Socially dominant, aggressive males are poor influencers of group-consensus in a social fish

Mariana Rodriguez-Santiago[1,2]†, Paul Nührenberg[3,4,]†, James Derry[1], Oliver Deussen[4], Linda K Garrison[1], Sylvia F Garza[1,3,4], Fritz Francisco[3,4], Hans A Hofmann [1,2]*, Alex Jordan[1,3,4] *

Affiliations:

1. Department of Integrative Biology, The University of Texas at Austin
2. Institute for Neuroscience, The University of Texas at Austin
3. Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz
4. Centre for the Advanced Study of Collective Behaviour, University of Konstanz

† Denotes co-first authorship

*Authors for correspondence: hans@utexas.edu; ajordan@ab.mpg.de

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Abstract

In many species, cultures, and contexts, social dominance reflects the ability to exert influence over the behavior of others. Yet the behavioral attributes of those in dominant positions, and the behaviors of actually influential individuals may not be the same, and the behavioral attributes that generate influence in one social context may reduce influence in others. The question of what makes an effective leader is therefore not straightforward, and has many answers depending on the context in which leadership and influence is to be manifested. Most importantly, social *dominance* cannot always be assumed to be equivalent with social *influence.* Here we examine whether socially dominant males in the cichlid fish *Astatotilapia burtoni* are more effective in exerting social influence than socially subordinate males. Using machine-vision based automated tracking of behavior, we find that dominant males in this species display behavioral traits that typify leadership across taxonomic systems – they are aggressive, occupy central social network positions, and lead group movements, whereas subordinate males are passive, socially peripheral, and have little influence over typical group movement. However, in a more complex group-consensus task the influence of dominant males breaks down, and subordinate males become more effective agents of social change. In a more sophisticated group consensus task involving a visual association task, the behavioral attributes that define male dominance – aggression, rapid movement, and increased physical distance to others – interfere with the ability of dominant males to generate group to consensus. Dominant males occupy more spatially distant positions, and had lower signal-to-noise ratio of informative behavior in the association task, while subordinate males are typically is close physical association with their group members, have high signal-to-noise behaviors in the association task, and equal visual connectivity to other group members as dominant males. The attributes that define effective social influence are therefore highly context-specific in this species. These results demonstrate that in this and many other species including humans, behavioral traits that are typical of socially dominant individuals may be the same that reduce their social influence in other contexts.

Introduction

In human and many non-human animal groups, hierarchy is considered a defining feature of social interactions (1–4). Within groups, hierarchical differences can influence access to resources, mating opportunities, and patterns of conflict (5, 6). Dominance is also frequently associated with leadership in either movement or opinion (7–9). Dominance structures can also modify influence in groups, specifically through differences in attention to dominant and subordinate individuals (10). The behavioral attributes that define social dominance may also directly increase social influence, for example confidence and assertiveness in humans (11), so much so that *social dominance* is often considered to be equivalent to *social influence* (for discussion, see 12). Yet dominance may also be associated with aversive behavioral traits, meaning that individuals able to rise to socially dominant positions are the most damaging for group performance. For example, aggression and competitiveness are traits commonly associated with social dominance, yet can potentially lead to the phenomenon of 'toxic leadership' in organizations (13, 14).

Dissociating the factors that interact to mediate *dominance* and *influence* is therefore crucial for understanding how social hierarchy affects group performance and function, but manipulative experiments in humans can be ethically and logistically challenging. In contrast, social animals can provide excellent models for examining dominance and influence since social dominance is correlated with or, a direct result of, higher aggression (15–19). However, it can be challenging to dissociate the effects of dominance status itself from the behavior of the dominant individual. Group movement may be disproportionally influenced by dominant individuals, potentially due to affiliative social bonds (e.g. 9), but influence over movement can similarly be achieved through repulsive interactions, which may be predicted when interacting with aggressive dominant individuals. Thus, the link between the influence of socially dominant individuals and the behaviors of those individuals may be context-specific. While dominance and influence may be associated in competitive scenarios, the same aggressive traits may reduce social influence and be detrimental to group function and cohesion in others contexts (20, 21). The difficulty in separating behavioral elements limits our ability to understand the development, evolution, and expression of behavioral traits and their interactions in social contexts, as well as the adaptive significance of dominance (22, 23) and social influence (6).

Here we examine how consensus responses in a socially-facilitated group association task are influenced by social hierarchy. We explore how the behavioral traits that define social *dominance* in the male cichlid fish *Astatotilapia burtoni* (24) interact with their *influence* in different contexts. *Dominant* males of this species have clear phenotypic signatures of social status; they are territorial, brightly colored, and highly aggressive, while *subordinate* males are non-territorial, non-aggressive, and cryptically colored. Additionally, the presence of these distinct male types can differently influence the behavior of other group members (25). Depending on social context, males can switch between these phenotypes in as little as 20 minutes when the opportunity for social ascension arises (26, 27). Dominant males also have higher centrality than subordinates in behavioral social networks (28), frequently exchanging aggressive displays with other males, attacking and chasing, and courting females. Using this species, we allow dominant and subordinate males to learn a group association task, then place these individuals into new groups of naïve individuals. We ask how the social status of the informed individual affects the time taken for the naïve group to reach consensus and move as a cohesive group to the correct conditioned stimulus. We hypothesize that socially dominant informants with higher network connectivity will have stronger influence on group level behavior if information flows along behavioral interaction edges. Alternatively, the behavioral traits of *dominant* males may prove an aversive source of social information and make those males ineffective agents of social *influence*.

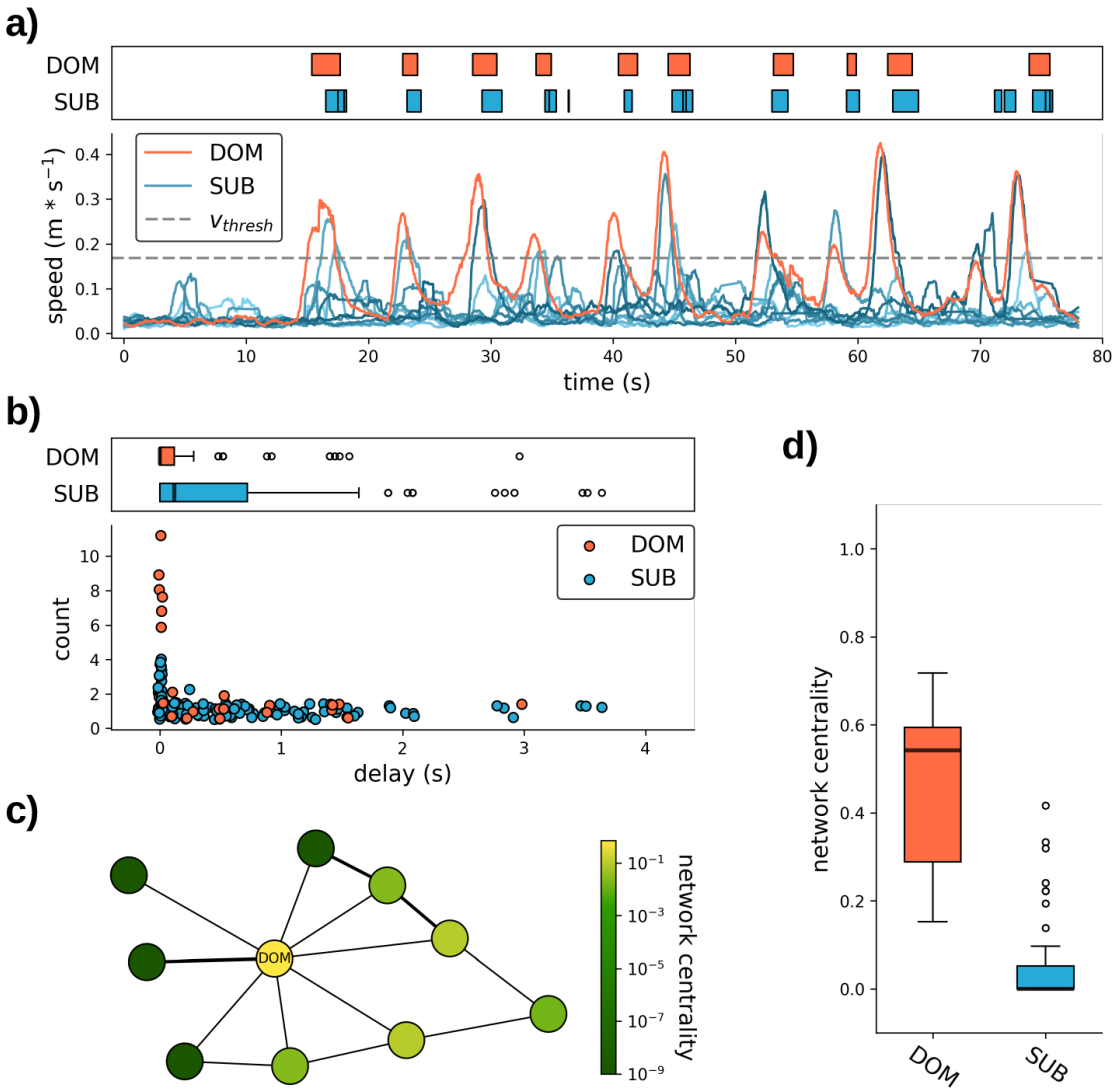

Figure 1. a) Representative examples of speed traces of dominant (DOM) and subordinate (SUB) males. Upper panel represents onset and duration of speed events that exceed a Q_{95} threshold of all speeds ('v_{thresh}'). **b)** Onset of speed events across all dominant and subordinate male event initiations (delay = 0) and responses (delay > 0), with upper panel demonstrating a temporal offset in which dominant males more often initiate rapid movements (Wilcoxon signed-rank test, $p < 0.001$). **c)** Example of a social network graph created from directed, pairwise initiator/responder counts (graph directedness omitted for visualization). Node color denotes network (betweenness) centrality of dominant and subordinate group members. **d)** Aggregation of all individuals from the standard condition recordings showing the effect of social status on network centrality ($p < 0.01$).

Results

Phenotypically dominant males are more central in social networks and lead group movements

We first examined whether dominant males occupy more central social network positions (Figure 1c), which was indeed the case (Bonferroni corrected α-level = 0.01 Wilcoxon signed-rank tests; *dominant vs subordinate centrality* $p < 0.01$; Figure 1d). When we analyzed the onset and duration of speed events that dominant and subordinate males either initiated or responded to (Figure 1a), we found that dominant males were also more effective initiators of group movements than subordinate males (Bonferroni corrected α-level = 0.01 Wilcoxon signed-rank tests; *dominant vs subordinate motion delay* $p < 0.001$; Figure 1b).

Groups with subordinate informants reached consensus faster than those with dominant informants

We then asked whether inclusion of an informed individual in otherwise naïve groups increased speed to reach group consensus. Groups containing dominant male informants did not reach consensus faster than naïve groups (Bonferroni corrected α-level = 0.17; *dominant informant* vs. *naïve* $p = 0.288$; Figure 2), whereas groups containing a subordinate male informant achieved consensus significantly faster than both naïve and dominant male informant groups (*subordinate informant* vs. *naïve* $p < 0.001$; *subordinate informant* vs. *dominant informant* $p = 0.015$; Figure 2).

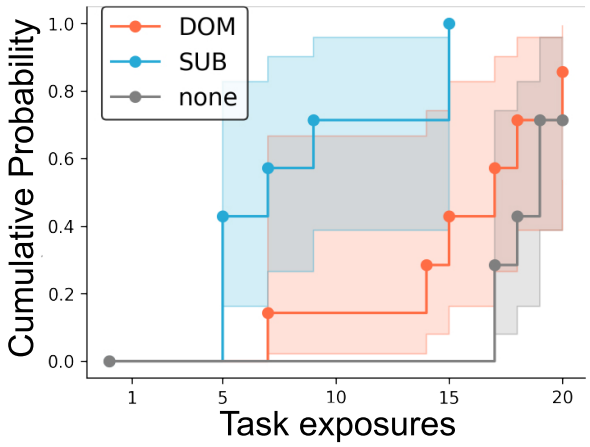

Figure 2. The cumulative probability of group consensus response in an association task over the course of 20 exposures. Groups with a *subordinate* (SUB) male informant had a higher probability of response than those with a *dominant* (DOM) male informant or those without an informant (none).

Dominant males had greater spatial separation and lower behavioral signal-to-noise ratio

Finally, we determined whether dominant and subordinate individuals differed in their visual connectivity or mean distance to other group members (Figure 3a). We found that dominant males were more distant from other group members than were subordinate males (Bonferroni corrected α-level = 0.01; *dominant vs subordinate mean pairwise distance* $p < 0.01$; Figure 3c), but there was no difference in the visual connectivity to other group members between dominants and subordinates (*dominant vs subordinate mean angular area subtended on retina* $p = 0.149$; Figure 3b). Also, dominant males were significantly more likely than subordinate males to swim as fast or faster than the average speed of informed individuals moving towards the unconditioned stimulus during the association task (*dominant vs subordinate speed threshold event ratio* $p < 0.001$; Figure 3d). Last, we used principal component analysis (PCA) to examine the trajectory and network analyses with the phenotypic indicators of dominance. Dominant and subordinate individuals clearly separate along PC1, demonstrating that the metrics we derived from the data are consistent (Figure 3e).

Discussion

In many species, cultures, and contexts, social dominance reflects the ability to control the behavior of group partners (16). Yet social influence is not unidimensional; it can be achieved in numerous ways, and the behavioral attributes that typify influence in one context may be the same that reduce influence in another. The question of what makes an effective leader is therefore not straightforward, and has different answers depending on the context in which leadership and influence are manifested.

Here we demonstrate that dominant male cichlid fish display behavioral traits frequently associated with leadership and increased social influence in many animal species including humans; such as higher aggression, social network centrality, and leadership in group movement (12). Yet groups that contained dominant males as sources of information were slower to reach consensus in an association task. Rather, subordinate males, who occupy peripheral social network positions and have little influence over group movements, are the most effective in generating group consensus. The links between social *dominance* and social *influence* are therefore not straightforward and are highly context-specific.

The attributes that differentiated dominant and subordinate males, and likely their efficacy as agents of social influence, were social, spatial, and temporal. Dominant males occupied more central positions in interaction networks – a common trait of dominant individuals across species (9). This effect was driven by aggressive interactions of dominant males with other group members, whom they frequently chased and attacked. Group members continually fled from dominant males, and such aggressive behavior was rarely displayed by subordinate males. Consequently, dominant males had greater spatial separation from the rest of the group as they both chased away and were avoided by other group members, whereas subordinate males had higher spatial proximity to other group members (Figure 3c). This spatial and visual separation likely led to lower opportunity for processes like physical leadership, spatial enhancement of stimuli, or observational learning. These differences may ultimately contribute to the slower time to group-consensus in groups with a dominant male informant. In contrast, the visual connectivity among naïve and informed individuals, although correlated to their spatial proximity, was not different for dominant and subordinate informants (Figure 3b). This suggests that visual access to social cues was similar for both subordinate and dominant males, potentially increasing the influence of dominant individuals (10). That dominant males had lower group influence, despite similar opportunity for visual attention, suggests that the social cues from aggressive dominant males may have a negative valence compared to cues from passive subordinate males.

Dominant individuals were also less reliable sources of social information due to their frequent, aggressive chasing of other group members. In the association task, informed individuals swam quickly and directly towards the 'correct' feeder, inducing following behavior in other group members. Such a rapid change in speed is also known to be an important social cue influencing collective behavior in zebrafish (29). However, this mode of swimming – rapid and straight – was a rare behavior for subordinate males, who typically moved at slow speeds, stayed with the group, and moved without abrupt changes in speed. In contrast, dominant males frequently made rapid accelerations around the arena as they chased other individuals, which subsequently induced accelerated flight responses in subordinates. Thus, the frequent rapid movements of dominant males likely masked the informative social cues of a rapid swim towards the correct stimulus in the association task. Dominant males have a lower signal-to-noise ratio of informative motion cues, likely contributing to their poor influence over group-consensus.

Overall, dominant males were behaviorally, spatially, and socially differentiable from subordinate males, consistent with many previous studies on this system (Figure 3e). These behavioral differences facilitated, and in fact defined, their dominant position and influence over normal group behavior, but these same behaviors lowered their influence in a more sophisticated group task. This finding demonstrates that the attributes that define effective leaders may be highly context-specific, and traits

commonly observed in socially dominant individuals may be the very traits that make them poor effectors of social change in other contexts. Thus, a passive process of leadership ascension, in which the most aggressive individuals rise to positions of influence, may be counter-productive in contexts where group consensus is prioritized.

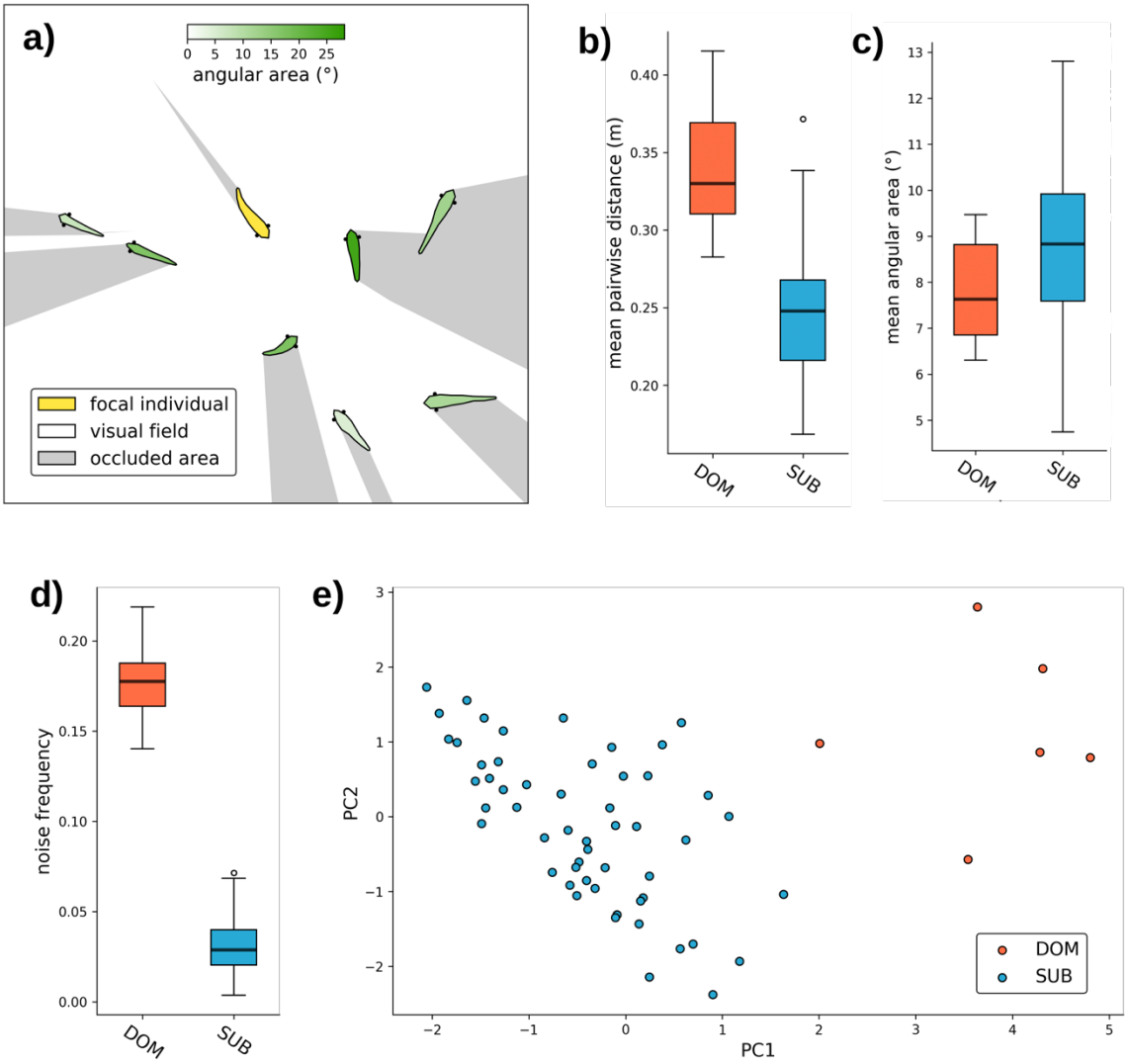

Figure 3. a) Schematic of visual field computation. **b)** and **c)** Aggregated data from all standard condition recordings, comparing mean pairwise distance ('association' connectivity) and mean angular area (visual connectivity) between *dominant* (DOM) and *subordinate* (SUB) males with other group members (Wilcoxon signed-rank tests, $p < 0.01$ and $p = 0.149$). **d)** Hypothetical signal-to-noise ratio in social learning context (rapid, directed swimming) compared by social status ($p < 0.001$). **e)** PCA on all metrics derived from trajectory and network analyses, comparing dominant and subordinate males in this social parameter space.

Materials and Methods

Captive *Astatotilapia burtoni* descended from a wild caught stock population (30) were maintained in stable communities until transfer to the experimental paradigm. Groups consisted of both males and females, though only males were used as informants since these have clear phenotypic indicators of social dominance, whereas females, although likely having social dominance hierarchies, have no reliable visual indicators of dominance status. All work was conducted in compliance with the Institutional Animal Care and Use Committee at The University of Texas at Austin.

Behavioral paradigm

The behavioral task measured the time taken to reach group-consensus in a simple association task using a food reward and colored light-emitting diodes. Experiments were conducted in large, oval PVC tubs (205 liters, 108 x 54.6 x 42.7 cm) with two automatic fish feeders (EHEIM) mounted on opposite ends of each tank. The motor control pins of the feeders were rewired and externally controlled by a digital I/O switch slaved to an Arduino Uno microcontroller that also controlled one diffuse RGB LED mounted directly under each feeder (code available in supplementary material). Four times a day (0830, 1130, 1430, 1730) for five consecutive days, the Arduino randomly selected which fish feeder's tumbler would turn, the LEDs simultaneously displayed one of two colors (RGB 255,60,0 [orange] or 0,255,255 [cyan]) for three seconds, followed by three seconds of no stimulus; then the tumbler of the feeder that displayed the orange stimulus would turn, spilling out a provision of Tetramin flake food. Neither of these color stimuli elicits an innate response in the focal animals (due for example to inherent color preferences; , 31), allowing their use as conditioned stimuli in an association learning paradigm. However, the color of the rewarded stimulus affected the speed at which the association was achieved, and we therefore kept the rewarded stimulus color consistent throughout all trials and randomized the location of colors to prevent spatial learning. A networked Logitech HD 1080p webcam was mounted above each tank and automatically scheduled to record for one minute before and after each training event using iSpy open source security camera software.

Group-consensus task

Using the protocol described above, groups of eight *A.* burtoni (4 males, 4 females) underwent the training four times a day for five days. Group behavioral response to the task during all trials was scored as the proportion of individuals in the group that responded to the light stimulus by swimming towards it before the delivery of food. A successful group response was defined as seven or more of the eight group members swimming directly toward the positive stimulus in less than one second of stimulus onset, in two or more consecutive trials.

Within the five-day training period, all groups showed a behavioral shift from initial fear of the light stimulus and lack of coordinated movement, through to a consensus movement toward the conditioned stimulus. After five days, all naïve groups reached consensus movement towards that correct cue, and subsequently one dominant male ("*dominant*") and one subordinate male ("*subordinate*") were placed into new groups (3 males, 4 females; total group size 8 individuals) that were naïve to the association task. For groups with *dominant* males, all three other males were smaller than the *dominant*, while for groups with *subordinate* males, at least one male was larger than the *subordinate*. We did not observe any dominance shifts (i.e. a *dominant* becoming a *subordinate* in a new group, or vice-versa) in these group transitions. Seven groups each with either a *dominant or subordinate* informant were then placed in identical training protocols as previously and the time taken to group-consensus measured. In total, 168 fish were used.

Deep-learning based automated tracking and analysis of behavior

We trained an implementation of a Mask and Region based Convolution Neural Network (Mask R-CNN) on a subset of manually labeled images to accurately detect and segment individual fish in the videos, resulting in pixel masks for each video frame and individual respectively (32, 33). The masks were then skeletonized using morphological image transformations, allowing to estimate fish spine poses as seven equidistantly spaced points along the midline of each mask's long axis. The first and second spine points represent head position and orientation, and were used to automatically

reconstruct continuous fish trajectories using a simple, distance-based identity assignment approach. Accuracy and high detection frequency were visually verified with a Python-based GUI developed within the lab, that was also used to manually correct false identity assignments and losses (32).

Behavioral, visual, and spatial connectivity analysis

In order to examine baseline differences in the behavior of *dominant* and *subordinate* males in social contexts, we placed seven additional groups of 10 individuals in identical tanks as described above and filmed their behavior in the absence of external stimuli. We calculated the behavioral, visual, and spatial interactions between all fish of each group. To estimate the number of behavioral interactions that dominant and subordinate males had with other group members, trajectory data was used to determine events with elevated swimming speed ($>Q_{95}$ of the speed distribution). The first two individuals passing this threshold in such events were treated as event initiator and responder, and a delay time between the two individuals was calculated (Figure 1a,b). We created behavioral interaction networks using the event count as the weights of the directed edges between network nodes (initiator to responder), that allowed the calculation of betweenness centrality as a measure of behavioral influence in standard conditions (Figure 2). Additionally, the ratio of the sum of event durations to the duration of the recording was calculated for each fish, constituting the individuals' hypothetical noise frequency in the social training context (fast, directed movement in absence of LED stimulus). Spatial connectivity between group members was calculated as their mean pairwise distances. Finally, we computed the visual connectivity as the mean angular area subtended by each individual on the retinas of all other group members using a ray-casting approach with the contours of the Mask R-CNN detection results as occluding objects (Figure 3a). Casting rays from both eyes of a focal fish towards to these contours (including the focal individual), we modelled the nearly complete field of view known from other freshwater fishes (34). These measures generated three connectivity scores for each dominant and subordinate group member: a behavioral ('interaction') connectivity, spatial ('association') connectivity, and visual connectivity. Finally, we conducted a principal component analysis (PCA) on the speed threshold event ratio (noise frequency) and connectivity scores to assess the overall consistency of metrics derived from trajectory and network analyses with the phenotypic indicators of dominance (Figure 3e).

Data analysis and statistics

For time-to-consensus movement analysis, we conducted a Kaplan-Meier Survival Analysis (35), using the first of two consecutive trials in which seven or more individuals responded to the stimulus onset as time to criterion and right-censoring groups that did not complete the social learning task. We used log-rank tests to compare the survival estimates of naïve groups to informed groups, and to compare naïve and informed groups split by social status of the informed individual (Bonferroni-corrected for n = 3 comparisons). For comparisons of the baseline behaviors of dominant and subordinate fish, we performed multiple Wilcoxon signed-rank tests with the social status of group members as predictor and network centrality, mean angular area, mean pairwise distance, speed threshold event ratio and delay times as response variables. Here, a Bonferroni correction for n = 5 comparisons was applied.

Author Contributions
AJ, JD, and HAH designed experiments; AJ and JD wrote code for automated data acquisition; AJ, MRS, LKG and SFG performed experiments; PN performed machine-vision tracking; AJ and SFG performed image-based tracking; PN, AJ, LKG, FF, and MRS performed statistical analysis; AJ, PN, and MRS wrote the manuscript; AJ, HAH, and OD revised manuscript.

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References

1. W. C. Allee, The social life of animals. (1938).

2. J. C. Magee, A. D. Galinsky, 8 social hierarchy: The self-reinforcing nature of power and status. *Academy of Management annals* **2**, 351–398 (2008).

3. A. Mazur, A biosocial model of status in face-to-face primate groups. *Social Forces* **64**, 377–402 (1985).

4. G. P. Murdock, Social structure. (1949).

5. R. F. Bales, F. L. Strodtbeck, T. M. Mills, M. E. Roseborough, Channels of communication in small groups. *American Sociological Review* **16**, 461–468 (1951).

6. J. Berger, S. J. Rosenholtz, M. Zelditch Jr, Status organizing processes. *Annual review of sociology* **6**, 479–508 (1980).

7. R. W. Byrne, How monkeys find their way: leadership, coordination, and cognitive maps of African baboons. *On the move. How and why animals travel in groups*, 491–518 (2000).

8. E. W. De Kwaadsteniet, E. Van Dijk, Social status as a cue for tacit coordination. *Journal of Experimental Social Psychology* **46**, 515–524 (2010).

9. A. J. King, C. M. Douglas, E. Huchard, N. J. Isaac, G. Cowlishaw, Dominance and affiliation mediate despotism in a social primate. *Current Biology* **18**, 1833–1838 (2008).

10. M. CHANCE, *The Social structure of attention*, M. R. A. Chance, R. R. Larsen, Eds. (Wiley, 1976).

11. C. Anderson, G. J. Kilduff, Why do dominant personalities attain influence in face-to-face groups? The competence-signaling effects of trait dominance. *Journal of personality and social psychology* **96**, 491 (2009).

12. T. E. Rowell, The concept of social dominance. *Behavioral biology* **11**, 131–154 (1974).

13. K. Matos, O. O'Neill, X. Lei, Toxic leadership and the masculinity contest culture: How "win or die" cultures breed abusive leadership. *Journal of Social Issues* **74**, 500–528 (2018).

14. G. E. Reed, Toxic leadership. *Military review* **84**, 67–71 (2004).

15. M. S. Di Bitetti, C. H. Janson, Social foraging and the finder's share in capuchin monkeys, Cebus apella. *Animal Behaviour* **62**, 47–56 (2001).

16. C. Drews, The concept and definition of dominance in animal behaviour. *Behaviour* **125**, 283–313 (1993).

17. R. E. Flynn, L.-A. Giraldeau, Producer–scrounger games in a spatially explicit world: tactic use influences flock geometry of spice finches. *Ethology* **107**, 249–257 (2001).

18. C. Janson, Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology* **18**, 125–138 (1985).

19. J. Krause, R. James, D. W. Franks, D. P. Croft, *Animal social networks* (Oxford University Press, USA, 2015).

20. S. B. Hrdy, Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* **1**, 13–40 (1979).

21. T. M. Glomb, H. Liao, Interpersonal aggression in work groups: Social influence, reciprocal, and individual effects. *Academy of Management journal* **46**, 486–496 (2003).

22. N. A. Chagnon, Life histories, blood revenge, and warfare in a tribal population. *Science* **239**, 985–992 (1988).

23. C. Von Rueden, M. Gurven, H. Kaplan, Why do men seek status? Fitness payoffs to dominance and prestige. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2223–2232 (2010).

24. K. P. Maruska, R. D. Fernald, Astatotilapia burtoni: a model system for analyzing the neurobiology of behavior. *ACS chemical neuroscience* **9**, 1951–1962 (2018).

25. J. K. Desjardins, H. A. Hofmann, R. D. Fernald, Social Context Influences Aggressive and Courtship Behavior in a Cichlid Fish. *PLoS ONE* **7**, e32781 (2012).

26. H. A. Hofmann, Gonadotropin-releasing hormone signaling in behavioral plasticity. *Current Opinion in Neurobiology* **16**, 343–350 (2006).

27. K. P. Maruska, R. D. Fernald, Behavioral and physiological plasticity: rapid changes during social ascent in an African cichlid fish. *Hormones and Behavior* **58**, 230–240 (2010).

28. S. M. Maguire, D. Peter, A. L. Jordan, H. A. Hofmann, Social network dynamics predict hormone levels and behavior in a highly social cichlid fish. *In review*.

29. B. Lemasson, *et al.*, Motion cues tune social influence in shoaling fish. *Scientific Reports* **8** (2018).

30. R. D. Fernald, N. R. Hirata, Field study of Haplochromis burtoni: Quantitative behavioural observations. *Animal Behaviour* **25**, 964–975 (1977).

31. B. Egger, Y. Klaefiger, A. Theis, W. Salzburger, A sensory bias has triggered the evolution of egg-spots in cichlid fishes. *PLoS one* **6**, e25601 (2011).

32. F. A. Francisco, P. Nührenberg, A. L. Jordan, A low-cost, open-source framework for tracking and behavioural analysis of animals in aquatic ecosystems. *bioRxiv*, 571232 (2019).

33. K. He, G. Gkioxari, P. Dollár, R. Girshick, Mask r-cnn in *Proceedings of the IEEE International Conference on Computer Vision*, (2017), pp. 2961–2969.

34. D. Pita, B. A. Moore, L. P. Tyrrell, E. Fernández-Juricic, Vision in two cyprinid fish: implications for collective behavior. *PeerJ* **3**, e1113 (2015).

35. E. L. Kaplan, P. Meier, Nonparametric estimation from incomplete observations. *Journal of the American statistical association* **53**, 457–481 (1958).