

Stress coping style predicts aggression and social dominance in rainbow trout

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Abstract

Social stress is frequently used as a model for studying the neuroendocrine mechanisms underlying stress-induced behavioral inhibition, depression, and fear conditioning. It has previously been shown that social subordination may result in increased glucocorticoid release and changes in brain signaling systems. However, it is still an open question which neuroendocrine and behavioral differences are causes, and which are consequences of social status. Using juvenile rainbow trout of similar size and with no apparent differences in social history, we demonstrate that the ability to win fights for social dominance can be predicted from the duration of a behavioral response to stress, in this case appetite inhibition after transfer to a new environment. Moreover, stress responsiveness in terms of confinement-induced changes in plasma cortisol was negatively correlated to aggressive behavior. Fish that exhibited lower cortisol responses to a standardized confinement test were markedly more aggressive when being placed in a dominant social position later in the study. These findings support the view that distinct behavioral–physiological stress coping styles are present in teleost fish, and these coping characteristics influence both social rank and levels of aggression.

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Introduction

In many animal species, social defeat is a powerful stressor that can lead to drastic alterations in physiology and behavior. Behavioral effects of social defeat include appetite inhibition (Kramer et al., 1999; Meerlo et al., 1997; Øverli et al., 1998), reduced aggression (Blanchard et al., 1995; Höglund et al., 2001), decreased reproductive behavior (D'Amato, 1988; Perret, 1992), and increased submissive and defensive behaviors towards conspecifics (Blanchard et al., 1993; Siegfried et al., 1984). Social defeat is also

frequently used as a paradigm to study the neuroendocrine mechanisms underlying stress-induced behavioral inhibition, depression, and acquisition and expression of fear conditioning (Berton et al., 1999; Fuchs and Flügge, 2002; Gould et al., 1997; Jasnow and Huhman, 2001; Keeney and Hogg, 1999; Koolhaas et al., 1990; Shively et al., 1997; but see also Marrow et al., 1999). It is, however, sometimes difficult to discern whether the physiological and behavioral differences between dominant and subordinate individuals are causes or consequences of social rank. Furthermore, the time course with which these changes occur is often of fundamental interest (Summers, 2002; Summers et al., 2003), but with most experimental techniques data acquisition cannot be carried out until contests for dominance are already settled and animals with established dominant or subordinate status can be sacrificed. It would therefore be of interest to

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investigate whether the outcome of contests for social dominance among individuals with similar social histories can be predicted from observations made before social interaction.

Both in the wild and in captivity, a range of factors such as age, body size, sex, kinship, secondary sexual characteristics, prior dominance experience, or residence in a particular territory have been shown to affect social rank (Abbott et al., 1985; Beacham, 1988; Beauprand and Cotnoir, 1996; Cote, 2000; Renison et al., 2002; Sprague, 1998). The majority of these studies do not address what innate or acquired traits initially helped individuals gain the characteristics that accompany dominance. Some studies, however, suggest that differences in behavior and physiology predispose an animal for a certain social rank, at least in a predictable and stable experimental environment (McCarthy, 2001; Morgan et al., 2000; Plusquellec et al., 2001; Pottinger and Carrick, 2001).

In a breeding program with rainbow trout (*Oncorhynchus mykiss*), two lines of fish with divergent cortisol responsiveness have been created (high-responding, HR; and low-responding, LR) (Pottinger and Carrick, 1999). Fish from the LR line show a strong tendency to become dominant over HR individuals in staged fights for social dominance between pairs (Pottinger and Carrick, 2001). The LR fish also show a reduced locomotor response to a simulated territorial intrusion test and a more rapid resumption of feed intake after transfer to a new environment (Øverli et al., 2002a). Thus, the HR and LR lines of rainbow trout might represent selection for different behavioral–physiological stress coping styles, as defined by Koolhaas et al. (1999). In the study reported here, we investigate whether individual differences in behavioral and physiological components of stress coping style predict social rank even in an unselected population (i.e., no prior identification of LR or HR lineage) of rainbow trout.

Methods

Experimental and analytical procedures

Rainbow trout weighing 332 ± 9 g (population mean $\pm$ SEM, $n = 100$) were obtained from the Gavins Point National Fish Hatchery, Yankton, SD, USA. These fish were kept indoors in a circular holding tank for at least 2 weeks before experiments (volume: 2500 l, water flow: 10 l/min, photoperiod light–dark: 12–12 h, temperature: 8–12°C). While in the holding tanks, fish were hand fed once daily with pelleted food (1/8" Silver Cup Trout Pellets, Nelson and Sons, Inc., Murray, UT, USA) corresponding to 2% of the biomass in the tank. Experiments took place under similar environmental conditions in glass aquaria (length $\times$ width $\times$ depth: 122 $\times$ 47 $\times$ 53 cm), which were divided into four equal compartments by removable opaque PVC walls.

Test fish ($n = 36$) were weighed and selected so that their weight was close to the mean of the population in the holding tank before being transferred to isolation in observation aquaria. Neighboring fish were size matched for later pairing (maximum size difference: 10%) and marked by a small cut in the upper or lower part of the tail fin. At 2 h after transfer to isolation and once daily after that, fish were hand fed to satiety or to a maximum of 2% body weight/day, with daily records made of which individuals took food. Previous experiments have shown that holding juvenile salmonid fish in isolation for approximately 1 week with sufficient access to food is highly effective in inducing territoriality and motivation to express aggressive behavior (Øverli et al., 1999a; Pottinger and Carrick, 2001).

After 3 days in isolation, experimental fish were subjected to a standardized confinement test (30 min in an opaque 5-l enclosure), anaesthetized in 500 mg/l tricaine methanesulfonate (MS-222), and a blood sample was taken from the caudal sinus of each fish.

Fish were then returned to isolation for three more days, and on day 7 following the initial transfer, pairs of fish were formed by removing the PVC walls separating individual compartments. This resulted in escalated fights in all pairs, involving rapid circling and biting directed against the fins and all parts of the body from both opponents. As in previous experiments (Øverli et al., 1999a), all fights inevitably ended with one of the opponents retreating and ceasing to retaliate to aggressive attacks from the other fish. From this point in the interaction, aggressive behavior was unidirectional, and a retreating subordinate and an aggressive dominant individual could clearly be identified.

In an experimental environment with no opportunity for withdrawal or escape, the situation described above is highly stressful for the subordinate individual. Studies with fish (Øverli et al., 1999a) as well as lizards (Summers, 2002; Summers et al., 2003) show that the dominant animal, in contrast, exhibits a rapid cessation of the stress response resulting from the fight. In the current study, experiments were terminated 5 min (eight pairs) or 3 h (five pairs) following identification of social status, with dominant and subordinate individuals being netted rapidly and anaesthetized in 500 mg/l MS-222. Blood samples were obtained from the caudal sinus, and fish were killed by decapitation and then dissected to determine sex. Control ($n = 10$) samples were obtained from isolated fish that had not participated in fights, but had otherwise been treated as above.

Blood samples were centrifuged to separate plasma, which was drawn off and frozen at -80°C within 3 min of the fish being removed from water. Plasma cortisol was later analyzed by a previously validated radioimmunoassay technique (Winberg and Lepage, 1998; modified from Olsen et al., 1992). The minimum detectable level of cortisol in this assay is 0.5 ng/ml, intra-assay coefficient of variation is 2.1%, and inter-assay coefficient of variation is 7.1%.

In all pairs, the number of aggressive acts performed by dominant fish was counted for 5 min after stable domination–subordination relationships had been established. In the 3-h pairs, aggression was also quantified at 60–70 and 120–130 min. An aggressive act was defined as a bite or a rapid approach not including biting that resulted in displacement of the subordinate (Øverli et al., 2002b).

Data analysis

Parametric methods (*t* test or ANOVA followed by Tukey–Kramer post hoc test) were applied to analyze both behavioral and endocrine data using Levene's test and normal probability plots to confirm homogeneity of variance and normality of distribution. Binominal test was used to test whether proportions of individuals falling in two different categories (i.e., subordinate vs. dominant) differed among populations grouped according to the duration of stress-induced appetite inhibition. Pearson statistics and ANCOVA were used to analyze correlations between endocrine and behavioral measures. When confinement-induced cortisol was plotted against a measure of aggressive behavior in fish that later became dominant (the frequency of aggressive acts performed during the first 5 min after the formation of stable dominant–subordination relationships), it appeared that the data were distributed along two different regression lines. We used the method suggested by Armitage (1980) to test whether the regression slopes were different (using the *t* statistics) and whether the lines were significantly separated (using the *t* statistics for adjusted constants). The latter test corresponds to a covariance analysis with individual fish assigned to two different groups based on proximity to each regression line (groups 1 or 2, see Fig. 2) using group as independent variable, aggression as dependent variable, and confinement-induced cortisol as covariate.

Results

Although the fish used in this study were quite large, postmortem dissection revealed that all were reproductively immature. Including 10 controls, 36 fish were used in the study, and 25 females and 11 males were identified. There were only three male–female pairs formed, and two of these contests were won by females and one by a male. Among the remaining 10 pairs, 7 were female–female and 3 were male–male. Thus, there were only four male winners in total. There were no significant effects of sex on stress responsiveness, aggressiveness, or social dominance (data not shown). Data for males and females were therefore pooled in the following analysis.

Behavioral stress coping

In all, 13 pairs of fish were tested for social dominance, with 8 pairs sampled at 5 min and 5 pairs sampled at 3

h following the formation of stable dominant–subordinate relationships. In four cases, the dominant and the subordinate individual had each started to feed on the same day following transfer from holding tanks. In eight out of the remaining nine pairs, the fish that started feeding first became dominant. This frequency difference was significant (Binominal test, $P = 0.02$). There was no weight difference between subsequently subordinate and dominant fish at the beginning of the experiment. However, although they most often started to feed later, subordinate fish were significantly larger than dominant fish at the end of the experiment, weight of dominant fish being 343.2 ± 16.2 g and weight of subordinate fish being 358.1 ± 16.4 g (mean $\pm$ SEM) ($t = 6.39$, $df = 24$, $P < 0.001$, paired *t* test).

Plasma cortisol

There was no difference in confinement-induced cortisol levels between fish that later obtained dominant or subordinate rank in pairs. Mean cortisol $\pm$ SEM in subsequently dominant fish was 83.3 ± 8.5 ng/ml, while confinement-induced cortisol in subsequently subordinate fish was 86.0 ± 9.4 ng/ml. The endocrine response to social interaction, however, differed between dominant and subordinate individuals (Fig. 1). At 5 min and 3 h following the termination of fights and the formation of stable dominant–subordinate relationships, only subordinate fish showed significantly higher plasma cortisol levels than undisturbed controls ($F_{(4,34)} = 20.79$, $P < 0.001$, for post hoc *P* values, see Fig. 1).

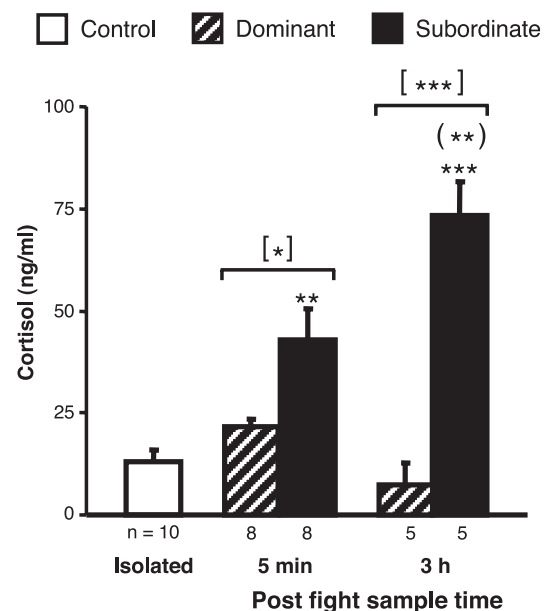


Fig. 1. Plasma cortisol in dominant and subordinate rainbow trout sampled at 5 min and 3 h after fights for social dominance had ended, and in undisturbed controls. Significant differences among groups are indicated by asterisks where $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, [*] refers to a significant effect of social rank, (*) indicates a difference to previous time point, and * denotes a difference to undisturbed controls (ANOVA followed by the Tukey–Kramer test).

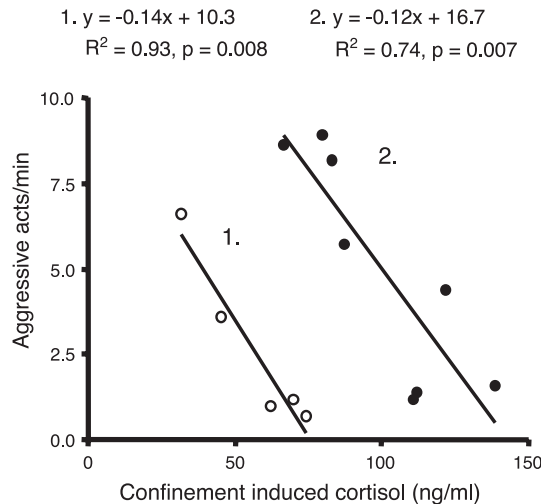


Fig. 2. Relationship between the cortisol response to 30-min confinement and the level of aggressive behavior during the first 5 min after becoming dominant in pairs formed 4 days after the stress test (pooled data for fish sampled at 5 min and 3 h following hierarchy formation). Assignment of individuals to groups 1 and 2 in the above graph were based on the existence of two different regression lines within the data set, confirmed statistically by analysis of covariance (ANCOVA). Line equations and Pearson r^2 and P values are shown.

While there was no indication that the endocrine response to confinement stress predicted social dominance, there was a strong negative correlation between the cortisol response to 30-min confinement and the level of aggressive behavior shown by fight winners in the 5-min period directly following fights. In other words, individuals exhibiting a lower cortisol response to confinement stress performed more aggressive attacks immediately following establishment of dominant social status. These data were distributed along two separate regression lines (differences between mean $y = -7.64$; $SD = 1.24$; $t = -6.18$; $df = 10$; $P < 0.001$) with very similar slopes (differences between slope $= 0.019$; $SD = 0.05$; $t = 0.37$; $df = 9$; $P = 0.72$) and high r^2 values (Fig. 2, pooled data from 5-min and 3-h groups).

No correlation was, however, seen between post-fight plasma cortisol values and aggression in 5-min dominant fish. Dominant fish sampled at 3 h showed a trend towards a positive correlation between post-fight plasma cortisol and the frequency of aggressive acts performed during all three observation periods ($r^2 = 0.69$, Pearson $P = 0.08$). However, the low sample size of this group ($n = 5$) hampered conclusions about the relationship between aggression and cortisol levels induced by continued social interaction.

Discussion

A striking result from the current study was that within pairs of fish, the individual that had most rapidly resumed feed intake after transfer to isolation nearly always won the subsequent fight for social dominance. Only in one out of nine cases did the fish that resumed feeding first become

subordinate after pair formation. The observed relationship between dominance and time to resume feeding did not rely on larger body size in dominant fish. Although weight differences were small, fish ending up subordinate had grown faster than those becoming dominant during the 1-week isolation period. This finding is consistent with previous observations that a high metabolic rate is predictive of dominant status (McCarthy, 2001). Additionally, this result implies that a rapid resumption of feeding after transfer to isolation does not provide a weight advantage during an agonistic encounter 1 week later. Instead, appetite inhibition after transfer to a new environment most likely reflects some aspect of the physiological response to stress, which could also influence the outcome of fights. As in mammals, stress-induced inhibition of food intake in fish is in part mediated by central signaling systems that are simultaneously involved in the control of physiological stress responses (Bernier and Peter, 2001; De Pedro et al., 1998), and the resumption of feed intake after a stressor is likely to reflect a downregulation of the physiological stress response (Øverli et al., 1998).

An initial difference between subsequently dominant and subordinate fish in hypothalamus–pituitary–interrenal (HPI) axis reactivity was not evident in this experiment. This observation might indicate that HPI axis dynamics did not affect the outcome of fights for social dominance. This stands in contrast to previous findings, where individuals with consistently high or low cortisol responses were pre-identified either by genetic selection for stress responsiveness (Pottinger and Carrick, 2001) or by repeatedly testing fish from a normal hatchery population (S. Winberg and A. Stoskus, unpublished data). In these studies, fish with consistently low stress-induced cortisol values showed a strong tendency to win fights for dominance. Also, Sloman et al. (2001) found that plasma cortisol was elevated in socially subordinate fish that had not been subjected to any other external stressor, both before and after social stress. More detailed studies of both the time course and magnitude of HPI axis activation are probably required to determine the role of initial differences in stress responsiveness for the outcome of contests for social dominance.

While achievement of dominance was not predicted by confinement-induced cortisol levels in the current experiment, plasma cortisol responses elicited by 30 min of confinement were strongly related to the level of aggressive behavior shown by dominant fish as soon as fights had been decisively won (cf. Fig. 2). Regarding Fig. 2, it should be noted that the separation between the regression lines was merely done on basis of the ANCOVA, none of the other variables measured in this experiment correlated to this distinction among groups of dominant individuals. There was, however, a very low probability ($P < 0.001$) that these data came from a uniform population. There was also very little overlap between the cortisol data range for each line, and lines were separated at a point very close to the overall mean with respect to confinement-induced plasma cortisol.

Thus, it seems likely that the distinction represents subsets of individuals with differing stress-coping profiles within the dominant group. Within each subset of fish, those showing the lowest HPI axis responsiveness were also the most aggressive.

An association between low hypothalamus–pituitary–adrenal (HPA) axis reactivity and high levels or abnormal forms of aggression has also been reported in several mammalian species (Haller et al., 2001; Ruis et al., 2000), including humans (McBurnett et al., 2000). Glucocorticoids have also been shown to have rapid effects on aggressive behavior in both mammals (Hayden-Hixon and Ferris, 1991) and fish (Øverli et al., 2002b). However, in the current study, there was no relationship between the immediate cortisol responses to pair formation and the level of aggressive behavior shown by dominant fish. Thus, it can be hypothesized that differences in HPI–HPA axis dynamics are associated with long-term organizational effects determining individual behavioral profiles (Delville et al., 2003; Halász et al., 2002; Koolhaas et al., 1999) as well as immediate hormonal effects on aggression.

The observation that social rank can be predicted with nearly 100% certainty based on the speed with which animals adapt to a new territory may be of considerable value for experiments aiming to dissociate the causes and consequences of social rank. There are large differences between the dynamics of social hierarchy formation in a laboratory environment and in the wild (Sloman and Armstrong, 2002) and among different species (Creel, 2001). Nevertheless, there is ample evidence that social subordination may affect glucocorticoid hormone release both in free living animals and under conditions of rearing in captivity (e.g., Øverli et al., 1999a,b; Sapolsky, 1990; Summers et al., 2003). But do these differences arise before, during, or after contests for social rank? For instance, the fact that subordinate fish displayed higher cortisol values than dominant ones directly following fights can depend on one or a combination of three different factors: either winners and losers showed a differential response to fighting (but not to confinement stress), the repeated stressors of confinement and fighting affected them differently, or the 5-min period of unidirectional aggressive behavior after fights caused increased cortisol values in subordinate fish.

Another question to address is whether fighting affects brain signaling systems involved in the control of aggressive behavior differently in winners and losers (Summers et al., 2003), or if metabolic changes during the fight force one of the contestants to give up earlier (see e.g., Haller, 1991, 1995). Questions regarding the neuroendocrine correlates of fight resolution can only be solved by obtaining samples from animals during a fight for dominance. The present study suggests that identification of eventually dominant individuals can be provided before actual fights.

Knowledge on individual coping styles may also be of great importance to improve welfare and performance of

animals in capture (Ruis et al., 2002). In an aquaculture environment, fish are held in large numbers under artificial conditions they would not normally encounter in the wild. These conditions are sometimes stressful and can affect fish health and welfare, and thus production (Barton, 2000; Barton and Iwama, 1991). In this context, it would be of interest to investigate whether feeding behavior in an unfamiliar environment is a consistent individual trait that is predictive of other behavioral and physiological features, and can be used as a criterion for selection in breeding programs.

In conclusion, this study shows that the ability to win fights for social dominance can be predicted by the duration of a behavioral stress response, in this case appetite inhibition. Moreover, stress responsiveness in terms of confinement-induced cortisol is negatively related to aggression after establishing rank relationships. These observations support the idea that distinct behavioral–physiological stress coping styles (Koolhaas et al., 1999) are present in teleost fish. Moreover, coping characteristics appear to be of importance in determining social rank and individual differences in aggressive behavior.

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