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

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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 emphasise 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, neighbours 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 behaviour (Christensen and Radford 2018; Ridley and Mirville 2018).

We discussed rival identity, particularly the comparison of responses to neighbours and strangers, as the core theme of our review (Christensen and Radford 2018). But we included 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 emphasised in the commentaries. For instance, Kranstauber & 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 behaviour, 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 behavioural 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 behaviour.

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 behaviour 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 behavioural ecology is grounded in complementary theoretical modelling and empirical testing, the theoretical basis of many aspects of intergroup conflict is not well-developed (Christensen and Radford 2018; Thompson and Cant 2018). While 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 modelling 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 neighbours and strangers; focusing solely on identity is too limiting; and post-interaction behaviour is as important as the interactions themselves. All of this, as well as the need for further development of theoretical modelling 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 behaviour 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 behavioural ecologists are well-equipped to tackle.

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REFERENCES
