



Variation in glucocorticoid levels in relation to direct and third-party interactions in a social cichlid fish



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HIGHLIGHTS

- Subordinate female cortisol levels linked to affiliativeness with dominant female
- Subordinate female cortisol levels linked to conflict between dominants
- Direct aggression had no impact on subordinate female cortisol levels
- Individual hormonal state can be influenced both directly and indirectly.

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ABSTRACT

In complex animal societies, direct interactions between group members can influence the behavior and glucocorticoid levels of individuals involved. Recently, it has become apparent that third-party group members can influence dyadic interactions, and vice versa. Thus, glucocorticoid levels may vary depending on interactions of other members of the social group. Using the social cichlid fish *Neolamprologus pulcher*, we examined the relationship between levels of the glucocorticoid hormone cortisol in subordinate females and 1) direct interactions with dominant group members, as well as 2) dyadic interactions between the dominant male and female, in which the subordinate female was not directly involved. Subordinate females that frequently engaged in non-aggressive interactions with dominant females had lower cortisol levels. There was no relationship between subordinate female cortisol and agonistic interactions between the subordinate female and either dominant. Subordinate females had higher cortisol levels when in groups in which the dominant breeding pair behaved agonistically towards each other and performed fewer courtship behaviors. For subordinate females in this species, variation in cortisol levels is associated with their own affiliative behavior, but also can be explained by the broader social context of interactions between dominant members of the group.

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1. Introduction

The effects of sociality and dominance status on individual glucocorticoid levels have received a great deal of attention in recent years. Glucocorticoids (hereafter GC) mediate an individual's physiological response to stressors that they perceive or encounter [43]. In the short term, the release of GCs redirects energy to processes essential for escaping a stressor. Examples of such shifts include increasing the available glucose in circulation [33,42] and upregulating circulatory system function while redirecting blood away from nonessential organs [43]. However, chronically elevated GC levels can impact organisms well past the conclusion of exposure to the stressor, and lead to reduced

investment in growth and reproduction [43]. Thus, GC levels can provide information about the stress level experienced by an animal, as well as potential lasting costs associated with exposure to a stressor.

Social species may face stressors associated with group living. Individuals in groups generally live in closer proximity and share resources, which may lead to frequent and potentially stressful interactions with other group members. On the one hand, repeated agonistic interactions over time can act as a stressor and elevate individual cortisol levels [56]. On the other hand, such social systems also provide opportunities to participate in non-aggressive interactions (hereafter “affiliative” interactions) as well as submissive behaviors which may reduce or prevent agonistic interactions, and these behaviors may be inversely related to individual cortisol levels [5].

In addition to the effects of the frequency and nature of social interactions, GC levels in organisms living in hierarchical groups may also be related to social status and stability. Elevated GC levels have been

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suggested as a cause of subordinate reproductive suppression [44,52,56], as well as a cost of dominance [12,13]. However, across animal groups there is great variation in the relationship between GC levels and social status ([1]; see reviews by [11,24]). In some systems subordinate group members have higher basal GC levels than more dominant group members (such as house mice, *Mus musculus* [7]), whereas in others dominant group members have higher basal GC levels than more subordinate group members (such as Florida Scrub Jays *Aphelocoma coerulescens* [44]). Yet other social vertebrates show no apparent differences in GC levels depending on social rank (such as gray wolves, *Canis lupus* [35]). Abbott et al. [1] suggested that this wide variation in relative GC levels is related to the number of stressors individuals face and the amount of social support available, both of which may vary among taxa and correlate with status in some systems. Similarly, Goymann and Wingfield [24] suggested that patterns of status-based differences in cortisol levels reflect status-based differences in “allostatic loads”, the summed burden on individuals due to physiological, environmental, and social factors, [46].

Social species exist in communication networks in which individuals can acquire information about other individuals through signals not necessarily intended for them [36]. In Siamese fighting fish, *Betta splendens*, and green swordtail fish, *Xiphophorus helleri*, individuals eavesdropped on dyadic conflicts and used acquired information to inform future decisions [17,40]. Contestants also adjust their aggressive actions depending on the presence and sex of eavesdroppers [16]. Individuals within communication networks thus have access to a great deal of information about group dynamics and stability. Therefore, individual behavior and GC levels may reflect information about others in the group, including information gained from observing the interactions of others. Indeed, the behavior of individuals influences and is influenced by both their own direct interactions with other group members and by indirect interactions among others in the group [21,22,26].

In cooperatively breeding systems, the presence of potentially reproductive subordinate group members may lead to conflict between the dominant breeders. While subordinate group members may provide alloparental care, which benefits both parents, subordinate attempts to reproduce within the group may impose a cost on the same-sex dominant, and a potential benefit to the opposite-sex dominant. Variation in subordinate behavior is causally linked to variation in conflict between dominant males and dominant females in a cooperatively breeding fish [26]. The outcome of this conflict between dominants may feedback directly and indirectly on subordinate group members' behavior and fitness, and these subordinates may respond to prevent or reduce negative effects. Thus, we expect that GC levels of subordinate individuals in cooperatively breeding systems will reflect the sum of stressors related to the frequency of direct interactions, as well as the indirect effects of behavioral interactions among other group members.

Neolamprologus pulcher is a cooperatively breeding cichlid endemic to Lake Tanganyika in East Africa [50]. This species has become a model system for the study of cooperative and other social behavior (see review by [54]). *N. pulcher* groups are characterized by a dominant breeding pair and a number of subordinates (1–14, [4]) that form a size-based dominance hierarchy [3,15,30,50]. Reproductive skew is high, but monopolization of reproduction by dominant group members is not complete. Extra-pair reproduction has been documented in *N. pulcher* for both male [29] and female [30] subordinate group members, as well as by non-group members [31,58]. In *N. pulcher*, levels of the GC hormone cortisol are higher in dominant individuals than in subordinate individuals [8,38], and are higher in subordinate group members than size-matched individuals maintained in non-breeding groups [6]. Further, Bender et al. [5] found that subordinate male submissiveness to dominant males is inversely correlated with cortisol, testosterone, and 11-ketotestosterone levels demonstrating that subordinate GC levels are influenced not only by social status but also individual behavior in *N. pulcher*.

We examined the relationship between cortisol levels in subordinate female *N. pulcher* and the behavioral interactions among subordinate females, dominant females, and dominant males. Specifically, we examined the relationship between subordinate female cortisol and affiliative and agonistic (aggression, and associated submissive and avoidance behaviors) interactions that directly involve subordinate females, as well as affiliative and agonistic interactions that occur between the dominant female and dominant male. We predict that affiliative behavior between the subordinate female and either dominant would be negatively correlated with subordinate female GC levels. Affiliative behavior may indicate a lack of conflict within the dyad, or prevent future agonistic interactions. We predict that agonistic interactions between the subordinate female and the dominant male or dominant female would be positively correlated with subordinate female GC levels as such interactions are likely stressful to the subordinate female. Finally, we predict that agonistic interactions within the dominant breeding pair would be negatively correlated with subordinate female cortisol levels. We predicted this for two reasons. First, dominants occupied in conflict with their mates may have less time to engage in suppression of, or other conflict with, the subordinate female. In this case we would expect subordinate female cortisol levels to be both negatively correlated with dominant conflict and positively correlated with direct agonistic interactions between the subordinate female and one or both dominants. Second, subordinate females with lower cortisol levels may be more likely to reproduce and thus create greater conflict between the dominant breeders.

2. Methods

Fish were either wild caught or F1 fish that originated in the region of Kipili, Tanzania (7°26'02"S, 30°35'59"E) of Lake Tanganyika. Wild caught fish had been in the lab population for >1 year, and there was no discernable difference in the behavior of wild caught and F1 fish. Groups of three fish (dominant male, dominant female, subordinate female) were maintained in 113.6 L aquariums (30.5 cm × 61 cm × 61 cm) with a sand substrate of an average depth of 30 mm. Each aquarium contained two halved clay flowerpots that served as a breeding substrate as well as a submersible heater. Each aquarium had a biweekly water change (20%), and appropriate water chemistry was maintained using commercially available *Tanganyika Buffer* (Seachem Laboratories, 1000 Seachem Dr., Madison, GA 30650). Water temperature was checked daily, and water chemistry was checked biweekly the day before the scheduled water change. Tank conditions were maintained to reflect those in Lake Tanganyika (mean temperature ± SD = 24.9 ± 1.6 °C, pH = 7.8–8.4). Fish received daily feeding ad libitum of either dry *TetraCichlid Cichlid Flakes* (Tetra Holding (US) Inc. 3001 Commerce St. Blacksburg, VA 24060) food (once daily on 5 days per week) or frozen daphnia (Hikari Sales U.S.A., Inc. 2804 McCone Ave., Hayward, CA 94545) and brine shrimp (San Francisco Bay Brand, Inc. 8239 Enterprise Drive, Newark, CA 94560) (once daily on the remaining 2 days per week). All tanks were kept on a 12 h L:12 h D illumination cycle.

Prior to introducing fish into the experimental tanks, all fish were measured for standard length (SL, mm) and mass (g), and given a dorsal fin clip in order to easily distinguish each from tank mates. Eight groups were created, each consisting of a dominant male (mean SL ± SD = 63.4 ± 4.98 mm), a dominant female (mean SL ± SD = 55.19 ± 1.38 mm), as well as a smaller female fish (mean SL ± SD = 38.3 ± 2.7 mm). All fish within a group were unrelated. In order to reduce conflict between the fish upon introduction, the subordinate female fish was released first and the dominant pair was released 24 h later. Groups then were observed regularly in the following days to ensure that there was no excessive aggression. While it never occurred, excessive aggression (which we defined as resulting in noticeable physical damage to fins or missing scales) the aggressing fish would have been isolated in

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