

Address correspondence to J.A. Stamps. E-mail: [jastamps@ucdavis.edu](mailto:jastamps@ucdavis.edu).

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## Dynamic conflict among heterogeneous groups: a comment on Christensen and Radford

Faye J. Thompson<sup>✉</sup> and Michael A. Cant<sup>✉</sup>

Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK

Christensen and Radford (2018) provide a stimulating review of one of many poorly understood aspects of intergroup conflict, “neighbour stranger response differences” or NSRD. We applaud Christensen and Radford for drawing together a disparate literature on group-living species, and for insightful discussion of the complexities of intergroup interactions. NSRD has been the topic of much research in nonsocial species, so it seems natural to ask whether this research helps to understand variation in conflict behavior between heterogeneous groups composed of individuals with varying interests. Sometimes, however, we believe that research on intergroup conflict can be obscured rather than clarified by

theory and hypotheses derived to explain individual-level conflict and territoriality.

In this case, we think that the focus on NSRD distracts from the most important and interesting feature of intergroup conflict: the intrinsic variability and dynamics of the parties involved. As Christensen and Radford’s review comprehensively demonstrates, neighbors and strangers alike can vary hugely in the threat they pose, depending on reproductive status (e.g. whether females are receptive to mating, or caring for young offspring), group size and composition (e.g. the number of individuals that are predominantly involved in fighting), and their motivation for interacting with a rival group (e.g. to gain territory, or compete for food or mates). Similarly, the threat to own group (and therefore the likely response to intergroup conflict) can also vary depending on own group traits. This variation within and between the parties involved in intergroup conflict is likely to obscure simple comparisons of responses to neighbors and strangers. Consequently, we think that the “two hypotheses” paradigm that characterizes individual-level NSRD research (i.e. “familiarity” versus “threat”; Temeles 1994) may be of limited use to guide investigation of variation in conflict between groups. Instead, we need general theoretical models that can predict how individual and group level intergroup responses change as the ecological and social environment changes. Any differential responses to neighbors versus stranger groups over and above those that emerge endogenously from these models would be interesting but, until we have such models, we suspect that NSRD among social groups will usually be attributable to other forms of ecological and social variability.

A challenge for research in this area is the wide gulf that exists between the assumptions of theoretical models of intergroup conflict and the types of social behavior that field and lab studies measure. Most fundamentally, almost all current models of intergroup conflict focus on the evolution of fixed genetic strategies that evolve on an evolutionary time scale, not the evolution of behavioral responses to conflict. To illustrate, it is widely assumed that groups under attack should pull together and become more cohesive, but we are unable to find any formal model to support this prediction in a biological context. What current population genetic and game theoretic models do predict is that an evolutionary history of conflict between groups can, over many generations, favor the spread of alleles for altruism (or reduced conflict effort) within groups, and alleles for hostility between groups (e.g. Choi and Bowles 2007; Lehmann and Feldman 2008; Gavrillets and Fortunato 2014; Barker et al. 2016). Radford and Fawcett (2014) have pointed out this gulf between the assumptions of current theory and the behaviors measured in empirical studies and recommended studying longer-term behavioral responses to try to bridge the gap from the empirical side.

From the theoretical side, there is a need for models that move beyond the assumptions of unitary actors and simultaneous fixed genetic strategies that characterize classic dyadic animal contest theory. One possibility is to build models that specify the sequence or timing of acts involved in conflict (e.g. Thompson et al. 2017), rather than assuming that actors employ simultaneous “sealed bids.” Economic models of “dynamic battles” (Konrad 2009) offer useful exemplars that evolutionary theorists might adapt and explore. Another approach is to solve for bargaining strategies (Binmore 2010), rather than evolutionarily stable fixed strategies. Developing an evolutionary framework to study conflict among heterogeneous and dynamic groups is a technical and conceptual challenge. But, unusually for behavioral ecology, this is a field where theory is lagging behind empirical research, and hence is rich with opportunity. Hopefully, Christensen and Radford’s review will help to motivate and inform new theory to match what empiricists observe and can test.

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Address correspondence to M.A. Cant. E-mail: [m.a.cant@exeter.ac.uk](mailto:m.a.cant@exeter.ac.uk).

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## Mating and/or social system to explain territorial responses: a comment on Christensen and Radford

**Bart Kranstauber and Marta B. Manser**

Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Studies investigating territorial interactions often find on the first glance seemingly contradictory results, in some cases the response to neighboring groups is stronger than the response to strangers (nasty-neighbor effect), whereas in other cases the response towards strangers is stronger (dear-enemy effect). Christensen and Radford (2018) provide a comprehensive and much needed review of the different responses for species that collectively defend a territory and what the causes and consequences of these variations may be. In group-living species, not only the identity of the intruder varies but also the resident group living in the territory consists of various individuals that have potentially differing interests and motivations. Therefore, studying these interactions in the context of group-living species is especially interesting, but also highly challenging.

## Strangers

Although the dichotomy between neighbors and strangers sounds convincing, in practice, much more complexity is to be expected. In the case of meerkats, for example, besides neighboring groups that have a similar group structure as the resident group, they can encounter stranger coalitions with hugely varying composition. These can be roving male coalitions, looking for extra matings, females that have been evicted from their natal group either alone or in groups, or males and females that grouped together to form a new group searching for territories (Clutton-Brock and Manser 2016). In group-living species, the diversity of these intruding groups is potentially much higher compared to solitary or pair bonded species.

The phenomena where both the intruding groups are diverse and the territory owner group consists different individuals with different interest, such as finding potential mates or defending their mates deserves more attention. Christensen and Radford (2018) in several places indicate this interest in the composition of the stranger group but we think it deserves special attention since in this situation the dynamics are expected to be truly different compared to neighbor–stranger response differences in solitary or paired territory owners.

## Causes of response variation

The authors emphasize the context-dependent variation and within group variation as important factors determining response variation. Convincing empirical evidence exists for the effect of population density, seasonal changes as well as encounter locations as context-dependent factors explaining response variation. However, what is not considered is the mating and/or social system determining the social structure of group-living species and as a consequence the dispersal of group members (Willems et al. 2013; Clutton-Brock 2016), which are crucial determinants in territorial defense. We predict that the social structure and dispersal strategies, philopatry in females or males, will likely explain some of the neighbor–stranger response differences between species, as the characteristics of the different categories of intruders are directly determined by these factors. It will also bring in the role of relatedness of intruders, how they are tolerated or competed, as has recently been shown in African wild dogs (Jackson et al. 2017), and what underlying cognitive processes may be required.

## Future directions

As a perspective for the future, Christensen and Radford (2018) identify three key areas of interest, first theoretical modeling, second physiological hormonal mechanisms, and last the influence of anthropogenic disturbances. As the authors point out the knowledge of the physiological underpinning of differential responses between neighbors and strangers is currently minimal even in solitary species. It is important to investigate this further, yet it might be more rewarding to first obtain a complete picture in the context of single individuals or pairs defending territories.

The last key point suggested to be investigated is how anthropogenic changes are going to change territorial interaction, for example, by changing population density and territory sizes through habitat loss and fragmentation or alternatively by signals or cues being masked by anthropogenic noise. For both these mechanisms, it needs to be carefully considered how the predictions on