

How does competition influence mate choice decisions for males and females in the monogamous convict cichlid fish, *Archocentrus nigrofasciatus*?

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Summary

It is understood that mate choice, competition, and sex differences produced by sexual selection underlie behavior, but few studies focus on their interactions within a system to understand how they shape behavior. Here, using the monogamous convict cichlid, *Archocentrus nigrofasciatus*, we examined the mate choice process of males and females in the presence of intrasexual competition. We compared and contrasted patterns reported in a previous study exploring this process in the absence of competition by using the same methodological paradigm. Specifically, two individuals (i.e., the competitors) were presented with a choice of two alternative, visually and tactilely isolated, mates and observed until one competitor (i.e., the primary competitor) spawned with one of the potential mates (i.e., the accepted mate). This was done for males and females separately. Both sexes spent more time with their mates while attacking and inhibiting the courtship of the other competitor (i.e., the secondary competitor). Only females expressed this time preference in the absence of competition (Santangelo & Itzkowitz, 2004), but both sexes visited accepted mates more in the presence of competition. These results suggest competition causes the adoption of a mate guarding tactic. Males exhibited more differences than females with the addition of competition suggesting that male mate choice patterns are more labile than females. We attribute this to the ability of males to be bigamous and the adoption of different strategies based on the level of male-male competition. Courtship was not affected by competition for either sex, however the courtship of secondary individuals did appear to be influenced by primary individuals. Competition did not eliminate a searcher's continuous assessment of potential mates, yet it was conducted to a lesser degree. Thus, mate guarding is an important strategy that must be balanced with an individual's inclination to continuously assess based on present competition levels.

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Introduction

Many studies explore mate choice in the presence of competition to simulate natural conditions where these two processes typically operate together (see reviews in Bateson, 1983; Clutton-Brock & Vincent, 1991; Andersson, 1994; Qvarnström & Forsgren, 1998). However, while mate choice studies over the past two decades have focused on how individuals find mates (e.g., Janetos, 1980; Real, 1990; 1991; Weigmann et al., 1996; see reviews in Gibson & Langon, 1996; Jennions & Petrie, 1997), relatively few have focused on how a search changes as competition is incorporated. This possibly has, in part, lent to the difficulty in applying mate search theory to natural populations. Furthermore, because much of the research on mate choice has been on species with only one choosy sex (i.e., non-monogamous systems), no study has explored if competition affects male and female mate choice differently. Thus, the two goals of this study are, (1) to explore the influence of intrasexual competition on the mate choice process of male and female monogamous convict cichlid fish (*Archocentrus nigrofasciatus*) and, (2) to compare and contrast the effect of competition between males and females.

Previous research has examined the mate choice process of both male and female convict cichlids in the absence of intrasexual competition (Santangelo & Itzkowitz, 2004). In that work, an individual selector (i.e., male or female) chose between two potential mates, one of which was ultimately chosen as the mate (i.e., accepted mate), and the other rejected (i.e., rejected mate). Female selectors visited accepted males as often as rejected males, but visits to accepted males were longer in duration (Table 1). Thus, females expressed a time preference for the males they accepted. In contrast, the time spent and number of visits male selectors made between accepted and rejected female mates did not differ. However, male selectors did court accepted females more than rejected females. This contrasted female selectors who courted accepted and rejected males similarly. Lastly, both sexes continuously assessed rejected mates (i.e., they continued to visit, spend time with, and court rejected mates until spawning).

Here, using the same paradigm, we test how male and female convict cichlids choose their mates under conditions of direct intrasexual competition. To

clearly state our predictions, it is necessary to define the terminology used hereafter delineating the competing and potential mate fish. Two fish (i.e., ‘competitors’) competed to mate with one of two other fish (i.e., ‘potential mates’). Once a competitor mated, it was termed the ‘primary competitor’ and the potential mate he or she spawned with the ‘accepted mate.’ The competitor who did not mate was termed the ‘secondary competitor’ and the potential mate not chosen the ‘rejected mate.’ Given how male and female convict cichlids choose their mates in the absence of competition (see above), and that competition is considered a cost during a search thus decreasing one’s choosiness (e.g., Real, 1990; Palokangas et al., 1992; Sikkel, 1998; Gotthard et al., 1999), we make the following predictions (also see Table 1). A decrease in choosiness should coincide with a decrease in preference expression, thus primary females will not spend more time with accepted males, yet will continue to visit and court both males similarly. Likewise, males who mate will no longer express a courtship preference, but will continue to visit and spend time equally between potential female mates. Possibly, secondary competitors will show a similar search pattern to primary competitors if each adjusts their search patterns similarly to manage competition costs.

However, intrasexual aggression could limit some individuals from acquiring particular mates (e.g., Beeching et al., 1998; Slagsvold, 1993), which alters our predictions (see Table 1). For example, if individuals exhibit more mate fidelity as a type of mate guarding tactic in the presence of a sex conspe-

Table 1. Summary of results from Santangelo & Itzkowitz (2004) (i.e., Non competing) compared to summary of alternative hypotheses of current study (i.e., Competing). Symbols explain direction of results regarding accepted mates versus rejected mates. For example, > under time means that a competitor spends more time with the accepted mate than the rejected mate.

Spawning competitors	Non-competing			Competing					
	Time	Visits	Courtship	If search patterns change due to a decrease in choosiness			If search patterns change due to adoption of a mate guarding tactic		
				Time	Visits	Courtship	Time	Visits	Courtship
Male	=	=	>	=	=	=	>	>	>
Female	>	=	=	=	=	=	>	>	<, >, or =

cific, then less time should be allotted for continuous assessment (see above). If so, then primary females will visit rejected males less than accepted males (in contrast to non-competing females), but spend more time with accepted males (similar to non-competing females). There is no evidence to suggest that mate guarding would alter female courtship intensity towards either male, thus we predict if mate guarding occurs, primary females should resemble non-competing females in courting both males at equal rates. If primary males mate guard, they will differ from non-competing males by spending more time with, and making more visits to, accepted females but will continue to exhibit more courtship towards accepted females. If primary competitors (male and/or female) are mate guarding, then secondary competitors should show the reverse pattern of primary competitors (e.g., spend more time with the rejected mate). Additionally, if mate guarding occurs, then secondary competitors will be attacked more when with the primary competitor's preferred mate than with the rejected mate.

There are no clear predictions regarding whether, or how, the sexes will be differentially affected by competition because it is unclear which sex, if either, undergoes more competition. In the field, both sexes actively compete with sex conspecifics for access to mates (pers. obsv.). However, because males have a higher reproductive potential (Townshend & Wootton, 1984; Wisenden, 1994) sexual selection theory predicts that males are less choosy and undergo more competition than females (reviewed in Andersson, 1994). Yet, females are more brightly colored than males predicting that females should be less choosy and undergo more competition (reviewed in Andersson, 1994). Either way, one sex could be influenced by competition more than the other.

Methods

Design and procedure

Apart from some minor points indicated below, methods mimicked those of Santangelo & Itzkowitz (2004) and were the same for male and female competition experiments. All procedures were approved under Lehigh IACUC protocol number DR/00. Fish were kept in 473.5 liter stock aquaria. Subjects were a combination of individuals bred in the laboratory, obtained from

local pet stores, and collected from their native country, Costa Rica. All populations behave similarly (Bockelman, 2004). Males and females were maintained at $20 \pm 2^\circ\text{C}$ with a 15L:9D hour cycle, housed in separate tanks, and fed trout crumbles every other day. Although the exact breeding experience of all fish was unknown, the majority, if not all, of experimental subjects had previously bred. Therefore, females were isolated for one month before experiments began to ensure their readiness to pair and spawn (see Townshend & Wootton, 1984; Barlow, 1991). We recorded the total length and mass of each fish (see Table 2a, b). Males were always larger than females to mimic natural populations (Wisenden, 1995; pers. obsv.) as well as the methodology of Santangelo & Itzkowitz (2004). Once used, subjects were kept separate from stock fish to avoid pseudoreplication.

We placed four fish in each experimental tank (two competitors and two potential mates). Although both males and females are expected to exhibit choice within a monogamous system, we designated the free-swimming individuals as the selectors (see Santangelo & Itzkowitz, 2004 for justification). Fish were given their designations after spawning as described above (see Introduction), and primary individuals never spawned with both potential mates.

Experiments were conducted in 284 liter ($120 \times 45 \times 50$ cm) aquaria partitioned into five sections (Figure 1). The outermost sections, (i.e., intruder compartments; A in Figure 1), were separated from the rest of the tank by clear plastic partitions. We placed one juvenile convict cichlid in each intruder compartment to mimic the design of Santangelo & Itzkowitz (2004). Adjacent to each intruder compartment were experimental compartments (B in Figure 1); each containing a spawning site (i.e., flower pot). Experimental compartments were delineated by the clear intruder compartment partition on one side and opaque partition on the other. The opaque partitions for both experimental compartments created a middle neutral section between them (C in Figure 1). Holes in these opaque partitions allowed only competitors access to both experimental compartments as potential mates were tethered in their compartments (see below). The hole diameters were 2 cm for female competitors and 3.5 cm for male competitors. The opaque partitions limited tactile and visual interactions between potential mates controlling for possible effects of interactions between the potential mates on the competitors mate choice process; holes in partitions were offset to further limit these visual interactions. The ability of competitors to interact and

Table 2. Size distributions for length, width, and mass of fish used in the (a) female competition experiment, (b) male competition experiment.

(a)	Female mean size	Female size range	Mean size differences between females	Size range differences between females	Male mean size	Male size range	Mean size differences between male mates	Size range differences between male mates
Length	61.5 cm	54.9-72.2 cm	2.1 cm	0.0-5.8 cm	68.7 cm	59.9-79.0 cm	3.3 cm	0.3-12.2 cm
Mass	5.0 g	3.3-7.3 g	0.3 g	0.0-1.0 g	6.2 g	3.8-9.7 g	0.9 g	0.0-3.2 g
(b)	Male mean size	Male size range	Mean size differences between males	Size range differences between males	Female mean size	Female size range	Mean size differences between female mates	Size range differences between female mates
Length	68.3 cm	60.5-83.0 cm	2.09 cm	0.1-4.6 cm	59.9 cm	50.3-70.9 cm	3.8 cm	0.2-10.6 cm
Mass	6.0 g	4.3-9.9 g	0.4 g	0.0-1.1 g	4.6 g	2.9-7.6 g	0.9 g	0.0-3.0 g

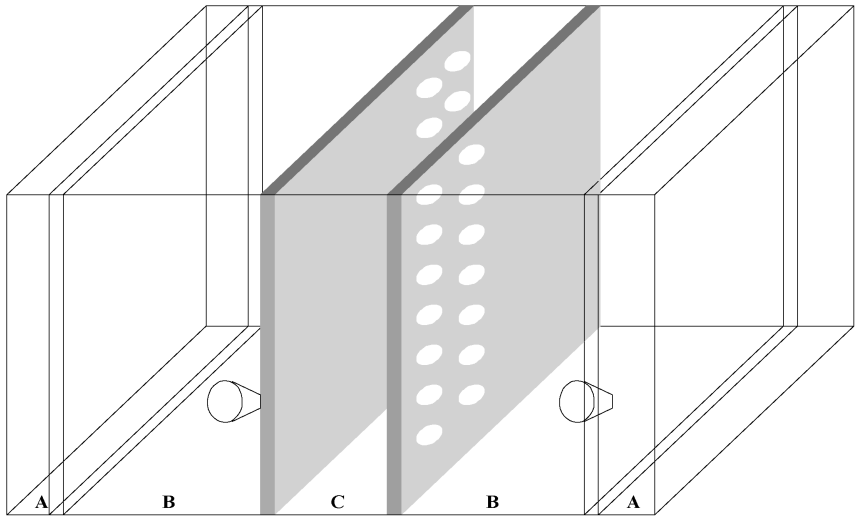


Figure 1. Diagram of the experimental setup. (A) intruder compartments. (B) experimental compartments with flowerpots. (C) neutral compartment.

spawn with potential mates allowed recording both mate 'choice' and mate 'preference' data (reviewed by Jennions & Petrie, 1997; Wagner, 1998; also see methods of Santangelo & Itzkowitz, 2004).

Each experimental compartment contained one potential mate tethered to restrict it to its respective compartment. Before tethering a fish, we anesthetized it using seltzer water (see Summerfelt & Smith, 1990). We then inserted a monofilament loop through the fish's dorsal musculature and let it recuperate for four days in a hospital tank prior to testing. On the fifth day, we attached a second monofilament line from a swivel to the fish's monofilament loop. The swivel was screwed into a board overhanging an experimental section. We allowed the tethered fish another day to acclimate to the tether before the competitors were introduced. This design provided potential mates with free movement in their compartment and access to the flowerpot while preventing their movement through the holed partition. Tethered convict cichlids are able to both successfully pair and rear offspring (pers. obsv.). Furthermore, their mate choice behavior is identical to non-tethered fish in the same experimental setup (refer to Santangelo & Itzkowitz, 2004; Santangelo, 2005). We feel this treatment follows all ethical concerns as these methods have been published before, authorized by an IACUC committee,

and most importantly, all fish fully recovered within days of having the tether removed.

After tethered potential mates acclimated to an experimental tank, selectors were tagged (see below), placed in the neutral compartment, and we began video taping immediately. We video taped each tank for a half hour each day until spawning occurred. The time of day recorded was randomized mimicking the methods of Santangelo & Itzkowitz (2004). We fed fish each day eight pellets of trout crumbles in each experimental compartment.

Competitors were similarly sized within a replicate (i.e., total length difference between selectors did not exceed 0.5 cm) and tagged for individual identification by injecting non-toxic white water soluble paint underneath the scales. One fish was tagged on the left flank, the other on the right flank. If a competitor incurred serious injury during a replicate, he or she was removed and isolated in a hospital tank. The remaining competitor (now consequently considered the primary competitor) was left in the tank and continued to be video taped each day until spawning. Sample sizes were as follows; female competition, $N = 15$; male competition, $N = 16$.

Video analysis began after all replicates had been completed and were watched with the observer blind to which fish was ultimately primary or secondary and which mate was ultimately rejected or accepted. Data recorded from the videotapes included courtship between potential mates and competitors, aggressive behavior between competitors, the number of times each competitor visited each compartment, and the duration of these visits (i.e., bouts). The mean number of visits made to potential mates per day by each competitor was calculated by dividing the total number of visits made by the number of days that competitor spent in the tank. We determined the mean bout by computing the mean bout for each day, and then calculating the mean of these means.

Data summary and analysis

Selection periods

Following Santangelo & Itzkowitz (2004), data for competitors (i.e., mean bouts, visits, and courtship rates) were calculated for different time periods of the mate choice process. However, due to the lack of any biologically significant interaction of period in that study, or this one, these results are not reported.

Courtship

Courtship behaviors (i.e., tailbeats, quivers, and brushes; see Santangelo, 2005 for description of behaviors) displayed by each individual was recorded. Similar to Santangelo & Itzkowitz (2004), all courtship behaviors followed similar trends and so were combined to generate an overall courtship score. We calculated the average number of courtship events exhibited per day by dividing the sum of all courtship events by the number of days spent in the tank. Because competitors might not spend the same amount of time with each mate, we also calculated a courtship rate. This was done by dividing total number of courtship events an individual exhibited toward another fish by the total amount of time the two fish spent together. Courtship rates for each day were averaged over all days giving each fish a mean courtship rate score.

Statistics

Each competitor's pattern of movement was analyzed as a 2 within \times 3 within subject ANOVA design (see Keppel, 1991) with competitor type as one factor (primary or secondary) and compartment type as the other factor (i.e., accepted, neutral, rejected; the potential mate that resided in a compartment defined compartment type). Individual comparisons within the ANOVA's were tested with paired planned comparisons or multiple comparison Tukey tests.

Courtship data did not conform to parametric assumptions. Therefore, Wilcoxon matched pairs (i.e., WMP) was used to compare courtship means and rates between individuals. Samples where a competitor could not court a potential mate because they never visited that mate, were removed. Therefore, some analyses were not carried out due to inadequate sample sizes ($N \leq 5$) for the matched design.

The time competitors spent together in each compartment was analyzed using a within subject ANOVA and the amount of aggression each competitor exhibited towards the other was analyzed using a sign test. A sign test was used because the data did not fit the assumptions of parametric testing and within the framework of the current study, discovering the competitor that was more often more aggressive has greater meaning than the magnitude of the aggression between the selectors.

Female competition

In one replicate the secondary female did not spend time with the rejected male; this replicate was excluded from courtship analyses involving the rejected male and secondary female. In two replicates, the secondary female was removed before the primary female spawned due to injury.

Male competition

In one replicate a secondary male never visited the accepted female. Therefore this replicate was excluded from courtship analyses involving the secondary male and the accepted female. In three replicates, the secondary male was removed before the primary male spawned due to injury.

Results

Female competition

The mean number of days primary females took to spawn was 6.47 ± 0.74 days. Female size, relative to the other female, was not a factor in determining the primary female (Binomial test; length: large 7, small 7, $p = 0.99$; mass: large 9, small 5, $p = 0.45$). Males were not accepted based on length (Binomial test; large 8, small 7, $p = 0.99$) or mass (Binomial test; large 8, small 6, $p = 0.80$). Sample sizes are not equal due to exclusion of tie scores.

(i) Time

Because average bout length per day and average time spent per day in each compartment show the same patterns save one exception, we report only bout patterns with the one exception elucidated below. There was a significant interaction between female type and compartment type ($F_{2,22} = 8.73$, $p = 0.001$, Figure 2a). Thus the effect of female type depended on the compartment in which the comparison is made. Compared to secondary females, primary females spent more time with accepted males (Planned comparison: $F_{1,11} = 5.31$, $p = 0.04$), and less time with rejected males per day (Planned comparison: $F_{1,11} = 9.79$, $p = 0.009$). Bouts of primary females were greater with accepted males than with either rejected males (Planned comparison: $F_{1,11} = 13.56$, $p = 0.003$), or in the neutral compartment (Tukey test: $p = 0.002$). However, these bouts by the primary females did

not differ between rejected males and the neutral compartment (Tukey test: $p = 0.99$). Secondary females showed a different trend such that their bout lengths were similar among all three compartments (accepted males vs rejected males; Planned comparison: $F_{1,11} = 2.19$, $p = 0.17$; accepted males vs the neutral compartment; Tukey test: $p = 0.99$; rejected males vs the neutral compartment; Tukey test: $p = 0.28$). However, while the bouts of secondary females did not differ among the compartments, due to their visits (see below), their average time per day was greater with rejected males than with accepted males (Planned comparison: $F_{1,11} = 9.65$, $p = 0.01$) and in the neutral compartment (Tukey test: $p = 0.01$). There was no difference between the neutral compartment and accepted males (Tukey test: $p = 0.92$).

Primary females were more often the more aggressive fish in the accepted male's compartment (sign test: non tie scores $N = 11$, $z = 2.41$, $p = 0.016$). Both females were similarly aggressive in the neutral compartment (sign test: non tie scores $N = 11$, $z = 0.00$, $p = 1.00$) and rejected male's compartment (sign test: non tie scores $N = 8$, $z = 0.35$, $p = 0.72$).

(ii) Visits

There was a significant interaction between female type and compartment type (within-subjects ANOVA: $F_{2,22} = 8.61$, $p = 0.002$; Figure 3a). Thus, as was the case for bout time (Figure 2a), the effect of female type on the number of visits depended on the compartment in which the comparison was made. Primary females visited accepted males more than did secondary females (Planned comparison: $F_{1,11} = 7.72$, $p = 0.018$), but both females visited rejected males a similar amount (Planned comparison: $F_{1,11} = 2.17$, $p = 0.17$). Primary females visited accepted males more than they visited rejected males per day (Planned comparison: $F_{1,11} = 8.12$, $p = 0.016$) while secondary females visited rejected males more than they did accepted males per day (Planned comparison: $F_{1,11} = 6.66$, $p = 0.025$).

(iii) Courtship

Primary females courted accepted males more than they courted rejected males per day (WMP: $N = 11$, $T = 9.00$, $z = 2.12$, $p = 0.033$), but did not court either male at significantly different rates per day (WMP: $N = 11$, $T = 32.00$, $z = 0.09$, $p = 0.93$; Figure 4a). Secondary females were

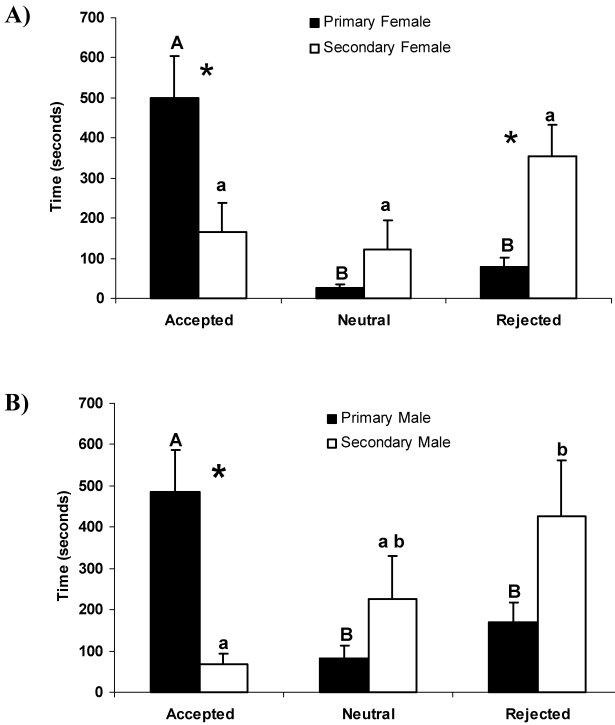


Figure 2. Mean and SE of bout lengths of primary (black bars) and secondary (white bars) female competitors (A) and male competitors (B). Different capital letters indicate significant differences between compartments within primary competitors; different lowercase letters indicate significant differences between compartments within secondary competitors. Significant differences within a compartment between competitors are indicated by (*); n.s. = no significant differences. All differences are $p < 0.05$.

different. They courted rejected males more than accepted males per day (WMP: $N = 11$, $T = 2.00$, $z = 2.59$, $p = 0.009$) and courted rejected males at a higher rate per day (WMP: $N = 11$, $T = 13.00$, $z = 1.78$, $p = 0.07$; Figure 4a).

Accepted males courted primary females more than secondary females (WMP: $N = 12$, $T = 0.00$, $z = 3.06$, $p = 0.002$), and at a higher rate per day (WMP: $N = 12$, $T = 14.00$, $z = 1.96$, $p = 0.04$, Figure 5a). Rejected males did not court females differently in either mean courtship (WMP: $N = 10$, $T = 24.00$, $z = 0.35$, $p = 0.72$), or rate of courtship per day (WMP: $N = 10$, $T = 15.00$, $z = 1.27$, $p = 0.20$; Figure 5a). Compared to accepted males, rejected males did not differ in their mean

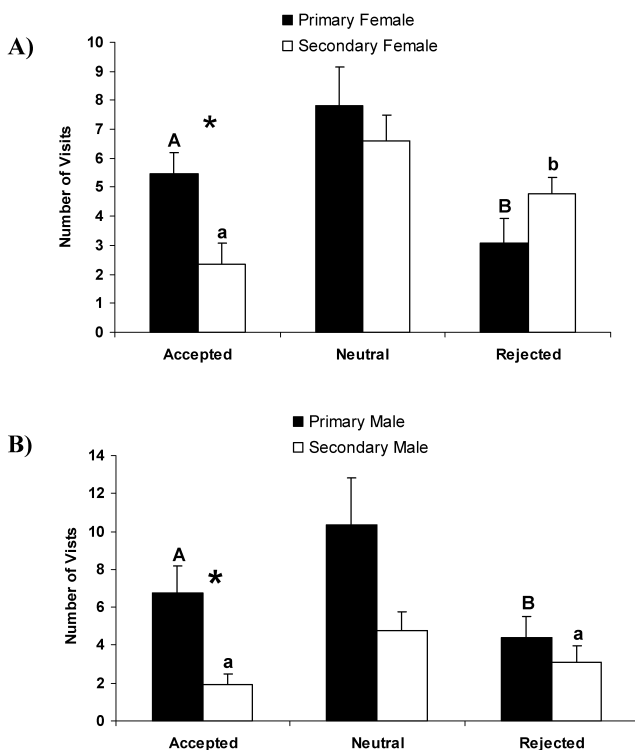


Figure 3. Mean and SE of number of visits for primary (black bars) and secondary (white bars) female competitors (A) and male competitors (B). See Figure 2 caption for more details.

courtship per day towards primary females (WMP: $N = 11$, $T = 23.00$, $z = 0.89$, $p = 0.37$), but did court primary females at a higher rate (WMP: $N = 11$, $T = 10.00$, $z = 2.05$, $p = 0.04$). Also, rejected males courted secondary females more than did accepted males in both mean courtship (WMP: $N = 11$, $T = 5.00$, $z = 2.48$, $p = 0.013$) and courtship rate per day (WMP: $N = 11$, $T = 24.00$, $z = 0.80$, $p = 0.42$).

Male competition

Females took an average of 6.19 ± 0.86 days to spawn. Females were not accepted based on length (Binomial test: 4 large, 12 small; $p = 0.07$) or mass (Binomial test: 5 large, 10 small; $p = 0.30$). Male size, relative to the other male was not a factor in determining the primary male (Binomial test; length: 7 large, 9 small; $p = 0.80$; mass: 11 large, 4 small; $p = 0.12$). Again, sample sizes are not all equal due to the exclusion of tie scores.

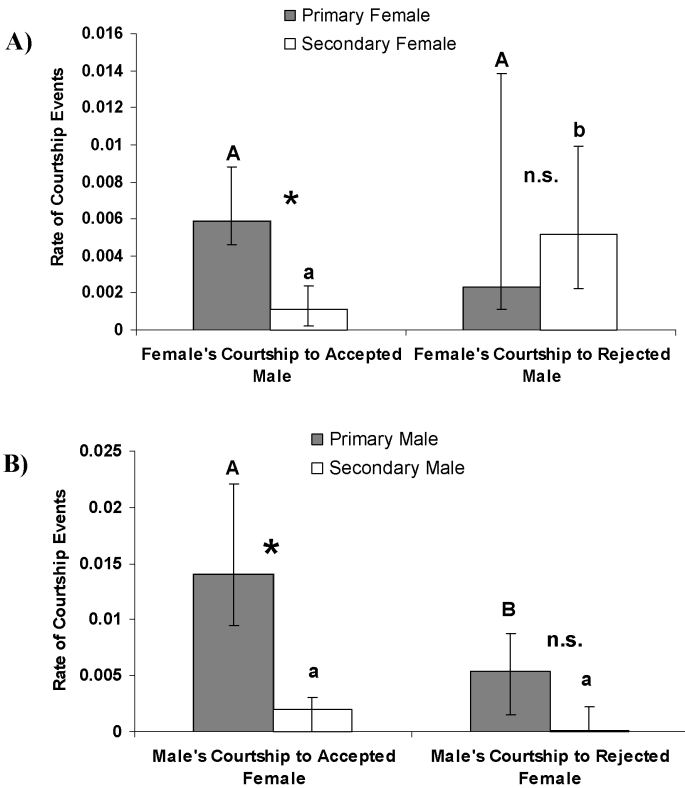


Figure 4. Median, 1st, and 3rd quartiles of primary (gray bars) and secondary (white bars) female (A) and male (B) competitor courtship rate towards accepted and rejected mates. See Figure 2 caption for more details.

(i) Time

Similar to the female competition results, average time spent and average bout length per day in each compartment show similar patterns here save one exception. Thus, again we report only bout patterns with the one exception elucidated below. There was a significant interaction between male type and compartment type (within-subject ANOVA: $F_{2,22} = 9.98$, $p < 0.001$, Figure 2b). Thus, the effect of male type depended on the compartment in which the comparison was made. There was no difference between males in bouts with rejected females ($F_{1,11} = 2.89$, $p = 0.12$), but primary males had longer bouts with accepted females (Planned comparison: $F_{1,11} = 17.37$, $p = 0.001$). However, secondary males spent a greater average amount of time per day with rejected females than did primary males (Planned com-

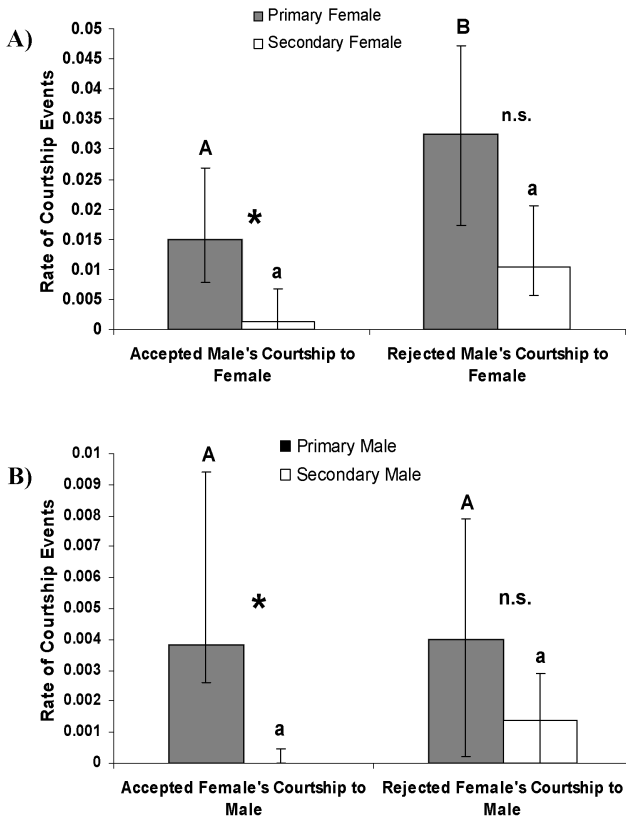


Figure 5. Median, 1st, and 3rd quartiles of the accepted and rejected mates' courtship rate towards primary (gray bars) and secondary (white bars) female (A) and male (B) competitors. See Figure 2 caption for more details.

parison: $F_{1,11} = 5.11, p = 0.045$). Primary males had longer bouts with accepted females than they did with rejected females (Planned comparison: $F_{1,11} = 7.85, p = 0.017$) or in the neutral compartment (Tukey test: $p = 0.10$). Primary male bout lengths between rejected females and the neutral compartment were similar (Tukey test: $p = 0.97$). Secondary males had longer bouts with rejected females than with accepted females (Planned comparison: $F_{1,11} = 6.61, p = 0.026$) while thier bouts in the neutral compartment did not differ from accepted females (Tukey test: $p = 0.74$) or rejected females (Tukey test: $p = 0.50$).

Similar to female competitors, primary males were more often more aggressive than secondary males in the presence of accepted females (sign test:

$z = 2.85$, $N = 10$, $p = 0.004$). Aggression between males was similar in the neutral compartment (sign test: $z = 0.95$, $N = 10$, $p = 0.34$) and in the rejected female's compartment (sign test: $z = 1.21$, $N = 11$, $p = 0.23$).

(ii) Visits

There was a significant interaction between male type and compartment type (within-subjects ANOVA: $F_{2,22} = 4.09$, $p = 0.030$; Figure 3b). Thus, the effect of male type depended on the compartment in which the comparison was made. Primary males visited accepted females more than they visited rejected females per day (Planned comparison: $F_{1,11} = 11.83$, $p = 0.005$). Secondary males did not differ in their visits to either female (Planned comparison: $F_{1,11} = 1.31$, $p > 0.27$). Primary males also visited accepted females more than did secondary males (Planned comparison: $F_{1,11} = 8.41$, $p = 0.014$), but males did not differ in number of visits to rejected females per day (Planned comparison: $F_{1,11} = 0.61$, $p = 0.45$).

(iii) Courtship

Primary males courted accepted females more than rejected females (WMP: $N = 12$, $T = 0.00$, $z = 3.06$, $p = 0.002$), and at a higher rate per day (WMP: $N = 12$, $T = 5.00$, $z = 2.67$, $p = 0.007$; Figure 4b). Secondary males did not court accepted and rejected females differently in number of courtship events per day (WMP: $N = 11$, $T = 14.00$, $z = 0.56$, $p = 0.58$) and courtship rate per day (WMP: $N = 11$, $T = 14.00$, $z = 0.56$, $p = 0.57$).

Between males, primary males courted accepted females more than did secondary males (WMP: $N = 11$, $T = 0.00$, $z = 2.93$, $p = 0.003$) and at a higher rate per day (WMP: $N = 11$, $T = 0.00$, $z = 2.93$, $p = 0.003$). Males did not differ in their courtship towards rejected females in number of courtship events per day (WMP: $N = 12$, $T = 31.00$, $z = 0.62$, $p = 0.53$), or courtship rate per day (WMP: $N = 12$, $T = 14.00$, $z = 1.96$, $p = 0.05$).

Accepted females courted primary males more per day (WMP: $N = 11$, $T = 0.00$, $z = 2.93$, $p = 0.003$) and at a higher rate (WMP: $N = 11$, $T = 1.00$, $z = 2.85$, $p = 0.004$; Figure 5b) than they did secondary males. No significant correlation existed between the accepted females courtship rate to primary males and the number of days until spawning (Spearman rank: $N = 12$, $r = 0.23$, $p = 0.46$). Rejected females did not court either male differently in number of courtship events per day (WMP: $N = 12$,

$T = 37.50$, $z = 0.12$, $p = 0.91$), or courtship rate per day (WMP: $N = 12$, $T = 19.00$, $z = 1.56$, $p = 0.12$). Compared to rejected females, accepted females courted primary males more (WMP: $N = 12$, $T = 6.00$, $z = 2.58$, $p = 0.009$) and courted secondary males less per day (WMP: $N = 11$, $T = 2.00$, $z = 2.24$, $p = 0.025$). However, accepted and rejected females did not differ in their courtship rates towards primary (WMP: $N = 12$, $T = 31.00$, $z = 0.63$, $p = 0.53$) or secondary males (WMP: $N = 11$, $T = 5.00$, $z = 1.82$, $p = 0.068$).

Discussion

Both male and female competitors spent their time differentially among compartments refuting the hypothesis that competitors will exhibit similar mate choice patterns. Nor did intrasexual competition cause either sex to eliminate mate preferences (i.e., for females a time preference; for males a courtship preference). However, competition did cause changes in these mate choice patterns. Primary females made more visits to accepted than to rejected males per day and these visits were longer in duration (i.e., bouts). In contrast, while non-competing females also expressed their mate preferences through bouts, they visited accepted and rejected males equally (Santangelo & Itzkowitz, 2004). Primary males spent more time, made more visits, exhibited longer bouts, and courted at a higher rate accepted than rejected females. Non-competing males also courted accepted females at a higher rate, but did not differentially visit or spend time between females (Santangelo & Itzkowitz, 2004). Thus, competition caused males to express their mate preferences in terms of time as well as courtship.

The change in behavior for both sexes due to competition is indicative of mate guarding (Table 1). Mate guarding is a common aspect of male mate choice in multiple species (reviewed by Andersson, 1994), and also in female mate choice of some monogamous species (e.g., Hunter et al., 1993; Petrie & Kempenaers, 1998). Mate guarding has been suggested as one function of extended pre-mating pair bonds (Walter & Trillmich, 1994; Yamamoto et al., 1999). Furthermore, female-female aggression in convict cichlids has been suggested as a method to limit a preferred male's contact with other females (Beeching et al., 1998). In support of these ideas, individuals in both sexes either spent more time with (i.e., males), and/or made more visits to

(i.e., males and females), preferred mates only in the presence of another competing searcher. Additionally, primary individuals were most aggressive in the presence of the accepted mate.

That both sexes only exhibit these mate guarding tactics in the face of competition indicates that they optimize their search behavior given the present level of competition. For example, in the current study, the difference in visits between potential mates was caused by primary individuals leaving their accepted mate, entering the neutral compartment, and then immediately returning. In contrast, in the absence of competition, individuals would continue through the neutral compartment and visit the rejected mate (Santangelo & Itzkowitz, 2004). This shows a decrease in continuous assessment of other potential mates in the presence of competition. That is, both sexes were more attentive to their preferred mate in the presence of a competing sex conspecific. In a variety of species, it has been shown that as competition among searchers increases, there is an increase in mate guarding behavior (e.g., hermit crab, *Pagurus middendorffi*: Wada et al., 1999; Mediterranean wrasse, *Symphodus ocellatus*: Alonzo & Warner, 2000; crab spider, *Misumena vatia*: Holdsworth & Morse, 2000; snow crabs, *Chionoecetes opilio*: Rondeau & Sainte-Marie, 2001; sleepy lizard, *Tiliqua rugosa*: How & Bull, 2002; also see pipefish, *Corythoichthys haematopterus*: Matsumoto & Yanagisawa, 2001). Because both male and female convict cichlids continuously assess when choosing a mate, mate guarding is of obvious importance. The results of the current study, together with that of Santangelo & Itzkowitz (2004; see Introduction), suggests that the benefit of mate guarding must be balanced with both the potential cost of leaving one's preferred mate in order to assess others, and the potential benefit of finding a higher quality mate.

We can make no direct conclusion about which sex was more affected by the addition of competition. However, the change in more levels for males suggests that the search process of males is more labile, which may be related to their higher reproductive potential relative to females (Townshend & Wootton, 1984; Wisenden, 1994; see below). It is curious that males only express a time preference in the presence of competition while females will do so regardless. For females, this suggests that there are other reasons for them to spend time with these males, or it is simply a matter of spending time on the territory preparing the nest. Given the current experimental design, we cannot separate out these two factors. For males, which show the ability to be

bigamous (Keenleyside et al., 1990), by having a more flexible continuous assessment strategy, they can take advantage of low competition levels (i.e., perhaps to attempt bigamy) while in high competition environments, mate guard.

Competitor courtship

Competition did not appear to alter the courtship patterns of either sex, but courtship patterns did differ between the sexes. Compared to rejected females, primary males courted accepted females more per day, and at a higher rate. This is the same for non-competing males (Santangelo & Itzkowitz, 2004) and it is unclear if competition had any influence on courtship itself. For example, competing males might have increased or decreased their courtship relative to non-competing males, but males that mated still courted accepted females more than rejected females. The courtship of primary females resembled non-competing females in that neither courted accepted and rejected males at different rates (Santangelo & Itzkowitz, 2004; Santangelo, 2005). So accepted males received more courtship from primary females, but only as a function of these females spending more time with accepted males. This supports the previous suggestion that individual females court at one rate regardless of the male they are courting (see Santangelo & Itzkowitz, 2004; Santangelo, 2005). Other studies show that females modify their mate advertisement signals less so than do males (i.e., contact calls in budgerigars, *Melopsittacus undulatus*: Hile et al., 2000; feather ornaments in European starlings, *Sturnus vulgaris*: Komdeur et al., 2005). The persistence of this pattern among species may be a general sexual selection phenomenon, such as the relative costs of mating between sexes, including monogamous species.

Secondary females exhibited different courtship rates between male potential mates, but this was likely due to the primary female's aggression towards the secondary female when with the accepted male, rather than secondary females choosing to court at a lower rate. Similarly, primary males appeared to inhibit the courtship of secondary males to both females. Males and females will court multiple individuals (up until they mate), regardless of who they ultimately choose (Santangelo & Itzkowitz, 2004; also see Mackerath & Keeleyside, 1993). Thus, protecting one's mate from other potential suitors is an important aspect to convict cichlid ecology. While

similar results have been shown in multiple species (i.e., baboons, *Papio cynocephalus*: Hausfater, 1975; elephant seals, *Mirounga leonine*: McCann, 1981; ring-necked pheasants, *Phasianus colchicus*: Mateos & Carranza, 1999; bluethroats, *Luscinia s. svecica*: Johnsen et al., 2003; raptors: reviewed in Mougeot, 2004) our studies are the first we know of to show this in a monogamous species that does not exhibit frequent extra pair matings.

Potential mate courtship

Courtship from potential mates also differed between the sexes. Rejected males courted primary females at a higher rate than did accepted males. This was also the pattern observed in the absence of female-female competition (Santangelo & Itzkowitz, 2004; Santangelo, 2005). It appears that a male's courtship level is related to how successful he is in acquiring a mate. Why rejected males might court at a higher rate has been previously discussed (see Santangelo, 2005), but in brief, could be because (1) rejected males are lower quality, or realize they are not preferred, and are attempting to manipulate female choice, (2) accepted males are higher quality, or realize they are preferred, so invest less in courtship, or (3) a combination of these. The occurrence of this effect in multiple studies on convict cichlids, and in other species (e.g., bower birds, *Ptilonorhynchus violaceus*: Patricelli et al., 2002), necessitates additional exploration for why these differences occur among males in their courtship.

Accepted males both courted more, and received more courtship from, primary females than secondary females. Therefore, similar to non-competing males (Santangelo & Itzkowitz, 2004), and to the competing males of the male competition experiment here, males that mated courted the females they mated with more. The courtship that rejected males exhibited and received did not differ between primary and secondary females. Although it is unclear why rejected males showed no courtship preference, we speculate that if lower quality individuals exhibit less choosiness (sensu Real, 1990), these males might not show a distinct preference for either female, as seen in pipefish (Mazzi, 2004).

Accepted and rejected females courted primary males at similar rates. It is unclear how this relates to our previous suggestion that males prefer 'high-courtiers' to 'low-courtiers' (Santangelo & Itzkowitz, 2004) as males in this study might simply not had this cue on which to base their choice. However, because primary males spent more time with accepted females, primary

males still received more courtship from accepted females. Males might be assessing the total amount of courtship they receive from a female and in general this supports hypotheses suggesting that searchers mate with those from which they receive the most information (Luttbegg, 1996). Clearly though, males are using some other cue in deciding with which female to spend their time thus enabling them to gather this information. In both experiments here, and in previous studies (Santangelo & Itzkowitz, 2004; Santangelo, 2005), receptivity is unlikely to be the information signaled through courtship as female courtship was not correlated to number of days to spawning.

Rejected females courted male competitors similarly, again supporting that an individual female courts all males equally (see above). However, similar to secondary females, accepted females here did not court both males equally. But, similar to primary females inhibiting secondary female courtship (see above), we feel here primary males caused accepted females not to court rejected males. We base this on that in every other instance, either within this study or our previous ones, females did not alter their courtship rate towards different males. In this case the primary male may have done so directly (i.e., his presence inhibits female courtship), or indirectly (i.e., he directly inhibits the competing male's courtship – see above). Either way, a mate guarding male appears to inhibit courtship between his female and other males.

Secondary individuals

Secondary males and females acted similarly; both spent more time with rejected mates than with accepted mates. It is unclear whether the patterns of secondary competitors were intrinsic to their mate choice, or to avoid primary competitors. However, the latter seems more likely, especially given the aggression of primary competitors in the presence of accepted mate. Given that secondary females visited rejected males more than accepted, and secondary males visited both potential mates equally, perhaps subordinate females are less likely to 'test' if a guarded mate has become available relative to subordinate males. Although the current study cannot answer what the secondary individuals would have done had they not been competing, and under natural conditions more than only one other potential mate would be available, secondary females did exhibit courtship to the male with whom they were 'forced' to spend time. Assuming there are no better quality mates

available, dominant individuals might indirectly 'force' sex conspecifics to mate with non-preferred mates, particularly if it is less costly to do so than to forgo reproduction. Potentially, dominant individuals directly and indirectly manipulate the mate searching, and the mate choice, of subordinate individuals.

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