Original investigation

The negative impact of heavy rains on the abundance of a Mediterranean population of European rabbits

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Abstract

European rabbits, Oryctolagus cuniculus, are the basic prey of several endangered predators and an important hunting bag in the area of its origin in southwestern Europe. Conversely, they are considered an undesirable species in other areas where they were introduced. Therefore, there is great interest in understanding the factors that influence population dynamics and abundance of this species. I studied the effects of relatively common heavy rains on inter-annual variations in rabbit density in four habitats of Doñana National Park and surrounding areas (southwestern Spain) during several years when rainfall was either lower or higher than average. I estimated spring and autumn rabbit densities by line transect sampling between autumn 1993 and autumn 1998, and counted rabbit warrens and entrances in two of the habitats (one with and the other without scrubland vegetation) in 1995, 1996 and 1997. Rabbit density significantly decreased in all habitats during the rainy years, densities being on average 5.3 and 4.6 times lower for spring and autumn censuses, respectively. Both number of warrens and entrances significantly decreased after two consecutive years of heavy rain in both habitat types, although in the scrubland habitats some recovery was observed during the second consecutive year of heavy rains. The area where warrens were apparently free of the effects of rains was only between 2.7 and 3.8% in the open habitat and 21.5% in the scrubland. At least for the open habitat, no clear relationship was observed between the height above sea level and whether warrens were affected by rain or not. The results indicate that heavy rains may be an important factor decreasing rabbit density, at least in flat areas, by negatively acting on warrens during the breeding period.

Key words: Oryctolagus cuniculus, flooding, warrens, interannual density

Introduction

The European rabbit, Oryctolagus cuniculus, is a species of extraordinary but contrary concern in both the area of its origin and places where it was introduced (Thompson and King 1994). In the areas of origin in southwestern Europe (Branco et al. 2000), rabbits are an important hunting bag and the staple prey of many endangered predators such as Iberian lynx, Lynx pardinus, or imperial eagle, Aquila adalberti.
(Delibes and Hiraldo 1981; Rogers et al. 1994), but in many other parts of its distribution, they are considered an undesirable species due to economic losses in agriculture or to damage of conservation actions for endangered species (e.g. Kolb 1994). Therefore, population dynamics of rabbits have received considerable attention by both field and theoretical biologists (e.g. Myers and Parker 1974; Pech et al. 1992; Smith and Trout 1994; Gibb and Fitzgerald 1998).

It has been well documented that rabbit populations undergo high intra-annual oscillations in abundance as a direct consequence of seasonality in reproduction (Delibes and Calderon 1979), triggered by the availability of food (Wallage-Drees 1983; Villafuerte et al. 1997). In Mediterranean environments of Europe, the breeding period can extend from mid autumn to the end of spring (Rogers et al. 1994). Myxomatosis, which is usually more virulent during summer and autumn in Europe, and viral hemorrhagic disease (RHD) have also a significant effect on intra-annual variations in rabbit numbers (Rogers et al. 1994; Villafuerte et al. 1994; Marchandeu et al. 1998; Mutze et al. 1998). In the same way, rabbit abundance also varies widely among years (e.g. Myers and Parker 1975; Rogers et al. 1994; Palomares et al. 2001), although not in a predictable way as in snowshoe hares, Lepus americanus, or small mammal populations in northern ecosystems (Krebs 1996). Between-year oscillations in rabbit abundance have been related to variations in the incidence of myxomatosis or RHD (Soriguer and Rogers 1981; Villafuerte et al. 1995), food availability (Villafuerte et al. 1997; Gibb and Fitzgerald 1998), drought periods (Myers and Parker 1975), or predator abundance (Pech et al. 1992; Banks 2000).

Here, I studied the effect of heavy rains on rabbit density on an inter-annual basis in an area of the Iberian Peninsula, where the European rabbit has its evolutionary origin (Branco et al. 2000).

**Material and methods**

**Study area**

The study was carried out in the north of Doñana National Park and surroundings, in an area called Coto del Rey (south-western Spain; 37°9'N, 6°26'W) between November 1993 and October 1998. The Doñana National Park is a flat, sandy area containing three main biotopes: scrubland, dunes, and marsh (Valverde 1958). The climate is Mediterranean sub-humid, with an annual rainy period usually starting in autumn and ending in spring, and a dry period when rain is very rarely lasting 3–5 months around summer. Annual rainfall is between 500 and 600 mm, although during the study period rainfall was lower than average during the first 2 years (annual totals of 413 and 253 mm, respectively; annual rainfall measured between dry seasons), followed by 3 rainy years (mainly the first 2 years) when annual totals were 1032, 885, and 629 mm, respectively. During these years, several times monthly rainfall exceeded 200 mm (Fig. 1a). In addition, the number of days with heavy rains (here considered as days with rainfall ≥25 mm) was much more frequent from winter 1995/96 onward than previously (Fig. 1b).

The low rainfall years of the study period were a continuation of a longer period that started in 1990/91 with rainfall close to or lower than average (480 mm for 1990/91, 494 mm for 1991/92, and 374 mm for 1992/93).

Coto del Rey is characterized by a mixture of relatively well-conserved areas of Mediterranean scrubland and ash stands where Pistacia lentiscus shrubs predominate, plantations of mainly Pinus pinea, and cleared areas for cattle grazing with isolated trees (Quercus suber and Olea europeae); marsh extends to the south of the study area. Ground heights in the study area range between 1–6.4 m a.s.l. More information on the study area can be found in Palomares et al. (2001).

The effect of the rain on rabbits was studied in 4 areas/vegetation types of Coto del Rey: Mediterranean scrubland, ash stands inside the National Park, ash stands outside the National Park, and pastureland. The first three areas were scrubland habitats, while the last was an open habitat (Palomares et al. 2001).

**Rabbit density**

Rabbit density was estimated twice per year between autumn 1993 and autumn 1998 in the 4 areas/vegetation types described. Rabbits were counted in October–November and June each year (a priori times of the lowest and highest rab-
Fig. 1. Monthly rainfall (a) and number of days with rainfall higher than 25 mm (b) between December 1992 and October 1998 in a meteorological station situated within the Doñana National Park to 12 km from the study area.

bit density; Soriguer 1981). Rabbit density in each area was estimated by line transect sampling and the program TRANSECT (Burnham et al. 1980; Buckland et al. 1993). Transects ranged from 1100 m to 1870 m per habitat and were slowly (ca. 1.5–2.5 km/h) surveyed on foot at dusk (15–20 min before sunset to 25–30 min after sunset). In total, there were 72 days of valid censuses, during which 110,580 m were walked and 3,176 rabbits were counted. More details on the methodology can be found in Palomares et al. (2001). Results are given as mean rabbit density and 95% confidence intervals of the estimated density.

Significant differences in rabbit densities between censuses carried out in drought (autumn 1993–autumn 1995) and rainy (spring 1996–autumn 1998) study periods were tested by general lineal mod-
els using the GLM procedure in SAS (SAS INSTITUTE INC. 1990), and a Type III sums of squares. In addition to general weather conditions, season and habitat were also included in the model to control for the possible effect of these variables on results of the test.

Warren surveys

Warren surveys were carried out in the most representative and distinct habitats of the study area (Mediterranean scrubland and pastureland) between April and October of 1995 (the end of inter-years drought period) and at summers 1996 and 1997 (both years with winters of heavy rains; see Fig. 1). Areas surveyed in each habitat were the same 342 ha each year for the pastureland and 126 ha for 1995 and the same 23 ha (included within 126 ha of 1995) for both 1996 and 1997 at the Mediterranean scrubland. Warren surveys consisted of recording the size (i.e. number of entrances) and position of every warren within these areas in U.T.M. coordinates using a Global Positioning System (GPS; model Garmin 75). Used and unused entrances were counted for each warren, but not collapsed ones. Used entrances were those with clear signals of use such as clean paths, absence of cobweb or presence of rabbit tracks, whereas unused ones lacked these signals. In the scrubland habitats of the study area, rabbits mainly use warrens during the breeding period (PALOMARES 2001). For warren mapping, teams of 3–5 persons slowly walked small sections of the area inspecting for warrens everywhere. Differences in the total number of warrens and entrances recorded in 1995 (before heavy rains) and 1996 and 1997 (after one and two years respectively) of heavy rains were tested by Chi-square tests considering the data from each habitat type independently.

In addition to these warren surveys, the immediate effect of rain on warrens was field-assessed on 2–3 February 1996 in the pastureland habitat, and on 12–13 January 1997 in both pastureland and Mediterranean scrubland habitats. In these surveys, I searched for warrens and considered that warrens were not affected by rain if they had at least one entrance apparently free of the effect of rain (i.e. the visible part of the entrance was not flooded or blocked by sand). Obviously, this approach was conservative because it is reasonable to think that in many cases warrens could actually be flooded although water could not be seen. These surveys were carried out 2–3 days after heavy rains in 1996 (22 l/m²/day), and 5–6 days after heavy rains in 1997 (41 l/m²/day).

Results

Rabbit density

Rabbit density oscillated between 55 and less than one individual per hectare in the Mediterranean scrubland during June 1994 and pastureland during both October of 1997 and 1998, respectively (Fig. 2). After the start of the rainy period in November 1995, rabbit density was lower in all habitats (Fig. 2). Density of rabbits was on average 5.3 times lower (range = 2.6–9.0 for the different habitats) in the rainy years than in the drought years for the June censuses, and 4.6 times lower (range = 2.4–8.3) compared with the October censuses. Differences between censuses carried out during drought and rainy periods were highly significant ($F = 74.03$, d.f. = 1, $p < 0.001$), once the effect of season and habitat was controlled.

Effect of rain on warrens

Warren densities in summer 1995 were 7.0 and 1.5 per hectare for the habitats Mediterranean scrubland and pastureland, respectively (Fig. 3). Density of total entrances were 38.1 and 18.2 per hectare for the same habitats (Fig. 3). Both the number of warrens and entrances decreased in both habitats after the first year of heavy rains (Fig. 3), although significant differences between 1995 and 1996 for both habitat types combined were only detected for the number of entrances ($\chi^2 = 17.7$, d.f. = 1, $p < 0.001$). During the second year of heavy rains, the number of warrens and entrances continued to decrease in the pastureland, but not in the Mediterranean scrubland where some recovery was observed (Fig. 3). This recovery was also observed in the direct rabbit censuses, which mirrored quite well what happened with warrens and entrances in both habitat types (Figs 2 and 3). The overall effect of rain on warrens after the two years of heavy rains was significant both for warrens ($\chi^2 = 28.5$, d.f. = 1, $p < 0.001$) and entrances ($\chi^2 = 161.0$, d.f. = 1, $p < 0.001$).
The winter surveys of the study area during 1996 and 1997 showed that not more than 3.8% in 1996 and 2.7% in 1997 of pastureland, and in 1997 21.5% of Mediterranean scrubland were at least partially free of the effect of the rain on warrens. In the pastureland no clear relation was observed between warrens with at least one entrance free of the effect of rain and the height above sea level. These warrens were located in 8 different sites that coincided quite well in both years and were between 2 and 6 m a.s.l. Many other warrens located at the same height were affected by rains. This probably depended more on the topography of the ground in each site.
Fig. 3. Summer warren and entrance densities in two habitats (Mediterranean scrubland and pastureland) of the Doñana National Park for 1995, 1996 and 1997.

where warrens were built than on the elevation above sea level. Most entrances were either flooded, or blocked by the ground falling off on the top of the entrance, or blocked by the sand carried down by water during the rain (Fig. 4). Conversely, the results were different in the Mediterranean scrubland as most warrens were not fully affected by rain (all except one) and situated higher than 4.6 m a.s.l.

Discussion

Factors determining the variations in rabbit density among habitats in the study area have already been discussed elsewhere (Palomares et al. 1996; 2001; Palomares and Delibes 1997), therefore I will focus here on between-years variations and the role of heavy rains.
The data presented suggest that an excess of rain, concentrated in a few months and even days, negatively affected rabbit populations of the study area. The effect was simultaneous and significant in different habitats, although rabbits in open habitats suffered the highest negative impact. Heavy rains acted directly, by flooding and collapsing most warrens, at the time of the year when rabbit reproduction is common in the study area (DELIBES and CALDERÓN 1979). Flooding and collapsing of warrens most likely directly killed most young rabbits that were unable to escape. COPSON et al. (1981), PARER et al. (1987) and Gibb (1993) reported young rabbit deaths in warrens due to wet weather. In addition, most rain in the study area was concentrated at the end of autumn and beginning of winter, the time of first litters (DELIBES and CALDERÓN 1979; CALZADA 2000). Young rabbits born at these times of the year are more healthy and experience a higher probability to survive than young rabbits born later (RICHARDSON and Wood 1982; Webb 1993). Furthermore, rabbits born at these times became reproductively active during the same breeding season. Therefore, the negative effect of rain on rabbit population dynamics is likely to be profound, as it hit the
more potentially productive fraction of young rabbits. Other factors such as the RHD could have caused the declined observed in the rabbit populations of the study area. Although this hypothesis cannot be totally discarded, it seems unlikely since in Doñana RHD arrived in 1989 (Villafuerte et al. 1994), and during both dry and wet years along the study, a few rabbits were found dead of RHD in the study area (C. Gortazar, pers. comm.; P. Matín, pers. comm.).

Even though rabbit populations in both open and scrubland habitats suffered from the negative effect of heavy rains, the effect was lower in the scrubland. This was probably because warrens were less affected in scrubland than in open habitats. There was even a slight recovery of warrens in the scrubland habitat during the second year of heavy rains. In scrubland habitats, most of the warrens are built between roots of tall shrubs (Palomares 2001), which can therefore help to prevent them from collapsing and being fully blocked by water-deposited sand as was very frequent in the pasturage. The recovery in Mediterranean scrubland could be produced by rabbits selecting new and safer places to build the warrens in the second year of heavy rains. However, in the pasturage, rabbits must be limited in their building capabilities because they are more exposed to predation while excavating warrens than in the Mediterranean scrubland (Villafuerte and Moreno 1997). In fact, in the pasturage, warren distribution seems to mainly be the consequence of human management of the area carried out in 1970 when scrubland vegetation was removed and warrens destroyed except in a few places (Palomares et al. 1996). Since then the spread of rabbits over the full area has been limited.

In this study, I show that inter-annual variations in rabbit abundance may also be caused by heavy rains, which had a particularly negative effect in altered-open habitats. However, the continuous decline observed in rabbit populations during the last decades in the Mediterranean ecosys-

tems where they originated (Rogers et al. 1994) may have been caused by other factors. On this larger temporal scale, competition with larger herbivores (Soriguer 1983), mesopredator release due to decline in numbers of top predators (Palomares et al. 1995), loss of traditional land management practices (Moreno and Villafuerte 1995), arrival of myxomatosis first (Rogers et al. 1994), and later the viral hemorrhagic disease (Villafuerte et al. 1995; Gortazar 1997), have been proposed as potential factors explaining the decline. Probably all these factors have acted jointly on rabbit populations to produce their present status.

Results of this study can have important management implications for rabbits. In addition to an important hunting bag (Rogers et al. 1994), rabbits are also the prey of species of great conservation value such as the Iberian lynx and the Spanish imperial eagle. Therefore, rabbit recovery plans are being undertaken in many places of the Iberian Peninsula (e.g. see Gortazar et al. 2000), including the Doñana region. Amongst the management activities undertaken, building of artificial warrens is common (Gortazar et al. 2000; Sanz-Zuasti and Pablos 2000). This study indicates that in flat or sandy areas, warrens should be built in places with low probability of being affected by heavy rains, perhaps simulating the levees that rabbits frequently use to built their warrens in the Camargue (Rogers 1981).

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Zusammenfassung

Der negative Einfluss von starken Niederschlägen auf die Abundanz einer mediterranen Population europäischer Wildkaninchen


References


Heavy rain impact on European rabbits


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