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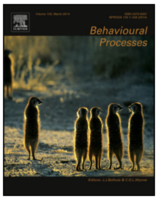

Context-dependent responses to neighbours and strangers in wild European rabbits (*Oryctolagus cuniculus*)

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ABSTRACT

Territorial animals defend their territories against intruders. The level of aggression directed to intruders depends on the familiarity and/or the relative threat they pose, and it could be modified by the context of the interaction. We explored in a wild social mammal, the European rabbit (*Oryctolagus cuniculus*), whether residents responded more aggressively to strangers or to neighbours (dear enemy or nasty neighbour effects, respectively). We simulated the intrusion of neighbours or strangers in different parts of the territory of wild European rabbits in a suburban area in central Spain. For that, we placed faecal pellets of neighbouring or stranger rabbits in the territory of 5 rabbit colonies. Resident rabbits counter-marked preferably the odour stations with stranger odour, compared to the ones with neighbour odour, and they did not make a difference between neighbour and a non-odour control stimuli. The results suggest that rabbits show a dear enemy effect. However, repeated intrusions escalated the responses of rabbits towards neighbours. The location within the territory or the sex of the stranger did not affect the level of response. We conclude that in rabbits the relative threat posed by the intruder triggers the intensity of the interaction.

1. Introduction

Many animals defend the resources contained in a territory from competitors (Davies and Houston, 1984). Different species use varied means of defence, such as vocalizations or visual signals. Mammals are usually crepuscular and live in complex environments, and scent-marking is one of the major ways of passive defence (Ralls, 1971; Johnson, 1973). Scent marks provide information about the resident and about its resource holding potential (Gosling, 1982). Many studies have shown that animals are able to discriminate among the odours of conspecifics, for example they are able to distinguish between kin and non-kin (Hurst et al., 2001; Boulet et al., 2009), between colony members and outsiders (O'Riain and Jarvis, 1997), or between neighbours and strangers (Höjesjö et al., 1998; Aragón et al., 2000). Scent-marking is economic, but it does not constitute a barrier against intrusions, and indeed, intrusions are commonplace. However, not all intruders necessarily pose a similar risk to the resident, and animals should discriminate among them, and respond accordingly, as overreaction might be maladaptive (Jaeger, 1981). Two main hypotheses are used to explain the differential responses of residents to intruders. One is the familiarity hypothesis (Ydenberg et al., 1988), that suggests that the participants in the contest engage in an asymmetric war of attrition, where the resident and the intruder gain information about each other, and as familiarity increases, the responses become de-escalated. The other is the relative threat hypothesis (Temeles, 1994). It considers that not all intruders pose the same level of threat, which depends, to a great extent, on the potential losses and gains derived from the interaction.

Frequently, neighbours are more familiar – the encounter rates between them are higher than with transient intruders – and they pose a lower threat to residents than non-neighbours – territorial neighbours might gain some mates, but strangers might try to gain the territory as well (Temeles, 1994). Under these conditions, most studies have found that residents are less aggressive to neighbours than to strangers, what is known as the dear enemy phenomenon (Jaeger, 1981; Fisher, 1954).

However, in other contexts, studies have failed to find a dear enemy effect. For instance, when the payoff of the contest is highly asymmetrical, neighbours might be, at least, as threatening as strangers (Granroth-Wilding and Magurran, 2013). The

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level of threat might also be sex-dependent (Bard et al., 2002; Tierney et al., 2013). In many species males defend territories containing reproductive mates, whereas females defend the breeding sites. Therefore, intruders might represent different threats for a male or a female. For instance, in red-winged blackbirds (*Agelaius phoeniceus*), males responded more to non-neighbours than to neighbours (Yasukawa et al., 1982), whereas females during the reproductive season reacted as aggressively to both types of intruders (Beletsky, 1983). Not only sex but also the season might render different payoffs, as resources, and the relative importance of monopolising them, might vary at different times of the year (Hyman, 2005; Palphramand and White, 2007). Moreover, the relative risk of an intrusion might depend on the location in the territory relative to its boundaries. Normally, intruders reaching the core area elicited more aggressions than those encountered in the boundaries (Furrer et al., 2011; Schradin, 2004). When neighbours pose a greater risk than strangers, they have been called 'nasty neighbours' (Müller and Manser, 2007).

Taking all that together, it seems that context is an important trigger of the responses of residents facing an intrusion. Whereas there are many studies in birds and reptiles focusing on particular aspects of the neighbour-stranger relationship, not many have used social mammals to explore context-dependent reactions in the wild. Therefore, we followed a comprehensive approach to know whether European rabbits, *Oryctolagus cuniculus*, (1) discriminate between neighbours and strangers and (2) show a dear enemy or a nasty neighbour effect. Moreover, we wanted to know (3) whether the responses were context-dependent. We looked at differences in responses according to the sex of the intruder, the location within the territory where the simulated intruder was found (periphery or core area), and the effect of repeated intrusions. For that, we set up an experiment where we simulated the presence of intruders by means of placing fresh pellets of neighbour and stranger rabbits within different locations of the territory of 5 rabbit colonies.

The European rabbit is a good animal model to test these hypotheses. Rabbits defend social territories using scent-marks disposed in latrines at different distances from the burrow, which is located in the core of the territory (Mykytowycz, 1968). Rabbit territories are relatively small, in our study area smaller than 100 m in diameter (Monclús and de Miguel, 2003), and the group consists of 2–12 adult members – 1–5 males and 1–7 females (Cowan, 1987; von Holst et al., 2002). The territories are stable and multi-purpose (territory and mates), where neighbours are usually familiar and some of them might be dispersing kin. In rabbits, dispersal is male-biased, most of the subadult males and 40% of the females disperse. Dispersal occurs when they are 4–5 months old, and females usually move to a neighbouring colony, whereas males move further away (Künkele and von Holst, 1996). Resident males from adjacent territories engage in ritualised agonistic interactions when encountering each other at a common border (Lockley, 1964; Bell, 1980). During these displays, neighbour males mark the shared border by paw-scrapping. Therefore, we would expect to find a dear enemy phenomenon in rabbits (Temeles, 1994; Ydenberg et al., 1988), as neighbours seem to be both more familiar and less threatening than strangers.

We expected to find differences in the responses to neighbours and strangers of different sex. In rabbits, intrasexual competition is the norm; males compete with other males for the access to females, whereas females compete with other females for the access to the breeding burrows (Mykytowycz, 1959; von Holst et al., 1999). Moreover, males are responsible for the boundary scent marking, and thus, they spend more time than females at the borders of the territory (Mykytowycz and Gambale, 1969). Therefore, we predicted that in the periphery male intruders might elicit a stronger response than female intruders, whereas in the core area, female intrusions might elicit a stronger response. Similarly, responses to intruding neighbours should be stronger in the core area than in the periphery.

2. Materials and methods

The experiment was conducted between November 2012 and March 2013 in a forest located next to Universidad Autónoma de Madrid, Spain (UTM 30TVK48). It is a suburban Mediterranean holm oak forest (*Quercus ilex ballota*) interspersed with some pine tree plantations (*Pinus pinea* and *Pinus pinaster*). Rabbits are abundant: the average rabbit density in the study area is 21 rabbits/ha (Monclús et al., 2009).

2.1. Experimental set-up

We selected a total of 5 rabbit colonies. Each colony was paired with at least another one, becoming neighbour colonies. The centre of the colony was defined by the colony burrow (Mykytowycz and Gambale, 1969). The contact area between two colonies was identified by the characteristic paw-scraping pattern left by the dominant males of the adjacent colonies during intrasexual dominance displays (Lockley, 1964). The colonies were on average 36 m radius (±13 S.D.).

At the beginning of the experiment we set 6 Petri dishes in the centre and 6 in the outer part of the territory of each colony to habituate the residents to the dishes. The Petri dishes were separated 1 m from each other. In total we used 66 scent stations in the different colonies. The Petri dishes were checked every other day to ensure that the rabbits were not disturbed by the inclusion of a novel object within their territory. We left the rabbits two weeks to habituate. After that, we confronted the rabbits with a fixed amount of fresh pellets collected in the neighbour colony (20 pellets per dish) or with fresh pellets from unknown rabbits collected in an animal facility at Universidad Autónoma de Madrid (20 pellets per dish). We used only one odour at a time, and half of the odour stations were randomly assigned to one of the odours and the other to controls (no odour). We checked for responses one week after disposing the odours. We registered as a positive response the paw-scrapping of the scent stations, which normally resulted in the dishes being moved away from their original location or even the disappearance of the dishes. Paw-scraps represent mixed marks (visual and chemical) as rabbits usually mark them with the secretions of the chin gland, as well as with anal secretions (Bell, 1980). Moreover, we considered as a positive response the addition of pellets, as counter-marking is a well-known response to competitor odours (Hurst et al., 1997; Sliwa and Richardson, 1998) or the disappearance of at least 10% of the original pellets. After recording the responses, all the Petri dishes were thoroughly washed with ethanol 96%, renumbered and placed again. To avoid habituation to a particular treatment, we alternated the treatments on a weekly basis.

The donors of the stranger odour were 2 males and one female. We did not mix the pellets collected but presented them separately during the stranger treatment. We presented in the core area and at the border either 1 Petri dish with female odour and 2 with male odour or 1 with male odour and 2 with female odour.

2.2. Data analysis

Our data followed a binomial distribution so we fitted Generalised Linear Mixed Models (GLMM) to analyse whether resident rabbits responded differentially to neighbour and strangers. All the analyses were performed with the function *glmer* of the package *lme4* from the software R, v.2.15.2 (R Development Core Team, 2012), using the binomial family with a logit link. In a first step we tested whether resident rabbits responded to other rabbit

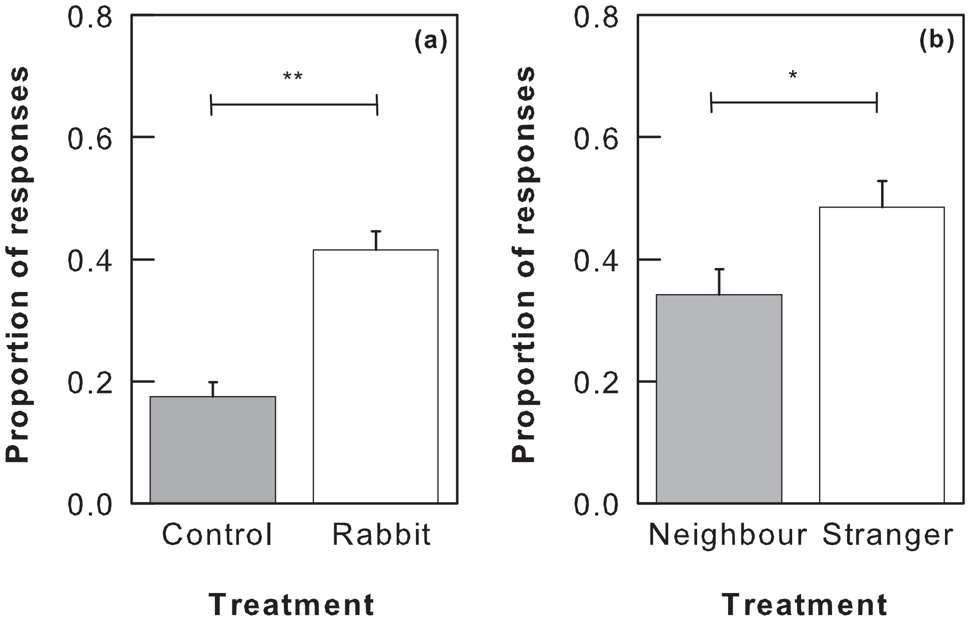

Fig. 1. Proportion of dishes eliciting a response to (a) control and rabbit scents and to (b) neighbour and stranger scents. Bars represent mean ± S.E. ** indicates $p < 0.01$; * indicates $p < 0.05$. See text for statistics.

odours. For that we compared the responses to any of the treatment dishes with the responses to control dishes (non-odour dishes). Then we tested the responses considering the treatments independently (neighbour vs. control and stranger vs. control). In the stranger treatments we also tested whether the responses depended of the sex of the odour donor. In all analyses we used *response* as the dependent variable, and we included *treatment* (control vs. odour), and *location* (inner vs. outer dish) as fixed factors. We included the date of the treatment as a covariate, to control for possible habituation to the odours. We considered the interaction between *treatment* and *location* and when non-significant they were removed from the final model (Engqvist, 2005). We included the colony and the colony nested with the scent station as random factors to control for potential preferences of the rabbits.

3. Results

Rabbits participated in 4 neighbour treatments and in 4 stranger treatments. In total we presented 516 Petri dishes in the five rabbit colonies. During a sampling event, we could not gather all the neighbour faeces needed, and thus, we had to reduce the number of Petri dishes presented. We obtained in total 152 responses. Resident rabbits responded significantly more to other rabbit odours than to control plates ($\beta = 1.225$, $n = 516$, $p < 0.001$; Fig. 1a). Moreover, resident rabbits responded more often to strangers than to neighbours ($\beta = -0.666$, $n = 258$, $p = 0.013$; Fig. 1b). The location of the plates (inner or outer) and the date were not statistically significant ($\beta = 0.047$, $n = 258$, $p = 0.854$; $\beta = 0.050$, $n = 258$, $p = 0.331$; respectively).

3.1. Context-dependent responses to neighbours

When rabbits were confronted with the odour of the neighbours, residents responded to both control and neighbour plates indistinctly ($\beta = -5.241$, $n = 252$, $p = 0.089$). Similarly, we did not find any difference between the responses in different locations ($\beta = 0.357$, $n = 252$, $p = 0.288$) and at different sampling events ($\beta = -0.009$, $n = 252$, $p = 0.222$). However, the interaction between date and treatment was statistically significant ($\beta = 0.019$, $n = 252$, $p = 0.027$): whereas residents decreased the number of responses to control plates along the course of the experiment ($\beta = -0.060$, $n = 126$, $p = 0.036$), they increased the number of responses to neighbour plates as time passed by ($\beta = 0.009$, $n = 126$, $p = 0.015$; Fig. 2). The interaction between treatment and location was not significant ($p > 0.1$) and was removed from the final model.

3.2. Context-dependent responses to strangers

Resident rabbits responded significantly more to strangers than to control plates ($\beta = 1.056$, $n = 264$, $p < 0.001$; Fig. 3). The number of

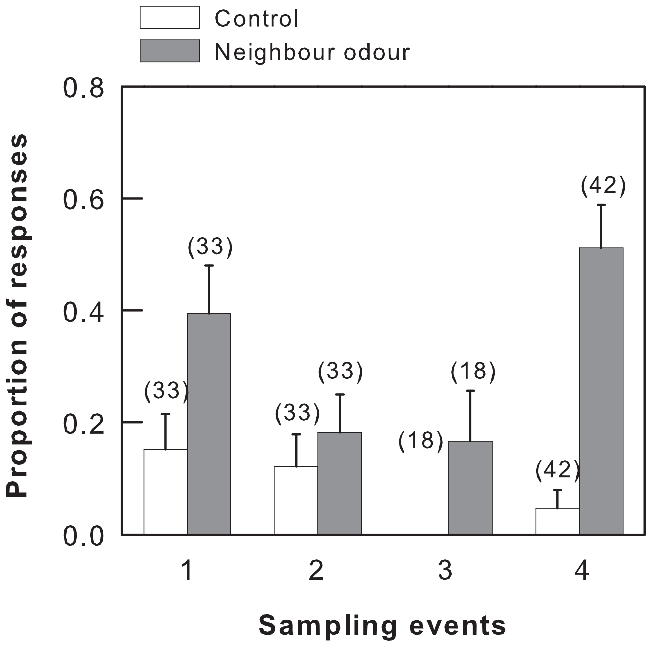

Fig. 2. Repeated simulated intrusions of neighbours increased the response of resident European rabbits whereas rabbits habituated to control plates. The number of plates used in each session are written in brackets. Bars represent mean number of dishes that elicited a response ± S.E.

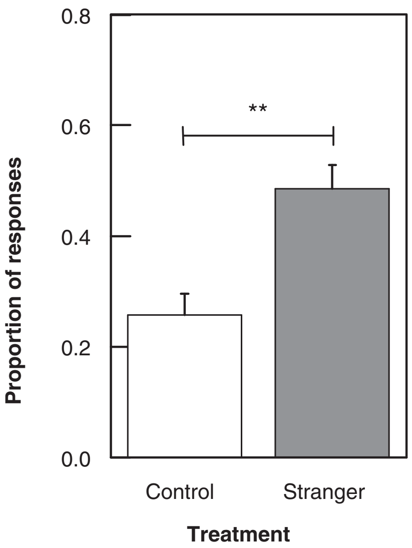

Fig. 3. Resident rabbits responded significantly more to stranger odours than to control plates. Bars represent mean number of dishes that elicited a response ± S.E, ** indicates $p < 0.01$. See text for statistics.

responses was independent of the location of the plate ($\beta = 0.375$, $n = 264$, $p = 0.204$) and of the date ($\beta = 0.001$, $n = 264$, $p = 0.797$). The interaction between treatment and location, as well as the interaction between treatment and date were non-significant (all $p > 0.1$) and were removed from the final model.

Residents responded equally to strangers independently of the sex of the donor of the odour ($\beta = 0.365$, $n = 132$, $p = 0.297$), or the interaction between sex of the donor and location ($\beta = 0.562$, $n = 132$, $p = 0.425$).

4. Discussion

Defending a territory is time and energy demanding. However, in many cases the payoff of monopolising the resources surpasses the costs (Brown, 1964). Territory holders defend these resources against intruders. Not all the intruders have similar objectives, and therefore, they do not represent the same risk to the territory holder. Therefore, it might not be adaptive to engage in escalated agonistic interactions independently of the actual risk (Jaeger, 1981). Therefore, a resident should discriminate among potential threats, and modulate the responses accordingly (Scharf et al., 2011).

With our study we could show that resident rabbits discriminated between neighbours and strangers and that the response was stronger to the latter. Moreover, they did not make a difference between control dishes and neighbour odours, suggesting that neighbours were not threatening. Thus, with this study we could confirm that European rabbits under field conditions showed a dear enemy effect. There are several non-exclusive explanations for the effect. Residents lack information about the competitive abilities and intentions of strangers, and therefore, they might represent a bigger threat than neighbours (reviewed in Temeles, 1994). On the other hand, the resident of a territory has probably measured its strengths several times with the residents of the neighbouring colonies, both through agonistic or non-agonistic interactions (del Barco-Trillo et al., 2009). Once the rules are set, the confrontations de-escalate. For instance, once the territory boundaries are defined, dominant rabbits exhibit ritualised displays in the presence of a neighbour dominant male in the overlapping area of both territories (Cowan, 1987). An alternative explanation could be that rabbits just spent more time investigating the stranger odours leading to the disturbance of the scent dishes. Animals have to gather chemical information about their environment, and this normally increases the time an animal is next to a new and unfamiliar odour. For instance, European rabbits spent more time next to odour stations when scented with fox faecal odour, presumably to gather information about the predator (Monclús et al., 2006). In the present study resident rabbits counter-marked more, both by defecating or by paw-scrapping, the scent stations with stranger odour than with neighbour odour, which suggests that they were not only spending more time there, but that the information gathered elicited an elimination response.

However, neighbours might become more threatening than perfect strangers (Müller and Manser, 2007; Newey et al., 2010). In a study with fiddler crabs, *Uca mjoebergi*, the authors experimentally increased the level of threat of a previously dear enemy neighbour. Resident crabs responded aggressively to the cheating neighbours, which supports the relative threat hypothesis (Booksmythe et al., 2010). Similarly, in our study, rabbits exposed to repeated simulated intrusions of a formerly dear enemy escalated the responses, probably because they perceived the neighbour was crossing a line. At the end of the experiment rabbits responded to neighbours as much as to strangers. Residents usually encounter neighbours in the outer part of the territory, and thus, intrusions into the core area of the territory might be perceived as a higher threat, independently of the familiarity of the intruder, because it could represent the potential loss of breeding opportunities (Schradin et al., 2010; Furrer et al., 2011). Similarly, other studies have found a clear increase in aggression towards intruding neighbours compared to non-intruding neighbours (Akçay et al., 2009). However, repeated intrusions do not always trigger a stronger response. For instance, repeated intrusions in the territory of brown toadlets, *Pseudophryne bibronii*, did not lead to increased aggressiveness, but to the assumption that the intruder had established in the neighbouring territory (Heap et al., 2012). Similarly, in European rabbits, the repeated intrusion of a stranger did not increase the responses of the resident individuals. Although we did not find an habituation to the stranger odour, as it has been found in other studies (Müller and Manser, 2007), the responses did not escalate as with the neighbour odour. Whereas rabbits usually encounter their neighbours, they never had physical contact with the strangers, and this lack of reinforcement of the scent matching could have driven the results (Gosling, 1982).

In our study we could not find any difference in the responses depending on the location of the intrusion within the territory. One possible explanation is that the presentation of scents simultaneously in the inner and outer parts of the territory created a high risk scenario, and the resident rabbits reacted to the higher risk cue (the intrusion in the core area). That might as well explain the lack of habituation to the odour of the strangers or the response independent of the sex of the stranger (Tierney et al., 2013).

In conclusion, European rabbits showed a plastic dear enemy response, which escalated after repeated simulated intrusions into the territory. Whereas familiarity might play a role modulating the responses, it seems more likely that the relative risk that an intruder poses defines the outcome of the interaction.

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