BRILL

Behaviour (2024) DOI:10.1163/1568539X-bja10271

Behaviour
brill.com/beh

Social fish use different submission signals depending on spatial position

Adam R. Reddon [a,*], **Christian Richardson** [a], **Amy Jose** [a],
Joachim G. Frommen [b] **and William T. Swaney** [a]
[a] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK
[b] Department of Natural Sciences, Manchester Metropolitan University, Manchester UK
[*]Corresponding author's e-mail address: a.r.reddon@ljmu.ac.uk
ORCID iDs: Reddon: 0000-0002-3193-0388; Frommen: 0000-0002-1752-6944;
Swaney: 0000-0002-5065-119X

Received 20 April 2024; initial decision 8 June 2024; revised 11 June 2024;
accepted 14 June 2024; published online 28 June 2024

Abstract

Animals often possess multiple distinct threat signals which indicate their level of aggressive motivation or resource holding potential. In contrast, the diversity of submission signals is considerably lower. Still, some social species exhibit multiple distinct submission signals which could have different strategic functions or serve to enhance signal transmission. In the current study, we examine submission signalling in the daffodil cichlid (*Neolamprologus pulcher*), a cooperatively breeding fish which produces two distinct submission signals: a tail quiver, and a head-up posture. Observing interactions within stable social groups revealed that submission signal selection depends on the location of the interaction, with tail quivers being preferentially displayed near the substrate, and head-up postures being deployed when the interaction takes place further away from the substrate. Our findings suggest that variation in submission signalling in daffodil cichlids may serve to enhance signal transmission across spatial contexts rather than to convey distinct information.

Keywords

agonism, communication, *Neolamprologus pulcher*, signalling, submissive.

1. Introduction

Agonistic signalling is an essential component of the communicative repertoire of social animals (Arnott & Elwood, 2009; Frommen, 2019; Reddon

Published with license by Koninklijke Brill BV | DOI: 10.1163/1568539X-bja10271
| ISSN: 0005-7959 (print) 1568-539X (online)

et al., 2022). Animals avoid the costs of escalated conflict by signalling their aggressive motivation through threat and submission signals (Maynard Smith & Harper, 2003). Many species produce several threat signals which might indicate increasing motivation to escalate a conflict (Hurd & Enquist, 2001) or serve in redundancy to ensure signal transmission (Partan & Marler, 1999). Submission signals by contrast are typically less diverse, with many species producing only one signal (Bradbury & Vehrencamp, 2011). There may be little benefit to signals that convey variation in submissive motivation because dominant animals are unlikely to accept a signal of partial submission from a subordinate (Matsumura & Hayden, 2006; Reddon et al., 2022). Nevertheless, there exists both continuous and categorical variation in submission signalling across the animal kingdom (e.g., Schenkel, 1967; Pereira & Kappeler, 1997; Van Dyk & Evans, 2008).

Rather than indicating different levels of submissive motivation, variation in submission signalling may serve to enhance signal transmission across different environmental contexts. Signal diversity can partly be explained by selection to maximise signal effectiveness across contexts (Schaefer & Ruxton, 2015). For example, little blue penguins (*Eudyptula minor*) have four distinct submission signals, which are used differentially depending on the distance to the receiver and the environment in which the interaction occurs (Waas, 1990). Salmonid fishes darken their body and eyes to signal submission (O'Connor et al., 1999), and the magnitude of this darkening is increased in turbid water conditions where the change may be more difficult to perceive (Eaton & Sloman, 2011). They, hence, use the same signal but vary the intensity to facilitate signal transmission depending on the environment.

Compared to aggressive signalling, studies on variation in submission signalling are rare (Reddon et al., 2022). Cooperatively breeding lamprologine cichlids are a promising model system to elucidate the significance of variation in submission signalling. For many lamprologine cichlids 'tail quivering' is used as a submission signal, which terminates agonistic encounters (e.g., Taborsky, 1985; Heg & Bachar, 2006; Saeki et al., 2022; Satoh et al., 2022; Manara et al., 2023). Additionally, fishes in this taxon often show further submission signals during within species interactions, which typically are species-specific. For example, *Neolamprologus meeli* shows a behaviour termed 'down-swim', where the submissive individual quickly dashes back and forth under the dominant fish (Saeki et al., 2022), while in *Julidochromis* *ornatus*, subordinates perform submissive zig-zag movements in proximity to the dominant (Heg and Bachar, 2006). Other species perform submissive head-up postures which may display their underside to the opponent (Hick et al., 2014; Bose et al., 2021). The reason for such variation in submission signals remains elusive. We aim to contribute to filling this knowledge gap using cooperatively breeding daffodil cichlids (*Neolamprologus pulcher*) as a study species. These fish are endemic to Lake Tanganyika (Konings, 1998) where they form long lasting social groups that defend joint territories over extended periods (Balshine-Earn et al., 1998; Jungwirth et al., 2023). Groups consist of 3-20 adult and subadult members (Groenewoud et al., 2016) organised into linear dominance hierarchies based on body size (Dey et al., 2013). The largest male–female pair is socially dominant and generally monopolises reproduction within the group (Hellmann et al., 2015). Agonistic interactions are frequent within groups with more dominant group members showing aggression to less dominant members, and subordinates responding with submission signals (Fischer et al., 2014; Reddon et al., 2019).

Daffodil cichlids produce two distinct submission signals: a ‘tail quiver’ in which the signalling fish rapidly oscillates their tail back and forth (see Video 1 at https://stream.cadmore.media/player/7fdf7dfd-0402-465b-b928-fce840652387), sometimes accompanied by a tilting of the body to one side, and a ‘head-up’ posture (Manara et al., 2023) in which the signalling fish tilts their body upward in the water column exposing their ventral surface to the receiver (see Video 2 at https://stream.cadmore.media/player/46fba2ba-ec81-439d-8535-917703b860b4). These signals can be used separately or in conjunction and may be repeated in response to a single act of aggression received. In response to threat displays (aggressive signals that do not involve physical contact with the receiver), subordinate daffodil cichlids are more likely to produce a tail quiver than a head-up posture, whereas both signals are used about equally in response to more overt forms of aggression such as biting or chasing (Manara et al., 2023). While this suggests possible strategic deployment of these two signals depending on the social context of the interaction, wider evidence for these two signals conveying distinct information is scarce. An alternative explanation is that the spatial context of the agonistic interaction affects submission signal choice in these fish. Informal observations in the laboratory and the field indicate that the tail quiver display often takes place near the substrate where it can stir up loose sand into the water which could make this signal more conspicuous and/or disrupt the attacker (ARR, JGF; pers. obs.). On the other hand, the head-up posture is more three-dimensional in its form, involving a vertical body pitch compared to the tail quiver which is predominantly lateral in its movement. As a result, the head-up posture may be more conspicuous in open water.

We examined the use of tail quiver displays and head-up postures in subordinate daffodil cichlids responding to dominant aggression in laboratory housed groups. Using a within-subjects design, we compared the frequency of each signal near the substrate versus further away. We predicted that focal subordinate fish would produce more tail quiver displays when near to the substrate and more head-up postures when further away.

2. Methods

We examined 12 social groups of daffodil cichlids (*Neolamprologus pulcher*) under laboratory conditions at Liverpool John Moores University. Each social group consisted of between 4 and 6 adult or subadult individuals of mixed sex and unknown relatedness. Each group was housed in a 90-litre (53 × 43 × 38 cm) glass aquarium furnished with 4 terracotta caves, a foam filter, a heater, and a thermometer. The bottom was covered with a 1–2 cm layer of fine coral sand. The aquaria were maintained at 27 ± 1°C and fish were fed daily on dried prepared cichlid flake food (Tropical Tanganyika). Groups were first established by adding subordinate-sized fish, haphazardly selected from our stock aquaria, into the group housing aquaria, before introducing a larger female and a larger male as dominant breeders 24 hours later (Ruberto et al., 2024). Groups had been established for at least one month prior to the start of the study and did not show any continuous harassment of single individuals that might have led to persistent escape behaviours limited by the tank walls.

Each group was video recorded 4 times for 20 min each, using a Sony AX700 video camera at 4k/60fps. Recordings were conducted on 4 separate days spread across 2 weeks resulting in 80 min of video footage for each group. Thirty minutes prior to video recording, the heater, filter, and thermometer were removed from the aquaria, leaving only the 4 terracotta caves and the sand substrate (Figure 1).

For each group, the focal individual was the largest subordinate (third largest fish overall, mean ± SEM standard length = 44.75 ± 2.73 mm; indeterminate sex). We chose this fish as the focal individual for ease of identification and for consistency with previous work in this species (Ruberto et

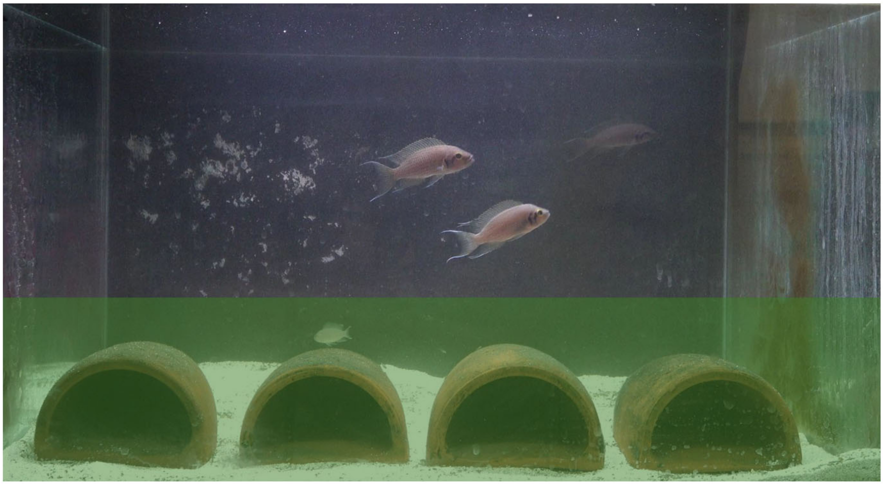

Figure 1. Screenshot from one of the video recordings. Interactions were scored as taking place near the substrate (close) if they were initiated within one focal fish length from the sand or the outer surface of the caves, as illustrated approximately by the zone shaded in green, or as taking place higher in the water column (far) if they occurred more than one body length away (i.e., above the green shaded area). The green shading is for illustration purposes, and it was not present during video recording or scoring.

al., 2020, 2024; Manara et al., 2023; Hirons-Major et al., 2024). An observer blind to the study hypotheses (CR) recorded all instances of aggression (chasing, ramming/biting, and threat displays; see Manara et al. (2023) for an ethogram) directed by either member of the dominant male-female pair towards this focal subordinate, and the number of head-up postures and/or tail quivers the focal subordinate produced in response to each aggression across the 80 min of observation. We recorded whether the interaction took place within approximately one body length including the caudal fin (total length) of the subordinate fish from the sand or external surfaces of the caves (‘close’) or higher up in the water column (‘far’; Figure 1) as judged by the observer.

We used paired samples t-tests to compare the number of (1) tail quiver displays and (2) head-up postures that each focal subordinate performed per aggression received from dominant fish, comparing whether displays occurred close to or far from the substrate. Analysis was conducted with SPSS (v 29.0) and Figure 2 was made using R (v 3.6.2).

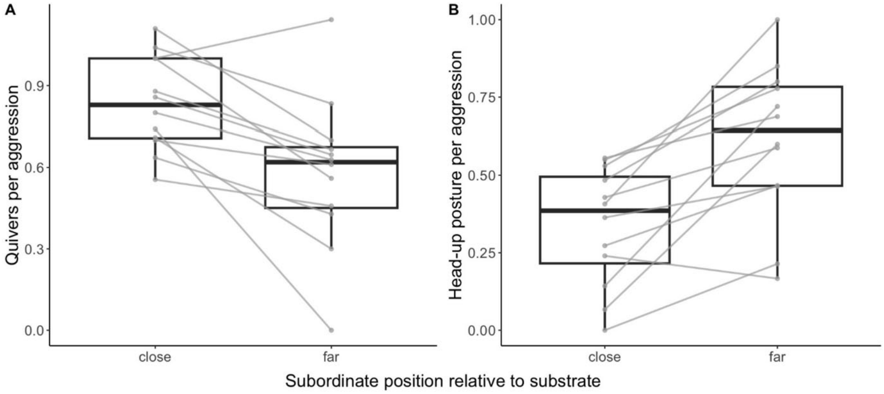

Figure 2. The number of (A) tail quivers or (B) head-up postures shown by focal subordinates per aggression received from the dominant breeding pair, depending on whether the interaction took place close to or far from the substrate. Focal subordinates showed significantly more tail quivers close to the substrate and significantly more head-up postures far from the substrate. The bold lines indicate median value and the boxes indicate the interquartile range. The grey dots represent individual datapoints, and the grey lines connect the responses of each individual fish across the two conditions.

2.1. *Ethical approval*

Animal housing and handling protocols were approved by the Liverpool John Moores University Animal Welfare and Ethics Steering Group (approval number: AR_AJ-KC/2022-6) and adhered to the guidelines of the Animal Behaviour Society and the Association for the Study of Animal Behaviour. All fish were monitored daily for any sign of social exclusion or injury and would have been removed from the group if detected. All observations were drawn from stable social groups showing species typical levels of agonism. Following the study, all fish remained in their social groups or were returned to stock housing aquaria for use in later studies.

Research data are available in Table A1 in the Appendix.

3. Results

Focal subordinate daffodil cichlids were more likely to show tail quivers to an aggressing dominant fish when the interaction took place close to the substrate than when the interaction was further away (paired $t_{11} = 3.96$, $p = 0.001$; Figure 2A).

Focal subordinate fish were more likely to display a head-up posture in response to aggression from a dominant group member when the interaction took place further than one body length from the substrate than when the interaction took place close to the substrate (paired $t_{11} = 4.65$, $p < 0.001$; Figure 2B).

4. Discussion

The existence of multiple signals conveying the same message may be explained by the requirement to communicate successfully in diverse signalling environments (Endler, 1992; Schafer & Ruxton, 2015). We found that the location of the interaction relative to the substrate affected the choice of submission signal in subordinate daffodil cichlids responding to aggression from the dominant breeding pair. The subordinate fish was more likely to show a tail quiver when close to the substrate compared to further away and to assume a head-up posture when far from the substrate compared to close. This differential use of these two distinct signals depending on the spatial context of the interaction suggests that the signal may be chosen to maximise salience rather than because the two signals convey distinct information.

In keeping with the notion that both submission signals convey a similar message in different contexts, vigorous tail quivers can result in a roll on the longitudinal axis revealing the underside of the signalling fish to the receiver much like the head-up posture (JGF pers. obs.). Guppies (*Poecilia reticulata*) produce a submission signal known as the side-tilt where the submitting fish rolls sideways on its longitudinal axis directing its underside towards the recipient, which interrupts aggression and often allows the signaller to escape without being further attacked (Gorlick, 1976). The tail quiver may have evolved from a form of side-tilting behaviour and might therefore be similar to the head-up posture in revealing the underside of the signaller, only with the rotation occurring on an alternate body axis to suit a different spatial signalling context.

A previous study on the use of the head-up posture by subordinate daffodil cichlids found that fish that produced this display in response to aggression from a dominant group member experienced a longer interval before receiving subsequent aggression from the recipient compared to interactions in which the head-up posture was not shown (Ruberto et al., 2020). Whether the two different submission signals are used tactically to improve communication efficiency in daffodil cichlids can be tested using an approach comparable to Ruberto et al. (2020). If signal efficiency is maximised by signal-context matching, then each signal should be more successful in delaying future aggression in the receiver when used in the spatial context in which it is more commonly deployed, compared to instances in which there is a signal-context mismatch.

Tail quivering also may temporarily restrict swimming ability in the signaller and is mutually incompatible with escape behaviour (Baerends, 1986). Reduced swimming capacity, even briefly, may be riskier when higher in the water column, further from shelter, where predation risk is more acute. As a result, tail quivering may be more perilous further away from the substrate. The head-up posture by contrast may not interfere with swimming to the same degree and could even act as the first movement in an escape response. The head-up posture may be a ritualisation (Zahavi, 1980) of the initial direction change component of an escape response (Domenici et al., 2011) which is used higher in the water column where it carries a lower risk than does the tail quiver.

Future work should also examine the behaviour of the aggressing fish in a more granular way (e.g., threat displays versus overt attacks, which can affect the choice of submission signal; Manara et al., 2023) as well as the direction of approach of the attacker. Subordinate fish near the substrate may be more likely to be approached from above, while those higher in the water column may be more likely to be approached from below, and these differences could affect the choice of submission signal given in response. Confirming the pattern of signal choice that we observed in the laboratory among wild, free-living daffodil cichlid groups would also be valuable, as the laboratory context is relatively simple compared to the natural habitat of the daffodil cichlid.

Cooperative breeding evolved several times independently within lamprologine cichlids (Dey et al., 2017; Tanaka et al., 2018). Examining submission signalling in some of the other cooperatively breeding species closely related to the daffodil cichlid (e.g., *Neolamprologus savoryi*, *or N. brichardi*) and comparing them to more distantly related cooperatively breeding lamprologine species (e.g., *N. multifasciatus*, *N. meeli*, *N. bifasciatus*, or members of the genus *Julidochromis*) would be valuable to elucidate the evolution of submission signals in highly social groups depending on the spatial and ecological context.

In the current study we examined the differential use of two distinct submission signals in the cooperatively breeding daffodil cichlid: the tail quiver, and the head-up posture. We found that tail quivers are more likely to be used close to the substrate, whereas the head-up posture is used more often further away from the substrate. Our data suggest that the coexistence of these two submission signals may be driven in part by signal efficacy under different signalling contexts. Social complexity can drive signalling complexity and repertoire size, as more intricate social relationships may require more nuanced signalling systems (Freeberg et al., 2012; Sewall, 2015). However, the ecological and environmental context of the interaction also needs to be considered when trying to understand communication in social animals (Ord & Garcia-Porta, 2012). Our data suggest a key role for the spatial context in driving agonistic signal repertoire and signal choice in a highly social vertebrate.

Acknowledgements

This work was supported by Liverpool John Moores University School of Biological and Environmental Sciences Research Development Funds to ARR and WTS.

References

Arnott, G. & Elwood, R.W. (2009). Assessment of fighting ability in animal contests. — Anim. Behav. 77: 991-1004.

Baerends, G.P. (1986). On causation and function of the pre-spawning behaviour of cichlid fish. — J. Fish. Biol. 29: 107-121.

Balshine-Earn, S., Neat, F., Reid, H. & Taborsky, M. (1998). Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. — Behav. Ecol. 9: 432-438.

Bose, A.P.H., Nührenberg, P. & Jordan, A. (2021). Female–female conflict is higher during periods of parental care in a group-living cichlid fish. — Anim. Behav. 182: 91-105.

Bradbury, J.W. & Vehrencamp, S.L. (2011). Principles of animal communication, 2nd edn. — Sinauer, Sunderland, MA.

Dey, C.J., Reddon, A.R., O'Connor, C.M. & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. — Anim. Behav. 85: 395-402.

Dey, C.J., O'Connor, C.M., Wilkinson, H., Shultz, S., Balshine, S. & Fitzpatrick, J.L. (2017). Direct benefits and evolutionary transitions to complex societies. — Nature Ecol. Evol. 1: 0137.

Domenici, P., Blagburn, J.M. & Bacon, J.P. (2011). Animal escapology I: Theoretical issues and emerging trends in escape trajectories. — J. Exp. Biol. 214: 2463-2473.

Eaton, L. & Sloman, K.A. (2011). Subordinate brown trout exaggerate social signalling in turbid conditions. — Anim. Behav. 81: 603-608.

Endler, J.A. (1992). Signals, signal conditions, and the direction of evolution. — Am. Nat. 139: S125-S153.

Fischer, S., Zöttl, M., Groenewoud, F. & Taborsky, B. (2014). Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. — Proc. Roy. Soc. Lond. B: Biol. Sci. 281: 20140184.

Freeberg, T.M., Dunbar, R.I.M. & Ord, T.J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. — Phil. Trans. Roy. Soc. Lond. B: Biol. Sci. 367: 1785-1801.

Frommen, J.G. (2019). Aggressive communication in aquatic environments. — Funct. Ecol. 34: 364-380.

Gorlick, D.L. (1976). Dominance hierarchies and factors influencing dominance in the guppy *Poecilia reticulata* (Peters). — Anim. Behav. 24: 336-346.

Groenewoud, F., Frommen, J.G., Josi, D., Tanaka, H., Jungwirth, A. & Taborsky, M. (2016). Predation risk drives social complexity in cooperative breeders. — Proc. Natl. Acad. Sci. USA 113: 4104-4109.

Heg, D. & Bachar, Z. (2006). Cooperative breeding in the Lake Tanganyika cichlid *Julidochromis ornatus*. — Environ. Biol. Fish. 76: 265-281.

Hellmann, J.K., Ligocki, I.Y., O'Connor, C.M., Reddon, A.R., Garvy, K.A., Marsh-Rollo, S.E., Gibbs, H.L., Balshine, S. & Hamilton, I.M. (2015). Reproductive sharing in relation to group and colony-level attributes in a cooperative breeding fish. — Proc. Roy. Soc. Lond. B: Biol. Sci. 282: 20150954.

Hick, K., Reddon, A.R., O'Connor, C.M. & Balshine, S. (2014). Strategic and tactical fighting decisions in cichlid fishes with divergent social systems. — Behaviour 151: 47-71.

Hirons-Major, C., Ruberto, T., Swaney, W.T. & Reddon, A.R. (2024). Submissive behaviour is affected by group size in a social fish. — Roy. Soc. Open Sci. 11: 240539.

Hurd, P.L. & Enquist, M. (2001). Threat display in birds. — Can. J Zool. 79: 931-942.

Jungwirth, A., Zöttl, M., Bonfils, D., Josi, D., Frommen, J.G. & Taborsky, M. (2023). Philopatry yields higher fitness than dispersal in a cooperative breeder with sex-specific life history trajectories. — Sci. Adv. 9: eadd2146.

Konings, A. (1998). Tanganyika cichlids in their natural habitat. — Cichlid Press, El Paso, TX.

Manara, V., Ruberto, T., Swaney, W.T. & Reddon, A.R. (2023). Subordinate submissive responses are predicted by dominant behaviour in a cooperatively breeding fish. — Behaviour 160: 124-144.

Matsumura, S. & Hayden, T.J. (2006). When should signals of submission be given? — A game theory model. — J. Theor. Biol. 240: 425-433.

Maynard Smith, J. & Harper, D. (2003). Animal signals. — Oxford University Press, Oxford.

O'Connor, K.I., Metcalfe, N.B. & Taylor, A.C. (1999). Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*?. — Anim. Behav. 58: 1269-1276.

Ord, T.J. & Garcia-Porta, J. (2012). Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups. — Phil. Trans. Roy. Soc. Lond. B: Biol. Sci. 367: 1811-1828.

Partan, S. & Marler, P. (1999). Communication goes multimodal. — Science 283: 1272-1273.

Pereira, M.E. & Kappeler, P.M. (1997). Divergent systems of agonistic behaviour in lemurid primates. — Behaviour 134: 225-274.

Reddon, A.R., Dey, C.J. & Balshine, S. (2019). Submissive behaviour is mediated by sex, social status, relative body size and shelter availability in a social fish. — Anim. Behav. 155: 131-139.

Reddon, A.R., Ruberto, T. & Reader, S.M. (2022). Submission signals in animal groups. — Behaviour 159: 1-20.

Ruberto, T., Talbot, J.L. & Reddon, A.R. (2020). Head up displays are a submission signal in the group-living daffodil cichlid. — Behav. Process. 181: 104271.

Ruberto, T., Swaney, W.T. & Reddon, A.R. (2024). Submissive behaviour is affected by territory structure in a social fish. — Curr. Zool.: zoae014.

Saeki, T., Satoh, S., Frommen, J.G., Kohda, M. & Awata, S. (2022). Kin-structured cooperatively breeding groups due to limited dispersal in the obligate shell-brooding cichlid *Neolamprologus meeli*. — Behav. Ecol. Sociobiol. 76: 89.

Satoh, S., Saeki, T., Kohda, M. & Awata, S. (2022). Cooperative breeding in *Neolamprologus bifasciatus*, a cichlid fish inhabiting the deep reefs of Lake Tanganyika. — Ecol. Freshw. Fish 31: 640-649.

Schaefer, H.M. & Ruxton, G.D. (2015). Signal diversity, sexual selection, and speciation. — Annu. Rev. Ecol. Evol. Sys. 46: 1-20.

Schenkel, R. (1967). Submission: its features and function in the wolf and dog. — Am. Zool. 7: 319-329.

Sewall, K.B. (2015). Social complexity as a driver of communication and cognition. — Integr. Comp. Biol. 55: 384-395.

Taborsky, M. (1985). Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. — Behaviour 95: 45-75.

Tanaka, H., Frommen, J.G., Koblmüller, S., Sefc, K.M., McGee, M., Kohda, M., Awata, S., Hori, M. & Taborsky, M. (2018). Evolutionary transitions to cooperative societies in fishes revisited. — Ethology 124: 777-789.

Van Dyk, D.A. & Evans, C.S. (2008). Opponent assessment in lizards: examining the effect of aggressive and submissive signals. — Behav. Ecol. 19: 895-901.

Waas, J.R. (1990). Intraspecific variation in social repertoires: evidence from cave-and burrow-dwelling little blue penguins. — Behaviour 115: 64-99.

Zahavi, A. (1980). Ritualization and the evolution of movement signals. — Behaviour 72: 77-80.

Table A1.
Research data.

ID	HUP/Agr_close	HUP/Agr_far	Quiver/agr_close	Quiver/agr_far
2803	0.53	0.85	1.11	0.70
2903	0.07	0.6	0.8	0.63
3003	0.00	0.21	1.00	1.14
3103	0.36	0.46	0.64	0.43
3303	0.24	0.17	1.04	0.83
3403	0.41	1.00	0.74	0.00
3503	0.43	0.59	0.86	0.65
3703	0.48	0.80	0.71	0.30
3803	0.27	0.47	0.88	0.67
4103	0.56	0.69	0.56	0.46
4403	0.14	0.72	1.00	0.56
4503	0.55	0.78	0.70	0.61