

SEX DIFFERENCES IN THE MATE SELECTION PROCESS OF THE MONOGAMOUS, BIPARENTAL CONVICT CICHLID, *ARCHOCENTRUS NIGROFASCIATUM*

by

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Summary

Compared to polygynous species, monogamous males and females are considered more similar in their mate choosiness, yet few studies have explored the mate selection process between the sexes. Here, we examined this mate selection process in the monogamous convict cichlid, *Archocentrus nigrofasciatus*. We presented an individual (*i.e.* the selector) of each sex with a choice of two alternative, visually and tactilely isolated, mates. Tanks were video taped each day until the selector fish spawned with one of the potential mates (*i.e.* the accepted mate). The number of visits, length of visits, and courtship interactions were recorded. Selecting females spent significantly more time with accepted *versus* rejected males (*i.e.* females expressed a time-based preference for their chosen males), but there was no significant difference in the number of visits made to either male. Selecting females did not court accepted and rejected males differently, but rejected males courted at a significantly higher rate than did accepted males. Although selecting females expressed a time-based preference for accepted males, they continued to visit and court rejected males throughout the mate choice process; thus females did not terminate their selection process until they spawned. In contrast to selecting females, selecting males did not spend a significantly different amount of time with accepted and rejected females while visiting both females equally. Furthermore, selecting males courted accepted females significantly more than they courted rejected females. Thus, males expressed their mate preferences through courtship whereas females expressed them through time spent. Males also courted more than females. Many of these sex differences

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curiously resemble those of a polygynous social system, which we suggest perhaps indicates polygynous ancestral origins.

Keywords: assessment, courtship, mate preferences, mate searching.

Introduction

Most theoretical and empirical studies on mate choice emphasize how a searching individual finds a suitable mate (theoretical studies: *e.g.* Janetos, 1980; Parker, 1983; Wittenberger, 1983; Real, 1990, 1991; Dombrovsky & Perrin, 1994; Mazalov *et al.*, 1996; Wiegmann *et al.*, 1996; empirical studies: *e.g.* Bensch & Hasselquist, 1992; Dale *et al.*, 1992; Itzkowitz *et al.*, 2001; Uy *et al.*, 2001). However, many of these studies focus on only the searcher whereas how searchers and potential mates associate could also affect search patterns. For example, the behaviors exhibited by a searcher could influence how a potential mate responds, and *vice versa* (*e.g.* Patricelli *et al.*, 2002). In this way, these interactions could affect the overall assessment process. Although theoretical studies (*e.g.* Luttbeg, 1996) have addressed behavioral differences directed towards and received from the potential mates sampled, very few empirical studies have described this interaction and related it to the ultimate mate choice (but see Patricelli *et al.*, 2003; Santangelo, in press). Here, we compare the behavioral interactions between an individual choosing a mate (*i.e.* the selector) and the individual accepted as a mate (*i.e.* the accepted mate) *versus* one that is rejected (*i.e.* the rejected mate) in the monogamous biparental convict cichlid fish (*Archocentrus nigrofasciatus*).

For such monogamous species, both sexes are expected to be choosy when selecting a mate (Clutton-Brock & Parker, 1992; Kokko & Johnstone, 2002); thus we used both males and females as selectors and asked whether the mate choice patterns exhibited by selectors between accepted and rejected mates are similar for males and females. If both sexes incur equal costs and benefits from mate choice processes, then it has been predicted that both will behave similarly when inspecting a potential mate (see Real, 1991). However convict cichlid males have a higher reproductive rate due to their faster processing times (defined as production of gametes, copulation, nest building, and parental care; see Clutton-Brock & Parker, 1992; Johnstone *et al.*, 1996) than females (Townshend & Wootton, 1984; Wisenden, 1994a) and

only males have been observed to maintain bigamous associations (Keenleyside, 1985). These resemblances to polygynous species may indicate that female convict cichlids are more choosy than males (see Clutton-Brock & Parker, 1992; Owens *et al.*, 1994). Yet males might be similarly choosy because they exhibit parental care, female intrasexual competition is quite common (Beeching *et al.*, 1998; Cleveland, 2003), and female biased sex ratios are commonly found in Costa Rican streams (Wisenden, 1994b; Cleveland, 2003). Thus, this system is ideal for exploring potential sex differences in the mate choice process.

Irrespective of the searcher's sex, our initial hypothesis is that as an individual progresses through the selection process, the selector will show a preference for one potential mate. Mate preferences are often shown by a bias in time spent with a particular individual (see Wagner, 1998) and field observations indicate that convict cichlids spend more time with the individuals they ultimately choose as their mate than with other individuals (Mackereth & Keenleyside, 1993; pers. obs.). Thus, we expect these preferences to be similarly expressed in both sexes as more time spent with the one potential mate relative to the other potential mate.

We also considered the courtship between the selector and the potential mates. Courtship is typically viewed as a method for potential mates to advertise their quality (*e.g.* birds, Reid, 1987; fish, Knapp & Kovach, 1991; Santangelo *et al.*, 2002; flies, Hoikkala *et al.*, 1998; reviewed in Andersson, 1994) and individuals engaged in courtship have the appearance of assessing each other. If convict cichlid courtship also resembles the polygynous pattern, we hypothesize that males will exhibit more courtship than females to potential mates. Alternatively, the female's lower reproductive potential may cause her to invest more in courtship so to gain more information about a male (*sensu* Hoi, 1997). In this case, the female selector's courtship rate should, at least, match or surpass the rate of a male selector.

Lastly, we considered the behavior of the potential mates towards the selector. Again, if convict cichlid courtship is similar to polygynous species, we hypothesize that a female potential mate will exhibit less courtship than a male potential mate (see above). We also anticipated sex differences between accepted and rejected potential mates. There are few examples of this in the literature regarding females of other species, therefore we posit the null hypothesis that there will be no courtship differences between accepted and rejected female potential mates. However, there are examples of rejected

males in other species showing less courtship (Sargent *et al.*, 1986; also see Itzkowitz & Haley, 1999) or more courtship (Patricelli *et al.*, 2002) than accepted males. Specifically, rejected convict cichlid males have been shown to court more than accepted males (Santangelo, in press) and therefore, here we expect the same.

Methods

Design and procedure

Except for some minor points as indicated below, all methods were the same for male and female selector experiments. Fish were kept in 473.5 liter stock aquaria. Subjects were a combination of individuals bred in the laboratory, individuals obtained from local pet stores, and individuals collected in their native country, Costa Rica. All populations behave similarly (pers. obs.; pers. comm. Cleveland; Gagliardi). Males and females were housed in separate tanks and fed trout crumbles every other day. Stock and experimental aquaria were maintained at $20 \pm 2^\circ\text{C}$ with a 15L : 9D hour cycle. The exact breeding experience of the stock fish was unknown, although the majority, if not all, of the subjects had previously bred. Therefore, prior to the start of the experiments, females were isolated for one month to ensure their readiness to pair and spawn (see Townshend & Wooten, 1984; Barlow, 1991). At the end of each replicate, all subjects were housed separately from the stock fish to avoid pseudoreplication.

The total length, width, and mass of each fish used were recorded (see Table 1). Males were always larger than females to mimic natural populations (Wisenden, 1995; pers. obs.). Because size reflects mate quality in convict cichlids (*i.e.* larger individuals are higher quality than smaller; Wisenden, 1995; Itzkowitz *et al.*, 1998), and the distribution of quality among potential mates can influence the selecting process in multiple ways (Real, 1990; Wiegmann *et al.*, 1996), potential mates were similar sizes (*i.e.* total length difference between potential mates ≤ 1 cm). That is, because it is not known how size relates specifically to fitness in convict cichlids, it would be difficult to interpret any results under these conditions (refer to Wiegmann *et al.*, 1999; Wiegmann & Mukhopadhyay, 1998). Thus, we aimed to remove the influence of any arbitrary size difference between potential mates in order to get a 'baseline' of mate search behavior.

Experiments were conducted in 284 liter ($120 \times 45 \times 50$ cm) aquaria. The aquaria were partitioned into five sections (Fig. 1). The outermost sections (*i.e.* intruder compartments; A in Fig. 1), were separated from the rest of the tank by clear plastic partitions. One juvenile convict cichlid was placed in each intruder compartment because pair bond formation is facilitated by the presence of conspecific intruders (see Itzkowitz & Draud, 1992; pers. obs.). Juveniles were used because they would not be considered a potential mate for the selector. Adjacent to each intruder compartment were the experimental compartments (B in Fig. 1). Each experimental compartment contained a flowerpot (*i.e.* spawning site). The experimental compartments were delineated by the clear plastic partition of the intruder compartment on one side and an opaque partition on the other side (see Fig. 1). The middle neutral section was bounded on either side by the opaque partitions from the experimental sections (C in Fig. 1). Holes were drilled in these opaque partitions to allow the selecting individual access to both experimental compartments. Holes were 2 cm in diameter for female selectors and 3.5 cm in

TABLE 1. *Size distributions of individuals in female selector and male selector experiments*

	Female selector experiment				Male selector experiment			
	Female mean size	Female size range	Male mean size	Male size range	Male mean size	Male size range	Female mean size	Female size range
Length (cm)	5.66	5.17-6.71	6.76	5.34-7.20	6.9	5.97-8.17	5.96	5.03-7.40
Width (cm)	0.84	0.69-1.00	0.88	0.78-1.09	0.91	0.74-1.15	0.88	0.69-1.12
Mass (g)	3.6	2.8-6.0	5.7	5.2-6.6	6.1	3.7-9.8	4.4	2.3-8.6

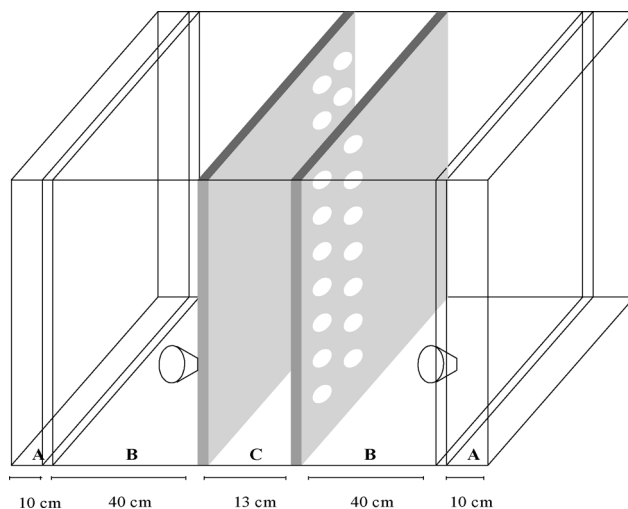


Fig. 1. Diagram of the general experimental set up. (A) intruder compartments. (B) experimental compartments with flowerpots. (C) neutral compartment.

diameter for male selectors. The partitions limited tactile interactions between the potential mates and the holes in both partitions were offset to limit visual interactions between these individuals. Limiting the interaction between potential mates was done because both sexes interact with other individuals of the same sex when selecting a mate, and these intrasexual interactions are expected to have a direct effect on the mate choice process (Weber & Weber, 1976; Siepen & Crapon de Caprona, 1986; Wisenden, 1995; Beeching & Hopp, 1999; pers. obs.). The ability of selecting individuals to interact and spawn with potential mates allowed the recording of both mate 'choice' and mate 'preference' data (reviewed by Jennions & Petrie, 1997; Wagner, 1998). That is, 'mate preference' delineates an individual's inclination to mate with a particular individual, but does not necessarily indicate their ultimate mating

partner. By allowing individuals to actually reproduce, we can not only determine which potential mate is preferred during the choice process, but also who is chosen.

One potential mate (either male or female depending on the experiment) was placed within each experimental compartment. These potential mates were tethered to restrict them to their respective compartments. To tether a fish, the fish was first anesthetized using seltzer water (see Summerfelt & Smith, 1990), then a monofilament loop was placed through the fish's dorsal musculature. The fish was allowed to recuperate in a hospital tank for four days prior to the start of testing. On the fifth day, a second monofilament line was attached to a swivel screwed into a board overhanging the experimental sections. This line was then attached to the fish's monofilament loop. The tethered fish were allowed one day to acclimate to the tether before the selector fish was introduced. This design provided potential mates with free movement and access to the flowerpot while preventing their movement through the partition. Tethered convict cichlids are able to both successfully pair and rear their offspring (pers. obs.) and their mate choice behavior is identical to non-tethered fish in the same experimental setup (refer to Santangelo, in press). This procedure was approved under IACUC protocol number DR/00.

At the start of each replicate, the selector was introduced into the central neutral compartment thus eliminating any bias potentially caused by starting on an experimental side (Bakker & Millinski, 1991; Collins, 1995). Once the selector was introduced, tanks were video taped every day for 2 hours until a pair formed and spawned. The time tapings began was randomized controlling for possible circadian rhythm effects on the examined behaviors. Eight pellets of trout crumbles were placed in each experimental compartment every day for food thereby eliminating any bias in resource quality between potential mates. All replicates ended once spawning had occurred. Potential mates that spawned with the selecting subject were termed 'accepted' mates whereas the other potential mates were termed 'rejected' mates. Replicates that ran for 21 days without a spawning were excluded from analyses as we assumed the selector made no choice.

Data recorded from the videotapes included the number of times selectors visited each compartment and the duration of these visits. Therefore, for each selector, the mean number of visits made to each potential mate per day was calculated by dividing the total number of visits made to a potential mate by the number of days until spawning. The average duration of each visit (*i.e.* bout length) was calculated by finding the mean bout length for each day of the selecting process, and the mean of these means was calculated.

Sample size

The goal was to complete 12 replicates that were successfully video taped. Once 12 replicates were videoed successfully, the experiment was stopped. However a total of 17 replicates were completed for the female choice experiment and 25 for the male choice experiment and these larger sample sizes were used in the analysis of who was chosen based on size and number of days to spawn.

Designation of selector and potential mates

Although convict cichlids are monogamous (*i.e.* both males and females are expected to exhibit choice), we designated the free-swimming individual within our design as the selector and the two tethered individuals as the potential mates. A single male and a single female

convict cichlid placed within an aquarium will almost always mate (as long as the male is similar in size or larger than the female; pers. obs.). Thus, here we presume that the presence of two potential mates makes the free-swimming individual the selector.

Data summary and analysis

Selection periods

In order to examine how a selection process proceeds (*i.e.* whether the patterns exhibited by the selector at the beginning of the process were similar to those at the end of the process); the selector's mean bouts, visits, and courtship rates (see below) were calculated for different periods of the selection process. This was accomplished via the number of days spent selecting divided into three equal time periods. For any particular sample where days were not equally divisible by three, the middle selection period (*i.e.* the second selection period) was one day less, or one day more, than the first and third selection period. Thus, the means for the beginning and end of the selection process always had equal weight.

Courtship

The number of courtship behaviors (*i.e.* tailbeats, quivers, and brushes) each individual exhibited was recorded. The duration of each courtship event is negligible and convict cichlids exhibit courtship sporadically during the time a male and female are together (pers. obs.). Each courtship behavior followed similar trends, thus they were combined to generate an overall number of courtship events for each individual. The average number of courtship events exhibited per day was calculated by summing the total number of courtship events an individual exhibited divided by the number of days until spawning. A courtship rate was also calculated because selectors might not spend the same amount of time within each compartment, thereby influencing the total amount of courtship observed between individuals. Courtship rate was calculated by dividing the total number of courtship events exhibited by an individual on each day divided by the total amount of time that individual spent with the one they were courting. Courtship rates for each day were averaged over all days giving each individual a mean courtship rate score.

Statistics

The selector's pattern of movement between the compartments was analyzed as a within-subject ANOVA design. Analyzing the data through periods required comparing accepted mates to rejected mates within each period; a 2 within \times 3 within ANOVA design was used (*i.e.* both factors were within-subject factors; see Keppel, 1991). Potential mate type (*i.e.* accepted or rejected) was one factor and selection period was the other. Individual comparisons both within and between periods of mate type were only conducted if a significant interaction was present. Then, the comparisons were tested using paired *t*-tests. Post-hoc comparisons were conducted using Tukey tests.

To compare the courtship of the potential mates, matched pair designs were used because both potential mates were responding to the same selector. Wilcoxon signed ranks were used for comparisons where the data did not conform to the assumptions of parametric testing. A Friedman ANOVA was used for the analysis of courtship over periods for selectors whose data also did not conform to the assumptions of parametric testing. In these cases, because

non-parametric ANOVA's cannot test for interactions, comparisons within each period were always carried out using Wilcoxon signed ranks. Comparisons between periods were only carried out if a significant effect was found in the overall ANOVA. Comparisons of courtship between sexes were carried out using Mann-Whitey U -tests. Spearman rank correlations were used to test correlations between courtship and number of days until spawning.

In two replicates the female did not spend any time in the rejected male's compartment. Therefore these two replicates were excluded from courtship analyses regarding rejected males.

Results

Female selection process

The mean time selecting females took to spawn was 8.24 (SE \pm 4.49) days. Females did not select longer males (10 large, 6 small; two tailed binomial test: $p = 0.993$), wider males (9 large, 8 small; two tailed binomial test: $p = 0.994$), nor heavier males (12 large, 4 small: two tailed binomial test: $p = 0.992$). Sample sizes are not all equal due to the exclusion of tie scores.

There was a main effect of male type on where females spent their time. That is, females spent significantly longer bouts with the male they eventually accepted than with the male they rejected ($F_{1,11} = 5.48$, $p = 0.039$; Fig. 2). Selection period had no effect on how females distributed their time between accepted and rejected males ($F_{2,22} = 1.41$, $p = 0.26$; Fig. 2). These relationships existed throughout the selection process as there was no significant interaction between male type and selection period for bout length ($F_{2,22} = 0.90$, $p = 0.41$).

There was no main effect of male type on the number of visits females made to each male ($F_{1,11} = 0.024$, $p = 0.87$; Fig. 3). Nor was there a main effect of selection period on the number of visits females made per day to each male ($F_{2,22} = 0.494$, $p = 0.61$; Fig. 3). These relationships also existed throughout the selection process as no significant interaction existed between male type and selection period for visits ($F_{2,22} = 0.482$, $p = 0.62$).

Females did not significantly differ in the mean amount of courtship events they exhibited per two hour session to accepted and rejected males until spawning (Wilcoxon signed ranks: $z = 1.27$, $T = 15.00$, $p = 0.20$). Nor did females significantly differ in their courtship rate per two hour session between accepted and rejected males over the entire selection process (Wilcoxon signed ranks: $z = 0.25$, $T = 25.00$, $N = 10$, $p = 0.79$; Fig. 4),

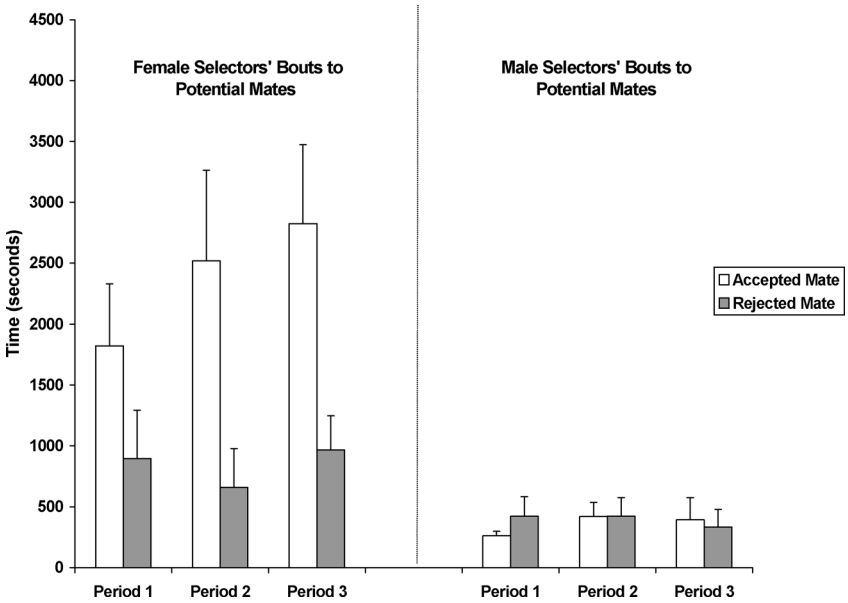


Fig. 2. Mean and SE of bout length selectors spent with potential mates in each period. White bars indicate accepted mates; gray bars indicate rejected mates. Left side of graph represents female selectors; right side represents male selectors. Overall, female selectors spent significantly more time with accepted than rejected mates ($p = 0.039$) whereas there was no significant difference in the time male selectors spent between potential mates ($p = 0.84$). No comparisons within any period were carried out as there was no significant interaction between rejected and accepted mates for both female ($p = 0.41$) and male selectors ($p = 0.46$). See text for details.

as well as within each period (Wilcoxon signed ranks; period 1: $z = 0.56$, $T = 14.00$, $N = 9$, $p = 0.57$; period 2: $z = 0.42$, $T = 15.00$, $N = 8$, $p = 0.67$; period 3: $z = 1.27$, $T = 15.00$, $N = 10$, $p = 0.20$; Fig. 4). It is curious that even though the rates were not significantly different and the female did spend more time with the accepted male (see above), that her average number of courtship events per two hour sessions was not significantly higher with the accepted male. However, females did exhibit a trend for courting at a lower rate towards the accepted male, which perhaps lessened the mean amount of courtship to the accepted male per two hour session. Female courtship appeared to have a similar structure to both males throughout the selection process as there was no significant effect between periods for female courtship rate per two hour session towards accepted males (Friedman ANOVA, $N = 11$, $df = 2$, $\chi^2 = 0.182$, $p = 0.91$; Fig. 4) or towards

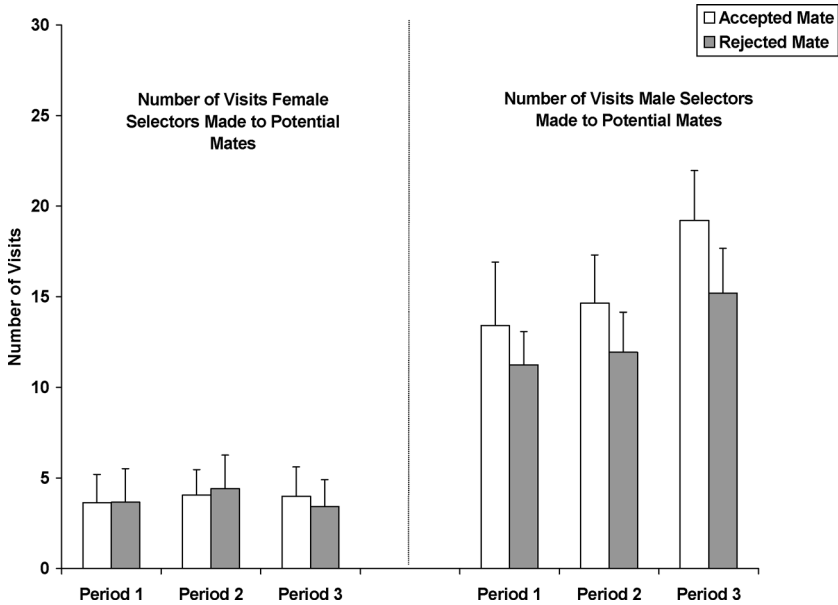


Fig. 3. Mean and SE of number of visits selectors spent with potential mates in each period. See Fig. 2 legend for more details. Overall, there was no significant difference in the number of visits per day between accepted and rejected mates for female selectors ($p = 0.87$) and male selectors ($p = 0.09$) and no significant interaction between rejected and accepted mates for both female ($p = 0.62$) and male selectors ($p = 0.55$). See text for details.

rejected males (Friedman ANOVA, $N = 11$, $df = 2$, $\chi^2 = 4.32$, $p = 0.11$; Fig. 4). Her courtship rate per two hour session to either male was not significantly correlated to the number of days females took to spawn (Spearman rank correlation: accepted males; $r = -0.54$, $N = 12$, $p = 0.07$; rejected males; $r = -0.53$, $N = 10$, $p = 0.11$).

Accepted and rejected males did not differ in their number of courtship events exhibited per two hour session to females (Paired t -test: $t_{10} = 0.858$, $p = 0.41$), however rejected males displayed a higher courtship rate in these sessions than accepted males (Wilcoxon signed ranks: $z = 1.98$, $T = 8.00$, $N = 10$, $p = 0.046$).

Male selection process

The mean time selecting males took to spawn was 6.76 (SE \pm 3.99) days. Males did not select longer females (12 large, 12 small; two tailed binomial test: $p = 0.995$), wider females (15 large, 10 small; two tailed binomial test:

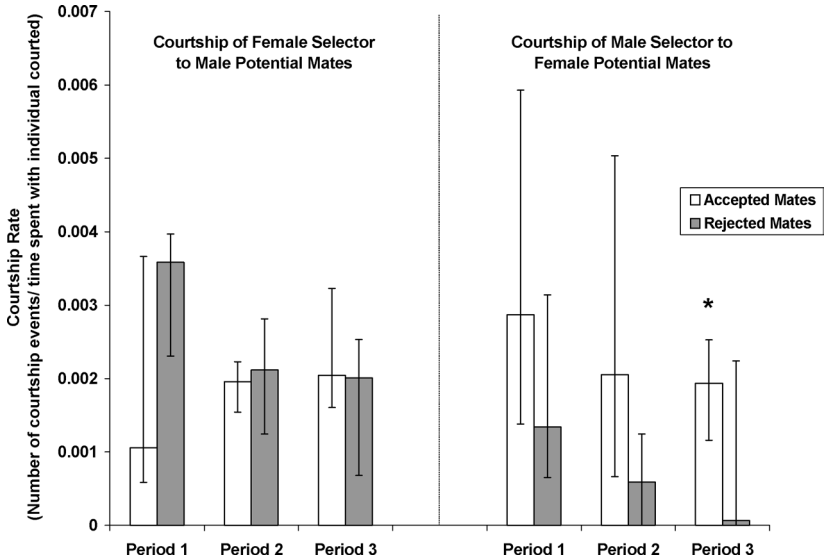


Fig. 4. Median, 1st and 3rd quartiles of selectors courtship rate to potential mates. See Fig. 2 for more details. (*) indicates a significant difference at $p < 0.05$.

$p = 0.994$), nor heavier females (13 large, 12 small; two tailed binomial test: $p = 0.994$). Sample sizes are not all equal due to the exclusion of tie scores.

There was no main effect of female type on the selecting male's bout length ($F_{1,11} = 0.04$, $p = 0.84$; Fig. 2). Selection period also had no effect on how males distributed their time among females ($F_{2,22} = 0.12$, $p = 0.89$; Fig. 2). These trends were consistent throughout the selection process as there was no significant interaction between selection period and female type for male bouts with each female ($F_{2,22} = 0.79$, $p = 0.46$).

There was also no main effect of female type on the number of visits males made to each female ($F_{1,11} = 3.33$, $p = 0.09$; Fig. 3). Nor was there a main effect of selection period on the number of visits males made per day to each female ($F_{2,22} = 2.66$, $p = 0.09$; Fig. 3). There was no significant interaction between female type and selection period for visits ($F_{2,22} = 0.61$, $p = 0.55$).

Males courted accepted females significantly more per two hour session than they did rejected females (paired t -test: $t_{12} = 4.82$, $p = 0.0005$). Males also courted accepted females at a significantly higher rate per two hour session (paired t -test: $t_{12} = 4.10$, $p = 0.001$; Fig. 4). Male courtship appeared to have a similar structure to both females throughout the selection

process as there was no significant effect of period on courtship rate per two hour session towards accepted females (Friedman ANOVA, $N = 11$, $df = 2$, $\chi^2 = 0.727$, $p = 0.69$; Fig. 4) or towards rejected females (Friedman ANOVA, $N = 11$, $df = 2$, $\chi^2 = 4.20$, $p = 0.12$; Fig. 4). Whereas males showed a steadily increasing trend through the periods of courting accepted females at a higher rate per two hour session than rejected females, it was only in period 3 that this difference was significant (Wilcoxon signed ranks; period 1: $z = 0.863$, $T = 28.00$, $N = 12$, $p = 0.38$; period 2: $z = 1.78$, $T = 13.00$, $N = 11$, $p = 0.07$; period 3: $z = 2.27$, $T = 10.00$, $N = 12$, $p = 0.022$; Fig. 4).

Accepted females courted the male more per two hour session (paired t test: $t_{10} = 3.32$, $N = 12$, $p = 0.006$) and at a significantly higher rate (paired t -test: $t_{12} = 2.68$, $p = 0.021$) than rejected females. Similar to female selectors, the courtship rate per two hour session of accepted females was not significantly correlated to the number of days until spawning (Pearson Product-Moment correlation: $r = -0.26$, $N = 12$, $p = 0.41$). The rejected female's courtship rate per two hour session was also not significantly correlated to the number of days until the accepted female and male spawned (Pearson Product-Moment correlation: $r = 0.19$, $N = 12$, $p = 0.55$).

Male versus female courtship

Male selectors courted accepted females at a significantly higher rate per two hour session than female selectors courted accepted males (Mann-Whitney U ; male selector $N = 12$, female selector $N = 12$, $z = -2.83$, $p = 0.004$). However, there was no significant difference in courtship rate per two hour session between male and female selectors towards their respective rejected mates (Mann-Whitney U ; male selector $N = 12$, female selector $N = 10$, $z = 0.329$, $p = 0.74$). The courtship rate per two hour session of male potential mates was also greater than that of female potential mates. That is, accepted males courted significantly more intensely than accepted females (Mann-Whitney U ; accepted male $N = 12$, accepted female $N = 12$, $z = 3.23$, $p = 0.001$) and rejected males courted significantly more intensely than rejected females (Mann-Whitney U ; rejected male $N = 12$, rejected female $N = 10$, $z = 3.89$, $p = 0.005$).

Discussion

Males and females select differently

Compared to female selectors, convict cichlid male selectors courted their accepted mates more, and, in this way, resembled polygynous species. There were also unexpected differences in how male and female selectors interacted with their potential mates. Male selectors exhibited no difference in the number of visits or bout length between accepted and rejected females and this was consistent across all periods. However, male selectors did show their preference by directing more courtship to accepted females, which became apparent during the third period. In contrast, female selectors expressed their mate preferences for accepted males by spending more time with them *versus* rejected males, yet courted both males similarly. These females generated this time-based preference by having longer bouts with the accepted male while visiting both males with equal frequencies. Whereas male selectors showed their courtship-based preference for the accepted mate during the third period, the female's time-based preference for her accepted mate was present throughout all three periods (*i.e.* there was no significant interaction between period number and potential mate type). Thus, while the choosiness for a mate is typically considered more similar between monogamous males and females relative to polygynous species, we show the process both sexes use to select mates are different.

The absence of a time-based preference expression by males for their accepted mates differs from previous studies where convict cichlid males expressed a time-based preference for particular females (*e.g.* Nutall & Keenleyside, 1993; Beeching & Hopp, 1999). However, those studies tested male preferences for female size (*i.e.* size indicates quality; see Methods) and so females were selected to differ greatly in size (differences were ≥ 1 cm). Because an individual's choosiness should increase as the differences in quality among potential mates increases (Parker, 1983; Hubbell & Johnson, 1987; Real, 1990); female size within the present study might not have differed enough for males to express a time-based preference. Furthermore, males might be more inclined to spend more time with a preferred female as a mate guarding tactic when there is obvious competition for her. However, males of the current study still expressed a courtship-based preference for accepted females indicating that males did still show some level of choosiness. In this

way, the courtship of convict cichlid males differs from a polygynous system and, combined with the fact that females courted accepted and rejected mates similarly, explains why there was no difference in courtship between male and female selectors towards rejected mates. Still, females did express a time-based preference under the same paradigm (*i.e.* no competition for mates and size equal potential mates). Thus, while it is yet unclear why males did not show a time-based preference, this remains a clear sex difference. Future studies may be able to further explain the ultimate reasons for these sex differences perhaps by testing the influence of direct intrasexual competition, or varying differences in the quality distribution among potential mates, to explore differences or similarities to the mate selection patterns presented in this study.

The continued attention (both in time and courtship behavior) to rejected mates by both sexes supports a previous suggestion that had been applied only to monogamous females. Although preferring certain males, females will continuously assess other available males until mating (Logan, 1991). This appears to be a type of bet-hedging tactic. So, while individuals might favor a particular potential mate during a mate search (indicated by mate preferences), they also will continue to invest, to some degree, in assessing other potential mates. This is further supported in convict cichlids because both males and females often switch mates (after a pair bond is organized but before spawning occurs) when a higher quality mate appears (Triefenbach & Itzkowitz, 1998).

Males and females act differently as potential mates

As potential mates, males and females were again different. Similar to the relationship between male and female selectors, female potential mates exhibited a lower courtship rate than male potential mates. Comparing accepted to rejected mates, accepted females courted at a higher rate than rejected females, whereas the reverse was true of males (*i.e.* rejected males courted at a higher rate than accepted males), thus supporting a previous study on convict cichlid male courtship (Santangelo, in press). Possibly, females exhibit a consistent courtship rate (with higher courting females being accepted) whereas males might have the ability to adjust their courtship. For example, selecting females did not show the ability to adjust their courtship rates (*i.e.* females courted both male potential mates similarly) whereas selecting

males did show this ability (i.e. males courted accepted females more than rejected females). However, it is possible that individuals as potential mates are different than individuals as selectors. Only potential mates were tethered and selectors saw two individuals of the opposite sex whereas potential mates always only saw one. Thus, female potential mates could have been mimicking the courtship levels of the selector males (or *vice versa*), whereas male potential mates were simply courting at their own individual intensity.

Still, the difference in courtship between accepted and rejected mates might be an attempt to manipulate the selectors choice. These differences between accepted and rejected mates may have resulted from one, or both, individuals raising or lowering their courtship rates. For example, rejected males might have attempted to manipulate the female selector's decision by courting at a high rate, thus exceeding that of the accepted male. Males with higher courtship rates are potentially more attractive as they have been shown to be more reproductively successful in other species (*e.g.* Knapp & Kovach, 1991; bicolor damselfish; Gibson, 1996; sage grouse; Forsgren, 1997; sand gobies; Møller *et al.*, 1998; barn swallows; Vinnedge & Verrell, 1998; salamanders; Martín-Vivaldi *et al.*, 1999; hoopoe; Cubillos & Guderley, 2000; three-spined sticklebacks; Olivera *et al.*, 2000; rock blennies; Santangelo *et al.*, 2002; beaugregory damselfish). This could also explain why selector males accepted females that exhibited higher courtship rates. Alternatively, accepted males might have invested less in their courtship because they were initially preferred (*sensu* Reynolds, 1993), thus their courtship was less than that of rejected males. Additionally, some studies have suggested that intense courtship is an indication of a poor quality individual (*e.g.* Kruijt & Hogan, 1967; Petrie & Hunter, 1993). In male satin bower birds, Patricelli *et al.* (2002) showed that while high courtship intensity is attractive to females, too high of an intensity threatens females and they flee. Possibly this is the case for convict cichlids since aggressive interactions are a common aspect of courtship (reviewed by Baerends, 1986; Barlow, 2000). In fact, in related species of monogamous cichlids, high levels of aggression inhibit pair bond formation (Barlow *et al.*, 1977; midas cichlid; Itzkowitz & Draud, 1992; Texas cichlid). Thus, males courting at too high a rate might be seen as a threat to females whereas females, who are rarely threatening to males (*i.e.* as long as they are similar or smaller in size, pers. obs.), can court at high rates to attract males.

In conclusion, this is one of the few studies showing that males and females of a monogamous species express their mate preferences differently. It remains unclear why such differences exist but may be the remnants of an ancestral polygynous social system with males relying on courtship to attract preferred females, and females finding and remaining with preferred males. Furthermore, for the most part, females courted less intensely than males; another similarity to a polygynous social system. Care must be taken in the future from putting too much emphasis on mate preferences since in this study, even after showing a preference, both sexes continued to visit and court rejected mates. Finally, our results show that care must also be taken when researchers choose a particular behavior pattern to indicate mate choice. Here we show that the behaviors used to indicate mate choice can differ between males and females.

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