SYMPOSIUM

Social Transitions Cause Rapid Behavioral and Neuroendocrine Changes

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Synopsis In species that form dominance hierarchies, there are often opportunities for low-ranking individuals to challenge high-ranking ones, resulting in a rise or fall in social rank. How does an animal rapidly detect, process, and then respond to these social transitions? This article explores and summarizes how these social transitions can rapidly (within 24 h) impact an individual's behavior, physiology, and brain, using the African cichlid fish, *Astatotilapia burtoni*, as a model. Male *A. burtoni* form hierarchies in which a few brightly-colored dominant males defend territories and spawn with females, while the remaining males are subordinate, more drab-colored, do not hold a territory, and have minimal opportunities for reproduction. These social phenotypes are plastic and reversible, meaning that individual males may switch between dominant and subordinate status multiple times within a lifetime. When the social environment is manipulated to create males that either ascend (subordinate to dominant) or descend (dominant to subordinate) in rank, there are rapid changes in behavior, circulating hormones, and levels of gene expression in the brain that reflect the direction of transition. For example, within minutes, males ascending in status show bright coloration, a distinct eye-bar, increased dominance behaviors, activation of brain nuclei in the social behavior network, and higher levels of sex steroids in the plasma. Ascending males also show rapid changes in levels of neuropeptide and steroid receptors in the brain, as well as in the pituitary and testes. To further examine hormone–behavior relationships in this species during rapid social ascent, the present study also measured levels of testosterone, 11-ketotestosterone, estradiol, progestins, and cortisol in the plasma during the first week of social ascent and tested for correlations with behavior. Plasma levels of all steroids were rapidly increased at 30 min after social ascent, but were not correlated with behavior during the initial rise in rank, suggesting that behavior is dissociated from endocrine status. These changes during social ascent are then compared with our current knowledge about males descending in rank, who rapidly show faded coloration, decreased dominance behaviors, increased subordinate behaviors, and higher circulating levels of cortisol. Collectively, this work highlights how the perception of similar social cues that are opposite in value are rapidly translated into adaptive behavioral and neuroendocrine changes that promote survival and reproductive fitness. Finally, future directions are proposed to better understand the mechanisms that govern these rapid changes in social position.

Introduction

To promote survival and reproductive fitness, individuals living in dominance hierarchies must have mechanisms that rapidly adapt their behavior and physiology to changes in social position. This ability is even more crucial in species living in dynamic habitats in which environmental fluctuations and social interactions may trigger alterations in availability of resources or territories. This shuffling of resources can lead to changes in relative social rank among individuals in the population, with some rising to higher status and some falling to lower status. Since reproductive opportunity and fitness is often greater for individuals of high social position, these transitions in rank have important consequences for growth, survival, and reproduction (Altmann et al. 1995; Sapolsky 2005; Young 2009). How do animals make these quick decisions on whether or not to

change social status, and how quickly do behavior and physiology adapt? While there are many animals, including humans, in which adaptive changes occur quickly in response to social or environmental cues (Sapolsky 2005; Summers et al. 2005; Chiao et al. 2009; Maruska 2014), less is understood about the cellular and molecular mechanisms that govern these crucial transitions.

Rapid transitions in social status are possible because animals constantly assess their surroundings via multiple sensory systems, and integrate this information with appropriate neural circuits that modulate behavioral outputs and physiology. This ability to quickly match their behavior and physiology to the current environmental and social conditions is crucial for an individual's fitness. The relationship between behavior, the brain, and levels of circulating hormones is dynamic in most vertebrates, but serves as an integrative neuroendocrine substrate for mediating changes in social status, particularly those tightly linked to reproductive function. Across vertebrates, for example, steroid hormones can modulate neural circuits that influence behaviors and fertility (Remage-Healey and Bass 2006; Campbell and Herbison 2014), but social and environmental signals can also induce rapid changes in levels of steroids in the plasma and in the functioning of the brain (Wingfield et al. 1990; Pradhan et al. 2010). In many cases, these changes in hormones, behavior, and neural-circuit function can occur on very short (seconds to hours) timescales. Importantly, rapid changes can also occur on different organizational levels, ranging from whole-animal behavior to hormone levels to cellular physiology to molecular-level changes in gene expression. To study the mechanisms involved in transitions in status on all of these biological levels requires a model system in which changes in social status can be reliably induced, with tractable phenotypes, and genomic resources (Renn et al. 2008; Robinson et al. 2008; Harris and Hofmann 2014; Maruska and Fernald 2014). One such system is the African cichlid fish *Astatotilapia burtoni*, which will be used here as a framework for discussing the rapid behavioral, hormonal, and molecular changes associated with transitions in social status. While "rapid" is a relative term with varying contextual meanings across fields, the focus here will be on changes that occur on the timescale of minutes to hours (e.g., within the first 24 h) following a switch in social status between subordinate and dominant phenotypes.

The African cichlid fish *A. burtoni* is an ideal model for examining the mechanisms involved in rapid and adaptive changes in social position (see Hofmann and Fernald (2001); Fernald and Maruska (2012); Maruska and Fernald (2013); Maruska (2014); Maruska and Fernald (2014) for reviews). Males of this species form dominance hierarchies in which a small percentage (10–30%) of individuals are dominant, are brightly-colored, aggressively defend a territory used for feeding and spawning, and are reproductively active. On the other hand, the majority of males in the population are subordinate and have a suppressed reproductive system, dull coloration, and typically shoal with females rather than maintain a territory. When a territory does become available, however, subordinate males can rapidly change their coloration, behavior, and physiology to that of the dominant male's phenotype. Similarly, resident dominant males can be challenged for their territory through agonistic interactions with rival males and may lose their resources and position in the dominance hierarchy and fall in rank. Thus, the dynamic physical and social living conditions of *A. burtoni* facilitate frequent changes in relative rank within the population, which has important consequences for survival and reproductive fitness.

Capitalizing on the ideally-suited *A. burtoni* model for studying transitions in social status, the goals of this article are several-fold. First, to better understand the relationship between circulating steroids and behavior during changes in status, the present study reports new data on changes in levels of steroids (androgens, estradiol, progestins, cortisol) in the plasma and behaviors during social ascent at the same times used in previous studies on *A. burtoni* (Maruska and Fernald 2010a, 2011a; Maruska et al. 2011). These data contribute important new information on the relationships between behavior and levels of circulating steroids that are induced by a rise in social position, thereby increasing the utility of this emerging model system for comparative studies. Second, this article reviews and summarizes our current knowledge on how behavior and physiology in male *A. burtoni* changes following a rise or fall in social rank, with a specific focus on those changes occurring on a short timescale (within 24 h of transition in status). Finally, directions for future work are proposed based on insights from the rapid social and reproductive plasticity exemplified by the *A. burtoni* model system.

Methods

Animals, experimental paradigm, sampling, and behavioral analyses

Adult male *A. burtoni* (SL = 68.5 7.8 mm; BM = 9.1 2.8 g) used for these experiments were from a laboratory-bred population that was derived

from wild-caught stock from Lake Tanganyika, Africa. Fish were maintained in aquaria under environmental conditions similar to their native equatorial habitat (28–29°C, pH 8.0, 12 h light: 12 h dark, constant aeration), and fed cichlid flakes daily. Aquaria contained gravel-covered bottoms and halved terra cotta pots to serve as territory shelters. Experimental procedures were approved by the Stanford Administrative Panel for Laboratory Animal Care.

The experimental paradigm and quantification of fish behaviors used here was identical to those described by Maruska and Fernald (2010a) and used in other studies (Maruska and Fernald 2011a, Maruska et al. 2011, 2013b, Carpenter et al. 2014), so will only be briefly described here. For these experiments, the following groups of males were generated: stable subordinate, stable dominant, and males ascending in rank that were sampled at 0.5, 6, 24, 72, and 120 h after social opportunity. To create ascending males, subject males were initially suppressed by large dominant males in a community tank for 4–5 weeks to create subordinate individuals that would be given an opportunity to rise in rank. Following the period of suppression, subject subordinate males were moved to the center compartment of an experimental tank that contained one larger resident dominant male and three to four females. Subject males remained in the center compartment for 2 days during which their subordinate status was confirmed by behavioral observations. The center compartment was bordered on either side by mixed-sex communities behind clear acrylic barriers so that experimental fish could see but not physically interact with these neighbors. On the day of ascent, the large resident male was removed in the dark with a net by a researcher wearing night-vision goggles. The resident was removed 1 h prior to the onset of light, thus ensuring that visual absence of the resident occurred consistently at light-onset for all subject males. Stable subordinate and dominant males were also used as comparisons to the males rising in social rank. Stable subordinate males were suppressed in community tanks for 4–5 weeks as described above, and on the day of ascent, a net was dipped into the tank prior to the onset of light, but the resident dominant male was not removed. Stable dominants were dominant males that maintained their high status in community tanks for a 4–5 week period and were then moved to the experimental tank with the 3–4 females but no large resident dominant male. On the sampling collection day, a net was dipped into the tank prior to light-onset to simulate a fish's removal. Stable dominant males were collected at 30 min

after displaying dominance behaviors at a rate of three behaviors per minute, similar to that of ascending males. Stable subordinate males were collected at 40–45 min after the onset of light, which matches the average collection time of both stable dominant males and those males that were given a social opportunity and ascended in rank.

Fish were videotaped in the experimental compartment for 45 min at the start of light-onset in the morning on the day before, day of, and for each of 5 days after social ascent. Videos were quantified by observers blind to the experimental condition. The following stereotypical behaviors were quantified as described in previous studies: fleeing (submissive behavior); frontal displays, lateral displays, border fights (territorial/agonistic behaviors); chasing, courtship quiver displays, leads, pot shelter entries, and digging (reproductive behaviors) (Fernald 1977; Fernald and Hirata 1977; Maruska and Fernald 2010a). Behavioral data on the day the fish were collected were used to test for correlations with levels of circulating steroids measured at the same timepoint (Pearson product moment test).

Sampling of blood and assays of steroid hormones

To measure circulating steroid hormones in subordinate, dominant, and ascending male fish at different times after social ascent (0.5, 6, 24, 72, and 120 h), fish were first anesthetized in ice-cold tank water, and measured for standard length (SL) and body mass (BM). Within 2 min of capturing a fish, heparinized 100-μl capillary tubes were used to collect blood samples from the caudal vein. Blood was centrifuged at 8000 rpm for 10 min, and then plasma was removed and stored at 80°C. Testes were also removed and weighed to calculate gonadosomatic index (GSI = [gonad mass/BM] * 100) as a measure of reproductive investment.

Enzyme ImmunoAssay (EIA) kits (Cayman Chemical, Inc.) were used to measure concentrations of testosterone (T; No. 582701), 11-ketotestosterone (11-KT; No. 582751), estradiol (E$_2$; No. 582251), progestins (P; No. 582601), and cortisol (No. 500360) in the plasma at different times after social ascent. While a previous study measured levels of 11-KT in the plasma at these same times (Maruska and Fernald 2010a), circulating concentrations of T, E$_2$, P, and cortisol were unknown. Plasma samples (10 μl) from each individual were extracted three times with 200 μl of diethyl ether, evaporated under a fume hood, and then reconstituted in assay buffer prior to analysis (1:40–1:55 dilutions). For cortisol assays, samples

were directly diluted 1:50 in assay buffer without extraction. Instructions provided by the manufacturer were then strictly followed. All samples were assayed in duplicate, plates were read at 405 nm using a microplate reader (UVmax Microplate reader, Molecular Devices), and hormone levels determined based on a standard curve run for each steroid and plate. Mean intra-assay coefficients of variation (CV) were: P (5.8%), T (9.5%), 11-KT (5.2%), E_2 (8.1%), cortisol (7.3%). Inter-assay CVs were: P (13.6%), T (4.3%), 11-KT (5.9%), E_2 (6.7%), cortisol (10.1%). The EIAs for cortisol, T, 11-KT, E_2, and P were previously validated and used to measure levels of circulating steroids in this species in other studies (Maruska and Fernald 2010b; O'Connell and Hofmann 2012; Kidd et al. 2013; Maruska et al. 2013 b). In some cases, steroid concentrations were log-transformed prior to statistical analyses (ANOVA, SigmaPlot 12, Systat software).

Results

Subject subordinate males rapidly displayed both territorial and reproductive behaviors within the first 30 min of social ascent (Fig. 1). While the number of territorial behaviors per minute was higher than the number of reproductive behaviors at the 30 min time point, by 6 h after ascent, these behavioral priorities switched to more reproductive behaviors, which were then sustained at similar levels over subsequent days (Fig. 1). The mean time to ascend (e.g., reach a rate of three behaviors per min) was 11.9 1.4 min after the onset of light, which did not differ from that measured in our previous study (12.7 1.2 min) (Student's t-test; $t = 0.872$; $P = 0.447$) (Maruska and Fernald 2010a). Behaviors (type and timing) of subordinate, ascending, and dominant males quantified here were nearly identical to those described in detail previously, using the same experimental paradigm and sampling regime (Maruska and Fernald 2010a), and will not be discussed here. The focus of this study, rather, was to test for correlations between these behaviors and levels of circulating steroids, which is reported below.

Gonadosomatic index, an indicator of reproductive investment, and plasma levels of circulating steroid hormones across the different times are plotted in Fig. 2. As in previous studies, subordinate males had similar GSI values to males rising in rank (all timepoints sampled), and subordinate and ascending males had lower GSI values than did dominant males (ANOVA, $F_{(6,63)} = 10.47$, $P < 0.001$; SNK, $P < 0.05$). For all circulating steroid levels measured, dominant males had higher levels than did subordinate males.
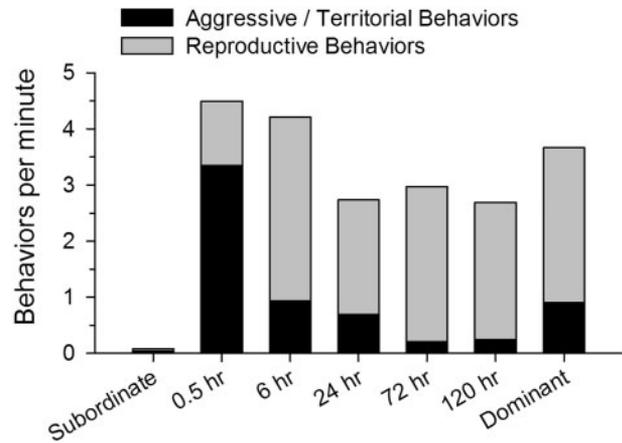
Fig. 1 Male *Astatotilapia burtoni* rising in social rank rapidly produce both aggressive and reproductive behaviors within the first 30 min of social ascent. Within a few hours (6 h timepoint), aggressive behaviors decrease and reproductive behaviors increase. Sample sizes are $N = 8$–12 per timepoint.

Further, there were rapid increases in circulating levels of cortisol (ANOVA, $F_{(6,63)} = 3.16$, $P = 0.010$; SNK, $P < 0.05$), E_2 (ANOVA, $F_{(6,63)} = 11.96$, $P < 0.001$; SNK, $P < 0.05$), T (ANOVA, $F_{(6,63)} = 4.19$, $P = 0.001$; SNK, $P < 0.05$), 11-KT (ANOVA, $F_{(6,63)} = 5.72$, $P < 0.001$; SNK, $P < 0.05$), and P (ANOVA, $F_{(6,63)} = 9.63$, $P < 0.001$; SNK, $P < 0.05$) at 30 min after social ascent compared with levels measured in stable subordinate males (Fig. 2).

Correlation analyses performed on all males used in this study ($N = 70$) between behaviors, levels of plasma steroids, and GSI, are summarized in Table 1. As expected, plasma levels of T, 11-KT, E_2, and P were all positively correlated with each other. In contrast, circulating levels of cortisol were not correlated with any other steroid levels, or GSI, or any of the quantified behaviors. Fleeing behavior was negatively correlated with circulating levels of T, 11-KT, E_2, and P. Furthermore, territorial behaviors were not well correlated with the levels of any circulating steroids. For example, only frontal displays showed positive correlations with levels of 11-KT and E_2. In contrast, all reproductive behaviors were positively correlated with T, 11-KT, E_2, and P, but not with cortisol. The only exception was the absence of a correlation between digging behavior and levels of 11-KT (Table 1).

Since one of the goals of this study was to focus on rapid changes associated with social transitions, correlation analyses were also run between behaviors and levels of circulating steroids within those individuals collected at the 30-min, 6-h, and 24-h timepoints. Within each of these rapid timepoints, there were no significant correlations between any of the
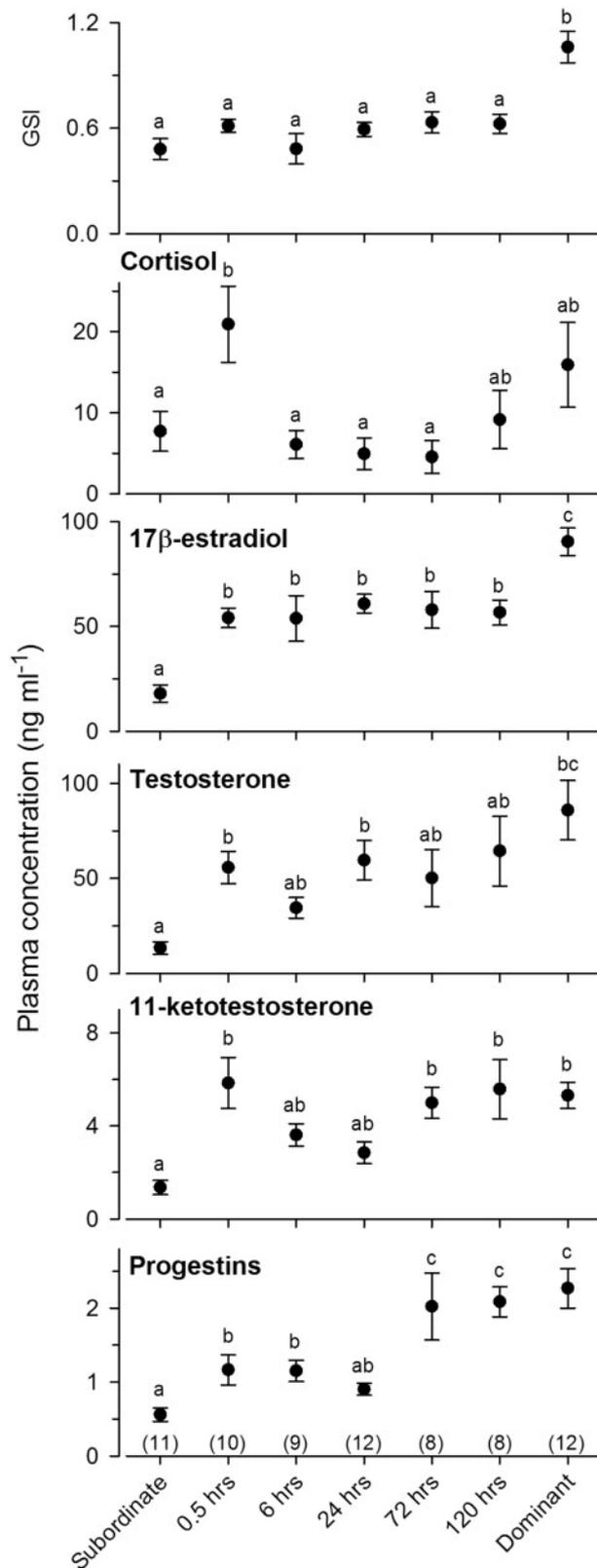
Fig. 2 Circulating levels of steroid hormones are rapidly elevated at 30 min after subordinate male *Astatotilapia burtoni* are provided with an opportunity to rise in social rank. Despite their small testes and low gonadosomatic index (GSI), ascending males show higher levels of cortisol, estradiol, testosterone, 11-ketotestosterone (a fish-specific androgen), and

individual behaviors and any of the levels of steroids in the plasma (Pearson correlation, all $P > 0.05$).

Discussion

Subordinate male *A. burtoni* showed increases in dominance behavior and circulating levels of the steroid hormones cortisol, T, 11-KT, E_2, and P within the first 30 min of rising in social rank. This rapid hormonal response is likely triggered by the social interactions, which are primarily agonistic in nature during the first 30 min, before switching to more reproductive behaviors several hours later. These new data show that the social opportunity is associated with quick increases in several steroid hormones, which then fluctuate differently over the next several days depending on the steroid. The absence of correlations between steroid concentrations in the plasma and behaviors, however, suggests a decoupling between endocrine state and behavior during the initial transition to a higher ranking status. It is important to keep in mind, however, that correlations do not imply causation, and there are likely other variables important for interpreting the relationship between behaviors and levels of steroid hormones that require further investigation. Nevertheless, a mismatch between outward and inward phenotypes may have evolved because it had a fitness benefit under the conditions of the dynamic environmental and social habitat, in which opportunities for social ascent are frequent.

Rapid changes in steroid hormones often are not well correlated with expression of behaviors in the short-term (Adkins-Regan 2005). Since behavior ultimately is controlled by the brain, the expression of different behaviors can change without the canonical steroid-producing tissues like the gonads. For example, removal of the gonads does not affect rapid displays of territorial and reproductive behaviors in a sex-changing fish (Godwin et al. 1996), and castration does not influence aggressive or sexual behaviors in some mammals (Demas et al. 1999; Scotti et al. 2008; Carter et al. 2014). In male *A. burtoni*, circulating sex steroids were not correlated with aggressive or territorial behaviors, but were positively correlated

Fig. 2 Continued

progestins at 30 min after given a social opportunity compared with subordinate males. Dominant males also typically show higher levels in the plasma compared with subordinate males for all steroids measured. Data are plotted as mean ± SE for subordinate, 0.5, 6, 24, 72, and 120 h after social ascent, and dominant males. Sample sizes shown in parentheses indicate the number of individuals measured per timepoint. Different letters indicate statistical differences among groups at $P ≤ 0.05$.

Table 1 Matrix of correlations between social behaviors, gonadosomatic index (GSI), and levels of plasma steroids in male *Astatotilapia burtoni*

	Flee	Frontal display	Lateral display	Border fight	Chase	Court quiver	Lead	Dig	Shelter entry	GSI	T	11KT	E$_2$	P	Cortisol
Flee		-0.28 **0.020**	-0.25 **0.036**	-0.19 0.100	-0.50 **<0.001**	-0.49 **<0.001**	-0.45 **<0.001**	-0.25 **0.030**	-0.50 **<0.001**	-0.30 **0.011**	-0.39 **<0.001**	-0.42 **<0.001**	-0.56 **<0.001**	-0.39 **<0.001**	-0.04 0.741
Frontal display			0.44 **<0.001**	0.52 **<0.001**	0.12 0.310	0.22 0.063	0.39 **<0.001**	0.04 0.712	0.09 0.451	0.15 0.212	0.20 0.101	0.28 **0.022**	0.30 **0.011**	0.03 0.844	0.12 0.332
Lateral display				0.75 **<0.001**	-0.11 0.352	0.16 0.200	-0.06 0.644	-0.20 0.091	-0.07 0.552	-0.03 0.792	0.12 0.321	0.17 0.152	0.07 0.562	0.02 0.862	0.06 0.611
Border fight					-0.08 0.521	0.05 0.662	-0.10 0.411	-0.17 0.162	-0.14 0.273	0.04 0.722	0.06 0.633	0.22 0.071	0.15 0.233	0.03 0.832	0.22 0.072
Chase						0.50 **<0.001**	0.50 **<0.001**	0.36 **0.002**	0.41 **<0.001**	0.33 **0.005**	0.36 **0.002**	0.27 **0.023**	0.48 **<0.001**	0.39 **<0.001**	-0.07 0.543
Court quiver							0.66 **<0.001**	0.40 **<0.001**	0.55 **<0.001**	0.03 0.783	0.28 **0.017**	0.39 **<0.001**	0.32 **0.007**	0.34 **0.004**	-0.05 0.661
Lead								0.41 **<0.001**	0.49 **<0.001**	0.33 **0.005**	0.35 **0.003**	0.30 **0.012**	0.48 **<0.001**	0.38 **0.001**	-0.08 0.493
Dig									0.62 **<0.001**	0.17 0.164	0.23 **0.050**	0.18 0.133	0.27 **0.020**	0.29 **0.013**	-0.13 0.293
Shelter entry										0.29 **0.014**	0.25 **0.038**	0.37 **0.002**	0.33 **0.006**	0.30 **0.012**	-0.10 0.411
GSI											0.36 **0.002**	0.12 0.34	0.59 **<0.001**	0.43 **<0.001**	0.12 0.321
T												0.60 **<0.001**	0.54 **<0.001**	0.64 **<0.001**	0.13 0.29
11KT													0.34 **0.004**	0.47 **<0.001**	0.01 0.953
E$_2$														0.64 **<0.001**	0.21 0.081
P															0.19 0.112
Cortisol															

Notes: Levels of steroids are negatively correlated with submissive behaviors (flee), positively correlated with many reproductive behaviors (chase, court quiver, lead, dig, shelter entry), and show minimal correlations with territorial aggressive behaviors (frontal display, lateral display, border fight). Dark gray (red online), negative correlation; medium gray (green online), positive correlation; light gray, no correlation. Significance at $P \leq 0.05$ is also indicated in bold. Males from all seven groups were included in the analysis ($N = 70$). Correlation coefficients (top values) and P-values (bottom values) from Pearson product moment correlation tests are shown. T, testosterone; 11KT, 11-ketotestosterone; E$_2$, estradiol; P, progestins.

with reproductive behaviors when all males were examined together. This suggests that sex steroids may play a role in the expression or modulation of reproductive behaviors during the social transition, but that aggressive behaviors may be regulated by independent mechanisms. In another study of *A. burtoni*, however, T and E$_2$ levels in the plasma were positively correlated with aggressive index (Huffman et al. 2012), but this difference may be due to the longer timeframe (2 weeks) of social ascent used in the Huffman et al. experiments compared with the 5 days used in the present study. In the related tilapia *Oreochromis mossambicus*, castration decreases reproductive behaviors, but has no effect on aggressive behaviors (Almeida et al. 2014), demonstrating a similar reliance of gonadal steroids on reproductive behavior but not on aggression. Thus, there is increasing support for decoupling of aggressive behaviors from gonadal steroids, suggesting independent central mechanisms for reproduction and aggression. In the mammalian hypothalamus, for example, there is evidence for overlapping, but distinct, neural populations involved in fighting versus mating, suggesting that there are separate reproductive and

aggressive circuits in some regions of the brain (Lin et al. 2011). The rapid expression of aggressive and reproductive behaviors in *A. burtoni* may be controlled by independent neural circuits, in which differential expression of steroid receptors in different regions of the brain may moderate/modulate context-dependent behaviors. It is possible, therefore, that rapid changes in sex steroids during social transitions serve to quickly modulate appropriate behavioral expression rather than being required to initiate it. The rapid timecourse of this behavioral plasticity suggests mechanisms related to modulation of existing neural circuits. In fact, male *A. burtoni* rising in rank show activation of, and increases in, the expression of different subtypes of androgen and estrogen receptors in several regions of the social behavior network (SBN) (Fig. 3), a collection of interconnected brain nuclei hypothesized to mediate social decisions (Newman 1999; Goodson 2005). These rapid changes in neural circuits can then be followed by genomic-level changes if the social and environmental conditions dictate more long-term phenotypic changes.

Since levels of circulating steroids may not always be good predictors of behavior, particularly during
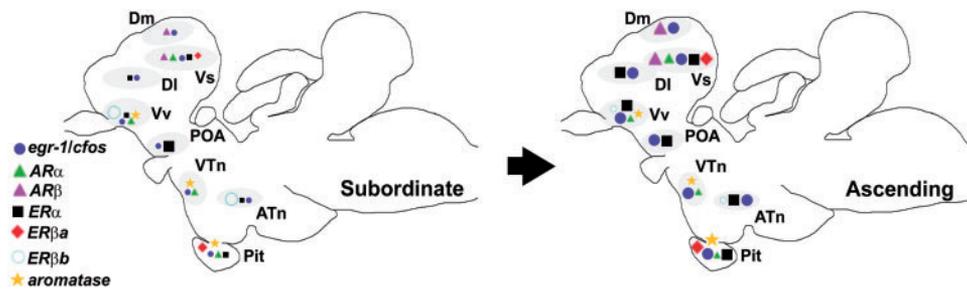
Fig. 3 Rapid changes in mRNA levels of IEGs (*egr-1/cfos*) and sex steroid receptors in social-processing regions of the brain associated with *Astatotilapia burtoni* males rising in social rank. Relative size of the symbols in each schematic sagittal section of the brain indicates the relative mRNA levels of each gene between subordinate males (left) and males ascending in social rank at 30 min after ascent (right). Within each identified nucleus of the brain (gray ovals), only those genes that showed differences between subordinate and ascending males are shown. Note that the ascending phenotype has higher mRNA levels (i.e., more large symbols) of several types of steroid receptors within many regions of the brain compared with the subordinate phenotype. Locations of each nucleus within the fish brain are depicted to minimize overlap and are therefore only approximate. Rostral is to the left. ARα, ARβ, androgen receptor subtypes α and β; ATn, anterior tuberal nucleus; Dm, medial zone of the dorsal telencephalon; Dl, lateral zone of the dorsal telencephalon; ERα, ERβa, ERβb, estrogen receptor subtypes α, βa, and βb; Pit, pituitary; POA, preoptic area; Vs, supracommissural nucleus of the ventral telencephalon; VTn, ventral tuberal nucleus; Vv, ventral nucleus of the ventral telencephalon. Modified from Maruska et al. (2013b). (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

periods when there is decoupling of physiological traits from phenotypic traits of color and behavior, then what is the purpose of rapidly increased plasma steroids during a change in social status? One possibility is that socially-induced changes in levels of circulating steroids are not related to the immediate context, but may modulate behavioral expression in future social interactions (Oliveira and Oliveira 2014). This "winning hypothesis" postulates that the probability of winning future interactions is governed by the success in previous ones, possibly mediated by transient changes in androgens (Oyegbile and Marler 2005; Hsu et al. 2006; Oliveira et al. 2009). Thus, it is likely that rapid increases in sex-related and stress-related steroids at social ascent in *A. burtoni* function to modulate expression of variables required for success in subsequent social interactions, as well as to initiate expression of physiological traits needed for dominance status and reproductive competence. While most previous research on this topic has focused on androgens (Oyegbile and Marler 2005; Oliveira et al. 2009; Fuxjager et al. 2010; Tibbetts and Crocker 2014), similar effects by other steroids (e.g., estrogens, progestins, cortisol) on cognitive processing also likely exist.

Summary of rapid changes along the brain–pituitary–testis axis during social ascent

In addition to the quick switch in behavioral repertoire and increases in levels of circulating steroids, the social transition from subordinate to dominant in male *A. burtoni* is associated with rapid physiological changes in the brain, pituitary, and testes (Fig. 4) (reviewed by Maruska and Fernald (2011b, 2013, 2014), Fernald and Maruska (2012), Maruska (2014)). These types of physiological changes along the reproductive axis also occur in other taxa in response to social transitions (Sapolsky 2005; Young 2009; Alonso et al. 2012; Fernald and Maruska 2012; Stevenson et al. 2012), and are important for allowing animals to properly allocate energy between growth and reproduction, thereby promoting survival and fitness. Within the first 24 h of social ascent in *A. burtoni*, many adaptive changes are initiated as the male transitions to a higher status. In the brain, for example, there are increases in cell proliferation in many regions (Maruska et al. 2012), activation of SBN nuclei measured by immediate early genes (IEGs) (Maruska et al. 2013b), increases in mRNA levels of sex steroid receptors in several SBN regions (Maruska et al. 2013b), and up-regulation of the gonadotropin-releasing hormone (GnRH1) neurons in the preoptic area as demonstrated by increases in GnRH1 somata size and mRNA expression (Davis and Fernald 1990; Maruska and Fernald 2013). Within 15 min of social ascent, there are also changes in mRNA expression of corticotropin-releasing factor (CRF) and its receptors in the brain, suggesting that the CRF system is involved in rapid shifts in social status (Carpenter et al. 2014).

In the pituitary gland, there are rapid increases in mRNA levels of the β-subunits of the two gonadotropin hormones, luteinizing hormone (LH), and follicle stimulating hormone (FSH) (Maruska et al. 2011). The levels of circulating LH and FSH are also
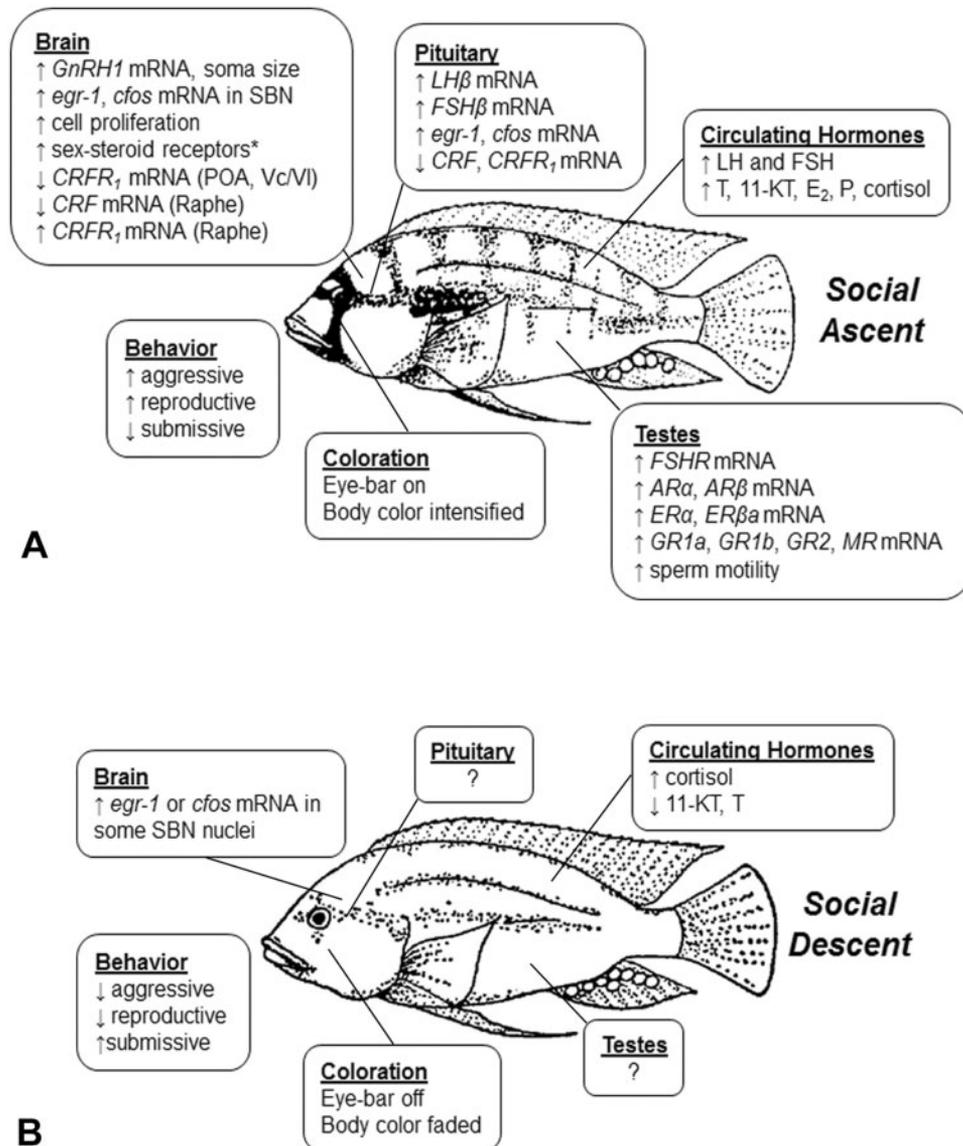
Fig. 4 Summary of rapid phenotypic changes in *Astatotilapia burtoni* males that are ascending (**A**) or descending (**B**) in social rank. Changes that occur within the first 24 h of males rising or falling in rank are shown. These adaptive phenotypic changes occur on similar timescales, but are often opposite in valence. Compared with social ascent, less is known about rapid physiological and molecular changes during social descent, but some cellular changes and changes in level of gene expression along the brain–pituitary–testes axis occur more slowly (days to weeks) (White et al. 2002). Data are compiled from Parikh et al. (2006), Maruska and Fernald (2011a), Maruska et al. (2011), Kustan et al. (2012), Maruska et al. (2012, 2013a, 2013b), and Carpenter et al. (2014).

rapidly elevated within 30 min of social ascent (Maruska et al. 2011), suggesting quick activation of the testes that promotes both spermatogenesis and steroid production. This coincident increase in pituitary mRNA levels and circulating mature hormones suggests that GnRH1 release to the pituitary rapidly up-regulates transcription (or liberates mRNA via other mechanisms) and causes release of already synthesized LH and FSH to the bloodstream. During the first 30 min of ascent, there are also increases in levels of circulating steroid hormones (T, 11-KT, E_2, P), suggesting that the suppressed testes

have enough steroidogenic potential to initiate this increase, or possibly that other steroid-producing tissues are involved. Importantly, although unknown in *A. burtoni*, in several other species of fish there is evidence that both LH and FSH can simultaneously stimulate steroid production and spermatogenesis (Garcia-Lopez et al. 2010; Levavi-Sivan et al. 2010), thereby providing the potential for rapid steroid release and sperm production from the suppressed testes within minutes of the ascent.

In the testes, there are increases in mRNA levels of FSH receptor, several sex steroid receptors (ARα,

ARβ, ERα, ERβa), and corticosteroid receptors (GR1a, GR1b, GR2, MR) within the first 24 h of social ascent (Maruska and Fernald 2011a). Further, within this same short timeframe, the quality of sperm also increases and these rising males can successfully court and spawn with females to sire viable offspring (Kustan et al. 2012). Male *A. burtoni* rising in social rank, therefore, show rapid and adaptive physiological changes along the brain–pituitary–testes axis that facilitate their transition to a dominant reproductive member of the population. In fact, the plasticity seen during the social ascent of *A. burtoni* represents one of the most rapid and extensive socially-induced transformations of the entire reproductive axis thus far described for any vertebrate. Because *A. burtoni* shows these rapid socially-induced changes, it will serve as an ideal model system for uncovering the neural and physiological mechanisms that govern cellular and molecular plasticity along the reproductive axis during changes in relative social position. The recent genome sequencing of *A. burtoni* and other African cichlids (Brawand et al. 2014) will also facilitate comparative and genetic manipulative studies to better understand the mechanisms controlling status and reproductive plasticity, as well as the selective pressures driving their evolution.

Social ascent versus social descent

Rising and falling in relative social rank can occur frequently in species that maintain dominance hierarchies, but how do social ascent and social descent differ? In *A. burtoni*, as in many animals, the transitions in status often require rapid behavioral and physiological changes that are similar, but opposite in direction (Fig. 4). For example, ascending males quickly turn on their aggressive eye-bar, intensify the coloration of their body, and begin performing dominance behaviors, while descending males turn off their eye-bar, fade their coloration, and adopt submissive behaviors within the same period of time (White et al. 2002; Burmeister et al. 2005; Maruska and Fernald 2010a; Maruska et al. 2013a). These outward changes in appearance and behavior that occur within minutes are likely an adaptation to quickly signal their new status to conspecifics, thereby reducing potential costly social interactions, and represent a period when the animal's outward and inward phenotypes do not necessarily match. This temporary dissociation of behavior and physiology in the short-term is likely a consequence of the additional time required to generate cellular and physiological changes (e.g., protein expression), and the need for

rapid mechanisms was likely selected over evolutionary time because it offered an advantage during these types of social transitions.

Behavioral plasticity relies on a nervous system that can perform rapid integrative and adaptive responses to changing conditions. This ensures that individuals with better or faster mechanisms of assessing, recognizing, and changing social status will have higher fitness, and will be more likely to pass their genes on to the next generation. The rapid behavioral changes in male *A. burtoni* observed during both social ascent and social descent conform to this premise, and therefore, make evolutionary sense. It is possible, however, that different neural mechanisms exist for rising versus falling in rank. For example, the degree of reversibility may be greater in one direction compared with the other, which necessitates involvement of different neurons, circuits, or cellular and molecular processes. In fact, the pattern of activation within SBN nuclei measured by IEGs (*cfos*, *egr-1*) differs between social ascent and social descent in *A. burtoni* (Maruska et al. 2013a). Thus, while the perception of a needed change in relative social position is rapidly registered by the brain for transitions in both directions, the conversion into transcriptional control of late-response genes that are necessary for phenotypic change likely differs and may also occur on different temporal scales.

Aside from the rapid fading of coloration, turning off of the eye-bar, increased submissive behaviors, and activation of the brain, little is known about how quickly physiological changes occur as males fall in social rank (Fig. 4) (White et al. 2002; Parikh et al. 2006; Maruska et al. 2013a). Within 30 min of social descent, however, there are increases in circulating levels of cortisol and decreases in levels of androgens (Maruska et al. 2013a). Males showing the greatest change toward more submissive behaviors also had the highest levels of cortisol, suggesting that this stress hormone may facilitate the behavioral switch from dominant to submissive behaviors as part of an adaptive strategy for coping with new conditions. Physiological changes along the reproductive axis such as shrinking of GnRH1 neuron size and testes size appear to occur more slowly over days to weeks (White et al. 2002). This protracted timescale may be an adaptation that retains reproductive potential and opportunities as long as possible in anticipation of acquiring a territory, thereby making a reversal in phenotype to the status of dominance faster. Future studies are needed, however, to determine whether there are other cellular or molecular changes along the brain–pituitary–gonad axis, or elsewhere, that occur rapidly during social descent.
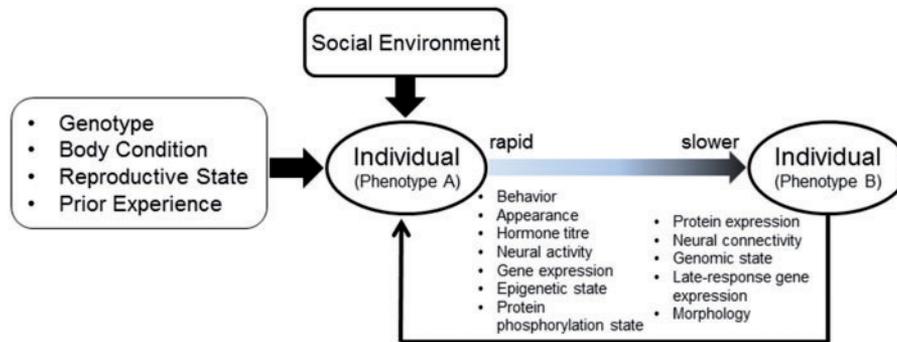
Fig. 5 Conceptual framework for transitions in social status. An individual's phenotype is shaped by many inputs including genotype, body condition, reproductive state, and prior social experience. Animals living in social societies constantly evaluate the social environment by interacting with and watching other individuals in the population. Individuals of one phenotype (phenotype A) then integrate all of these inputs and make adaptive decisions on whether or not to transition to an alternative phenotype (phenotype B). This transition in social status is associated with many changes that can occur on a continuous timescale from rapid (seconds to hours) to slower (days to weeks). Examples of variables and traits most likely to occur on rapid timescales versus slower ones are indicated on the figure. These changes in phenotype take place on many biological levels (e.g., from whole-animal behavior to gene expression) and are often reversible, but may occur on different temporal scales depending on the direction of the transition (e.g., rising versus falling in social rank). Resulting phenotypes also have important consequences for survival and reproductive fitness. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

Concluding comments and future directions

Neuroendocrine systems governing social behavior and reproduction are well-conserved across vertebrates and very sensitive to external cues such as social signals, environmental cues, and previous experience, as well as to internal cues such as hormone levels, body condition, and life-history stage. Social stimuli may trigger shared pathways that drive adaptive behavioral responses, which can then be modified in a species-specific manner and match an organism's unique environment. Transitions in social status within an individual can be envisioned as an integration of many inputs (prior experience, genotype, body condition, reproductive state, and social stimuli) that are used to decide whether or not to change rank, and therefore shape the response-dynamics of the individual's phenotype (Fig. 5). This conceptual framework for transitions in status requires constant evaluation of social stimuli from conspecifics, and the resultant changes can occur both on shorter and longer temporal scales to produce the new adaptive phenotype. Since dominance hierarchies exist across the animal kingdom (Chase 1974; Fernald and Hirata 1977; Sapolsky 2005; Bonoan et al. 2013; Jandt et al. 2014), understanding the mechanisms that mediate transitions in social position at behavioral and molecular scales is important. Many of the mechanisms involved in rapid behavioral and neuroendocrine changes, however, are still enigmatic.

Rapid transitions in social status likely involve multiple mechanisms acting on different temporal and organizational scales (Fig. 5). Because of the speed inherent in behavioral plasticity, it is more likely that changes in behavioral state or repertoire are mediated by modulation of activity within existing neural networks. For example, changes in neural activity, possibly influenced by modulators (e.g., neuropeptides, steroids, monoamines), likely precede changes in neurogenomic states across different nodes within social-decision-making networks in the brain (O'Connell and Hofmann 2011; Cardoso et al. 2015). If the behavioral change is transient, the organism can quickly and seamlessly revert to its original state via similar modulatory mechanisms. If the change is long-lasting, however, as is the case in loss or gain of territory-ownership and dominance, other mechanisms at the genomic or epigenetic level may be recruited to prepare the animal for a new social, behavioral, and physiological state. Baseline neural activity can therefore be shifted at the level of single neurons, or more global neural circuits, to initiate rapid changes in functional connectivity. These neural changes can then be made more permanent (e.g., changes in the morphology of neurons; synaptic connections) depending on feedback from the social environment. Focused experiments in the future that take advantage of the natural social transitions in *A. burtoni* should provide important insights toward identifying the cellular and molecular mechanisms that govern rapid behavioral plasticity, and how they may differ from maintenance of dominant and subordinate phenotypes.

Moving forward, there are many unanswered questions that deserve future study. For example,

how is the perception of social valence rapidly translated into adaptive phenotypic changes? What are the mechanisms that mediate both rapid short-term and slower long-term phenotypic changes associated with transitions in social rank? Relevant to this question would be an investigation into the potential role of neurosteroids in mediating rapid behavioral changes in *A. burtoni*. Localized release of brain-generated steroids in response to social signals occurs in several taxa (Remage-Healey et al. 2008, 2011; Do Rego et al. 2009), and is a likely candidate for being involved in social transition in *A. burtoni* as well. This neuromodulatory role of steroids is especially promising in light of the rapid nuclei-specific changes in the expression of steroid receptors observed in the brain of ascending males (see Fig. 3), and the lack of correlations between levels of circulating steroids and behavior in transitioning *A. burtoni*.

Of further interest are the questions of whether the mechanisms controlling social transitions are conserved across all taxa that exhibit social/dominance hierarchies, or are they species-specific? How do the mechanisms that mediate rising in rank differ from those of falling in rank? What role(s) have these mechanisms played in the evolution of social societies? While there are many ways to approach these questions, it is clear that both integrative (across levels of biological organization) and comparative (across species and taxa) studies are needed to advance the field. One important strategy would be to use reverse genomics that combines large-scale "omic" approaches (e.g., transcriptomics, proteomics, methylomics, metabolomics) to identify important genes (or gene modules), proteins, signaling pathways, or epigenetic mechanisms involved in social transitions, followed by manipulative tests (e.g., siRNA, pharmacology, CRISPR/Cas gene editing, optogenetics) to assign specific functions to the molecules or neural circuits identified by these approaches. Since fishes represent approximately 50% of all vertebrates and are increasingly appreciated as excellent models for understanding the complexities of social interactions (Bshary et al. 2014), cichlids in particular are poised to contribute significant new information on how an animal's social environment rapidly impacts behavior and physiology during adaptation to a changing world.

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