



## Familiarity with neighbours affects intrusion risk in territorial red squirrels



Erin Siracusa<sup>a, \*</sup>, Stan Boutin<sup>b</sup>, Murray M. Humphries<sup>c</sup>, Jamieson C. Gorrell<sup>b, 1</sup>,  
David W. Coltman<sup>b</sup>, Ben Dantzer<sup>d, e</sup>, Jeffrey E. Lane<sup>f</sup>, Andrew G. McAdam<sup>a</sup>

<sup>a</sup> Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

<sup>b</sup> Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

<sup>c</sup> Department of Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne-de-Bellevue, QC, Canada

<sup>d</sup> Department of Psychology, University of Michigan, Ann Arbor, MI, U.S.A.

<sup>e</sup> Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.

<sup>f</sup> Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

### ARTICLE INFO

#### Article history:

Received 3 April 2017

Initial acceptance 15 May 2017

Final acceptance 30 June 2017

MS. number: A17-00294R

#### Keywords:

dear enemy  
familiarity  
intrusion  
kin selection  
neighbourhood  
red squirrel  
social environment  
territoriality

Interactions with conspecifics are an important aspect of an individual's environment. Although it is well known that the presence of conspecifics can have important effects on behaviour, in general it is also now acknowledged that the composition of the social environment can vary, and that this variation may have profound effects on individual behaviour and fitness. Using a wild population of North American red squirrels, *Tamiasciurus hudsonicus*, we investigated the importance of the composition of the social environment in a territorial species by assessing whether the risk of intrusion faced by territory owners varied with the degree of relatedness and familiarity in their social neighbourhoods. To test this, we conducted temporary removals of territory owners and observed the time until intrusion and the identity of intruding individuals. We found that individuals in neighbourhoods with low average familiarity faced a higher risk of intrusion and that unfamiliar neighbours were more likely to intrude. Surprisingly, we found that related neighbours also posed a higher risk of intrusion. The results from our study suggest that familiarity with neighbours may be an ecologically and evolutionarily relevant measure of the social environment, even in a species considered to be 'asocial'. Future studies should consider the potential importance of the social environment, which has heretofore been mostly overlooked, as a relevant selective pressure in asocial, territorial species.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

An important aspect of an organism's daily life consists of interactions with conspecifics, comprising what we consider to be an individual's social environment. Such interactions with social partners are increasingly recognized to be important to individual behaviour and fitness (Moore, Brodie, & Wolf, 1997; Saltz, 2013; Wilson, Gelin, Perron, & Réale, 2009; Wolf, Brodie, & Moore, 1999). In the broadest sense, the presence of conspecifics may cause individuals to change the frequency with which they engage in certain behaviours (Beauchamp, 2003; Dantzer, Boutin, Humphries, & McAdam, 2012), or may modulate the behavioural tactics that individuals use (Bugnyar & Heinrich, 2006; Fischer,

Schwartz, Hoke, & Soares, 2015; Grand & Dill, 1999; Hellmann & Hamilton, 2014). However, variation in the composition of social groups can have effects on behaviour and fitness above and beyond the mere presence or number of conspecifics in an individual's environment. For instance, the presence of kin in social groups can reduce aggressive interactions and vigilance behaviour while increasing the proportion of time spent foraging or feeding (Brown & Brown, 1993, 1996; Davis, 1984; Viblanc, Pasquaretta, Sueur, Boonstra, & Dobson, 2016) and may positively influence survivorship and reproductive success (Hokit & Blaustein, 1997; Moses & Millar, 1994; Viblanc, Arnaud, Dobson, & Murie, 2010). Social units with stable composition (familiar associations among individuals) benefit from undisrupted dominant and subordinate roles, which results in increased tolerance and resource sharing for all group members (Senar, Camerino, & Metcalfe, 1990). In degus, *Octodon degus*, group stability has been demonstrated to have a modulating effect on the relationship between group size and

\* Correspondence: E. Siracusa, Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, ON N1G 2W1, Canada.

E-mail address: [erinsiracusa@gmail.com](mailto:erinsiracusa@gmail.com) (E. Siracusa).

<sup>1</sup> J. C. Gorrell is now at the Biology Department, Vancouver Island University, Nanaimo, BC V9R 5S5, Canada.

fitness (Ebensperger et al., 2016). Social instability (number of changed neighbours), on the other hand, has been demonstrated to result in increased aggressive signalling in *Betta splendens* (Matessi, Matos, Peake, McGregor, & Dabelsteen, 2010).

For territorial species the social environment is often defined by agonistic interactions. A variety of definitions for territoriality have been given, including but not limited to, the exclusive use of a fixed area (Pitelka, 1959), the active defence of an area from conspecifics (Brown & Orians, 1970), or a fixed area where an individual has priority of access to an important resource (Kaufmann, 1983). All definitions, however, necessitate that territoriality involves social interactions, via defence of one's territory, mutual avoidance or cooperation among neighbours. Most territorial species live in socially complex environments with a composition of neighbours that vary in relatedness (Brown & Brown, 1993), familiarity (Beletsky & Orians, 1989), sex (Eckenweber & Knörnschild, 2013), body condition (e.g. size; Booksmythe, Hayes, Jennions, & Backwell, 2012), aggression (Hyman & Hughes, 2006) or resource-holding potential (Parker, 1974), among other possibilities. Given that territoriality is not adaptive unless the benefits of increased access to resources outweigh the expenditure of time and energy in defending one's territory (Brown, 1964; Brown & Orians, 1970), it should be expected that the composition of neighbours around an individual's territory matters, as those individuals will directly influence the frequency, and therefore cost, of territorial defence. However, the role of neighbours remains contentious and appears to vary based on both the conditions and the system of study under observation (Carpenter, 1987).

One of the most widely documented patterns of differential behaviour among neighbouring individuals is the reduced aggression of territory owners towards familiar individuals relative to unfamiliar individuals (Fisher, 1954; reviewed in Temeles, 1994). Coined by Fisher in 1954, the 'dear enemy effect' is a cooperative phenomenon of reduced aggression among long-term neighbours, which has been hypothesized to occur either because long-term neighbours pose less of a threat to resources than unfamiliar neighbours or strangers (Temeles, 1994), or because the chances of role mistakes becomes less likely with increased familiarity ('asymmetric war of attrition'; Ydenberg, Giraldeau, & Falls, 1988). In either case, the function of the dear enemy effect is believed to be reduced engagement in expensive conflicts, which allows for increased time devoted to reproduction and growth. Familiarity with neighbouring individuals has been demonstrated to increase reproductive success in red-winged black birds, *Agelaius phoeniceus* (Beletsky & Orians, 1989) and great tits, *Parus major* (Grabowska-Zhang, Wilkin, & Sheldon, 2012), confer immediate fitness benefits through faster predator-evasion responses in brown trout, *Salmo trutta* (Griffiths, Brockmark, Hojesjo, & Johnsson, 2004), enhance survival and body condition in Arctic char, *Salvelinus alpinus* (Seppä, Laurila, Peuhkuri, Piironen, & Lower, 2001), as well as improve the survival and reproductive success of kangaroo rats, *Dipodomys stephensi*, following translocation (Shier & Swaisgood, 2012). However, neighbours have also been demonstrated to be important territorial intruders (Paton & Carpenter, 1984; Smith & Ivins, 1986), and in cases where competition between territory owners is particularly intense, individuals display increased aggression towards neighbours ('nasty neighbour effect': Müller & Manser, 2007; Newey, Robson, & Crozier, 2010; Yoon, Sillett, Morrison, & Ghalambor, 2012).

Despite evidence that the composition of individuals in the social neighbourhood does matter for behaviour and fitness, our understanding of the effects of social composition on territorial interactions remains limited. For many species, territoriality is maintained through vocalizations, displays and scent markings as a means to establish borders and exclude potential competitors.

However, territorial borders are not impenetrable and competitors may intrude as a means to increase access to resources. Hinsch and Komdeur (2010) have shown mathematically that the evolutionary stability of territoriality depends on the rate of intrusions from territorial neighbours. Since territoriality is an energetic trade-off between access to, and defence of, resources, intrusion by neighbours has significant potential to undercut the benefits of maintaining a territory (as a result of resource theft) while at the same time increasing the costs of defence (Hinsch & Komdeur, 2010; Hixon, 1980; Schoener, 1987). Understanding the social conditions under which territory owners face higher intrusion risk when defensive signalling cues are eliminated may provide insight into how territory owners should be expected to allocate defensive time and energy expenditure in response to their social environment in order to minimize costly intrusions.

North American red squirrels, *Tamiasciurus hudsonicus*, in the northern boreal forest harvest and cache newly matured white spruce, *Picea glauca*, cones in a larder hoard at the centre of their territory, called a 'midden' (Fletcher et al., 2010). Red squirrels depend heavily on these cached cones for overwinter survival and defend exclusive, nonoverlapping territories surrounding their midden (Smith, 1968). Defence occurs primarily through the use of territorial vocalizations called 'rattles' (Smith, 1978). Rattles are an important mechanism for communication between neighbours and function to deter intruders (Siracusa et al., 2017), thus minimizing potential costly physical interactions (Lair, 1990; Smith, 1978). Although physical interactions between individuals occur infrequently (Dantzer et al., 2012; Gorrell, McAdam, Coltman, Humphries, & Boutin, 2010), red squirrels obtain information about their social environment through the acoustic information contained within neighbouring rattles. A squirrel's social environment, therefore, is defined by the 130 m radius at which rattles can be detected (Smith, 1978). Within this acoustic social neighbourhood, red squirrels use rattles to assess local population density and adjust their behaviour (Dantzer et al., 2012) and life history (Dantzer et al., 2013) accordingly. Playback experiments have demonstrated that red squirrels are able to recognize kin through rattles (Wilson et al., 2015) and that squirrels may also distinguish between neighbour and stranger vocalizations (Price, Boutin, & Ydenberg, 1990; but see Wilson et al., 2015). The use of acoustic signalling, therefore, allows for the establishment of a rich social network, one that has so far been demonstrated to affect both behaviour and life history in a species typically considered to be 'asocial'.

While the importance of the quantity of individuals in the social environment has been demonstrated in red squirrels (Dantzer et al., 2012, 2013), the composition of red squirrel social neighbourhoods are also likely to vary in two important ways: relatedness and familiarity (length of time as neighbours). Juveniles will sometimes settle next to their mother, as breeding females are known to sometimes bequeath part or all of their territory to offspring (Berteaux & Boutin, 2000; Price, 1992; Price & Boutin, 1993). However, it is also common for juveniles to disperse from their natal territories and settle next to siblings, their father, or in many cases mostly unrelated neighbours (Berteaux & Boutin, 2000), creating variation in relatedness among neighbourhoods. In addition, overturn of middens can occur through the death of a territory owner or occasionally through bequeathal. As a result some squirrels may occupy different territories each year, setting the stage for an environment with variation in familiarity (duration of tenure as neighbours).

The purpose of this study was to examine under what social conditions and from which individuals red squirrels face increased risk of territorial intrusion in the absence of territory defence. By measuring intrusion risk, we aimed to better understand how red

Download English Version:

<https://daneshyari.com/en/article/5538308>

Download Persian Version:

<https://daneshyari.com/article/5538308>

[Daneshyari.com](https://daneshyari.com)