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

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8
9 We are grateful for the thoughtful and positive commentaries (Kranstauber and Manser 2018;
10 McGregor and Bee 2018; Ridley and Mirville 2018; Stamps 2018; Thompson and Cant 2018) written
11 about our recent review on the causes and consequences of variation in the responses of group-
12 living species to territorial intrusions (Christensen and Radford 2018). A clear consensus among the
13 commentators and ourselves is the need for more studies in this research field. Here we emphasise
14 some key future directions, which reflect both general ideas pertaining to variation in territorial
15 responses (relevant not just to groups but also to individual and pair-bonded territory holders) and
16 ideas more specifically relevant to the study of group-living species.

17
18 **VARIATION IN TERRITORIAL RESPONSES**

19 When investigating interactions between territory holders and other conspecifics, it is important to
20 consider what different responses might mean rather than just demonstrating that a different
21 response is shown to, for instance, neighbours and strangers (Ridley and Mirville 2018; Stamps
22 2018). At least in part, that is because such interactions may be about information exchange rather
23 than representing conflict; some interactions may include elements of both. Relatively peaceful
24 interactions between territory holders and outsiders are potentially more common than implied by a
25 focus on 'rivals' and 'conflict'; a more balanced approach, including information exchange and
26 negotiation, will further our understanding of territorial behaviour (Christensen and Radford 2018;
27 Ridley and Mirville 2018).

28
29 We discussed rival identity, particularly the comparison of responses to neighbours and
30 strangers, as the core theme of our review (Christensen and Radford 2018). But we included
31 mention of other factors that are likely to be (just as) important in determining how territory holders
32 respond to intruders; some of those factors, and some additional ones, have been emphasised in the
33 commentaries. For instance, Kranstauber & Manser (2018) highlight the need to consider social

34 structure, dispersal strategies and relatedness; McGregor and Bee (2018) illustrate the importance
35 of interaction location and timing; Thompson and Cant (2018) mention the need to consider
36 variation in group size and the motivation for intruding in the first place. We agree that for further
37 progress to be made in understanding territorial behaviour, studies need as far as possible to move
38 away from examinations of individual factors to a more inclusive approach; as a general example, we
39 like the suggestion of McGregor and Bee (2018) to think about “location, identity, time”.

40

41 For understandable logistical reasons, the greatest emphasis in territorial research has been
42 on the interaction period itself; studies have focused on which individuals invest and to what extent,
43 and what determines whether contests are won or lost. However, capturing the full range of costs
44 and benefits needs consideration of the post-interaction period (Radford et al. 2016; Christensen
45 and Radford 2018; Ridley and Mirville 2018). Researchers are starting to investigate behavioural
46 effects in the immediate aftermath of an interaction and even consequences apparent many hours
47 later; the overall threat level from territorial outsiders can also influence current behaviour.
48 Expanding the range of species in which such consequences are investigated, the timeframe over
49 which they are considered, and the range of impacts is likely to prove a profitable avenue for future
50 work.

51

52 **RESPONSES BY GROUP-LIVING SPECIES**

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

63

64 Surprisingly, given that much behavioural ecology is grounded in complementary theoretical
65 modelling and empirical testing, the theoretical basis of many aspects of intergroup conflict is not
66 well-developed (Christensen and Radford 2018; Thompson and Cant 2018). While starting with
67 existing simple models (in this case, those designed for contests between individuals) has value, the

68 added complexities of within-group differences in motivation need to be taken into account. In
69 general, a narrowing of the gap between the assumptions of current models and empirical
70 knowledge is crucial (Thompson and Cant 2018), and future modelling should consider not just
71 participation in territorial interactions (Gavrilets 2015) but post-interaction consequences too
72 (Radford et al. 2016; Christensen and Radford 2018).

73

74 **CONCLUSION**

75 Our overall message is that we should be wary of simplifying research investigating territorial
76 responses: it is not all about conflict; when considering rival identity, there is not just a dichotomous
77 comparison between neighbours and strangers; focusing solely on identity is too limiting; and post-
78 interaction behaviour is as important as the interactions themselves. All of this, as well as the need
79 for further development of theoretical modelling to provide testable predictions, is true for species
80 in which individuals or mated pairs hold territories; the complexities escalate when considering
81 group-living species and the variation inherent in the behaviour of different group members.
82 Challenging though it is, getting to grips with these issues is critical for our understanding of social
83 evolution; it is a challenge that behavioural ecologists are well-equipped to tackle.

84

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88

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90

91 **REFERENCES**

- 92 Christensen C, Radford AN. 2018. Dear enemies or nasty neighbors? Causes and consequences of
93 variation in the responses of group-living species to territorial intrusions. *Behav Ecol*. In press.
- 94 Gavrilets S. 2015. Collective action problem in heterogeneous groups. *Phil Trans Biol Sci*.
95 370:20150016.
- 96 Kranstauber B, Manser MB. 2018. Mating and/or social system to explain territorial responses: a
97 comment on Christensen and Radford. *Behav Ecol*. In press.
- 98 McGregor PK, Bee, MA. 2018. Where, who, and when? Key drivers of territorial responses: a
99 comment on Christensen and Radford. *Behav Ecol*. In press.
- 100 Radford AN, Majolo B, Aureli F. 2016. Within-group behavioural consequences of between-group
101 conflict: a prospective review. *Proc Biol Sci*. 283:20161567.

- 102 Ridley AR, Mirville MO. 2018. The importance of understanding costs and benefits: a comment on
103 Christensen and Radford. Behav Ecol. In press.
- 104 Stamps J. 2018. Criteria for studies of dear enemy and nasty neighbour effects: a comment on
105 Christensen and Radford. Behav Ecol. In press.
- 106 Thompson FJ, Cant MA. 2018. Dynamic conflict among heterogeneous groups: a comment on
107 Christensen and Radford. Behav Ecol. In press.