

or increased group instability, increasing the chances of group extinction (Angulo et al. 2018). The costs of territorial defense and intergroup interactions may therefore be much higher than realized for some species.

However, the use of the words “intrusion” and “defense” repeatedly seen in studies of intergroup interactions emphasizes the fact that most studies investigate “conflict” between groups. In so doing, a potentially highly valuable aspect of intergroup interactions is missed. As Christensen and Radford (2018) point out, some individuals may not participate in intergroup conflict. They may, however, peacefully interact with extra-group members. These peaceful interactions, which have been observed in a number of species (Angulo et al. 2018), may be as informative as competitive intergroup interactions in understanding the causes and consequences of variation in response to territorial incursions. Although information exchange between groups may be one of the recognized outcomes of intergroup interaction, the acquisition of such information does not necessarily have to involve conflict. The occurrence of, and patterns of investment in, peaceful interactions between groups warrants further investigation. For example, long-term research of intergroup interactions in mountain gorillas, (*Gorilla beringei beringei*), a species often identified as having highly aggressive intergroup interactions, reveals that up to 20% of intergroup interactions are peaceful (Mirville 2018). This suggests a potentially important role of peaceful interactions as a mechanism of social information exchange or resource negotiation between groups, and expands the potential costs and benefits of intergroup interactions, beyond those that are associated with aggressive encounters. Such a possibility remains relatively unexplored and we suggest, combined with the excellent suggestions of Christensen and Radford (2018), that this be a fruitful avenue of future research.

Address correspondence to A.R. Ridley. E-mail: amanda.ridley@uwa.edu.au.

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Variation in group territorial behavior: a response to comments on Christensen and Radford

Andrew N. Radford[✉] and Charlotte Christensen

School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

We are grateful for the thoughtful and positive commentaries (Kranstauber and Manser 2018; McGregor and Bee 2018; Ridley and Mirville 2018; Stamps 2018; Thompson and Cant 2018) written about our recent review on the causes and consequences of variation in the responses of group-living species to territorial intrusions (Christensen and Radford 2018). A clear consensus among the commentators and ourselves is the need for more studies in this research field. Here, we emphasize some key future directions, which reflect both general ideas pertaining to variation in territorial responses (relevant not just to groups but also to individual and pair-bonded territory holders) and ideas more specifically relevant to the study of group-living species.

VARIATION IN TERRITORIAL RESPONSES

When investigating interactions between territory holders and other conspecifics, it is important to consider what different responses might mean rather than just demonstrating that a different response is shown to, for instance, neighbors and strangers (Ridley and Mirville 2018; Stamps 2018). At least in part, that is, because such interactions may be about information exchange rather than representing conflict; some interactions may include elements of both. Relatively peaceful interactions between territory holders and outsiders are potentially more common than implied by a focus on “rivals” and “conflict”; a more balanced approach, including information exchange and negotiation, will further our understanding of territorial behavior (Christensen and Radford 2018; Ridley and Mirville 2018).

We discussed rival identity, particularly the comparison of responses to neighbors and strangers, as the core theme of our review (Christensen and Radford 2018). But, we included the mention of other factors that are likely to be (just as) important in determining how territory holders respond to intruders; some of those factors, and some additional ones, have been emphasized in the commentaries. For instance, Kranstauber and Manser (2018) highlight the need to consider social structure, dispersal strategies, and relatedness; McGregor and Bee (2018) illustrate the importance of interaction location and timing; Thompson and Cant (2018) mention the need to consider variation in group size and the motivation for intruding in the first place. We agree that for further progress to be made in understanding territorial behavior, studies need as far as possible to move away from examinations of individual factors to a more inclusive approach; as a general example, we like the suggestion of McGregor and Bee (2018) to think about “location, identity, time.”

For understandable logistical reasons, the greatest emphasis in territorial research has been on the interaction period itself; studies have focused on which individuals invest and to what extent and what determines whether contests are won or lost. However, capturing the full range of costs and benefits needs consideration of the post-interaction period (Radford et al. 2016; Christensen and Radford 2018; Ridley and Mirville 2018). Researchers are starting

to investigate behavioral effects in the immediate aftermath of an interaction and even consequences apparent many hours later; the overall threat level from territorial outsiders can also influence current behavior. Expanding the range of species in which such consequences are investigated, the timeframe over which they are considered, and the range of impacts is likely to prove a profitable avenue for future work.

RESPONSES BY GROUP-LIVING SPECIES

A clear element of group territorial behavior is that the interests of different group members are unlikely to be perfectly aligned (Christensen and Radford 2018; Kranstauber and Manser 2018; Ridley and Mirville 2018; Thompson and Cant 2018). That is true of both territory holders and outsiders (Kranstauber and Manser 2018), and will have consequences for both interaction involvement and post-interaction behaviours (Radford et al. 2016; Christensen and Radford 2018). Establishing the different motivations of individuals will help us to explain within-group variation in participation—in response to the same threat, different group members might become involved in physical contests, just signal from a safe distance, or not engage at all with the outsiders; considering just an overall group response hides much inherent and interesting inter-individual variation that underpins social evolution.

Surprisingly, given that much behavioral ecology is grounded in complementary theoretical modeling and empirical testing, the theoretical basis of many aspects of intergroup conflict is not well developed (Christensen and Radford 2018; Thompson and Cant 2018). Although starting with existing simple models (in this case, those designed for contests between individuals) has value, the added complexities of within-group differences in motivation need to be taken into account. In general, a narrowing of the gap between the assumptions of current models and empirical knowledge is crucial (Thompson and Cant 2018), and future modeling should consider not just participation in territorial interactions (Gavrilets 2015) but post-interaction consequences too (Radford et al. 2016; Christensen and Radford 2018).

CONCLUSION

Our overall message is that we should be wary of simplifying research investigating territorial responses: it is not all about conflict; when considering rival identity, there is not just a dichotomous comparison between neighbors and strangers; focusing

solely on identity is too limiting; and post-interaction behavior is as important as the interactions themselves. All of this, as well as the need for further development of theoretical modeling to provide testable predictions, is true for species in which individuals or mated pairs hold territories; the complexities escalate when considering group-living species and the variation inherent in the behavior of different group members. Challenging though it is, getting to grips with these issues is critical for our understanding of social evolution; it is a challenge that behavioral ecologists are well equipped to tackle.

Address correspondence Andrew N. Radford. E-mail: andy.radford@bristol.ac.uk

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