

Concordant female mate preferences in the cichlid fish *Tropheus moorii*

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Abstract Discriminating female mate preferences enhance the variance in reproductive success among males of a population and create a potential for sexual selection, which can account for trait evolution and diversification. Fish color patterns are among the prime targets of mate choice-driven sexual selection. Populations of the cichlid *Tropheus* from Lake Tanganyika display remarkable geographic color pattern variation, but the role of female choice in their rapid and rich phenotypic diversification is unclear. Males and females establish a pair bond prior to spawning monogamously, but as brood care is strictly maternal, female investment in reproduction is high and the operational sex ratio is male-biased. Therefore, variance in male reproductive success can accrue if individual males succeed repeatedly in securing a mate. To test this prediction in the red colored *Tropheus moorii* “Chimba”, four pairs of males were presented to a series of females and female mate preferences were inferred from pairwise interactions. There was a significant difference in mating success between the males of each pair ($P < 0.001$ over all

trials), as—with one exception—females shared preferences for the same males. Male courtship activity was strongly correlated with female choice. Our experiment suggests that female choice contributes to the variance in male reproductive success in the tested population.

Keywords Mate choice · Sexual selection · Cichlidae · Courtship · Lake Tanganyika

Introduction

Variance in reproductive success among individuals in a population results from both selection and random events and is a prerequisite for evolutionary change, population differentiation, and finally speciation. The potential for intra- and intersexual selection to produce high variance in mate and offspring numbers is considered to be greater in either polygynous or polyandrous mating systems than in monogamous species (Awise et al., 2002). Congruently, sexual dimorphism, considered a consequence of sexual selection, is prevalent and most pronounced in polygynous and polyandrous species (Awise et al., 2002), and vice versa, the degree of sexual dimorphism has been used as a proxy to quantify the strength of sexual selection in a species (e.g., Lande, 1980; Owens et al., 1999) and to provide evidence for the correlation between sexual selection and species richness (e.g., Barraclough et al., 1995; Møller &

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Cuervo, 1998; Stuart-Fox & Owens, 2003; Mank, 2007; but see Gage et al., 2002; Morrow et al., 2003; Ritchie et al., 2005).

In the cichlid species flocks (tribe Haplochromini) of the East African Lakes Malawi and Victoria, the predicted relationship between mating system, sexual dimorphism, and divergence rate seems to hold (Turner, 1994; Seehausen, 2000). Maternal brood care in the way of mouthbrooding without male participation creates male-biased operational sex ratios and allows for polygamy and female mate choice (Kellogg et al., 1995; Balshine-Earn, 1996; Kokko & Johnstone, 2002).

Body coloration of haplochromine cichlids is cryptic in females but elaborate and often conspicuous in males, and females of some species were shown to base their mate choice on male coloration (Maan et al., 2004; Pauers et al., 2004). Moreover, male color pattern is one of the first traits to diverge between closely related species and populations (Van Oppen et al., 1998; Seehausen & Schluter, 2004; Genner & Turner, 2005), and is able to sustain reproductive isolation between sympatric populations (Seehausen, 1997; Seehausen et al., 1998). Finally, an astonishing number of species and intraspecific color morphs evolved in each of the two lakes within a short period of time (Turner et al., 2001). Hence, it has been argued that the divergence into colorful but eco-morphologically similar species and populations was driven by sexual selection through female choice operating on eco-morphologically divergent lineages created by natural selection (Seehausen & van Alphen, 1999; Danley & Kocher, 2001; Allender et al., 2003).

The cichlid species assemblage of the third Great Lake of East Africa, Lake Tanganyika, comprises several genetically, ecologically and morphologically highly divergent tribes with distinct evolutionary histories (Koblmüller et al., 2008a), one of which—the Tropheini—is closely related to the haplochromine species of Lakes Malawi and Victoria (Salzburger et al., 2005; Koblmüller et al., 2008b). Within the Tropheini, species and allopatric populations of the genus *Tropheus* have evolved a stunning diversity of color patterns (e.g., Konings, 1998; Schupke, 2003; Egger et al., 2007). Mate choice experiments between color morphs of *T. moorii* revealed variable degrees of reproductive isolation

between four different morphs (Egger et al., 2008, 2010); by and large, there is evidence that isolation is more complete between phenotypically highly distinct morphs than between similar morphs (Salzburger et al., 2006; Egger et al., 2010). However, it remained questionable whether mate selection is also able to provide for variance in reproductive success within populations, especially as some of the traits commonly associated with sexual selection are lacking in *Tropheus*. Most populations are sexually monomorphic with both genders displaying the same—population specific—color pattern, and both sexes use color signals in social interactions such as the defense of their individual territories (Wickler, 1969; Sturmbauer & Dallinger, 1995). The peculiar mating system of *Tropheus* can be described as ‘serial monogamy’: Males and females establish temporary pair bonds in the males’ territories prior to spawning, upon which the females abandon their mates and mouthbrood their eggs and fry by themselves (Yanagisawa & Nishida, 1991). Genetic analysis of wild-caught mouthbrooding females and their fry revealed a complete absence of multiple mating, as offspring genotypes were consistent with a single sire per brood (Egger et al., 2006).

With uniparental maternal brood care and long spawning intervals (Yanagisawa & Sato, 1990), female investment in reproduction is high and their reproductive cycles are long, but males also invest time and resources when they allow the females to feed heavily from their territories during the pair bonding period (Yanagisawa & Nishida, 1991; Schürch & Taborsky, 2005; Schütz et al., 2010). Nonetheless, in computer simulations of mating and reproduction based on field data of *Tropheus* and using different assumptions on mate choice behavior and reproductive biology, the operational sex ratio was strongly male-biased and similar to that retrieved from simulations of a polygynous system without male investment in reproduction (Sefc, 2008). Moreover, variances in simulated male reproductive success in *Tropheus* were nearly as high as in the simulated polygynous system, and within the range of estimates from natural populations of some sexually dimorphic birds and fishes. Importantly, the simulations showed that the distribution of “quality traits” among males and the ability of females to distinguish between males of different “quality” were the strongest determinants of variance; male “quality trait” values were interpreted

to summarize attractiveness based on all possible mate choice cues including the males' territories (Sefc, 2008).

In other words, if individual males succeed repeatedly in securing a mate, considerable variance in male reproductive success may accrue despite pair bonding and monogamous spawning. The mate choice experiment in this paper was set up in order to test this prediction. Pairs of males were presented to a suite of females, and we asked whether different females would show concordant preferences.

Methods

Experimental protocol and data analysis

The individuals used in our experiments were wild-caught adult *Tropheus moorii* from Chimba, Zambia (Fig. 1). *Tropheus* "Chimba" is one of a series of red colored populations, which inhabit the shoreline of northwestern Zambia and southern Congo and are differentiated from each other by slight variations in hue and the position of bright red color patches (Schupke, 2003). The fish were housed in individual aquaria before trials (60 × 30 × 30 cm). All fish were weighed, and their total length was measured. Total length, i.e., including the caudal fin, was measured in order to represent the entire body presented to the females. Individual and experimental tanks were filtered with internal box filters, kept at 25–27°C by an internal heater and illuminated with an overhead white light on a 12:12 h light–dark cycle. One-third water changes were carried out at least every 2 weeks. Fish were fed up to three times a day with a mixture of pellets with high plant content and flake food.

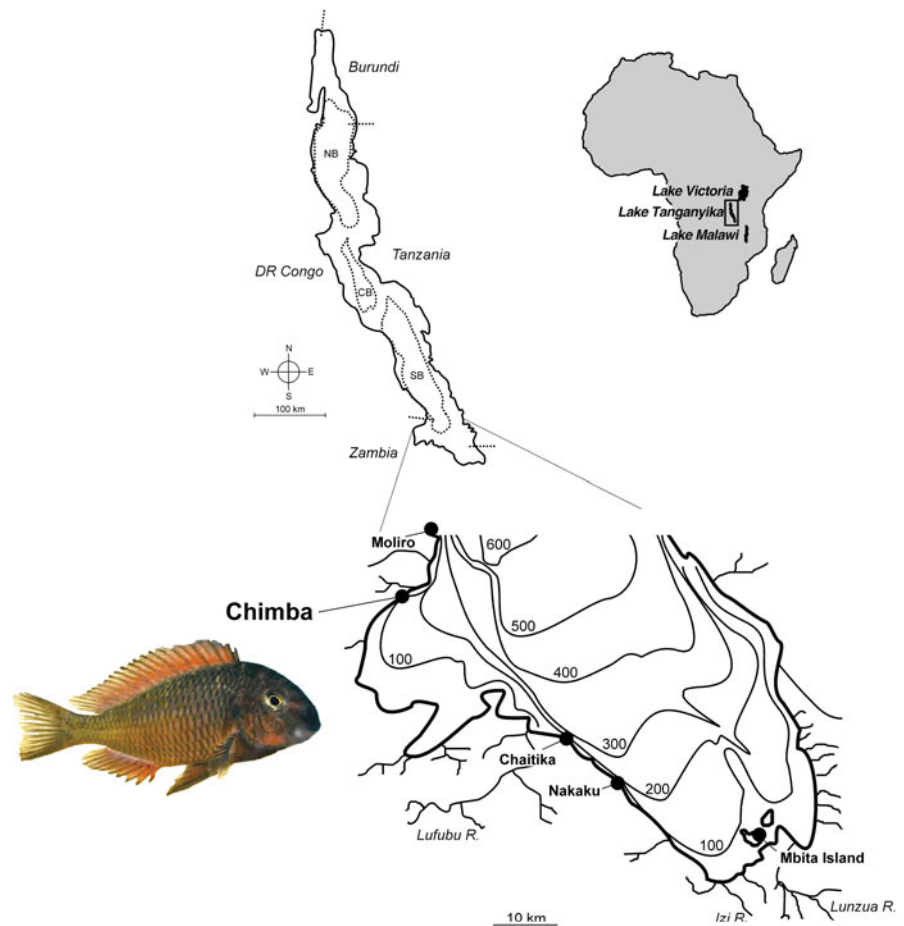
The setup of the experimental tanks was as in Egger et al. (2008): Four experimental tanks (150 × 70 × 50 cm) were divided by mesh partitions (mesh size 13 mm) into two outer compartments with a length of 45 cm each for males and one central compartment with a length of 60 cm for the female. Hollow bricks (clay bottle stands; one in each of the male's compartments and three in the female's compartment) served as hiding place and territory focus as well as spawning place.

Two of the experimental tanks were stocked with males of similar size (tank 1: male M1a with 30.1 g and 8.8 cm, male M1b with 29.1 g and 9.0 cm; tank

3: male M3a with 30.5 g and 9.1 cm, male M3b with 30.8 g and 9.1 cm); the other two tanks received males of different sizes (tank 2: male M2a with 31.5 g and 9.5 cm, male M2b with 28.8 g and 9.1 cm; tank 4: male M4a with 25.7 g and 8.6 cm, male M4b with 30.6 g and 9.0 cm). Mate choice trials followed the procedure developed by Egger et al. (2008). For 4 days, females and males were kept with mesh partitions in place in order to allow the females to examine and evaluate both of the males under standardized conditions (the 'decision phase' of Egger et al., 2008). Next, females were permitted free access to one male at a time ('sequential access phase' of Egger et al., 2008), and their interactions with the males were observed and scored. Test sessions were carried out twice a day, in the morning and in the afternoon, for a maximum of 8 consecutive days; some trials were terminated earlier, when the female preference was clear either because she had spawned with one of the males (six times) or when aggression between the female and the non-preferred male was too intense (once). The partition between the female and one of the males was removed for 30 min, while an opaque plastic plate was placed between the female's territory and the territory of the other male. In the second session of that day, the female was allowed to interact with the second male. The order of access to the males was assigned randomly in each trial, but preserved on consecutive days of the trial. In the middle of each trial (i.e., after 4 days observation sessions) the two males switched sides to control for a potential tank side bias in the females' choice.

The interactions of the pairs were categorized as spawning, pseudospawning, courtship, pairing and aggressive behavior. Aggressive displays in *Tropheus* include chasing, expelling, circling, and mouth-fighting, while courtship and spawning behaviors include lead swimming by the male, quivering by both sexes, release and snapping up of eggs by the female, and nuzzling of the male's anal fin by the female (Nelissen, 1976). Pseudospawning contains the same behavioral sequences as spawning, but without release of eggs. Intensive courtship of both sexes was scored as 'courtship'. When females remained in one male's territory without aggressive behavior but rejected the alternative male consistently during all access sessions, the behavior was scored as 'pairing'. Spawning, pseudospawning, courtship and pairing were

Fig. 1 Photograph of *Tropheus moorii* “Chimba” and map showing the location of this population in Lake Tanganyika



interpreted to indicate a preference of the female for that male (Egger et al., 2008).

A total of 38 trials were conducted, of which 22 yielded interaction scores allowing the inference of a female preference for one of the males. Lack of interactions or aggressive behavior towards both males prevented the identification of female preferences in the remaining 16 trials. Results were obtained from ten different females: three of these females scored with all four pairs of males, three females scored with two pairs of males, and four females scored with only one of the pairs. The proportion of successful trials in this experiment is similar to that achieved in Egger et al. (2008).

Early on during the experiment, we started to suspect that female choice and the courtship activity of the males were correlated. As a crude measure of activity levels, we counted the number of observation sessions per trial, in which either courtship, aggression or neutral behavior predominated. For example, in a

trial consisting of eight observation sessions, a male might show courtship activity in four sessions, aggression in one session, and neutral activity in three sessions. Behavior was classified as neutral when individuals did not interact with each other at all during the observation session, irrespective of movements between their own and the other animal's territories. Activity data for both males and females were collected in 15 of the 22 successful trials.

Statistical analyses

Chi-square statistics were calculated to test whether mating success (i.e., trials classified as either spawning, pseudospawning, courtship or pairing) was distributed evenly among the two males of each pair. Differences in the activity between chosen and rejected males and differences in female activity towards chosen and rejected males were assessed by generalized linear model analyses (SPSS Statistics v.

19) with “females” nested within “male pairs” to account for the repeated testing of males and females. Male status (preferred vs. rejected) and male size were used as fixed factor and covariate, respectively. As the activity data are counts of events within a variable number of observations, a binomial distribution with a logit link function was specified.

Genetic analysis of clutches spawned outside the observation period

In five trials, the females spawned with one of the males outside the observation period. Despite the mesh partitions between their compartments, the eggs were fertilized in four of these cases, and paternity was determined by microsatellite analysis. These four trials were scored as “spawning”. DNA extraction followed a standard Chelex protocol (Walsh et al., 1991) and a Wizard[®]SV Genomic DNA Purification System (Promega Corporation) for adult tissue and eggs, respectively. Adults and eggs were genotyped at four microsatellite loci, TmoM11 and TmoM27 (Zardoya et al., 1996), UME002 and UME003 (Parker & Kornfield, 1996). The PCR reactions followed the protocol in Egger et al. (2006) with an annealing temperature of 54°C. Fragment size analysis was carried out on an ABI 3130xl automatic sequencer (Applied Biosystems) using GeneScan-500 ROX (Applied Biosystems) as an internal size standard. The electropherograms were analyzed in Genemapper 3.7 (Applied Biosystems).

Results

Among three pairs of males, the same male was preferred by all tested females ($n = 5, 6,$ and 7 females, respectively) and equal mating success of the two alternative males was rejected with P values < 0.05 (Fig. 2). Interestingly, the females preferred the smaller of the two males in the two pairs with dissimilar body sizes. Only four females yielded preference scores with the fourth, same-size pair of males, three of them agreeing in their preference for one male (M1b), and one female pairing with the other male. The bias in favor of male M1b was not significant (Fig. 2). Across all pairs of males, Fisher’s combined probability (Fisher, 1948) for equal mating success of males in a pair amounts to $P = 0.0005$ ($\chi^2 = 27.9, df = 8$).

In each trial except the one with the disparate preference for male M1a (Fig. 2), the preferred males displayed higher courtship activity and less aggression than their rejected competitors. On average, the level of neutral behavior was slightly higher in the rejected males. The differences in activity scores between preferred and rejected males were confirmed by a significant effect of the males’ status (preferred vs. rejected) on the males’ courtship and aggression scores, but not on neutral behavior (Table 1). Consistent with our qualitative inference of female preferences, female courtship scores were higher, and female aggression scores were lower, with the preferred than with the rejected males (Table 1). On

Fig. 2 Female mate preferences. The shaded bars represent the number of mate choice trials scored as pairing, courtship, pseudospawning, and spawning with the males given on the x-axis. Spawning with a male was either observed or determined by genetic analysis of the fertilized eggs. Broken vertical lines separate the four pairs of males. P values are the probability for equal mating success of the two males in each pair

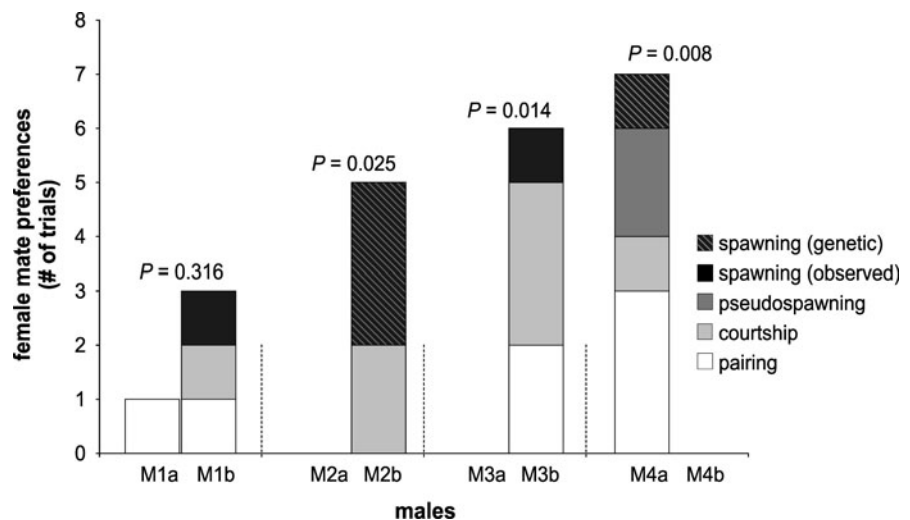


Table 1 Effects of males status (preferred vs. rejected) and male size on activity levels of males and females

	Male courtship		Male aggression		Male neutral		Female courtship		Female aggression		Female neutral	
	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P
Male status	13.65	<0.001	9.04	0.003	3.58	0.058	16.31	<0.001	8.85	0.003	3.70	0.054
Male size	0.56	0.453	0.217	0.642	0.10	0.754	0.268	0.605	0.513	0.474	1.70	0.193

average, levels of neutral behavior were higher in interactions with the rejected males, but the difference was not significant (Table 1). Male size, which was included as a covariate in the analysis, had no effect on male and female behavior scores (Table 1).

Discussion

Due to the concordant preferences of the tested females, mating success differed substantially between the two alternative males in each tank. Hence, in our experiment, female *Tropheus* appeared sufficiently discriminating to create considerable variance in male reproductive success and consequently potential for directional sexual selection. Agreement among females in repeated tests with the same males was also observed in laboratory rats, although the degree of concordance was somewhat lower than in our study (Lovell et al., 2007). In the rose bitterling, females did not agree in their preferences for particular males when males were presented simultaneously, whereas preferences for sequentially presented males were congruent among females in one study (Casalini et al., 2009), but not in another (Agbali et al., 2010). Similarly, no unanimous female preferences for particular males were detected in experiments testing fixed pairs or groups of males with different females in sand gobies (Lehtonen & Lindström, 2008) and guppies (Brooks & Endler, 2001), where variation in female preferences and hence the lack of a universally attractive male phenotype allows the persistence of polymorphism in sexually selected traits. Moreover, discordant female preferences suggest that females base their choice on genetic compatibility, whereas a quest for good genes is expected to result in congruent female preferences (Agbali et al., 2010).

Our experiment was not designed to identify the cues according to which females make their choices. Male coloration is obviously a candidate cue in a colorful cichlid fish, and individual body coloration varies among individual males and females of the Chimba population. Part of this variation is probably due to differences in the amount of integument pigment content, but a proportion of any momentarily observed variation results from the rapid physiological color changes associated with communication among individuals (Nelissen, 1976; Sturmbauer & Dallinger, 1995), which makes quantitative comparisons between individuals difficult. Visual assessment of male courtship color patterns in our experiment suggested high within-individual variation among observation sessions, and there was no obvious and consistent difference in overall red color intensity and the size of a red cheek patch between the preferred and rejected males. Hence, the here made observations do not allow to draw a connection between female preference and male redness. In other fish species, for example sticklebacks (Milinski & Bakker, 1990; Bakker & Mundwiler, 1994), guppies (Karino & Urano, 2008) and the cichlid *Pundamilia nyererei* (Maan et al., 2004), the redness of males is the most important criterion for female choice, and in the cichlid *Labeotropheus fuelleborni*, females preferred males with higher chroma and color contrast (Pauers et al., 2004). In contrast, male coloration was not related to female choice and male mate quality in rose bitterling (Agbali et al., 2010; Casalini et al., 2009). Interestingly, in a previous experiment, *Tropheus* “Chimba” females did not discriminate against similarly colored but clearly distinguishable males of the Moliro population; nor did Moliro females discriminate against Chimba males (Egger et al., 2010). The observed mate preferences, both between and within populations, suggest that the mating decisions of Chimba females do not heavily rely on

slight differences between male color patterns and intensities.

Female preferences for large males have been documented in several fish species (e.g., Ptacek & Travis, 1997; Rosenthal & Evans, 1998; Basolo, 2004; Hudman & Gotelli, 2007). No effect of male size on female choice was observed in the present and in previous mate choice experiments with *Tropheus* (Egger et al., 2008, 2010). In the field, the average body size of paired territorial males did not differ from that of unpaired territorial males (Yanagisawa & Nishida, 1991).

The preferred *Tropheus* males of the present experiment displayed higher courtship activity than their rejected counterparts. Female preferences for more active males have been observed in several species of fish (Bischoff et al., 1985; Knapp & Kovach, 1991; Carvalho et al., 2003; Maan et al., 2004; Reichard et al., 2005), the mallard (Bossema & Kruijt, 1982; Kruijt et al., 1982), and a wolf spider (Shamble et al., 2009). Male courtship vigor could either be cause or consequence of female attention (Takahashi et al., 2008). In our experiment, the observation of female courtship behavior never preceded the occurrence of courtship by the male. Although this temporal sequence would suggest that females responded to rather than elicited male courtship, it cannot be excluded that females communicated their preferences in an unobserved manner, e.g., by olfactory signals, early on in the trial and thereby encouraged the preferred males to increase their courtship vigor. In addition to signaling vitality (Knapp & Kovach, 1991; Mariette et al., 2006; Pekkala et al., 2009; Weir & Grant, 2010), the movements involved in the courtship of many fish species also serve to produce or enhance other signals. In several cichlid species including *Tropheus moorii*, a component of courtship (the quiver) is associated with the production of sound (e.g., Nelissen, 1978; Amorim et al., 2008; Smith & van Staaden, 2009), and courtship sound has been shown to influence the preferences of females in a Lake Victoria cichlid (Verzijden et al., 2010). Moreover, courtship movements may disperse odor and thereby support olfactory signaling (Blais et al., 2007; Agbali et al., 2010).

Notwithstanding the obvious mating advantage of some males over others in the present experiment, it is necessary to remember that potential mate choice

cues, such as territory size and male-male interaction, were not available to the females in our experiment. In the absence of parasitic reproduction (Egger et al., 2006), territory possession is a prerequisite to mating success of male *Tropheus*, but only a proportion of territorial males succeed to attract females (Yanagisawa & Nishida, 1991). Both in the field and in laboratory mate choice experiments, the size and composition of the males' territories have an effect on their mating success (Yanagisawa & Nishida, 1991; Hermann & Sefc, unpublished). Supplementary information from additional cues might further reinforce the observed discriminative abilities of females, but it could also result in a reduction of the variance in male mating success, if the males' territories or intrasexual aggressive displays compensate for deficiencies in other traits, or if females vary in their preferences for different cues (Candolin, 2003). Furthermore, variance in male mating success in the natural environment may decline in situations when females cannot afford to be as discriminating as they proved to be in the experiment (Atalo et al., 1988; Real, 1990; Milinski & Bakker, 1992). Obviously, the most relevant assessment of the variance in reproductive success would be obtained from parentage reconstructions in natural populations (e.g., Weatherhead & Boag, 1997; Coltman et al., 1999; Friedl & Klump, 1999; Serbezov et al., 2010), with the caveat that this approach depends on the comprehensive sampling of juveniles and potential parents. The large census size of *Tropheus* (Sturmbauer et al., 2008) impedes the identification of closely related individuals in a randomly drawn sample; for example, the probability of an individual's parent being included in population samples of 200–300 *Tropheus* was estimated to be only 1–7%, and only 4–10 individuals were assigned a parent in these samples (Koch et al., 2008).

The presented experiment complements a simulation of *Tropheus* reproduction, which suggested that pair bonding and monogamous spawning do not necessarily curb the potential for sexual selection, if concordant female preferences provide for variance in male reproductive success (Sefc, 2008). This prediction was fulfilled in the present mate choice experiment, as females discriminated clearly between different males and some males accumulated significantly more matings than others.

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