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Comparative conflict resolution: cooperative cichlids outperform less social species

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Evolution towards complex forms of sociality is dependent on overcoming conflicts of interest between prospective social partners. Competition for limited resources is a key aspect of such conflicts. Behaviour that results in conflict resolution without termination of the social relationship is thus predicted to be more prevalent in more social species. We here tested this hypothesis by staging contests between conspecifics over a crucial resource, using three lamprologine cichlid species that differ in their sociality. The cooperatively breeding species (*Neolamprologus pulcher*) indeed demonstrated improved conflict resolution, showing more egalitarian sharing of the resource and establishing mutually tolerant relationships more often compared to the pair-bonded species (*Variabilichormis moorii*) and the mostly solitary species (*Lepidiolamprologus elongatus*). We suggest that this is the result of behavioural differences between these cichlids: *N. pulcher* already showed more de-escalating behaviour during the earliest stages of the contests and increased rates of de-escalating behaviours more in response to heightened levels of aggression. Our results thus provide comparative support for the notion that socially competent behaviour, resolving conflicts while maintaining social relations, is a key behavioural aspect of evolutionary transitions to complex societies.

Competition for limited resources is a key cause of conflicts in biology and as such a major force in evolution (Germain et al., 2018). While competition is observed across all levels of biological organization, it is predicted to be particularly fierce where individuals have the same resource needs (Queller & Strassmann, 2018). As such, both ecological and social factors influence the severity of competition and the degree to which conflicts can be resolved: competition may be reduced where ecologies allow for the exploitation of alternative resources (e.g. by divergent specialization; Araújo et al., 2011), but sociality often increases the likelihood that a given resource is targeted by multiple individuals with conflicting interests (e.g. because of limited dispersal; West et al., 2007). Indeed, the rich literature on animal contests highlights that escalated competition is prevalent where mutually exclusive interests of individuals directly collide (Palaoro & Peixoto, 2022; Pinto et al., 2019).

The outcome of conflicts over resources is typically influenced by traits of the resource and of the contestants (Pinto et al., 2019): fights for more valuable resources are usually more severe and individuals with increased resource-holding potential are more likely to win a contest (Elwood & Arnott, 2012). An individual's resource-holding potential, in turn, is determined by its current relation to the resource (e.g. residency effects; Kemp & Wiklund, 2004), its current competitive ability relative to the opponent (e.g. relative body size; Arnott & Elwood, 2009), its past experience in general (e.g. winner–loser effects; Rutte et al., 2006), and its past experience with the opponent (dear-enemy and familiarity effects; Ydenberg et al., 1988). Winners of conflicts then tend to completely monopolize the contested resource, with losers being driven off, terminating the social relationship between the contestants (Strassmann & Queller, 2014). However, not all competition results in aggressive contests and individuals may resolve conflicts without potentially costly fighting, for example via appeasement

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(Quiñones et al., 2016), threats (Cant, 2011) or sharing of the resource (Samuni et al., 2018).

Resolving conflicts without escalated aggression is particularly important for social evolution (Queller & Strassmann, 2018). This is because competition for the same food, mates or breeding sites is considered a major hurdle for the evolution of advanced sociality (Korb & Heinze, 2016). For sociality to emerge and for transitions towards complex societies to be possible, competition between individual animals must thus be resolved by either closely aligning fitness interests (Rubenstein & Abbot, 2017) or behavioural interactions that do not result in the termination of the social relationship (Taborsky & Oliveira, 2012; Taborsky, 2021). Indeed, behavioural repertoire size (Leighton, 2017; McComb & Semple, 2005), postconflict reconciliation (Aureli et al., 2002; Thierry et al., 2008), and the quality and durability of interindividual relationships (‘social bonds’; Ostner & Schülke, 2014; Tobias et al., 2016) have been shown to vary along gradients of sociality. In addition, submissive signals appear to be more prominent in group-living animals, likely because they help cease agonistic interactions without parting ways (Reddon et al., 2022). This incomplete list highlights that there is some support for the notion that more social animals behave more socially competent in the sense that they are more likely to resolve conflicts while maintaining social relationships (Taborsky, 2021).

Nevertheless, more data are needed to get a clearer picture of the suggested coevolutionary link between sociality and social competence (Taborsky, 2021) and the expected knock-on effects this may have on various other biological traits, for example brain size (Dunbar & Shultz, 2007) or life history (Lucas & Keller, 2019). Comparative studies are especially scarce in this respect, likely due to the issue of designing experiments that accurately probe social behaviour across different species (Burkart & Schaik, 2013). Conflict resolution, as a key aspect of socially competent behaviour and a necessary precondition for the establishment of social groups and complex societies, is a promising target for comparative approaches. This is because intraspecific contests can be staged with relative ease and in a standardized way that is identical (or at least very similar) for many species (Reichert & Quinn, 2017). Fish may prove particularly useful in this regard for at least three reasons. First, fish are the most species-rich group of vertebrates, encompassing an incredible range of ecological adaptations (Helfman et al., 2009) and social organizations (Taborsky & Wong, 2017), providing great opportunities for comparative research. Second, fish are experimentally highly tractable, especially with regard to behavioural analyses of contests (Balshine et al., 2017; Balzarini et al., 2014). The hormonal and neuronal control of conflict resolution in fishes can also be probed in experiments (Chou et al., 2016; Desjardins et al., 2005). Third, likely due to the previous points, there already exists a rich literature on conflict resolution in fishes (Hsu et al., 2011) and the proximate mechanisms involved in it (Maruska et al., 2022). This helps to identify taxa that are most suitable for investigating a given question and enabling meta-analytical approaches (Moore et al., 2020).

The lamprologine cichlids of Lake Tanganyika represent one such taxon of interest. These closely related fish (Ronco et al., 2021) are ecologically (Muschick et al., 2012) and socially (Jordan et al., 2021) highly diverse, but all rely on a substrate for breeding (Sefc, 2011). This typically takes the form of either crevices in/under rocks (Jungwirth et al., 2021) or snail shells (Lein & Jordan, 2021). This opens up the possibility of staging contests over a resource between conspecifics of a wide range of species with divergent ecologies and sociality (Jordan et al., 2021). Indeed, this paradigm has frequently been used in lamprologines to investigate (among others) (1) the impact of social rearing conditions on social behaviour (and brain morphology; Fischer et al., 2015), (2) how individual and environmental traits influence social behaviour (Reddon et al., 2019) and (3) intrasexual conflict (Brandtmann et al., 1999). However, the majority of such studies have focused on a single species and comparative data are still scarce (but see Balshine et al., 2017; Hick et al., 2014 for notable exceptions).

We here set out to study conflict resolution in three lamprologine cichlids that differ in key aspects of their ecology and sociality (see Methods for additional details about the species). We staged contests between two differently sized conspecifics competing for a resource that each fish had previously monopolized alone (see Methods for details). Specifically, we used this setup to test the following hypotheses and predictions. First, we hypothesized that individuals with greater resource-holding potential, in our case represented by an individual's size relative to that of its opponent, will win contests more often. We thus predicted that within each experimental pair, larger fish would show more aggressive behaviour (biting and displays) and less de-escalating behaviour (submissions and fleeing), as well as occupying the contested resource more compared to smaller fish. Second, we hypothesized that more social species have improved abilities to resolve conflicts without potentially costly escalated fighting. We thus predicted reduced rates of aggression and increased rates of de-escalation in the more social species. Third, we hypothesized that social species more often resolve conflicts without terminating social relationships between contestants. We thus predicted that the highly social species would more often be mutually tolerant and show an increased rate of resource sharing among the contestants. Taken together, our experiments should thus provide comparative evidence for or against the notion that conflict resolution abilities coevolve with social systems (Queller & Strassmann, 2018; Reddon et al., 2022; Taborsky, 2021).

METHODS

Study Species

We studied three lamprologine cichlid species from Lake Tanganyika: *Lepidiolamprologus elongatus*, *Neolmprologus pulcher* and *Variabilichromis moorii*. While taxonomically closely related (Ronco et al., 2021) and sharing similarities in reproductive biology (all are substrate breeders with biparental care; Sefc, 2011), these species differ in their sociality: *L. elongatus* is a largely solitary species, forming loose (interspecific) groups for hunting (Yuma, 1994) and temporary pairs for a given breeding attempt (Sefc, 2011); *N. pulcher* is a cooperative breeder, living in permanent groups with stable membership and size-based hierarchies (Taborsky, 2016); and *V. moorii* forms stable pairs for extended periods of time (Bose et al., 2018). As such, we observe a gradient of increasing sociality from *L. elongatus* to *V. moorii* to *N. pulcher*. Crucially, in our aquarium settings, all three species readily accept half flowerpots as substrate for breeding and as shelters. Contests over access to such flowerpots are frequently observed in our stock tanks, and the largest tank mates typically monopolize a given flowerpot, also outside of breeding attempts. Note that our focal species differ in additional aspects of their biology, particularly their feeding ecology, their body size and their reproductive biology. We address the potentially confounding effects of these differences in detail in the Discussion below.

Housing Conditions and Fish Stock

All experimental individuals had been housed in 160-litre stock tanks in groups of same-age full siblings throughout their lives, under standard housing conditions: 12:12 h light:dark cycle, 26 ± 2 °C, water chemistry resembling that of Lake Tanganyika, fed six times a week with a mix of dried and frozen aquarium pet food. These conditions were also maintained in the experimental tanks. All fish were F1 offspring of wild-caught individuals from the southern part of Lake Tanganyika.

Experimental Procedure

Experiments were carried out at the Konrad Lorenz Institute of Ethology, Vienna, Austria, in two blocks. Block 1 extended from 12 July 2022 to 5 August 2022 and block 2 extended from 21 October 2022 to 13 December 2022. For the initial habituation phase (see below), each experimental 160-litre tank was divided in half with an opaque plastic sheet, resulting in two compartments of equal size, each outfitted with an air stone. Quarter flowerpots (original diameter: 13 cm) were placed at the back of the tank and against the opaque divider, thus providing each compartment with a shelter. On day 1 of a given trial, two test fish were introduced into the experimental tanks, one each per compartment, forming an experimental pair in a given tank. Upon moving to the experimental tank, individuals were allowed to habituate to their compartment for approximately 72 h (habituation phase). Throughout the habituation phase, we frequently checked that each experimental fish had accepted its respective shelter, as indicated by hiding in it and/or clear signs of digging activity. All individuals fulfilled this criterion for inclusion in the study, and we thus observed 138 individual test fish in 69 pairs, 23 per species. Each test fish was consequently considered a ‘resident’ or ‘territory owner’, making our set-up ‘symmetric’ in the sense that both contestants entered their encounter with the same relationship to the contested resource (in contrast to ‘asymmetric’ staged contests between ‘winners and losers’, ‘residents and intruders’, etc.; Hsu et al., 2011). Test fish within a given pair were chosen to be of the same species, but to have a discernible size difference (this also allowed for reliable tracking during observations and rehousing after the experiments), and to be unfamiliar with one another (ensured by choosing fish from different stock tanks: members of an experimental pair had never encountered each other prior to this study). The size (cm, standard length [SL] to the nearest mm) and sex of each individual were determined upon its capture from its home tank. We did not assign individuals to pairs by their sex, but by their size alone; sex composition of pairs was thus a haphazard result of our size selection. Individual *L. elongatus* in our experiments had an average SL of 9.3 cm (range 6.1–13 cm), and average size difference within pairs was 2.1 cm (range 0.6–4.5 cm). For *N. pulcher*, we recorded an average SL of 4.9 cm (range 2.9–6.6 cm), with within-pair size difference being on average 1.9 cm (range 0.5–3.5 cm). Our *V. moorii* were on average 4.6 cm long (SL; range 2.5–7 cm), with an average size difference within pairs of 1.5 cm (range 0.5–2.2 cm). For each experimental pair, we calculated its size ratio, i.e. the SL (cm) of the smaller fish divided by the SL (cm) of the larger fish (larger values indicating more similar sizes of the two fish). Following the habituation phase, the divider was removed and the two quarter flowerpots were replaced with a half flowerpot of identical original diameter (13 cm), thus providing a single shelter in the tank at the location where previously the two quarter flowerpots had been positioned.

Videos and Behavioural Recordings

We video recorded the first 30 min after the removal of the divider, using a single camera (block 1: Akaso EK7000; block 2: Canon Vixia HF R300) per experimental tank placed approximately 50 cm in front of the aquarium to ensure the whole experimental tank was in view. Following established ethograms for Lake Tanganyika cichlids (e.g. Balzarini et al., 2014; Hick et al., 2014; Reddon et al., 2019; Manara et al., 2022 and references therein), we recorded the following behaviours by visual inspection of the videos: (1) the time (s) each fish spent in the shelter (half flowerpot), (2) the number of times each fish bit the other, (3) the number of frontal displays each fish showed, (4) the number of lateral displays each fish showed, (5) the number of times each fish fled from the other and (6) the number of submissive postures (quivering) each fish showed. We considered behaviours 2–4 as aggression and behaviours 5–6 as de-escalation; while biting and displays serve to establish dominance over another fish in these species, fleeing and submissive quivers tend to reduce the number of aggressive behaviours an individual receives, indicating a relatively lower dominance rank (Dey et al., 2013; Reddon et al., 2019; Ruberto et al., 2020). This view is further supported by the observation that behaviours 2–4 are positively correlated with use of the contested resource (time in the shelter; linear model (LM): $t = 2.275$, $P = 0.025$, slope = 1.195), while behaviours 5–6 are negatively correlated with it (LM: $t = -3.427$, $P < 0.001$, slope = −5.741).

Crucially, the behavioural repertoires of all three species generally overlap when using the broad categories we applied here (Balzarini et al., 2014; Hick et al., 2014; Manara et al., 2022; Reddon et al., 2019). While more detailed analyses of ‘displays’ may be appropriate when investigating a single species, for example distinguishing between lateral displays with or without an s-bend or distinguishing between frontal displays with or without head-down posture (Hick et al., 2014), small behavioural differences between the species make such a level of detail infeasible (Balzarini et al., 2014). Importantly, however, all three species follow the general pattern of behavioural escalation where conflicts start with lateral displays, move towards frontal displays, and escalate to biting if not terminated at an earlier stage. As such, our reduced level of resolution in the behavioural recordings should appropriately represent differences in contest severity between the species, despite small differences in the exact behaviours used when described at the highest level of detail.

In addition, we noted whether (7) the fish were mutually tolerant 24 h after first encountering each other (Zöttl et al., 2013). To this end, we assessed a 5 min video taken at that time (set-up identical to above), i.e. 24 h after the removal of the divider. We scored fish as not mutually tolerant (1) if one fish was hiding in a corner and/or near the surface and received aggression from the other fish when leaving such a location, (2) if one fish permanently occupied the shelter and behaved aggressively when the other fish approached the shelter entrance and (3) if one fish constantly behaved aggressively towards the other and chased it around the tank. Conversely, we scored fish as mutually tolerant (4) if both fish communally shared the shelter or (5) if both fish freely roamed the tank without signs of overt aggression between them. Upon this final observation, each test fish was rehoused to its original stock tank.

Ethical Note

All experiments reported here were approved by the Austrian Federal Ministry of Education, Science and Research (Bundesministerium für Bildung, Wissenschaft und Forschung, BMBWF; Zl. ETK 016/02/2021, GZ 2021–0.297.650) and follow the ASAB/ABS Guidelines for the treatment of animals in behavioural research (ASAB Ethical Committee/ABS Animal Care Committee, 2023). Sample sizes were determined following power analyses assuming small effect sizes and using a model structure including a maximum of four explanatory variables. No fish suffered obvious injuries during this work. The most severe aggression we observed were mouth fights, which were very brief (included in counts of biting due to their rare occurrence) and bites towards an opponent's fins and flanks. Neither of these aggressive behaviours appeared to damage a fish's tissue. We monitored the fish throughout the entire observation period at least twice daily and would have terminated any trial in which a fish would have been at risk of suffering lasting injuries or death. However, this was never necessary, likely because the size of the experimental tanks (160-litre) afforded losing individuals with enough space to avoid the aggressive winner. All fish used in these experiments were successfully reintroduced to their respective stock tanks at the end of their experimental trial.

Statistical Analyses

All analyses were carried out in R version 4.1.0 (R Development Core Team, 2013), using the package lme4 (Bates et al., 2013) to fit models, the package DHARMa (Hartig, 2020) to derive model diagnostics and the package insight to get variance components (Lüdecke et al., 2019). Model results were extracted using ‘summary’ and ‘drop1’ using a chi-square test statistic, and model diagnostics were extracted using ‘testResiduals’. Full information for each model can be found in the Appendix (Results: Tables A1–A7; diagnostics: Figs A1–A7). In short: to analyse factors influencing within-pair differences in behaviour, we fitted three negative binomial generalized linear mixed-effects models (nbGLMM). In each model, we fitted the respective response variable (aggression, de-escalation, share of the resource [time spent in the shelter]) and included species identity and relative size (either large or small) as explanatory variables. We also initially included the two-way interaction between the two explanatory variables but removed it and refitted the models where its effect was not significant. The sex of both fish and the observer's identity were included as random effects. To analyse whether the species differed in the relative sharing of the resource, we fitted a linear mixed-effects model (LMER). We fitted the difference between the large and the small fish in time spent in the shelter in a given trial as the response variable and included species identity as explanatory variable, as well as including the sex of both fish and the observer's identity as random effects. To analyse behavioural differences between the species, we used two chi-square tests, one each for the species-specific total counts of aggression and de-escalation. To analyse factors influencing de-escalating behaviour shown by a given experimental pair, we fitted an LMER. We fitted our counts of de-escalating behaviours shown by both fish as the response variable and included three explanatory variables: species identity, the size ratio between the two fish and aggression shown by the two fish. We also included the two-way interaction between species identity and aggression; the two-way interaction between species identity and size ratio was initially included but was removed due to its nonsignificant effect. In addition, we included two random effects: the sex of both fish and the observer's identity. A corresponding model was fitted to specifically investigate the de-escalating behaviour of the small fish in response to aggression by the large fish. This LMER included de-escalation by a small fish as response variable, species identity, the size ratio between the two fish of the pair and aggression shown by the large fish in the pair as explanatory variables, and the two-way interaction between species identity and aggression by the large fish (the two-way interaction between species identity and size ratio was initially included, but was removed due to its nonsignificant effect). To analyse factors influencing mutual tolerance, we fitted a binomial generalized linear mixed-effects model (bGLMM). In this model, we fitted whether or not both fish were mutually tolerant (yes/no) as the binomial response variable. We included four explanatory variables: species identity, the size ratio between the two fish, aggression shown by the two fish and de-escalation shown by the two fish. In addition, we included two random effects: the sex of both fish and the observer's identity. We initially also included all two-way interactions between species identity and all the other explanatory variables, but stepwise removed them due to their nonsignificant effect.

RESULTS

Does Body Size Predict Behaviour During Contests?

Within an experimental pair, larger fish showed more aggression than smaller fish (nbGLMM: $N = 138$ individuals, likelihood ratio test, $LRT = 93.004$, $P < 0.001$; Fig. 1a, Table A1), and this effect did not differ between the species (nonsignificant interaction between individual status and species identity). Conversely, smaller fish showed more de-escalation than larger fish (nbGLMM: $LRT = 147.754$, $P < 0.001$; Fig. 1b, Table A2), which did not differ between the species (nonsignificant interaction between individual status and species identity).

Do the Species Behave Differently During Contests?

The species differed in the frequencies of aggressive (chi-square test: $\chi^2_6 = 280.54$, $P < 0.001$; Fig. 2a) and de-escalating ($\chi^2_4 = 30.31$, $P < 0.001$; Fig. 2b) behaviours that they showed. In addition, the frequency of de-escalation generally decreased with increases in the size ratio between the two fish (i.e. de-escalation was reduced where individuals in a pair were more similar in size; LMER: $N = 69$ pairs, $LRT = 7.613$, $P = 0.006$; Table A5). De-escalating behaviour was most strongly predicted by species-specific effects of aggressive behaviour ($LRT = 36.298$, $P < 0.001$; Fig. 2c). Specifically, *N. pulcher* increased the frequency of de-escalation at a greater rate as frequencies of aggression increased compared to *L. elongatus* and *V. moorii* (albeit still showing considerably less than one de-escalating behaviour per aggressive behaviour). This pattern was also observed when only investigating the de-escalating behaviour of the smaller fish in response to aggression shown by the larger fish: smaller fish showed less de-escalation when they were closer in size to the larger fish (LMER: $N = 69$ pairs, $LRT = 4.136$, $P = 0.042$; Table A6), and the increase in de-escalation in response to increased received aggression was species specific (with *N. pulcher* showing the strongest increase; $LRT = 35.216$, $P < 0.001$; Table A6, Fig. A8).

Does Contest Outcome Differ Between the Species?

There was a significant interaction between an individual's status as either the large or small fish in an experimental pair and species identity in the analysis of the time a fish spent inside the shelter (nbGLMM: $LRT = 7.771$, $P = 0.021$; Table A3): the difference in time spent inside the shelter between large and small fish was more pronounced in *L. elongatus* and *V. moorii* compared to *N. pulcher* (LMER: $N = 69$ pairs, $LRT = 16.371$, $P < 0.001$; Table A4, Fig. 3a).

Of the 69 pairs included in this study, 18 were scored as composed of two mutually tolerant individual conspecifics 24 h after removing the divider (ca. 26%). The three species differed in their tolerance (bGLMM: $N = 69$ pairs, $LRT = 9.221$, $P = 0.009$; Table A7, Fig. 3b), with the highly social cooperative breeder *N. pulcher* showing greater rates of tolerance (13 of 23 pairs, ca. 57%) than the other two species ($P = 0.006$; Table A7). The pair-bonded *V. moorii* had slightly higher rates of tolerance (three of 23 pairs, ca. 13%) than the mostly solitary *L. elongatus* (two of 23 pairs (ca. 9%), but this did not constitute a statistically significant difference ($P = 0.577$; Table A7). None of the other variables we included

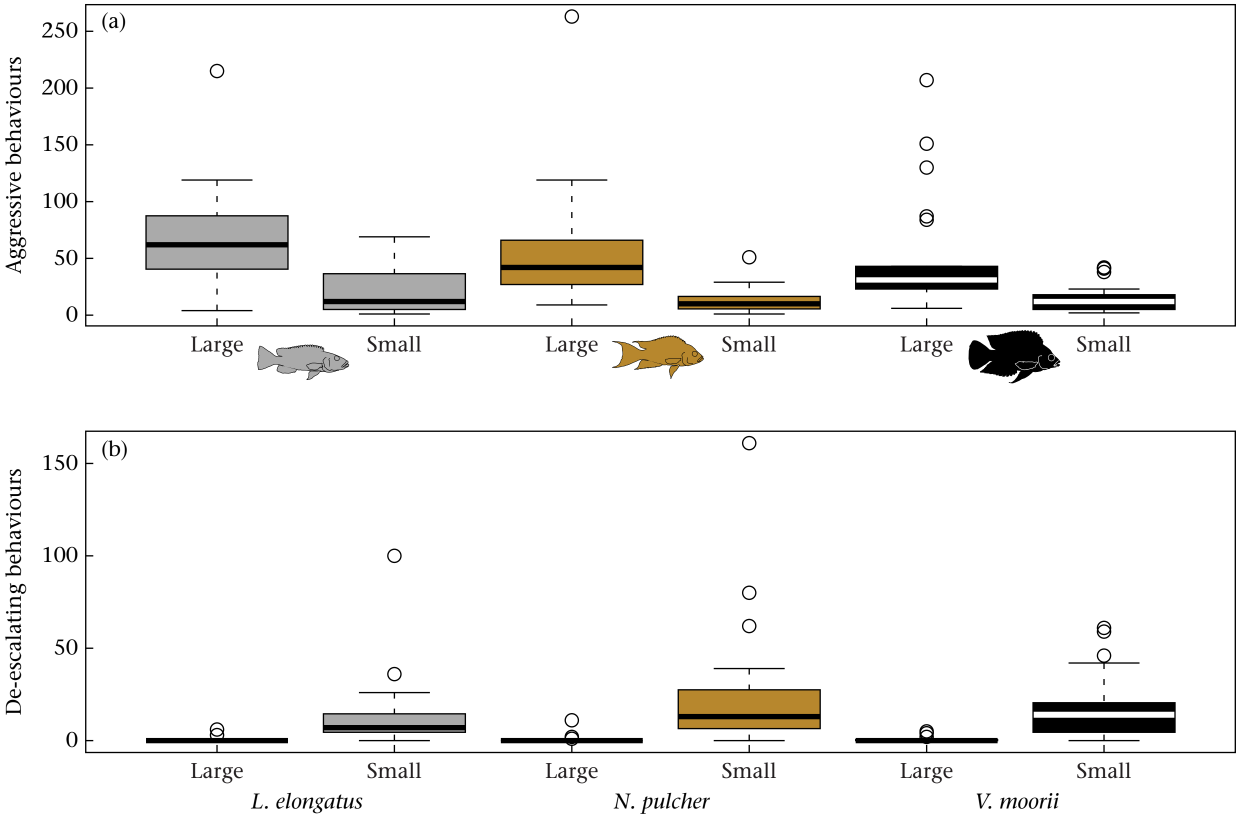

Figure 1. Behavioural differences between individuals of different relative size (large or small within their experimental pair) for each species (*Lepidiolamprologus elongatus* (grey), *Neolamprologus pulcher* (beige), *Variabilichromis moorii* (black)). (a) The sum of all aggressive behaviours (bites, frontal displays, lateral displays). (b) The sum of all de-escalating behaviours (fleeing, submissive quivers). Each box represents data for 23 individuals recorded during the first 30 min of both fish encountering each other, showing medians (central line), interquartile ranges (boxes), range without outliers (whiskers) and outliers (points outside 1.5 times the interquartile range above the upper quartile and below the lower quartile).

significantly predicted whether a pair would be mutually tolerant (size ratio between the two individuals: LRT = 1.061, $P = 0.303$; sum of all aggressive behaviours shown during the initial 30 min of encountering each other: LRT = 2.027, $P = 0.155$; sum of all de-escalating behaviours shown during the initial 30 min of encountering each other: LRT = 0.519, $P = 0.471$), and we found no support for any interactive effect between species identity and any of these variables.

DISCUSSION

We have shown that species of lamprologine cichlids differ in their conflict resolution when competing for a crucial resource: compared to the pair-bonded *V. moorii* and the mostly solitary *L. elongatus*, the cooperatively breeding *N. pulcher* showed a more egalitarian sharing of the shelter (Fig. 3a) during the initial stages of a conflict with a previously unfamiliar conspecific and ultimately had higher rates of establishing mutual tolerance (Fig. 3b). This suggests that the more social species is indeed better able to settle conflicts without terminating social relationships. This view is further supported by the behavioural analyses that showed increased rates of de-escalating behaviour in *N. pulcher* (Figs 1 and 2). Importantly, the fact that our experimental set-up replicated two well-known findings from previous work on conflicts among fishes across all three of our focal species lends some confidence to our comparative results regarding conflict resolution: larger individuals behaved more aggressively and won contests more often (Figs 1 and 3a) and contests included less de-escalating behaviour when the contestants were more similar in size (which could be interpreted as increased severity of the contests; see Results; Hsu et al., 2011).

The Lamprologini of Lake Tanganyika are the only fishes described as living in complex societies in the sense of cooperating via alloparental brood care, division of labour and establishing permanent groups with stable group membership (Taborsky & Wong, 2017). It has been suggested that this evolutionary transition has occurred independently several times in this taxon (Dey et al., 2017), making it even more surprising that other highly social fish, for example coral-associated Gobiidae and Pomacentridae (Wong & Buston, 2013), have not reached this same degree of sociality (Taborsky & Wong, 2017). While ecological factors are certainly important in setting the stage for complex sociality in lamprologines (Dey et al., 2017; Jungwirth et al., 2021; Lein & Jordan, 2021; Taborsky & Wong, 2017; Tanaka et al., 2018), it is ultimately the behaviour of individual fish that determines whether cooperation persists or whether social relationships are terminated (Fig. 1). This is especially true for social cichlids, because indirect fitness gains from assisting close relatives appear to be of minor importance for the adaptive value of their cooperation (Awata et al., 2005; Josi et al., 2021; Jungwirth & Taborsky, 2015; Tanaka et al., 2015) compared to, for example, eusocial insects (Bourke, 2019). Persistence of cooperative groups thus relies on successful behavioural negotiations between group members (Quiñones et al., 2016); in other words, on socially competent behaviour (Taborsky, 2021; Reddon et al., 2022).

For lamprologines, a key behaviour in this respect appears to be submissive quivering (Manara et al., 2022; Reddon et al., 2019), which the more social species show more frequently during

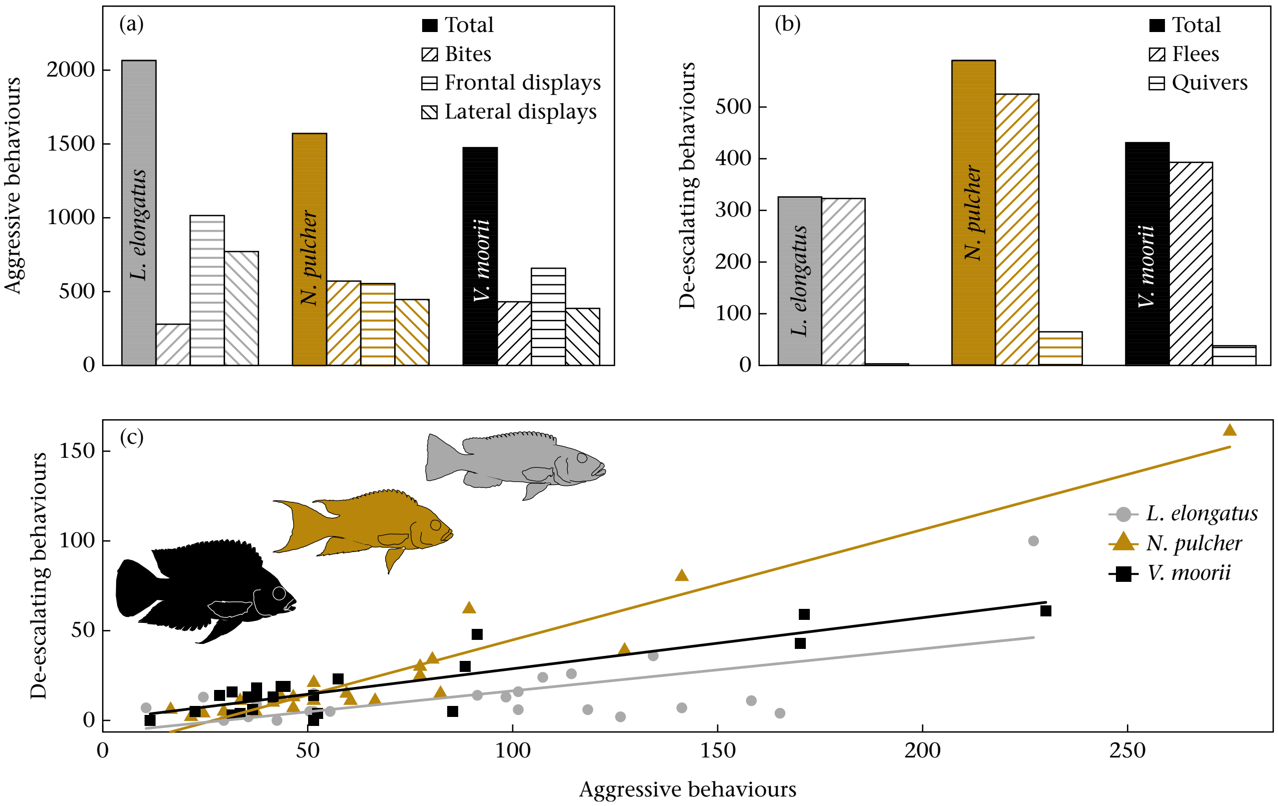

Figure 2. Behavioural differences between the three focal species (*Lepidiolamprologus elongatus* (grey), *Neolamprologus pulcher* (beige), *Variabilichromis moorii* (black)) as recorded in the first 30 min after two experimental fish encountered each other. (a) Aggressive behaviours (counts/30 min): sum of all aggressive behaviours recorded and the number of bites, frontal displays and lateral displays. (b) De-escalating behaviours (counts/30 min): sum of all de-escalating behaviours recorded and the number of fleeing behaviours and submissive quivers. (c) The sum of all de-escalating behaviours shown by an experimental pair plotted as a function of the sum of all aggressive behaviours shown by the same pair (counts/30 min). Each point represents data for a single pair ($N = 69$, 23 per species). Lines show the values predicted by the respective species-specific linear models.

contests compared to species with a less complex social organization (Balshine et al., 2017; Hick et al., 2014; Fig. 2b). Quivering itself is not exclusively shown by social lamprologines, but is a behaviour expressed during mating in a wide range of cichlids (including the social lamprologines; Alward et al., 2020; Amorim et al., 2004; Baylis, 1976; Wright et al., 2017). Its role as a de-escalating behaviour during social conflicts thus appears to represent a behavioural neofunctionalization during social evolution among Lake Tanganyika's Lamprologini (Rubenstein et al., 2019). However, to conclusively show that what researchers have categorized as ‘quivering’ in two different contexts (mating and conflict de-escalation) indeed constitutes ‘the same’ behaviour, further investigations of the genetic, neuronal and motor control of quivering (Alward et al., 2020) and, crucially, its effect on receivers (King et al., 2022) are needed (Jordan et al., 2021). Irrespective of the outcome of such studies, de-escalating behaviour in general and submissive quivering in particular constitute important aspects of conflict resolution and social competence in social cichlids (Manara et al., 2022; Reddon et al., 2019; Ruberto et al., 2020; Fig. 2), lending support to the idea that submissive behaviours play a key role in social evolution (Reddon et al., 2022).

Previous studies of social conflict in cichlids had already used a set-up similar to ours (Balshine et al., 2017; Hick et al., 2014), demonstrating the viability of using the same experimental design for different species. This is a powerful approach to studying social behaviour in a comparative setting, but is often challenging in other taxa (Rubenstein & Abbot, 2017; but see Burkart & Schaik, 2013, Tchabovsky et al., 2019 for additional notable exceptions). Most work aiming to compare socially competent behaviour between species of diverging social complexity has focused on qualitative descriptions of behaviours and estimating behavioural repertoire size (e.g. Leighton, 2017; Manser et al., 2014; Nehring & Steiger, 2018). While such studies are invaluable for characterizing species, for identifying potential behaviours and contexts of interest, and for highlighting the ecological settings in which sociality evolves, they are often limited in the scope to which they can experimentally control for confounding variables. Specifically, controlling for the relative resource-holding potential between contestants (Prenter et al., 2008), the social and reproductive status of prospective cooperators (Cram et al., 2019) or the out-group options available for individuals (Bergmüller et al., 2005) is necessary (among other aspects) for pinning down differences in social competence between species. Otherwise, the observed behavioural differences may well be caused by other ecological and life history differences present at the time of data collection, and not necessarily interspecific variation in social competence.

Our own work has some shortcomings in precisely this aspect. First, we did not explicitly control for the sex of our experimental individuals, having assumed that they were not yet sexually mature. This resulted in an imbalanced data set with regard to the sex mix among experimental pairs (Table A8; the variance explained by sex mix relative to the total residual variance differed across our different models; see respective Tables in the Appendix). While we did include this information in our models, we also recognized it as a confounding factor that may well have biological relevance and should thus be targeted explicitly in the future. This is particularly true for our focal species, as the relationships within and between the sexes differ markedly between them: *N. pulcher*

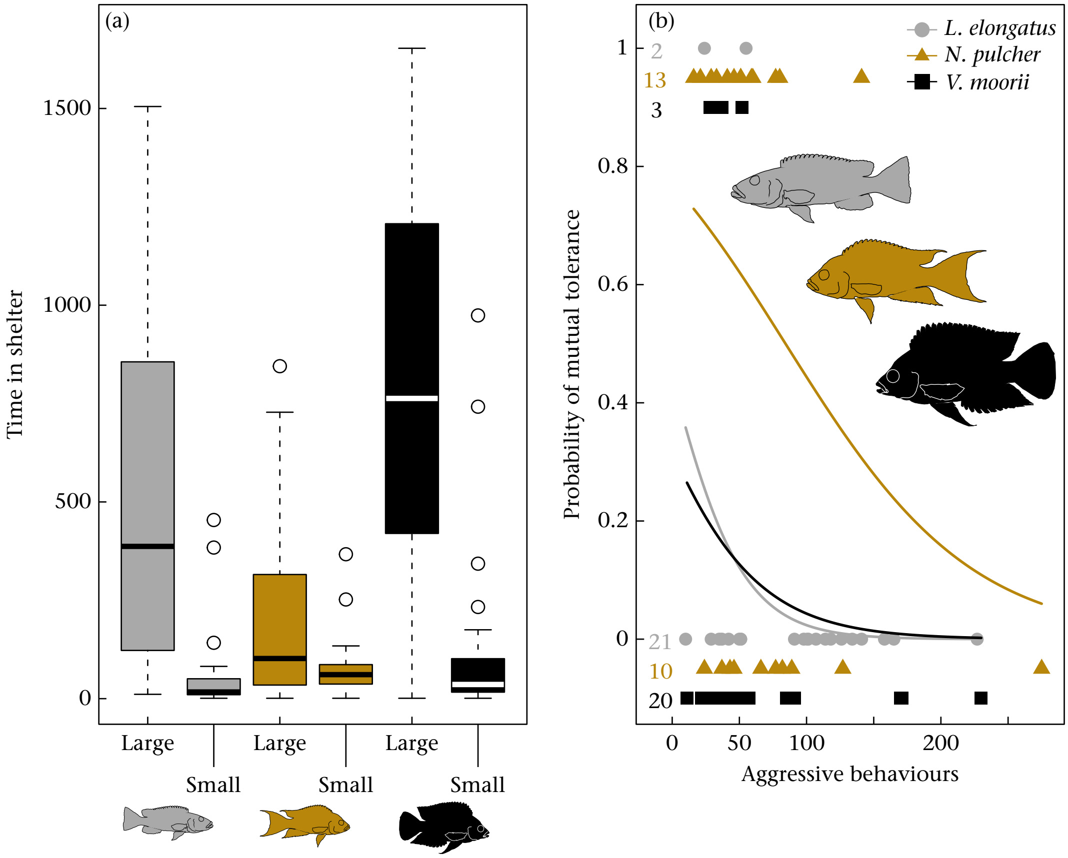

Figure 3. Conflict resolution of the three focal species (*Lepidiolamprologus elongatus* (grey), *Neolamprologus pulcher* (beige), *Variabilichromis moorii* (black)). (a) Time (s) spent using the resource, the half flowerpot shelter, during the first 30 min of the two experimental fish encountering each other for large and small individuals of each species. Each box represents 23 individual fish, showing medians (central line), interquartile ranges (boxes), range without outliers (whiskers) and outliers (points outside 1.5 times the interquartile range above the upper quartile and below the lower quartile). (b) The probability of being scored as mutually tolerant for a pair of experimental fish 24 h after first encountering each other plotted as a function of the total aggression both fish showed during the first 30 min of their encounter. This probability is given as 1 (mutually tolerant) or 0 (not tolerant). Each point represents a single pair for each of the three focal species ($N = 69$ pairs, 23 per species), and data for *N. pulcher* and *V. moorii* were offset in the *y* direction to increase visibility. Numbers next to points give the respective sample sizes of tolerant and nontolerant pairs per species. Curves show the values predicted by the respective species-specific generalized linear models (no offset was applied to curves).

are socially polygynous (Jungwirth et al., 2016) and exhibit moderate genetic polygamy (ca. 20% extrapair parentage, with resident males losing slightly more paternity than resident females lose maternity; Hellmann et al., 2015) whereas *V. moorii* are socially monogamous and exhibit a high level of genetic polyandry (ca. 40% extrapair paternity with no reports of lost maternity; Bose et al., 2018; Zimmermann et al., 2023). For *L. elongatus*, no analyses of the genetic mating system could be found, but they are socially (serial) monogamous (Sefc, 2011). These reproductive patterns are likely linked to the observed size dimorphism in each species, where males are the larger sex in *L. elongatus* and *N. pulcher* while the opposite is true in *V. moorii* (Sefc, 2011). In line with this, we have anecdotal evidence from observations of our stock tanks suggesting that male–male aggression is increased in *L. elongatus* and *N. pulcher* and female–female aggression is increased in *V. moorii*, but a dedicated investigation of this is required before any conclusions can be drawn. Second, there is a huge 'blind spot' in our data between the end of the behavioural observations (30 min after removing the divider) and our recording of mutual tolerance (24 h after removing the divider). This may explain the lack of a significant effect of counts of either aggressive or de-escalating behaviours for the establishment of tolerance in a given trial: the fact that we did not find a clear relationship between our behavioural recordings and the final outcome of the staged conflicts may well be because mutual tolerance was established at a later stage. Longer observations, potentially with the aid of automated behavioural recordings (Jordan et al., 2021), may thus provide further insight into when and how cichlids differ in their social competence. This is related to a third point, namely that our behavioural recordings were conducted by a range of human observers. While we did strive towards reducing between-observer variation by comparing scores recorded during initial observer training, observer bias remains an issue in ethological work (Tuyttens et al., 2014). This is particularly true in a study like ours where blinding observers to species identity (and thus social system) is impossible. Again, automated data collection may prove useful to reduce this issue in future research to more definitively probe the impact of initial behavioural interactions on eventual tolerance (Jordan et al., 2021). Fourth, our focal species differ in their diet: *L. elongatus* is a piscivorous predator, while *N. pulcher* and *V. moorii* are plankton and Aufwuchs feeders (Muschick et al., 2012). It is thus reasonable to assume that competition for food is greater among individual *L. elongatus* than among the other two species. The respective prediction, namely that *L. elongatus* should be more aggressive and less tolerant, found mixed support in our data: the predatory *L. elongatus* did show more aggression than the two plankton/Aufwuchs feeders (Figs 1 and 2), but they were not less tolerant than at least one of the nonpredatory species (Fig. 3b). Finally, while our focal species all require a crevice or cave for breeding (Sefc, 2011), they differ in the degree to which they are associated with this substrate outside breeding attempts (Jungwirth et al., 2021): *N. pulcher* spend their entire life around the shelters they maintain and defend (Jungwirth et al., 2023), *V. moorii* permanently defend territories once they start breeding and *L. elongatus* are mostly transient. We indeed observed differences between the species in the total amount of time spent in the shelter during our observations (Fig. 3a), but we do not have data on shelter use outside this. As such, the 'value' of the resource over which we staged contests may still differ between the species (Hsu et al., 2011), an aspect that may be worth investigating more explicitly in the future. However, the direction in which these differences could be expected to be expressed (resource value and thus contest severity and shelter use: *N. pulcher* > *V. moorii* > *L. elongatus*) would be opposite to our findings.

In summary, we have shown that the resolution of conflicts over a crucial resource differed between three lamprologine cichlid species that differ in their sociality: the cooperatively breeding species (*N. pulcher*) showed improved conflict resolution, sharing the resource more equally and establishing tolerance more often, compared to the pair-bonded (*V. moorii*) and the mostly solitary species (*L. elongatus*). We thus provide comparative support for the notion that social competence, i.e. appropriate social behaviour that resolves conflicts without terminating social relationships, coevolves with social complexity (Taborsky & Oliveira, 2012; Taborsky, 2021). Further studies applying our general approach, i.e. using the same experimental set-up for a range of socially divergent but closely related species, will show whether this indeed constitutes a broad and widespread phenomenon.

Author Contributions

S.F. and A.J. conceptualized the study. S.A., X.G., B.R., D.Y. and A.J. collected and curated the data. S.F. and A.J. conducted the analyses. A.J. wrote the initial draft of the manuscript. All authors contributed to revisions.

Data Availability

All data included in this manuscript are uploaded as Supplementary Material, as is the R script used for data curation, the analyses and the production of the figures.

Declaration of Interest

We declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2023.12.006.

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Appendix

Additional Information on Analyses of Status (Relative Size) Effects

To analyse factors influencing within-pair differences in aggressive, de-escalating and territorial behaviour, we fitted three nbGLMMs. These models were identical in the initial structure of the explanatory variables, but differed in the respective response variable: one model each was fitted with (1) the sum of all aggressive behaviours a fish showed during the first 30 min of encountering its partner, (2) the sum of all de-escalating behaviours a fish showed during the first 30 min of encountering its partner and (3) the time (s) it spent inside the shelter (half flowerpot) during the first 30 min of encountering its partner as response variable. In each such model, we included (1) the individual's species identity (three level factor: *L. elongatus*, *N. pulcher*, *V. moorii*) and (2) its status (two-level factor: being the larger or smaller of the two fish in an experimental pair) as explanatory variables. In addition, we included two random effects: (1) the sex mix of the two fish (three-level factor: both fish are females, both fish are males, one fish is a female and one a male), and (2) the observer's identity (four-level factor: S.A., X.G., B.R., D.Y.). We initially also included the two-way interaction between species and status but removed it due to its nonsignificant effect in the models of aggressive and de-escalating behaviours. This interaction was retained in the model of time spent in the shelter, where it proved to be significant. To gain a better understanding of these interspecific differences in resource sharing, we then fitted a linear mixed-effects model (LMER) that included the difference in time spent in the shelter between the large and the small fish as response variable, species identity as the explanatory variable, and sex mix and observer identity as random effects. We subsequently performed post-hoc analyses using orthogonal contrasts. First, we set the contrast of the model to compare the cooperative breeding species (*N. pulcher*) with the mean of the two noncooperatively breeding species (*V. moori* and *L. elongatus*; see factor 'cooperative versus noncooperative' in Table A7). Second, we compared the species that forms stable pairs (*V. moori*) with the species that has a mostly solitary lifestyle (*L. elongaus*; see factor 'stable pairs versus solitary' in Table A7).

The initial full models thus had the following structures:

$$\text{Aggression} \sim \text{Species} * \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$\text{De-escalation} \sim \text{Species} * \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$\text{TimeInShelter} \sim \text{Species} * \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$(\text{TimeInShelterLarge-TimeInShelterSmall}) \sim \text{Species} + (1|\text{SexMixes}) + (1|\text{Observer})$$

The final models, the results of which are reported in the main text, thus had the following structures:

$$\text{Aggression} \sim \text{Species} + \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$\text{De-escalation} \sim \text{Species} + \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$\text{TimeInShelter} \sim \text{Species} * \text{Status} + (1|\text{SexMixes}) + (1|\text{Observer})$$

$$(\text{TimeInShelterLarge-TimeInShelterSmall}) \sim \text{Species} + (1|\text{SexMixes}) + (1|\text{Observer})$$

Additional Information on Analyses of De-escalating Behaviour

To analyse factors influencing de-escalating behaviour during the first 30 min of two experimental fish encountering each other (see Methods for definitions and details), we fitted two LMERs, assuming a Gaussian error structure. The first model considered all behaviours recorded for both fish, while the second model more specifically looked at the expected dominance relationship between the two fish, considering aggression shown only by the larger fish and de-escalation shown only by the smaller fish. In the first model, we fitted our counts of de-escalating behaviours shown by both fish (fleeing behaviours and submissive quivers) as the response variable. We included three explanatory variables: (1) species identity (three-level factor: *L. elongatus*, *N. pulcher*, *V. moorii*), (2) the size ratio between the two fish (SL of the smaller fish divided by SL of the larger fish, larger values indicating more similar sizes of the two fish), and (3) all aggression shown in the first 30 min after the two fish first encountered each other (sum of bites, frontal displays and lateral displays shown by both fish). In addition, we included two random effects: (1) the sex mix of the two fish (three-level factor: both fish are females, both fish are males, one fish is a female and one a male), and (2) the observer's identity (four-level factor: S.A., X.G., B.R., D.Y.). We initially included the two-way interactions between species and aggressive behaviours and between species and size ratio. The second model had the same general structure, but we fitted it with the de-escalating behaviours shown by the smaller fish only as the response variable, and aggression shown by the larger fish only as one of the explanatory variables. The initial full models thus had the structure:

De-escalationAll~Species * SizeRatio + Species * AggressionAll + (1|SexMix) + (1|Observer)

De-escalationSmall~Species * SizeRatio + Species * AggressionLarge + (1|SexMix) + (1|Observer)

We subsequently removed the interaction between species and size ratio due to its nonsignificant effect in both models. The final models, the results of which are reported in the main text, thus had the structure:

De-escalationAll ~ SizeRatio + Species * AggressionAll + (1|SexMix) + (1|Observer)

De-escalationSmall ~ SizeRatio + Species * AggressionLarge + (1|SexMix) + (1|Observer)

Additional Information on Analyses of Mutual Tolerance

To analyse factors influencing whether two fish would be mutually tolerant 24 h after first encountering each other (see Methods for definitions and details), we fitted a GLMM with a logit link function, assuming a binomial error structure (bGLMM). In this model, we fitted whether or not fish were mutually tolerant (yes/no) as the binomial response variable. We included four explanatory variables: (1) species identity (three-level factor: *L. elongatus*, *N. pulcher*, *V. moorii*), (2) the size ratio between the two fish (SL of the smaller fish divided by SL of the larger fish; larger values indicate that fish were more similar in size), (3) all aggression shown in the first 30 min after the two fish first encountered each other (sum of bites, frontal displays and lateral displays shown by both fish), and (4) all de-escalation shown in the first 30 min after the two fish first encountered each other (sum of fleeing behaviours and submissive quivers shown by both fish). In addition, we included two random effects: (1) the sex mix of the two fish (three-level factor: both fish are females, both fish are males, one fish is a female and one a male), and (2) the observer's identity (four-level factor: S.A., X.G., B.R., D.Y.). To check for species-specific effects of size or behaviour, we initially also included all two-way interactions between species identity and all the other explanatory variables. The initial full model thus had the structure:

MutTol ~ Species * SizeRatio + Species * Aggression + Species * De-escalation + (1|SexMix) + (1|Observer)

All interactions were removed stepwise due to their nonsignificant effects. The final model, the results of which are reported in the main text, thus had the structure:

MutTol ~ Species + SizeRatio + Aggression + De-escalation + (1|SexMix) + (1|Observer)

To subsequently investigate the significant effect of species identity on mutual tolerance with regard to differences in social organization between the species, we used the same orthogonal contrasts for the post hoc analysis of this model as described above (Additional Information on Analyses of Status (Relative Size) Effects).

Table A1

The results of the final model (without any two-way interactions) of the analysis of aggressive behaviour shown by individual fish

	df	Estimate	SE	AIC	LRT	*P*
Intercept		4.081	0.16	1215.4		
Species	2			1216.4	4.964	0.084
Status	1	−1.362	0.138	1306.4	93.004	<0.001
Cooperative versus noncooperative		−0.04	0.052			
Stable pairs versus solitary		−0.193	0.089			

In this model, the ratio of the variance explained by the random effect ‘SexMix’ and the total residual variance was <0.001. *df*: degrees of freedom (1 for continuous data; levels minus 1 for factors); AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test; the reference category for Status was ‘large’; cooperative versus noncooperative: comparing the cooperatively breeding species (*N. pulcher*) with the two noncooperatively breeding species (*L. elongatus* and *V. moorii*); Stable pairs versus solitary: among the noncooperatively breeding species, contrasting the species forming long-term stable pairs (*V. moorii*) with the mostly solitary species (*L. elongatus*); refer to these two-way orthogonal contrasts for estimates of the three-level factor Species.

Table A2

The results of the final model (without any two-way interactions) of the analysis of de-escalating behaviour shown by individual fish

	df	Estimate	SE	AIC	LRT	*P*
Intercept		−0.644	0.23	684.24		
Species	2			683.08	2.838	0.242
Status	1	3.559	0.281	830	147.754	<0.001
Cooperative versus noncooperative		0.126	0.092			
Stable pairs versus solitary		0.167	0.164			

In this model, the ratio of the variance explained by the random effect ‘SexMix’ and the total residual variance was <0.001. *df*: degrees of freedom (1 for continuous data; levels minus 1 for factors); AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test; the reference category for Status was ‘large’; cooperative versus noncooperative: comparing the cooperatively breeding species (*N. pulcher*) with the two noncooperatively breeding species (*L. elongatus* and *V. moorii*); Stable pairs versus solitary: among the noncooperatively breeding species, contrasting the species forming long-term stable pairs (*V. moorii*) with the mostly solitary species (*L. elongatus*); refer to these two-way orthogonal contrasts for estimates of the three-level factor Species.

Table A3

The results of the final model (including the two-way interaction between Status and Species) of the analysis of time spent in the shelter by individual fish

	Estimate	SE	AIC	LRT	*P*
Intercept	6.261	0.337	1731		
Species:Status			1734.7	7.771	0.021

In this model, the ratio of the variance explained by the random effect ‘SexMix’ and the total residual variance was 0.025. AIC: Aikaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test; for further details and additional estimates of the interaction Species:Status see Table A4.

Table A4

The results of the final model of the analysis of the difference in time spent in the shelter between large and small fish in the same trial

	Estimate	SE	AIC	LRT	*P*
Intercept	407.11	89.3	1052.5		0.031
Species			1064.9	16.371	<0.001
Cooperative versus noncooperative	−166.38	39.97			<0.001
Stable pairs versus solitary	76.99	73.61			0.3

The table includes the results of the orthogonal contrasts analysis which was performed after confirming that the three-level main effect ‘Species’ was significant. In this model, the ratio of the variance explained by the random effect ‘SexMix’ and the total residual variance was <0.001. AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test; cooperative versus noncooperative: comparing the cooperatively breeding species (*N. pulcher*) with the two noncooperatively breeding species (*L. elongatus* and *V. moorii*); stable pairs versus solitary: among the noncooperatively breeding species, contrasting the species forming long-term stable pairs (*V. moorii*) with the mostly solitary species (*L. elongatus*); refer to these two-way orthogonal contrasts for estimates of the three-level factor Species.

Table A5

The results of the final model (with the two-way interaction between Species and all Aggression) of the analysis of all de-escalating behaviour by an experimental pair

	df	Estimate	SE	AIC	LRT	*P*
Intercept		23.575	12.706	539.91		
Size ratio	1	−44.61	16.547	545.52	7.613	0.006
Species:Aggression	2			572.21	36.298	<0.001

In this model, the ratio of the variance explained by the random effect 'SexMix' and the total residual variance was 0.041. *df*: degrees of freedom (1 for continuous data; levels minus 1 for factors); AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test.

Table A6

The results of the final model (with the two-way interaction between Species and Aggression by the large fish) of the analysis of de-escalating behaviour by the small fish

	df	Estimate	SE	AIC	LRT	*P*
Intercept		10.64	9.533	505.84		
Size ratio	1	−24.57	12.388	507.98	4.136	0.042
Species:Aggression	2			537.06	35.216	<0.001

In this model, the ratio of the variance explained by the random effect 'SexMix' and the total residual variance was 0.039. *df*: degrees of freedom (1 for continuous data; levels minus 1 for factors); AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test.

Table A7

The results of the final model (without any two-way interactions) of the analysis of mutual tolerance

	df	Estimate	SE	AIC	LRT	*P*
Intercept		2.401	2.922	68.689		
Species	2			73.91	9.221	0.009
Size ratio	1	−4.175	3.763	67.75	1.061	0.303
Aggression	1	−0.029	0.022	68.715	2.027	0.155
De-escalation	1	0.029	0.039	67.208	0.519	0.471
Cooperative versus noncooperative		0.687	0.252			0.006
Stable pairs versus solitary		−0.333	0.597			0.577

The table includes the results of the orthogonal contrasts analysis which was performed after confirming that the three-level main effect 'Species' was significant. In this model, the ratio of the variance explained by the random effect 'SexMix' and the total residual variance was 0.311. *df*: degrees of freedom (1 for continuous data; levels minus 1 for factors); AIC: Akaike information criterion; LRT: likelihood ratio test; *P*: as calculated on the basis of a chi-square test; cooperative versus noncooperative: comparing the cooperatively breeding species (*N. pulcher*) with the two noncooperatively breeding species (*L. elongatus* and *V. moorii*); stable pairs versus solitary: among the non-cooperatively breeding species, contrasting the species forming long-term stable pairs (*V. moorii*) with the mostly solitary species (*L. elongatus*); refer to these two-way orthogonal contrasts for estimates of the three-level factor Species.

Table A8

The sample sizes per species for pairs that were composed of different sex mixes

	FF	FM	MM
L. elongatus	10 (0)	7 (0)	6 (2)
N. pulcher	3 (1)	10 (5)	10 (7)
V. moorii	7 (0)	12 (1)	4 (2)

FF: female/female; FM: female/male; MM: male/male. Numbers in parentheses give the number of such pairs that were then recorded as mutually tolerant. For each species, 23 pairs were observed, but sex mixes were not explicitly balanced.

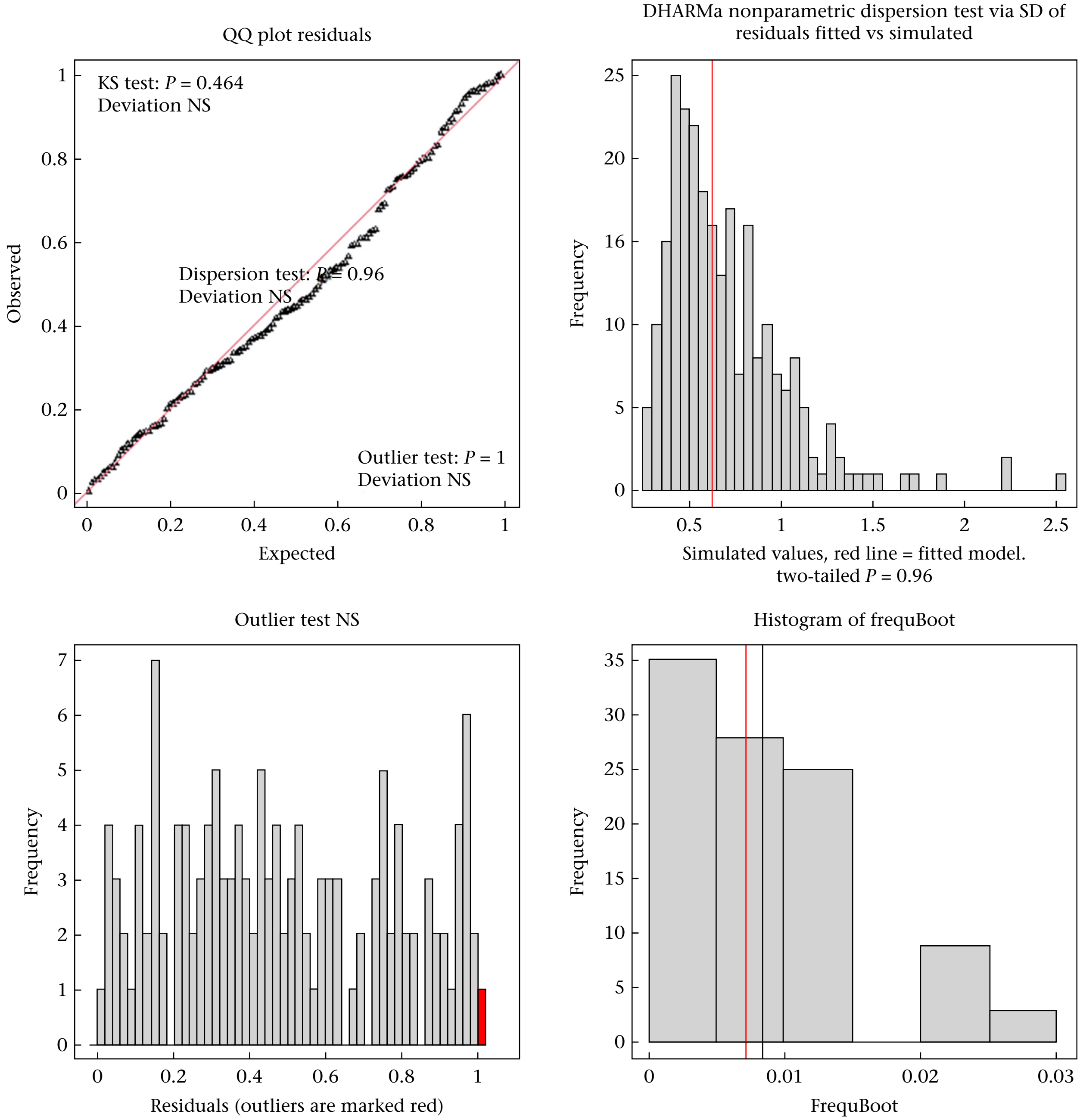

Figure A1. Model diagnostics for the results of the final model of the analysis of aggressive behaviour shown by individual fish, as derived with ‘testResiduals’ from DHARMa.

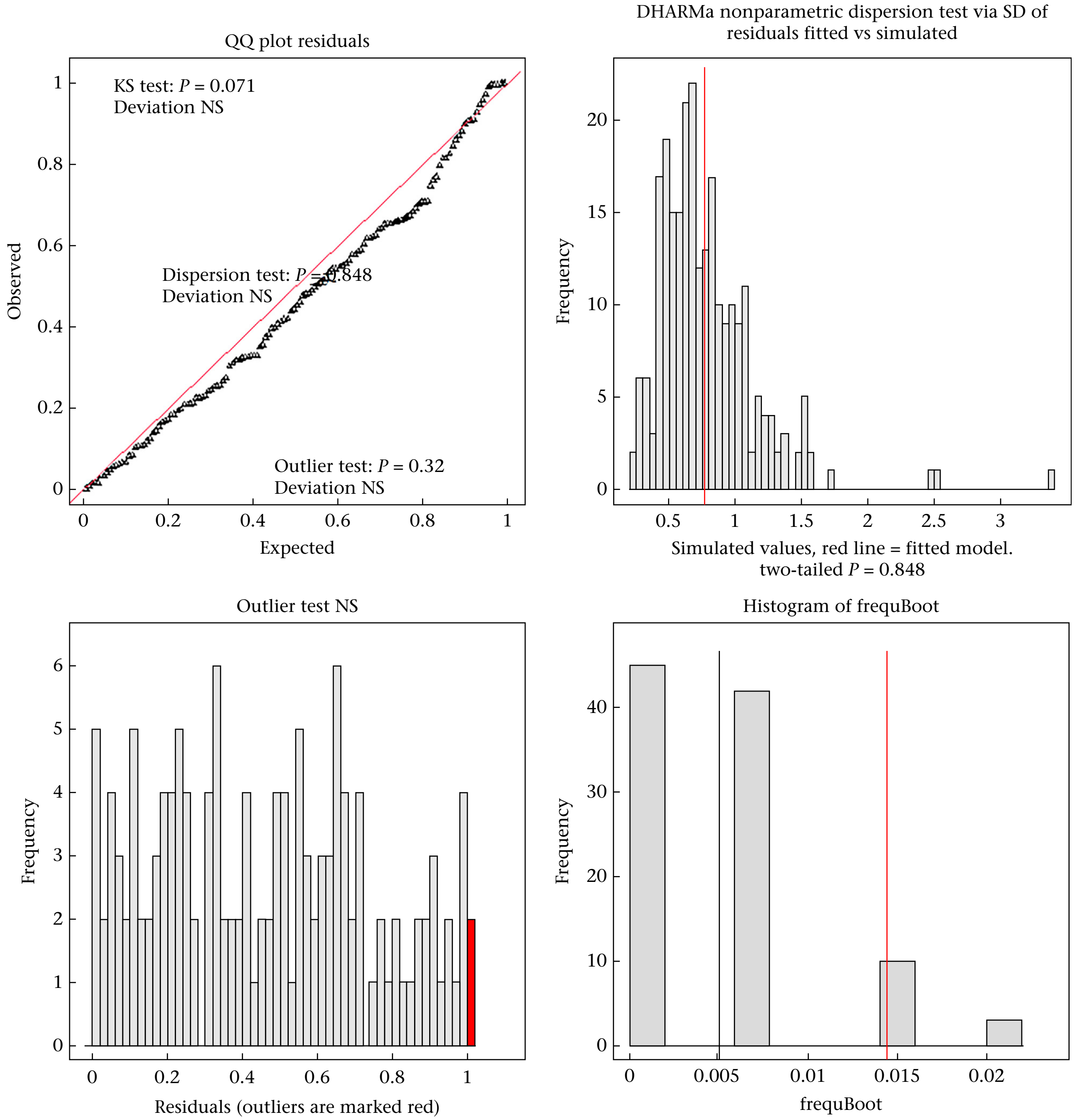

Figure A2. Model diagnostics for the results of the final model of the analysis of de-escalating behaviour shown by individual fish, as derived with ‘testResiduals’ from DHARMa.

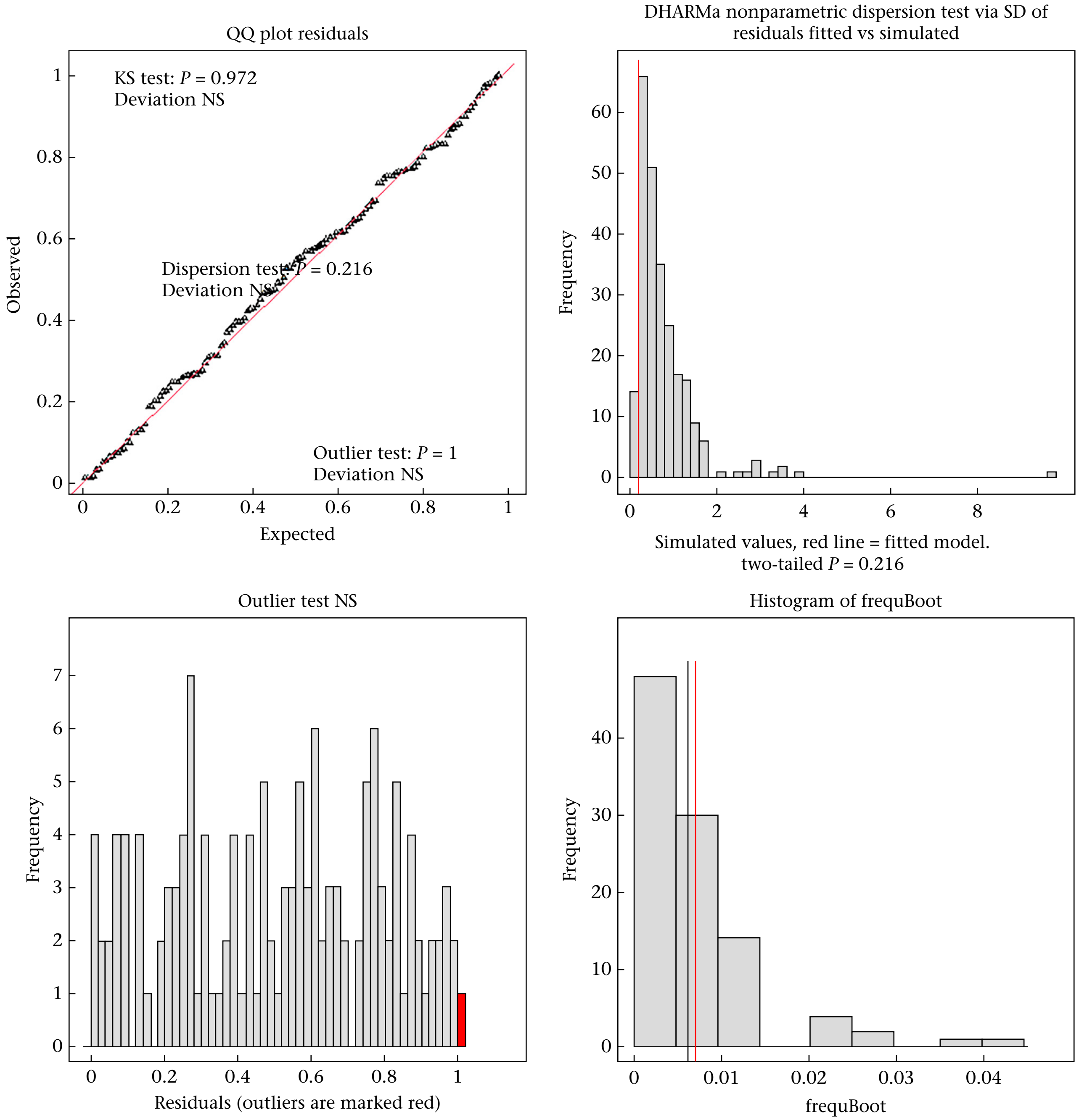

Figure A3. Model diagnostics for the results of the final model of the analysis of time spent in the shelter by individual fish, as derived with ‘testResiduals’ from DHARMa.

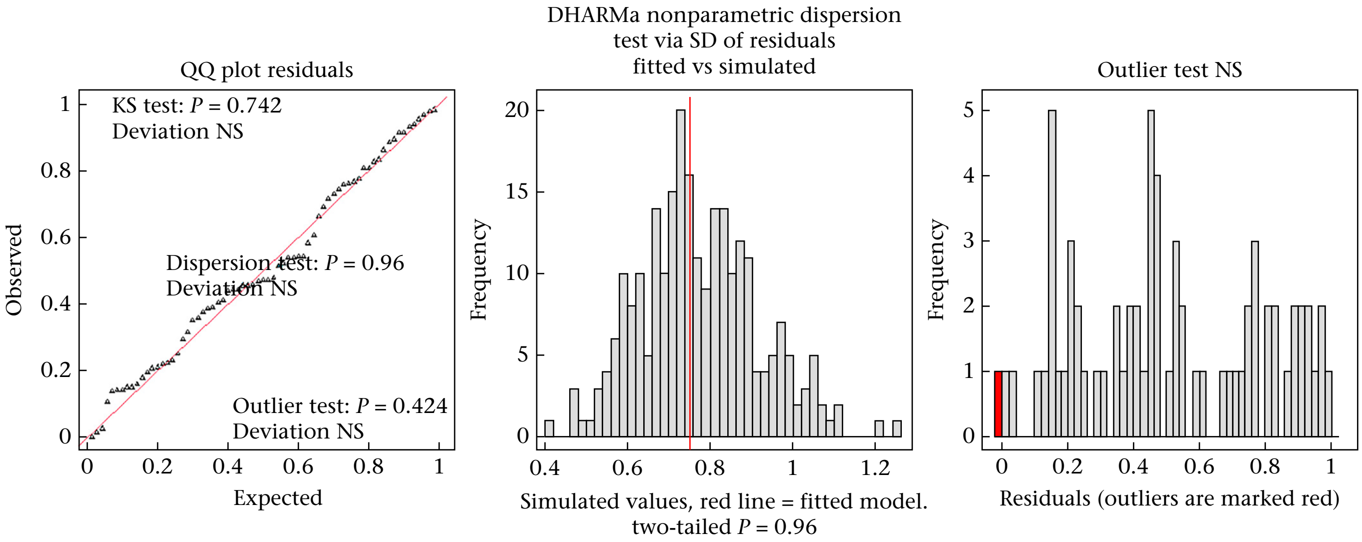

Figure A4. Model diagnostics for the results of the final model of the analysis of the difference in time spent in the shelter between large and small fish in the same trial, as derived with 'testResiduals' from DHARMa.

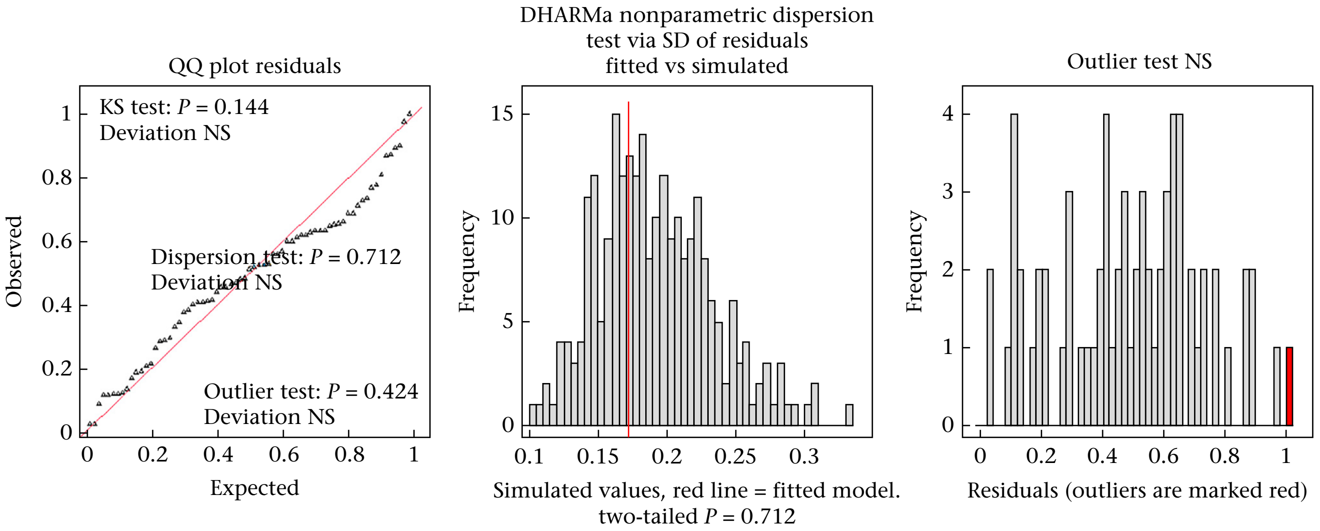

Figure A5. Model diagnostics for the final model for the analyses of factors influencing de-escalating behaviour, as derived with 'testResiduals' from DHARMa.

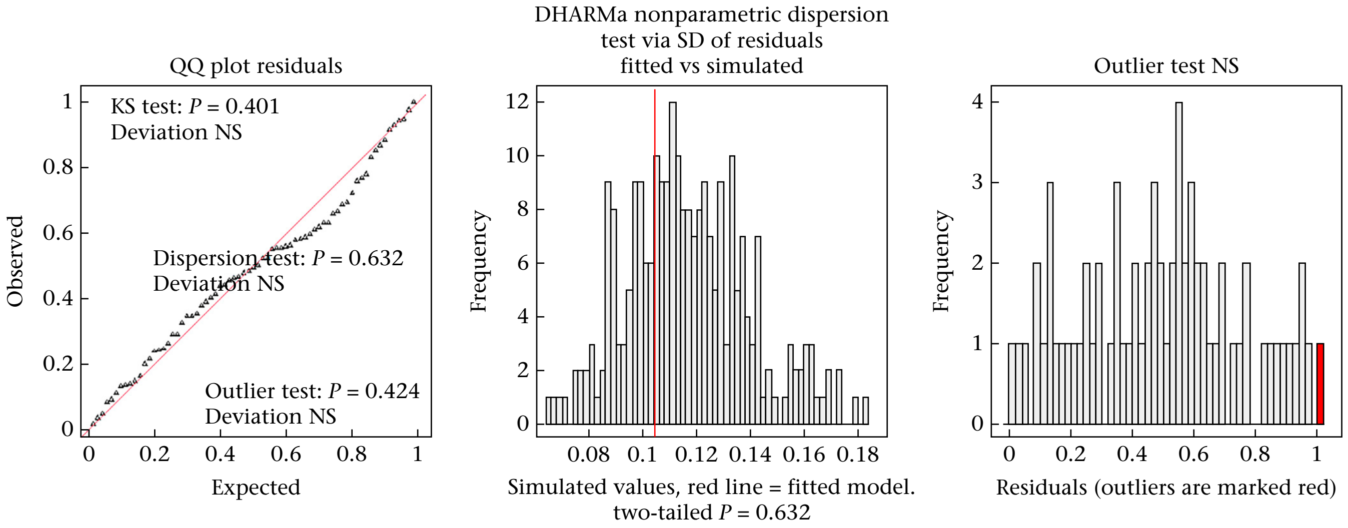

Figure A6. Model diagnostics for the final model for the analyses of factors influencing de-escalating behaviour by small fish, as derived with 'testResiduals' from DHARMa.

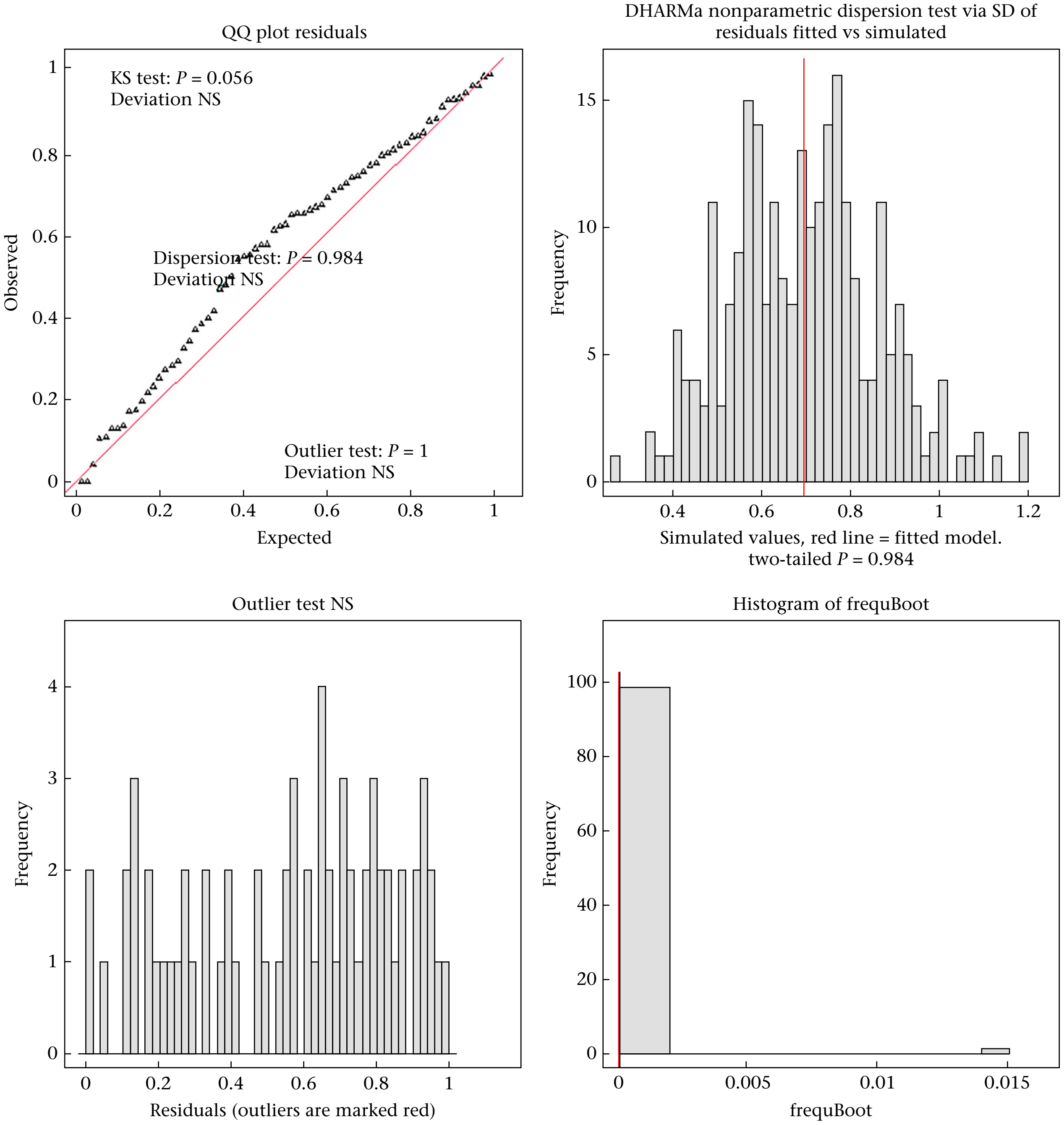

Figure A7. Model diagnostics for the final model for the analyses of factors influencing mutual tolerance, as derived with ‘testResiduals’ from DHARMa.

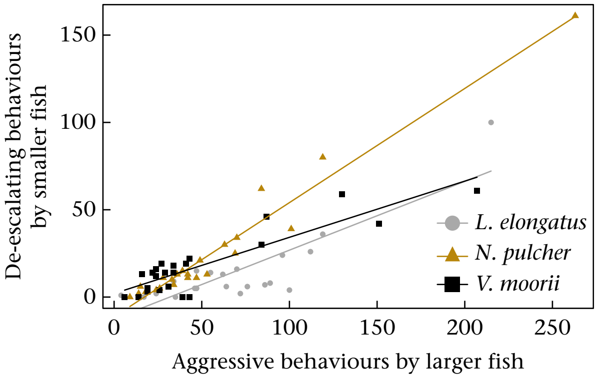

Figure A8. Behavioural differences between the three focal species (*Lepidiolamprologus elongatus* (grey), *Neolamprologus pulcher* (beige), *Variabilichromis moorii* (black)) as recorded in the first 30 min after two experimental fish encountered each other. The sum of all de-escalating behaviours shown by the smaller fish in an experimental pair is plotted as a function of the sum of all aggressive behaviours shown by the larger fish in the same pair, both as counts/30 min. Each point represents data for a single pair ($N = 69$, 23 per species). Lines show the values predicted by the respective species-specific linear models.