowest variation in population growth rates with changes in the hunting timing (Figs 3e and f). Thus, it seems that responses to a good strategy are stronger (i.e., high population growth rate) when the quality of the population is better, and thus number of rabbits is higher.

The simulation results indicate that, in general, higher population growth rates are reached when the hunting period is in the first half of the year than in the second half. In particular, the maximum population growth rate is attained when the first hunting month is March, April or May, while minimum population growth is found when the first hunting month is September or October. When the strategy simulated is to hunt both adults and juveniles, the maximum and minimum population growth rates shift to earlier hunting periods (first hunting month March/April and September, respectively) than when the age-selection strategy is simulated (May and October, respectively).

When the age-selection strategy is simulated (Figs 3a and c), the effects of the different hunting rates on population growth rate are homogenous between different hunting timings (i.e., the lines are parallel). When hunting is indiscriminate (Figs 3b and d), however, the variability of the effects depends on the timing of hunting, with less variability being observed when the hunting period begins in the first six-months (lines are convergent in the first six-months and divergent in the second six-months). This is clearly an effect of the relative number of adults and juveniles, and their reproductive status at different hunting rates and at different times of the year. Most females reproduce in the first six-months (Table 1). If the hunting rate is increased in the first six-months (i.e., +10%) and the strategy is to hunt only adults, the increase in hunting causes a sharp reduction in the breeding population, greatly affecting the population growth rate. If adults and juveniles are hunted, mainly the latter are affected by the hunting increase in the first six-months, and thus the effect of a reduction in hunting on the population growth rate is low. Similarly, if the hunting rate is reduced in the first six-months (i.e., –10%), the reduction affects only adults when hunting only adults, but affects more juveniles than adults when hunting both age-classes. Therefore, the simulation results suggest that the

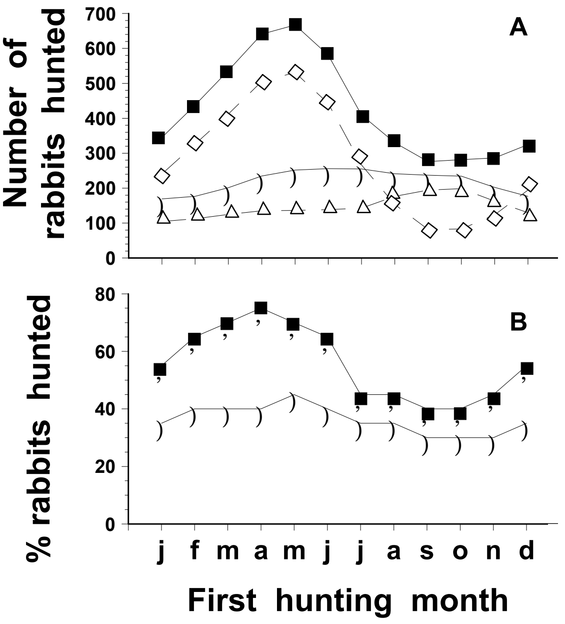

Figure 4. Maximum number (A) and maximum percentage (B) of rabbits hunted, while maintaining a stable good population when hunting is simulated during a consecutive 3-month period. Black circles: simulations of age-selective hunting (only adults hunted). Black squares: simulations of non-age-selective hunting. Additionally, non-age-selective data are broken down into number of adults hunted (open triangles) and number of juveniles hunted (open diamonds).

benefits of reducing the hunting rate in the first six-months are higher when the age-selection strategy is employed.

In non-age-selective hunting, adults and juveniles are shot depending on their relative proportion in the population. Differences in their proportions throughout the year appear in the Fig. 4a, which represents the maximum number of adults and juveniles (open triangles and diamonds respectively) that can be hunted while maintaining a stable good population. The number of juveniles that can be hunted is higher than the number of adults throughout much of the year, especially in spring. The exception is autumn, when the number of adults that can be hunted exceeds the number of juveniles. Hunting in autumn reduces overall population breeding potential for the next season, resulting detrimental to the maintenance of the population.

In the simulations of age-selective hunting, the maximum number of adults that can be hunted (black circles in the Fig. 4a) while maintaining a stable population shows little dependence on the month in which the hunting period commences. For this reason, variation of the hunting rate does not present different effects on the population growth rate when hunting is simulated at different periods of the year (Figs. 3a and c).

In general, age-selective hunting results in a lower number of hunted rabbits than the non-age-selective hunting (Fig. 4a, black circles and black squares respectively). When the values predicted by the model are expressed as percentages (simulations always run with the same initial population structure), the predicted percentage of rabbits hunted varies from approximately 30 to 45% (only adults hunted) or from 40 to 75% (adults and juveniles hunted) depending on the timing of the hunting season (Fig. 4b). Thus, maximum benefits can be obtained by hunting adults and juveniles and by starting in spring.

3.2. Interviews

In the light of the modelling results, interviews with hunters were performed with two goals: (1) to ascertain whether hunters would accept a change of the timing of hunting, and (2) to determine whether hunters adjust their hunting pressure in response to their perception of rabbit population quality with the overall aim of conserving populations. The second issue is of great importance, especially when the rabbit population quality is bad (i.e., low rabbit density), because the effect of the timing of hunting is less important than the hunting pressure applied (Fig. 3e and f).

Sample size (n) of different analysis vary among 204 and 230: Pellet counts could not be performed in 9 areas; the interviewer could not find an adequate person to interview in 16 areas, and both situations together occurred in 19 areas (Fig. 1). An additional number of areas were partly invalid when the interviewed did not answered all questions.. Almost half the hunters interviewed disagreed with the current timing of rabbit hunting stipulated by the Spanish government (46.4%, n = 224). Only 39.1% of interviewees indicated that they would abide by any changes to the permitted hunting period (*n* = 230). Regarding self-imposed restrictions on the hunting pressure, we found that 67.9% of hunters interviewed already reduced hunting days, 44.1% reduced the number of rabbits hunted per day, 41.4% reduced the number of hunting hours per day, and 39.1% reduced the number of hunters per day (*n* = 220). Only 21.7% currently applied all the above-mentioned voluntary hunting restrictions, 27.4% did not employ any of them, and the rest (50.9%) applied some.

Table 2. Observed rabbit abundance in areas with different hunting restrictions (Mean ± SD values of pellet number / 0.5 m^2). Student t-test was performed with log-transformed values.

Restriction of	Yes	No	*n*	*t-value*	*P-value*
Hunting days	1.11 ± 1.75	1.34 ± 2.41	204	-1.38	0.2
Hunters per day	1.16 ± 2.47	1.29 ± 2.16	205	-1.21	0.23
Rabbits hunted per day	1.22 ± 2.03	1.34 ± 2.35	198	-1.00	0.32
Hunting hours per day	1.67 ± 2.42	1.11 ± 2.12	214	2.61	0.01

Correlation analysis between rabbit abundance in particular areas and the application of specific hunting restrictions in those areas showed that only the reduction of hunting hours per day is related to rabbit abundance; employed where rabbits were abundant (Table 2). Next, we compared rabbit abundance between areas in which all hunting restrictions were applied, areas in which some of the restrictions were applied, and areas in which no restrictions were applied. Analysis revealed significant differences between these three groups (ANOVA, *F* = 3.92, *d.f.* = 221, *P* = 0.021). Exploring these differences, areas with no hunting restrictions applied had lower rabbit abundance, while areas with some restrictions applied had higher abundance (Fig. 5). Areas with all hunting restrictions applied showed a medium average rabbit abundance, but without significant differences with the other two groups; therefore, areas with all restrictions applied may have a broad range of rabbit abundance.

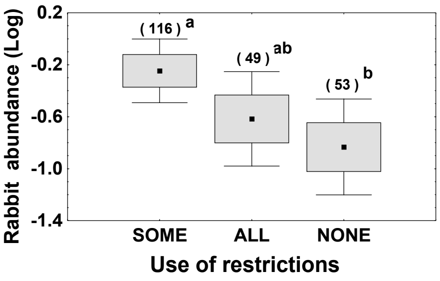

Figure 5. Rabbit abundance (log-transformed pellet number / 0.5 m^2) at different intensities of hunting restriction. Groups that were not significantly different based on Tukey post-hoc test share a common letter. Numbers in parentheses indicate the number of valid questionnaires. Central black square is the mean, box limits mark standard error and vertical lines mark ± 1.96 * standard error.

4. Discussion

For centuries, rabbit control was a regular and necessary strategy to protect crops in many countries including Spain. In areas where rabbits were introduced, control measures also served to protect against native species loss. Although rabbit control is an ongoing necessity in many countries, it is now clear that rabbit numbers are decreasing in Southwestern Europe. In this region, many hunters want a large number of rabbits in their hunting lands, and conservation agencies want healthy rabbit populations to maintain endangered predators and thereby preserve Mediterranean ecosystem diversity (Palma et al., 1999, Palomares, 2001).

Obviously, any hunting management strategy that aims either to control or to conserve the population must take into account the quality of the population (i.e., the population density and its evolution), because the consequences of management decisions may vary considerably depending on the quality of the population (Milner-Gulland, 1997). In our model, we have simulated hunting at three different levels of population quality to include the likely variability of wild rabbit populations in Southwestern Europe. The population quality, and hence the population growth behaviour, was varied by modifying the juvenile survival parameter. Juvenile survival is the most variable population parameter of rabbit populations (Simonetti and Fuentes, 1982; Gibb and Williams, 1994; Rogers et al., 1994) and greatly affects population quality (Smith and Trout, 1994).

The simulated evolution of a population with a medium population quality over a period of nine years showed similarities with field data obtained from a natural population of rabbits in Spain. However, the field data show some years of low rabbit abundance that are not observed in the model results. These drops are attributed to stochastic events that were not considered in the model. In Mediterranean ecosystems, inter-annual variations in rabbit numbers is mainly determined by annual rainfall or length of drought. Such variations lead to greater variability in field data than in data from simulations. Therefore, weather and other factors would be expected to cause greater fluctuations in the population growth rate than those simulated in this study. For this reason, the real situation is expected to be less optimistic than predictions in our modelling in scarce or declining populations (Lande et al., 1997). In addition, given the simplistic nature of the model, exact values of harvest rates or harvested rabbits are not useful as management tools, but are subject of concern when focusing on the relative importance of different options.

Our simulations suggest that the current governmental policy regarding the timing of hunting in Southwestern Europe, especially in Spain, is not optimal for conserving rabbit populations. Our model simulations show that the current choice of hunting period (October to December) offers a suboptimal prognosis for maintaining healthy wild rabbit populations. This result concurs well with previous studies of rabbit populations in other geographical areas, which were undertaken to determine the optimal time for rabbit control (Darwin and Williams, 1964; Smith and Trout, 1994; Smith, 1997). Interviews conducted in the present study indicated that almost half of the hunters in Southern Spain disagree with the current policy on the timing of hunting, and many would like it changed.

Our results show that hunting in late spring (currently allowed in Spain for rabbit control) optimises hunting extraction, because during this period even high hunting rates are sustainable. On the other hand, hunting in late autumn (the current hunting period) has the greatest detrimental effect on rabbit populations and the lowest hunting bag is obtained. These results lead to the conclusion that the current timing of rabbit hunting and control in Spain should be changed to enhance conservation of healthy wild rabbit populations, needed to conserve their predators.

This result could be explained by the annual variability of wild rabbit abundance and seasonal reproduction. Again, we agree with the results of previous studies (Darwin and Williams, 1964; Smith and Trout, 1994) carried out on rabbit populations in other geographical regions; this agreement suggests that the effects tested are greater than the differences between population parameters. These authors showed that more young rabbits are killed when control is carried out in late spring and more adults are killed when control is performed in winter. The current hunting period in Southwestern Europe is from late autumn to early winter, when rabbit numbers are at a minimum, while a late spring harvest coincides with the end of the reproduction and with maximum rabbit abundance (Beltrán 1991; Villafuerte et al., 1997). Although the same proportion of the population is hunted in both cases, Lande et al. (1997) have shown that the effects on population conservation are dramatic when hunting is carried out in areas with low abundance because population stability is reduced. In this sense, our results clearly show that hunting rates in scarce or declining populations are not sustainable in the long term.

The strategy of age-based hunting is related to the results mentioned above. If only adult rabbits are hunted, the benefit of changing the hunting period is not as marked as when adults and juveniles are hunted. The ability to hunt juveniles may mean fewer adults are killed, especially towards the end of the breeding period. This is a good strategy for increasing the survival of pregnant or reproductive females and therefore to maintain the population. Our results show that the higher proportion of juveniles in spring allows more variability in hunting rates with lower impact on population growth rate, because a lower proportion of reproductive females is killed by hunting.

Although the age-selection strategy could be difficult to apply strictly in the field, the tendency of hunters to select rabbits of higher body weight due to their higher economic value (Beddington, 1974) acts to bias hunting toward adult rabbits. In addition, different hunting or capture methods can be biased toward a particular age class of rabbits (Daly, 1980; Smith et al., 1995). On the other hand, in our simulations of non-age-selective hunting, we assumed that hunters shoot different ages depending on their proportion in the population. Thus, we ignored a variety of factors that influence the selection of hunted animals, for example age-related differences in rabbit detectability or rabbit behavioural characteristics. Further research is needed to assess potential biases affecting the hunting of wild populations.

Other important limitations were assumed in order to simplify the model. For example the model is density-independent and hunting is modelled without compensatory responses. The lack of compensatory reduction in mortality or increase in fecundity would result in a higher negative effect on population dynamics when juveniles are hunted, and when hunting is performed during breeding (Smith and Trout, 1994). However, compensatory or additive hunting in natural populations is much debated and probably varies among populations (Kokko, 2001).

Associations of hunters are responsible for regulating and managing hunting quotas in their hunting areas. As more than 70% of Spanish territory is covered by hunting areas, the management of these areas has important consequences for the conservation of wild species, should be considered by national organizations, and guided through ecological studies. In many cases, economic interests or lack of information lead hunters to mismanage game or non-game species, thereby putting some endangered predators at risk (Villafuerte et al., 1998). For example, results of our interviews indicate that when rabbit abundance is low, hunters either opt not to employ any hunting restrictions or to employ all hunting restrictions. These two attitudes are diametrically opposed, the former clearly representing mismanagement in the long term (caused by applying high hunting pressure during the legal hunting period) and the latter the best strategy for rabbit recovery. When such management decisions are considered in the light of our modelling results, which show that in bad quality populations the timing of hunting has less effect on the population growth rate than hunting pressure, we conclude that hunter mismanagement in areas of low rabbit abundance may affect populations in these areas and should be corrected to conserve rabbit populations and their predators.

When rabbit abundance is high, hunting societies currently employ some or all of the restrictions to conserve rabbit populations for coming years, making for suitable management. The relationship between the use of hunting restrictions and rabbit abundance also could be explained as an effect of management; however, given that we found no correlation between the application of the most stringent limitation (applying all hunting restrictions) and rabbit abundance, this explanation can be ruled out. In addition, our results are not supposed to involve causality because decisions on the use of restrictions can change each year depending on the hunter’s perception of rabbit abundance. However, we did not attempt to study the effectiveness of hunting restrictions in this paper.

Our results show that almost 75% of hunters currently employ some or all of the self-imposed restrictions on hunting pressure, making for suitable management. Thus, when they notice a drop in rabbit abundance, they restrict hunting to some degree. However, not all hunting restrictions are easily applied. Our results indicate that hunters are willing to reduce the number of hunting days, the number of rabbits shot or even the number of hunting hours per day, but are unlikely to reduce the number of hunters per day. If the hunting season were changed to late spring, the number of hunters could be maintained and the number of rabbits killed could even be increased, and other restrictions would be less necessary.

Management decisions based on hunting modelling should be supported by scientific information on the applicability and acceptance of the changes proposed. Most hunters agreed with a change in the timing of hunting in Spain, and our model predicts that moving the hunting season from late autumn (the current hunting period) to late spring should improve rabbit populations. We recommend management agencies to review rabbit hunting policies to adapt them to the current situation, and encourage hunters in low rabbit abundance areas to implement measures to conserve rabbit populations. Spanish policy was not changed after the introduction of myxomatosis in the 1950s, nor was it modified following rabbit haemorrhagic disease in the 1980s. Both diseases caused rabbit numbers to drop, and therefore hunters, conservationists and predators have been affected by the poor management of rabbit populations. However, a change in the hunting season may give rise to other conflicts (e.g. disturbing effects on breeding species) that should be assessed in a broad context and monitored to avoid unforeseen problems. Finally, it should be of great concern for conservation agencies to apply an effective management of hunting resources in the areas of potential interest for predators. In the current situation of decline of wild rabbit populations, hunting restrictions should be applied in such areas to maintain and increase their abundances and thus to conserve predator community.

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Note:

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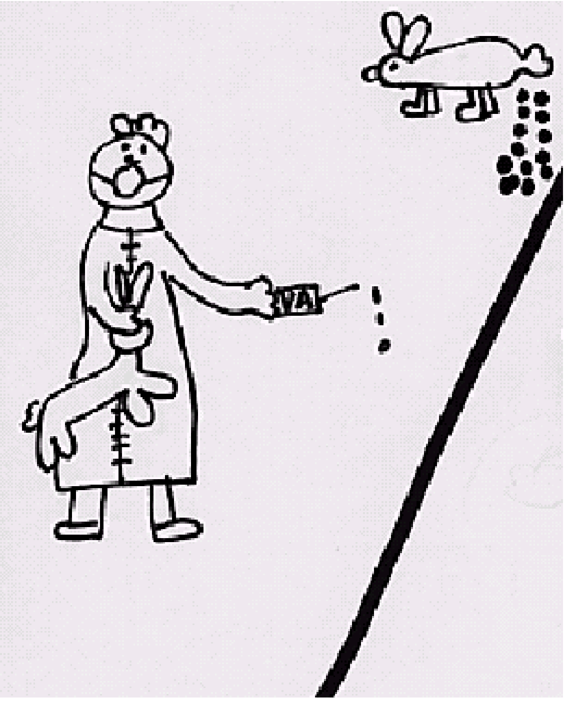

CAPÍTULO 4

Las enfermedades del conejo. Las nuevas herramientas de gestión a través del uso de virus modificados genéticamente

CAPÍTULO 4

Las enfermedades del conejo. Las nuevas herramientas de gestión a través del uso de virus modificados genéticamente

Resumen

En este capítulo se discuten las técnicas moleculares que se están desarrollando actualmente para la gestión del conejo a escala mundial. Estas técnicas se basan en la modificación genética del virus de la mixomatosis, que sería posteriormente liberado en las poblaciones de conejo silvestre. Dos líneas de ecología aplicada son la base del desarrollo de estos virus recombinantes: por un lado, la investigación en la lucha contra las enfermedades del conejo para la conservación de sus poblaciones en el Sudoeste de Europa, y por otro lado, la investigación sobre la lucha biológica contra los propios conejos en los lugares donde son una especie invasora.

Teniendo en cuenta ambas líneas de investigación aplicada, totalmente opuestas en sus objetivos finales, y considerando que los resultados de ambas investigaciones proponen la suelta de un virus genéticamente modificado en las poblaciones de conejo silvestre, el objetivo básico de este trabajo es profundizar sobre el posible impacto de dicha suelta.

En la primera publicación que se adjunta se realiza una previa exposición breve del problema. En la segunda publicación, se aborda el mismo a través de la información recopilada sobre la problemática de las poblaciones de conejo a nivel mundial, las bases moleculares de ambas líneas de investigación, el posible impacto de los virus recombinantes resultantes (basados en la historia previa de las enfermedades del conejo), y las normas legales que existen hasta la fecha (tanto nacionales como internacionales) que podrían regular su uso.

Durante el siglo XX aparecieron las dos enfermedades del conejo, la mixomatosis y la enfermedad hemorrágica (EHV). Para entender adecuadamente el potencial de los virus recombinantes (a liberar en poblaciones silvestres de conejo) es básico conocer la historia de estas enfermedades. La mixomatosis se descubrió en 1896 en Montevideo, donde unos conejos europeos de granja se infectaron con un virus que afectaba de manera leve a algunas especies de conejo americano. Dada la alta mortalidad que produjo, el virus se ensayó como método de control biológico para las poblaciones de conejo, tanto en Europa como en Australia. La primera liberación exitosa se produjo en Australia en 1950; no tardó en liberarse en Francia en 1952, foco de su expansión natural al resto de Europa. También se produjeron liberaciones ilegales en otros continentes. Las mixomatosis produjo mortalidades de hasta un

99% en las poblaciones de conejo. La rápida capacidad de cambio del virus ha permitido la recuperación en diferentes grados de muchas poblaciones.

La EHV apareció en 1984 en granjas de conejo doméstico en China; en 1987 llegó a las granjas italianas, y posteriormente se detectó en el campo. La EHV cruzó de forma natural a Gran Bretaña en 1992; en 1995 se escapó de una isla experimental cruzando los 5 km. que le separaban del continente australiano; por último, fue introducida ilegalmente en Nueva Zelanda. La EHV supuso mortalidades variables en campo, pero siempre mayores al 50%. Aún no se conoce el origen de este virus; una de las hipótesis más aceptadas es que procede de la mutación de un virus inocuo, que existiría de forma natural en algunas poblaciones silvestres como en Gran Bretaña.

En la lucha contra estas enfermedades, un grupo de investigación español, ha desarrollado un virus vacunal contra las dos enfermedades a través de la modificación genética del virus de la mixomatosis. El gen de la proteína viral del virus de la EHV se inserta en el genoma del virus de la mixomatosis. Al expresarse dicho gen dentro de los conejos, produce inmunidad contra la EHV, mientras que al escoger una cepa muy atenuada de mixomatosis el virus recombinante actúa como vacuna contra la misma. Por otro lado, en la lucha contra el conejo como especie invasora, un equipo australiano de investigación ha modificado el virus de la mixomatosis insertándole un gen que produce una proteína esencial para la unión del óvulo con el gameto. Una vez en el conejo, el animal produce anticuerpos contra esa proteína, que interfieren con la reproducción, produciendo infertilidad en las hembras. Este proceso se denomina inmunocontracepción mediada por virus y se está investigando también para otras especies en distintos centros australianos.

El desarrollo exponencial de las técnicas moleculares de modificación genética (surgidas en los años 1970) no ha ido paralelo al de una legislación que regule su uso, algo que sería muy necesario. En Europa, la Directiva 219 CEE de 1990 regulaba las liberaciones de organismos modificados. En la Directiva actual, 18 CE de 2001, todos los países deben estar de acuerdo en la decisión que ha tomado uno de ellos (la fecha para transponer esta Directiva en España era octubre de 2002). En Australia, no ha habido una normativa legal hasta 2001. En esta ley, el virus recombinante fue clasificado en la categoría de “organismo confinado no destinado a la liberación en el campo”. Respecto a las normas internacionales, la mayoría de organismos emiten recomendaciones que no son útiles como normas legales.

Silicon philanthropists follow a great tradition

Sir — What is being called ‘venture philanthropy’ in your News feature ‘Biomedical philanthropy, Silicon Valley style’ (*Nature* **410,** 140–143; 2001) is hardly a new concept — it is an example of what has traditionally characterized ‘thoughtful philanthropy’. In fact, it is very like the ‘old’ strategic philanthropy envisioned and practised by many private foundations established at the beginning of the twentieth century.

Robert Kohler’s book *Partners in Science* (Univ. Chicago Press, 1991) provides many examples of the essential role private funders played in the development of modern molecular biology, genetics, public health and other biomedical research fields. The Silicon Valley entrepreneurs interviewed in your feature are following a tradition long established by private funders who viewed their money as providing venture capital for the common good and who long held the view that philanthropy should invest in the acquisition of new knowledge and in its responsible application. Further, the staff of the new foundations are following in the footsteps of a profession first defined by the Rockefeller Foundation ‘circuit riders’ — programme officers knowledgeable in their fields, actively seeking out promising research projects needing support.

I do not intend to detract from the laudable efforts of these new philanthropists to pursue thoughtful giving that takes risks and invests in new ideas with a minimum of hassle and red tape. But I do not see why they need to be flattered into thinking they are inventing something new — or that, as some of them seem to believe, they have a new model that needs to be emulated by all funders. Just as there is a certain dishonesty in the communication between researchers and government funders (the ‘proposal’ describing work already completed), there is a growing risk of dishonest dialogue between scientists and some of the philanthropists identified by the anecdotes Trisha Gura relates (‘No one but you has the keen insight to recognize my brilliant idea’).

The number of projects and researchers supported by private philanthropy will remain small compared with those receiving government support, and private funding relies on its partnership with public dollars. Peer review may not be perfect, but neither is investing in whoever grabs someone’s attention or ear.

The true richness of private philanthropy is found in its diversity of approaches and its distributed decision-making processes that allow many different points of view — and many different grant-making approaches — to flourish.

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When DNA research menaces diversity

Sir — The Nature Science Update “Synthetic viruses just around the corner”[1] reported a discussion about scientists’ imminent ability to synthesize new viruses for producing better vaccines or for devising deadlier biological weapons. I would like to give an example where genetic engineering of viruses can undermine careful management of natural resources.

Two new rabbit virus strains are being developed for opposing reasons. On the one hand, a group in Australia is modifying rabbit myxoma virus to transmit reproductive sterility and so reduce numbers in a region where rabbits constitute a pest[2]. On the other, a European group is modifying myxoma virus to express rabbit haemorrhagic disease virus capsid protein[3] to protect rabbits against both diseases and encourage the recovery of wild populations within the species’ original distribution area.

Each goal is logical within its regional context. However, the history of rabbit viruses shows that outcomes can conflict with initial goals. First recorded in Montevideo in 1896, myxoma virus was successfully released in Australia in 1950 to control rabbit populations, but an illegal release in 1952 in France led to the virus spreading throughout Europe. Similarly, rabbit haemorrhagic disease, which spread naturally from Chinese rabbitries throughout Europe in 1987, spread in Australia after an accidental release from a trial island and in New Zealand after an illegal release in 1997.

The new modified viruses could spread worldwide as easily as myxomatosis and rabbit haemorrhagic disease initially spread. The establishment of modified myxoma virus into inappropriate regions could have disastrous effects on biodiversity. The preservation of Australasian ecosystems, as well as the conservation of endangered predators in Europe, depends on the same species: the wild rabbit, the target of both modified viruses.

It is therefore essential that modified viruses are very carefully and appropriately used. Biotechnology policies on the release of modified organisms rely on national authorities. But rabbits are distributed throughout the world, so it is essential to guide the development, release and regulation of rabbit virus biotechnology, and to enforce international controls to prevent accidental spread of genetically modified viruses.

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Gulf syndrome research has passed peer review

Sir — Your News report (*Nature* **410,** 135; 2001) mentioned the negative comments made by a former US Department of Defense (DoD) employee, Bernard Rostker, and by Philip Landrigan, a Clinton committee appointee, about our published research on Gulf War syndrome. Because your story stated that our work was supported by a private foundation and non-peer-reviewed grant funds, and involved small patient samples, readers might be left with the impression that our findings are invalid.

This is not true. Over the past four years we have published 12 papers in prominent scientific journals establishing that there is a new syndrome with three variants in Gulf War veterans of a naval reserve battalion (see, for example, ref. 1). Our study of 63 cases and 186 controls identified strong associations with risk factors for exposure to sarin nerve gas and related chemicals. We have also identified affected brain regions and a genetic predisposition using a variety of techniques. Our design and sample sizes are equivalent to those used by the Centers for Disease Control and Prevention in such classic epidemic investigations as toxic shock syndrome, Four-Corners hantavirus pneumonia and AIDS.

The funding proposals for all our studies were rejected by the DoD’s peer-review system but were funded by a private foundation or after appeal to higher government levels. Our results later passed rigorous peer review before publication in respected scientific journals. A consistent publishing record is a better indicator of scientific merit than the sources of funding, particularly in the politically charged environment of Gulf War research.

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COMMENTARY

First synthesize new viruses then regulate their release? The case of the wild rabbit

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Abstract

European wild rabbits originated in southwestern Europe but have been introduced into many other countries world-wide, becoming serious pests in many instances. As a consequence of rabbits being regarded so differently, applied research for their management often has opposing goals, namely their conservation or their control. Furthermore, modern gene technology has led to the concept of using genetically modified myxoma viruses for rabbit management, again with quite contrary aims in mind. In this paper we explain the possible ecological and economic consequences of using these genetically modified viruses inappropriately and we consider whether national and international regulations are sufficient to prevent improper use. If international regulations are inadequate, molecular biologists and ecologists must consider the consequences of their research and advice beyond their own country to avoid unwanted impacts.

Keywords: conservation, GMO, myxomatosis, *Oryctolagus cuniculus*, rabbit haemorrhagic disease, wild rabbit

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Introduction

Organisms modified using gene technology are commonly referred to as genetically modified organisms (GMOs). They are now widely used in industry, agriculture, health care, and biological control, usually involving releases into the environment.

Nevertheless, developments in this area have often progressed faster than the legislation that provides for their safe use and Tiedje *et al.* (1989) have recommended that research should be carried out within a framework of science-based regulation that encourages innovation without compromising environmental values. As GMOs may be spread beyond political boundaries, it is essential to achieve international co-ordination in developing such regulations.

Here we present the case of genetically modified rabbit viruses, one developed to help conserve rabbits, the other developed for their control, in which the lack of effective international co-ordination and control could compromise the management of rabbit populations in countries other than those in which the viruses were developed (Angulo 2001).

Current distribution and ecological problems concerning wild rabbits

The European wild rabbit, *Oryctolagus cuniculus*, originated in southwestern Europe on the Iberian peninsula (Fig. 1). It is a prolific species and has always supported a diverse predator community. In Spain it is the staple prey of two endangered predators, the imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*) (Delibes & Hiraldo 1981). Humans have also taken advantage of rabbit abundance: over one million hunters generate an estimated US\$ 1.2×10^9 annually in Spain (Villafuerte *et al.* 1998). However, in the last 50 years wild rabbit populations have undergone a sharp decline caused mainly by the appearance of two viral diseases, myxomatosis and rabbit haemorrhagic disease (RHD) (Queney *et al.* 2000). Hunters and conservationists alike are concerned.

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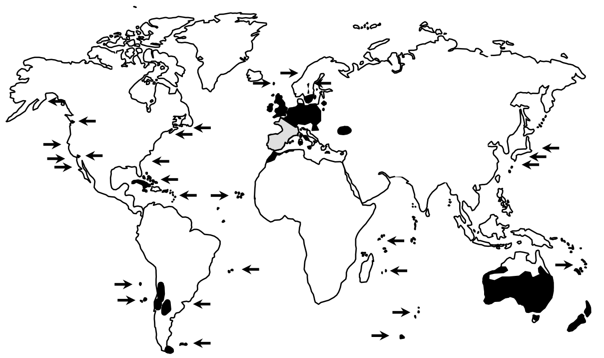

Fig. 1 Current distribution of European wild rabbits. Arrows indicate small areas where rabbits have been introduced. Natural populations marked in grey and introduced populations in black.

Besides spreading naturally into other European countries, rabbits have been distributed world-wide by man for food and hunting (Fig. 1). In many areas rabbits have become a real pest, multiplying 'like rabbits' in an optimal environment and with the lack of effective predators (Holland 1999). In Australia, rabbits cause erosion, land degradation and loss of native plants (Fenner & Fantini 1999) and rabbit control and agricultural losses cost US$ 310 million annually (Robinson *et al.* 1997). In Britain, crop damage is estimated at over US$ 170 million annually (R. C. Trout, personal communication).

New rabbit management programmes: Australian vs. Spanish GM viruses

Given the two distinct lines of research for the management of wild rabbits, conservation and pest control, it is intriguing that, for each, a solution is being sought through the genetic manipulation of the myxoma virus (MV) originally derived from cottontail rabbits (*Sylvilagus* spp.) in the Americas.

In trying to deal with diseases in wild rabbits in southwest Europe hunters and conservationists have increasingly turned to molecular technology. Immunization of rabbits against myxomatosis has long been possible using cell culture-attenuated MV strains. However, during the last few years, researchers have explored ways of developing recombinant vaccines that express the RHD virus (RHDV) capsid protein. These include the use of baculovirus (Laurent *et al.* 1994), poxivirus (Fischer *et al.* 1997), plant viruses such as potyvirus (Fernández-Fernández *et al.* 2001), or plants (Castañón *et al.* 1999). Most importantly, Bertagnoli *et al.* (1996) produced a recombinant vaccine based on an attenuated MV that expressed RHDV capsid protein to protect simultaneously against both diseases. Most of the systems listed rely on direct inoculation of individual rabbits, and consequently are not suited for large-scale wild rabbit vaccination. However, Spanish scientists have recently developed an alternative GM virus, based on an attenuated but transmissible field strain of MV, genetically modified to provide protection against RHD as well. It is capable of horizontal transmission by contact between rabbits; thus, only a few rabbits need to be initially vaccinated to achieve immunization of the greater population (Bárcena *et al.* 2000). The Spanish National Committee of Biosafety authorized the experimental test release of this recombinant on a Mediterranean island, Isla del Aire, to assess its potency and safety. Infected rabbits produced antibodies against both viruses, and horizontal transmission to about 50% of uninoculated rabbits in the field was observed during the short trial period (Torres *et al.* 2001). Scientists are hopeful of widespread release soon.

The same concept of natural spread of virus to affect rabbit populations on a wide scale is also being considered to control rabbits. One initiative of the Pest Animal Control Cooperative Research Centre (PAC-CRC) in Australia is the use of GM MV to reduce rabbit fertility through transmissible (virally vectored) immunocontraception. This concept was proposed at the Conference on Fertility Control in Wildlife held in Melbourne in 1990. The idea was to develop recombinant viral vectors that can transmit immunogens to induce a specific immune response in the target animal against reproductive proteins. Specific and contagious viruses, in this case MV, could disseminate the contraceptive agent into the population (Tyndale-Biscoe 1991). The recombinant MV produces the rabbit zona pellucida glycoprotein B and initial experiments have induced temporary infertility in 25% of female rabbits (Kerr *et al.* 1999).

Impact of GM rabbit viruses: the world-wide spread of MV and RHD

While both GM viruses could be valuable in managing rabbits in the countries where they are being developed, the problem is that they may cause an entirely unwanted effect in another country, and the history of rabbit viruses shows clearly that they are well suited to global spread.

Myxomatosis was first recorded in Montevideo, in 1896 (Fig. 2a) when it was spread from the native South American cottontail rabbit, *Sylvilagus brasiliensis* to European rabbits. Soon after its discovery, MV was suggested as a possible tool for the control of rabbits in Australia. During the 1920s–1940s, there was great debate over the use of MV to control rabbits, but it was nevertheless legally released in Australia in 1950 (Ratcliffe *et al.* 1952). The success of myxomatosis in Australia led a French landowner to release the virus illegally in 1952, and subsequently myxomatosis spread naturally through the rest of Europe (Muñoz 1960; Sellers 1987). Myxomatosis was illegally

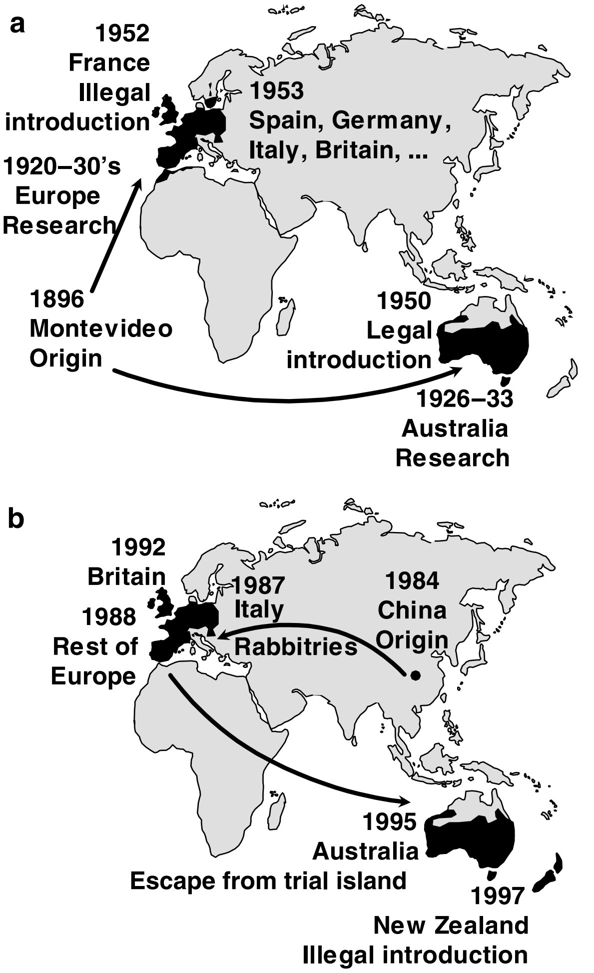

Fig. 2 (a) Origin and expansion of myxoma virus. (b) Origin and expansion of rabbit haemorrhagic disease. (Virus spread in rabbitries outside the wild rabbit distribution has not been shown.)

used by Argentinean landowners to control the spread of wild rabbits and was illegally distributed in Britain (Fenner & Fantini 1999).

Myxomatosis initially reduced British wild rabbit populations by 99% (Flowerdew *et al*. 1992). In Australia MV was also highly effective at first but attenuated into less virulent strains and rabbits developed genetic resistance to the disease so that today there is a dynamic balance between virulence and host resistance in which myxomatosis kills between 40 and 60% of infected susceptible rabbits (Kerr & Best 1998). This also explains why rabbits were relatively rare in Britain for about 25 years (Lloyd 1981) and why MV continues to regulate their populations today (Trout *et al*. 1992).

MV has caused major declines in native wild rabbit populations of southwest Europe. In Spain, it resulted in a reduction of hunting activity (Muñoz 1960), and negatively affected endangered predators (Delibes & Hiraldo 1981). MV also had negative environmental (Flowerdew *et al*. 1992) and economic impacts (Fenner & Fantini 1999).

In 1984, a new disease, RHD [also known as rabbit calicivirus disease (RCD) in Australasia], appeared in rabbitries in China (Fig. 2b). In 1987 it appeared in Italy and broke out simultaneously in several other European countries, transmitted largely through trade in domestic rabbits. It quickly expanded into wild rabbit populations, even crossing the English Channel into Britain by 1992 (Chasey & Trout 1995). In 1995, before it was fully evaluated as a new rabbit control agent in Australia, RHD escaped from an experimental trial on a quarantined island and crossed 5 km of sea to mainland Australia where it soon became established (Kovaliski 1998). In 1997 it was illegally introduced in New Zealand (O'Keefe *et al*. 1999).

In Australia, the initial effectiveness of RHD was variable, with the highest levels in arid and semiarid areas where mortality reached 95%, leading to the collapse of rabbit commerce (Fenner & Fantini 1999). Meanwhile, RHD had sharply reduced native wild rabbit populations in southwest Europe. The first RHD epizootics caused mortality rates between 70 and 90% in domestic rabbits, and between 50 and 60% in wild rabbits (Villafuerte *et al*. 1994), although Marchandeau *et al*. (1998) detected mortality rates up to 80% in wild rabbits. In Spain, few populations have recovered to prior levels, directly affecting hunting activity and endangered predators (Fernández 1993; Villafuerte *et al*. 1998; Martínez & Calvo 2001).

A single pathogenic RHDV serotype seems to exist to date (Asgari *et al*. 1999). But a nonpathogenic rabbit calicivirus related to RHDV has been described in domestic rabbits (Capucci *et al*. 1996). Besides, seropositive rabbits, apparently carrying antibodies raised against a related nonvirulent calicivirus and protected from severe RHD, have been found in Europe (Trout *et al*. 1997), Australia (Nagesha *et al*. 2000) and New Zealand (O'Keefe *et al*. 1999). Mutation of an avirulent form of the calicivirus is a possible explanation for the origin of RHD (Rodak *et al*. 1990).

Can viruses be contained within target populations or distinct geographical areas?

For both the Spanish GM virus, which vaccinates rabbits against myxomatosis and RHD, and the Australian virus, aimed at reducing the fertility of rabbits, it is envisaged that active viruses that retain their capacity to spread would be most useful. This is important because it would not be necessary to vaccinate every rabbit. A naturally spreading vaccine could be introduced into some rabbits then spread to a greater part of the population. However, it is precisely this characteristic that would make them so difficult to contain.

The ready spread of both MV and RHDV raises many questions about our ability to contain such viruses. Clearly landholders interested in reducing rabbit problems deliberately spread MV and RHDV. There is also a risk, as happened with RHDV in Australia, of underestimating the role of insect vectors in transmitting the virus over very long distances. Sea birds have also been implicated in the spread of both MV and RHDV. It is therefore quite conceivable that recombinant MV could be used in areas where such risks were not fully considered. Indeed, the most recent trials with a GM MV were carried out on Isla del Aire, only 1 km offshore from one of the larger Balearic Islands and where there is a seagull colony and regular hunting activity.

Other issues also need to be fully understood. These include the potential for interaction between GM viruses and field strains of MV (Tyndale-Biscoe 1994) including genetic exchange between GM viruses and wild viruses which may have different virulence or greater ability to compete. It is also necessary to understand and counter any potential impact of GM viruses on *Sylvilagus* spp., the original hosts of MV.

Although such questions are being considered with the idea of developing safeguards in the GM viruses, the idea of using actively spreading viruses remains problematic. As we have seen, MV and RHDV are difficult to contain within distinct geographical areas. It is essential to ask whether it would be possible to prevent the potential for spread of GM rabbit viruses into inappropriate regions through currently available mechanisms such as international controls and regulations.

What regulations cover research and release of GMOs at national levels?

During the 1970s many countries launched biotechnology policies and management plans. Most distinguish between contained GMO work and deliberate releases into the environment with separate legislation. A national authority generally regulates approval for release following risk assessment that may include scientific and ethical considerations as well as public consultation.

For example, in 1990, the European Union allowed for releases of GMOs through Directive 90/219/EEC (EEC 1990). Within that framework a national authority could evaluate risks. This directive resolved the problems on a national level but created a problem on the European level, as other Member States could not discuss the decision. In April 2001 a new Directive 2001/18/EC was adopted (EC 2001), whereby the release of a GMO in any country needs the agreement of the European Commission and the rest of the member states. The final date for Member States to comply with this Directive is October 2002 (although it has not yet been adopted in Spain). Until this date, GMO applications (i.e. recombinant vaccine MV) may be subject to the Directive 90/220/EEC.

In New Zealand, the Hazardous Substances and New Organisms Act covers the importation, development, field-testing and the intentional release of GMOs into the environment (http://www.hsno.govt.nz/). For GM viruses, an assessment would obviously be made in terms of their capacity to cause disease. But, it is not clear whether international risks or consequences are considered by this legislation.

Gene technology was subject to voluntary assessment in Australia from 1975 until June 2001. Responsibilities were held by different committees, but their recommendations were not enforced. In 1997 Australia began preparing new legislation to tighten assessment. Called the Gene Technology Act 2000, it commenced operation in June 2001 (Radke 2001). For the release of GMO into the environment, the Gene Technology Regulator may consult international experts. The Gene Technology Regulator can impose conditions to limit the spread or persistence of the GMO in the environment. However, the release may be approved, claiming isolation distances or physical barriers to other continents. Currently, research on modified MV done by the Pest Animal Control CRC and Australian National University is licensed as a dealing not involving intentional release into the environment.

International agreements on research and release of GMOs

International organizations such as the Organization for Economic Cooperation and Development (OECD), World Trade Organization (WTO), the World Organization for Animal Health (OIE), the World Health Organization, or the Convention on Biological Diversity, try to unify national regulations. However, international organizations only develop recommendations and guidelines, and these may or may not necessarily be adopted by individual countries.

The OECD seeks to ensure safety, develop effective regulatory oversight and facilitate trade in biotechnology products between the 29 member countries. The OECD has organized international meetings on GMOs, mainly on modified food and crops. Similarly, the WTO has developed the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) to protect animals and plants from pests and diseases and GMOs were discussed during SPS Committee meetings in November 2001. The OIE informs countries of the occurrence of animal diseases, harmonizes regulations for trade in animals or animal products, and develops recommendations to prevent disease spread.

The Convention on Biological Diversity adopted an agreement known as the Cartagena Protocol of Biosafety in

January 2000, to protect biological diversity from potential risks posed by GMOs. It established a procedure specifically focusing on cross-border movement of GMOs in which risks are assessed by national authorities but final decisions regarding the importation or release of GMOs must be communicated to the Convention. By November 2001 only eight countries had ratified the Cartagena Protocol, but neither countries of the European Community nor Australia and New Zealand were signatories.

We conclude that, while there are some regulations focused on the research and release of GMOs there appear to be few agreements that specifically address safe research, handling and release of GMOs at an international level. Moreover, regulations are very general, or focus on safety issues regarding GM food trade and importation, and their effectiveness is weak, as shown by the discovery of GM crops growing in areas where permission had not been granted (Dalton 2001; Jayaraman 2001). Regulations for nontradable GMOs or GM viruses seem to be even less well considered.

Conclusion

Applied research for the management of wild rabbits in different parts of the world has opposing goals. This may lead to the creation and release of antagonistic GM viruses, one aimed at conservation, the other aimed at rabbit control. The use of virally vectored immunocontraception to control pests is currently being investigated for a number of different species (Tyndale-Biscoe 1991), including possums (Sutherland *et al*. 1996), foxes (Holland 1999), cats (Courchamp & Cornell 2000) and rodents (Ylönen 2001). Bearing in mind the facility with which viruses spread or can be intentionally spread and the difficulty of virus control in the field (Fenner & Fantini 1999) mere legislation is not enough. To avoid unexpected effects of the introduction of new GMOs for wildlife management, it is essential to get international agreement and co-ordination in the development and use of such strategies.

It is essential that research on rabbit control and conservation try to achieve realistic management goals where risks are minimized (Angulo 2001). Certainly, Australian and Spanish scientists follow the guidelines established in their respective countries (Robinson *et al*. 1997; Bárcena *et al*. 2000), but a greater effort should be made to promote the international communication between scientists and national and international authorities (Tyndale-Biscoe 1994). Evaluating the possible impact of release of GMOs into the environment requires expertise in many scientific disciplines. Between them, molecular biologists, veterinarians and ecologists must consider the consequences of their decisions, beyond their own country.

This paper takes a step in that direction by pointing out some potential impacts of GMOs being developed for managing wild rabbit populations. Past studies have focused on general ecological and evolutionary aspects (Tiedje *et al*. 1989) or particular legal and ethical issues (Tyndale-Biscoe 1994), but none has provided a thorough assessment of the risks. We make no specific recommendations about a course of action that can be taken other than to list some questions that might be raised in international scientific or regulatory meetings. These include asking: (i) whether accidental or illegal spread could be prevented by existing international controls or conventions that regulate cross-border GMO movements; (ii) what international scientific structures should be established to enable the rational development of GMOs for wildlife management; (iii) how can international regulations on GMO releases be designed to be acceptable to and implemented within individual countries?

In essence, there is a need for scientific and regulatory structures that guide the development and release of GMOs by (i) evaluating their potential to escape and establish abroad; (ii) assessing whether or not risks are internationally acceptable at scientific, economic and environmental levels; and (iii) developing specific regulation of their use.

In the meantime, ecologists, veterinarians and molecular biologists must keep an international perspective on their work and devise measures to reduce the risk of unwanted ecological and economic impacts, of the kind illustrated here for viruses being designed to manage wild rabbits.

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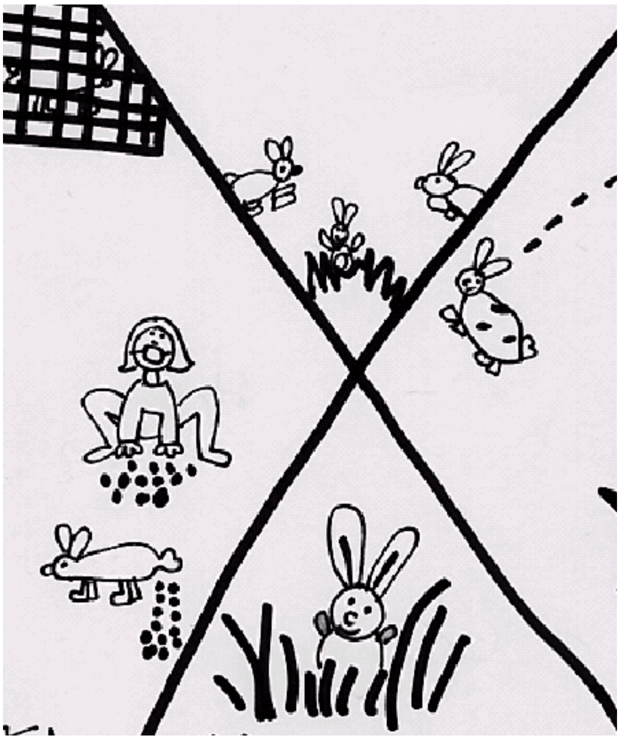
This review stems from Elena Angulo's PhD thesis on the ecological factors influencing abundance and distribution of wild rabbit populations in Spain. This work showed that diseases were among the most important limiting factors. Brian Cooke is a Principal Research Scientist with CSIRO. He has been involved with research on the biological control of wild rabbits in Australia for 35 years, working mainly with rabbit haemorrhagic disease over the last 14 years.



DISCUSIÓN GENERAL

DISCUSIÓN

Las poblaciones de conejo en Andalucía: el comienzo de una síntesis

La presente Tesis contiene cuatro capítulos que mediante diferentes aproximaciones analizan algunos de los factores que afectan o limitan la distribución y abundancia de las poblaciones de conejo en Andalucía. Para responder al objetivo de la tesis, en esta discusión general se pretende dar una visión integradora de lo expuesto por separado en cada uno de los capítulos, identificar los principales resultados obtenidos y sintetizarlos con la literatura científica disponible.

Autocrítica a la metodología utilizada

Dado que esta Tesis pretende analizar los efectos de determinados factores sobre las abundancias y la distribución del conejo, necesita examinar la existencia de relaciones de causalidad. Sin embargo, tales relaciones son difíciles de analizar en las poblaciones silvestres, puesto que usualmente se requiere de experimentación y, generalmente, una serie larga de años para poder cuantificar a largo plazo los efectos de los diferentes factores. Ello no ha sido posible por una limitación de tiempo y de medios adecuados y hemos debido conformarnos con realizar una aproximación para establecer relaciones entre los factores estudiados y el conejo. Se han utilizado dos herramientas para explorar de manera indirecta estas relaciones de causalidad: modelos lineares generalizados y modelos matemáticos de simulación.

En el Capítulo 1, se utilizan los modelos lineales generalizados para modelizar la abundancia y presencia de conejo en relación a factores tanto de hábitat como históricos. Estos modelos, basados en datos observacionales, describen los patrones de relación entre las especies y el entorno. Tienen como desventaja que son específicos de un determinado momento, lugar y condiciones ambientales, y por esta razón no debe asumirse que tengan un alto poder predictivo. Sin embargo, son muy interesantes para obtener información sobre las condiciones actuales que determinan la presencia o abundancia de una determinada especie en unas determinadas condiciones, y también como método para establecer hipótesis sobre los posibles efectos que pueden afectar al futuro de la especie (Morrison et al. 1998; Seoane y Bustamante 2001).

En el Capítulo 3, para analizar los efectos de la caza se ha utilizado un modelo matemático de simulación de la dinámica poblacional. Al ser un método indirecto, está sujeto a una serie de asunciones, además de las propias del modelo. Este modelo matemático utiliza como base los parámetros demográficos de una población de conejos andaluza. Sin embargo, no hay que olvidar que un modelo es siempre una abstracción del sistema real de estudio que nos permite enfocar más claramente un aspecto del mismo (Johnson 1996). Por tanto, aunque los resultados del modelo indiquen diferencias entre los escenarios modelados, la medición precisa de tales diferencias debería ser analizada más profundamente con estudios experimentales. El ajuste de la presión de caza o de las temporadas de caza resultantes del modelo, debe ser flexible a las posibles fluctuaciones de la población por factores no controlados. En este sentido, uno de los principios básicos de la explotación cinegética induce al gestor a tener un comportamiento conservador en las tasas de caza a aplicar. Caughley y Sinclair (1994) establecieron un margen mínimo del 25% cuando el conocimiento sobre la población es escaso o la población es muy variable. Además, en el caso de poblaciones a baja densidad, como es la situación actual de muchas de las poblaciones ibéricas de conejo, el gestor debe ser aún más conservador ya que ha de tener en cuenta que los efectos estocásticos son mucho mayores (Lande et al. 1997).

Por otro lado, al modelo utilizado en el Capítulo 3 para analizar los efectos de la caza, se le han impuesto una serie de asunciones, con objeto de mantener la sencillez del modelo y de la interpretación de los resultados. Estas asunciones del modelo son tres: la falta de densodependencia y de estocasticidad en el modelo y la caza añadida como mortalidad aditiva. La densodependencia es un factor crucial en los modelos de dinámica poblacional, sin embargo, cuantificar su efecto es muy dificultoso (Shenk et al. 1998). En el caso del conejo, las informaciones son contradictorias por lo que se decidió no incorporar en el modelo este efecto (Trout y Smith 1998; Twigg y Williams 1999; Smith1997). Puesto que la mayoría de las abundancias de conejo en la Península están a niveles tan bajos, esta asunción es relativamente poco importante.

El modelo es parcialmente determinista, es decir, no tiene en cuenta factores aleatorios. Esto ya se observa al comparar las predicciones del modelo con los datos de campo de la población de origen: los datos simulados mantienen una evolución lineal mientras que esto no ocurre en la población natural. En el ecosistema mediterráneo las oscilaciones interanuales a nivel climático son muy importantes, lo cual afecta a la reproducción del conejo de un año a otro y, por tanto, a su productividad anual (Wallage-Drees 1983; Beltrán 1991; Villafuerte et al. 1997). La estocasticidad que se asume debería ser tenida en cuenta a la hora de interpretar los resultados. Especialmente en los efectos de los diferentes escenarios en las poblaciones de baja densidad, puesto que es de esperar que las oscilaciones estocásticas produzcan en estas poblaciones unas fluctuaciones mayores que en poblaciones de mayor abundancia, pudiendo llevar al colapso a dichas poblaciones (Lande et al. 1997). Sin embargo, puesto que estas simulaciones se hacen para comparar entre diferentes escenarios de caza, las oscilaciones interanuales en los parámetros son relativamente poco importantes, ya que suceden en todos los escenarios por igual.

Se ha observado que algunas causas de mortalidad, como la depredación o la mixomatosis, pueden estar actuando de forma aditiva en las poblaciones de conejo (Trout et al. 1992; Hone 1999). Al añadir la caza como mortalidad aditiva, se aplica a la población simulada el peor efecto que puede tener la caza. En este sentido, basándonos en Smith y Trout (1994), la falta de una respuesta compensatoria que reduzca la mortalidad o incremente la fecundidad podría resultar en un mayor efecto negativo, sobre todo cuando se cazan los juveniles o cuando la caza se efectúa durante el periodo de reproducción. En resumen, actualmente hay un cierto debate sobre incluir la caza como mortalidad aditiva o como compensatoria, y es probable que el ser una cosa u otra sea dependiente de la población (Kokko 2001).

Por último, el Capítulo 2 (sobre los métodos de gestión) y parte del Capítulo 3 (sobre la reducción de la presión de caza), se basan en la relación entre los métodos de gestión cinegética y la abundancia actual de conejos. Estas relaciones se pueden interpretar desde el punto de vista de la efectividad de los métodos de gestión sobre las abundancia de conejos, o simplemente que esos métodos de gestión se lleven a cabo precisamente en las áreas de mayor abundancia de conejo. Puesto que las estrategias de gestión utilizadas en Andalucía varían de un año a otro, las relaciones no implican efectividad de la gestión en la mayoría de los casos.

En este sentido, cabe destacar las sugerencias realizadas por Strickland et al. (1996), quienes indican que el ideal en la gestión de cualquier especie silvestre es que el gestor sea capaz de evaluar de una manera fiable los progresos de la población, es decir, asegurarse de que las estrategias de manejo que utiliza están siendo adecuadas. Esto implica que los objetivos de la gestión deben ser cuantificables. Según los mismos autores, la determinación del éxito de la gestión debe basarse en el seguimiento a lo largo de los ciclos anuales de la abundancia poblacional de la especie y de las actuaciones aplicadas. Para ello, las estrategias de gestión deben ser establecidas para periodos de tiempo largos, puesto que en periodos cortos no se puede determinar el éxito de la gestión. En definitiva, con el actual sistema de gestión en Andalucía (y posiblemente en el resto de España) que, desgraciadamente, no se rige por las sugerencias de Strickland et al. (1996), es difícil establecer un clara efectividad de las herramientas utilizadas sobre las especies a las que va dirigida la gestión.

El paisaje como modulador de la distribución y abundancia de conejos

Los resultados obtenidos en el Capítulo 1 demuestran que las abundancias de conejo en Andalucía están a muy bajos niveles. Este hecho coincide con otros estudios recientes y con los que se están llevando a cabo en la actualidad en la Península Ibérica (Fa et al. 1999; Carlos Calvete, comunicación personal; Néstor Fernández, comunicación personal). Es evidente que el conejo en Andalucía está atravesando uno de los peores momentos de su historia reciente.

En cuanto a la distribución de las poblaciones, los conejos no están repartidos al azar en Andalucía sino que existe un patrón espacial en su distribución. Teniendo en cuenta que el declive del conejo en España se produjo de forma más drástica en los paisajes menos aptos para el mismo (Villafuerte et al. 1995), es posible explicar este patrón espacial en función del paisaje. Intrínsecamente, el paisaje está estructurado de manera espacial, por lo que el patrón espacial que muestra la distribución del conejo podría estar asociado a los paisajes preferidos por la especie.

En los resultados expuestos en el Capítulo 1 de esta tesis, se muestra como el conejo sigue siendo dependiente del paisaje, puesto que sus abundancias están relacionadas con la vegetación natural, los cultivos y los ecotonos. En este sentido, los resultados obtenidos corroboran estudios anteriores en los que los conejos aparecen asociados a los ecotonos entre diferentes estructuras del paisaje, especialmente cuando estas estructuras son mosaicos de cultivos o pastizales con vegetación natural (Rogers y Myers 1979; Fa et al. 1999; Virgós et al. en prensa). Según la teoría del "aprovisionamiento óptimo", el conejo como especie presa debe optimizar los recorridos entre los lugares de refugio y de alimentación. La calidad del refugio afecta a esta relación de manera que refugios de mejor calidad (por ejemplo, más espesos) permiten alejarse más a los conejos durante el aprovisionamiento (Villafuerte y Moreno 1997). Así, en el Capítulo 1 se muestra cómo las abundancias de conejo están relacionadas con la superficie cubierta por vegetación natural, en este caso bosques y matorral, que le ofrecen un buen refugio. Por otro lado, un alimento de alta calidad favorece que las hembras adquieran una buena condición física y puedan reproducirse, lo que a largo plazo supondría mayores abundancias de conejo (Wallage-Drees 1983, Wallage-Drees y Michielsen 1989; Villafuerte et al. 1997). En este sentido, las abundancias de conejo en Andalucía están en relación directa con la superficie de pastizal y de cultivos mixtos, o con la superficie de cultivos homogéneos cuando éstos son de secano. A través de estudios de dieta, se ha observado que el conejo selecciona las gramíneas, especialmente durante la época de reproducción, lo cual puede explicar la relación del conejo con los cultivos de secano, normalmente constituidos por trigo y cebada (Homolka 1988; Chapuis y Gaudin 1995).

Los efectos humanos: el abandono del campo

Las conclusiones del Capítulo 1, se pueden resumir en que, a pesar de las bajas abundancias medias obtenidas para el área de estudio y a pesar de los cambios que se han producido en el ecosistema por efecto del hombre (Rundel 1998), la abundancia de conejo en Andalucía sigue estando modelada por el paisaje. En este sentido, los resultados del análisis global de la distribución y abundancias de conejo, incorporando factores históricos, indican que el conejo está relacionado negativamente con el abandono del campo. Es más difícil encontrar un población de conejos en lugares donde ha habido abandono rural y, en el caso de encontrarla, tiene una baja abundancia de conejos. El abandono del campo tiene un componente espacial importante (ya que desaparece en los modelos de presencia de conejo realizados al incorporar la autocorrelación espacial), posiblemente porque el abandono del campo está ligado a un determinado tipo de paisaje (Etienne et al. 1998; Schröder 1998). Gortázar et al. (2000) muestran cómo el abandono del campo en Aragón ha favorecido a las especies de caza mayor y desfavorecido a las de caza menor; también Boag (1987) observa claramente los efectos negativos de la intensificación de la agricultura sobre la abundancia de conejos. En el caso del lince, uno de los depredadores más directamente ligados a las poblaciones de conejo, varios autores establecen el abandono del campo como una de las causas más importantes de su declive (Palma et al. 1999; Rodríguez y Delibes 2002). En especial, Palma et al. (1999) asocian el abandono del campo en zonas serranas con la pérdida de usos tradicionales beneficiosos para mantener altas poblaciones de conejo.

Las enfermedades del conejo : una carga del pasado, del presente y del futuro

En el Capítulo 1 se analizan, de manera global, cómo otros factores diferentes al paisaje pueden explicar la presencia y la abundancias de conejo. Las variables incorporadas se refieren a hechos del pasado que pueden estar asociados a la distribución actual de las poblaciones de conejo. Los resultados indican que la carga histórica que soporta el conejo está determinando su distribución en mayor medida que los efectos del paisaje, carga histórica que está asociada a las enfermedades, a la actividad cinegética y a la gestión de las especies cinegéticas realizada a lo largo de las últimas tres décadas.

Tanto la presencia de conejos como su abundancia están relacionadas con la intensidad de la recuperación de las poblaciones ante la enfermedad hemorrágica. Esto coincide con lo visto por Villafuerte et al. (1995) y Gortázar et al. (2000), quienes observan cómo las poblaciones con mayor densidad de conejos se han recuperado más que las poblaciones con menor densidad. Los mismos resultados se obtienen con respecto al efecto de la intensidad de la recuperación de las poblaciones de conejo tras la entrada de la mixomatosis. Esto parece indicar que la recuperación de las poblaciones ibéricas tras la entrada de la mixomatosis no ha sido total, puesto que las abundancias actuales todavía reflejan su efecto (como se muestra en el Capítulo 1) y, además, los efectos de la EHV se han añadido a los anteriormente provocados por la mixomatosis en las poblaciones silvestres ibéricas (Gortázar et al. 2000). Como se ha mostrado en el Capítulo 4, tanto la mixomatosis como la EHV, produjeron en su primera entrada en las poblaciones de conejo, grandes mortalidades (99% en el caso de la mixomatosis, y entre 50-90% en el caso de la EHV), reduciendo gravemente sus abundancias. Los efectos de la mixomatosis fueron superados por muchas poblaciones debido a la coevolución entre el virus y el conejo (Kerr y Best 1998), pero esto no parece haber ocurrido en el caso de la EHV. En este sentido, Queney et al. (2000) no han detectado una pérdida de variabilidad genética en las poblaciones de conejo tras la entrada de la EHV, lo que indica que todas las variedades genéticas de conejo son susceptibles por igual a la enfermedad.

Por otro lado, las abundancias de conejo en Andalucía están asociadas negativamente a la detección de la mixomatosis (a través de ejemplares enfermos). La mixomatosis es más fácil de detectar en poblaciones de alta abundancia, porque los individuos enfermos serán también más abundantes; por ello en el modelo del Capítulo 1 la detección de la enfermedad por los entrevistados indica una alta probabilidad de encontrar poblaciones de conejo. Sin embargo, considerando únicamente la abundancia de conejo, la detección de la enfermedad está asociada a bajas abundancias. Como se dice en el Capítulo 4, la enfermedad sigue controlando de forma natural las poblaciones de conejo manteniéndolas a bajos niveles de abundancia (Ross et al. 1989; Trout et al. 1992). Es claro este efecto, si tenemos en cuenta la mortalidad que produce la enfermedad en las poblaciones de conejo silvestre. Aunque existen muchas diferencias entre estudios, en general se señalan unas mortalidades de entre el 5 y el 20 % de la población, llegando en algunos casos hasta el 60% de los individuos susceptibles (Wood 1980; Flowerdew et al. 1992; Kerr y Best 1998).

Además del efecto de la mixomatosis sobre las poblaciones, hay que tener en cuenta que la EHV puede estar también en la misma población. Las mortalidades estimadas actualmente para la EHV son de entre el 15-20% de los adultos y el 50% de los juveniles (Moriarty et al. 2000; Calvete et al. 2002). Estas mortalidades varían en función de la densidad poblacional y de la proporción de conejos susceptibles de cada población, ya que se refieren a las mortalidades observadas, es decir, que son resultado tanto de la mortalidad producida por el virus entre los conejos infectados susceptibles a la enfermedad (patogenicidad del virus) como de la morbilidad (proporción de conejos en la población que son infectados por el virus). En el caso de que ambas enfermedades estén presentes en la misma población, las estimaciones observadas en los juveniles para cada una de ellas se confunden, por la dificultad que implica diferenciar el impacto de ambas enfermedades (Calvete et al. 2002). Esto no ocurre para el caso de los adultos, ya que la mayoría son resistentes a mixomatosis y el impacto de la EHV es más fácil de estimar.

Por último, las enfermedades siguen constituyendo un problema para el futuro de las poblaciones de conejo. Si, como se expone en el Capítulo 4, los virus modificados genéticamente llegaran a liberarse en las poblaciones de conejo, nuevas investigaciones deberán realizarse para analizar sus efectos. En especial se hará necesario un seguimiento de su interacción con los virus que ya existen de forma natural en las poblaciones, de su efectividad (para lo que han sido creados) a largo plazo, y del control de su dispersión entre diferentes continentes.

La lucha contra las enfermedades

Como se muestra en el Capítulo 2 (sobre los métodos de gestión de la caza menor), la lucha contra las enfermedades del conejo es un método de gestión cinegética que se ha incrementado en las últimas tres décadas. Este incremento en el uso de los manejos estaría relacionado con una mayor percepción, por parte de cazadores y gestores, de la importancia del efecto de las enfermedades sobre las poblaciones de conejo.

Actualmente la gestión de las enfermedades se utiliza en un 15% de las áreas andaluzas, pero sigue siendo una de las herramientas de manejo que menos se aplica debido a su alto costo económico y su relativamente baja efectividad. Como se expone en el Capítulo 2 las herramientas de prevención de enfermedades y parásitos (a través de vacunaciones, desparasitaciones y medicación suplementaria) en las poblaciones de conejo silvestre cuestan un promedio de 4 790 euros al año por cada 2 000 ha. manejadas. Un control efectivo de los vectores de las enfermedades a través de la desparasitación de las madrigueras, como el mostrado por Trout et al. (1992) en Gran Bretaña, no ha sido exitoso al llevarlo a cabo en la Península Ibérica (Osácar et al. 1996). Es posible que esto se deba a una mayor cantidad de vectores en los ecosistemas mediterráneos y a su diferente presencia y fenología por los factores abióticos que los controlan (Cooke 1990; Cooke 1999; Osácar et al. 2001a,b).

Como se muestra en el Capítulo 4, la información existente sobre las vacunas pone de manifiesto que son efectivas a corto plazo (únicamente durante seis meses) evitando el contagio de los animales cuando entran en contacto con la enfermedad (Calvete, 2000; Gortázar et al. 2000). Ello hace que no sean efectivas para su uso en el campo, puesto que los métodos de captura para ser vacunados implican causar estrés y mayores mortalidades en la población que las que causarían las propias enfermedades (Letti et al. 2000). Por este motivo actualmente se ensaya la utilización de virus vivos genéticamente modificados como vacunas recombinantes. En principio, su dispersión en el campo sería la misma que el propio virus, permitiendo teóricamente una inmunización permanente en la población y transmisible entre los diferentes individuos (Bárcena et al. 2000a,b; Torres et al. 2001a,b).

Tanto las vacunaciones como las desparasitaciones (internas y externas) son herramientas básicas asociada a las translocaciones de individuos. Son necesarias para evitar la diseminación de agentes patógenos y sus vectores de unos lugares a otros (Spalding y Forrester 1993; Woodford 1994; Calvete et al. 1997). Sin embargo, algunos autores han establecido efectos negativos de las vacunaciones sobre los conejos. Twiig et al. 1997 observaron reacciones leves en el punto de inoculación, mientras que Calvete et al. (en prensa) observan una mayor mortalidad de los conejos vacunados durante los primeros días después de la translocación. Aunque uno de dichos autores considera que las vacunaciones aumentan la supervivencia de los individuos a más largo plazo (Carlos Calvete, comunicación personal).

Como se muestra en el Capítulo 1, el empleo de translocaciones y de estrategias de gestión destinadas a la prevención de enfermedades y parásitos están asociadas negativamente a la distribución del conejo. Asumiendo que la efectividad de ambas estrategias no es negativa para las poblaciones de conejo, se puede dar una explicación lógica a este hecho. Las translocaciones de conejos se llevan a cabo cuando la abundancia poblacional es escasa o cuando la población se ha extinguido (Calvete et al. 1997). Esto ocurre de forma general en todas las translocaciones de especies silvestres, ya sean cinegéticas o no (Wolf et al. 1996; Griffith, 1989; Fisher y Lindenmayer 2000; Gortázar et al. 2000b, Watson y Thirgood 2001).

La gestión cinegética y la abundancia de conejos

La gestión del conejo es de gran importancia en Andalucía. Como se ha descrito en el Capítulo 2, más del 95% de las áreas andaluzas usan estrategias para recuperar a las poblaciones y su uso ha aumentado en las últimas tres décadas. Las estrategias más utilizadas son llas más sencillas de ejecutar, menos costosas y más tradicionales (los manejos de hábitat y el control de depredadores), mientras que las menos usadas son las más complejas de realizar y más costosas (como las de prevención de enfermedades y parásitos) o menos tradicionales (como la reducción de la caza).

El gasto medio en gestión cinegética de caza menor está entre 4 500 y 8 800 euros al año por cada 2 000 ha., gastándose más dinero en los lugares donde las abundancias de conejo son mayores. Por un lado, esto podría estar indicando que la gestión cinegética se realiza con mayor intensidad en las áreas donde la actividad cinegética es un negocio, puesto que éstas generalmente tienen mayores abundancias. Por otro lado, indicaría la falta de una gestión adecuada en los lugares en los que la abundancia de conejos es más baja. En este sentido conviene recordar, como ya se ha dicho, que las poblaciones a baja densidad pueden sufrir oscilaciones estocásticas que las lleven al colapso con mayor frecuencia que las poblaciones de alta densidad (Lande et al. 1997), por lo que estas poblaciones deberían ser objeto de un mayor interés por parte de la Administración encargada de la conservación natural.

Resultados similares se han obtenido en el Capítulo 3 al analizar los efectos de la caza. Las estrategias de reducción de la caza (reducción del número de cazadores, del número de días de caza, del número de piezas obtenidas y del horario de caza) resultaron más frecuentemente utilizadas en los lugares con mayor abundancia de conejos. En las áreas de baja abundancia aparecen dos decisiones diametralmente opuestas. En la primera se restringe la caza con todas las medidas posibles, lo cual es beneficioso para permitir la recuperación de las poblaciones. Esta era la gestión que se esperaba al realizar el estudio. En la segunda decisión no se utiliza ninguna de estas medidas de restricción de caza a pesar de la baja abundancia de conejo. En este caso, parece que los cazadores no son conscientes de que su participación es crucial para la recuperación de las poblaciones mediante la reducción de la caza. De cualquier modo, muchas de estas áreas pueden corresponder a zonas libres de caza, que con la nueva normativa andaluza de fauna y flora van a ser eliminadas al imponerse la obligatoriedad de su planificación cinegética (BOPA, 2003).

Los efectos de la caza sobre las poblaciones de conejo

Desde el punto de vista ecológico, la caza puede entenderse como la extracción de una especie silvestre del medio en el que vive. Esta extracción afecta a la población de la especie que se caza y, en mayor o menor medida, al ecosistema al que pertenece (Bennet y Robinson 2000a). En el Capítulo 3 se muestra como el período actual de caza es el más desfavorable para el mantenimiento de las abundancias de conejo. De hecho, estos resultados concuerdan con los obtenidos en estudios realizados en otras áreas para establecer el momento óptimo para llevar a cabo un control de las poblaciones de conejo (Darwin y Williams 1964; Smith y Trout 1994; Smith 1997). Lógicamente, si se caza durante la época previa a la reproducción, se extrae un alto porcentaje de hembras adultas lo cual reduce el potencial reproductor de la temporada. Según el modelo, la caza causa menos daños cuando se lleva a cabo al final de la primavera, porque hay más juveniles en la población que absorben la mayor parte de la mortalidad (Beltrán 1991; Villafuerte et al. 1997). Por otro lado, al final de la primavera la abundancia de la población es mayor, por la incorporación de los juveniles en la población, por lo que la presión cinegética empleada también podría ser mayor. La selección de la temporada de caza es una herramienta fundamental en la gestión de las especies cinegéticas, especialmente cuando dichas especies tienen un período reproductor claramente definido. Quizá por ello, la mayoría de los estudios científicos sobre este factor han sido realizados sobre aves acuáticas (Gruver et al. 1984; Kokko et al. 1998; Kokko y Lindström 1998). En estas especies, el período del año es importante porque también está afectado por la cronología de la migración y por la experiencia de los individuos (Dehorter y Tamisier 1998; Heusmann 1999; Madsen 2001).

Los resultados de las simulaciones indican que tanto la caza antes del comienzo del período de reproducción, como la caza en poblaciones de mala calidad (definida ésta tanto desde el punto de vista de la abundancia como de la tendencia poblacional) no son recomendables para la conservación de las poblaciones de conejo. Esto se puede explicar porque las consecuencias de la caza dependen totalmente de la densidad de la población, siendo los resultados mucho más variables o menos predecibles en los casos en que la abundancia de la población sea baja (Milner-Gulland 1997; Lande et al. 1997). La UICN/UNEP/WWF define la caza sostenible en los siguiente términos: la caza es sostenible cuando no afecta significativamente a la población (World Conservation Strategy 1980). Bennet y Robinson (2000b) consideran esta definición demasiado utópica y proponen una definición más laxa: la caza es sostenible si no provoca una tendencia constante y negativa en la abundancia, si no reduce la abundancia a niveles vulnerables o cercanos a la extinción, a niveles en que reduzca el papel ecológico de la especie en el ecosistema o a niveles en que deje de ser un recurso significativo para el hombre. Según estas sugerencias, la caza del conejo en Andalucía debería prohibirse en las poblaciones con tendencia negativa, limitarse en las poblaciones de baja abundancia y en todos los casos la temporada cinegética debería cambiarse al final de la primavera. A pesar de que, como muestran los resultados del Capítulo 3, la mayoría de los cazadores estarían dispuestos a aceptar un cambio en la temporada de caza, es preciso evaluar los posibles conflictos que puedan surgir, como por ejemplo la interacción con otras especies cinegéticas o los posibles efectos de sobrecaza por percibir mayores abundancias.

Por último, y como conclusión al estudio de los efectos de la gestión de la propia actividad y de las especies cinegéticas, se destaca como herramienta imprescindible el seguimiento de las poblaciones. Este seguimiento permite analizar tanto los efectos de los escenarios de caza a que se somete la población como los efectos de las medidas de manejo aplicadas. Quizás el objetivo final de la gestión cinegética deba ser encontrar un “modelo adaptativo” que combine los resultados científicos con los objetivos del gestor, que en muchos casos dependen de la presión de los cazadores y la historia de la actividad cinegética en la zona (Sutherland 2001).

La gestión cinegética y la conservación natural

El 96.8% de la superficie de Andalucía (y el 75% de la superficie de España) está catalogada como terrenos cinegéticos. Los cotos privados de caza suponen en Andalucía más de 7 millones de ha, de los cuales 5 millones y medio corresponden a los cotos de caza menor (el 70% de la superficie de Andalucía) (MAPYA 2000; Consejería de Medio Ambiente 2002).. La gestión cinegética de caza menor en Andalucía es intensa, repercutiendo dichos manejos sobre todo el ecosistema. Por ello, se hace necesario evaluar y guiar los actuales métodos de gestión cinegética tanto desde el punto de vista de las especies hacia las cuales se orienta como hacia el resto de las especies del ecosistema.

En el Capítulo 2 se muestra cómo una mayor intensidad en la aplicación de medidas de restricción de la actividad cinegética está asociada a un mayor nivel de conservación natural de las áreas, estimado éste a través de la cantidad de especies de fauna silvestre que se encuentran en la zona y el valor ambiental de cada una de ellas (basado en su rareza en Andalucía). Las mayores restricciones de la actividad cinegética ocurren en las áreas con un mayor grado de conservación. La restricción de la caza ha sido sugerido para favorecer la conservación de muchas especies (Beringer et al. 1998; Carrillo et al. 2000; Barbosa 2001; Cullen et al. 2001; McComb et al. 2001). Algunos autores han sugerido un mayor control de la presión de caza como medida a tomar para la conservación de ciertos depredadores en los ecosistemas mediterráneos (Castro y Palma 1996; Real y Mañosa 1997). Sin embargo, es también un hecho que la mayoría de las áreas mejor conservadas son gestionadas por la Administración competente en materia de medio ambiente y una de las medidas más utilizadas es la reducción y el control de la caza. A pesar de ello, los espacios protegidos constituyen un escaso porcentaje de las áreas estudiadas, por lo que no se espera que los resultados estén sesgados por la presencia de espacios naturales en la muestra.

En el mismo Capítulo se observa cómo un mayor grado de conservación natural de las áreas se asocia al manejo de hábitat. El manejo de hábitat es una herramienta tradicionalmente usada, tanto por conservadores como por cazadores, para la recuperación o el mantenimiento de un hábitat que favorezca a las especies a las que el manejo va dirigido; por ejemplo, los manejos de hábitat se han mostrado efectivos para el incremento de conejo (Moreno y Villafuerte 1995). Por otro lado, la conservación del hábitat es esencial para la conservar los depredadores amenazados del ecosistema mediterráneo, por lo que los manejos de hábitat que realizan los gestores cinegéticos, aunque no van dirigidos a estas especies, son aprovechados de manera indirecta por ellas (Litvaitis et al. 1996; Real y Mañosa 1997; Carrete et al. 2002). Por ejemplo, en el caso de la conservación del lince ibérico y del águila imperial, es necesario mantener un hábitat adecuado por lo que los manejos están orientados hacia la mejora del hábitat para el conejo (Castro y Palma 1996; Ferrer y Harte 1997; Palma et al. 1999; Rodríguez y Delibes 2002).

Las poblaciones de conejo en Andalucía: el final de una síntesis

Estos últimos párrafos quieren sintetizar las aportaciones realizadas para intentar responder a la pregunta de fondo de la presente Tesis, obviando las ya citadas limitaciones metodológicas expuestas al comienzo de esta Discusión, para permitir una visión más personal sobre los resultados del trabajo realizado.

¿Cómo una especie tan prolífica ha pasado a ser poco abundante y en declive en su área de distribución original?

En esta Tesis se ha constatado que, efectivamente, las abundancias de conejo en Andalucía están seriamente mermadas respecto a los valores anteriores. Las enfermedades parecen haber sido el agente principal del declive del conejo, puesto que la presencia y abundancia de conejo están ligadas en gran medida al potencial de la población para recuperarse tras la entrada de las dos enfermedades (mixomatosis y EHV). Ambas enfermedades parecen seguir teniendo un efecto negativo muy importante sobre la abundancia de las poblaciones que permanecen en la actualidad, especialmente en las poblaciones de menor abundancia.

Queda clara la dificultad para determinar el efecto de las estrategias de gestión de la caza menor sobre las abundancias actuales de conejo o sobre el declive de la especie en una escala regional amplia (como es toda Andalucía). Ello se debe en gran medida a que diferentes estrategias de gestión se aplican de manera conjunta en la misma zona y durante un corto espacio de tiempo, cambiando las estrategias sin dar tiempo a que puedan analizarse los resultados a medio plazo. Por este motivo y porque en Andalucía la gestión es intensa, frecuente e importante económicamente, es necesario profundizar sobre este tema en futuros estudios. A pesar de no poder determinar los efectos de las medidas de manejo, los resultados que se han expuesto en esta tesis indican que son las poblaciones más densas las que se benefician de una mayor intensidad de gestión, que a su vez propicia un mayor nivel de conservación natural. Por el contrario, las poblaciones menos densas están sufriendo una mala gestión cinegética, posiblemente una situación que se ha mantenido a través de los años propiciando el declive de la especie. El problema de gestión que ocurre en estas poblaciones se puede desglosar en dos tipos: la ausencia de gestión y la alta presión cinegética.

Respecto a la propia actividad cinegética, se puede concluir que en el último siglo se ha estado cazando el conejo en la Península Ibérica durante la temporada más adecuada para favorecer el declive de la especie. Este hecho es de suma importancia si, además, se tiene en cuenta que la presión cinegética en las áreas de menor abundancia ha sido muy alta y el comportamiento de las poblaciones menos densas es impredecible y variable.

A través de los resultados obtenidos en la presente Tesis se puede realizar una reconstrucción hipotética sobre como ha podido ser el declive del conejo en Andalucía (y por tanto en el resto del área de distribución original de la especie). Todos los factores aquí mencionados posiblemente han estado actuando sobre las poblaciones de conejo de manera conjunta y sobre todo, a lo largo de muchos años. Si se considera que los efectos actuales sobre las poblaciones menos densas han podido ocurrir en el pasado en múltiples ocasiones, obtendríamos un patrón de declive del conejo en el que son las poblaciones menos densas las que tienen todas las papeletas para extinguirse. E inicialmente las poblaciones menos densas debían distribuirse en los ambientes menos óptimos para el conejo. Este patrón sería confirmado por la distribución actual de las poblaciones. Estas poblaciones presentan un patrón espacial que puede relacionarse con los paisajes preferidos por el conejo. Las mayores abundancias se encuentran en los paisajes que le son más óptimos, en base a su condición de presa (generalmente mosaicos de vegetación natural y cultivos o pastizales).

What next?

Esta es la pregunta final tras todo trabajo de investigación:

¿qué líneas de trabajo se perfilan como continuación de los resultados expuestos en la presente Tesis?

La contestación se puede desglosar en función de las áreas de investigación más importantes que se incluyen en la tesis:

- La gestión cinegética

La gestión cinegética de caza menor a una escala regional amplia necesita un mayor esfuerzo en la coordinación de las medidas de gestión a nivel temporal y espacial. La utilización de estrategias múltiples de gestión debe basarse en unos objetivos claros y mantenerse a medio-largo plazo de manera que se pueda estimar su eficacia. Para ello, las Administraciones encargadas deben favorecer el estudio y la creación un sistema regional coordinado de monitorización y gestión. Dicho sistema podría estar basado, por ejemplo, en las actuales unidades de gestión que son los cotos de caza, lo que implicaría una mayor participación de los cazadores en esta gestión coordinada. Esta monitorización debe ser guiada desde una perspectiva científica que a largo plazo pueda ofrecer resultados claros sobre la efectividad diferencial de las estrategias utilizadas en la gestión cinegética. Dichos resultados deben volcarse a las unidades de gestión que las integran.

- La conservación natural

Se ha comprobado que la intensidad de las medidas de gestión de caza menor en los lugares de alta abundancia de conejo están relacionadas con un mayor nivel de conservación natural. Sin embargo, esta gestión cinegética (aplicada en la mayoría de los casos por los cazadores) debe ser orientada para que no existan conflictos con el resto de fauna silvestre no cinegética. En este sentido, una línea de investigación aplicada que actualmente se está investigando, es el estudio de los conflictos entre la caza y la conservación en un marco tanto ecológico como socio-económico (RegHab, 2002). Por otro lado, queda un vacío de gestión en los lugares de baja abundancia de conejo, sobre los que se debe centrar la conservación natural.

Posiblemente, la recuperación de los paisajes óptimos para el conejo y una mayor conexión entre dichos paisajes favorecerían los niveles actuales de conservación natural en Andalucía. Queda abierta una línea para estudiar de forma más profunda las relaciones entre el hábitat y el conejo siguiendo una dimensión temporal y considerando, por un lado, que estos cambios en el paisaje pueden ser los que han inducido la desaparición del conejo, y por otro lado, que la propia desaparición del conejo ha podido provocar un cambio paralelo en la estructura del paisaje, que frenaría su re-colonización.

- La investigación básica

Además de las líneas de investigación aplicada sugeridas anteriormente, queda una línea abierta de investigación básica sobre las enfermedades del conejo desde el punto de vista ecológico, especialmente sobre la EHV, como han propuesto otros autores (Calvete 2000; Cooke 2002). Investigación sobre las cepas no patógenas en España, sobre la dinámica de las enfermedades en las poblaciones de conejo, sobre los factores que la afectan y sobre la persistencia y dispersión del virus a escala temporal y espacial.

Por último, queda abierto un campo muy interesante de investigación desde el punto de vista ecológico, social y económico de la diferente visión del conejo a nivel mundial. La integración de las dos visiones, la especie invasora y la especie a conservar, constituye un amplio marco para resolver estudiar los conflictos a los que la especie se enfrenta en este nuevo milenio.

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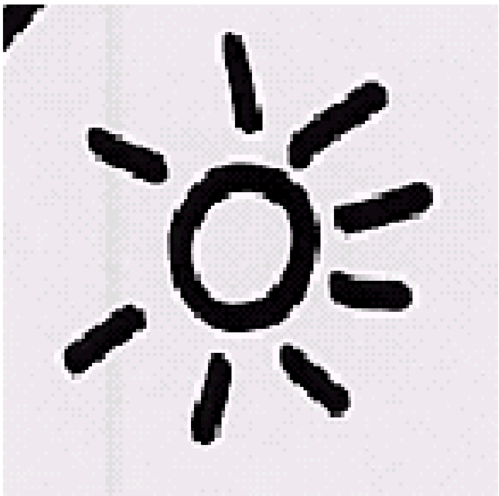

CONCLUSIONES

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1. La presencia actual de las poblaciones de conejo en Andalucía responde a un patrón espacial relacionado con los paisajes más óptimos para el conejo. Las mayores abundancias están asociadas a un mayor número de ecotonos, mayores superficies de vegetación natural y de cultivos mixtos. Menores abundancias están asociadas con el abandono del campo.

2. La presencia actual de las poblaciones de conejo está relacionada con un mayor grado de recuperación de las poblaciones tras la entrada de la mixomatosis y de la enfermedad hemorrágico vírica. Dichas enfermedades han tenido y siguen teniendo un efecto negativo muy importante sobre las abundancias poblacionales.

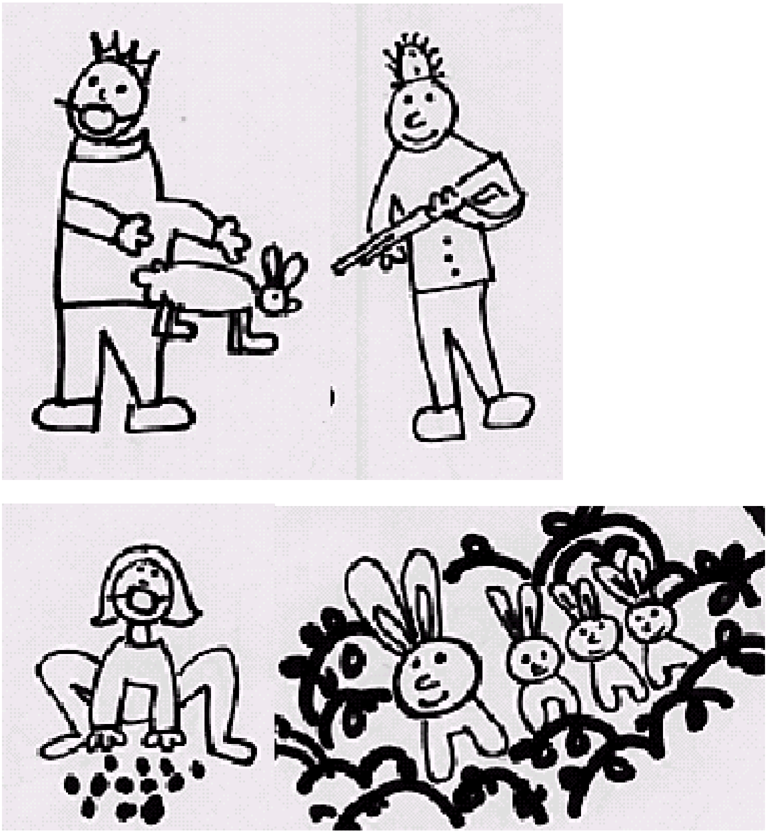
3. La presencia actual de las poblaciones de conejo se relaciona con las estrategias de gestión. La gestión de la caza menor, en la cual se engloban las estrategias de gestión del conejo, es muy frecuente e intensa en Andalucía y se ha incrementado en las últimas décadas. Las estrategias más utilizadas son los manejos de hábitat y el control de depredadores.

4. En las áreas con mayor abundancia de conejo se realiza una mayor intensidad de manejo, y esta intensidad está relacionada con un mayor grado de conservación natural. En las áreas donde el conejo es menos abundante, la gestión es escasa, y deberían ser objeto de mayor esfuerzo de conservación.

5. La reducción de la presión cinegética se utiliza en más del 75% de las áreas andaluzas. Sin embargo, su utilización es más frecuente e intensa en las áreas de mayor abundancia de conejo. Los lugares donde el conejo es escaso sufren una mayor presión cinegética que donde el conejo es abundante. Los resultados de las simulaciones de caza indican que cuando el conejo es escaso o la población no crece los efectos de la presión cinegética producen el colapso de la población. Por ello, es necesaria una mayor participación de los cazadores, a través de la reducción de la caza, para conservar estas poblaciones de baja abundancia de conejo.

6. Los resultados de las simulaciones sobre la temporada de caza indican que la temporada actual de caza es la más perjudicial para la conservación de las poblaciones de conejo. La temporada que afecta menos a las poblaciones es el final de la primavera, una vez finalizado el período de reproducción, por la contribución de los ejemplares juveniles en la bolsa de caza.

7. Las investigaciones actuales sobre virus modificados genéticamente para el control del conejo, a través de inmunocontracepción mediada por virus, ponen en peligro a las poblaciones ibéricas de conejo, ante la falta de normativas legales nacionales e internacionales operativas. De las misma manera, las vacunas recombinantes que se ensayan en España pueden poner en peligro la gestión del conejo en aquellos lugares en los que actúa como una especie invasora.



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