Hydrobiologia (2023) 850:2405–2423
https://doi.org/10.1007/s10750-022-04980-z

ADVANCES IN CICHLID RESEARCH V

Behavioral changes during social ascent and descent in replicate social networks of an African cichlid fish

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Received: 8 April 2022 / Revised: 16 July 2022 / Accepted: 30 July 2022 / Published online: 2 September 2022

Abstract Within social dominance hierarchies, rank has a major impact on health and fitness. Dominance hierarchies are rarely stable as individuals may change rank due to changes in the social environment. Here we describe general group-level social network properties and changes in social ties and behavior during rank transitions in 16 communities of the cichlid *Astatotilapia burtoni*. Social networks based on chases were dense with dominant males frequently chasing subordinate males and females. This intense territoriality of dominant males was also reflected by a high degree of 'power' inequality. Compared to chase-based networks, display-based networks were characterized by a high degree of reciprocity due to display behaviors mostly occurring bidirectionally among a few highly ranked males. Territory ownership is tightly linked to social dominance and territory loss (i.e., social descent) was, as expected, associated with a sharp reduction in aggression level and an increase in chases received. However, although territory acquisition (i.e., social ascent) was an abrupt process, ascending males displayed elevated aggression prior to ascent, in sharp contrast to previous studies carried out in less complex settings. Together, our results provide novel insights into dynamic changes in behavior in cichlid dominance hierarchies.

Keywords Aggression · Social rank · Territory defense · Social network

Guest editors: S. Koblmüller, R. C. Albertson, M. J. Genner, K. M. Sefc & T. Takahashi / Advances in Cichlid Research V: Behavior, Ecology and Evolutionary Biology

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-022-04980-z.

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Introduction

Competition for access to resources, such as mates, food, or territory resources, may lead to the emergence of dominance hierarchies. Dominance hierarchies help structure social societies and reduce conflict by making social relationships more predictable (Taborsky & Oliveira, 2012). The position of an individual within a dominance hierarchy has a dramatic impact on behavior and physiology (Dijkstra & Border, 2018; Snyder-Mackler et al., 2020). In many vertebrates, low-ranking individuals behave submissively and experience reduced reproductive opportunities, while high-ranking individuals show aggressive behaviors and monopolize resources and reproductive opportunities (Drews, 1993; Sapolsky, 2005; Chase & Lindquist, 2016). However, individuals never maintain the same rank during their lifetime due to changes in the social environment or developmental changes, such as increased body size or fighting ability. For example, a territory owner (high-ranked male) may fall victim to predation, triggering competition among lower-ranked individuals for the newly vacated territory. During this process, the new territory owner undergoes social ascent which is associated with dramatic behavioral and neuroendocrine changes to attain and signal higher dominance status (Milewski et al., 2022). Conversely, dominant males may undergo social descent if they are no longer able to incur the cost of maintaining their dominance status. This may lead to the dominant individual being evicted from his territory by a lower ranking male, which coincides with rapid changes in behavior and physiology in the descending male. Both social ascent and descent have been widely studied in laboratory settings to understand the behavioral and neuroendocrine shifts that occur with rank change (Larrieu & Sandi, 2018). For example, social descent using a resident-intruder test is widely used to impose repeated social defeat (mostly in rodents but also in cichlids). This social defeat paradigm can be used to investigate dysregulation of neuroendocrine systems and depression-like states (Bouvier et al., 2017; Lim et al., 2020). Social defeat studies are often done in an artificial setting, whereby the focal male is transferred into the home cage of a territory owner (resident) forcing the intruder male into submission. However, social hierarchies in a group setting results in more natural social organization and may lead to completely different physiological or behavioral outcomes relative to more artificial conditions (Dijkstra et al., 2010; Williamson et al., 2016). Consequently, studying the dynamics of social hierarchy formation and maintenance in these more natural settings is key to understanding how the social environment influences the link between rank and fitness (Dijkstra & Border, 2018; Larrieu & Sandi, 2018; Strauss & Shizuka, 2022). However, investigating changes in behavior and social relationships in individuals that undergo a rank change within a complex social hierarchy is challenging. Social network analysis is a useful approach for examining social behavior at the individual and group levels and it can be used to quantify how relationships are formed, maintained, and adjusted over time (Hobson et al., 2013; Bierbach et al., 2014; Pinter-Wollman et al., 2014; Williamson et al., 2016). An increasing number of studies in cichlid fish have used social network approaches to quantify general group structure, social stability, or social prominence of certain group members (Schürch et al., 2010; Dey et al., 2015; Border et al., 2019; Maguire et al., 2021; Piefke et al., 2021). However, very few studies have used social network approaches to quantify changes in behavior and connectivity of individuals within social groups during rank transitions in cichlid fish (Piefke et al., 2021).

The East African cichlid, *Astatotilapia burtoni*, is an emerging model system to study how the social environment influences the brain, behavior, and physiology (Dijkstra et al., 2017; Alward et al., 2020; Rodriguez-Santiago et al., 2020; Butler & Maruska, 2021). As is the case in many haplochromine cichlids, dominant males in this species are brightly colored, vigorously defend territories, and court females, while subordinate males are drab in color, school with the females, and do not typically reproduce (Maruska & Fernald, 2018). Dominant males also tend to be larger than subordinate males. In *A. burtoni*, males keep track of other members in the hierarchy, and changes in the physical and/or social environment can induce rapid changes in social status, altering the individual's physiology and behavior (Hofmann et al., 1999; Maruska & Fernald, 2010; Desjardins et al., 2012; Huffman et al., 2012). Because of the extremely obvious phenotypic markers of social dominance and rich behavioral repertoire, *A. burtoni* as well as many other cichlid species (Dijkstra et al., 2007; John et al., 2021; Culbert et al., 2022) provide excellent opportunities to study behavioral changes during rank transitions. Previous studies in *A. burtoni* have shown that social ascent and descent are linked to rapid changes in behavior, with males dramatically increasing or decreasing territorial aggression, respectively (Burmeister et al., 2005; Maruska & Fernald, 2010; Huffman et al., 2012; Maruska et al., 2013; Fialkowski et al., 2021). However, these studies were carried out in relatively isolated conditions with only a limited number of competitors, resulting in social dynamics that do not necessarily reflect the situation in the wild. The goal of the current study was twofold. First, we describe general social network properties of experimental *A. burtoni* social hierarchies relative to how group members are connected, and power is distributed in large mixed-sex groups (16 groups each consisting of 12 males, 14 females). This goal will also expand on recent efforts to use a social network perspective to quantify cichlid social dynamics in *A. burtoni* (Border et al., 2019; Rodriguez-Santiago et al., 2020; Maguire et al., 2021; Piefke et al., 2021). Second, using these experimental communities, we will define behavioral changes in males that either ascend (i.e., gain a territory) or descend (i.e., lose a territory). To this end, we quantified behavioral interactions at regular intervals to obtain snapshots of the social network over a 19-day period in replicate mixed-sex communities. On day 16, a vacant territory was experimentally created through the removal of a dominant male in several replicate communities of *A. burtoni*. In principle, vacating a territory provides the opportunity for a subordinate male to become dominant by monopolizing the vacant territory. In addition, this increased competition was also expected to lead to changes in the hierarchy, potentially triggering more descents as well. We quantified behavioral changes in these ascending and descending males three days prior to their rank change and the first three days when males were in their new rank. We predicted that ascending males and descending males rapidly increase or decrease their rate of aggression, respectively, leading to a behavioral phenotype that is consistent with their new rank.

Methods

Animals and housing

For this experiment, adult *A. burtoni* were bred from a laboratory population originally derived from Lake Tanganyika, Africa. The fish were housed in 110-l tanks, maintained at 28 °C on a 12:12-h light/dark cycle and fed cichlid flakes (Omega Sea Ltd.) every morning. All experimental tanks were setup with partial terracotta pots placed in each corner to create four defendable territories per tank. A total of 16 groups were studied, each composed of 12 males ($N = 192$) and 14 females ($N = 224$). All fish were individually tagged through the dorsal musculature using a stainless steel tagging gun and colored beads. Experimental groups were given four weeks to settle and stabilize before observation began. All procedures were approved by Central Michigan University's Institutional Animal Care and Use Committee.

Experimental design

The experimental design of this experiment has been described elsewhere in a study on the link between social rank and oxidative stress (Border et al., 2019). A graphical depiction of the experimental design is shown in Fig. 1A. In brief, groups were filmed over a 19-day period (on days: 1, 3, 5, 7, 9, 11, 13, 14, 15, 16, 17, 18, and 19) for 10 min per session using a Canon EOS Rebel T5i for later quantification. The experiment was originally designed to induce community-wide social instability and the effects of male removal on community-wide instability and overall aggression were published elsewhere (Piefke et al., 2021). To manipulate social instability, groups were randomly assigned to either the dominant-male removal treatment ($N = 9$) or the subordinate-male removal treatment ($N = 7$): in the dominant-male removal treatment, a dominant male was removed from an experimental group and a mock removal was performed on a randomly chosen subordinate male by netting and immediately releasing him. In the subordinate-male removal treatment, a subordinate male was removed from the group and a mock removal was performed on a randomly chosen dominant male. The subordinate removal controlled for changes in fish density in the dominant-removal groups. Male removals were performed immediately following the filming on day 16.

The dominant-removal treatment created a vacant territory over which males in the group competed for ownership. We hypothesized that this would trigger social ascent of a previously subordinate male (Fig. 1B). In addition, we also observed several social descents (for more details, see "Results" section), allowing us to quantify behavioral changes in both ascending and descending males.

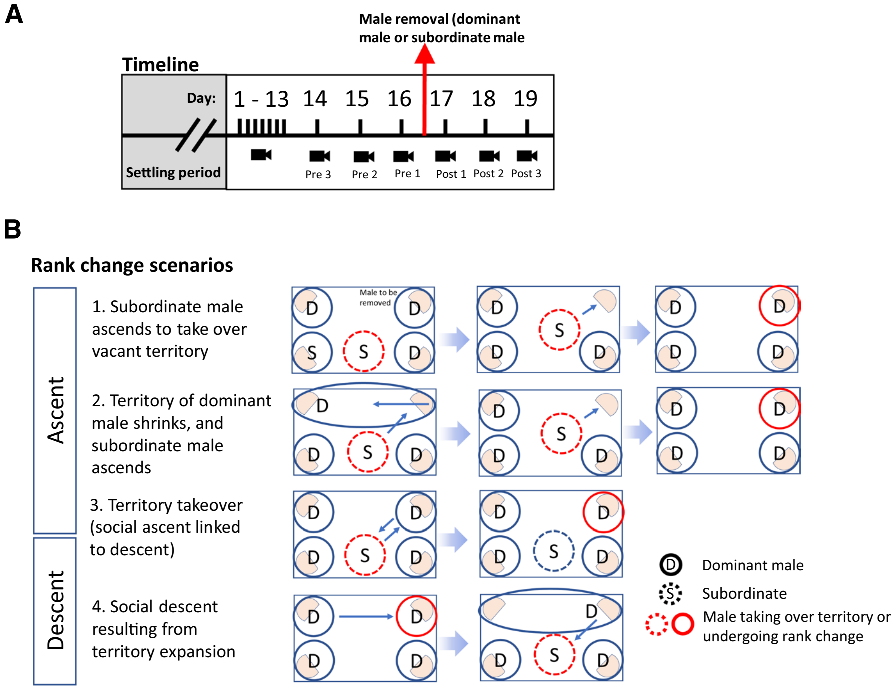


Fig. 1 **A** Experimental design. To induce social rank changes and social instability, we removed a dominant male after filming on day 16 in nine experimental groups. A subordinate male was removed in seven control groups. We filmed groups for 10 min either every other day from day 1 to day 13 or daily from day 13 to day 19. For each video, we recorded social status of each male and we reconstructed weighted and directed social networks. Pre-3, -2, and -1 denote the number of days prior to a rank change and Post-1, -2, and -3 indicate the number of days after attaining the new rank. On 'Post-1', ascended males occupied a flowerpot (territory) while descended males had lost their flowerpot. Note that most rank changes occurred from day 16 to day 17, but we also recorded several that took place one or two days later (for details, see "Results" section). **B** Potential scenarios of social ascent and descent. Shown are schematic top views of experimental communities containing a flowerpot in each corner of the tank. Dominant males (D) occupy one or two flowerpots, whereas subordinate males (S) shoal with females and other subordinate males. Not all community members are indicated (each community contained 12 males and 14 females)

Behavioral observation

Using all-occurrence sampling for each 10-min video, the following behaviors were recorded among all members in each group: fleeing, chasing, lateral displays, and border displays (Piefke et al., 2021). Fish that are a target of a chase typically swim away (flee) from the aggressor. Display behaviors are usually not followed by flee and are typically used in symmetrical interactions with two males engaging in border or lateral displays simultaneously toward one another. For both chase and display behaviors, we recorded the initiator of the behavior as well as the target.

For each video, individual males were categorized as either dominant or subordinate. Dominant males were categorized as defending a flowerpot, whereas subordinate males were not. Dominant males also expressed bright yellow or blue coloration, expressed a dark eye bar, and exhibited more aggression and courtship behavior compared to subordinate males. Most subordinate males avoided dominant males, showed frequent fleeing behavior from dominant males, and shoaled with females and other subordinate males. However, some subordinate males showed bright coloration, a dark eye bar, and defended space in the aquarium (but no flowerpot) while occasionally showing (behavioral) traits that are typical to subordinate males, such as fleeing, shoaling, and no dark eye bar (for more details, see "Results" section). For each video, we also recorded which flowerpot(s) each dominant male defended.

Ethical note

Cichlids were studied under protocols approved by the Animal Care and Use Committees of Central Michigan University (IACUC protocol 15-22). This research adhered to the ASAB/ABS Guidelines for the use of animals in research. We attempted to reduce stress of the animals during the experiment by ensuring sufficient enrichment in the form of flowerpots. This also facilitated the establishment of multiple territories and social stability in the dominance hierarchy, avoiding excessive aggression by a single *alpha* male.

Social network analysis

We constructed and analyzed two social networks for each 10-min video. The chase aggression social network was based on chases, while the display aggression social network was based on lateral and border displays. Representative chase and display networks are shown in Fig. 2A. The chase network is useful for characterizing social dominance relationships with a clear winner (the chaser) and loser (the fish fleeing from the aggressor). While all fish may perform chases, most chases are performed by dominant males toward subordinate males and females. In contrast to chases, displays are often used during symmetrical territorial interactions among dominant males trying to establish territorial boundaries. Hence, these two network types represent distinctly different agonistic networks that can provide a more comprehensive perspective on overall community structure and social change when observed separately. Statistical analyses were performed using R v3.4.4 (R Core Team, 2018). Social networks were created for each video using the R package igraph v1.1.2 (igraph Development Team, 2018). Using these networks, we computed weighted outdegree (referred to as 'outstrength'), unweighted outdegree (referred to as 'outdegree'), weighted indegree (referred to as 'instrength'), and unweighted indegree (referred to as 'indegree') for each male for both the chase and display networks as measures of individual connectivity or prominence within the network. Outstrength and instrength are equivalent to the total number of chases or displays a male performs or receives, respectively. Outdegree and indegree are the number of fish to whom the behavior was directed or the number of fish that directed behavior to the focal male, respectively.

Group-level analysis

One aim of the current paper is to describe general properties of *A. burtoni* social hierarchies relative to the distribution of aggression across group members, overall connectivity within the social network, and consistency (i.e., stability) of the hierarchy over time. All group-level metrics were calculated for 10-min social network separately. For our analysis, we focused on the social networks derived from video recordings obtained prior to the male removal on day 16 to avoid male removal and social instability from influencing these findings.

To characterize how power is distributed among males in each community, we calculated the *Gini coefficients* for each chased-based social network using chases performed (chase outstrength). We calculated Gini coefficients using the R package 'ineq' (Zeileis & Kleiber, 2014). Gini coefficients range from 0 (even distribution of power) to 1 (completely uneven distribution of power) (Wittebolle et al., 2009; McDonald & Shizuka, 2012). In addition, we also calculated Gini coefficients for dominant males only to evaluate the degree of inequality among dominant males in each community. We did not calculate Gini coefficients using display data because most lateral and border displays are used during bidirectional interactions with no clear winner or loser.

We calculated group-level social network metrics for each chase and display social network: (a) *Network density* is the proportion of actual connections that are created compared to all possible connections that could be made between individuals within a community (Wasserman, 1994). (b) *Network reciprocity* is the likelihood of vertices being mutually linked within a network and evaluates how often interactions occur in both directions between a target and its source (Schino & Aureli, 2010). Network reciprocity is measured from 0 (interactions always performed in one direction) to 1 (interactions always performed equally in both directions). (c) *Network diameter* is representative of the linear size of a network and is calculated as the shortest path between the two most distant nodes (Wasserman, 1994). (d) *Eigencentrality* is the average of each node's influence over the entire network based on

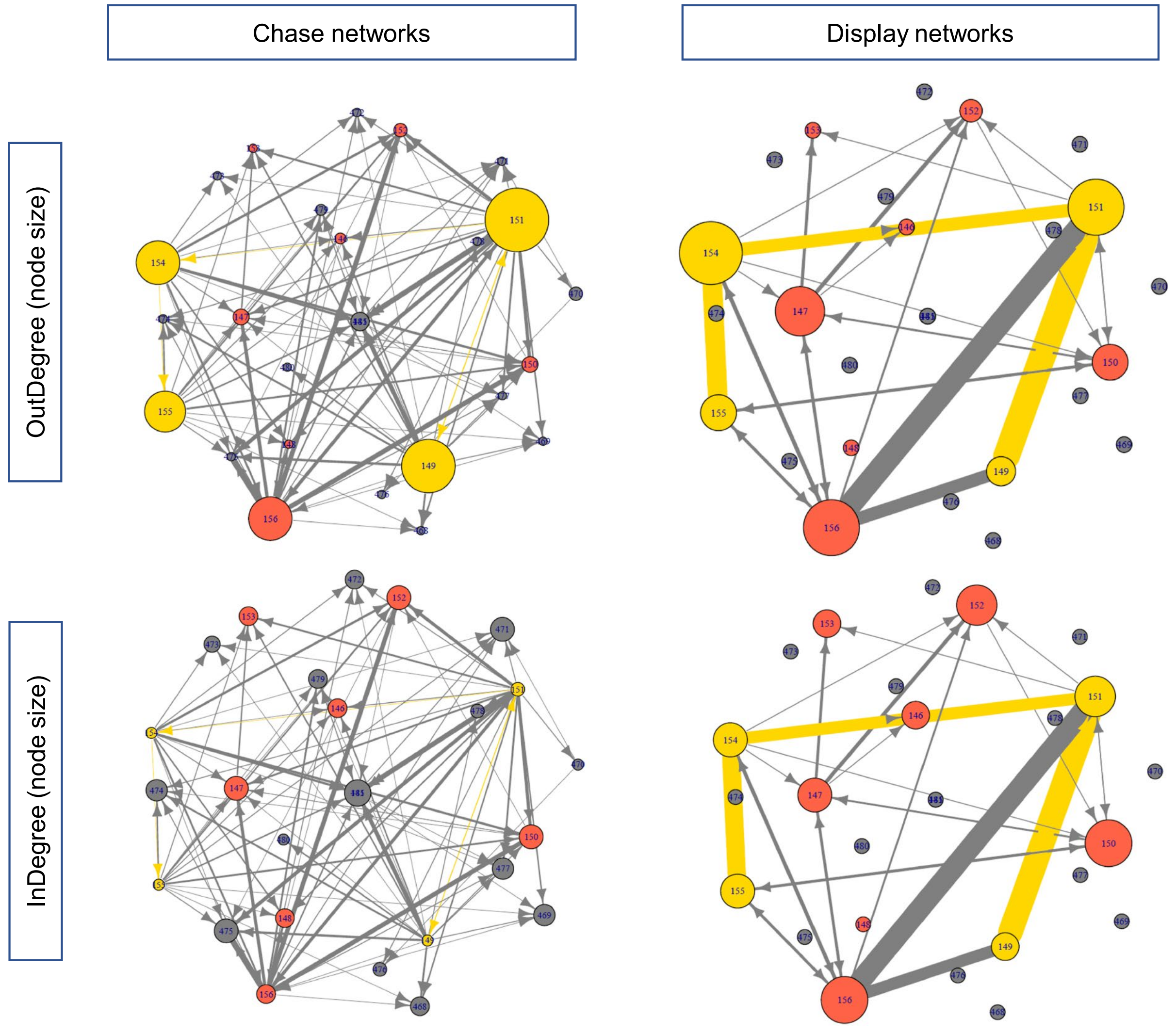


Fig. 2 Chase (left) and display social networks (right) of a representative group based on the same 10-min video. Edge width represents outstrength (arrows going out) and instrength (arrows coming in). Node size represents outdegree (top) and indegree (bottom). Dominant males (yellow) tend to be more aggressive than subordinate males (red) and females (gray). Interactions between dominant males are indicated as yellow edges and tended to be more common in display social networks than in chase social networks. Also note that chase social networks are considerably denser than display social networks. Numbers within each node indicate fish ID

the number of links it has to other nodes and how well those other nodes are connected within the network (Alvarez-Socorro et al., 2015).

To determine network stability over time, we calculated the average correlation between sequential chase and display-based matrices (networks) in each group using Pearson's r correlation. Correlations were based on a scale of -1 to 1, where -1 was total negative correlation, 0 meant no correlation, and 1 was a total positive correlation between chase or display rates from one matrix to the next.

Statistical analysis

We used linear mixed models (LMM) and generalized linear mixed models (GLMM) using the R packages lme4, MASS (Bates et al., 2015), and glmmTMB (Brooks et al., 2017).

Gini coefficients and group-level social network metrics were calculated for each social network (each is based on a 10-min video). We then calculated the mean values across all pre-manipulation networks. Gini coefficients and group-level social network metrics were compared between different categories using Wilcoxon signed ranked tests or Mann–Whitney *U* tests for paired or unpaired tests, respectively.

We tested whether chase and display social network metrics (outstrength, outdegree, instrength, and indegree) changed the day after the rank change relative to the day just prior to the rank change using GLMMs assuming a Poisson or negative binomial distribution. To increase the time window before and after rank change, we also analyzed data for the 3 days before and three days after the rank transition. GLMMs were fitted for ascending and descending males separately using male ID as a random effect and period (before versus after rank change) as factor. Model assumptions were verified by plotting residuals against fitted values. For all effects we report estimates and standard error. Data and code will be archived on Dryad upon acceptance.

Results

General dominance hierarchy characteristics

A small number of males maintained social dominance (3–4 in each community) while the rest of the males shoaled with the females. Each dominant male defended a territory that contained one or two flowerpots (there were 4 flowerpots in each community). Most chases were performed by these territorial males toward subordinate males and females. More specifically, as can be seen in the distribution of chase-based outdegree and indegree in all networks (Fig. 3A),

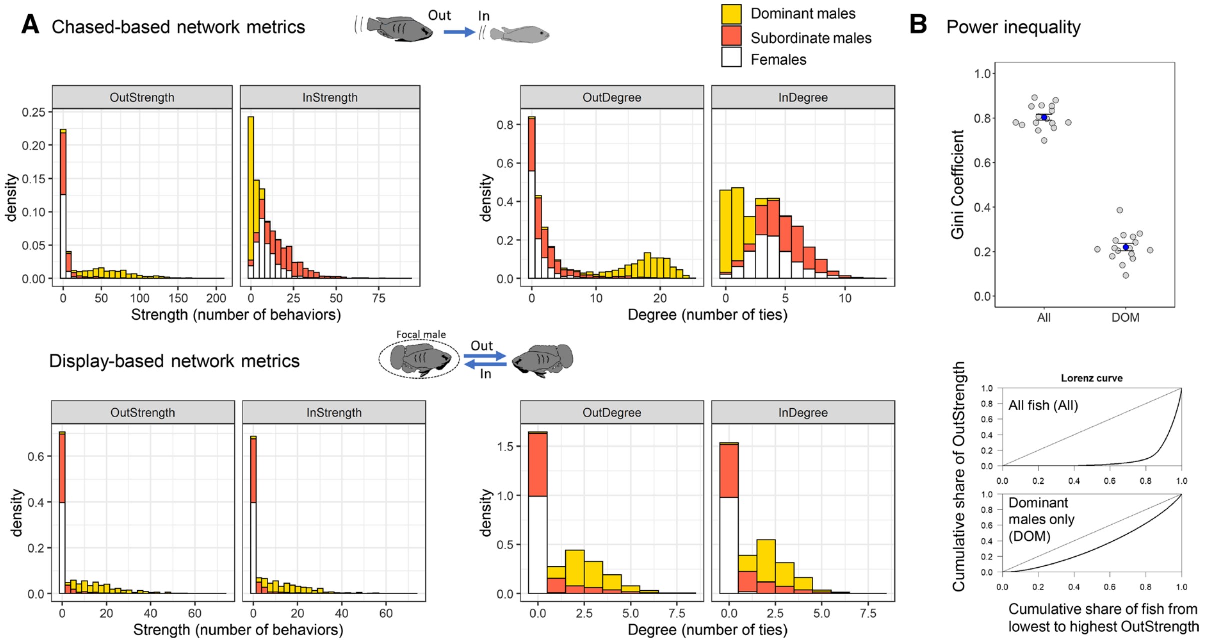


Fig. 3 **A** Distribution of outstrength, instrength, outdegree, and indegree for chased-based networks and display-based networks. Shown is the distribution of all pre-manipulation social networks (each based on a 10-min video) for all communities ($N = 16$) combined. **B** Gini coefficients calculated for all fish in a community (All) or among the dominant males in a community (DOM). The raw values shown are the average Gini coefficient for all social networks of a given community obtained between days 1 through 16 (i.e., all pre-manipulation social networks, each based on a 10-min video). Shown are the mean ± SE. The Gini coefficients for each network were calculated using chase-based outstrength, which corresponds to the rate of winning. High Gini coefficient values correspond to high levels of inequality, and low values indicate that the distribution of power is more even. The Lorenz curves, which are used to derive the Gini coefficient, show the distribution of power based on all pre-manipulation social networks (each based on a 10-min video) and all communities combined ($N = 16$). The diagonal represents completely even distribution of chase outstrength

most fish chased none or few fish (low outdegree values) and only a few males performed chases toward a relatively large number of community members (high outdegree values), with some males showing chases toward over 20 fish (> 75% of the community) during a single 10-min video. Hence power was distributed very unevenly among community members as indicated by high Gini coefficients for chase outstrength (Fig. 3B). This means that dominant males had the most influence over their community. The Gini coefficients for dominant males only was substantially lower than those for the entire community (Wilcoxon signed ranks test: $V=0$, $N=16$, $P<0.00001$), suggesting that power was relatively evenly distributed among dominant males.

Group-level social network metrics are shown in Fig. 4 (for representative chase and display networks, see Fig. 2). Both network density (proportion of actual connections relative to all possible connections) and network diameter (linear size of the network as measured by the shortest path between the most distant nodes) were generally lower for display networks compared to chase networks (Wilcoxon signed ranks test, network density: $V=0$, $N=16$, $P<0.00001$; network diameter: $V=0$, $N=16$, $P<0.00001$). This most likely reflects the fact that display behaviors are mostly performed among a few dominant males and aggressive subordinate males, resulting in smaller, more strongly connected social networks for display behavior compared to chase behavior. Display-based network reciprocity was much higher than chase-based network reciprocity (Wilcoxon signed ranks test: $V=136$, $N=16$, $P<0.00001$, Fig. 4). This is due to display behaviors involving symmetrical interactions between two males. For example, border display typically involves two neighboring dominant males flaring their fins and opercula toward each other in rapid alternating fashion. The high level of reciprocity is also evident when comparing display instrength and outstrength, which had very similar distribution both in terms of shape and magnitude (Fig. 3A). The average Pearson correlation coefficient between adjacent networks was positive (generally > 0.5, see Fig. 4), suggesting that both chase and display networks are consistent across time. A sequence of daily social networks of a representative community is shown in the supplementary figure.

How do changes in rank influence social behavior and connectivity?

Most males remained either dominant or subordinate and did not change their rank for the duration of the experiment (143 out of 192 males). However, each community had at least one male that experienced a shift in status during the 19 days of observation. We observed 49 males that ascended or descended in rank at least once for a combined total of 62 status changes (31 ascents and 31 descents). All ascenders and descenders either claimed or lost their flowerpot, respectively. To examine behavioral changes during social ascent or descent, we focus on males that

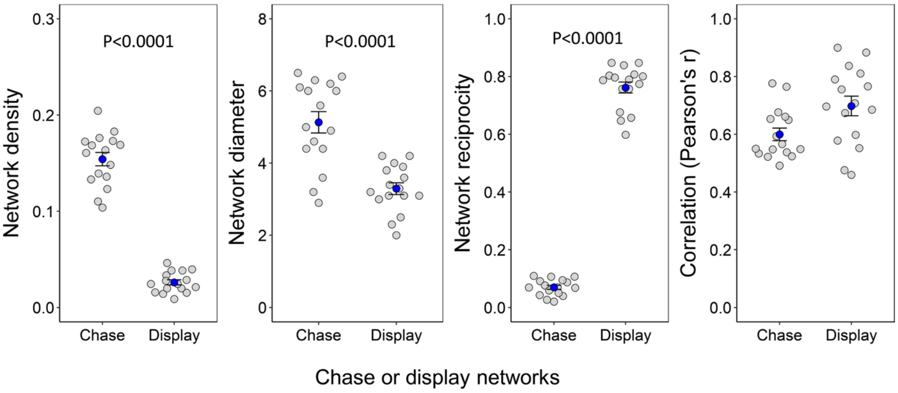


Fig. 4 Community-level social network parameters. Social network measures are the average for all social networks of a given community obtained between days 1 and 16 (i.e., all pre-manipulation social networks, each based on a 10-min video). Shown are the mean ± SE and raw values for all 16 communities across all pre-manipulation videos for social networks based on chases or display behavior

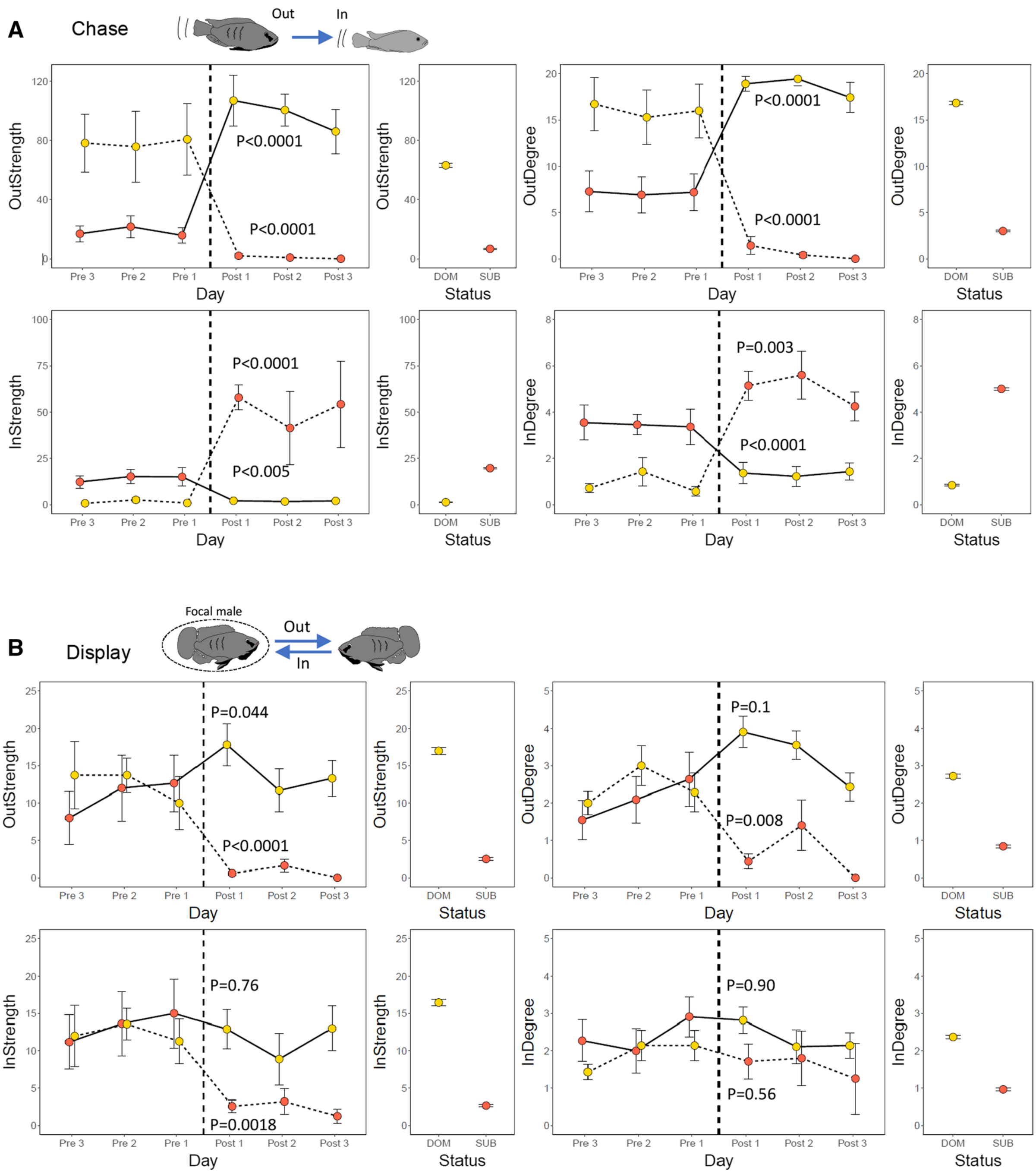
changed ranks during day 13 to 19 because for this timeframe we have daily observations.

Most males in this subset were in a dominant-male removal community: of the 11 ascenders, 10 males were from a dominant-male removal community and of the 7 descenders, 4 males were from a dominant-removal community. As noted above, when we designed the experiment, we expected that removing a dominant male would lead to social ascent, with the ascending male occupying the newly vacated territory (as shown in Fig. 1B, scenario 1). However, the day after the dominant-male removal, the vacated flowerpot was taken over by a previously subordinate male in five instances, while in the remaining four instances, the vacant territory was taken over by an already existing dominant male expanding his territory. The other ascents involved territory takeovers of flowerpots that were not vacated by the dominant-male removal, such as a flowerpot takeover from an already existing dominant male who owned two flowerpots (leading to the dominant male shrinking his territorial space and essentially giving up one flowerpot, Fig. 1B, scenario 2) or rank takeover resulting in social defeat of the territory owner that was evicted by the ascending male (Fig. 1B, scenario 3). We note that these variable cases of ascents may have been indirectly triggered by the male removal, because removing an influential male may lead to changes in space use and the distribution of aggression across the entire community, potentially increasing opportunities for rank changes.

We tested whether the behavior the day after the rank change was significantly different from the behavior just prior to the rank change (Fig. 5). Here, we report P values in the text only (for complete statistical results, see Table 1). We note that findings are qualitatively the same when the analysis was based on the three days before and the three days after the rank transition (Table 1). Social network metrics are shown for three days prior and three days after social ascent or descent for data computed from chases and display networks separately (Fig. 5, for visualization of social networks of a representative community before and after male removal, see supplementary figure). We found that males ascending in rank exhibited a dramatic increase in the number of chases performed, as shown by an abrupt and highly significant increase in chase outstrength ($P < 0.0001$) and outdegree ($P < 0.0001$) on the first day after ascent compared to the day before ascent (Fig. 5). We also expected to see a reduction in the number of chases received after social ascent. Accordingly, chase instrength and indegree exhibited highly significant differences between the day before and after ascent (both Ps < 0.0001, Fig. 5). However, measures of display received were not significantly different the day before and after ascent (display instrength: $P = 0.857$; display indegree: $P = 0.52$, Fig. 5). This suggests that prior to ascent, these males were frequently engaged in territorial disputes (border displays and lateral displays) even before they assumed dominant status. A similar pattern is evident in display behavior performed. Although both display outstrength ($P = 0.007$) and display outdegree ($P = 0.0016$) showed a highly significant increase the day after ascent compared to the day before ascent, they were already elevated the day prior to ascent, with display outstrength and outdegree prior to ascent being almost indistinguishable from those observed in stable dominant males (Fig. 5).

To further understand these patterns, we examined the degree of social dominance prior to ascent. Of the 11 males that ascended, 7 were fully subordinate males that were shoaling with other fish and showed all characteristics of subordinate males, including suppressed coloration and frequent fleeing. However, the remaining 4 males had a dark eye bar (a sign of social dominance) and, while also occasionally shoaling and displaying some subordinate behaviors, were also seen defending a defined space in the aquarium despite not owning a flowerpot. Although we considered these males subordinate in the analysis, these males can also be considered 'intermediate males.' As can be seen in Fig. 6, these four intermediate males showed higher display outstrength prior to ascent. We found that intermediate males were likely to transition to social dominance status: we recorded a total of five intermediate males prior to male removal on day 16: of these males, all except for one ascended to social dominance status. Combined, our data suggest that males that are about to rise in status are more likely to show dominance-like behaviors prior to ascent.

We recorded a total of seven males undergoing social descent between day 14 and day 19. In five cases, we recorded a social ascent that was linked to a social rank takeover, whereby a subordinate male overthrew a dominant male, with the latter undergoing social defeat (Fig. 1B, scenario 3). The remaining



2 social defeats resulted from an already existing dominant male moving or expanding his territory and forcing the original territory owner away (Fig. 1B, scenario 4). The behavioral changes in descending males were less gradual compared to social ascending males, with descended males rapidly assuming phenotypic traits of subordinate males, such as fleeing, shoaling, and drab coloration. Specifically, descended males experienced a sharp decrease in the number of chases being performed and a large increase in the number of chases received, as indicated by a significant decrease in chase outstrength

◂**Fig. 5** Behavioral changes as a function of social status (dominant: yellow, subordinate: red) and social status change (ascent: solid line, $N=11$, descent: dashed line, $N=7$). The behavioral metrics are based on chase (**A**) and display (**B**) networks. Outstrength is the frequency of behavior performed by the focal male (equivalent to sum of behaviors) and outdegree is the number of fish to which that behavior was directed. Instrength is the frequency of behavior received by the focal male and indegree is the number of fish that directed the behavior to the focal male. A chase received was always associated with a fleeing event performed by the focal males, whereas displays directed to the focal male were often followed by the focal male directing a display back. Behavioral metrics for stable dominant and stable subordinate males are also shown (based on all observations prior to male removal). *P* values are indicated comparing the change in behavior between Pre-1 and Post-1 (the day before and after the rank transition, indicated by the dashed line) following the statistical findings reported in Table 1. Shown are the mean ± SE

($P<0.0001$) and outdegree ($P<0.0001$) and a highly significant increase in chase instrength ($P<0.0001$) and indegree ($P<0.0001$) the day after descent compared to the day prior to descent (Fig. 5). Descended males also exhibited a highly significant reduction in both display outstrength ($P<0.0001$) and outdegree ($P<0.0001$, Fig. 5). There was also a highly significant reduction in display instrength ($P<0.0001$) in descending males; however, there was no difference in display indegree between the day before and after descent ($P=0.52$, Fig. 5). Our data suggest that behavioral changes in response to losing dominance status (social descent) are abrupt.

Discussion

In the current study, we examined how behavior and social relationships change in males that undergo rank changes in replicate social hierarchies of *A. burtoni*. Before we discuss these effects, we first describe some general characteristics of the *A. burtoni* social networks that we studied.

Cichlid communities are characterized by high-power inequality, dense chase networks, and display-based networks that connect mostly dominant males

Consistent with previous studies in *A. burtoni* (Maruska & Fernald, 2010; Huffman et al., 2012; Maruska et al., 2013) and other cichlids (Dijkstra et al., 2010; Dey et al., 2013; Almeida et al., 2014), we found that there were rank-dependent differences in aggression, with dominant males performing chases and display behaviors more frequently and toward more community members, as indicated by higher outstrength and outdegree, respectively, compared to subordinate males. Dominant males were rarely the target of chases compared to subordinate males, as indicated by lower chase instrength and indegree in dominant males. The fact that dominant males performed chases frequently while not being the target of chases themselves was also supported by extremely low levels of reciprocity in the chase networks relative to display networks. Dominant males did not only show a high level of display behavior, but other males also targeted display behavior toward them. We observed that display behavior was often shown in symmetrical territorial disputes where both males engaged in display behavior directed to each other during the same bout. Accordingly, there was a high level of reciprocity in the display networks. These data are consistent with the observation that in *A. burtoni* males maintain their dominant position within the community by chasing subordinate males and females and by engaging in symmetrical displays with neighboring territorial males (Desjardins et al., 2012; Piefke et al., 2021). As has been reported for other animal species (Holekamp & Strauss, 2016), individual cichlid males behaved appropriately according to their social rank. While this is not surprising, given that in any animal species with a dominance hierarchy, dominant and subordinates should exhibit behaviors that are typical of their social rank, it does raise a number of interesting questions as to how the dominance hierarchy is maintained in a group setting (see for instance Chase et al., 2002). These types of stable social relationships within a group require a high level of social competence involving the ability to distinguish between males of different ranks, to learn about one's own social rank relative to others, and to recognize which territory belongs to which male (Bond et al., 2003; Grosenick et al., 2007; Weitekamp et al., 2017).

We found that in all 16 communities, social hierarchies consisted of 3–4 dominant males with established territories. The remaining males were subordinate as is typically seen in experimental *A. burtoni* communities (Maruska & Fernald, 2018). Our measure of power inequality, Gini coefficients, indicated that power was centralized to a few territorial males

Table 1 Effect of rank transition on social network metrics

	OutStrength			OutDegree			InStrength			InDegree		
	Estimate	*Z*	*P*	Estimate	*Z*	*P*	Estimate	*Z*	*P*	Estimate	*Z*	*P*
Change in social network metric before and after rank change (1 day prior and after)												
Ascent												
Chase	− 1.95 ± 0.23	− 8.67	**< 0.0001**	− 1.19 ± 0.19	− 6.17	**< 0.0001**	1.69 ± 0.22	7.69	**< 0.0001**	0.89 ± 0.19	4.59	**< 0.0001**
Display	− 0.70 ± 0.26	− 2.7	**0.007**	− 0.51 ± 0.16	− 3.15	**0.0016**	0.042 ± 0.23	0.18	0.857	− 0.017 ± 0.17	− 0.01	0.922
Descent												
Chase	4.05 ± 0.49	8.26	**< 0.0001**	3.21 ± 0.41	7.81	**< 0.0001**	− 2.80 ± 0.37	− 7.51	**< 0.0001**	− 1.72 ± 0.26	− 6.75	**< 0.0001**
Display	2.61 ± 0.43	6.13	**< 0.0001**	1.37 ± 0.35	3.93	**< 0.0001**	1.58 ± 0.28	5.56	**< 0.0001**	0.16 ± 0.25	0.65	0.52
Change in social network metric before and after rank change (3 days prior and after)												
Chase	− 1.94 ± 0.35	− 5.60	**< 0.0001**	− 1.21 ± 0.26	− 4.60	**< 0.0001**	1.98 ± 0.31	6.43	**< 0.0001**	0.90 ± 0.31	2.95	**0.003**
Display	− 0.73 ± 0.36	− 2.01	**0.044**	− 0.39 ± 0.15	− 1.64	0.10	− 0.10 ± 0.33	− 0.31	0.76	0.032 ± 0.25	0.13	0.90
Descent												
Chase	2.91 ± 1.04	2.80	**0.005**	2.37 ± 0.65	3.66	**< 0.0001**	− 4.21 ± 0.41	− 10.24	**< 0.0001**	− 2.20 ± 0.53	− 4.17	**< 0.0001**
Display	2.86 ± 0.51	5.57	**< 0.0001**	1.67 ± 0.63	2.66	**0.008**	1.39 ± 0.44	3.123	**0.0018**	0.22 ± 0.39	0.58	0.56

(Top) Comparing behavior the day prior and the day after the rank transition. (Bottom) Comparing behavior three days prior versus three days after rank transition. Shown is the effect of 'period' (i.e., comparing metrics before versus after the rank transition, mean ± SE) using generalized linear mixed models. Significant effects are shown in bold

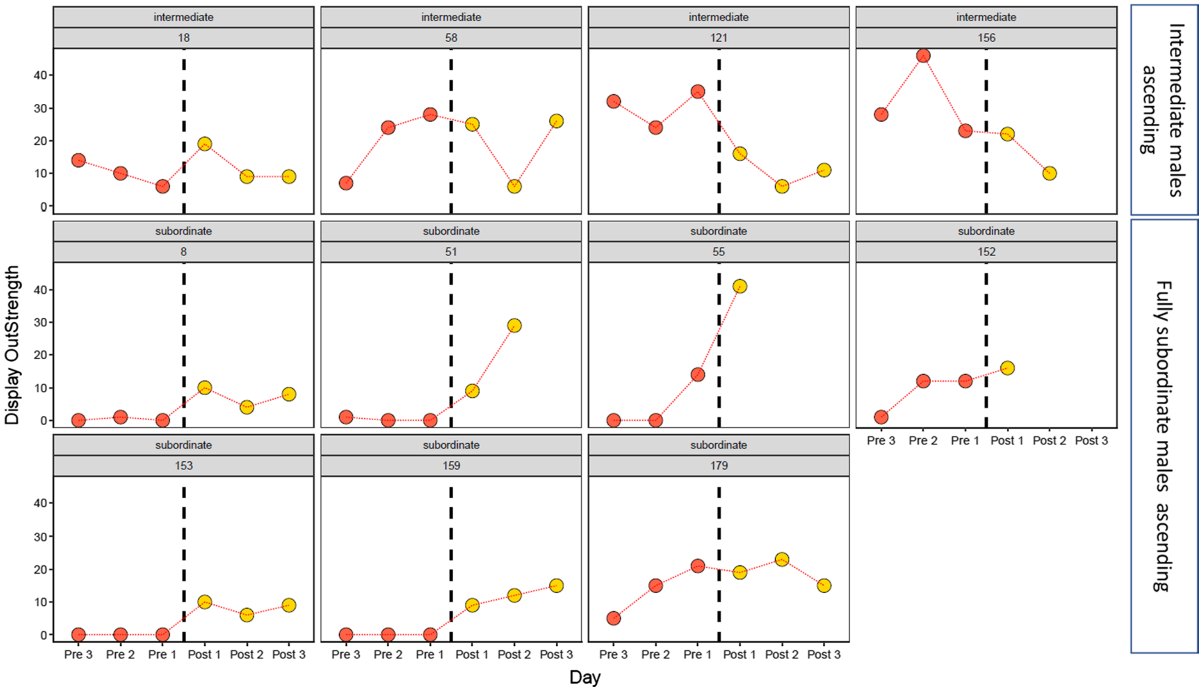


Fig. 6 Behavioral changes in display outstrength in individual males that were intermediate males or completely subordinate males prior to ascent (dominant males: red, subordinate, or intermediate males: blue). Note that in the previous figures, intermediate males were considered subordinate. Display outstrength is the frequency of border and lateral displays performed by the focal male. The numbers indicate unique male IDs

in each community, with only a few males performing most chases (chase outstrength). It is important to note that our cichlid communities differ greatly from more despotic social hierarchies with a single dominant male in a social group. For example, in replicate communities of mice, there was a single *alpha* male, which exhibited the vast majority of wins within a community (Williamson et al., 2016). By contrast, in our study each community contained multiple dominant males who each staked out their own territories. However, despite power being distributed across multiple dominant males, the Gini coefficients for our cichlid communities were considerably higher (corresponding to more inequality) than those reported in the study of Williamson's et al. (2016): in their study the mean Gini coefficient was 0.68, whereas in our study Gini coefficients were around 0.8 and often higher. A previous study reported Gini coefficients ranging from 0.08 to 0.41 in 40 dominance hierarchy datasets, which included data collected in mammals, birds, one insect and one fish species (McDonald & Shizuka, 2012). However, in their study Gini coefficients were calculated based on Elo rating, which can be helpful for dynamic assessment of social rank based on sequential dyadic interactions, but less so for evaluating the distribution of aggression or power in static social networks. Therefore, our Gini coefficients cannot be compared to those reported in McDonald & Shizuka (2012). Nevertheless, the considerable uneven distribution of power most likely reflects the distinct stratification in cichlid societies, with dominant males showing a high frequency of chase behaviors but rarely being chased themselves.

We found that network density was lower for display social networks than chase social networks. The lower level of connectivity in display social networks was mostly because display behaviors were less frequent than chases and performed predominantly by dominant males establishing territorial boundaries. However, as can be seen in Fig. 2, display behaviors were also commonly performed between dominant males and highly ranked subordinate males. Consequently, display social networks mostly connected highly ranked males within social groups. This also resulted in sparser display-based social networks with fewer well-connected fish, as indicated by lower network diameter in display-based social networks relative to chase-based social networks. By contrast, chase networks were much denser because chases occur even among subordinate fish, including females. In addition, dominant males exhibit a high rate of chases toward many subordinate males and females. We conclude that chase and display social networks connect group members in radically different ways relative to (1) how different categories of fish are connected (e.g., dominant to dominant versus dominant to females), (2) the nature of these connections (symmetrical interactions versus win–lose), and (3) the distribution of aggression among group members. Hence, we recommend using these different network types rather than collapsing all behaviors into a single-agonistic social network in future studies.

Rank transitions are associated with changes in behavior and social connectivity

Previous studies have shown that males can gain or lose a territory extremely rapidly and that these changes are accompanied by dramatic changes in behavior (Maruska & Fernald, 2010; Huffman et al., 2012; Maruska et al., 2013; Alward et al., 2019). However, these studies were carried out in more isolated conditions using a single dominant male that was either removed or added to induce social ascent or descent, respectively. Our study shows that males reduce their rate of aggression after descent, consistent with a previous social defeat study in the same species (Maruska et al., 2013). A community setting may be a more ecologically relevant way to study social dominance hierarchies. For example, phenotype-specific contest outcome in dyads may differ from more realistic group settings, as was shown in the cichlid *Pundamilia* where red males socially dominated blue males in dyadic contests but not in a larger group setting (Dijkstra et al., 2005, 2008a, 2010). The need to study social rank in a group setting has also been suggested for studies focusing on the neurophysiological consequences of low social rank in rodents (Tamashiro et al., 2005; Langgartner et al., 2015). In resident-intruder tests, the socially defeated male is solely targeted by the resident male often leading to severe social suppression (for an example in *A. burtoni*, see Alcazar et al., 2016). By contrast, in a larger group setting the descended male becomes part of the shoal where multiple fish are potential targets of aggression. In addition, in a larger group setting, multiple males will attain social dominance and hence dominant males have less time to direct aggression to subordinate males as they are also engaged in time and energy-consuming territorial displays toward neighboring males. Consequently, a descended male receives less territorial aggression in a group setting, which better resembles the situation in the wild.

The notion that social hierarchies should be studied in more complex group settings rather than artificial small groups or dyads also has potential animal welfare implications. In *A. burtoni*, dominant–subordinate relationships are often studied in male dyads housed with several females, whereby the subordinate male receives a disproportionate amount of aggression from the dominant male (Korzan et al., 2008; Alward et al., 2020; Fialkowski et al., 2021). These extreme levels of subordination may in some cases lead to injury (Alcazar et al., 2016; Alward et al., 2020). In some instances, trials where aggression is excessive need to be aborted (Dijkstra, unpublished data), which can lead to unwanted biases in experimental designs (Webster & Rutz, 2020). However, the dyad setup is still widely used for two reasons. First, social status can be reliably assigned in a dyad setting by ensuring a size asymmetry in each pair (the larger male typically assumes social dominance, while the smaller male is forced into the subordinate position). However, assigning social status in a group setting is much harder with for instance larger males not always being able to attain or maintain dominance status due to complex group dynamics and intrinsic factors that influence success in competition, including motivational state, body strength, and body coloration. Secondly, many *A. burtoni* studies rely on suppression of the reproductive axis in subordinate males, with the gonadosomatic index often being significantly lower in subordinate males than in dominant males in a dyad setting (Fialkowski et al., 2021) but not consistently in a group setting (Border et al., 2021).

We found that males ascending in rank experienced a large increase in chase outstrength and outdegree the day after ascent, consistent with previous studies in more isolated conditions in which males rapidly assumed territorial behavior after a dominant-male removal [social opportunity paradigm behavior, which involves subordination of the focal male by a so-called suppressor male for several weeks, followed by removing the suppressor male which allows the focal male to ascend to the dominant position (Maruska & Fernald, 2010; Huffman et al., 2012; Alward et al., 2019; Fialkowski et al., 2021)]. However, to our surprise we found that several days prior to the day of ascent, displays received and performed were elevated in males that subsequently ascended in rank. This suggests that the subordinate males that are most likely to claim a territory initiated more dominant-like behaviors in the days leading up to social ascent. Some of the ascending males were intermediate males prior to ascent, that is, males that do not own a flowerpot but who exhibit territorial behavior by defending space and showing dominance characteristics, such as a high level of chase and display behavior as well as visual markers of social dominance (dark eye bar and brighter nuptial coloration). Interestingly, of the five intermediate males recorded across all communities prior to male removal on day 16, all except for one male ascended to social dominance status by the next day. This suggests that intermediate males are more likely to transition to social dominance status than fully subordinate males. This is consistent with a previous study where intermediate *A. burtoni* males were also more likely to transition than stable subordinate males in unmanipulated communities (Fulmer & Preuss, 2017). In this study, however, the authors did not mention space use of intermediate males but defined them based on behaviors that were distinctly different from stable dominant and subordinate males, with intermediate males showing more conflict behavior and ignoring displays (‘threats’) more frequently than stable dominant males (Fulmer & Preuss, 2017). As mentioned above, the social opportunity paradigm has been used to study experimental social ascent in *A. burtoni* (Maruska & Fernald, 2010; Huffman et al., 2012; Alward et al., 2019; Fialkowski et al., 2021). In these studies, males showed much lower levels of dominance behaviors prior to ascent. However, in the social opportunity paradigm, social ascent was experimentally imposed by removing a single dominant ‘suppressor’ or *alpha* male. By contrast, in the current study, we observed naturally occurring status transitions in a broader hierarchy after experimentally vacating a territory. The fact that intermediate males were more likely to ascend is also supported by other studies in cichlids (Oliveira & Almada, 1996; Alonso et al., 2012) and fish more generally (Rueger et al., 2022). For example, in the neotropical cichlid *Cichlasoma dimerus*, highly ranked individuals were more likely to ascend (Alonso et al., 2012). It is also consistent with studies in other vertebrates, such as birds, where males are queuing (Bruinzeel & Van De Pol, 2004) or form more connections with other males (McDonald, 2007) prior to ascending to dominance status.

Our current study adds to a large body of literature on dominance hierarchies and competition in cichlids (Dijkstra et al., 2008b, 2009; Almeida et al., 2014; Jordan et al., 2016; Fulmer & Preuss, 2017; Ziegelbecker et al., 2018; Vitt et al., 2020; Maguire et al., 2021; Fialkowski et al., 2022; Madge Pimentel et al., 2022). Cichlid dominance hierarchies mostly emerge from social dominance interactions, which enables researchers to isolate the effect of social dominance rank emerging from dominance behaviors without potential confounding factors such as grooming, coalitionary behaviors, or hereditary components of social dominance as is seen in some mammalian species (Snyder-Mackler et al., 2020). This makes cichlids, in our opinion, ideally suited for studying the physiological consequences of social rank and competition in a realistic social setting (Border et al., 2019, 2021). Importantly, the intense territoriality of cichlids allows for direct quantification of agonistic interactions and therefore social networks can be reconstructed based on real interactions as opposed to some indirect indicator of social interaction, such as association time. The quantification of social dynamics in cichlids is also highly efficient: although we computed social networks based on 10-min video recordings, we found that ~ 5-min intervals are sufficient to obtain repeatable estimates of social network metrics in *A. burtoni* communities (Dijkstra, unpublished data). We note that we quantified social interactions by eye, but automatic tracking approaches will most likely facilitate future social network studies in cichlids (Rodriguez-Santiago et al., 2020).

Here, we describe general group-level and individual-level properties of different network metrics in the cichlid *A. burtoni*. We show that power is unequally distributed in each dominance hierarchy, with a relatively small subset of territorial males affirming their social dominance by chasing nondominant fish and showing symmetrical aggressive displays to each other to establish territorial boundaries. These findings are consistent with the pronounced territoriality typically seen in many haplochromines and other cichlid species (Maan et al., 2004; Genner & Turner, 2005; Salzburger, 2009). We found rapid changes in behavior after social rank transitions; however, to our surprise males that attained social dominance already exhibited dominant-like behaviors prior to social ascent (i.e., territory acquisition). We believe our study provides more insight into the overall structure of dominance hierarchies and complex social-specific behaviors, which may form a basis for future studies aimed at understanding social dynamics of social status or rank in complex group settings. This approach can further studies on the link between behavioral dynamics and the physiological causes and consequences of social rank (Sapolsky, 2005; O'Connell & Hofmann, 2012; Border et al., 2021; Ord, 2021). Characterizations of social rank within dominance hierarchies are also key to studying the role of male–male competition in driving diversification in fitness-related traits, such as body coloration and social behavior (Kohda, 1998; Dijkstra & Groothuis, 2011; Pauers et al., 2012; Lehtonen, 2014; Tinghitella et al., 2018).

Acknowledgements We thank members of the Dijkstra lab for providing helpful comments to earlier drafts of the manuscript. Gabi DeOliveira, Shana Border, Tayler Brown, and Hannah Janeski are thanked for help with data collection. We thank Ellisif Cline for help with fish care. Two anonymous reviewers provided helpful comments that improved the manuscript. This work was supported by a Faculty Research and Creative Endeavors research grant from Central Michigan University to P.D.D.

Declarations

Conflict of interest The authors declare no competing interests.

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