Social network dynamics predict hormone levels and behavior in a highly social cichlid fish

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ABSTRACT

Group living confers many benefits while simultaneously exposing group members to intense competition. An individual's rise to prominence within a group may conflict with the overall functioning of the group. There is therefore a complex and dynamic relationship between the behavioral displays that directly benefit an individual, the consequences of these actions for the community, and how they feed back on individual-level fitness. We used a network analysis approach to study the link between behavior, social stability, and steroid hormone levels in replicate communities of the cichlid fish, *Astatotilapia burtoni,* which live in social groups with a dominance hierarchy. We demonstrate that individual behavior can have direct and indirect effects on the behavior of others while also affecting group characteristics. Our results show that *A. burtoni* males form stable social networks, where dominant individuals act as hubs for social interactions. However, there was variation in the temporal stability in these networks, and this variation in stability impacted hormone levels. Dominant males had higher testosterone levels, however, the differences in testosterone levels between dominant and subordinate males were greatest in stable communities. In sum, our analyses provide novel insights into the processes by which individual and community properties interact.

1. Introduction

Animal societies are often characterized by complex social hierarchies (Chase and Seitz, 2011; Landau, 1951a, 1951b). While group living confers substantial benefits (e.g. access to mates, predator avoidance, shared resources, efficient foraging, and other forms of cooperation; (Clutton-Brock and Harvey, 1977; Krause and Ruxton, 2002)), constant conflict with other group members ensues, as each individual aims to maximize their share of resources and reproductive opportunities (Hofmann et al., 2014). Awareness of the social environment allows animals to maximize opportunities while avoiding costly interactions with other group members. When making behavioral decisions, animals must integrate external social and environmental information with their internal physiological state (e.g., condition and experience) in order to make the appropriate social decisions (Taborsky and Oliveira, 2012). Each animal inhabits a social environment composed of the overlapping networks of behavioral interactions that it participates in (e.g., aggressive or affiliative interaction networks).

Perturbations to one part of the system can affect the stability and properties of other parts, potentially creating social opportunities and conflicts (Border et al., 2019; Dakin and Brandt Ryder, 2020; Jordan et al., 2016).

Relationships between individual behavior, individual rank, and community structure have been explored in several group living species. For example, in Pig-tail Macaques, *Macaca nemestrina,* removal of dominant males (who typically police aggressive interactions in the group) results in a destabilization of the aggressive interaction network as well as a fragmentation of affiliative networks such as playing and grooming (Flack et al., 2006). In human social networks, community structure and social interactions have been linked to the spread of obesity, smoking cessation, and depression (Christakis and Fowler, 2008; Christakis and Fowler, 2007; Rosenquist et al., 2011). Together, these studies suggest that network dynamics of social groups play an important role in individual fitness. Additionally, individual rank within a social hierarchy has important consequences for survival and reproduction. For example, in house finches, *Carpodacus mexicanus,* and wire-

tailed manakins, *Pipra filicauda*, social network position influences mating success (Oh and Badyaev, 2010; Ryder et al., 2009, 2008). House finch males can modify the effects of sexual selection by choosing social environments where they are relatively more attractive (Oh and Badyaev, 2010). Hence, both social network dynamics, as well as individual rank within the network, are important components of fitness for group living animals.

The African cichlid fish, *Astatotilapia burtoni,* forms naturalistic communities with social hierarchies in the laboratory, providing a tractable model system highly amendable to studies exploring the causes and consequences of social life. Males of this species can be either dominant (DOM) or subordinate (SUB), and have the ability to transition between these phenotypes at any time, depending on the availability of territories and the outcome of territorial contests. DOM males are brightly colored, highly aggressive, territorial, and sexually active; SUB males are cryptically colored, less aggressive, non-territorial, and rarely show sexual behavior (Hofmann, 2003; Maruska and Fernald, 2013). Furthermore, individuals exhibit a repertoire of socially cognitive abilities (Weitekamp and Hofmann, 2014; Wallace and Hofman, 2021), including transitive inference of dominance rank (Grosenick et al., 2007) and cooperative territory defense (Weitekamp and Hofmann, 2017). Additionally, SUB males have the ability to adjust their behavior based on whether or not DOMs are watching (Desjardins et al., 2012), and females are able to recognize individual males in a mate choice paradigm (Desjardins et al., 2010). The dynamic nature of this social system provides an ideal setting to explore how social dynamics influence individual behavior and physiology.

A number of physiological processes interact with the social environment to modulate behavior. Steroid hormones such as androgens and glucocorticoids are one example, as these hormones dynamically respond to changes in the social environment and have dramatic influences on individual behavior. Testosterone, in particular, is associated with social dominance across vertebrates (Hirschenhauser and Oliveira, 2006), and is a critical component of an individual's response to aggressive challenges across vertebrates (Hirschenhauser et al., 2004; Wingfield et al., 1990). Likewise, glucocorticoids mediate behavior by regulating the vertebrate stress response to both physical and psychosocial stressors (Wendelaar Bonga, 1997). Furthermore, while much remains to be understood, these two steroid hormones are thought to interact (Emerson and Emerson and Hess, 2001; Grebe et al., 2019; Knight et al., 2020), illustrating the complex regulatory dynamics of behavior. In some species, cortisol can suppress testosterone levels by acting directly on the androgen-producing Leydig cells in the testes (Sapolsky, 2005; Welsh et al., 1982). Additionally, testosterone can impinge on the hypothalamic-pituitary-adrenal axis and suppress the secretion of cortisol (Handa et al., 1994). The relationship between androgens, glucocorticoids, and social status varies across species and depends on the social system (Sapolsky, 2005). For example, in some species of primates, where hierarchies are less stable and dominant animals have to defend their rank constantly, glucocorticoids are higher in dominant individuals compared to subordinates. Conversely, when dominance rank is maintained without physical interactions, the opposite pattern exists (Sapolsky, 2005). This divergence highlights the complex and dynamic nature of interactions within a specific social context, and the need for careful experimental approaches towards untangling the specific nature of these interactions.

A. burtoni is a well-suited model for addressing these complexities. In this species, circulating testosterone responds to changes in social status and is associated with both aggression and courtship (Huffman et al., 2012; Maruska, 2015; Maruska and Fernald, 2010; O'Connell and Hofmann, 2012a). In DOM males, circulating testosterone levels are elevated compared to subordinates, and are often positively correlated with aggressive behavior (O'Connell and Hofmann, 2012a; Weitekamp and Hofmann, 2017), but see (Alward et al., 2020, 2019; Maruska, 2015). Further, androgen receptor agonists increase courtship behavior in DOMs, while antagonists have the opposite effect (O'Connell and

Hofmann, 2012a; Alward et al., 2019). If presented an opportunity to ascend in status, SUB males show an instantaneous behavioral response and rapid surge in testosterone (Huffman et al., 2012; Maruska and Fernald, 2013, 2010). During status descent, DOM males display a significant decrease in testosterone 24 h after loss of rank (Parikh et al., 2006). Cortisol levels in this species are dependent on social status and the social environment. In communities where DOM males change status very infrequently SUB males have higher cortisol levels, while in communities characterized by an unpredictable social environment cortisol levels are more variable (Fox et al., 1997).

To address how community dynamics influence individual behavior, quantitative measurements of social structure are needed. Social network analysis (SNA) provides a useful approach in addressing this issue. SNA provides descriptive statistics of a social group by examining how interactions among individuals form distinct community structures. Utilizing SNA to explore animal networks has generated valuable insights into: the contact structure of animal societies (Croft et al., 2004; Lusseau, 2003; Lusseau et al., 2003), the influence of individuals on network structure (Flack et al., 2006; Lusseau and Newman, 2004; Williams and Lusseau, 2006), fitness consequences of an individual's position in the network (Jordan et al., 2016; Oh and Badyaev, 2010; Ryder et al., 2009, 2008), disease transmission (Craft et al., 2011; Godfrey et al., 2010; Grear et al., 2009), and collective decision making (Aplin et al., 2014; Ward et al., 2002). Taken together, these studies highlight the need to explore community dynamics outside the level of individual behavior. While these works have identified the importance of community structure, we know little about how properties of social networks regulate individual physiology; SNA presents an exciting approach to address such questions.

Here we quantify the behavioral interactions between all males from eight naturalistic communities of *A. burtoni* over a 10-day period, examining how changes in social structure interact with individual behavior and circulating hormone levels. Specifically, we test how connectedness (in-degree and out-degree centrality), or interactions among individuals within the network, is associated with aggression and courtship behavior and how community structure influences individual levels of circulating androgens and glucocorticoids.

2. Materials and methods

2.1. Animals

Animals used in this study were adult *A. burtoni* (males were between 5.1 and 8.0 cm in standard length, females were not measured) from a population originally derived from Lake Tanganyika, Africa (Fernald and Hirata, 1977). Fish were fed cichlid flakes (Omega Sea Ltd.) every morning before behavioral observations, and were maintained at 28 °C on a 12:12 h light/dark cycle. The present study comprises eight communities, each consisting of eight males and ten females. All aquaria (110 l) contained a sufficient number of terra cotta pots to serve as territorial shelters for up to four males, although in some communities only three males became dominant. Communities were established and allowed to acclimate for two weeks prior to the start of observations. All males were individually tagged with plastic beads of varying colors as described in (Trainor and Hofmann, 2006); females were not tagged. All procedures were approved by The University of Texas at Austin Institutional Animal Care and Use Committee.

2.2. Behavioral observations

Communities were recorded on video at 09:30 h for 30 min each on days 1, 3, 6, 7, 8, 9, and 10 using a Sony digital Handycam. All animals were fed 1 h before behavioral observations. We conducted 5-min focal observations of each male from these recordings (i.e., 7 observations per individual); the identities of the recipients of all displays were recorded as well. In total, this study includes 210 observations on 30 individual

DOM males and 238 observations on 34 individual SUB males. Males were identified as individuals based on their tag colors and females were identified by sex, but not as individuals. DOM males display an eye bar (most of the time), hold a territory, and have bright yellow or blue nuptial colors. While these color morphs show distinct differences in behavior and physiology (Dijkstra et al., 2017; Korzan et al., 2008; Whitaker et al., 2021) these differences did not substantially affect the results of the present study and were therefore not distinguished. Aggressive behavioral displays, including: chasing (aggressive approaches form one individual to another), border conflicts (ritualized aggressive displays between dominant males), and lateral display, as well as courtship behaviors including: leading and quivering directed towards females, were scored by a naïve observer (PD) following established ethograms (Fernald and Hirata, 1977). Aggressive displays towards males and females were analyzed separately as they may serve different functions depending on the sex of the targeted individual.

2.3. Tissue collection and hormone measurements

After behavioral observations on the 10th day, males were weighed and measured, and blood was drawn through the dorsal aorta using heparinized 26-gauge butterfly needles (Surflo) after application of a local anesthetic (lidocaine). Time from removal from aquarium to blood collection ranged from 1 min to 7.5 min, with one blood sample collected at 11 min. Plasma was then separated by centrifugation (3000 rpm for 15 min) and stored at -80 °C until further processing. Animals were euthanized immediately following blood collection. Gonads were removed and weighed to ascertain the gonadal somatic index (gonad weight / body weight * 100). Finally, brain and skin tissue were collected for use in a separate study (Dijkstra et al., 2017). We measured circulating testosterone ($n = 59$) and cortisol ($n = 61$) using ELISA (Assay Designs). Plasma samples were diluted 1:30 following (Kidd et al., 2010), and assays performed following manufacturer's instructions. The coefficient of variation within the testosterone and cortisol assay plates averaged 1.91% and 2.58%, respectively. Across testosterone and cortisol assay plates the coefficient of variation was 4.44% and 4.33%, respectively.

2.4. Statistical analysis

All statistical analyses were conducted in R (R Core Team, 2016). All relevant data are available as supplemental materials.

2.4.1. Social network analysis

Social networks were constructed using the R package, igraph (Csárdi and Nepusz, 2006). Networks were created for each tank on each day separately. Nodes represent individuals while edges represent the sum of aggressive interactions (chases, border conflict, and later displays combined) directed from one individual to another. The width of each edge is weighted by the rate they occurred. Females are represented by a single aggregate node, comprising the sum total of aggressive interactions between males and females during the observation period. Female to female aggressive interactions are rare and were not scored (Renn et al., 2009). Using these networks, we extracted indices of node importance: in-degree and out-degree centrality (defined as the sum of the weights of incoming and outgoing ties for each node, respectively). We conducted analyses at the individual and community level using linear mixed models (LMM) and generalized linear mixed models (GLMM), created with the R package lme4 (Bates et al., 2015). The distribution of in-degree and out-degree centralities were compared between DOM and SUB males with a GLMM that included status as a fixed effect and random effects to control for community membership and fish identity. To assess significance of these models compared to the null expectation we used datastream permutations to create simulated networks as suggested by Farine and Whitehead (2015). Swapping was allowed across time points between males of the same community and

social status. We reran all of our mixed models on 1000 permuted data sets and compared model parameters obtained from the observed data to parameters obtained from the randomized data to calculate empirical *p*-values.

To assess the robustness of our community stability estimates, we also analyzed autocorrelation patterns across time, correlating all sequential time point combinations of each network (Hobson et al., 2013). We calculated correlation coefficients and assessed their significance using the set of 1000 permuted replicate networks of the quadratic assignment procedure (QAP) implemented in the SNA R package (Butts, 2014). This procedure iteratively re-labels the nodes of the network, repeating the correlation calculation each time. Nodes were swapped randomly without regard for social status. *P*-values are given as the proportion of those randomized replicates that have a greater correlation coefficient than the observed correlation coefficient, with the null hypothesis that the two matrices are unrelated. We calculated a stability index by averaging the Pearson correlation coefficient of each network compared between sequential time points.

2.4.2. Individual level analysis

To examine the effects of behavior received by individuals on their behavior towards others, we used GLMMs with a Poisson error structure (appropriate for count data) and a log link function (to account for the non-normal distribution of the data). We created four separate models, using behavior received from DOMs and behavior received from SUBs as the response variables. DOM and SUB individuals were modeled separately. We included random effects to account for repeated observations of individuals and communities. Furthermore, we included a random effect at the level of each observation to account for over-dispersion (zero-inflation) in our count data using the method described by (Elston et al., 2001). To avoid over-parametrization, we used a forward fitting procedure, fitting each parameter and all two-way interactions one at a time. In each round we chose the parameter that improved the model the most, based on a chi square test and Akaike Information Criterion (AIC) score, until the model could no longer be significantly improved. The covariates we considered in this model included all outward social behaviors (aggression towards DOM, aggression towards SUB, aggression towards females (FEM) and courtship towards FEM), as well as non-social behaviors (foraging, shelter visitation, and digging).

2.4.3. Analysis of hormone measurements

To meet parametric assumptions, testosterone data were square root transformed and cortisol measurements were log transformed. The log transformed cortisol measurements showed a significant correlation with the time elapsed during blood sampling ($r^2 = 0.29$, $p = 4.67 \times 10^{-6}$) similar to previous studies in this species (Dijkstra et al., 2017; Fox et al., 1997). To control for this sampling effect we used the (normally distributed) residuals from this regression in all of our analyses. As reported previously (Dijkstra et al., 2017), there was no significant relationship between sampling time and testosterone levels and therefore no correction was necessary. Community effects on hormones were analyzed using ANOVA with fixed effects for community and status. Comparisons of hormones and behavior included only the behavior on day 10, when the hormones were sampled. We used LMM with random effects for community. *P*-values were calculated using ANOVA with Wald Chi-square tests implemented in the car R-package (Fox and Weisberg, 2011).

2.4.4. Community-level analyses

Connectedness based on social status was calculated by averaging the connections between members of a particular social status (Royle et al., 2012). For analyses of connectedness and hormones we included only the day 10 networks, when the hormones were sampled. We used LMM with random effects for community. For analyses of how connectedness of DOMs affected connectedness of SUBs and vice-versa, all data were included and we used LMM with random effects for

community and day. In both cases P-values were calculated using ANOVA with Wald Chi-square tests.

The stability index (average Pearson correlation coefficient of the networks over time, see above) was compared to the hormone data in two ways. In the first approach, we averaged the hormone data for each social status in each community and subtracted the average DOM hormone level from the average SUB level. We then tested for a correlation by calculating the non-parametric Kendall's tau statistic and assessed the significance by comparing it to the set of permuted networks. In the second approach, we included all of the hormone data and used a LMM with stability, status, and their interaction as main effects and a random effect for community, again assessing significance of the coefficients by permutation analysis. The results of both methods were concordant.

3. Result

3.1. Social networks of A. burtoni

We quantified behavior in eight communities based on seven observation periods over ten days and visualized the emergent social networks based on the sum of the total aggressive behavioral interactions. As can be seen in a representative community shown in Fig. 1, a typical community consisted of three or four DOMs. We observed that DOMs were hubs in the network and most of the aggressive interactions are directed from DOM animals towards other DOMs, SUBs, and females, while aggressive displays from SUBs are lower in frequency and usually directed towards other SUBs or females. To formalize this observation, we examined the degree densities of incoming (in-degree) and outgoing (out-degree) edges in the network as a function of social status. As expected, we found strong evidence that DOMs had higher aggressive in-degree than SUBs (GLMM Status: 0.255 $\pm$ 0.107, $p = 0.0176$) and much higher aggressive out-degree than SUBs (Fig. 2, GLMM Status: 3.278 $\pm$ 0.236, $p < 0.001$). To assess the stability of individual associations over time, we calculated a stability index by correlating association matrices representing the networks across all eight pairwise, sequential time points and used permutation analysis to

assess significance. We found that in highly stable communities, associations between individuals were strongly correlated across sequential time points with 43.75% of these comparisons having a p-value <0.05 (Fig. 2). In less stable communities, some comparisons were not stronger than the correlations in the permutated dataset. This is likely due to the dynamic interactions that DOM and SUB males typically display, driving fairly high correlations between networks even when individual DOM and SUB males are permuted.

3.2. Effects of social network position on behavior

We then asked how an individual's position in the social network affects its behavior. Table 1 summarizes the following results. Among DOMs, interacting aggressively with other DOMs was associated with increased courtship displays and decreased aggression towards SUBs. Among SUB males, the more aggressive behavior they received from DOMs the higher was the reciprocal aggression from those SUB males back towards DOMs, while their aggression towards other SUB males decreased. SUB males that are intermediate in the dominance hierarchy are largely responsible for this relationship, as most other SUB males do not show aggression towards DOMs. When we examined the DOM males that were targeted by these intermediate SUB males, we find that receiving aggression from SUB males was positively associated with a reciprocal increase in aggression back towards those SUBs (similar to the effect seen in the previous model) and negatively associated with aggression towards other DOMs and females.

3.3. Individual-level analysis of hormones and behavior

Steroid hormones have long been known for their role in regulating social behavior. We therefore examined relationships between social status, steroid hormones and individual behavioral displays on observation day 10 (when steroid levels were assayed). Not surprisingly, we found that testosterone was higher in DOM males (Supplemental Fig. 1A: 1.590 $\pm$ 0.879, $\chi^2 = 6.343$, $p = 0.0118$). However it was not correlated to overall aggression ($\chi^2 = 2.043$, $p = 0.153$). We then partitioned aggressive displays into those directed against DOMs, SUBs, or
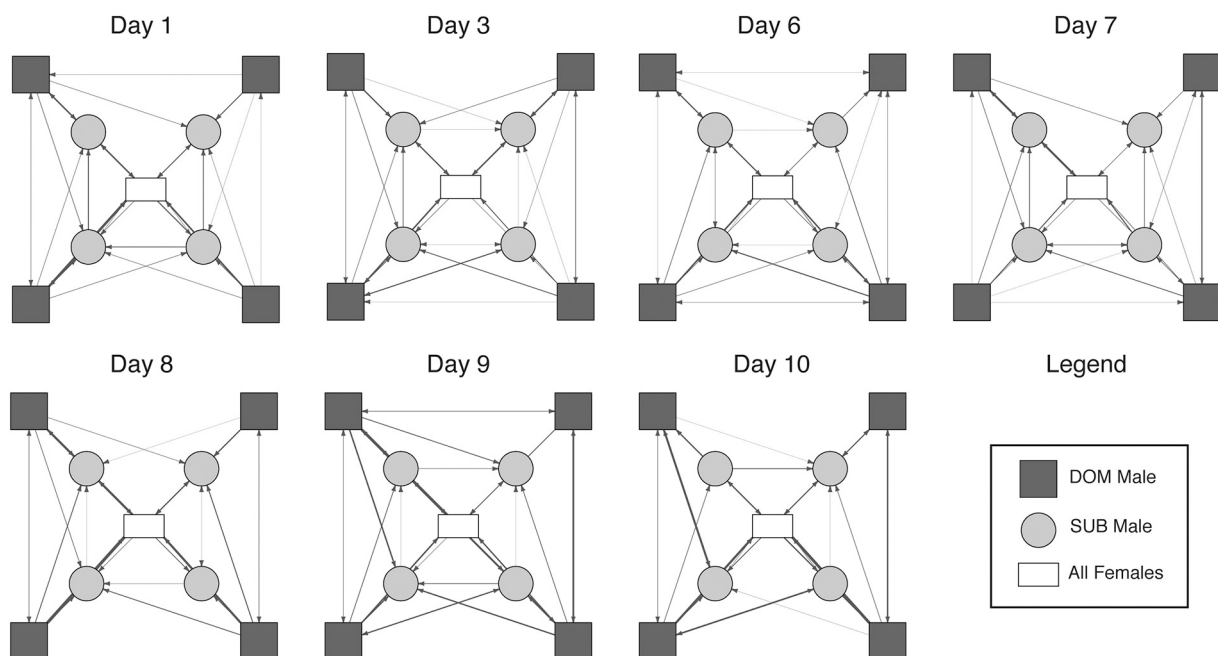

Fig. 1. Example networks of a single *A. burtoni* community over time. DOM and SUB Individuals are depicted in the same position on each day. DOM males (dark gray squares) are depicted in the corner of the tank aquarium that they occupied, while SUB males (light gray circles) are arranged randomly. Females (white rectangles) were not identified individually and are depicted as an aggregate node representing all eight females. The lines (edges) indicate interactions between individuals, with the weight and arrow representing the strength and directionality of the interaction, respectively.
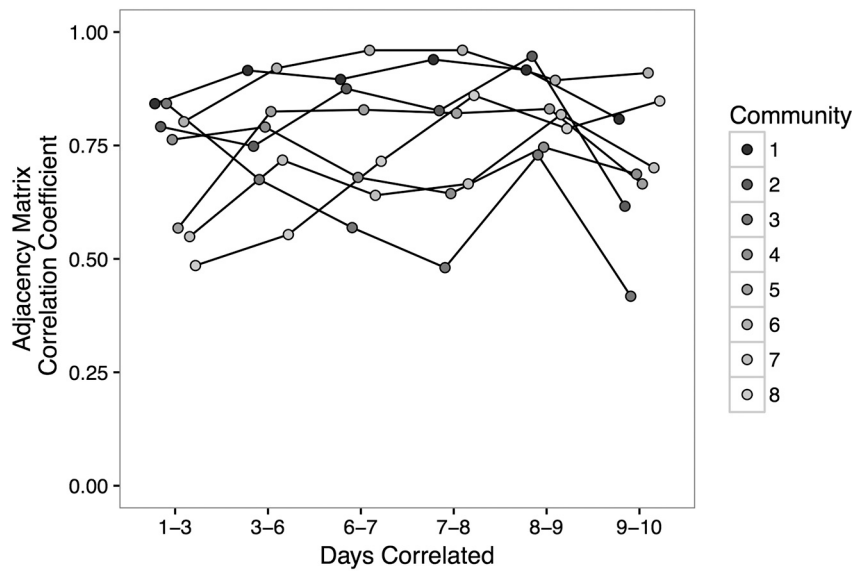
Fig. 2. Networks are stable over time. Points represent correlation coefficients of the matrices representing networks of each community correlated across consecutive days and are plotted with small random noise added to avoid overlap for the purpose of visualization. Each community is depicted in a different shade of gray and connected by a line.

Table 1

Receiving aggression from other community members correlates to the behavior that those individuals express. Results of four mixed models comparing the aggression received from DOMs (first two rows) or SUBs (last two rows) depending on the social status of the receiver. Significant effects are shown in bold.

Incoming behavior	Status	Outgoing behavior	Estimate	Permutation *p*-value
Aggression from DOM	DOM	**Aggression to SUB**	**−0.282**	**<0.001**
		Aggression to FEM	−0.079	0.470
		Courtship	**0.307**	**<0.001**
	SUB	**Aggression to DOM**	**1.041**	**0.001**
		Aggression to SUB	**−0.120**	**0.015**
		Aggression to FEM	**−0.316**	**0.048**
		Courtship	0.138	0.162
Aggression From SUB	DOM	Aggression to DOM	−0.036	0.124
		Aggression to SUB	**0.405**	**<0.001**
		Aggression to FEM	**−0.120**	**0.009**
		Courtship	−0.028	0.252
	SUB	Aggression to DOM	−0.068	0.254
		Aggression to SUB	−0.074	0.904
		Aggression to FEM	−0.085	0.259
		Courtship	0.030	0.420

females, respectively, finding that testosterone levels were not associated with aggression towards DOMs ($\chi^2 = 0.222$, $p = 0.637$) or SUBs ($\chi^2 = 0.020$, $p = 0.887$). However, we found a significant association between testosterone levels and aggression towards females, controlling for social status (Supplemental Fig. 1B: 0.082 ± 0.055, $\chi^2 = 4.005$, $p = 0.045$). Testosterone was not associated with the amount of courtship displays in either DOMs or SUBs. Next, we created similar models with cortisol as the response variable. We found that DOM males had lower cortisol levels than SUB males (Supplemental Fig. 1A: -0.152 ± 0.068,

$\chi^2 = 5.000$, $p = 0.025$). We found no relationships between cortisol and courtship or any aspects of aggressive behavior.

3.4. Community level regulation of hormones and behavior

We first asked whether community level behavioral variables could explain the amount of DOM and SUB aggression in these communities. Specifically, we looked at whether the aggressive output of the DOM males within the community predicted the aggressive output of SUB males and vice versa. We found that DOM-FEM connectedness (the average amount of DOM aggression towards females) was strongly negatively correlated to SUB male aggression in the community (Fig. 3: -0.241 ± 0.114, perm p = 0.04). The average amount of direct interactions between DOMs and SUBs did not correlate with SUB aggression and neither did DOM-DOM connectedness. No aspects of SUB male behavior in the community correlated with DOM male aggression.

Steroid hormones have well known roles in individual social behaviors, but how they are related to properties of the social group is less well understood. We therefore asked whether testosterone and cortisol
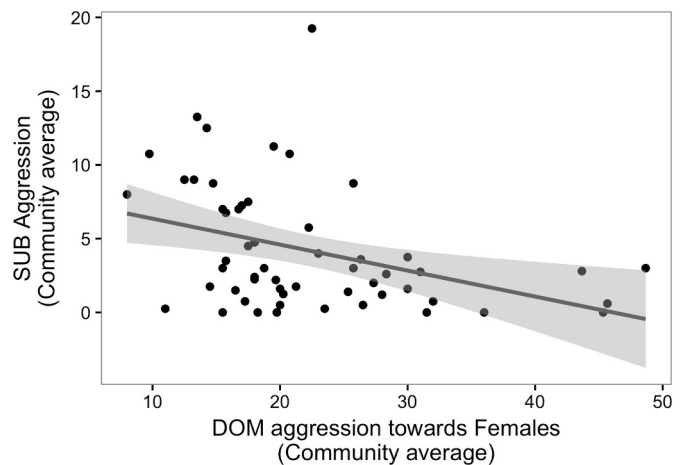

Fig. 3. Indirect effects of the DOM-FEM connectedness (the average amount of aggression directed from DOM males towards females in a community) negatively correlate to SUB male aggression.

were regulated by community membership, using ANOVAs with social status and community membership as fixed effects. We found significant main effects for community membership and status as well as the community by status interaction with both hormones (Testosterone ANOVA community * status: F = 3.504, p = 0.005; Cortisol ANOVA community * status F = 2.745 p = 0.018). Finally, we used two different modeling approaches to examine the extent to which community-level regulation of androgens was related to overall network stability. In the first approach, we subtracted the average DOM testosterone level from the average SUB testosterone level for each community, and regressed those differences against the stability index and compared the results to a set of permuted networks (to assess significance). We found a positive correlation such that the difference between DOM and SUB testosterone levels increased with community stability (Fig. 4: Kendall's rank correlation, tau = 0.643, perm p = 0.046). To assess whether this was a robust result, we used another approach: Specifically, we used a LMM with random effects for community membership and stability index and status as fixed effects, and compared the results to a set of permuted networks (again, to assess significance). Concordant with the result reported above, we found a stability index-by-status interaction effect, such that in DOMs, testosterone increased with increasing stability index, whereas in SUBs testosterone decreased with increasing stability index. Consequently, the differences in testosterone between DOM and SUB animals were greatest in stable communities (Fig. 4: stability-by-status: perm p = 0.001). The effect of community membership on cortisol levels (see above) was not correlated to the stability index.

4. Discussion

Social connections are linked to physiology, cognition and fitness (Cacioppo et al., 2014; Christakis and Fowler, 2007; Eisenberger and Cole, 2012; Rosenquist et al., 2011; Silk, 2007; Rodriguez-Santiago et al., 2020). Here we show that dyadic and community-level factors are correlated with individual-level behavior and physiology. We found that *A. burtoni* form stable social networks with social interactions that are highly correlated across days. DOM males act as hubs for social interactions, receiving and displaying more behavior than other community members. Furthermore, group dynamics also influence physiological characteristics of individuals within the community. Specifically, the difference in testosterone levels between DOMs and SUBs increases as communities become more stable. Thus, the direct and indirect relationships between individuals and their social partners ultimately affect the physiology of individual group members as well as
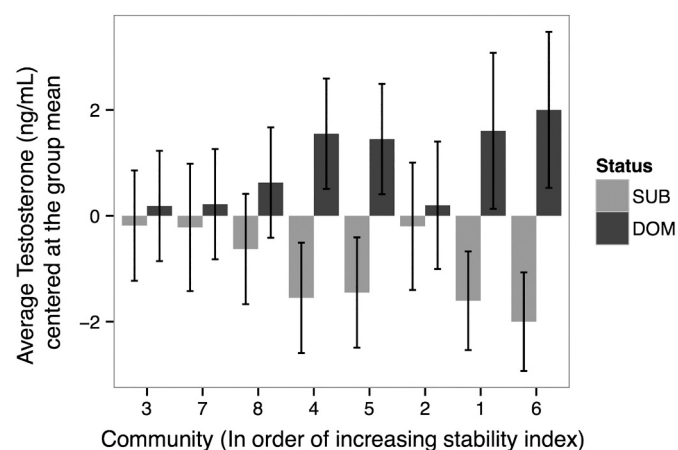

Fig. 4. The community effect on testosterone. The stability of social networks is positively correlated with increased differences in testosterone levels between DOMs and SUBs. Average and standard error of DOM (dark gray) and SUB (light gray) testosterone levels, centered on the whole community average, plotted for each community. Communities are shown in order of increasing stability index.

the stability of the social network and the likelihood of social change.

4.1. Individual-level analyses

On an individual level, we found correlations between circulating testosterone levels and behavior. Specifically, even though there was no association between androgen levels in DOM males and aggression towards males (which is sometimes but not always found in this species, see O'Connell and Hofmann, 2012a; Maruska, 2015; Weitekamp and Hofmann, 2017; Alward et al., 2020), androgens levels in DOM males were correlated with chases of females. Interestingly, courtship displays (such as quivering and leading) frequently follow ritualized chases directed at females. Thus, "aggressive" chases in this context may be related to reproduction, while ritualized chases directed at SUBs have a policing function. It is possible, of course, that courtship displays are not directly regulated by circulating androgens but by estrogens after the conversion of testosterone to estradiol by the enzyme aromatase (Czajka-Oraniec and Simpson, 2010). However, O'Connell and Hofmann (2012a) showed previously that courtship behavior is directly regulated by androgen receptors (AR) in *A. burtoni*, although their study did not pinpoint the responsible AR subtype. This finding was recently corroborated by Alward et al. (2019), who then also used transgenic methods to demonstrate that ARα, but not Arβ, is required for courtship behavior (Alward et al., 2020). In line with these and our findings (O'Connell et al., 2013b), a recent revision (Goymann et al., 2019) of the Challenge Hypothesis (Oliveira et al., 2002; Wingfield et al., 1990) suggested that androgen levels are responsive to reproductive opportunities. In polygynous lekking species, such as *A. burtoni* (Fernald and Hirata, 1977), where trade-offs between mating opportunities and parental care are absent for males, androgens are predicted to regulate interactions with females (Goymann et al., 2019). Consistent with this idea, our results show that in stable communities – where DOM males have more time available to court females and suppress SUBs – differences in T levels between DOMs and SUBs are greater.

Estrogens have been implicated in regulating aggressive behavior in a range of species (Trainor et al., 2006), including *A. burtoni* (O'Connell et al., 2013), likely via the nuclear estrogen receptor (O'Connell and Hofmann, 2012a). We did not assay estrogen levels in the present study, although future research should examine its role in a social network context in both stable and unstable communities.

In the present study, we did not analyze females at an individual level. Although reproductively active female *A. burtoni* can form dominance hierarchies under certain circumstances (i.e., in the absence of males, see Renn et al., 2012, 2016), they normally lack phenotypic indicators of social dominance, such as the aggressive displays, nuptial coloration, and lachrymal stripe typically seen in DOM males (Rodriguez-Santiago et al., 2020; White and Fernald, 1993). As a consequence, in naturalistic communities, females rarely initiate aggressive displays and do not alter group dynamics, yet aggression networks were the focus of our study. However, more research is needed to determine how female behavior and physiology relate to community dynamics (Rodriguez-Santiago et al., 2020).

4.2. Social network position and behavior

We found that DOM males were better connected within each network than SUB males with both higher levels of in-degree and out-degree. This higher connectedness is consistent with other studies showing that dominant or breeding individuals are 'hubs' in the social network. For example, in the cooperatively breeding cichlid, *Neolamprologus pulcher*, interactions were more frequent at the top of the dominance hierarchy and breeders had more connections than non-breeders within the group (Dey et al., 2013). Network theory suggests that well-connected individuals or nodes may have a disproportionate impact on the group structure and stability (Sih and Watters, 2005), and recent work has indeed indicated that removing these well-connected

DOM males creates social instability in *A. burtoni* networks (Piefke et al., 2021).

On a dyadic level, we found evidence of both direct and indirect correlations between status and behavior. We discovered social status-dependent correlations between the behavior that individuals direct towards others and the behavior they receive. DOMs that directed fewer aggressive displays towards females and other DOMs received more aggressive displays from SUBs. This result suggests that SUB males challenge DOMs they perceive as being lower in the dominance hierarchy. Consistent with this notion is our finding that lower aggression towards females is associated with lower androgen levels. In DOM males, interacting more with other DOMs was correlated to higher levels of sexual behavior and lower levels of aggression towards SUB males. This may indicate that higher ranking DOM males interact more with other DOMs, are not as threatened by SUB males, and are more sexually active. In SUB males, receiving aggression from DOMs was correlated to a reciprocal increase in aggression towards DOMs. This effect is driven by intermediate males, which challenge DOM males and in turn are targeted by them (Desjardins et al., 2012). These patterns in reciprocal aggression between DOMs, and between SUB males and (presumably lower-ranking) DOM males, involved mostly border conflicts and lateral displays. These ritualized agonistic displays, which typically do not result in a winner or loser (as defined as fleeing from the aggressor) are important for establishing and maintaining territorial boundaries and "dear enemy" relationships between neighboring DOM males, and can facilitate cooperative territory defense (Weitekamp and Hofmann, 2017). In SUB males, receiving aggression from other SUBs was correlated to lower amounts of aggression towards SUBs. This is consistent with a dominance hierarchy among SUB males, where the least aggressive SUBs are targeted the most by other higher-ranking SUBs.

4.3. Community-level analyses

Behavior and physiology of group living animals may be intimately tied to the structure of their community (Krause and Ruxton, 2002). We found that both circulating levels of testosterone and cortisol were strongly correlated to community membership and social status. The amount of DOM-DOM interactions within a group was negatively correlated with circulating levels of testosterone. Both DOM and SUB males likely perceive high aggression between DOM males as stressful, and therefore higher cortisol levels could cause decreases in testosterone through feedback mechanisms on the hypothalamic-pituitary-gonadal axis. While DOM males are active participants, this effect in SUB males is likely mediated by third-party observation of DOMs by SUBs. This is consistent with previous works showing that third-party observations can significantly affect the physiology of the observer (Desjardins et al., 2010; Weitekamp and Hofmann, 2017). While DOM-DOM interactions correlated with testosterone and cortisol across DOMs and SUB, DOM-FEM interactions are positively correlated with testosterone in DOMs only, having no effect in SUB males. In DOM males, testosterone increases in response to reproductive opportunities (Huffman et al., 2012; Maruska and Fernald, 2010; O'Connell et al., 2013), and hence, this effect is likely explained by aggressive behaviors prompted by mating opportunities and may consequently be explained by the correlation between testosterone and DOM-FEM interactions at the individual level.

In wire-tailed manakins (*Pipra filicauda)*, males can be either territory holders or (subordinate) floaters, and testosterone can affect behavior in a status dependent manner (Brandt Ryder et al., 2020). Territory holders and floaters often form cooperative coalitions, which benefit both types by increasing their mating opportunities. Interestingly, androgen-mediated behavior is dependent on social status: increased testosterone levels reduce cooperation in territory holders, while they have the opposite effect in floaters. In *A. burtoni,* DOM males decrease their aggression and testosterone response as they become familiar with a territorial neighbor and even form resource defense

coalitions against unfamiliar intruders (Weitekamp and Hofmann, 2017). SUBs, however, do not cooperate with DOMs in this species. Instead, we speculate that SUBs may increase their testosterone levels in times of social instability, when they have a higher chance to ascend in the hierarchy or encounter more mating opportunities as DOM males are pre-occupied with frequent territorial disputes.

In human and non-human primates both testosterone and cortisol have been linked to social network parameters (Brent et al., 2011; Kornienko et al., 2016; Sapolsky, 2005). In humans, higher cortisol levels correlated with turnover of friendships and fewer friendships overall, while higher levels of testosterone are correlated to more numerous and longer lasting connections (Kornienko et al., 2016, 2014, 2013). Similarly, in Rhesus macaques (*Macaca mulatta*), third party interactions were correlated to cortisol levels, indicating that indirect interactions can determine hormone levels in highly social groups across vertebrates (Brent et al., 2011). Our results are consistent with this literature as we examined replicated social networks, show that community structure can affect testosterone and cortisol levels, and provide evidence for a physiological effect of third-party interactions.

At the behavioral level, increased DOM-FEM interactions correlated with lower aggression in SUBs. Importantly, this effect is independent of direct interactions between DOMs and SUBs and instead suggests an indirect effect of viewing DOM male aggression towards females suppressing SUB male aggression. Finally, the amount of SUB-SUB aggression in the community correlated with higher testosterone among SUB males. Interestingly, at the individual level, a SUB's testosterone level was not correlated with the amount of aggression it showed towards other SUBs. Thus, simply viewing many aggressive interactions between SUBs may be sufficient to increase SUB's testosterone levels, even if they do not necessarily display increased aggressive behavior themselves. These results join a small but growing body of literature showing the importance of indirect interactions. For example, in manakins, third party interactions correlate to the likelihood of a male to rise in the social hierarchy and reproductive success (McDonald, 2007; Ryder et al., 2009, 2008), while in yellow-bellied marmots*,* the amount of indirect interactions predict a female's likelihood to disperse or stay within their natal group (Wey and Blumstein, 2010). Additionally, in humans, the likelihood of consuming alcohol or becoming depressed was associated with an individual's social connections (Niels Rosenquist et al., 2010; Rosenquist et al., 2011).

Finally, we calculated a metric for social network stability. Remarkably, we found that the community effect on testosterone levels was correlated with social network stability. As stability increased, DOM testosterone levels increased as well, while SUB testosterone levels decreased (Fig. 4.). In relatively unstable communities DOM and SUB male testosterone levels were similar, and in stable communities DOM males had higher levels of testosterone than SUBs. Males of SUB status may play a passive or active role in this process; unstable communities may give SUB males an opportunity to increase their social rank, leading to associated behavioral and physiological changes (Huffman et al., 2012; Maruska et al., 2011; Maruska and Fernald, 2011). Alternatively, SUBs with increased aggression and high androgens may actively destabilize dominance hierarchies by acting aggressively towards DOM males, particularly in communities where DOM-FEM aggression is low, which could also be indicative of lower testosterone among DOMs. Such a behavioral tactic may well come with fitness benefits. For example, we have previously shown that such "intermediate" SUB males are four times more likely to ascend to dominance as other SUBs (Desjardins et al., 2012).

5. Conclusions

The cichlid fish *A. burtoni* is ideally suited for analyses of complex community dynamics. Experiments using social engineering techniques (such as removing or adding individual community members; (Flack et al., 2006; Maldonado-Chaparro et al., 2018) or pharmacological

manipulations that subtly alter the aggressive or sexual behavior of specific individuals (O'Connell and Hofmann, 2012a) will help untangle cause and effect relationships in these complex community interactions. For example, removing a dominant male can lead to dramatic changes in *A. burtoni* networks (Piefke et al., 2021). These perturbation approaches can then be extended to investigating the molecular and neural substrates involved in shaping complex social dynamics and structure (O'Connell and Hofmann, 2012b) as well as the underlying molecular substrates (O'Connell et al., 2013; Williamson et al., 2016). Ultimately, this approach will provide insight into the causal mechanisms by which social plasticity spreads across a community and may enlighten our understanding of our own sociality.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2021.104994.

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