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Size-assortative mating in the absence of mate choice

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Running headline: Mechanisms of size-assortative mating

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Size-assortative mating is one of the most common mating patterns in nature. Nevertheless, the underlying behavioural mechanisms have received little attention. Assortment is typically assumed to result from mate choice, which can be coupled with differences in competitive potential. We investigated the behavioural mechanisms underlying size-assortative mating in a monogamous, biparental goby cichlid, where mutual mate choice should be expected. We performed three field experiments with females and males of *Eretmodus cyanostictus* to test for the existence of mate preferences in general and with regard to size, (i) a sequential presentation of differently sized potential partners, (ii) a removal of partners combined with surveillance until re-pairing with a new partner, and (iii) the simultaneous release of new and original partners on the experimental territories. In the removal experiment, we found evidence for weak preferences for large partners relative to own size and to the original partner's size, but pairs were formed irrespective of these preferences. The ecological importance of being paired appears to reduce choosiness and to override mate preferences. Territory ownership was quickly decided by aggressive interactions between original and new partners, and in both sexes the larger contestant won and was immediately accepted as partner by the resident. Our results suggest that strong intra-sexual competition can be a powerful promoter of size-assortative mating even in the absence of active mate choice.

KEYWORDS: assortative mating, size, mating preferences, mate choice, intra-sexual competition, monogamy, biparental care, cichlids, *Eretmodus cyanostictus*

Size-assortative mating defined as a positive correlation between the body sizes of male and female partners ranks among the most common mating patterns in nature (Ridley 1983, Crespi 1989, Rowe & Arnqvist 1996). It has been described in a wide range of taxa, including flatworms (Vreys & Michiels 1997), molluscs (e.g. Cruz et al. 2004), annelids (Michiels et al. 2001), arthropods (Crespi 1989), fish (e.g. Kolm 2002, Olafsdottir et al. 2006), amphibians (Arak 1983), reptiles (Olsson 1993, Shine et al. 2001), birds (Delestrade 2001, Helfenstein et al. 2004) and mammals (Preston et al. 2005). Surprisingly, the behavioural mechanisms leading to size-assortative mating have been explored only rarely (Rowe & Arnqvist 1996), which hampers our understanding of evolutionary mechanisms underlying this mating pattern. Most often size-assortative mating is thought to result from mate choice for large size by one or both sexes (Crespi 1989, Harari et al. 1999). A preference for large partners is often coupled with a size-dependent competitive potential allowing larger individuals to obtain the preferred partners by excluding smaller, physically inferior competitors (Crespi 1989, Olsson 1993, Harari et al. 1999). Mating with large females is beneficial if these are more fecund (Roff 1992) or produce larger eggs (Kolm 2001), while females may benefit from mating with large males if the latter are less likely to be sperm-limited (MacDiarmid & Butler 1999), or better able to defend or provide resources for offspring (Gagliardi-Seeley & Itzkowitz 2006), or contribute 'good genes' for offspring (Riechert & Johns 2003).

Alternatively, size-assortative mating may result from a choice of matching size, in which case small individuals should reject large potential partners even if these would be willing to mate. 'Prudent' mate choice should evolve when mating with a large partner bears costs for small individuals, which are not outweighed by size-related advantages (Härdling & Kokko 2005). For example, mating with a larger partner may increase the risk of predation (Michiels et al. 2001) or of asymmetric exploitation (Vreys & Michiels 1997), or intra-sexual competition may make it too costly for small, inferior individuals to strive for the best available option (Alatalo et al. 1992, Shine et al. 2001).

In the study of size-assortative mating we must distinguish between mating preferences for a certain partner size and the process that actually produces the observed size assortment. Other factors influence mate choice besides preferences, such as the costs of choice, the availability of potential mates (Jennions & Petrie 1997) and, most importantly, intra-sexual competition of potential partners and their complex interactions with mating preferences (reviewed in Wong & Candolin 2005). Mechanisms that do *not* involve mate choice have received little attention so far, and appear to apply only under limited conditions. Size assortment of mates (i) may be a by-product of a correlated distribution of male and female body sizes in space (Johannesson et al. 1995) or time (Miyashita 1994), or (ii) may arise if mechanical constraints render mating between mismatched partners inefficient or impossible (Crespi 1989, Brown 1993, Otronen 1993).

We investigated the behavioural mechanisms of pair formation in the long-term monogamous, biparentally mouthbrooding cichlid *Eretmodus cyanostictus* from Lake Tanganyika, in which sizes of male and female partners are highly correlated (Morley & Balshine 2002; this study, Fig. 1). In this species, *mutual* mate choice should be favoured by selection, as offspring survival depends greatly on biparental care (Kokko & Johnstone 2002). A single *E. cyanostictus* cannot brood the clutch for the entire incubation period of three weeks (Grüter & Taborsky 2004). Both pair partners contribute a substantial share to the parental care duties. In *E. cyanostictus*, mutual choice for *large size* might be expected because larger females are more fecund (Morley 2000), large females and males can hold larger clutch volumes in their mouth (Morley 2000, M. Steinegger & B. Taborsky, unpubl. data), and large males may be more efficient in defending the territory (both sexes defend the territory jointly, but males are on average bigger and take a greater share of defence; Morley 2000). Alternatively, both sexes might prefer a partner of *matching* size, if they run the risk to be expelled from their territory by larger competitors when having a large and too attractive partner ('prudent mate choice', Härdling & Kokko 2005). In *E. cyanostictus*, both mechanical mating constraints and heterogeneous spatio-temporal distributions of size classes can be excluded as potential causes of size-assortative mating.

We conducted three experiments in the field to investigate the relative importance of mating preferences and intra-sexual competition for pair formation in *E. cyanostictus*; (i) experimentally widowed individuals were given a choice between caged fish of defined sizes; (ii) experimental widows ('residents') were allowed to interact with the natural range of unconfined potential partners in the presence of natural levels of competition for partners and space; (iii) during the latter experiment residents quickly paired up with a new partner; in a subsequent test we released new and original partners simultaneously at the resident's territory to test for effects of status (original or new partner) and size on ultimate pair formation.

As *E. cyanostictus* is a species with long-term monogamy, the loss of a partner should be a critical event in the life history inducing extensive mate assessment before a new pair is formed. Therefore, we expected to find clear evidence of mate preferences and expected these preferences to ultimately influence pair formation. As this species mates size-assortatively, we expected mate preferences to be size-dependent. Furthermore, we expected that larger individuals would obtain preferred partners more easily due to size-dependent differences in resource holding potential.

METHODS

Study Site and Species

We conducted our experiment at the southern tip of Lake Tanganyika at Kasakalawe Point (8°46.849'S, 31°04.882'E) near Mpulungu, Zambia, between mid September and end of November 2005. All data were obtained at water depths of 3.0 to 3.5m using SCUBA diving.

E. cyanostictus pairs co-defend all-purpose territories along the rocky shores of the lake. By far the most of territory defence is directed towards conspecifics, and males show more defence behaviour than females (Morley 2000, p. 34). At a depth of 3m, territories at Kasakalawe Point comprise an area of about 2.0m^2 (= median, Morley 2000) and contain up to three layers of granite stones. *E. cyanostictus* feed almost exclusively on turf algae covering the stone surfaces, and they use crevices between the stones as shelters. Brood care is strictly biparental. Females brood the clutch for 7-10 days before transferring them to the male to be brooded for another 12-16 days, and the actual shares taken by each partner depend on the parents' energetic state (Steinegger & Taborsky 2007) and operational sex ratio (Grüter & Taborsky 2005).

General Field Methods

To select experimental territories haphazardly we dived parallel to the coastline from a defined starting point at a depth of 3m and stopped every 4-6m. We observed the fish in front of us until we roughly knew the boundaries of their territories, and then used the territory closest to us as experimental territory. Pairs can be easily recognized by courtship behaviour, joint feeding and joint defence against conspecifics (cf. Morley & Balshine 2002). Experimental territories were marked by numbered stones placed near the centre. Any stationary individual can be identified by its unique pattern of light-blue, iridescent spots (Morley & Balshine 2002). To catch a fish we waited until it stayed motionless under a stone. Then we placed a tent-shaped, fine-meshed net over the stone and coaxed the fish to swim into it by carefully lifting the stone. All body size measurements were taken under water to minimize handling stress. We placed the fish on a framed measuring board with a 1-mm grid, adjusted it to the left and lower frames of the board and read its standard and total lengths to the nearest mm. We used total length (TL) as measure of body length for all analyses. None of the fish used in our experiments were mouth-brooding at the time of catching or during the course of the experiment.

Presentation experiment

In this experiment, we tested female preferences. Compared to males, females are more likely to discriminate between potential partners, as is it more difficult for males to find a new partner because of a biased sex ratio (see 'Results'). At the beginning of each of 10 trials we determined and marked an experimental territory, identified the territory owners by sketches of their individual colour spot patterns and estimated their sizes. We captured three males from an area at least 20 m away from the experimental territory (sex was confirmed by inspection of genital papilla) that were smaller ($\bar{x}$ ±SD= 6.47±0.36 cm, N=10), similar (7.26±0.39 cm, N=9) and larger (8.33±0.48 cm, N=10) in size, respectively, than the male owner of the experimental territory, and we also caught the territorial male (7.37±0.80 cm, N=10). We placed the four males in separate mesh cages a few metres away from the experimental territory. We waited for 10 min to allow the territorial female to recognize the absence of her partner. We considered this time span as adequate because territories are small, and females usually started to swim around in the entire territory and to inspect shelters soon after we caught the male. Then we presented the males sequentially in a randomly chosen order (the respective sequence of treatments was determined before each dive), and observed the female resident for 15 min (see below). Males were presented in a clear plexiglas tube of 15.0 cm length and an inner diameter of 8.2 cm, which was closed on one end by a 1 mm-mesh allowing for water exchange, and on the other end by a removable plastic lid. After all presentations were finished, we caught the territorial female to measure its size ($\bar{x}$ ±SD= 6.54±0.49 cm, N=10), then we released all fish at the respective places of their capture.

Behavioural recordings

We placed the tube with the male in the centre of the experimental territory and immediately started a 15-min behavioural recording. We continuously noted all behaviours by the female or any other fish directed towards the tube, and every 30 s we estimated the female's distance from the tube. Furthermore, we recorded the female's feeding rate, and any interactions with other fish, and we noted behaviour of the male in the tube.

Partner Removal and Release Experiments

Removal experiment

We completed nine trials of male removals and ten trials of female removals. Another five trials had to be terminated prematurely - three times the resident left its territory at some stage after the removal of its partner, and two times the removed partners escaped from their holding cages and returned to their original territory before the end of the removal phase. We included these five trials in our analyses as far as possible.

We caught the pair member that we had designated beforehand to stay on the territory (further called 'resident'), measured its standard and total lengths and marked it by excising half of one dorsal fin ray to facilitate quick identification during focal observations. Then we released the resident in a central shelter of its territory and left the territory undisturbed for 1-2 days before removing its partner.

All removals were done in the morning. We first recorded the behaviour of the resident for 15 min (see 'Behavioural recordings'). Then we caught the pair member that had been designated to be removed (the 'original partner') and put it into a mesh cage until its release. The cage was equipped with four medium-sized stones (major axis approx. 15-20 cm) arranged in a pyramid to form a high-quality shelter with several entrances. As stones were covered with turf algae they also provided food for the caged fish. Each cage was checked for the well-being of its inhabitant once a day. During these checks, fish either moved around in the cage while scraping algae from stones, or they were using their shelter. Further 15-min behavioural recordings of the resident were done (i) 45 min after capturing its partner, (ii) in the early and (iii) late afternoon of the same day (separated by an interval of 2 h) and (iv) in the morning of day 2. If the resident had not re-mated by that time, additional recordings were done in the afternoon of day 2 and, if it was still single, also in the morning of day 3. A removal trial was terminated after the last recording of this observation schedule.

Release experiment

During the first morning or afternoon dive after completion of a removal trial, we caught the new partner, measured its length and caged it temporarily, while taking the resident's old partner from its cage and measuring its length as well. Both fish were marked by fin clipping as described above for quick identification. Then we released both fish ('new' and 'original partner') in the centre of the territory simultaneously in two nearby shelters. We immediately did a 15-min behavioural recording, and we did a second recording either in the afternoon of the same day (if the release was in the morning), or in the morning of the following day. The day after the end of each release trial, we checked which individuals were present in the territory. At 12 territories we made between 1 and 8 further checks on later days spread over a period of day 2 to day 37 after the end of the release experiment. No further partner changes were detected during these additional checks.

Behavioural recordings

During 15-min behavioural observations we continuously recorded all social behaviours (see Appendix 1) between the resident and any other fish. Together with the behaviour, we noted whether it was shown *by* or *towards* the resident, or reciprocally by both fish, and we estimated the difference between TL of conspecific visitors and residents in mm (the residents' TL was measured before). We validated our estimates by first estimating and then measuring the TL of 9 new partners (mean deviation of measured TL=3.8%). We noted any information available about the identity of the other fish (e.g., whether it was a territory neighbour or an unknown conspecific, or if it was another species). We counted the total number of feeding bites by the resident per 15 min and recorded the time it was hiding and the time out of sight using two stop watches. Whenever possible we also noted social interactions between the resident's partner and other fish, even if the resident itself was not involved.

Definitions

Behaviour: Appendix 1 describes the behaviours recorded during the 15-min observations, subdivided in three categories: contact behaviour, partner-directed behaviour and aggressive behaviour.

Pair: We considered a conspecific to be a partner of a resident if it was fully tolerated on the territory during one or more recordings, and if the two fish acted together repeatedly, that is they showed mutual S-bends or courtship, they were seen feeding or hiding together, or they jointly defended the territory against other fish. This criterion was met by all original pairs before partners were removed, and it was also applied for new partners.

Time to re-pairing: The time between removal of the old partner and pairing up of the resident with a new partner. As re-pairing was not directly observed during the removal experiment, we used the mean of the period between the last sighting of a resident being single and the first sighting when it was together with a new partner as an estimate for the time of re-pairing. These estimates include only the 13 daylight hours, as *E. cyanostictus* are inactive at night (B. Taborsky, pers. obs.).

Sex: Male and female *E. cyanostictus* are monomorphic and can only be told apart unambiguously by inspection of their genital papilla after capture. Males are on average larger than females, but the size distributions overlap. For data analysis we assigned a sex to each fish that had entered a territory during the behavioural recordings to determine the number of potential partners. We used a criterion based on the size distributions of sexes obtained from fish of known sex captured during our experiments. We based our criterion on the 10th percentile of the male size distribution (=6.7 cm; $\bar{x}$ ±SE= 7.5±0.11 cm, N=36) and the 90th percentile of the female distribution (=7.1 cm; $\bar{x}$ ±SE= 6.7±0.063 cm, N=38). An intruder was considered to be male if observed on a territory with a female resident and if its estimated size was ≥ 6.7 cm. An intruder was considered to be female if observed on a territory with a male resident and if its size was ≤ 7.1 cm. This rule included some size overlap of the sexes and may therefore include some false assignments. We also tested a more stringent criterion, assigning intruders to be males only if they were ≥ 7.1 cm and to be females only if they were ≤ 6.7 cm. This criterion necessarily causes less errors of sex assignment but it also causes neglect of data. The results did not change qualitatively when we analyzed the data with the more stringent criterion, therefore these analyses are not reported here.

Potential partner: An apparently unmated individual of opposite sex to the resident entering a resident's territory.

Winners/losers: The final partner of the resident and winner of territory ownership was defined as the fish present at a territory and interacting with the resident during the terminal check(s) after the end of the release trials. The final winner was always either the 'original' or the 'new partner', and only one of them was present during all final checks; the fish absent during the final checks was considered to be the loser.

'Best matching size': In our study population, partners differed by 11.95% in total length ($=\bar{x}$; ±0.7 SE, N=77; Fig. 1). Therefore we defined a potential partner to have the 'best matching size', if the size difference between the fish was 12% of the mean size of both fish, with males exceeding females in size.

Analysis

Statistical analyses were done with SPSS v13.0. All statistical tests are two-tailed. The behavioural data were analysed using non-parametric statistics as they did not fulfil the requirements for parametric testing. For descriptive statistics we give medians and quartiles. In the removal experiment, when we tested the influence of visitor sizes on the residents' behaviour, we used three different measures to describe the size of visitors. The α-level of these tests were adjusted by Bonferroni correction.

For each statistical test we give the respective sample sizes, which are sometimes smaller than the number of performed trials due to missing values. In the partner removal trials, missing values result from the fact that we analysed rates of behaviour per visiting fish, yielding an undefined value when the numerator (the number of fish) was zero. Furthermore, in four trials re-pairing occurred so fast, that we could not record unpaired fish in these trials.

RESULTS

Presentation Experiment

In accordance with our hypotheses about the potential mechanisms underlying size-assortative mating in *E. cyanostictus*, we expected females to prefer at least one of three from the four categories of males presented to them, either large (L; preference for large size) or intermediately sized (I) males (preference for matching size) over small (S) males, or the own partners (O), if females were able to recognize them. However, we found no significant difference in median distances kept from the tube (Friedman two-way ANOVAs by ranks: χ^2_3=4.36, P=0.22, N=8; medians [qu.]: L: 13.7 [9.4, 41.2], I:5.5 [0, 30.0], S:8.7 [3.7, 24.4], O: 12.5 [6.9, 24.4]), in contact behaviour (χ^2_3=3.01, P=0.39, N=8; L: 1.0 [0, 2.2], I:1.0 [0.5, 7.5], S: 4.0 [1, 8.2], O: 2.0 [1.0, 3.5]) or aggression directed towards the tube (χ^2_3=4.46, P=0.22, N=9; L: 0.5 [0, 2.7], I: 40.0 [1.0, 66.0], S: 26.0 [4.0, 106.3], O: 0 [0, 4.0]) between the four types of presented males. We performed additional analyses to test the ability of females to distinguish their own partner from the unknown males by pooling the data of the latter. Also in these tests the median distances from the tube (Mann-Whitney U-test: U=95.5, P=0.98, N=24,8), the frequency of contact behaviour (U=81.5, P=0.63, N=23,8) and aggression (U=83.5, P=0.15, N=27,9) shown towards the fish in the tube did not differ between presentations of the own partner vs. all other males.

Partner Removal and Release Experiments

Pair-formation after partner removal

After the old partner had been removed, residents paired up again quickly (median time to re-pairing=314 min [qu.: 102, 370]. Also newly formed pairs were size-assorted (Pearson correlation: r=0.62, P=0.005, N=19). In 17 trials, residents had only one new partner, while in two trials two new partners occurred (once in succession; once temporarily two males were simultaneously present, each defending half of the territory).

We never observed the actual pair formation directly during this experiment. On five other occasions we witnessed prospective new partners arriving at a territory. By coincidence, in all 5 cases the male had been removed (during 4 male presentation trials with tubes (see above) and during 1 pilot trial done in 2003 for the removal experiment). These cases suggest that the re-pairing process is very fast (Table 1). In all cases new males arrived soon after removal of the original partner (within 1.5h) and, after first being ignored or attacked by the resident, they were quickly accepted. Already soon after acceptance they behaved as 'partners' (acting together, see 'Methods'; in 3 cases the new partners started to defend the territory). In one case, the new male even spawned with the resident female after two days.

Availability of potential partners after partner removal

During those behavioural recordings when residents were unpaired, 0-11 'potential partners' (see definition above; median [qu.]= 2 [1, 3.25]) entered the experimental territories.

Usually, potential partners arrived at the experimental territories sequentially. Compared to the recordings when residents were paired (i.e. before partner removal and after re-pairing), more conspecifics of the opposite sex entered the experimental territories while residents were unpaired (One-sample Chi-square test, male removals: $\chi_1^2=3.80$, P=0.05, N=61 visitors; female removals: $\chi_1^2=17.95$, P<0.0001, N=69 visitors), while there was no difference in the frequencies of visiting same-sex fish (male removals: $\chi_1^2=0.35$, P=0.55, N=61; female removals: $\chi_1^2=0.0096$, P=0.92, N=107; expectations for one-sample test derived from the observation times with or without partner).

Behaviours shown between pair members and non-pair members

Overall, most of the recorded social behaviours among conspecifics were either contact and partner-directed interactions between mates (median [qu.]= 57.8% [45.4, 69], N=19 trials) or aggressive interactions between residents and conspecifics other than their partners (37.7% [28.4, 51.1]). Aggression among partners (0% [0,0], N=19), or contact and partner-directed interactions between residents and non-partners (1.7% [0, 5.1]) were rare.

Social interactions with other fish species occurred only rarely and were always aggressive. These interactions made up 20.2% (=median; qu: 14.1, 27.6) of all aggressive interactions between residents and fish other than their partners. In all analyses presented below we focus only on intraspecific social interactions.

Evidence for partner preference

We tested four predictions of the hypothesis that partner preferences play a role in pair formation of *E. cyanostictus*.

(1) Behaviour of resident towards potential partners: In general, unpaired residents should be eager to find a new partner, and therefore should seek more contacts with and be less aggressive towards potential partners than paired fish, which usually evict all conspecifics regardless of sex. Accordingly, unpaired residents should show more contact behaviour (S-bend) and less aggression than paired fish towards opposite-sex visitors (potential partners) but not towards same-sex fish. Overall, unpaired residents showed more S-bend per visiting conspecific than paired fish (Mann-Whitney U test: U=160, P=0.046, N=24,20). However, when analysed separately, S-bend rates towards same sex fish (U=185, P=0.46, N=22,19) or opposite-sex fish (U=112.5, P=0.29, N=21,13) did not differ between paired and unpaired residents. Rates of aggressive behaviour did not differ between paired and unpaired fish towards visiting conspecifics in general (U=176.0, P=0.28, N=23,19), or towards the same (U=167.5, P=0.40, N=22,18) or the opposite sex (U=148.0, P=0.76, N=21,15). By comparing the rates of behaviour using Mann-Whitney U tests, we were able to include all trials in the analysis despite some missing values in the paired data. The results did not differ when using Wilcoxon signed-ranks tests making use of the paired data structure.

(2) Sex differences: Compared to females, males should be more willing to accept potential partners, as it is more difficult for males to pair up again. The Kasakalawe Point population has a male bias of 1.4:1 (Neat & Balshine 1999, Morley & Balshine 2002), and males take longer than females to re-pair (Morley & Balshine 2002; this study, Mann-Whitney U-test: U=21, P=0.05, N=9,10). Consequently, unpaired males should show a higher frequency of contact behaviour and a lower level of aggression towards potential partners than unpaired females do. However, there was no significant difference between sexes (Mann Whitney U-test, S-bend: U=15.0, P=0.24, N=5,8; aggression: U=20, P=0.54, N=5,10)

After repairing, males were expected to guard new partners more closely than females do. We analysed the sums of 'approaches' and 'follows' (behaviours thought to serve mate guarding; Appendix 1) considering the behavioural rates during those recordings of the removal trials when the resident had a new partner. Contrary to our expectation, resident males showed lower rates of mate guarding than females (Mann-Whitney U-test: U=4.5, P=0.008, N=8,6). The mate guarding propensity of new partners towards residents did not differ between sexes (U=23.5, P=0.95, N=8,6).

(3) Size-related behaviour by residents: As size-assortative mating is assumed to result from size-based choice, either relatively large opposite-sex fish or fish of a matching size should be preferred. First we tested if aggression frequencies of unpaired residents depended on the size of potential partners. As the latter differed in size, potential partners are the independent units for this analysis. All correlations between size measures (difference to resident's size, difference to original partner's size, deviation of best match) and aggression frequency were non-significant, both for female (N=19 dyads) and male residents (N=35 dyads; all P>0.1, Spearman rank correlations). Contact behaviour with potential partners was too rare to be analysed statistically.

Second, we analysed whether interactions between mates *after* re-pairing depended on size. As in the removal experiment we never observed the pair formation directly, we analysed the first recording after re-pairing as the closest possible measure of this process. Contact behaviour was the only category with sufficiently high frequencies to be quantitatively analysed. Male residents tended to show more S-bends towards females that were larger relative to the size of original partners (r_s=0.75, P=0.02, N=9; adjusted α-level: 0.017), whereas correlations with the other two size measures, and all correlations between the contact behaviour of female residents and male size and were not significant (all P>0.1). Combining data of both sexes, again the size differences between new and original partners correlated significantly with S-bend frequency (r_s=0.60; P=0.008, N=18). S-bends shown by new mates towards the residents did not correlate with any of the size measures, neither in males, females or the combined data (all P>0.1).

Third, we tested whether the propensity of mate guarding ('approaches' plus 'follows') depends on size. Resident females showed more mate guarding per time towards their new partners when the latter were larger (Spearman rank correlation, difference to female size: r_s=0.93, P=0.001; difference to original partner's size: r_s=0.86, P=0.006, all N=8; adjusted α-level: 0.017), while mate guarding did not relate to the deviation of best-matching size. None of these comparisons was significant for resident males, nor for male or female new partners (all P>0.1).

(4) Final pair formation: If a mate preference results in the actual choice of a partner, residents faced with a simultaneous choice between original and new partner should exhibit a clear preference for one of the two and, most importantly, the preferred fish should gain partner and territory. To test for a resident's preference during the release trials, we focused on the period *before* the first encounter of the two same-sex fish, because this first encounter usually decided about territory ownership (see below). When only one partner was present at a territory, the resident always consorted with this fish. Only in six trials, original and new partners were shortly present simultaneously before they first met and started an escalating conflict, which indicates that the chances of the resident to exhibit a preference for either partner in these short periods were very limited. We compared the sum of all contact and partner-directed behaviours of focal residents shown towards or simultaneously with the later winners and later losers of territory

ownership performed during the short periods before the onset of intrasexual aggression. They did not differ significantly (Wilcoxon signed-ranks test: T=4.0, P=0.34, N=6).

An anecdotal observation suggests that residents might show preferences but cannot influence the outcome of the encounter between original and new partner and therefore the subsequent pair formation. In one trial, the resident male spawned with its *original* partner shortly after the latter's release suggesting a preference for this female. Nevertheless, in the end the *new* partner gained the territory and paired up with the resident male after expelling her mouthbrooding competitor.

(5) Who gains the territory?

In 17 trials (89.5%) we were present when ownership of the experimental territories was decided. In all 17 cases, decisions resulted from actions by one of the two same-sex fish. In 6 trials one of the same-sex fish left stealthily after having stayed hidden in the territory for several min after the release and was never seen again at the territory. In 11 trials territory ownership was determined by aggression between the same-sex fish. The winner of the aggressive encounters always obtained the experimental territories and paired up with the resident (one-sample Chi-square test, χ_1^2=11.0, P=0.001). In 9 of the 11 trials (81.8%) the winner of the *first* direct encounter between the two same-sex fish was also the ultimate winner of the territory (χ_1^2=4.45, P=0.035).

Across the 19 successful trials, size and prior ownership (original or new partner) were unrelated to each other (Fig. 2a; Paired t-test: t=-0.62, P=0.54, N=19). Prior ownership did not influence the likelihood to become the final territory owner (Fig. 2b; One-sample Chi-square test: χ_1^2=0.47, P=0.49, N=19). In contrast, body size strongly determined the likelihood of winning.

With one exception, always the larger same-sex fish became territory owner (Fig. 2c; Paired t-test, t=4.71, P<0.001, N=19). Winners were on average 0.45 cm (range: -0.15–1.55 cm) or 6.2% larger than losers.

DISCUSSION

Altogether, four experiments have been done to test for mate preferences in *E. cyanostictus*, three of them in the field (this study) and one in the lab (Morley 2000). In two of them opposite-sex fish were presented behind transparent barriers either sequentially (tube presentation) or simultaneously (lab experiment, Morley 2000), whereas in the other two tests all fish interacted freely while potential mates were present sequentially (removal experiment) or simultaneously (release experiment). Out of the three experimental manipulations reported here, only the removal experiment provided some evidence for a preference of large-sized partners. Morley's (2000) lab study revealed no size preferences, but rather a preference for more active and less aggressive fish (causes and effects of activity and aggression were not disentangled though).

In our experiment, 'widowed' residents paired up rapidly suggesting that they were not or only marginally choosy, accepting more or less the first intruder arriving. In the release trials, residents did not interfere in the competitive interactions of same-sex fish about territory ownership, and they had no detectable influence on final pair formation. This suggests that mate choice is unlikely to cause size assortment in *E. cyanostictus*. In contrast, we found evidence that pair formation was determined by a strict competitive advantage of larger fish over smaller ones in direct encounters between same-sex individuals.

Evidence for Mating Preferences

The tube presentations did not reveal evidence for preferences by the focal test fish, not even for the own partners. Therefore, we cannot exclude that the fish presented in the tube were not recognized as possible partners. Moreover, several factors may influence female behaviour, which would obscure possible preferences. These include the behaviour of the presented males, which ranged from motionless to aggressive, and the presence of scale eaters (*Perissodus microlepis*) or dominant space competitors (*Lamprologus moorii*) close to the tube in some trials.

In the removal experiment these confounding factors did not exist, but still there were no indications of mate preferences with regard to pairing status, sex or size *before* re-pairing. More opposite-sex fish entered territories when a resident was single than when it was paired, and unpaired residents showed higher rates of S-bend per visitor than paired fish. The first result does not necessarily reflect an interest of visitors to settle in a territory. Visitors may have simply taken advantage of the absence of one of the territory owners by using the territory for trespassing or feeding. The increased contact rate by residents towards visitors, however, might indicate a propensity to re-mate. *After* re-pairing two results indicate that residents responded to their new partners' sizes. (i) Residents showed more S-bends when the new partner was larger relative to their own size or to the size of their original mate; and (ii) resident females showed more mate guarding the larger new partners were. Although these relationships became apparent only *after* re-pairing, they might point towards a weak preference for large-sized partners.

According to Jennions and Petrie (1997), mating preferences comprise an individual preference function and 'choosiness', i.e. the effort an individual is prepared to invest in mate assessment. While there are some indications that the preference function of residents ranked large individuals higher, we are lacking any evidence for choosiness. (i) In most trials, time to re-pairing was too short to allow for extensive assessment of the range of possible partners. (ii) In five cases where we observed the entire process of a conspecific arriving at a territory and being accepted (Table 1), these fish were almost immediately tolerated after the first contact between resident and incoming fish. In three of the five cases the resident was first aggressive towards the incoming fish before switching quickly to partner-directed behaviour. (iii) Residents did not interfere in the contest between original and new partners, and readily accepted the winners as their partners.

Are the Incoming Fish Tolerated by Widowed Residents Really New Partners?

We propose that this is the case. First, none of the new partners, which won the contest with the original owner, had left the territory at our checks done until 2-37 d after the end of the release tests. Second, regular long-term checks of 70 territories showed that single territory owners do not occur (B. Taborsky, unpub. data). *E. cyanostictus* forms long-term pair-bonds and partners stay together on average for 226 days (B. Taborsky et al., in prep). Females need to have a partner around for joint brooding at any time as they reproduce year-round. It is unlikely that they would tolerate fish to stay in their territory if they could not breed with them, because of competition for food and shelter. For the same reason, males should only tolerate prospective spawning partners.

Where do New Partners Come from?

One might argue that re-pairing is quick and preferences are difficult to detect, because the prospective partners know each other already from previous interactions. While this cannot be completely excluded, usually new partners are at least not recruited from directly adjacent territories. The latter case occurred only once during a pilot trial in 2003. The two involved females, the experimental widow and the current partner of a male that tried to switch between neighbouring territories engaged in extensive mouthfights. In no other trial we ever saw such fights between same-sex neighbours.

From partner removal trials done in *E. cyanostictus* in a different experimental context (Taborsky, B., Guyer, L. & Demus, P., unpub. data), we know that new partners can be recruited from distances exceeding 10 m. Our data indicate that potential new partners available to experimentally widowed fish span the full spectrum of body sizes of adult territorial fish. In a 20x20 m area we detected 53 territorial pairs exhibiting a size variation between 6.5-8.5 cm in males and 6.0-7.5 cm in females (Taborsky, B., Guyer, L. & Demus, P., unpub. data), and in addition, a population of floating individuals is present in our study area (Morley 2000).

Why is Mate Choice absent despite weak Size Preferences?

Mate choice is influenced not only by preference, but also by mate availability and the costs of choice (Jennions & Petrie 1997). When the costs of choice are high, choosiness for partners may be reduced, for instance when predators are present (reviewed in Magnhagen 1991, Jennions & Petrie 1997). In *E. cyanostictus*, the predominant risk is the loss of the territory and the resources it provides due to intense space competition. Virtually all lake bottom area at our study site was occupied by territories of *E. cyanostictus* or one of their space competitors. Experimentally-created, vacant territories were quickly taken over by neighbouring pairs (Morley & Balshine 2002). Furthermore, 14.6% of a total of 48 *E. cyanostictus* experimentally widowed by Morley & Balshine (2002) and by us left their territories within 5 days after partner removal without having re-paired. In species that defend all-purpose territories, the loss of a partner may be detrimental if one individual alone is not able to defend the territory against intruders. Hence quick re-pairing may be crucial for singletons in order to keep the territory, which provides food, shelter and breeding opportunities. Likewise, in the absence of vacant space, incoming conspecifics should have a strong interest to pair up quickly to obtain a territory and a partner. This should be true if vacancies open up only rarely, which is likely to be the case, and it should especially hold for male floaters, which exist in excess in our population. Rather than being driven by mate choice this system appears to represent 'opportunistic' monogamy, where having *any* partner is highly advantageous over having no partner. Strong competition for breeding sites appears to override the importance of mate quality also in a monogamous, biparental bird, the guillemot (*Uria aalge*, Jeschke et al. 2007). We would like to stress that we were able to detect opportunistic mating behaviour because we performed our trial in the presence of natural competitor densities and the possibility of direct interactions between prospective partners. It would have been impossible to simulate natural competitor densities and the entire spectrum of potential partners in a controlled laboratory situation.

How can Size-Assortative Mating arise in the Absence of Active Choice?

Given the importance of territory possession and the strictly size-dependent potential to win competitive encounters, it is conceivable that larger singleton floaters expel smaller, physically inferior territory owners, thereby forcing the original resident pair to divorce. 'Forced divorce' (*sensu* B. Taborsky & M. Taborsky, pers. comm. with Choudhury 1995), when pair bonds are terminated by intruders, appears to be the commonest source of divorce in a number of monogamous bird species (Williams & McKinney 1996, Taborsky & Taborsky 1999, Heg et al. 2003, Jeschke et al. 2007) living at densities at or near their carrying capacity. Each expulsion of a resident naturally creates a new singleton, hence forced divorce might result in suites of expulsions and new pair formations.

While it is possible that frequent replacements of smaller territory owners by larger same-sex conspecifics may generate a tendency for size assortment, it is unlikely that this mechanism suffices to generate the strong correlation between sizes of mating partners as observed in *E. cyanostictus*. Moreover, the presence of size preferences after re-pairing has happened suggests that there are fitness effects of partner size. The effort of an active mate choice for size may not be necessary, however, if a different, simpler mechanism has similar effects. Habitat choice, a common factor promoting non-random settlement in animals (e.g. Rodenhouse et al. 1997), is a good candidate for an alternative mechanism, as in *E. cyanostictus* territories vary considerably in habitat quality. If larger fish dominate the access to high-quality territories as suggested by our results, size-assortative mating may result as a by-product of habitat preferences (B. Taborsky, L. Guyer & P. Demus, unpub. data).

Conclusions

Even in species with long-term monogamy pairs may be formed opportunistically rather than by mate preference, if the presence of a pair partner is crucial for territory maintenance. Intra-sexual competition combined with a size-dependent competitive advantage had been proposed to promote size-assortative mating caused by mate choice for large size. Here we showed that it can act also in the absence of active mate choice, although the evolution of strong size assortment requires probably additional mechanisms.

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Appendix 1

Social behaviours, which were observed during the 15-min behavioural recordings and recorded as frequencies (c.f. also Morley 2000, Appendix C for a description of some of these behaviours)

Contact behaviour

'S-bend': A fish curves its body into an 'S' shape in front of a conspecific. This is the second most prominent behavioural category within the social behaviours (531 times observed; only aggressive behaviour was observed more often; N= 603), while all remaining social behaviour types were observed rarely. As S-bend is mostly shown towards the partner and also occurs before and during spawning, it has been classified previously as courtship behaviour (Morley 2000). However, the fact that it occurs in peaceful, neutral and aggressive contexts suggests that its function is much broader. Therefore, an analysis of the function of this behaviour was required, and we analysed the context of each of the 531 recorded S-bends. Overall, S-bends were shown about 6 times more often towards partners than towards visitors (3.72 and 0.61 times per 15-min recording, respectively). Partners either showed no response or did an S-bend simultaneously. Occasionally, unilateral or mutual S-bends between partners occurred within a behavioural sequence containing also S-shake, circling, following or approaches (see descriptions below). Between partners, S-bend never occurred together with aggression. When the conspecific was *not* a partner, in 55.3% S-bend was not accompanied by any other behaviours, while in 44.7% of the cases it was immediately followed by aggression (44.7%), usually by the individual performing the S-bend (87.5% of 42 cases with aggression). Only 5 times (5.3%) S-bend towards a conspecific was directly followed by partner-directed behaviour.

S-bends directed towards visitors occurred about three times more often when only a single resident occupied the territory (i.e. during the removal phases before re-pairing; N=0.59 per visitor, as compared to 0.19 when a partner was present) and residents were more likely to show an S-bend towards visitors (63.6%) than the other way round (36.4%). Overall, S-bends were shown at similar rates by male and female residents (0.19 and 0.21 times per visitor, respectively), whereas among visitors only males showed S-bends. Furthermore, S-bends were shown at similar rates towards both sexes (towards a male: 0.30 times per resident-visitor dyad; towards a female: 0.25 times per dyad). Analysing both sexes involved in a dyad, S-bends occurred most often between males and females (0.41 times per dyad) and between males (0.32 times per dyad), while they were observed only rarely between females (0.08 times per dyad).

In summary, S-bend occurs predominantly between partners, where it occurs in combination with partner-directed behaviour or in 'neutral' interactions (=no obvious detectable context). When shown towards non-partners, there are no obvious differences regarding the sex by which and towards which it is shown, and the context is usually either aggressive or neutral. From these observations and the fact that it occurs so frequently, we conclude that S-bend serves a very general contact function. It probably serves to reveal the own presence and identity, and at the same time to collect information about the identity and intention of the recipient. As it is usually shown in front of a (moving) conspecific, it may also serve to stop possible intruders early to proceed on their way into the territory. In a metaphorical sense, we think this behaviour is a combination between an exclamation mark and a question mark, i.e. it does not convey a specific meaning, but serves to catch attention and to release a response.

Partner-directed behaviour

We classified the behaviours in this section as 'partner-directed', as they occur almost exclusively between pair members. Over all recordings, only 8 times a behaviour of this category was directed to a non-partner.

'S-shake': Similar to S-bend, but at the same time the fish shakes it whole body with varying intensity. Partners often show this behaviour simultaneously while positioned in parallel. S-shake has never been observed in an aggressive context.

'Circling': Partners turn around each other in tight circles, each following the other. In some cases they circle while one fish (usually the female) points with its head towards the flank of the other fish (usually the male) ('T-position'). When in T-position, often the first fish directs bites towards the flank of the second fish but without actual body contact ('intentional bite'). These behaviours are an intensive form of courtship, which also directly precede spawning.

'Approach': A fish swims directly towards its partner at a moderate speed; the approach is not followed by a threat, a chase or a fight. After an approach, usually the two involved fish stayed together in close proximity for some time.

'Follow': A fish follows a conspecific approximately at constant distance and at a moderate speed; the behaviour is not followed by a threat, a chase or a fight.

By 'Approach' and 'Follow' fish attain or maintain a close distance to their partner, suggesting that these behaviours may function as mate guarding.

'Feeding together': Pair partners feed at close proximity (up to 30 cm distance), usually positioned parallel to each other. We counted continuous bouts of this behaviour, which may consist of a few to several tens of bites in quick succession. Accordingly, their length is highly variable. This behaviour occured only between partners and it might be an important component of mate guarding. We did not assign it to the mate guarding behaviours, however, as obviously its main function is food uptake; it was hence not included in our statistical analyses of social behaviour, but it was part of our criterion to indentify pairs (see 'Methods').

Aggressive behaviours

'Restrained attack': A moderately fast forward movement towards another fish, which is accompanied by spreading the unpaired fins. The movement is stopped before the opponent is reached.

'Overt attack': A fish approaches another fish at high speed, obviously trying to hit it. In contrast to a 'chase', the focal fish does not continue to follow its opponent once the latter flees from the attacker.

'Chase': One fish follows another fish at high speed, while the other fish is fleeing. If the other fish is reached, the chaser directs a bite towards its opponent's tailfin.

'Bite': One fish bites another fish anywhere on the body.

'Pseudo-mouthfight': Two fish swim head to head back and forth while maintaining a constant distance between each other's heads. This behaviour is frequently seen between territorial neighbours close to their common territory border.

'Mouthfight': Two fish fight by locking their jaws and wrestling.

Table 1: Summary of five cases where males were observed arriving and being accepted at territories by female residents after the original owners had been experimentally removed

date	type of experiment	female's response before accept.[1]	pair-typical behaviour[2]	male defends?[3]	time to 1st contact[4]	time to accept.[5]	time to leaving[6]
25.10.03.	male removal	aggression	mutual S-bend	yes	20	20	stayed[a]
4.10.05.	male presentation	ignores male	feed together, approach, follow	no	51	5	25
6.10.05.	male presentation	weak aggression	mutual S-bend	yes	75	1-5	stayed
7.10.05.	male presentation	aggression	feed together	yes	82	7	10[b]
15.10.05.	male presentation	pair-typical behaviour	mutual S-bend	not recorded	53	0	stayed

[1] Initial response of female towards the new male before both engaged in 'pair-typical' behaviour

[2] Behaviours shown that are typical for pair members (for details see definition 'Pair' in 'Methods')

[3] Was the new male aggressive against conspecifics within the territory?

[4] Time interval after removal of original partner until first contact and interaction between resident female and new male

[5] Time interval from first contact to onset of pair-typical behaviour ('acceptance')

[6] Time interval from acceptance of new male to time male left again, if it left at all; 'stayed' indicates that male stayed at least until end of the observation period (i.e. 2 days in male removal trial and 2-3 hours in male presentation trials).

[a] on day 2 after its arrival the new male spawned with the resident female

[b] male left territory while we caught the female, probably because of disturbance

Figure Legends

Fig. 1: Correlation between the total lengths of male and female pair partners of unmanipulated pairs in Kasakalawe Bay (Pearson correlation: $r=0.73$, $P<0.001$, $N=77$). The dashed line denotes equal sizes of pair members. Males are usually larger than their female partners (almost all data points are below the dashed line), and relative size differences between pair members increase linearly with increasing absolute size.

Fig. 2: Results of the release phases of 19 experimental trials; (a) mean ±SE total lengths of original (black) and new (grey) partners; (b) number of original (black) vs. new (grey) male and female partners that took over the experimental territories and stayed until the end of the experiment (='winners'); (c) mean ±SE total lengths of 'winners' (black) and 'losers' (grey).

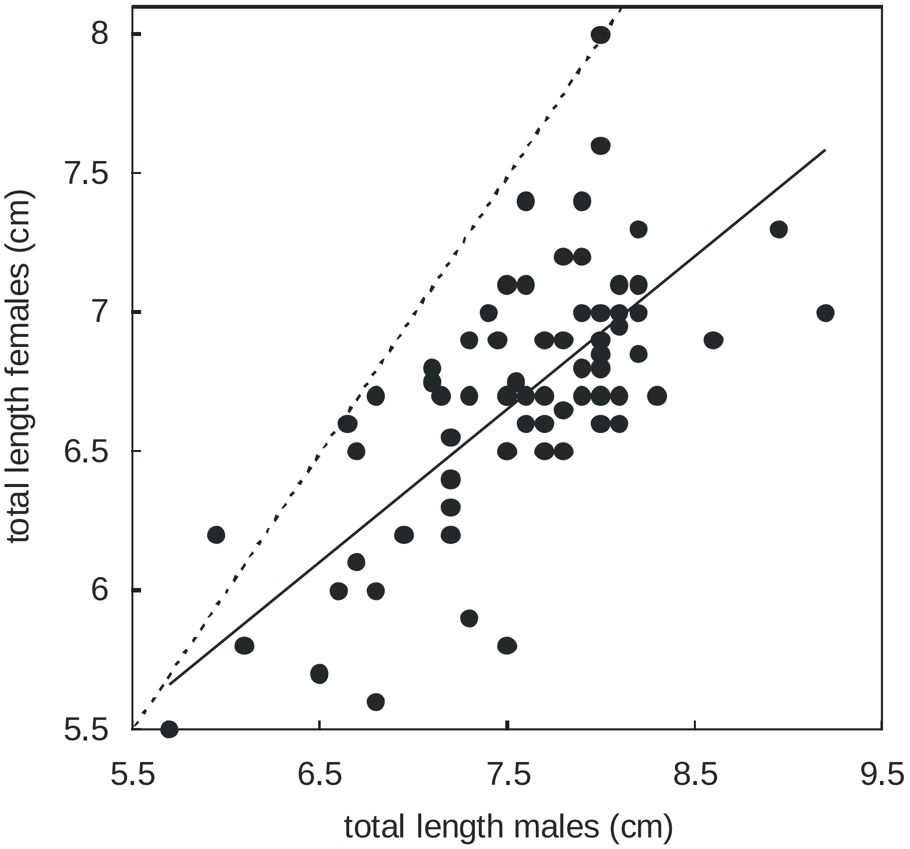
8
7.5
7
6.5
6
5.5
5.5
6.5
7.5
8.5
9.5
total length females (cm)
total length males (cm)

Figure 1

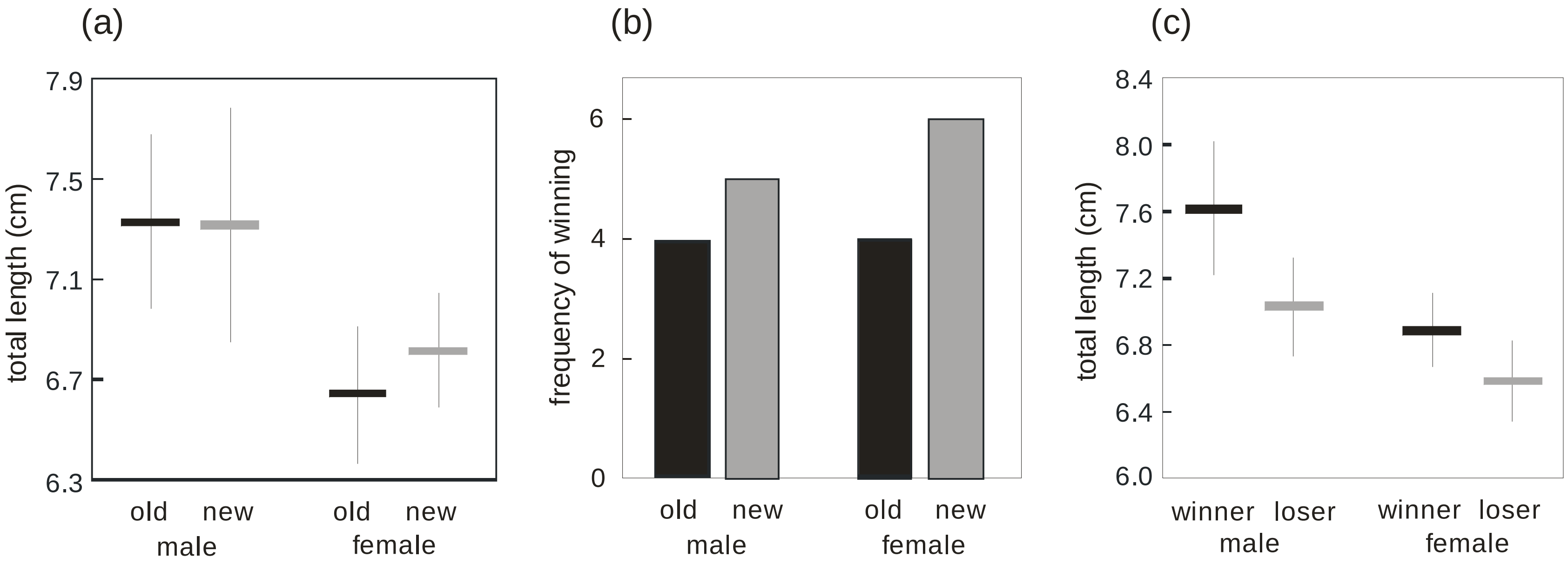
(a)
7.9
7.5
7.1
6.7
6.3
total length (cm)
old
new
male
old
new
female
(b)
6
4
2
0
frequency of winning
old
new
male
old
new
female
(c)
8.4
8.0
7.6
7.2
6.8
6.4
6.0
total length (cm)
winner
loser
male
winner
loser
female

Figure 2