Courtship in the monogamous convict cichlid; what are individuals saying to rejected and selected mates?

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I examined the relation between courtship and mate choice in convict cichlids by presenting females with the option of courting and spawning with one of two males that were isolated from each other. I quantified the amount of courtship performed by females towards males they selected as mates and males they rejected, and the amount of courtship performed by each male towards the female. I measured courtship using two rates: (1) daily courtship rate, the total number of courtship events per number of days until spawning; and (2) contact courtship rate, the total number of courtship events per day per total time spent with a given individual. Females showed similar contact courtship rates to each male, whereas both types of courtship rates between females and only rejected males were significantly and positively correlated. Females showed a nonsignificant tendency to select larger males. Females spent significantly more time with the males they selected and therefore females' daily courtship rate towards selected males was significantly higher than that towards rejected males. Although females showed a preference early in their search for the male they eventually selected, they continued to spend time with, and court, the rejected male until spawning with the selected male, indicating that females continuously assess males throughout their search. Male courtship differed from female courtship in that while the daily courtship rates towards the females did not differ significantly between males, the contact courtship rate of rejected males was significantly higher than that of selected males. Thus, rejected males may court more because they know they are not the preferred male, or selected males may court less because they know they are the preferred male, or a combination of both.

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Although behaviourists have hypothesized that courtship serves a variety of functions (e.g. Baerends 1986), courtship is typically viewed as a means for potential mates to advertise their quality (e.g. flies: Hoikkala et al. 1998; fish: Knapp & Kovach 1991; birds: Reid 1987) and/or location (e.g. crabs: Christy et al. 2001; flies: Ritchie et al. 1998; fish: Itzkowitz & Haley 1999; frogs: Arak 1988; Gerhardt 1994; birds: Dale et al. 1990; Hasselquist & Bensch 1991). However, courtship can be more complex. For example, in many species, courtship between males and females can continue for extended periods, suggesting that it might be an interactive process (i.e. a dialogue between the male and female), but few studies have examined how this type of courtship process relates to mate choice decisions (but see below). Therefore, similar to studies that explore mate searching by comparing the time that individuals invest in potential mates (e.g. Real 1990; Sullivan 1994; Luttbeg

1996; Weigmann et al. 1996), here I examine courtship patterns shown by individuals towards two potential mates, one of which they ultimately select. Here, 'select' in this study means a mating has occurred.

There is extensive evidence within the literature across taxa that courtship has a definite role in the mate choice process. For example, male beaugregory damselfish, *Stegastes leucostictus*, with high-quality territories court more and receive more eggs than males with low-quality territories (Santangelo et al. 2002). In multiple species of frogs, females prefer males that produce courtship calls at higher rates (reviewed by Gerhardt 1994). The mating success of male sand gobies, *Pomatoschistus minutus*, is associated with the intensity of male courtship (Forsgren 1997), and female whitethroats, *Sylvia communis*, mate with males that show more variable courtship songs (Balsby 2000). While it is difficult to do justice here to all courtship studies that have been conducted (reviewed in Andersson 1994), these studies generally indicate that courtship influences the mate choice decisions made by both sexes. However, we do not yet know if, or how, courtship patterns differ when individuals direct them

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towards multiple potential mates, particularly when only one of these potential mates is selected.

The possibility that courtship is uniquely 'tuned' to the courtship of each potential mate encountered has received some support. For example, the courtship of female white-throats influences male courtship, indicating that courtship can both be a message to the opposite sex and a response to the courtship of the opposite sex (Balsby & Dabelsteen 2002). The courtship of male veiled chameleons, *Chamaeleo calyptratus*, varies depending on the courtship they receive from either receptive or nonreceptive females (Kelso & Verrell 2002). Similarly, males of some species can adjust their courtship displays to the response of the female so as not to 'frighten away' the female (Patricelli et al. 2002). These studies imply that courtship can be modulated to a particular potential mate, which suggests that courtship is involved in mate assessment. Therefore, the patterns of courtship between a searching individual and a potential mate that that searcher ultimately selects might differ from the courtship patterns between that same searcher and a potential mate that he or she rejects. However, without knowledge of which potential mates a searching individual does select, as well as which ones are rejected, it is difficult to determine the role that these courtship interactions play in mate choice decisions.

Here, I examine the courtship and mate choice of the serially monogamous convict cichlid, *Archocentrus nigrofasciatus*. I used a two-choice experimental design in which each female was given a choice between two alternative males as potential mates. The male with whom the female mated was deemed the 'selected' male, and the other male, the 'rejected' male. Using this design, I made the following hypotheses.

(1) Based on previous studies on convict cichlids (see below), females will spend more time with the males they ultimately select as mates than with those they reject.

(2) Because there is currently no data showing how selected males court relative to rejected males in convict cichlids, I posit the null hypothesis that the courtship behaviour of selected males will not differ from that of rejected males. Examples of alternative hypotheses, as well as the null hypothesis, can be found in other species. That is, males that are selected as mates, relative to those that are rejected, will court females more (Sargent et al. 1986; Itzkowitz & Haley 1999), less (Patricelli et al. 2002), or the same amount (Wiley 1973).

(3) For female courtship, again I posit the null hypothesis that females will not court rejected or selected males differently. This is based upon the paucity of data on female courtship and mate selection in convict cichlids, or in any other species. However, if females choose their mates early in the courtship period relative to when they spawn, I predicted that they would either stop courting rejected males, or, at least, court rejected males differently.

METHODS

Study Species

Convict cichlids are biparental substrate brooders. Both sexes will court multiple individuals, and spawning occurs only after a stable pair bond is established. Thus far, the only differences that have been observed between courting individuals is that individuals spend more time with the mates they select (Mackereth & Keenleyside 1993; personal observation). Larger males are considered to be of higher quality (i.e. have increased reproductive success) because they are better able to protect and care for the offspring (Wisenden 1994b; also see Perrone 1978) and, together with the female, show a greater ability to outcompete other pairs for breeding sites (Itzkowitz et al. 1998). As such, females generally prefer the largest of available males (Noonan 1983) and males prefer to mate with larger, more gravid females (Nutall & Keenleyside 1993). During the courtship process, males and females will switch partners in order to obtain a mate of better quality (Triefenbach & Itzkowitz 1998). Aside from size, courtship has been implicated in the assessment of individual quality. Keenleyside (1985) showed that although size influences mate choice in convict cichlids, size does not account for many of the observed pairings, suggesting that other signals, such as 'vigour and persistence of courtship', are of potential importance in mate selection. However, no study has yet quantified the courtship behaviour of mate-searching convict cichlids.

Experimental Design

The fish used in this study were kept in 473.5-litre stock aquaria and were bred in the laboratory. Original stocks of subjects were obtained from local pet stores. Once in the laboratory, males and females were housed in separate, visually isolated stock tanks, and fed trout crumbles every other day. The aquaria were maintained at $20 \pm 2\,^{\circ}\mathrm{C}$ on a 14:10 h light:dark cycle.

Experiments were conducted in 284-litre ($120 \times 45 \times 50$ cm) aquaria. The aquaria were divided into five sections using plastic partitions (Fig. 1). The two outermost sections, referred to as intruder compartments (sections labelled A in Fig. 1), were separated from the rest of the tank by clear plastic partitions. I placed one juvenile convict cichlid in each intruder compartment at the start of each trial because pair bond formation is facilitated by the presence of conspecific intruders (Itzkowitz & Draud 1992; personal observation). I used juveniles because they would not be considered another potential mate for the selecting female. The two adjacent sections were experimental compartments (sections labelled B in Fig. 1), each of which contained a flower-pot to be used as a spawning site for convict cichlid pairs. The central, neutral section (section labelled C in Fig. 1) was separated from the two experimental compartments by opaque partitions. I drilled holes (2 cm in diameter) in these opaque partitions large enough to allow the experimental female, but not the experimental males, access to all compartments. These holes were offset from each other, limiting tactile and visual interactions between the two males that could potentially influence male or female courtship. Permitting females to interact and spawn with the males allowed me to record mate 'choice' data, rather than only mate 'preference' data. Briefly, preference is an individual's
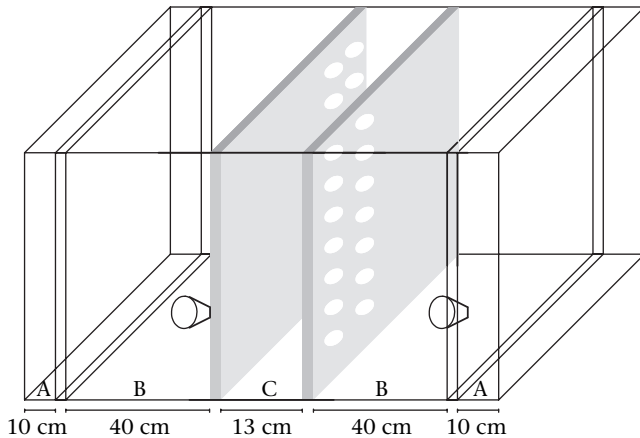
Figure 1. A diagram of the experimental set-up showing the two intruder compartments (A), the two experimental compartments (B), each equipped with a flower-pot, and the central neutral compartment (C). The intruder compartments were separated from the experimental compartments by clear plastic partitions. The experimental compartments were separated from the central compartment by opaque partitions into which 2-cm holes were drilled to allow the female access to both males.

inclination to mate with a potential mate, whereas choice is the actual outcome of the decision process, typically resulting in offspring (reviewed in Jennions & Petrie 1997; Wagner 1998).

Although the actual breeding experience of the fish used in the experiment was unknown, the majority, if not all, of them had previously bred. Therefore, females were not used until they had resided at least 1 month in their stock tank to ensure that all were equally ready to pair and spawn (see Townshend & Wootton 1984; Barlow 1991).

I recorded the total length of each adult fish to ensure that all males were larger than the female in order to mimic natural populations (Wisenden 1995). I then placed one juvenile intruder in each intruder compartment and one experimental male in each experimental compartment. Immediately following this, I placed a female in the central, neutral compartment. Fish were fed by dropping eight pellets of trout crumbles in each experimental compartment every day. This eliminated any bias in resource quality between potential mates (e.g. Grant & Guha 1993; Wisenden 1994a, b). Upon the introduction of the female, tanks were videotaped for 2 h every day until the female spawned with a male. All replicates ended after the female spawned with one of the males. At the end of each replicate, all individuals were housed separately from the rest of the fish stock to avoid pseudoreplication.

I tested 31 females. However, due to time constraints (i.e. females spawned an average of 8 days after being introduced), I randomly selected 12 videotaped trials for analyses of courtship behaviour. When I collected data from the videotapes, I had no knowledge of which male was ultimately selected for the particular tank I was watching.

The courtship of both male and female convict cichlids is characterized by movements (i.e. events) such as tail beating, quivering and brushing (see Baerends &

Baerends-van Roon 1950; Cole et al. 1980; Turner 1987). Tail beating is a lateral orientation towards the intended receiver, followed by strong quick lashes with the tail. During quivering, the body of the fish is tilted upward or downward at approximately a 45° angle and then the whole body is vibrated at a high frequency. Brushing is a mutual display and occurs when the female and male swim slowly past each other in close proximity and perform lateral displays.

I recorded tail beats, quivers and brushes between the female and each of the males from the videotapes. All courtship events followed the same trend, and therefore, were combined to generate an overall score of courtship events for each individual. However, for correlation analysis between males and females, I excluded brushing because it is a mutual display. For each individual, I determined the amount of courtship using two types of rates. First, I calculated the 'daily courtship rate' by summing the total number of courtship events performed by an individual divided by the number of days until spawning occurred. Because females might not spend the same amount of time with each male, which could influence the amount of courtship observed between individuals, I also calculated the 'contact courtship rate' by dividing the total number of courtship events performed by an individual on each day divided by the total amount of time that that individual was with the opposite-sex fish on that day. The contact courtship rate is most likely the most sensitive estimate of a courtship rate for convict cichlids because the duration of each courtship event is negligible and courtship will be performed sporadically throughout the period of time that a male and female are together. For each courtship rate, I summed each individual's scores for each day, and then averaged these values to obtain a mean courtship rate score for each individual.

Because I presented each female with two males and compared the female's behaviour towards each male (e.g. the selected male versus the rejected male), I analysed the difference in the time the female spent with both males as a within-subject design, and analysed female courtship with paired t tests. Similarly, because both males responded to the same female, I also analysed male courtship as matched pairs. In two replicates, the female never went to the rejected male's side, and thus no courtship events were possible. Therefore, these two replicates were excluded from any courtship analyses regarding the rejected male. All data conformed to the ANOVA assumptions. Correlations reported are Pearson product-moment coefficients. Some variables were used twice in different tests and correlations. Therefore, as per the Bonferroni correction, all correlations were tested at an α of 0.025. Power analyses, taken from Zar (1999), accompany all nonsignificant correlations. The program Statistica was used to analyse all data.

RESULTS

Females did not select the larger male significantly more often (21 chose the large male, 10 chose the small male; one-tailed binomial test: $N = 31$, $P = 0.05$). Nor did the

female select the larger male significantly more often within the replicates chosen for videotaped courtship analyses (eight chose the large male, four chose the small male; one-tailed binomial test: $N = 12$, $P = 0.25$).

Females spent more time per day with the males they eventually selected as mates than they did with males they eventually rejected (planned comparison: $F_{1,11} = 33.41$, $P = 0.0001$). Females also spent more time with the selected male than they did in the neutral compartment (Tukey test: $P < 0.05$), but did not differ in the amount of time they spent with rejected males and in the neutral compartment (Tukey test: $P > 0.05$).

Although the daily courtship rates of selected and rejected males towards females did not differ significantly ($t_9 = 1.18$, $P = 0.26$), the contact courtship rate of rejected males was significantly higher than that of selected males ($t_9 = 2.87$, $P = 0.018$). Females, in contrast, showed a significantly higher daily courtship rate towards selected males than towards rejected males ($F_{1,9} = 8.92$, $P = 0.015$), but did not differ significantly in their contact courtship rates towards selected and rejected males ($F_{1,9} = 2.04$, $P = 0.18$).

The daily courtship rate between the selected male and female was not significantly correlated (Pearson correlation: $r_{11} = 0.39$, $P = 0.21$, power $= 0.85$; Fig. 2a). Similarly, the contact courtship rate between the selected male

and the female was also not significantly correlated ($r_{11} = 0.57$, $P = 0.052$, power $= 0.62$; Fig. 2b). However, both correlations yielded high positive r values, indicating strong positive trends. Both aspects of the rejected male's courtship were positive and significantly correlated with the female's courtship (daily courtship rate: $r_9 = 0.95$, $P < 0.0001$; contact courtship rate: $r_9 = 0.72$, $P = 0.018$; Fig. 2a, b). The daily courtship rate correlation between the selected male and female differed significantly from that between the rejected male and female ($P = 0.014$), whereas the contact courtship rate did not ($P = 0.61$).

DISCUSSION

Females tended to select the larger male, but this tendency was not significant. Although Noonan (1983) found that female convict cichlids did choose the larger male significantly more often, her design limited direct contact between males and females. When observing pair formation between individuals in an artificial pond, Keenleyside (1985) found that male size could not fully explain female choice. His results, and the results of the current study, suggest that size is not the only measure females use to assess male convict cichlids. Under natural conditions, individuals are in direct contact with one another during
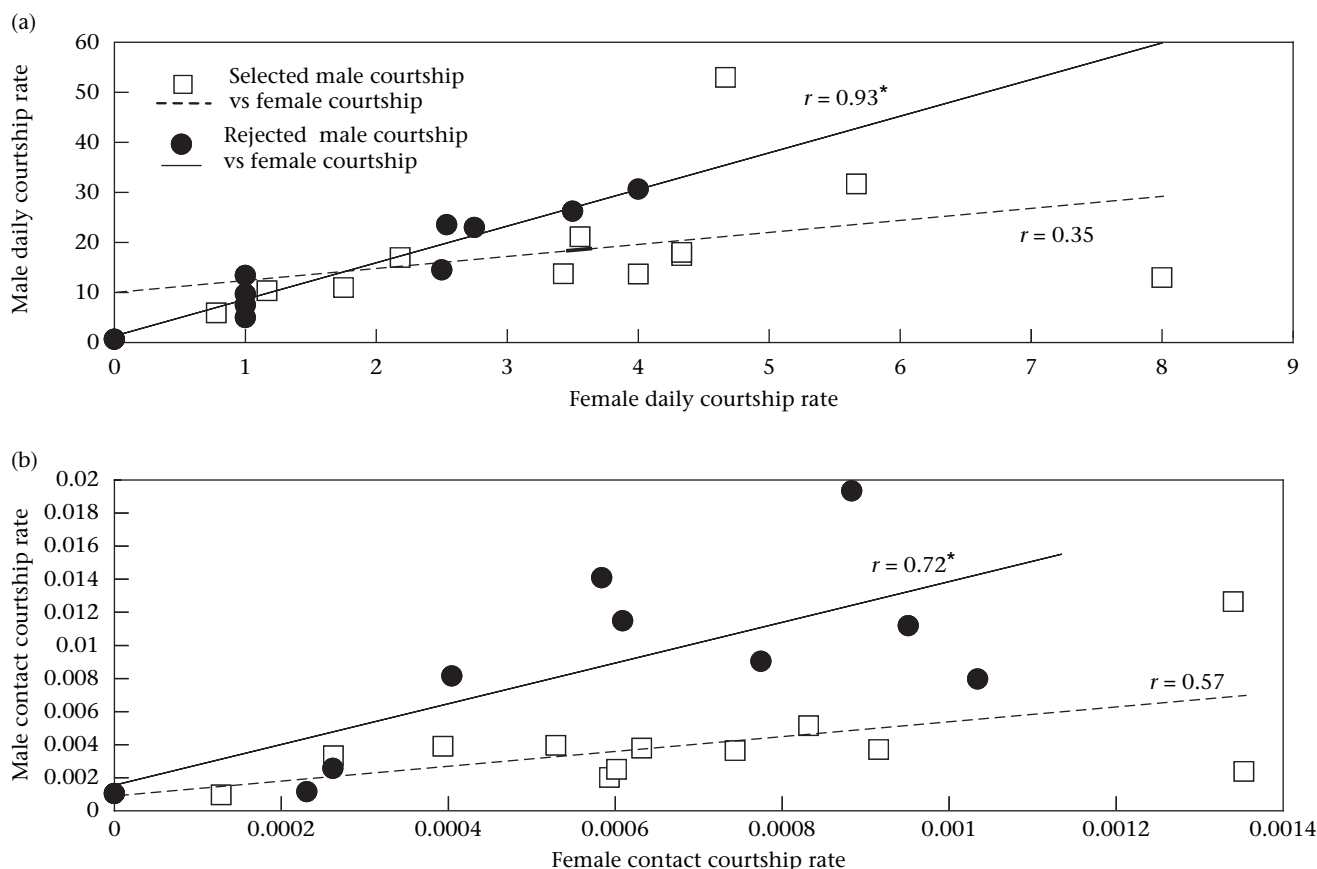

Figure 2. Correlations of courtship rates between selected males and females and between rejected males and females. (a) Average daily courtship rate (i.e. the total number of courtship events performed, divided by the number of days until spawning) and (b) average contact courtship rate per day (i.e. the total number of courtship events performed by an individual each day, divided by the total time that that individual spent with an individual of the opposite sex on that day). Significant r values (*) tested at $\alpha = 0.025$.

pre-pairing behaviour (personal observation). Thus, when making a mate choice decision, females might place more importance on male size when physical contact with males is limited, but use other signals and traits when physical contact is not limited.

The null hypothesis for female courtship was supported in that females showed a similar courtship contact rate to each male per day. However, the hypothesis that females would spend more time with selected males per day was also supported, and consequently, females showed a higher daily courtship rate towards males they selected. So, while females do not appear to modulate courtship between particular males (i.e. contact courtship rate), they do modulate the time they spend with these males, which influences their overall courtship patterns (i.e. daily courtship rate). Further support for this idea is reflected in the fact that the contact courtship rate correlations between the female and each male did not significantly differ, whereas the daily courtship rate correlations did.

The null hypothesis for male courtship was rejected because courtship rates of selected and rejected males differed significantly. Rejected males showed a significantly higher contact courtship rate than selected males, but males did not differ significantly in the average number of courtship events they directed towards the female per day. The lack of a significant difference between males for the daily courtship rate was, again, most likely influenced by the female's behaviour (i.e. where the female spent her time). It is unclear whether the rejected male increased his contact courtship rate relative to that of the selected male, or whether the selected male decreased his contact courtship rate relative to that of the rejected male, or both. That is, if the female conveys to the 'rejected' male that he is not the preferred male, then the rejected male might attempt to manipulate the female's decision by courting her at a higher rate. For example, males with higher courtship rates are more reproductively successful in other species (e.g. bicolour damselfish, *Stegastes partitus*: Knapp & Kovach 1991; sage grouse, *Centrocercus urophasianus*: Gibson 1996; sand gobies, *Pomatoschistus minutus*: Forsgren 1997; barn swallows, *Hirundo rustica*: Møller et al. 1998; hoopoe, *Upapa epops*: Martín-Vivaldi et al. 1999; three-spined sticklebacks, *Gasterosteus aculeatus*: Cubillos & Guderley 2000; rock blennies, *Parablennius sanguinolentus parvicornis*: Oliveira et al. 2000; beaugregory damselfish, *Stegastes leucostictus*: Santangelo et al. 2002). Alternatively, if a male 'knows' that he will be selected, he might invest less in courtship (sensu Reynolds 1993), thereby lowering his courtship rate. Of course, males might not alter their courtship rate at all, but be rejected simply because they are 'high courters' and thus females would spend less time with them. Some studies on courtship have suggested that intense courtship is an indication of a poor-quality individual (e.g. Kruijt & Hogan 1967; Petrie & Hunter 1993). Patricelli et al. (2002) showed that although high courtship intensity is attractive to female satin bowerbirds, *Ptilonorhynchus violaceus*, when courtship intensity is too great, females are threatened and flee. This may be especially relevant for convict cichlids because aggressive interactions are a prominent aspect of courtship (reviewed by Baerends 1986; Barlow 2000) and high levels of aggression inhibit the formation of a pair

bond in related species of monogamous cichlids (midas cichlid, *Amphilophus citrinelium*: Barlow et al. 1977; Texas cichlid, *Herichthys cyanoguttatum*: Itzkowitz & Draud 1992).

Both measures of courtship between rejected males and females were significantly correlated, whereas neither measure of courtship between selected males and females was significantly correlated. These results are counterintuitive because they suggest that males that 'match' the courtship behaviour of females are rejected. This process of 'matching' a partner's courtship activity can be found in other species, but typically is associated with mating pairs (e.g. de Gaudemar et al. 2000). It is unclear why coordinated courtship in convict cichlids is associated with rejected mates and more work is clearly needed to address this question. However, this result does indicate that there are more differences in the courtship process of selected and rejected mates than just their contact courtship rates.

Females began to spend more time with the mate they ultimately selected relatively soon after inspecting both males (e.g. Fig. 3), but the females continued to visit and to court the 'rejected' male up until the day they spawned. Continuous attention to rejected males supports a previous claim that, although monogamous females prefer certain males, they will continue to assess other available males in the population until mating (Logan 1991). Continuous assessment could be a bet-hedging strategy; one will not completely invest in obtaining a particular mate while ignoring all other mating options. For example, both male and female convict cichlids can switch mates before spawning if a higher-quality mate appears (Triefenbach & Itzkowitz 1998); thus, if the female is unsuccessful in mating with her initially selected male (i.e. he chooses a different female), this strategy would allow her the opportunity to continue investing in the next best option.

Ultimately, further experimentation is needed to discover why coordinated courtship between pairs is associated with mate rejection. Furthermore, do males adjust their courtship, and if not, what are the underlying
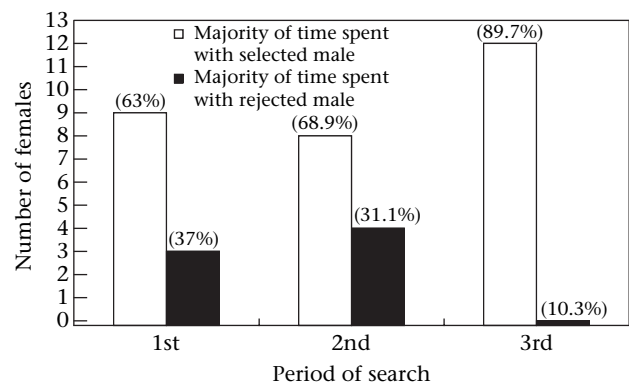

Figure 3. The number of females who spent the majority of their time with the male they selected and with the male they rejected summed over the first, second and third periods of the search (i.e. numbers of days until spawning/3). The middle day was removed for searches not evenly divisible by three. Parentheses represent the average percentage of time that females spent with each male in each period of search. (Note that females spent some portion of their time with rejected males in each period of the search).

reasons for the differences observed between selected and rejected male courtship? However, if males are aware that females continuously assess them, then it follows that males would adjust their courtship during a female's search in an attempt to become more attractive.

Acknowledgments

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