

# Behavioral coping strategies in a cichlid fish: the role of social status and acute stress response in direct and displaced aggression

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## Abstract

The African cichlid fish, *Astatotilapia burtoni*, has a complex social system with a sophisticated social hierarchy that offers unique opportunities to understand how social rank and its physiological substrates relate to behavioral strategies. In *A. burtoni*, a small fraction of the males are dominant (T, territorial), as distinguished by being large, brightly colored, reproductively active, and aggressively defending territories. In contrast, the majority of males are non-dominant (NT, non-territorial), being smaller, drably colored, sexually immature, and typically schooling with females. The social system is regulated by aggressive interactions between males and behavioral responses to aggression can be direct or displaced with respect to the animal that acts. To determine whether direct and displaced behaviors are differentially exhibited by T and NT males, individuals were shown a video presentation of a dominant male displaying aggressively. Analysis of aggressive acts toward the video display and displaced activity toward a tank mate revealed that T males exhibited more direct behavior (toward the video display), while NT males engaged in more displaced behavior (toward tank mates). Because similar experiments with primates suggest that shifts in behavioral strategies are linked to changes in the stress response (as measured by circulating cortisol levels), we measured cortisol levels of T and NT males following exposure to the aggressive stimulus. Although in some animals subordinate males are reported to have higher cortisol levels, here we show that in *A. burtoni* the endocrine response to specific situations can vary considerably even among animals of the same status. Interestingly, NT males with intermediate cortisol levels showed more directed behavior while NT males with both high and low cortisol levels showed more displaced. This suggests an optimal physiological stress response in NT males that predisposes them to challenge aggressors perhaps making it more likely for them to ascend in status.

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## Introduction

Within a group, individuals compete for resources and when asymmetries in size, strength, or fighting ability exist, dominance relationships often develop. This leads to some individuals consistently winning aggressive bouts against opponents that then defer and ultimately submit. Such dominance relationships are found in most animal communities where social behavior is regulated by the dynamics of these relationships (for a review, see [Langen and Rabenold, 1994](#); [Gilbert, 2001](#); [Newton-Fisher, 2004](#); [Smuts et al., 1987](#); [Wilson, 1975](#)).

Dominant and subordinate animals can influence each other by overt behavioral acts or simply by their mere presence ([McBride, 1971](#); [Wiley and Hartnett, 1980](#)). Varying behavioral strategies are also reported among individuals of the same status. One class of actions, displacement activity, has been found to characterize some individuals within both the dominant and subordinate populations. For example, in subordinate primate males, it has been reported that a subset of males displace aggression by initiating a fight with a third party of equal or lesser status after losing an aggressive bout ([Vigin and Sapalosky, 1997](#)). At feeding sites, subordinate primates often show displacement activities when in close proximity to dominant males. Even the risk of aggression associated with assessment of social status has been found to result in increased displacement

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activities in primates. For example, Schino et al. (1990) reported that when unfamiliar female macaques (*Macaca mulatta*) were housed in close proximity, any delay in the establishment of clear dominance relationships caused increased scratching and autogrooming, both forms of displacement behavior. During non-social stress such as extended food restriction, an increase in self-grooming and self-scratching has also been reported (Diezinger and Anderson, 1997). Thus, it appears that displacement activity is an important behavioral response to stress.

Among non-primates, cichlid fish have proven to be valuable model systems for understanding the physiological substrates responsible for dominant and subordinate behaviors. Specifically, the African cichlid fish, *Astatotilapia burtoni*, is known for complex behaviors that support a sophisticated social system that provides an opportunity to analyze the interaction between social rank and behavioral coping strategies. Since so much is already known about how the physiological state of *A. burtoni* is regulated by social status, we can assess whether social information is transmitted primarily by status, behavior, or both.

Social status in fish can be readily classified using the agonistic profile of an individual (e.g., dominant fish attack whereas subordinate fish flee; Dawkins, 1976). In their natural habitat, the shorepools of Lake Tanganyika (Fernald and Hirata, 1977), *A. burtoni* live in a lek-like social system, where a fraction of the males dominate food and nesting sites and hence have access to females. These dominant, territorial (T) males (10–35% of the population) are brightly colored (blue or yellow) with a dramatic black stripe through the eye, vertical black bars on the body, a black spot on the tip of the gill cover, and a large red humeral patch. T males vigorously defend contiguous territories, exchange threat displays with T neighbors, chase subordinate, non-territorial (NT) males, and solicit and court females. In stark contrast, NT males are cryptically colored and do not court females (Fernald and Hirata, 1979). Males can and do switch between these two states, typically on the basis of winning or losing a territory. Males that win a territory will become T males over the course of a week, while males that lose a territory will switch from T to NT state over the course of 3 weeks (White et al., 2002).

Previous work with *A. burtoni* showed that NT males in a controlled and stable social situation have higher basal cortisol levels (Fox et al., 1997); however, endocrine response to specific situations can vary considerably even among animals of the same status. Previous work with primates suggests that this variance in cortisol levels may be linked to different coping strategies used by males during a stressful event. For example, compared to the other subordinate primates, those that displace behavior have lower basal cortisol concentrations and elevated basal testosterone (Vigin and Sapalovsky, 1997). Lower cortisol concentrations were also reported among dominant males who were most likely to displace aggression after losing a fight (Sapolsky and Ray, 1989).

### **Experiment 1: direct and displaced behavioral responses to aggression in dominant and subordinate males**

In Experiment 1 we examined whether differential patterns of direct and displaced behavior occur within and/or across the status classes of male *A. burtoni*. Behavior of T and NT males was observed during a controlled, acute, stressful event using identical video clips of a dominant male displaying aggressively as a stimulus.

### **Experiment 2: acute physiological response to aggression in dominant and subordinate males**

In Experiment 2 we measured the physiological characteristics of the response to the stressful stimulus to discover how this is related to different behavioral strategies. We again tested T and NT males with the aggressive video stimulus in this experiment and then measured males' circulating cortisol levels to determine whether there is a general physiological stress response associated with social rank or, more specifically, a subtype of behaviors in response to stress.

## **General methods**

### *Subjects*

Twenty-eight male *A. burtoni* males (14 T and 14 NT) originally derived from a wild-caught stock population collected in Lake Tanganyika (Fernald and Hirata, 1977) were used as subjects. Prior to selection, the fish were maintained in aquaria under conditions similar to those of their natural environment (Fernald and Hirata, 1977; 28°C water temperature, pH 8 and a 12:12-h, light–dark cycle with full spectrum illumination). A layer of gravel covered the bottom of the aquaria and terra cotta pots were placed in each tank to allow establishment and maintenance of male territories. Fish were fed every morning ad libitum with cichlid pellets and flakes (AquaDine, Healdsburg, CA). All fish were bred and reared in the laboratory under controlled conditions.

Each community tank (90 × 30 × 45 cm) consisted of 2–3 territorial males, 4 or more non-territorial males, and 5–10 females. Animals were treated at all times in accordance with Stanford's Administrative Panel for Laboratory Animal Care (APLAC) approved animal treatment policies.

### *Selection of males*

Focal behavioral observations were made of males in their community tank for at least 1 week before being considered for testing. Males had been previously tagged to distinguish individuals and were observed for 3 min three times per week at the same time each day. Behaviors were

identified using a standard guide (Fernald, 1977) and included aggressive behaviors such as chasing or biting territorial males, threat and border displays, and fighting; reproductive acts including digging a spawning pit, courting, and spawning; and submissive acts such as fleeing. The number of occurrences of each behavior was recorded, as well as the overall coloration of the fish and the presence or absence of an eyebar. When a male occupied a territory, the location was noted. Because males engage in aggressive acts in defense of an existing territory as well as during the acquisition of a new territory, only males actually defending a discernable territory were classified as “territorial.” Following this classification, a total of 14 T and 14 NT males from the same community tank were selected and paired for testing. It should be noted that these communities initially were comprised of size matched males; however, following territorial establishment by some males, size differences can and do exist. For the purposes of this experiment we did not require that T and NT males be sized matched at the time of test rather we deemed it more important that males (originally sized matched) subsequently displayed phenotypic difference under the same community environment. During the video display test, T and NT males were placed side by side in the video test aquarium (partitioned by clear Plexiglas) thus to allow T males to suppress NT males during acclimation. Additionally, each male was housed and tested with a female. The females remained with the test male throughout the course of the experiment.

#### *Video display tank*

The video display tank was a (74 × 37 × 29 cm) tank fitted with computer monitors at each end (see Fig. 1). Monitor output was standardized using Apple Colorsync (Cupertino, CA). Resolution for each monitor was set at 1280 × 1024 with a refresh rate of 85 Hz. The tank was bisected by a clear barrier, used to separate the pairs of focal males along with their female tank mates during initial acclimation. On the day of test an opaque barrier was additionally inserted to ensure attention to the video screen. Each side of the tank had an identically sized half terra cotta pot, placed facing the video monitor. This pot gave the test subjects a shelter and was included to aid in the establishment of a territory by the focal male. Prior to each trial, between trials, and during baseline trials, a static display of the video background was presented on the monitors. During playback, on each monitor a 4 min 30 s digital video clip was shown of a territorial male aggressively displaying. The stimulus male displayed territorial colors and an eyebar throughout the demonstration while repeatedly charging and performing lateral threat displays in the direction of the camera. This video clip was taken from video of a T male while housed in the video test tank; thus, all background in the video was identical to the tanks housing the test subjects. The same video clip was shown to each male.

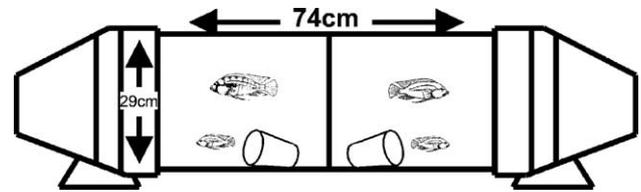


Fig. 1. Schematic illustration of the test aquarium. The test aquarium (74 cm long × 37 cm wide × 29 cm deep) was divided into two equal parts by a clear Plexiglas barrier and the focal males (one territorial and one non-territorial) were placed one into each part along with a female. At each end of the aquarium, a computer monitor was placed for presentation of the stimuli. The half terra cotta pot was oriented to face the computer monitor.

#### *Procedures*

Once a pair of males was selected, they were moved to the video display tank in order to acclimate for playback tests on the afternoon of the following day. At that time, one female was placed with each male and the fish remained housed in this manner while in the video display tank. Two hours prior to testing an opaque barrier was inserted between the two focal males and their respective tank mates and the static video display of the tank background were shown on the monitors. The opaque barrier was used to control male attention and guarantee that focal male behavior was in response to the aggressive video and not the behavior of the other focal male. During a test session, the video was played to one focal male/female pair while the other focal male and female received the static display. Thus, one male was given a test trial while the other was given a baseline trial. One trial block was composed of a baseline trial and a test trial with two intervening inter-trial intervals (ITI) of 2 min (one between each baseline and video, and one between trial blocks). Each animal received two trial blocks. The entire session was recorded using a camera viewing from the side and behavior was recorded for later scoring.

#### *Behavioral measures*

For baseline and test trials, the focal males' overall activity level was judged on a scale from 1 to 3: (1) stationary for more than half of the recorded time; (2) distinct behaviors, attending to video display and/or tank mate at least half of the recorded time; (3) distinct behaviors, actively interacting with the video display and/or tank mate at least two-thirds of the recorded time.

#### *Direct behaviors*

The frequency of behavioral acts directed toward the video display or in direct response to the video was recorded. Direct aggressive behaviors coded were as follows: tracking, charging, and lateral threat display specifically toward the video display. These behaviors were defined as follows: (1) tracking was scored as an event where the focal male approached the video monitor by swimming forwards and followed the video stimulus across the glass oriented with its mouth towards the glass; (2)

charging was scored when the focal male swam rapidly towards the video in an aggressive manner; and (3) lateral threat displays directed at the video were scored as every instance that the focal male raised his dorsal fin and lowered pelvic fins while facing the monitor.

#### *Displaced behaviors*

The frequency of displaced behavior (as defined as behavior directed toward the focal male's tank mate but not the video display) was coded for each focal male. Aggressive displaced behaviors coded were chasing and lateral threat display toward female. They were defined as follows: (1) chasing tank mate was scored as an event in which the focal male charged his tank mate and the tank mate reacted by fleeing; and (2) lateral threat displays directed toward the tank mate were scored as every instance that the focal male raised his dorsal fin and lowered pelvic fins facing his tank mate.

#### *Baseline control trial*

To control for behavior displayed by the focal males independent of the aggressive stimulus, the animals were observed without stimuli at the beginning of each session. Behavior was recorded for 4 min and 30 s (same duration as the aggressive video) while they viewed a static display of the video background scene. Following this baseline trial, an ITI of 2 min was given to prepare the video stimulus for display and allow an animal that had just viewed the aggressive stimulus to return to a baseline activity level.

The frequency of direct and displaced behavior observed during baseline was subtracted from the frequency during the video test to distinguish a subjects' general behavior from that which was a direct response to the aggressive stimulus. The corrected scores obtained for T and NT males were then compared.

#### *Video test trial*

After the ITI the video test was presented for 4 min 30 s. During this time, focal males viewed a previously recorded video of a territorial male aggressively displaying in the direction of the focal male. The recorded male was brightly colored, sustained an eyebar at all times, and repeatedly performed lateral threat displays. Following the video trial, focal males experienced another ITI. Once testing was complete, the opaque barrier was removed from the center of the tank and the individuals were returned to their home tank. Subjects in this study showed a pattern of responding consistent with recognizing the video sequence as a conspecific.

#### *Experiment 2*

Following the last video trial, blood samples were taken from each observed male. Samples of 50–200  $\mu$ l of blood

were drawn from each male into heparinized capillary tubes from the first brachial artery following which the males were returned to their community tanks. Blood samples were obtained within the first 3 min following capture to insure that any acute stress associated with the blood draw itself did not affect the obtained cortisol levels. The blood was centrifuged for 3 min at 14,000 rpm to isolate the plasma. The plasma was then stored at  $-80^{\circ}\text{C}$  until assayed. Cortisol concentration was measured in the plasma samples using an ELISA (Assay Designs Inc., Cortisol Correlate-EIA Kit, Ann Arbor, MI). Plasma samples were diluted 1:30 in assay buffer and then the kit protocol was strictly followed. The plates were read with a conventional plate reader at 405 nm ( $V_{\text{max}}$  Microplate Reader, Molecular Devices). To compute the circulating cortisol level, the percent bound for each of the standards was calculated and a logarithmic curve was generated. This curve was then used to compute the circulating hormone level for both T and NT males.

$P < 0.05$  was accepted as statistically significant for all measures taken and analyzed in Experiments 1 and 2.

## **Results and discussion**

### *Experiment 1*

We found that territorial males engaged in more direct behavioral acts while non-territorial males engaged in more displaced behavioral acts (see Fig. 2). Again, all measurements obtained during test trials were normalized against the corresponding baseline trial by subtracting the frequency of each behavior during baseline from the frequency during the test trial. The direct and displaced behaviors were calculated as a percentage of total behavior (both direct and displaced) for each animal. For T males, direct behavior was 70.7% of total behavior, whereas for NT males it was only 36.9%. These difference scores for T and NT males were found to be significantly different when subjected to a one-way ANOVA [ $F(1,10) = 11.46$ ;  $P = 0.010$ ].

The average activity level of T males and NT males was 2.15 and 2.10, respectively (on a scale from 1 to 3, 1 being less active 3 being most active). This difference was not statistically significant [ $F(1,10) = 0.628$ ,  $P = 0.451$ ].

These results indicate that social status can mediate the behavioral response to the aggressive stimulus. T males direct aggression toward the virtual intruder by visually tracking, charging and threatening with lateral threat displays. However, the NT males translate the virtual threat from the "intruder" into aggression toward a smaller tank mate. Instead of attacking the "intruder," these males chase and aggressively display to a tank mate that appears less likely to retaliate. Further, these results indicate that general activity between T and NT males does not differ but that the specific response to a stressful stimulus does.

Although these results show a clear distinction in displacement behavior between males of different social

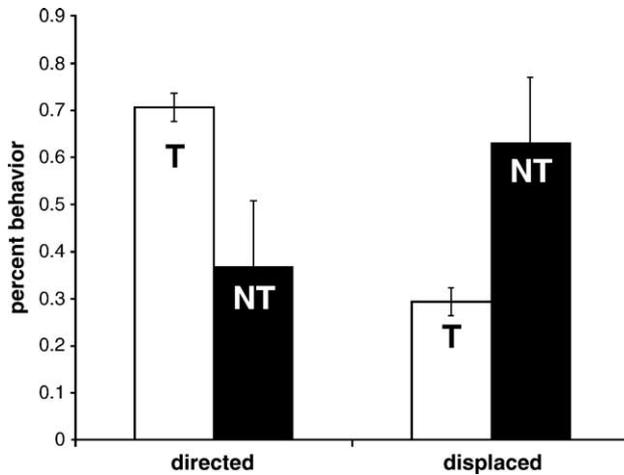


Fig. 2. Represents percent of direct and displaced behavior out of total aggressive behavior across status (means  $\pm$  SEM). NTs display significantly less percentage of direct behavior than Ts and significantly higher percentage of displaced behavior than Ts ( $P < 0.05$ ).  $N = 5$  for all categories.

ranks, there are also physiological differences associated with the T and NT phenotypes that may correlate with these behavioral patterns. Specifically, basal cortisol levels in NT males are reported to be higher than levels in T males in very stable social situations (Fox et al., 1997). However, under dynamic social conditions there is a pronounced variation in basal and socially modulated cortisol levels even among males of the same status (Greenwood et al., in preparation; Clement, unpublished data). The variation among members of the same status in *A. burtoni* appears greater than that which is reported in rainbow trout of similar dominant status (Øverli et al., 2004) and in general are more variable than higher vertebrates such as rats. These results may indicate that animals of different social status have similar physiological responses to acute stressors. Furthermore, the direct/displaced response pattern reported here may be a behavioral manifestation of these physiological differences.

## Experiment 2

### Cortisol levels

To understand how cortisol might relate to specific behavioral responses, measured blood cortisol concentrations from all males (T and NT) were divided into three categories: high [478–362 pg/ $\mu$  (total  $n = 4$ , T = 2, NT = 2)], medium [200–176 pg/ $\mu$  (total  $n = 5$ , T = 2, NT = 3)], and low [50–21 pg/ $\mu$  (total  $n = 3$ , T = 1, NT = 2)]. Note that values in the low range are not typical for a stress response but resemble baseline levels reported for *A. burtoni* (Fox et al., 1997).

### Direct/displaced behavior

The difference between the percentage of direct behavior and displaced behavior for T males with low, medium, and

high cortisol levels were  $-40.5\%$ ,  $35\%$ , and  $100\%$ , respectively (see Fig. 3). For NT males, those scores were  $-61\%$ ,  $150\%$ , and  $-52\%$ . A two-way mixed factors ANOVA performed on the corrected direct/displaced percentage scores revealed a status  $\times$  cortisol level interaction [ $F(2,16) = 6.75$ ,  $P = 0.029$ ]. When the data were further analyzed, it was found that for NT males, the differences in direct and displaced behavior did significantly vary with circulating cortisol levels [ $F(1,3) = 10.703$ ,  $P = 0.043$ ], whereas it did not in T males. In NT males, those with both high and low levels engaged in more displaced behaviors while those with moderate levels directed behaviors toward the offending stimulus. These data suggest that within NT males there is an optimal cortisol response, which produces behavior consistent with territorial defense. Although NT males with either low or high cortisol levels engage in more displaced behavior, the mechanism for the behaviors may be different. It may be that when NT males are not substantially aroused (as indicated by low cortisol levels consistent with baseline levels), they lack the motivation to engage in direct behavior and conversely NT males expressing a strong cortisol response are over stimulated and hypersensitive to aggressive interactions; thus, they misdirect their retaliation toward submissive tank mates to avoid further interactions with the aggressor.

## General discussion

The results of Experiment 1 show that when territorial and non-territorial males are presented with an aggressive stimulus they display significantly different responses. NT males displace their aggression from the seemingly more

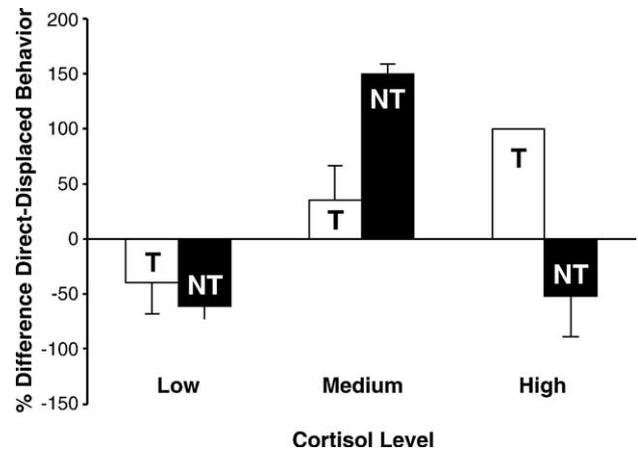


Fig. 3. Difference between percentage of total aggressive behavior that was directed and percentage of total aggressive behavior that was displaced (means  $\pm$  SEM) across status and circulating cortisol level. T males with high circulating cortisol levels ( $N = 1$ ) do not display significantly different behavioral profiles from T males with medium ( $N = 3$ ) or low ( $N = 2$ ) circulating cortisol levels. NT males with medium cortisol levels ( $N = 2$ ) show a significantly larger percentage of directed behaviors (versus percentage displaced behaviors) than do NT males at high ( $N = 2$ ) and low ( $N = 2$ ) circulating cortisol levels ( $P < 0.05$ ).

appropriate focus, the aggressive stimulus, by directing it toward their subordinate tank mate who is less likely to retaliate. Conversely, T males direct their aggression toward the stimulus. In Experiment 2, results indicate that among NT males the actual physiological stress response (as measured by circulating cortisol levels in plasma) corresponds to differential profiles of direct versus displaced behavior. Interestingly, those with a moderate stress response showed a behavioral pattern similar to that seen in T males. In contrast, T behavior appeared consistent regardless of the physiological stress response. These results suggest that displacement behavior in NT males may serve as an effective coping strategy when the physiological state is under duress. In other words, when cortisol levels are high or low, the animal is in a less than optimal condition, and the cost of retaliation toward the aggressive stimulus may be high. On the other hand, an optimal physiological stress response (i.e., moderate cortisol levels) may improve physical condition, therefore reducing the potential cost of challenging aggressors and making it more likely for NTs to ascend in status.

The causal and circumstantial physiological basis of status-linked behavior has received considerable attention. It has been reported that in rainbow trout and brown trout, specific cortisol levels both before and after social stress are correlated with subordination, suggesting an association between initial levels and social transition (Sloman et al., 2001). Modulation of behavior by status rank is also seen in another cichlid fish, the angel fish, *Pterophyllum scalare*. In a novel environment (e.g., isolated in a new aquarium), subordinate fish showed both an increase in swimming and a decrease in feeding as compared to dominant fish (Gomez-Laplaza and Morgan, 2003). Different coping styles displayed during a stressful event can also be indicative of future dominance. Øverli et al. (2004) reported that the duration of appetitive inhibition following transfer to a new environment is predictive of winning or losing a subsequent aggressive bout. However, since the stress response systematically varied between subordinate and dominant fish, with significantly higher levels of cortisol reported for subordinate males, it is unclear if such behavior is linked to social status per se or to a physiological correlate of status.

In *A. burtoni*, substantial physiological distinctions are associated with T males and NT males. T males are typically larger than NT males and have fully spermiated testes whereas NT males do not, rendering NT males incapable of reproduction (Fraley and Fernald, 1982). As in primates (Vigin and Sapalosky, 1997), androgen fluctuations are correlated with behavior but fail to differentially produce behavior. Territorial males have higher androgen levels than do NT males (Parikh et al., in preparation). However, changes in testosterone concentrations do not translate into changes in social status, behavior, or physiology seen in NT individuals (Soma et al., 1996). The exact causative role of cortisol in *A. burtoni* remains to be discovered.

Chronic stress has been thought to be responsible for the behavioral repertoire and sexual repression seen in non-

dominant animals (Blanchard et al., 1993; De Goeij et al., 1992; Manogue et al., 1975; Sapolsky, 1993). Corticosteroids generated from chronic stress have been shown to be effectors of change at each level of the hypothalamic–pituitary–gonadal (HPG) axis, the hypothalamus (Thibier and Rolland, 1976), the pituitary gland (Welsh and Johnson, 1981), and the gonads (Sapolsky, 1985). However, results reported here suggest that cortisol levels do not directly regulate status differentiating behavior in *A. burtoni* since these levels do not correspond to status but rather distinguish behavioral differences among subordinate males. In other fish, cortisol levels do distinguish males of varying social status. In juvenile yellowtail fish, *Seriola quinqueradia* (Temminck and Schlegel; Carangidae), whole-body immunoreactive cortisol levels that begin to rise around the of time aggressive behavior are higher for males that are behaviorally subordinate (Sakakura et al., 1998). However, among some primates such as vervet monkeys, *Cercopithecus aethiops sabaues*, cortisol levels do not differ between dominant and subordinate males in stable groups and among groups in which the dominant male is removed, the subsequent dominant male is reported to have higher cortisol levels than other males of the group (McGuire et al., 1986).

In rainbow trout following an aggressive bout, cortisol levels initially rise in both dominant and subordinate males but levels decrease rapidly in dominant males while continuing to increase in subordinate fish (Øverli et al., 1999). It is possible that a similar time course for cortisol exists in T and NT males. However, since plasma sampling for both T and NT males for the current experiment did not occur immediately following a stressor, levels in T males may have been descending while levels in NT males continued to ascend.

In *A. burtoni*, aggressive behavior in a subtype of subordinate males is contingent on the presence of a dominant male. Hofmann et al. (submitted for publication) report that this class of subordinate males display agonistic behaviors toward non-dominant, non-aggressor fish when a dominant male is not in view. If the dominant male is removed, these males are more likely to ascend to dominant status than males not performing this behavior, indicating that it may be an advantageous behavioral style or coping strategy within this species. This does appear consistent with reports in rhesus monkeys that intermediate ranking males are the only animals in the hierarchy to show increased displaced activity under conditions that produce frustration (Clarke et al., 1988; de Waal, 1982; Goodall, 1986; Smuts, 1986). In *A. burtoni*, however, displacement behavior was most consistently associated with subordinate males, while a subset of NT males produced behaviors consistent with those of T males. Thus, it could be that classifying males as either T or NT is too simple and may not reflect the full spectrum of male behavior. Intermediate males that appear NT who display the “optimal” cortisol level also exhibit an optimal behavioral profile that allows them to ascend in an unstable social situation. However, because conditions were not

altered to encourage NT to T transitions in the current experiments, it remains to be seen which coping style is most beneficial and if the same strategy is superior in all circumstances. The response variations seen here do mirror those reported in response to major stressors that can reflect differences in personality, coping style, and temperament strategy both within and between species (Clarke et al., 1988; de Waal, 1982; Goodall, 1986; Smuts, 1986).

The data presented here suggest that behavioral acts may determine the cortisol levels needed to sustain the particular strategy in play. Clearly, differential coping styles exist and are correlated with distinct physiological responses in teleost fish. The cause of these related factors is yet to be investigated.

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