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ORIGINAL PAPER

European rabbits recognise conspecifics in their predators' diets

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Abstract

Rabbits can successfully avoid their enemies by evaluating the risk of predation. They have various defensive strategies, such as morphological adaptations and behaviours patterns, which enable them to perceive their predators and thus reduce the risk of predation. It is well documented that rabbits recognise the scats of terrestrial predators and avoid those areas in which they are present. However, few studies show whether the prey species can recognise the presence of congeners in carnivores' scats, which would allow them to identify their predators in a more efficient manner. We have carried out a comparative analysis of the use of space made by rabbits on plots on which a neutral odour (water) or the odours of the ferrets' scats that had consumed either rabbit or another mammal (beef) were applied. Our results showed a lower number of rabbit pellets on those plots containing predator odours than on the control plots. During the first 6 days after applying the first odour, the number of rabbit pellets was lower on plots on which rabbit had been included in the diet when compared with scats obtained from a beef diet. However, no differences between the two experimental plots were recorded during the third visit (9 days after applying the first odour). Our results suggest that rabbits may be able to detect congeners in their predators' scats, thus leading them to, in the short term, avoid areas in which their terrestrial predators' diet is based on conspecifics, probably as the result of them perceiving a higher risk of predation.

Keywords Anti-predator strategies · *Oryctolagus cuniculus* · Predator diet · Predator-prey interaction · Predation risk

Introduction

Natural selection has provided animals with mechanisms that enable them to detect predators before being attacked, in addition to defensive strategies with which to minimise the risk of predation (Stankowich et al. 2014). Some behavioural strategies, such as temporal and spatial activity modifications, make it more difficult for the prey species to be captured by predators (Reichard 1998; Apfelbach et al. 2005).

Animals express action patterns because there is a conflict between their ecological needs to obtain food and reproduce, and that of dealing with the risk of dying as the result of predation, that is, there is a trade-off between benefits and costs. Lima and Bednekoff (1999) hypothesised that animals choose those habitats that offer a wide range of food and refuge against enemies with which they share their home range (Beltran 1991; Santilli and Bagliacca 2010). According to this hypothesis, the choice of space should be made by attaining a balance between the benefits of foraging and energetic costs, which are represented by the risk of being preyed upon in a foraging spot (Nersesian et al. 2011). In fact, it has been suggested that both the prey and the predator species can coexist owing to small-scale spatiotemporal heterogeneity, since prey species use those areas in which the densities of their predators are lower or from which they can shift to safe habitats (Viota et al. 2012). They can also change their daily activity patterns depending, amongst other factors, on predator activity (Diete et al. 2017). The coexistence of both species in local spaces is, therefore, permitted with a minor cost to the prey.

The risk of predation is perceived and evaluated by prey species, since they are able to detect cues left by predators in order to modulate their anti-predator strategies and defensive responses, thus avoiding high costs (Monclús et al. 2009). These signals can be perceived directly or indirectly by prey. Some authors have suggested that innate sympatric recognition mechanisms and a co-evolved predator-prey system could

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have resulted in an appreciation of signals left by both before a direct encounter, independently of the prey's previous experience of the predator (e.g. Caine and Weldon 1989; Jedrzejewski and Jedrzejewska 1990; Barreto and Macdonald 1999; Monclús et al. 2005; Cox et al. 2010). The faeces of carnivore predators emit volatile fatty acids (Apfelbach et al. 2005; Cox et al. 2010) and sulphur compounds resulting from the acquisition of animal protein digested from their diet (Monclús et al. 2005), which prey species are able to recognise (Vilhunen and Hirvonen 2003; Pereira et al. 2017). Previous studies have suggested that the remains of a prey contain an odour marker in the urine and faeces of predators, which could result in them smelling differently to other prey depending on the species that are digested by the predators. These odour markers are called kairomones, which are semiochemicals emitted by an organism that benefit another species, and have been identified as a component that is general to many carnivore odours that induces defensive behaviours, such as avoidance, in prey species (Ferrero et al. 2011; Rosen et al. 2015).

Some of these experiments have also attempted to determine whether individual prey are able to recognise consumed conspecifics through the odour of faeces, which could be interpreted as the presence of an active predator for their species. This might have a more aversive effect on those individuals that perceive the smells of congeners consumed by predators (Pillay et al. 2003; Cox et al. 2010). In fact, some studies with fish and amphibians have indicated that chemical cues from consumed conspecifics are alarm substances that favour the recognition of active predators (Vilhunen and Hirvonen 2003; Shaffery and Relyea 2015). The intensity of the anti-predator behaviour may also depend on the phylogenetic proximity of the digested prey species or a true alarm such as pheromones produced by prey species after being digested (Vilhunen and Hirvonen 2003; Preston and Forstner 2015).

Very few of these studies have been carried out with the principal objective of identifying congeners in the diet of an active predator (Vilhunen and Hirvonen 2003; Cox et al. 2010; Hettyey et al. 2016). Therefore, the objective of the study presented herein is to demonstrate preys' capacity to recognise and identify congeners in their predators' diet by means of the odour of faeces in a wild environment. The experiment was performed in completely natural conditions with a co-evolved prey and a sympatric predator, using the European rabbit (*Oryctolagus cuniculus*) as a prey and ferrets (*Mustula putorious furo*) as a predator. The European rabbit is, within its native range in the Iberian Peninsula, a key prey for more than 30 vertebrate predator species, including rabbit-specialist predators (Delibes-Mateos et al. 2007). As a consequence of this evolutionary pressure, rabbits have anti-predator behaviours (Monclús et al. 2009) that allow them to avoid direct encounters with predators and thus reduce the probability of being preyed upon (Beja et al. 2007; Barrio et al. 2010a).

The aim of this work is, therefore, to verify the possibility of rabbits recognising congeners in carnivore predators' diets by means of scents from faeces. We tested whether rabbits are able to identify enemies that consume rabbits, thus enabling them to reduce the risk of being preyed upon. We hypothesise that rabbits will be more inclined to avoid those experimental plots sprayed with the faeces of predators which have been fed with rabbit meat than those plots in which there are faeces of predators whose diet is based on the meat of other mammal.

Methods

Study area and experimental design

The study was conducted in four open-air agriculture areas (hereafter study sites) mainly devoted to the cultivation of olive crops in the province of Córdoba, Spain (37° 30′–37° 58′N, longitude 4° 17′–4° 56′W), in June 2014. The sites are characterised by a dry Mediterranean climate (average annual rainfall of 500 mm, temperatures 8–26 °C).

The four study sites were olive grove that were separated by more than 6 km. Three plots (90 m^2) were established on each site, which were 50 m apart from each other in order to avoid each plot being contaminated by odours from the others, in addition to ensuring that the same rabbit population could visit all the plots on the same site (Rödel et al. 2006; Barrio et al. 2010b). On each plot, 20 wooden stakes (3 m apart) were driven into the ground in two parallel rows of 10 units, and a lure element (commercial rabbit pellets at a constant weight) was placed close to each stake with the aim of attracting rabbits, since not much food is available in these areas as a result of agricultural practices (Guerrero-Casado et al. 2015; Carpio et al. 2017). This element was added only on the first days and was not replaced throughout the experiment because the objective was not to calculate the amount of food consumed, but rather to employ it as an attractive element to ensure that the rabbits would use the plots (Fig. 1). A total of 240 stakes (4 sites × 3 plots/site × 20 stakes/plot) were placed in the ground, and all the rabbit pellets around each stake within a circular sampling unit (1 m^2) were counted and removed before the beginning of the study. This count was used to estimate initial rabbit abundances at the plot level, and new pellets were again counted in (and removed from) the same sampling units 3, 6 and 9 days after the start of the experiment, which were known as visit 1, visit 2 and visit 3, respectively. Counting pellets as a measure of the space used by rabbits is a common method that is widely used to evaluate habitat use and rabbit abundance (Fernandez-de-Simon et al. 2011; Rouco et al. 2016).

One of the following three experimental treatments was randomly applied on each plot on each site: ferret scat odours containing (i) rabbit in the diet (hereafter 'treatment-rabbit'), (ii) beef in the diet (hereafter 'treatment-beef') or (iii) a

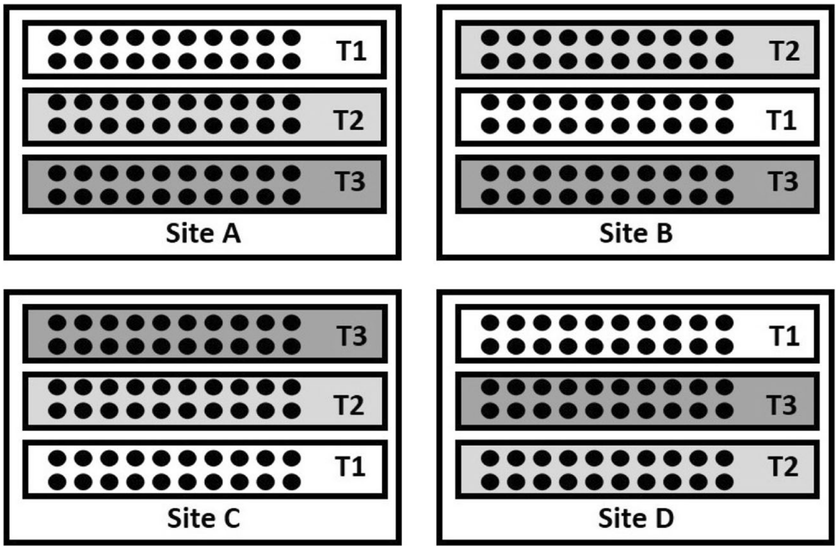

Fig. 1 Representation of the experimental design of the four sites (**A, B, C, D**), which were divided into three plots (T1, T2, T3). Each plot is corresponded to an applied treatment (T1 'water', T2 'beef-treatment', T3 'rabbit-treatment'), which were randomly arranged within sites. The points signal wooden stakes

procedural control (water). The stakes were sprayed daily for 9 days with either the predator odours (treatment-beef or treatment-rabbit) or water (control), using different spray bottles for each treatment. The experiment was stopped after 9 days because it is known that rabbits can become accustomed to odours if they do not detect active signals of predation (Tortosa et al. 2015).

Predator odours

The ferret (*Mustela putorius furo*) was used as a predator because this species has a sympatric and co-evolutionary history and has often been used in predator-prey studies (McPhee et al. 2010; Apfelbach et al. 2015). Moreover, the rabbits in the study area are frequently captured through the use of ferrets from warrens for restocking purposes (Guerrero-Casado et al. 2013) or in order to prevent agricultural damage (Ríos-Saldaña et al. 2013). It is, therefore, possible to assume that the predator and prey co-exist in the same area. Ferret faeces were collected from a group composed of eight captive male ferrets. Four of them were fed solely on rabbit for 2 weeks, and another group of four male ferrets was fed solely on beef during the same period. We used only those faeces expelled during the last week of each diet to ensure that no remains of other foods were in the digestive tract. According to Johnson-Delaney (2014), the gastrointestinal transit time in ferrets is approximately 3 h, because as an obligatory carnivorous, ferrets have a very short intestinal tract. A liquid extract was obtained from all mixed faeces belonged to a same group (rabbit diet or beef diet) by following the procedure described in Barrio et al. (2010b), i.e. mixing 50 g of faeces with 1 L water, leaving it for about 4 h and filtering it through coarse cloth to remove solid material. This method was applied in the same way in both treatments and using the same tools, which were cleaned after each use to prevent the mixing of components. Before being applied, the liquid was frozen to − 20 °C in order to homogenise it and thus avoid erroneous results owing to the loss of volatiles from the faeces of the extracts used on different days. Finally, the liquid extract was kept in bottles in order to spray constant doses around each stake.

Data analysis

Each stake was considered to be a sampling unit, and the variable response was the number of pellets counted on each visit. The effect of the experimental treatments on the rabbits' use of space measured as the number of pellets (pellets/m^2) was evaluated using a generalised linear mixed model (GLMM) with a Poisson distribution and a log function, in which the treatment (three levels: control, treatment-rabbit and treatment-beef) and the visits (three levels: visit 1, visit 2 and visit 3) were included as fixed factors. The interaction between both factors was also included. The initial rabbit abundance was also included as an explanatory variable to account for local variations in rabbit abundance, and the sampling plots and the study sites were included as random factors in order to accommodate the nestedness of the data. Post hoc tests (Fisher LSD) were subsequently carried out within the mixed model in order to explore the differences between the levels of the fixed factors.

Results

Overall, comparing with 'treatment-rabbit' plots (mean = 5.5 ± 0.65), the mean rabbit abundance (pellets/m^2) was higher on the control plots (15.2 ± 1.39; $Z = 4.2$, $p < 0.0001$) and on the 'treatment-beef' plots (8.69 ± 1.08; $Z = 2.54$, $p = 0.011$). The interaction between the treatments and the visits also showed significantly differences (Table 1), indicating that the effect of the treatments changed over the visits after their application (Table 1 and Fig. 2). According to the post hoc tests, the rabbit abundance was significantly ($p \leq 0.05$) lower on those plots that smelled of a predator than on those on which water was applied on visit 2 and visit 3, but no significant differences ($p > 0.05$) were found between the control and treatment-beef on visit 1 (Fig. 2). Moreover, significant differences ($p \leq 0.05$) between the two treatments composed of predator faeces were evidenced only on visit 1 and visit 2, being the rabbit abundance lower on the treatment-rabbit plots (Fig. 2), with no significant difference between treatment-beef and treatment-rabbit on visit 3.

Discussion

In this study, we have verified that, under natural conditions, prey (in this case rabbits) avoid areas with signals of predators that have consumed conspecifics. This conclusion was reached because, after counting the pellets on each plot, the number of excrements on the treatment-rabbit plots found on the first 6 days (visit 1 and visit 2) was lower than the number of pellets found on the treatment-beef plots. Moreover, we counted rabbit' excrement in order to test whether, in spite of the presence of food on all the plots in those areas in which food is scarce (Guerrero-Casado et al. 2015), rabbits minimised the number of visits to those plots containing predators' odours, compared with the control treatment (in which the number of excrements found were higher throughout the study).

Table 1 Results from the generalised linear mixed model for the effect of treatment, visit and initial abundance on rabbit use of plots

	Estimate	± SE	*Z* value	*p* value
Intercept	0.31	0.6	0.51	0.6098
Treatment-control	1.4	0.33	4.2	< 0.0001
Treatment-beef	0.85	0.34	2.54	0.011
Visit 2	0.13	0.07	1.74	0.0816
Visit 3	0.06	0.07	0.85	0.3939
Initial abundance	0.78	0.02	50.05	< 0.0001
Treatment-control × visit 2	0.08	0.08	0.96	0.3386
Treatment-beef × visit 2	− 0.12	0.09	− 1.4	0.1612
Treatment-control × visit 3	− 0.11	0.08	− 1.29	0.1978
Treatment-beef × visit 3	− 0.51	0.09	− 5.46	< 0.0001

Estimates for the level of fixed factors were calculated using reference values of 'treatment-rabbit' in the variable treatment, 'visit 1' in the variable visit and 'treatment-rabbit × visit 1' in the interaction

SE standard error

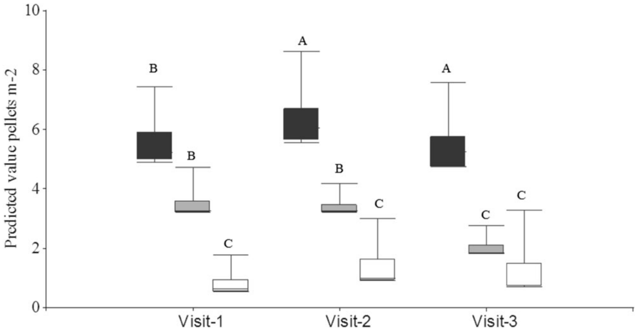

Fig. 2 Predicted values of the response variable (rabbit abundance) under three experimental treatments. The samples were collected on the third (visit 1), sixth (visit 2) and ninth days (visit 3). Different letters indicate significant differences amongst groups according to the post hoc test (p value < 0.05)

In accordance with others studies conducted with mammals in laboratories (Monclús et al. 2005; Apfelbach et al. 2015) or in semi-natural conditions (Cox et al. 2010), our results show that the European rabbit recognises the odour of sympatric predators and decreases its visits to those plots in which predators' odours are applied. Moreover, in the short term (during the first 6 days after the beginning of the experiment), we observed that this decrease was more significant in the treatment-rabbit plots than in treatment-beef plots. Upon detecting predator cues, rabbits evaluate the risk and respond by changing their array of action patterns and their use of space, such as reducing the frequency of their visits (Monclús et al. 2005; Díaz et al. 2005). The presence of conspecifics in the predators' diet could, therefore, be linked to an immediate and higher risk of predation, signifying that rabbits will avoid those areas more as adaptation and defensive behaviour measures to deal with an active predator (Pereira et al. 2017).

Furthermore, the recognition of congeners in the predators' diet supposes an evolutionary advantage because prey animals perceive a higher risk and, therefore, increase their level of antipredator behaviour (Shaffery and Relyea 2015; Scherer and Smee 2016; Pereira et al. 2017). According to the results of this study, it is, therefore, plausible to conclude that when rabbits recognise congeners in the scats of a predator, they respond with more aversion because it means for them a higher predation risk. Whether animals are able to identify predators for which they are not an active prey, then they will not be under a so high risk of being predated and will, therefore, decrease their defensive behaviour, thus enabling them to continue with other behaviours, such as foraging (Cox et al. 2010; Pereira et al. 2017). The absence of direct signals of predation, such as the presence of the predator and/or killed rabbits, may imply that rabbits devaluate the risk involved, signifying that they make new decisions such as increasing the number of visits in order to prioritise non-defensive processes, because maintaining anti-predator strategies over a longer period of time has a high cost (Cox et al. 2010; Cremona et al. 2014; Tortosa et al. 2015).

It has been determined that that anatomies of mammals, and specifically rodents, contain olfactory circuits with which to detect chemicals, and it is well known that these nuclei are influenced by fear, and thus trigger anti-predator responses (Parsons et al. 2018). However, some accessory olfactory structures, along with the mechanisms employed to recognise predators' congeners, are still unknown (Ferrero et al. 2011; Rosen et al. 2015; Parsons et al. 2018). It is, therefore, not yet possible to determine what chemical and physiological mechanisms are used by prey species to recognise conspecifics in the predator scats owing to the odours perceived. Indeed, it would be very interesting to investigate if the recognition of conspecifics in the predator scats is an innate mechanism or whether the animals learn to identify the scent of conspecifics in the predator wastes (Parsons et al. 2018). We consequently suggest that more studies regarding the chemical composition of faeces and their effects on animal behaviour should be carried out in order to attain a complete knowledge of the mechanisms involved in the avoidance of a predator, since this is essential information for the proper interpretation of prey-predator strategies.

In conclusion, in this study, we have shown that predator odours were obtained from both a diet based on rabbits and a diet based on beef act as a repellent, thus reducing the frequency that rabbits make of the use of space. Moreover, at the beginning of the experiment, the odour of the predators which had been fed with rabbits (conspecific) had a higher repellent effect because the use of space by rabbits was lower in those, which supports our hypothesis that rabbits could recognise active predators of their species in the predators' scats, which implies a higher cost as a consequence of the loss of benefits in resources (food provided). But in turn, they attain a higher benefit, which is the possibility of staying alive as the result of making more accurate decisions based on the information obtained from the predators' cues.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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