Reply

Expanding the Link between Out-Group Threats and In-Group Behavior

(A Reply to Kavaliers and Choleris)

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abstract: In social species, groups and their members face a variety of threats from conspecific outsiders. Such out-group conflict is predicted to influence within-group behavior, with empirical work demonstrating this link in humans, primates, and birds. In our note "Out-Group Threat Promotes Within-Group Affiliation in a Cooperative Fish," appearing in *The American Naturalist* in February 2016, we provided experimental evidence that simulated territorial intrusions result in subsequent increases in affiliation among groupmates in a cichlid fish (*Neolamprologus pulcher*). Martin Kavaliers and Elena Choleris, in their comment "Out-Group Threat Responses, In-Group Bias, and Nonapeptide Involvement Are Conserved Across Vertebrates," appearing in this issue, commented on our cichlid-fish article; they consider the conserved nature of the link between out-group threat and in-group behavior and bias in vertebrates, the influence of pathogens in the process, and the potential underpinning hormonal mechanisms. Here, we provide clarification and expansion of some of the core points that are discussed in the comment by Kavaliers and Choleris.

Keywords: hormonal mechanisms, intergroup conflict, out-group threat, postconflict behavior, sociality.

In a wide range of taxa, from ants to humans, stable groups of individuals face a variety of threats from conspecific outsiders (Radford 2003; Crofoot and Wrangham 2010; Batchelor and Briffa 2011; Christensen et al. 2016). These out-group threats, and any ensuing conflicts, are theoretically predicted to influence subsequent in-group behavior and the evolution of in-group social structure and dynamics (Hamilton 1975; Alexander and Borgia 1978). There has been extensive discussion and demonstration of such links in the human literature, with respect to both short-term behavioral responses (West et al. 2006; Gneezy and Fessler 2012) and evolutionary consequences (Choi and Bowles 2007; Bowles 2009). Evidence has also begun to emerge in nonhuman animals for in-group behavioral changes in the aftermath of out-group conflict (reviewed in Radford et al. 2016). Examples are now available from primates (Polizzi di Sorrentino et al. 2012; Crofoot 2013; Majolo et al. 2016), other mammals (Kavaliers and Choleris 2011; Mares et al. 2011; Christensen et al. 2016), and birds (Radford 2008*a*, 2008*b*; Radford and Fawcett 2014). Most recently, we provided experimental evidence that simulated territorial intrusions result in subsequent increases in affiliation among groupmates in a cichlid fish (*Neolamprologus pulcher*; Bruintjes et al. 2016). Kavaliers and Choleris (2017) commented on our cichlid-fish article and discussed the conserved nature of the link between out-group threat and in-group behavior and bias in vertebrates, the influence of pathogens in the process, and the potential underpinning hormonal mechanisms. Here, we provide clarification and expansion of some of the core points that are discussed in the comment by Kavaliers and Choleris.

Out-group threats come in many forms (Radford et al. 2016). Individuals or same-sex coalitions may challenge the position or breeding success of particular group members (Mares et al. 2011; Bruintjes et al. 2016), while groups may attempt to acquire certain resources or the whole territory of rivals (Radford 2003; Wilson and Wrangham 2003; Kitchen and Beehner 2007). As Kavaliers and Choleris (2017) point out, pathogen exposure and the risk of infection may represent an additional threat posed by outsiders. Stronger immediate responses might be expected to infected, as opposed to healthy, outsiders, in the same way that there are stronger responses to individuals or groups who represent a greater threat in other contexts—for example, differences in the relative threat posed by groups of different size (Radford and du Plessis 2004) and by neighbors and strangers (Radford 2005; Müller and Manser 2007) have been shown to be important—with knock-on consequences for in-group behavior (Radford 2008*b*; Bruintjes et al. 2016; Christensen

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et al. 2016). Moreover, exposure to pathogens can influence the response to subsequent out-group threats; pathogen "priming" can lead to more negative reactions toward outsiders (Navarette and Fessler 2006; Fincher et al. 2011). In general, external factors such as the location of the encounter (Crofoot et al. 2008) and prior experience of conflicts (Radford 2011) are likely to alter responses to out-group threats and their consequences.

In-group behavioral changes may be triggered directly or indirectly by out-group threats. Most obviously, encounters with rival conspecifics can lead to conflict; those encounters may occur on shared territorial borders or be the result of territorial intrusions (Radford and du Plessis 2004; Kitchen and Beehner 2007). In such cases, interactions can vary from extensive signaling exchanges (McComb et al. 1994; Golabek et al. 2012) to physical fights (Wich and Sterck 2007; Mosser and Packer 2009). During such encounters, there may be the opportunity to assess the pathogen threat presented by outsiders. However, in-group behavior can also be influenced by indirect cues to the recent presence of rivals; for example, when encountering urine or fecal deposits (Christensen et al. 2016). There is also some evidence that spending time in territorial areas where conflicts with rivals are most likely can lead to in-group behavioral responses similar to those seen following actual conflicts (Radford 2011). In these latter cases involving no physical interaction with actual outsiders, there can be no direct assessment of pathogen risk (unless such information is available from feces, for instance), but memory of prior experiences with rivals in that area could still have an impact (see above).

The in-group consequences of out-group conflict, arising as a result of increased anxiety, disrupted social relationships, and alterations in group composition or structure (Cords and Thurnheer 1993; Stamps and Krishnan 2001; Crofoot 2013), are manifested across a variety of time frames. Changes in the way group members behave toward one another can occur during the conflict itself; this is the time frame considered by most human studies using economic games (West et al. 2006; Puurtinen and Mappes 2009). The majority of the empirical work on nonhuman animals has focused on the immediate aftermath of conflicts with rivals (Radford et al. 2016), demonstrating changes in affiliation or aggression between group members and alterations in movement patterns (Radford 2008*a*, 2008*b*; Polizzi di Sorrentino et al. 2012; Crofoot 2013; Christensen et al. 2016). There is also the possibility of longer-lasting behavioral effects; recent work on a cooperatively breeding bird species has shown that out-group conflicts can influence roost choice, consensus decision making, and group cohesion many hours later (Radford and Fawcett 2014). Furthermore, out-group conflict has the potential to affect reproductive success and survival. The stress of territorial intrusions could delay breeding and affect offspring quality and survival through maternal effects (Mileva et al. 2011), while costly participation in defense and postconflict interactions could lead to reductions in parental care and thus lowered offspring survival and growth (Mares et al. 2012). Injury or even death can result from defense against outsiders (Wilson and Wrangham 2003; Mosser and Packer 2009), although these are likely to be relatively rare events because escalation to fighting is minimized by avoidance and signaling (McComb et al. 1994; Golabek et al. 2012). Finally, and especially if out-group conflicts carry fitness consequences, there will be selective pressure over evolutionary time; threats from outsiders have been suggested to play an important role in the evolution of group dynamics and social structure (Wrangham 1980; van Schaik 1989).

The starting premise for our work on *N. pulcher* (Bruintjes et al. 2016) was that out-group threats should influence in-group behavioral interactions. However, various feedback loops are likely to be involved. Kavaliers and Choleris (2017) emphasize one such possibility, suggesting that amplification of in-group attractiveness and the promotion of group favoritism, mediated through such factors as allogrooming and social immunity, may further enhance in-group affiliation and social behavior. We suggest that interactions and relationships within groups can in turn influence reactions to out-group threats. For instance, there tends to be considerable intragroup variation in participation in out-group conflicts (Radford 2003; Kitchen and Beehner 2007), not least because it represents a collective-action problem (Willems et al. 2015). Promotion of intragroup cohesion and the strengthening of bonds between group members, in addition to rewards and punishments, could operate to increase the likelihood of contributions to future out-group conflicts (Radford 2008*b*, 2011).

While there is increasing evidence of out-group influences on in-group behavior, little empirical work has considered potential underpinning mechanisms. Kavaliers and Choleris (2017) discuss evolutionarily conserved endocrinological systems in vertebrates in this regard. This makes sense, given that behavioral responses are known in general to be constrained or escalated by hormonal changes (Adkins-Regan 2005). In particular, they focus on nonapeptide systems, emphasizing oxytocin and vasopressin (and their homologs), which help to mediate responses to social information and the expression of social behavior (Choleris et al. 2013; De Dreu and Kret 2016). We agree that these hormones are likely to be critical, especially given their facilitation of positive responses to in-group members and negative responses to outsiders (De Dreu et al. 2011; De Dreu and Kret 2016), but other hormones would also be worth investigation. For instance, in addition to their primary role in stress and reproduction, respectively, corticosteroids (e.g., cortisol) and sex steroids (e.g., androgens) are essential for the coordination of social behavior (Goodson 2005; Soares et al. 2010) and thus are likely to be important in mediating the effects of out-group conflict. Indeed, territorial intrusions raise cortisol and androgen levels in defenders (Hirschenhauser et al. 2004; Sebire et al. 2007); prolonged increases in cortisol can in turn reduce sex steroid levels (Barton and Iwama 1991), which will reduce reproductive potential. Studying hormonal changes in relation to both behavioral responses and reproductive output would help to reveal the mechanistic link between out-group conflict and in-group processes.

Out-group threats are common in all social species, including our own; it should also be remembered that social animals typically exhibit obligate dispersal that would, by definition, necessitate interactions with unknown conspecifics. Burgeoning evidence on in-group behavior and biases suggests that there may be evolutionarily conserved consequences of such threats and ensuing conflicts with outsiders, although interspecific differences are also expected. Nonhuman research on out-group conflict not only provides insight into the evolutionary roots of human sociality but also offers the opportunity for experimental testing of functional and mechanistic consequences that have, to date, received little empirical consideration. We therefore support the call of Kavaliers and Choleris (2017) for more work in this field and thus the opportunity for comparative investigations (see also Radford et al. 2016).

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