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Expanding the link between out-group threats and in-group behaviour: A reply to Kavaliers and Choleris

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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 behaviour 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 behavioural 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 non-human animals for in-group behavioural 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 2008a, 2008b; 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 & Choleris (In press) commented on our cichlid fish paper and discuss the conserved nature of the link between out-group threat and in-group behaviour 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; Brintjes 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 (In press) 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 neighbours and strangers (Radford 2005; Müller and Manser 2007) have been shown to be important – with knock-on consequences for in-group behaviour (Radford 2008b; Brintjes et al. 2016; Christensen et al. 2016). Moreover, exposure to pathogens can influence the response to subsequent out-group threats; pathogen ‘priming’ can lead to more negative reactions towards 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 behavioural 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 signalling 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 behaviour can also be influenced by indirect cues to the recent presence of rivals; for example, when encountering urine or faecal 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 behavioural 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 faeces, 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 & Thurnheer, 1993;

Stamps & Krishan 2001; Crofoot 2013), are manifested across a variety of timeframes. Changes in the way group members behave towards one another can occur during the conflict itself; this is the timeframe considered by most human studies using economic games (West et al. 2006; Puurtinen and Mappes 2009). The majority of the empirical work on non-human animals has focussed 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 2008a, b; Polizzi di Sorrentino 2012; Crofoot 2013; Christensen et al. 2016). There is also the possibility of longer-lasting behavioural effects; recent work on a cooperatively breeding bird species has shown 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 impact 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 defence and post-conflict 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 defence against outsiders (Wilson and Wrangham 2003; Mosser and Packer 2009), although these are likely to be relatively rare events as escalation to fighting is minimised by avoidance and signalling (McComb et al. 1994; Golabek et al. 2012). Finally, and especially if out-group conflicts carry fitness consequences, then 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 *Neolamprologus pulcher* (Bruitjes et al. 2016) was that out-group threats should influence in-group behavioural interactions. However, various feedback loops are likely to be involved. Kavaliers and Choleris (In press) emphasise one such possibility, suggesting that amplification of in-group attractiveness and the promotion of group favouritism, mediated through such factors as allogrooming and social immunity, may further enhance in-group affiliation and social behaviour. We suggest that interactions and relationships within groups can in turn influence reactions to out-group threats. For instance, there tends to be considerable intra-group 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 intra-group 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 2008b, 2011).

While there is increasing evidence of out-group influences on in-group behaviour, little empirical work has considered potential underpinning mechanisms. Kavaliers and Choleris (In press) discuss evolutionarily conserved endocrinological systems in vertebrates in this regard. This makes sense given that behavioural responses are known in general to be constrained or escalated by hormonal changes (Adkins-Regan 2005). In particular, they focus on nonapeptide systems, emphasising oxytocin and vasopressin (and their homologs) which help to mediate responses to social information and the expression of social behaviour (Choleris et al. 2013; De Dreu and Kret 2015). 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 2015), 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 behaviour (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 behavioural 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 behaviour and biases suggests that there may be evolutionarily conserved consequences of such threats and ensuing conflicts with outsiders, although inter-specific differences are also expected. Non-human research on out-group conflict not only provides insight into the evolutionary roots of human sociality, but 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 (In press) for more work in this field and thus the opportunity for comparative investigations (see also Radford et al. 2016).

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Literature Cited

- Adkins-Regan, E. 2005. *Hormones and animal social behavior*. Princeton: Princeton University Press.
- Alexander, R. D., and G. Borgia. 1978. Group selection, altruism and the levels of organisation of life. *Annual Review of Ecology and Systematics* 9:449–474.
- Barton, B. C., and G. K. Iwama. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of Fish Diseases* 1:3–26.
- Batchelor, T. P., and M. Briffa. 2011. Fight tactics in wood ants: Individuals in smaller groups fight harder but die faster. *Proceedings of the Royal Society B: Biological Sciences* 278:3243–3250.
- Bowles, S. 2009. Did warfare among ancestral hunter-gatherer groups affect the evolution of human social behaviors? *Science* 324:1293–1298.
- Bruintjes, R., J. Lynton-Jenkins, J. W. Jones, and A. N. Radford. 2016. Out-group threat promotes within-group affiliation in a cooperative fish. *American Naturalist* 187:274–282.
- Choi, J. K., and S. Bowles. 2007. The coevolution of parochial altruism and war. *Science* 318:636–640.
- Choleris, E., D. W. Pfaff, and M. Kavaliers eds. 2013. *Oxytocin, vasopressin and related peptides in the regulation of behavior*. Cambridge, UK: Cambridge University Press.
- Christensen, C., J. M. Kern, E. Bennitt, and A. N. Radford. 2016. Rival group scent induces changes in dwarf mongoose immediate behaviour and subsequent movement. *Behavioral Ecology* 27:1627–1634.
- Cords, M., and S. Thurnheer. 1993. Reconciling with valuable partners by long-tailed macaques. *Ethology* 93:315–325.
- Crofoot, M. C. 2013. The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors. *American Journal of Physical Anthropology* 152:79–85.
- Crofoot, M. C., I. C. Gilby, M. C. Wikelski, and R. W. Kays. 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences USA* 105:577–581.
- Crofoot, M.C., and R. W. Wrangham. 2010. Intergroup aggression in primates and humans: the case for a unified theory. In *Mind the gap: tracing the origins of human universals* (eds PM Kappeler, J Silk), pp. 171–195. New York: Springer.
- De Dreu, C. K. W., L. L. Greeg, G. A. van Kleef, S. Shalvi, and M. J. Handgraaf. 2011. Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences USA* 108:1262–1266.
- De Dreu, C. K. W., and M. E. Kret. 2015. Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity and defense. *Biological Psychiatry* 79:165–173.

- Fincher, C. L., R. Thornhill, D. R. Murray, and M. D. R. Schaller. 2011. Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings of the Royal Society B: Biological Sciences* 275:1279–1284.
- Gneezy, A., and D. M. T. Fessler. 2012. Conflict, sticks and carrots: war increases prosocial punishments and rewards. *Proceedings of the Royal Society B: Biological Sciences* 279:219–223.
- Golabek, K. A., A. R. Ridley, and A. N. Radford. 2012. Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour* 83:613–619.
- Goodson, J. L. 2005. The vertebrate social behaviour network: Evolutionary themes and variations. *Hormones and Behavior* 48:11–22.
- Hamilton, W. D. 1975. Innate social aptitudes of man: an approach from evolutionary genetics. In *Biosocial anthropology* (ed R Fox), pp. 133–155. London: Malaby Press.
- Hirschenhauser, K., M. Tarborsky, T. Oliveira, A. V. M. Canario, and R. F. Oliveira. 2004. A test of the ‘challenge hypothesis’ in cichlid fish: simulated partner and territory intruder experiments. *Animal Behaviour* 68:741–750.
- Kavaliers, M., and E. Choleris. 2011. Sociality, pathogen avoidance, and the neuropeptides oxytocin and arginine vasopression. *Psychological Science* 22:1367–1374.
- Kavaliers, M., and E. Choleris. In press. Out-group threat responses, in-group bias and nonapeptide involvement are conserved across vertebrates. *American Naturalist*.
- Kitchen, D. M., and J. C. Beehner. 2007. Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour* 144:1551–1581.
- Majolo, B., A. de Bortoli Vizioli, and J. Lehmann. 2016. The effect of inter-group competition on intra-group affiliation in primates. *Animal Behaviour* 114:13–19.
- Mares, R., A. J. Young, and T. H. Clutton-Brock. 2012. Individual contributions to territory defence in a cooperative breeder: weighing up the benefits and the costs. *Proceedings of the Royal Society B: Biological Sciences* 279:3989–3995.
- Mares, R., A. J. Young, D. L. Levesque, N. Harrison, and T. H. Clutton-Brock. 2011. Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. *Behavioral Ecology* 22:594–600.
- McComb, K., C. Packer, and A. Pusey. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour* 47:379–387.
- Mileva, V. R., K. M. Gilmour, and S. Balshine. 2011. Effects of maternal stress on egg characteristics in a cooperatively breeding fish. *Comparative Biochemistry and Physiology A* 158:22–29.
- Mosser, A., and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour* 78:359–370.

- Müller, C. A., and M. B. Manser. 2007 'Nasty neighbours' rather than 'dear enemies' in a social carnivore. *Proceedings of the Royal Society B: Biological Sciences* 274:959–965.
- Navarette, C. D., D. M. T. Fessler. 2006. Disease avoidance and ethnocentrism: The effect of disease vulnerability and disgust sensitivity on intergroup attitude. *Evolution and Human Behavior* 27:270–282.
- Polizzi di Sorrentino, E., G. Schino, L. Massaro, E. Visalberghi, and F. Aureli. 2012. Between-group hostility affects within-group interactions in tufted capuchin monkeys. *Animal Behaviour* 83:445–451.
- Puurtinen, M., and T. Mappes. 2009. Between-group competition and human cooperation. *Proceedings of the Royal Society B: Biological Sciences* 276:355–360.
- Radford, A. N. 2003. Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. *Animal Behaviour* 66:1035–1044.
- Radford, A. N. 2005. Neighbour-stranger discrimination in the group-living green woodhoopoe. *Animal Behaviour* 70:1227–1234.
- Radford, A. N. 2008a. Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. *Proceedings of the Royal Society B: Biological Sciences* 275:2787–2791.
- Radford, A. N. 2008b. Type of threat influences postconflict allopreening in a social bird. *Current Biology* 18:R114–115.
- Radford, A. N. 2011. Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation. *Biology Letters* 7:26–29.
- Radford, A. N., and M. A. du Plessis. 2004. Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour* 68:803–810.
- Radford, A. N., and T. W. Fawcett. 2014. Conflict between groups promotes later defense of a critical resource in a cooperatively breeding bird. *Current Biology* 24:2935–2939.
- Radford, A. N., B. Majolo, and F. Aureli. 2016. Within-group behavioural consequences of between-group conflict: a prospective review. *Proceedings of the Royal Society B: Biological Sciences* 283:20161567.
- Sebire, M., I. Katsiadaki, and A. P. Scott. 2007. Non-invasive measurement of 11-ketotestosterone, cortisol and androstenedione in male three-spined stickleback (*Gasterosteus aculeatus*). 152:30–38.
- Soares, M. C., R. Bshary, L. Fusani, W. Goymann, M. Hau, K. Hirschenhauser, and R. F. Oliveira. 2010. Hormonal mechanisms of cooperative behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2737–2750.

- Stamps, J. A., and W. Krishan. 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. *American Naturalist* 157:154–169.
- van Schaik, C. P. 1989. The ecology of social relationships amongst female primates. In *Comparative socioecology: the behavioral ecology of humans and other mammals* (eds V Standen, RA Foley), pp. 195–218. Oxford: Blackwell.
- West, S. A., A. Gardner, D. M. Shuker, T. Reynolds, M. Burton-Chellow, E. M. Sykes, M. A. Guinee, and A. S. Griffin. 2006. Cooperation and the scale of competition in humans. *Current Biology* 16:1103–1106.
- Wich, S.A., and E. H. Sterck. 2007. Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. *Behaviour* 144:1583–1598.
- Willems, E. P., T. J. M. Arseneau, X. Schleuning, and C. P. van Schaik. 2015. Communal range defence in primates as a public goods dilemma. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370:20150003.
- Wilson, M., and R. Wrangham. 2003. Between-group relations in chimpanzees. *Annual Review of Anthropology* 32:363–392.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.