

Red foxes (*Vulpes vulpes*) use rabbit (*Oryctolagus cuniculus*) scent marks as territorial marking sites

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Received: 18 December 2007 / Accepted: 2 May 2008 / Published online: 4 June 2008
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Abstract One of the functions of chemical communication is territorial signalling. To achieve this, animals should mark their territories in a manner that increases the detectability of the marks, thereby maximising the probability that other animals detect the scent marks. In this study, we focused on the scent-marking behaviour of red foxes in relation to the abundance of their main prey, the European rabbit, in a suburban forest in Madrid, Spain. Our results reveal that foxes scent-marked more and increased the detectability of their marks in areas of higher rabbit density. It would appear that foxes defend food resources from competitors by increasing the number and the detectability of their scent marks.

Keywords Chemical signals ·
Predator–prey interactions · Rabbit · Red fox ·
Territorial marking

Introduction

The capacity of an animal to gather information from its environment has direct consequences on its fitness (Welton et al. 2003; Dall et al. 2005). Although animals may use any of their different sensorial channels to acquire this information, most mammals are nocturnal and live in dense vegetation and, consequently, olfactory sensorial data play a dominant role (Ralls 1971; Johnson 1973). Scent marking behaviour serves several functions (Eisenberg and Kleiman 1972; Halpin 1986; Wirant and McGuire 2003), including

the defence of the territory (Gosling 1982). One primary aim of animals appropriately scent-marking their territories, which would include marking and renewing the scents, is to demonstrate their competitive ability (Gosling 1982). An important feature of scent marking is that other individuals should be able to easily detect the marks (Gorman and Trowbridge 1989). Indeed, many studies have highlighted the association of scent marks with structural characteristics of the environment, such as landmarks (Gorman and Mills 1984; Alberts 1992; Roberts 1997; Gosling and Roberts 2001). In this context, faeces are especially advantageous in comparison to urine and gland secretions because they add a visual component to the chemical one. This visual component increases the probability of detection as well as the permanence of the mark (Macdonald 1985). Many mammals are known to scent mark their territories with faeces (Roper et al. 1993; Gese and Ruff 1997; Brashares and Arcese 1999; Hutchings and White 2000; Begg et al. 2003).

We conducted a study aimed at assessing the scent-marking behaviour of foxes (*Vulpes vulpes*) in relation to the presence of rabbits (*Oryctolagus cuniculus*). Both species rely largely on chemical communication (Mykutowycz 1968; Henry 1977; Bell 1980). Moreover, there is evidence that the scent-marking behaviour of foxes and rabbits follows a well-defined pattern and that both use clearings and landmarks to deposit their marks (Monclús and Miguel 2003a, b). Therefore, in those places where fox and rabbit coexist, there could be a conflict between the scent-marking behaviour of both species. We determined the spatial relationship between fox and rabbit. The results of previous studies suggest that foxes defend their food resource from conspecific and heterospecific competitors (Monclús and Miguel 2003a) and that rabbits constitute the main food item in the study area. Therefore, we would

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expect to find that foxes scent-mark more and increase the detectability of their marks in those areas where rabbit density is higher—in order to defend the main food resource. We considered differences in accessibility, disposition and connection to conspicuous elements in relation to rabbit density.

Materials and methods

The study was carried out in central Spain (Madrid) at an altitude of approximately 700 m a.s.l., UTM (Universal Transverse Mercator) coordinates 30TVK48. It is a suburban 300-ha Mediterranean holm oak forest (*Quercus ilex* ssp. *ballota*) with interspersed pine plantations (*Pinus pinea* and *Pinus pinaster*).

The study was conducted from October 2005 to April 2006. We used 25 fixed plots, each 50 × 50 m, randomly chosen, where we recorded rabbit density and fox scent marking. In order to have plots that were independent in terms of rabbit population, we ensured that the minimum distance between two plots was larger than the averaged diameter of a rabbit population (Parer 1982; Monclús and Miguel 2003b). The plots were visited weekly, and new fox faeces were recorded (see further details below). The rabbit density of each plot was determined using pellet counts as an estimate of the actual density of rabbits (Palomares 2001). In each plot, we used four grids, each measuring 1 × 1 m. We removed all of the pellets within the grids, and 1 week later we counted the new pellets. Since rabbit pellets are susceptible to be affected by weather factors, such as heavy rain, sunlight or vegetation characteristics (Taylor and Williams 1956), we corrected for the decay rate. We used an additional grid where a known number of fresh faeces were deposited. One week later, coinciding with the count of the new pellets in the 1 × 1-m grids, the control pellets were counted. We estimated the index of abundance, relating the number of pellets found (F) with the time between both collection days ($t = 7$ days), the defecation rate, $D = 560$ pellets/day (Taylor and Williams 1956) and the surveyed area (A). The formula utilised was $N_r = \frac{F}{tDA}$. The index of rabbit density varied among plots and the average was 21.93 ± 12.94 SD. We performed a median cut (21.56) and divided the plots into high- ($n = 12$) and low- ($n = 13$) density plots.

For every fox faecal sample present in the plot, we recorded the following data:

1. The accessibility of the mark to other individuals. We considered two main locations: roads and clearings. All paths were considered to be roads, regardless of width; clearings were defined to be clearings in the wood and the intersections.

2. Association or not to remains of rabbit activity. We considered that fox faeces were associated when they were directly located on a latrine or on a pawscrape.

We measured the availability of clearings and roads in each of the 25 plots. In 16 of the 25 plots we also scored the availability of potential landmarks, which consisted of remains of rabbit activity (latrines, pawscrapes) by measuring the number of latrines and pawscrapes as well as the area that they occupied. With the values obtained, we calculated the expected frequencies of occurrence of the associations, considering a regular distribution of the fox faeces in the plot.

Our data did not follow a normal distribution so all analyses were non-parametric. First, we analysed the general pattern of the scent-marking behaviour of foxes, then we considered the availability of the different landmarks to assess whether foxes selected special places to locate their scent marks. All analyses were performed in STATISTICA ver. 6.0 (StatSoft, Tulsa, USA).

Results

We found significantly more fox faeces ($n_{\text{total}} = 335$) where the density of rabbits was higher (Mann–Whitney U test: $Z = 2.148$; $n_{\text{high}} = 12$, $n_{\text{low}} = 13$; $P = 0.031$). We also found more faeces deposited in clearings than on roads (Wilcoxon matched pairs test: $Z = 2.104$; $P = 0.035$). However, the number of faeces deposited in clearings did not differ between plots with a high density of rabbits and those with a low density (Mann–Whitney U test: $Z = -0.835$; $n_{\text{high}} = 12$, $n_{\text{low}} = 13$; $P = 0.437$) nor did the number of faeces on roads ($Z = -0.876$; $n_{\text{high}} = 12$, $n_{\text{low}} = 13$; $P = 0.381$).

There were more fox faeces associated to rabbit remains in those plots where the rabbit density was higher (Mann–Whitney U test: $Z = 2.208$; $n_{\text{high}} = 12$, $n_{\text{low}} = 13$; $P = 0.026$; Fig. 1). Foxes associated their marks to rabbit remains significantly more than expected (Wilcoxon matched pairs test: $Z = 2.741$; $P = 0.006$) and higher than would be expected if at random ($Z = 2.840$, $P = 0.004$ and $Z = 2.637$, $P = 0.008$, for latrines and pawscrapes, respectively). Foxes defecated on pawscrapes more than on latrines (Wilcoxon matched pairs test: $Z = 2.520$; $P = 0.012$). However, the availability of pawscrapes was higher than that of latrines, so when we corrected for availability, the differences in selection were no longer significant (Wilcoxon matched pairs test: $Z = 1.499$; $P = 0.133$). The use of latrines was independent of rabbit density (Mann–Whitney U test: $Z = 0.105$; $n_{\text{high}} = 8$, $n_{\text{low}} = 8$; $P = 0.916$) as was the use of pawscrapes ($Z = 1.260$; $n_{\text{high}} = 8$, $n_{\text{low}} = 8$; $P = 0.208$).

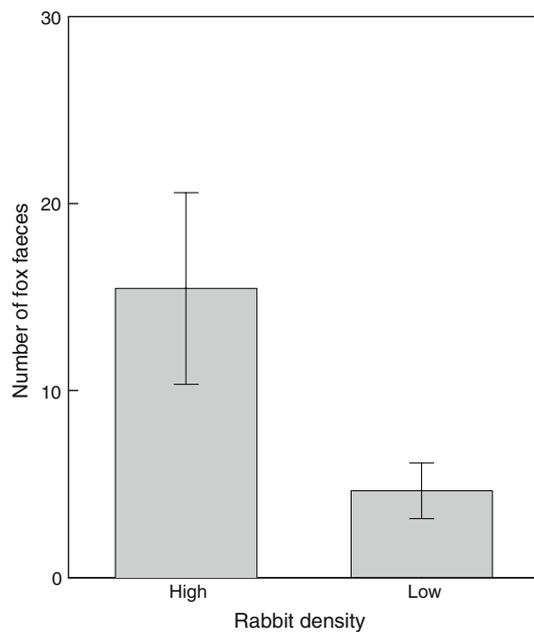


Fig. 1 Number of fox faeces related to rabbit remains depending on the density of rabbits (mean \pm SE)

Discussion

The main findings of our study were the close spatial association between foxes and rabbits. In those areas with a higher density of rabbits, foxes scent-marked and utilised the places of rabbit activity as landmarks more frequently.

More fox faeces were found in the plots with a high density of rabbits, which could be explained by a higher amount of time being spent by foxes in the ‘high-quality’ plots. It would appear that foxes were following an aggregational response, in that they adjusted their territory to that of their preys (Ricklefs and Miller 1999). However, in the patches with higher densities of rabbits the faeces were not located at random but instead associated to landmarks and, therefore, the foxes not only spent more time on those patches but also marked them more.

Some patterns of the scent-marking behaviour were independent of the density of rabbits. Foxes preferably located their faeces in clearings. Other studies carried out on wolves, *Canis lupus* (Barja et al. 2004), lynxes, *Lynx pardinus* (Robinson and Delibes 1988) and foxes, *Vulpes vulpes* (Monclús and Miguel 2003a), found that marking did occur mainly in clearings and crossroads, which are commonly considered to be more strategic places. Clearings constitute a special type of crossroad because they are the intersection of several small tracks that open out onto the clearing. Therefore, a mark deposited in a clearing has a higher chance to be found since different tracks lead to it. Moreover, the study area consisted of dense vegetation and, consequently, the clearings in the wood were nearly

the only places breaking the continuity of the environment. Considering the importance of discontinuities in the scent-marking behaviour, we consider that, in our study, foxes selected clearings independently of rabbit density.

The foxes also seemed to follow an additional strategy to increase the detectability of a mark: they associated their scent mark with conspicuous elements of the environment (Hebets and Papaj 2005), such as latrines and pawscrapes. Latrines and pawscrapes constitute complex signals, as they consist of visual and olfactory cues (Mykytowycz and Gambale 1969; Bell 1980). The addition of a further visual and chemical component, the fox faeces, may increase the probability of detection (Hebets and Papaj 2005) as it is known that in the early detection of a mark, the visual component plays an important role (Alberts 1992). Therefore, both latrines and pawscrapes constitute very conspicuous elements, which are used according to their availability. Moreover, the increased detectability of latrines and pawscrapes as scent marks could provide predators with information on the location of their prey (Rosell and Sanda 2006), thereby facilitating foxes to adjust their territories to those of their food resource.

Based on our results, we propose that foxes selected specific sites to locate their scent marks. We were able to distinguish two different behavioural patterns within the scent-marking behaviour of the foxes: one depended on the general characteristics of the environment, whereas the other depended on the abundance of the main prey. Indeed, foxes used the remains of rabbit activity as amplifiers for their scent marks.

Acknowledgments We are grateful to Heiko G. Rödel for his helpful comments on earlier drafts of this manuscript. The permits to carry out the study were kindly provided by the Consejería de Medio Ambiente de la Comunidad de Madrid.

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