



Group-size preferences in a shoaling cichlid

Loris Durrer^{a,*}, Michael Taborsky^a and Joachim G. Frommen^{a,b}

^a Division of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, 3032 Hinterkappelen, Switzerland

^b Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester M15GD, UK

* Corresponding author's e-mail address: loris.durrer@gmx.ch

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Abstract

Group size is an important criterion in social decisions. Accordingly, assessing quantities is common in many animals. In fishes, studies on numerical abilities focus on a limited range of species. Arguably, cichlids show the greatest variability of social patterns among vertebrates. Nevertheless, knowledge about their quantitative abilities is scarce. Here we use the Lake Tanganyika cichlid *Lamprologus callipterus* to scrutinize the quantitative abilities of fish in the context of shoaling. Females chose between different numbers of conspecifics, varying in absolute and relative number differences. In half of the trials both shoals were composed of familiar sisters, while all fish were unfamiliar non-kin in the other half. Test fish consistently preferred the larger of two shoals, irrespective of the ratios. Their activity differed significantly between familiarity/relatedness treatments, indicating recognition of this parameter. *L. callipterus* therefore has fine-tuned discrimination skills, adding to the evidence that quantitative abilities are widespread in fishes.

Keywords

shoaling preference, quantity discrimination, objective file system, *Lamprologus callipterus*, familiarity, relatedness.

1. Introduction

Group living is common in animals, at least during some stage of their life (Krause & Ruxton, 2002; Ward & Webster, 2016). It can generate a variety of fitness benefits, like reduced predation risk (Pulliam, 1973; Wrona & Dixon, 1991; Dittmann & Schausberger, 2017), enhanced foraging efficiency (Ward & Zahavi, 1973; Bijleveld et al., 2010; Cvikel et al., 2015; Harel et al.,

2017), or energy saving (Herskin & Steffensen, 1998; Marras et al., 2015). Such benefits often correlate positively with group size (Wrona & Dixon, 1991; Beauchamp, 1998). However, the costs of group living may also increase with group size, for instance through resource competition among individuals (Cresswell, 1998; Maszczyk et al., 2014) or enhanced conspicuousness to predators (Vine, 1973; Hebblewhite & Pletscher, 2002; Jackson et al., 2005). Other factors than group size may additionally influence the quality of a given group, for example the familiarity and relatedness among group members (Valsecchi et al., 1996; Ancillotto & Russo, 2014; Keller et al., 2017), which may influence aggression levels, the formation of stable hierarchies, or cooperation potential.

Consequently, individuals should integrate multiple factors when choosing to join, leave or change a group. The underlying social decisions have been studied in fishes aggregating in shoals or schools (Pitcher & Parrish, 1993; McGhee, 2019). Here, larger groups show increased foraging efficiency (Pitcher et al., 1982; Grand & Dill, 1999), a decreased individual risk of predation (Neill & Cullen, 1974), and better protection against macroparasite infection (Poulin & FitzGerald, 1989). On the other hand, smaller groups pose less competition for scarce resources (Krause, 1994; Krause & Ruxton, 2002) and they are less likely to be spotted by predators (Krause & Godin, 1994; Botham et al., 2005). Therefore, the decision to join a group may require assessment of costs and benefits of group size in dependence of ecological conditions, and the capability to differentiate between groups of different size.

The competence of numerical differentiation is widespread in animals including humans and has been shown to employ similar mechanisms across taxa (Xu, 2003; Feigenson et al., 2004), including fishes (Agrillo et al., 2012; Agrillo & Bisazza, 2018). In general, Weber's law suggests that when the ratio of two quantities approaches one, the difficulty of differentiating between said quantities increases (Weber, 1905; Krause et al., 1998). Hence, three is more easily distinguishable from four (ratio 0.75) than four is from five (ratio 0.8). Arguably, difficulty does not only increase with higher relative ratios, but also smaller absolute differences. For instance, three vs. five is more easily distinguishable than four vs. five. Studies on fishes have thus far investigated number differentiation mainly in the context of foraging (Lucon-Xiccato et al., 2015; Gómez-Laplaza et al., 2018), and shoaling (Hager &

Helfman, 1991; Krause, 1993; Agrillo et al., 2008; Gómez-Laplaza & Gerlai, 2011; Forsatkar et al., 2016; Bai et al., 2019). However, these studies focus on a limited range of species, with poecilids (see Agrillo & Bisazza, 2018 and citations therein), three-spined stickleback (*Gasterosteus aculeatus*; Krause, 1993; Krause et al., 1998; Frommen et al., 2009; Thünken et al., 2014; Mehlis et al., 2015; Mehlis-Rick et al., 2018) and angelfish (*Pterophyllum scalare*; Gómez-Laplaza & Gerlai, 2011, 2013; Gómez-Laplaza, 2012; Gómez-Laplaza et al., 2018) being overly represented.

Cichlids exhibit some of the most complex and diverse social systems among fishes (Taborsky, 2016; Taborsky & Wong, 2017), with familiarity and kinship being important drivers of social decisions (Jordan et al., 2009; Lee-Jenkins & Godin, 2013; Thünken et al., 2016). Nevertheless, the numerical abilities of cichlids are largely unknown, except from a few neotropical species (angelfish: Gómez-Laplaza & Gerlai, 2011; convict cichlids: Forsatkar et al., 2016). More generally, the integration of multiple factors potentially influencing shoal choice has rarely been studied. This is a severe drawback, because in nature the interplay of several factors usually affect the fitness consequences of social decisions. We scrutinize the effects of group size and familiarity/relatedness on shoaling decisions in the Lake Tanganyika cichlid *Lamprologus callipterus*. Besides anecdotal remarks (Brichard, 1989; Konings, 1998), little is known about the grouping behaviour of this species other than general formation of shoals outside of the reproductive context (Sato et al., 2004; Ota et al., 2010). Mating takes place several times throughout the year, with peak mating times following the lunar cycle (MT and JGF, pers. observation). Shoals are abandoned for breeding, as large males become territorial during the nest-holding period and females lay their eggs in snail shells within the nest (Sato, 1994; Taborsky, 1998; Schütz et al., 2010; Mitchell et al., 2014). Hence, individuals face the decision-making process to join a particular shoal at least after every breeding period, though fission-fusion events are most likely much more common. Consequently, this species appears to be an ideal model to study the integration of information in shoaling decisions, when several factors may vary independently of each other.

In this study, we asked whether *L. callipterus* females distinguish between groups that differ only slightly in size, predicting that in general they would prefer the larger of two available shoals. Furthermore, we asked whether and how familiarity or relatedness towards presented shoal fish would influence their behaviour.

2. Methods

2.1. Study species

Lamprologus callipterus is a cichlid fish endemic to Lake Tanganyika that breeds in empty gastropod shells. The particular breeding behaviour of this species explains its extreme size dimorphism, both between males and females (Schütz & Taborsky, 2000, 2005; Schütz et al., 2006) and between different male morphs, as males pursue alternative reproductive tactics (ARTs; Taborsky, 1998; Sato et al., 2004). Large bourgeois males collect empty snail shells in which females lay their eggs, whereas opportunistic sneaker males and specialized dwarf males attempt to fertilise eggs parasitically during spawning (Sato et al., 2004; Schütz et al., 2010). Dwarf males remain small for life, weighing on average only 2.5% of the body weight of bourgeois nest holders (Sato et al., 2004), and these two ARTs reflect a Mendelian genetic polymorphism (Wirtz-Ocaña et al., 2014). Differences in the two male morphs are not confined to their morphology, growth and breeding behaviour, but pertain also to their foraging behaviour and allocation of energy reserves (Schütz et al., 2010; von Kuerthy et al., 2015). Outside of breeding, *L. callipterus* forms size-assorted shoals for benthic foraging, which occurs mainly by digging out crustaceans and insect larvae from sand. These fission-fusion shoals are highly dynamic in both composition and movement, and they can reach sizes of up to about 100 individuals (MT and JGF, pers. obs.). Still, in comparison to their breeding behaviour, their shoaling behaviour is little understood.

2.2. Holding conditions

The experiments were conducted at the Ethologische Station Hasli, University of Bern, Switzerland, under license BE-73/15 of the Veterinary office of Kanton Bern. To avoid sex differences influencing the results (Ruhl et al., 2009; Rystrom et al., 2018) we used only adult *Lamprologus callipterus* females in this study, which were laboratory-bred F1–F3 offspring derived from wild-caught individuals from the southern end of Lake Tanganyika. We studied individuals from ten different families that were kept in 100 l and 200 l tanks, depending on group size. The size of the families varied between nine and 24 individuals, containing both males and females. Water temperature ($26 \pm 1^\circ\text{C}$) and illumination (13:11 L:D cycle) resembled natural conditions in Lake Tanganyika (cf., Taborsky, 1984). Fish were fed

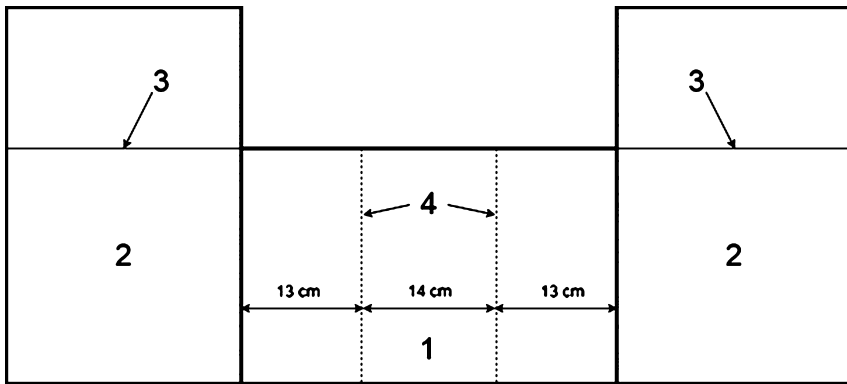


Figure 1. The experimental set-up (overhead view). The stimulus tanks (2) were placed at both ends of the focal subject's tank (1) and perpendicular to it. The stimulus tanks were size reduced with an opaque slate (3) so that the stimulus fish could not leave the visual field of the focal fish. Preference zones were indicated on the tank walls (4).

commercial flake food on five days a week, and on one day they were fed a mix of defrosted crustaceans and mosquito larvae. During the experimental phase, feeding took place after the observations in order to standardise the nutritional state of all fish (Krause, 1993; Frommen et al., 2007).

2.3. Experimental setup

For the experiment we used three 25 l tanks, measuring $40 \times 25 \times 25$ cm ($l \times w \times h$) each. The experimental tanks were kept under the same temperature and light conditions as the holding tanks. The tank for the focal fish was placed in the middle, while two stimulus tanks were positioned perpendicular to the focal tank on both of its sides (Figure 1). On the walls of the focal tank we indicated three sections using a black marker. The sections on the left and right measured $13 \times 25 \times 25$ cm ($l \times w \times h$) and marked the 'preference zones' on each side. The neutral zone in the middle measured $14 \times 25 \times 25$ cm. To avoid any influence from outside, the three tanks were visually isolated from the surrounding room with opaque black covers from three sides. Additionally, the bottom of each tank was covered with black plastic sheets to limit reflections and reduce stress for the fish (Merighe et al., 2004). Besides that, no further structure was added to the tanks, in order to continuously allow an uninterrupted line of sight. Such novel environment has been shown to increase the shoaling tendency in other fish species, most likely because the stimulus fish search the safety of the shoal under such

conditions (Thünken et al., 2014). The frontal side was left uncovered to allow recording of the focal fish using a recorder camera model Sony HDR CX-550V. To further avoid any disturbance from outside the whole setup including the camera was visually isolated from the surrounding room with a black curtain.

2.4. Experimental procedure

We conducted no training of our fish but observed spontaneous shoaling decisions. Test females were allowed to choose between two stimulus shoals that differed in size. To test their discrimination ability, we used three different combinations of ratios between the two shoals: 1 vs. 3 ($N = 34$), 1 vs. 2 ($N = 34$) and 2 vs. 3 ($N = 42$). Thus, shoals in different treatments differed both in absolute and relative shoal size. In half of the respective trials, all stimulus fish were familiar sisters of the test fish, while they were unfamiliar and unrelated in the other half. Hence, we could not differentiate whether potential differences in trials containing kin or non-kin were caused either by familiarity or by relatedness in this experiment.

The trials were run between 9:00 and 17:00. The three different combinations were tested on the same days and at comparable times in order to avoid time and sequence effects influencing the results. The stimulus and focal females were caught within 10 min before the respective observation. First, the two stimulus groups were caught using a net and their standard body length (SL) was measured on a measuring board to the nearest mm. They were then introduced to the two stimulus tanks so that the difference between the mean lengths of all fish in a shoal did not exceed 2 mm. Afterwards, the focal female was caught, measured and released in the middle of the focal tank. Recordings started immediately afterwards and lasted 30 min. After the recording, all fish were put back into their home tank. The water in the focal tank was renewed after every observation to prevent effects of olfactory cues from the previous fish (cf., Mehliis et al., 2015). Focal females were used only once. We minimised the number of stimulus fish to keep the total number of research animals low (Russell & Burch, 1959). Therefore, stimulus fish were presented in more than one shoal ratio treatment and in up to 3 trials per ratio treatment. However, shoals were never composed of the same individuals and we took care that fish were used in the smaller and larger group alike (cf., Frommen et al., 2009; Thünken et al., 2014). Therefore, individual differences in behaviour cannot explain potential effects of shoal

size. The location of the smaller and larger stimulus shoals was switched between trials in order to avoid potential side effects influencing the outcome.

2.5. Data acquisition and analyses

The recordings were analysed using Solomon Coder (<http://solomoncoder.com>). As a preference measure, we took the time each focal female spent in the zones in front of the respective stimulus groups. Furthermore, as a measure of sampling behaviour we counted how often the female entered and left each zone. A switch of zones was determined as soon as the eyes crossed the line indicated on the tank wall. The observer was blind to the respective treatment during data analysis.

We compared the times focal subjects spent near the larger and smaller shoal by evaluating the percentage of time spent near the larger shoal. A preference index was determined as follows:

$$\text{Index} = \frac{t(\text{large shoal})}{t(\text{large shoal}) + t(\text{small shoal})}$$

An index value of 0.5 indicates no preference for either shoal. A value above 0.5 indicates a preference for the larger, one below 0.5 for the smaller shoal. All statistical tests were performed using R (Version 3.2.5) and the stats and lme4 packages. All tests were two-tailed. We first ran a linear mixed model with the index being the dependent variable, testing for differences in preference between shoal ratios and familiarity treatments. We included family ID as a random factor, as we used multiple females of each family. The distribution of our index data was skewed to the left, we therefore conducted an antilog transformation of the index. Visual observation of the QQ-plot of the model confirmed all residuals to be within the confidence intervals. The model first included an interaction term between shoal ratio and familiarity, but we ultimately dropped the term as it was non-significant (Engqvist, 2005). We further tested the indices of each shoal ratio against a null-assumption of 0.5 using one-sample Wilcoxon tests.

We calculated overall time spent shoaling, i.e. the time spent in the two preference zones combined, for each fish. We used this value to determine whether our test fish spent more time in the preference zones than the percentage of area of the preference zones made up (65%). For this, we performed a one-sample Wilcoxon test, with a null-assumption of 0.65.

Finally, we ran a generalised linear mixed model on the number of zone changes. We again tested for effects of shoal ratio, familiarity and their

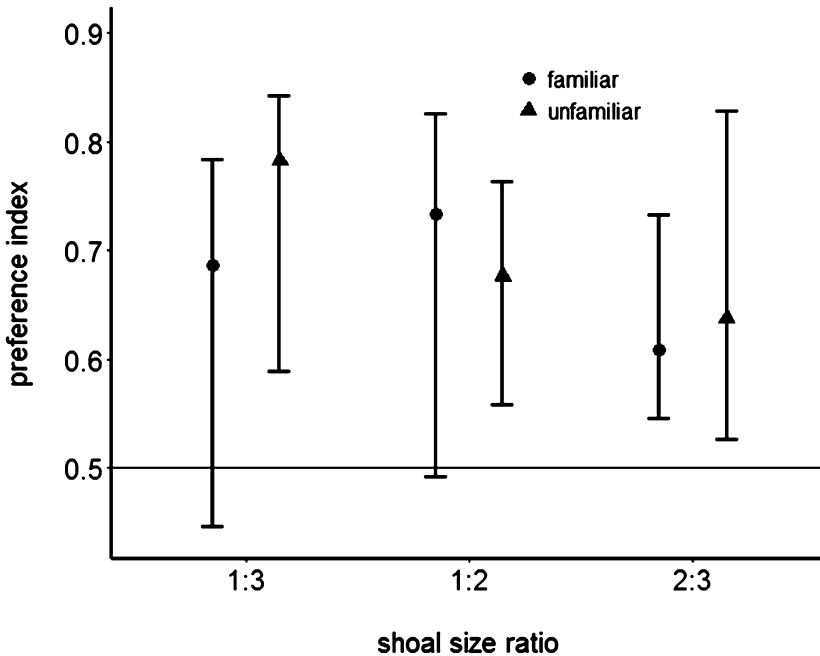


Figure 2. Shoaling preferences of females in different treatments. Values above 0.5 (marked by a horizontal line) indicate a preference for the larger shoal. At all presented shoal ratios, females significantly preferred shoaling with the larger shoal, while familiarity/relatedness had no effect on this preference (●familiar kin, ▲unfamiliar non-kin). Shown are medians and interquartile ranges.

interaction, using family ID as a random factor. The differences were then further analysed using unpaired Wilcoxon tests for each shoal ratio data group.

3. Results

The test females showed a significant preference for the larger shoal across all shoal ratios (one-sample Wilcoxon-test; 1 vs. 3: $N = 34$, $V = 497$, $p < 0.001$; 1 vs. 2: $N = 34$, $V = 452$, $p < 0.01$; 2 vs. 3: $N = 42$, $V = 752$, $p < 0.001$; Figure 2). Preference strength was comparable between shoal ratios (LMM, $N = 110$, $LRT = 0.93$, $p = 0.63$). Familiarity of the stimulus fish to the test female had no effect on this preference (LMM, $N = 110$, $LRT = 0.79$, $p = 0.38$). The test fish spent a significantly higher proportion of their time (arithmetic mean \pm SE: $89 \pm 6.8\%$) in the shoaling zone

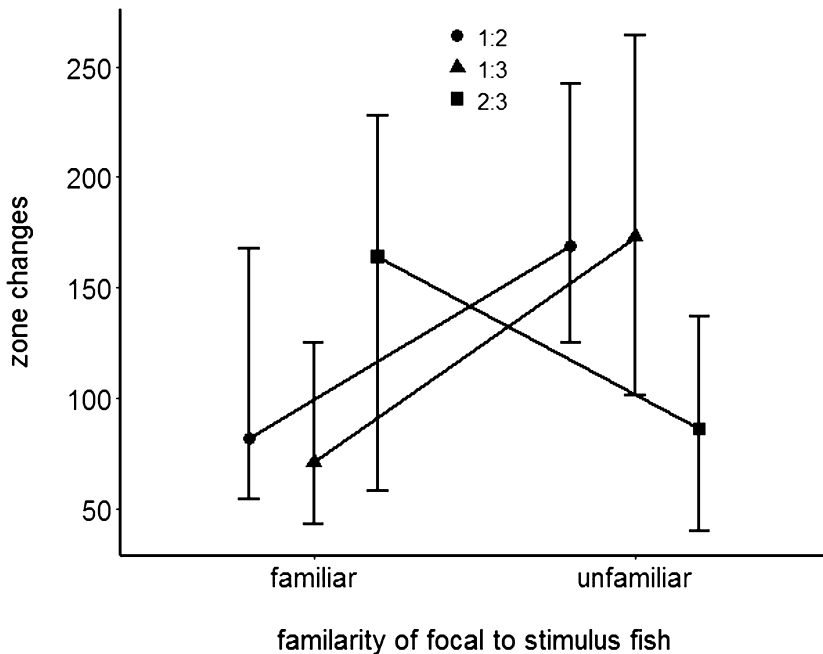


Figure 3. Familiarity/relatedness had a significant effect on the amount of zone changes. When focal subjects experienced shoal ratios of 1:2 (●) and 1:3 (▲), they switched between zones more often when the stimulus shoals contained unfamiliar non-kin than when shoal members were familiar kin. In contrast, they changed zones less often when choosing between shoals that contained unfamiliar non-kin when the shoal ratio was 2:3 (■). Shown are medians and interquartile ranges.

compared to what would be expected just from the proportion of the area (one-sample Wilcoxon-test, $N = 110$, $V = 6104$, $p < 0.001$).

Test females were highly active, with on average 140 zone changes in the recorded 30 min period. Individual activity was highly variable, indicated by a standard deviation of 100. The interaction between shoal ratio and familiarity had a significant effect on the amount of zone changes shown by the test females (GLMM, $N = 110$, $LRT = 677.07$, $p < 0.001$). When exposed to shoal ratios of 1 vs. 3 and 1 vs. 2, test females switched between zones significantly more often when encountering unfamiliar non-kin (unpaired Wilcoxon-test; 1 vs. 3: $N_{\text{non-kin}} = 17$, $N_{\text{kin}} = 17$, $W = 71.5$, $p < 0.05$; 1 vs. 2: $N_{\text{non-kin}} = 17$, $N_{\text{kin}} = 17$, $W = 76.5$, $p < 0.05$), while at a ratio of 2 vs. 3, they changed less often when tested with unfamiliar fish (unpaired Wilcoxon-test, $N_{\text{non-kin}} = 21$, $N_{\text{kin}} = 21$, $W = 297$, $p = 0.056$; Figure 3).

4. Discussion

Female *L. callipterus* showed a general preference to join the larger of two shoals, which conforms to previous studies on other fish species (reviewed in Agrillo & Bisazza, 2018). In our study, test subjects were exposed to varying discrimination intricacies. In the choice situation 1 vs. 3 and 1 vs. 2 conspecifics the fish experienced both relative and absolute number differences, whereas in the choice situation 1 vs. 2 and 2 vs. 3 conspecifics only relative number differences existed. Regardless, the performance of focal test subjects did not decrease in treatments with lower ratio. This indicates that female *L. callipterus* possess fine-tuned abilities when facing small relative and absolute differences. The absence of shoal ratio effects are compatible with the use of a nonverbal representational system postulated to account for discrimination of small number of items. Discrimination of quantities has been argued to rely on two systems: an object file system for representing small numbers ($\leq 3-4$) and an approximate number system for representing large numbers (> 4), which is affected by the numerical ratio (Feigenson et al., 2004). The ability of our test fish to discriminate 1 vs. 2, 2 vs. 3 and 1 vs. 3 with no differences between size ratios seems to support the operation of the object file system for small numbers. Currently, we do not know the abilities of *L. callipterus* to differentiate between higher shoal size ratios, such as between 3 and 4 or 8 and 9, and we cannot safely predict their abilities to differentiate between larger groups (for instance between 20 and 30). However, as *L. callipterus* often moves in large groups under natural conditions, we would expect similar capabilities, as has been observed in other fish species that successfully distinguish between larger shoal sizes (Agrillo et al., 2010; Piffer et al., 2012; Thünken et al., 2014; DeLong et al., 2017). Furthermore, studies on different vertebrate species suggested that the approximate number system might also be responsible for the estimation small numbers (Gallistel & Gelman, 1992; Rugani et al., 2013; Mehliis et al., 2015; Stancher et al., 2015; see also Agrillo et al., 2014 and further references therein). As larger numerosities or numerosities that spanned the boundary between the two systems were not tested in the present study, further studies are needed to elucidate the limits of the quantitative abilities of *L. callipterus*, as well as the exact mechanism of number discrimination in this species in more detail.

Besides potential numerical abilities, also non-numerical, continuous attributes such as density, cumulative surface area or overall space occupied by

a group might play a role in mediating preferences for larger shoals in *L. callipterus*. Indeed, several studies using various experimental approaches have dealt with that topic in other fish species (Frommen et al., 2009; Gómez-Laplaza & Gerlai, 2013; Piffer et al., 2013; Rugani et al., 2013). In our study, for example, the space available for all stimulus fish was the same, leading to less numerous shoals potentially being perceived as less dense. Such density differences have been shown to influence shoaling preferences in other fishes, for example in three-spined stickleback (Frommen et al., 2009). Ultimately, both mechanisms will lead to a preference for the larger of two groups in our study.

Shoal size is just one factor that can influence shoaling preference. In addition, the quality of a shoal, for example the size of individuals within a shoal, can affect shoaling preferences (Krause, 1994; Cattelan & Griggio, 2018), as well as environmental variables (Weetman et al., 1999; Fischer & Frommen, 2013), such as the presence of predators (Hager & Helfman, 1991; Hoare et al., 2004). Also, the specific state of the choosing individual, for example its health (Krause & Godin, 1994; Barber et al., 1995; Poulin, 1999), hunger (Krause, 1993; Frommen et al., 2007), or reproductive status (Frommen et al., 2012) may influence shoaling decisions. Several studies in different fishes have shown that familiarity and kinship to conspecifics can be recognised and affect shoaling preferences and behaviour (e.g., Frommen & Bakker, 2004; Gómez-Laplaza & Fuente, 2007; Davis et al., 2017; Cattelan et al., 2019; reviewed in Ward & Hart, 2003). Guppies (*Poecilia reticulata*), for instance, show mutual preferences for familiar conspecifics depending on previous social experiences (Cattelan et al., 2019). However, our fish did not change their intensity of preference for the shoals in either familiarity treatment, implying that they do not favour specific individuals. Furthermore, we did not observe any obvious behavioural differences, like aggressive displays expressed towards familiar or unfamiliar shoals. Nevertheless, focal fish showed different levels of zone changes, depending on the familiarity and relatedness of the presented stimulus fish. This indicates their capability of recognising familiar kin. While in shoal ratios of 1:3 and 1:2 we observed an increased amount of zone changes when test subjects were facing unfamiliar and unrelated individuals, the opposite effect appeared with the shoal ratio of 2:3. We currently cannot explain this divergence, yet it may imply that familiarity and kinship do not have straightforward effects on social decisions in this species. Nonetheless, we could show that *L. callipterus* can

distinguish between conspecifics on that level, which provides future opportunities to study the impact of familiarity and relatedness on their shoaling choices. It is important to note that in this study we did not assess whether our fish prefer to shoal with familiar over unfamiliar conspecifics, and we did not differentiate between familiarity and relatedness effects.

Activity of focal subjects was very high overall, which is in accordance with other studies where fishes were tested in a novel environment (Gómez-Laplaza & Morgan, 1991; Gerlai, 2010). The time spent shoaling was significantly higher than expected by random spacing patterns in the test tank. This implies that our fish indeed assessed the presented shoals and based their choice on the information thereby acquired.

In conclusion, by using spontaneous shoaling decisions without prior training, we show that *L. callipterus* has the ability to discriminate between shoals of different size. Furthermore, they recognised familiar kin and included such information into their shoal sampling behaviour. These findings increase our understanding of the general occurrence of number discrimination abilities in fishes by adding the hitherto unstudied African cichlids to the current literature.

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