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Group response to social perturbation: impacts of isotocin and the social landscape

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Conflict is an inherent part of group living, and the mediation of conflict is essential for the stability of social groups. Response to within-group social conflict should depend on the external social environment. Individuals in dense social neighbourhoods have greater opportunities to disperse and join a nearby group compared to individuals in sparse social neighbourhoods with few nearby groups. To explore the influence of the social neighbourhood on responses to conflict, we experimentally perturbed groups of wild *Neolamprologus pulcher*, a cooperatively breeding cichlid fish, by temporarily removing a subordinate individual. Such removals typically increase the amount of within-group aggression. As predicted, aggression towards the returning subordinate and the rate of eviction from the group increased with the density of neighbouring social groups. Furthermore, we predicted that the returning subordinate could improve its likelihood of reacceptance into the group by displaying submissively. To test this prediction, we attempted to manipulate submissive behaviour by injecting the removed individuals with isotocin, a nonapeptide hormone that has been shown in the laboratory to increase the expression of submissive behaviour in this species. As predicted, subordinates that received isotocin showed more submission when returned to their group. However, contrary to our prediction, these isotocin-treated fish received more aggression from their group-mates and were more likely to be evicted than fish receiving a saline control injection. Our results emphasize the importance of the social neighbourhood in determining within-group dynamics but surprisingly contradict the notion that submissive behaviour reduces aggression and facilitates group stability.
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Conflict is an unavoidable consequence of group living because individuals seek to maximize their share of resources and reproductive opportunities within the group, thereby reducing the resources and reproduction available for others. Conflict among individuals within a social group can counteract the benefits of group living, leading to reduced group productivity, injury, eviction and group dissolution (Aureli, Cords, & van Schaik, 2002). Therefore, in group-living species there should be strong selection for behaviours that mitigate conflict and reduce disputes within the group (Aureli et al., 2002; Bourke, 2011; Cant & Johnstone, 2009; Thompson, Donaldson, Johnstone, Field, & Cant, 2014).

Subordinate individuals often make use of submissive displays to appease dominant group members and increase their likelihood of being tolerated within the group (Bergmüller & Taborsky, 2005; Huntingford & Turner, 1987; Wilson, 1975). Subordinate individuals may perform submissive displays as an explicit signal of deference to dominant individuals in order to pre-empt or terminate a conflict. Submissive displays allow the signaller to concede a conflicted resourse without the need for further costly aggression (Lorenz, 1966; Matsumura & Hayden, 2006). They also allow the signaller to remain in the same spatial location rather than fleeing from the dominant (Issa & Edwards, 2006; Ligon, 2014; Matsumura & Hayden, 2006). Consequently, the expression of

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submissive behaviour is essential for the formation and maintenance of stable groups (Hick, Reddon, O'Connor, & Balshine, 2014; Schenkel, 1967).

The use of submissive displays may not be consistent across all social contexts, as the social environment may alter the amount of within-group conflict as well as the fitness consequences of unresolved conflict (Clutton-Brock, Hodge, & Flower, 2008; Kutsukake & Clutton-Brock, 2008a). For example, individual subordinate members may be more expendable in larger social groups than in smaller social groups (biological market theory; Kutsukake & Clutton-Brock, 2008a; Noë & Hammerstein, 1994). Similarly, groups living in densely populated areas may have a greater ability to attract new members from neighbouring groups, which may decrease the importance of current members and consequently, decrease dominant tolerance of subordinate behaviour (Noë & Hammerstein, 1994). Therefore, regardless of a subordinate's effort to moderate conflict, dominants may not reduce their policing or punishment of subordinates when there is a low cost to losing current subordinates. The social landscape can also alter a subordinate's willingness to avoid within-group conflict. An increased number of neighbouring groups can facilitate successful dispersal to another group (Bergmüller, Heg, Peer, & Taborsky, 2005; Drewe, Madden, & Pearce, 2009; Heg, Heg-Bachar, Brouwer, & Taborsky, 2008) and, therefore, in areas with many groups nearby, subordinates may have a decreased incentive to expend energy on mitigating conflict within their current group (Bergmüller, Heg, & Taborsky, 2005; Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013).

In this study, we sought to understand how the external social environment, the expression of submissive behaviour and the interaction between these factors affect group member responses to within-group conflict. We experimentally perturbed groups of wild *Neolamprologus pulcher*, a cooperatively breeding cichlid fish, by temporarily removing a subordinate group member and manipulating submissive behaviour by administering the nonapeptide hormone isotocin before returning the removed subordinate. *Neolamprologus pulcher* are endemic to Lake Tanganyika, East Africa where they live clustered in colonies composed of 2–200 distinct social groups (Heg, Brouwer, Bachar, & Taborsky, 2005; Stiver et al., 2007). Each social group consists of a dominant breeding pair and 1–15 subordinates (Wong & Balshine, 2011a) that jointly defend permanent territories. Subordinates form size-based dominance hierarchies and care for the offspring of the dominant breeders (Taborsky & Limberger, 1981) until reaching breeding status by inheriting their current territory (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Wong & Balshine, 2011a) or dispersing to fill vacant breeding positions in other territories (Bergmüller, Heg, Peer, et al., 2005; Stiver et al., 2007). Subordinate *N. pulcher* spend the majority of their time in their own territory, but also visit nearby groups (preferentially visiting groups within a 3 m radius; Heg et al., 2008) and receive little aggression when visiting these nearby groups (Bergmüller, Heg, Peer, et al., 2005). Subordinate removal treatments in *N. pulcher* simulate a dereliction of cooperative duties (Wong & Balshine, 2011a). Such removals also induce rank conflict among the remaining group members as they jockey for position in the perturbed hierarchy (Wong & Balshine, 2011b). Removals can result in punishment from the other group members, including eviction from the group (Balshine-Earn et al., 1998; Fischer, Zöttl, Groenewoud, & Taborsky, 2014). In the current study, we removed a subordinate fish for ~4 h. We predicted that removing subordinates would increase the amount of aggression they received from other group members and would increase the amount of submission given by the removed subordinate. Control fish were removed only briefly (~5 min) to account for potential effects of capture and handling, and to allow administration of the hormone treatment (see below).

Submissive signals are well developed in *N. pulcher* (Bender et al., 2006; Bergmüller & Taborsky, 2005; Bruintjes & Taborsky, 2008; Dey, Reddon, O'Connor, & Balshine, 2013; Reddon, O'Connor, Marsh-Rollo, & Balshine, 2012; Reddon et al., 2015; Reddon et al., 2011; Taborsky, 1985) and appear to facilitate social stability in this species (Hick et al., 2014). To explicitly examine the role of submissive behaviour in modulating the group's response to the focal subordinate, we gave each focal subordinate an injection of isotocin (IT), the teleost fish homologue of oxytocin (Godwin & Thompson, 2012; Thompson & Walton, 2013), or a saline vehicle control, before returning it to the group. In a previous study using a similar design in captive *N. pulcher* groups, we found that IT-treated fish increased their submissive behaviour upon return to their group, but did not show any change in aggressive or affiliative behaviours (Reddon et al., 2012). We predicted that individuals who received an injection of IT in the field would act more submissively, and that this submission would appease dominant group members, reducing the likelihood of these removed individuals being evicted from the group (Bergmüller & Taborsky, 2005).

We also expected that the social context would be an important predictor of both the focal fish's response and its group's response to the social conflict induced by the removal treatment. Because submissive behaviours are costly (Grantner & Taborsky, 1998), we would expect subordinates to scale their use to the potential cost of eviction. Therefore, submissive behaviours should be more valuable in low-density areas where individuals have a reduced ability to disperse to neighbouring groups (Bergmüller, Heg, & Taborsky, 2005; Cant & Johnstone, 2009). We also predicted that returned subordinates would receive more aggression from dominants and suffer increased rates of eviction in denser social neighbourhoods and in larger groups, due to the relative expendability of current subordinates when there are many subordinates in the group and/or a larger pool of potential subordinates that could join the group (Kutsukake & Clutton-Brock, 2008a; Noë & Hammerstein, 1994).

METHODS

We observed 40 *N. pulcher* groups from February to April 2013 in Kasakalawe Bay, Zambia (8°46′S, 31°46′E) using SCUBA. Our experimental groups were clustered in a single colony at a depth of 10–12 m. We mapped and measured the distances between each group in the colony using a 50 m measuring tape. We recorded the size of each experimental group and identified the dominant and subordinate fish in each group. We only considered individuals >10 mm in standard length (SL) in our calculation of group size, and any eggs, larvae or small juveniles that may have been present were not counted. Individuals were considered to be part of the focal group if they were in the territory and swam repeatedly under the rocks without eliciting aggression from other fish within the territory. We selected the largest subordinate in each experimental group as the focal fish for treatment in our experiment. All focal fish used were sexually mature (>35 mm SL; mean SL ± SE: 40.3 ± 0.66 mm; Taborsky, 1985). Between 0900 and 1700 hours, we observed each of these 40 focal subordinate fish for 10 min prior to capture and recorded all social behaviours produced and received. Following published ethograms for this species (Hick et al., 2014; Reddon et al., 2015; Sopinka et al., 2009), we categorized all social behaviours as overt physical attacks (ram, bite, mouth fight), restrained aggressive displays (operculum spreads, fin raises, head shakes), submissive displays (tail quivers, hook displays, submissive postures) or affiliative behaviours (parallel swims, follows, soft touches). We also recorded any aggression produced by the focal fish towards any

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