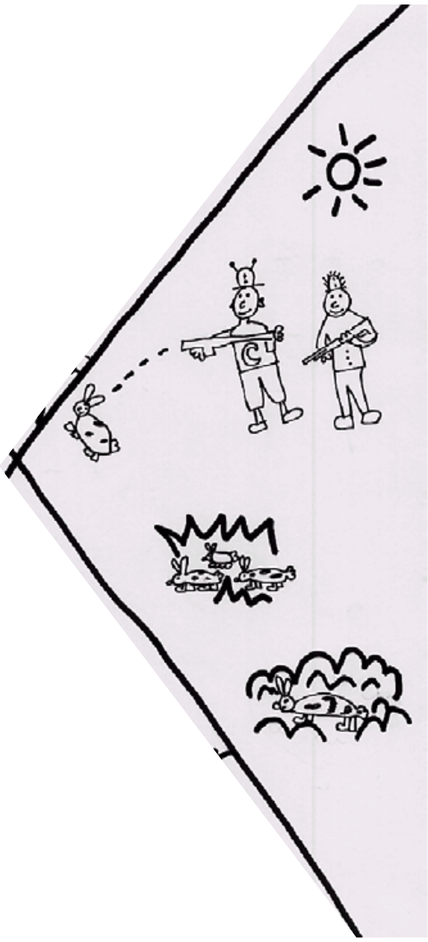

CAPÍTULO 3

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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"A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong when it tends otherwise"
Leopold 1933. Game Management

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 had collected insufficient data to distinguish seasonal differences, the relevant parameters were set to the average 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 leads to a higher frequency of the consumption of animals dead from disease as well as a higher frequency of predation not only of low body condition animals, but also of sick rabbits (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 hunting would cause such a 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:

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

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:

$$Dn_{(t)} = 0.5 * Da_{(t-1)} * F * R * \Delta t \qquad \text{eqn 2}$$

$$Dj1_{(t)} = Dn_{(t-1)} * (1-Mn) * \Delta t \qquad \text{eqn 3}$$

$$Dj2_{(t)} = Dj1_{(t-1)} * (1-Mj) * \Delta t \qquad \text{eqn 4}$$

$$Dj3_{(t)} = Dj2_{(t-1)} * (1-Mj) * \Delta t \qquad \text{eqn 5}$$

$$Dj4_{(t)} = Dj3_{(t-1)} * (1-Mj) * \Delta t \qquad \text{eqn 6}$$

$$Da_{(t)} = Dj4_{(t-1)} * (1-Mj) * \Delta t + Da_{(t-1)} (1-Ma) * \Delta t \qquad \text{eqn 7}$$

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 contribution to 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 zero and the variance of each parameter, which 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 the hunting component, because the 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 the 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 shown 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. This assumption both simplifies the model and means that we are 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 hunting, the most severe situation for a rabbit population, according to which hunters discriminate rabbit body size and shoot only adults; and (2) non-age-selective hunting, 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. This hunting strategy seems the most realistic; however, to our knowledge, there are no available data on the proportion of juveniles/adults hunted.

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). The geographic coordinates of survey points were selected using the geographic information systems software IDRISI (Eastman, 1997). Selection was carried out by means of a step-random sampling based on altitude and topography, to exclude areas unsuitable for rabbits. Areas lower than 1200 m in altitude and with slopes of less than 30% were favoured (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 an adequate person to interview (i.e., a person who was familiar with the hunting association decissions). 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, which was selected on the basis of a careful assessment showing it to be representative of 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 (i.e. number of hunting days, number of hunters per day, number of rabbits hunted per day, and/or 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.

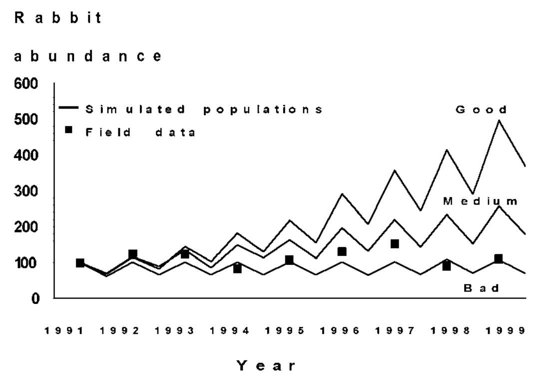

Figure 1. Population size estimates from modelling (black lines) and from vehicle surveys (black squares). Plots show the yearly maximum and minimum number of rabbits from simulations and the yearly average of rabbits seen per kilometre, respectively. Both data sets were normalized by setting the initial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

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

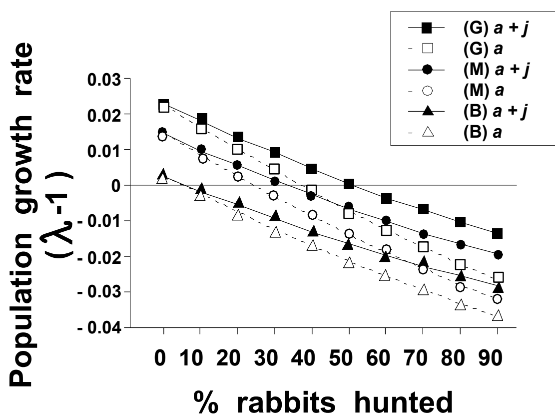

Figure 2. Effect of hunting rate on population growth rate (λ - 1) in good (G), medium (M) and bad (B) rabbit populations when a non-age-selection strategy (*a* + *j* : adults and juveniles hunted) or an age-selection strategy (*a* : only adults hunted) is simulated. Hunting rates are simulated in the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

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).

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.

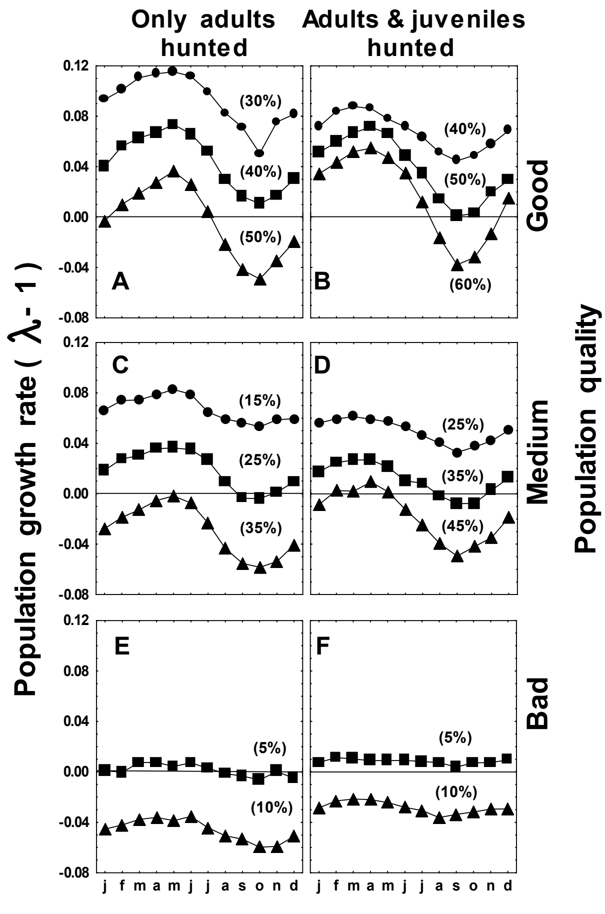

Figure 3. Effect of high (triangles), medium (squares) and low (circles) hunting rates on population growth rate (λ - 1) simulated during a consecutive 3-month period. (A). Good population, only adults hunted. (B) Good population, adults and juveniles hunted. (C) Medium population, only adults hunted, (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

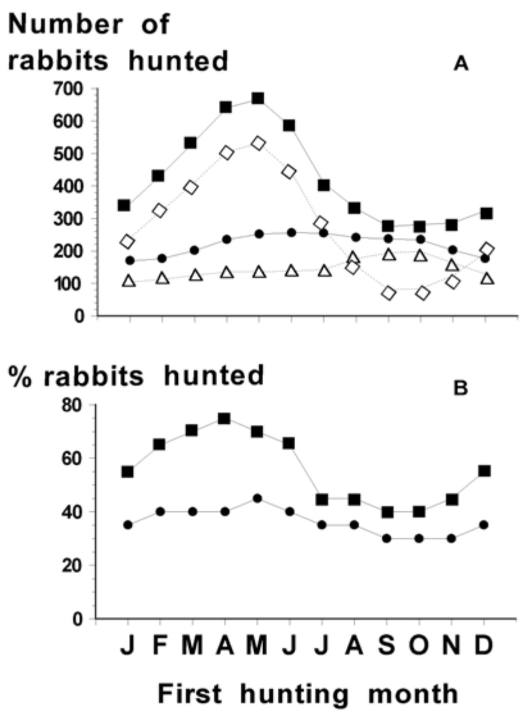

Figure 4. Maximum number (A) and maximum percentage (B) of rabbits hunted, while maintaining a stable good population when hunting is simulated during a consecutive 3-month period. Black circles: simulations of age-selective hunting (only adults hunted). Black squares: simulations of non-age-selective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

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 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).

The sample sizes (*n*) of different analysis varied from 204 and 230: pellet counts could not be performed in nine areas; the interviewer could not find an adequate person to interview in 16 areas, and both situations occurred together in an additional 19 areas (Fig. 1). Some other areas were partly invalid when the interviewed did not answered all questions. The mean size of the hunting areas surveyed was 3000 ha (range = 250–75000 ha, n = 240); thus, the total area surveyed covers 10.6% of southern Spain (the Andalusia region covers 8723200 ha), and 16.8% of the total official area for private small game hunting.

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,

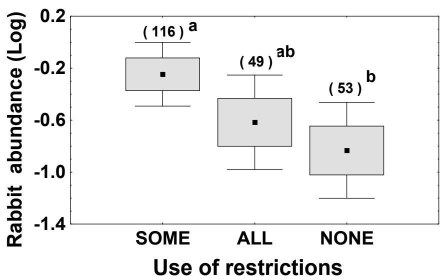

Figure 5. Rabbit abundance (log-transformed pellet number / 0.5 m^2) at different intensities of hunting restriction. Groups that were not significantly different based on Tukey post-hoc test share a common letter. Numbers in parentheses indicate the number of valid questionnaires. Central black square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

but without significant differences with the other two groups; therefore, areas with all restrictions applied may have a broad range of rabbit abundance.

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, the exact harvest rates or number of harvested rabbits derived from the model cannot be used as management tools; this data can only be used to assess 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 assumptions were made to simplify the model. For example, the model is density-independent and hunting is modelled without compensatory responses. The lack of compensatory reductions in mortality or increases in fecundity will 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, the issue of whether hunting mortality in natural populations is compensatory or additive 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 (82.8% of southern Spain) 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, conservation agencies should strive to ensure the effective management of hunting resources in areas of potential interest to predators. In the current situation of declining wild rabbit populations, hunting restrictions should be applied in such areas to maintain and increase rabbit abundance so as to conserve the predator community.

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