

Notes and Comments

Does Competition Allow Male Mate Choosiness in Threespine Sticklebacks?

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ABSTRACT: The theory of mate choice posits that intensified competition for mates can generate variation in either the strength or the direction of mate preferences within the competing sex. Here, we show that intensified male competition, manipulated through the operational sex ratio, induced differential mate choosiness among threespine stickleback males *Gasterosteus aculeatus*. In the absence of male competition, males were choosy independent of their condition when presented sequentially with a large and a small female. However, in a male-biased social setting, males in poor condition became indiscriminate, whereas good-condition males continued to be selective. Hence, competition induced condition-dependent mate choosiness. This was probably due to mating opportunities decreasing more for poor-condition than for good-condition males when competition intensified, resulting in condition-dependent cost of choice. Variation in condition and cost of choice could thus allow the persistence of male mate choosiness in populations experiencing intense male competition.

Keywords: assortative mating, courtship, intrasexual competition, mate competition, mate preferences, mutual mate choice.

Introduction

How choosy should an individual be when searching for a mate? This depends on the benefit of choice, which hinges on the variation in quality among potential mates, and on the cost of choice in terms of lost mating opportunities and reduced lifetime reproductive success (Johnstone et al. 1996; Kvarnemo and Simmons 1999; Kokko and Monaghan 2001; Kokko and Johnstone 2002). Intensified competition for mates is predicted to increase the cost of choice within the competing sex, since competition damages the mating prospects of choosy individuals when all competitors prefer the same subset of mates (Servedio and Lande 2006; Servedio 2007). Moreover, competition induces choosiness in the opposite sex, since it augments mating opportunities of the other sex, which further in-

creases the cost of choice in the competing sex (Kokko and Johnstone 2002).

In males, mate choice is usually weaker than in females as a result of lower cost of mating in terms of lost mating opportunities (Johnstone et al. 1996; Kokko and Johnstone 2002) and intense male-male competition that increases the cost of mate choice (Servedio and Lande 2006; Servedio 2007). However, males vary in their competitive ability, and intense competition could reduce mating opportunities more for subdominant males than for dominant males. This would generate variation in the costs of mate choice, which would favor the adjustment of choosiness to competitive ability (Fawcett and Johnstone 2003; Härdling and Kokko 2005). Males of different competitive ability could then maximize their mating success by differing in the strength or in the direction of their mate preferences, with subdominant males either being less choosy than dominant males or then preferring females that are rejected by dominant males (Fawcett and Johnstone 2003; Härdling and Kokko 2005). This could allow the persistence of some degree of male mate choosiness in populations experiencing intense male competition (Fawcett and Johnstone 2003; Härdling and Kokko 2005).

In support for competition inducing variation in the direction of mate preferences, a recent field study on the spider *Zygiella x-notata* finds intensified male competition to induce size-assortative mating preferences, whereby large males prefer large, more fecund females, while small males prefer smaller females (Bel-Venner et al. 2008). The other possible outcome of intensified competition, increased variation in the strength of preferences for a trait, has to our knowledge not been demonstrated. Under this scenario, only highly competitive males remain choosy when competition intensifies, while males of low competitive ability mate indiscriminately as a result of fewer mating opportunities and thus higher cost of mate choice.

Here, we experimentally investigated whether male mate choosiness is adjusted to competitive ability when the intensity of competition intensifies. This could allow the persistence of male mate choice under intense male-male competition. As a model species, we used a species with

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some degree of mutual mate choice, the threespine stickleback *Gasterosteus aculeatus*. The species has male parental care, and the reproductive rate of the male is restricted by the number of eggs that he can fit into his nest and by the 2–3-week-long parental phase. Males can therefore be choosy and prefer larger females, but the degree of choosiness is lower than in females, and only males court (Rowland 1982; Kraak and Bakker 1998; Rowland et al. 2002). Males in poor condition have fewer reproductive opportunities than do good-condition males over their lifetime, since they have a lower probability of surviving the parental period and completing additional breeding cycles (Candolin 2000a). Poor-condition males also suffer from lower current mating opportunities, since condition influences competitive ability, with dominant males in good condition dominating over poor-condition males in competition for females (Candolin 2000a). However, poor-condition males can momentarily increase their attractiveness in the absence of male competition, since male competition is needed to ensure honest signaling of male parental ability (Candolin 2000a, 2000b; Wong et al. 2007). Hence, mating opportunities depend on the social setting, with the mating opportunities of poor-condition males decreasing more than those of good-condition males when male-male competition intensifies. The cost of mate choice is therefore expected to vary depending on the relative condition of the male and the social setting, which could result in variation in mate choosiness among males.

Material and Methods

To determine whether intensified competition for females results in differential male mate choosiness, we varied the competitive ability of males by varying their condition and varied the intensity of competition by varying the operational sex ratio. Males in good or poor condition were then allowed to court two sequential dummy females of different size under either a male-biased or a female-biased sex ratio.

Sticklebacks were collected with Plexiglas traps (Candolin and Voigt 2001b) from the littoral of the Baltic Sea in southern Finland near Tvärminne Zoological Station before the breeding season. The fish were housed in flow-through aquaria at 18°C under natural lighting conditions in an outdoor facility. Males were separated from females on the basis of hints of nuptial coloration and randomly assigned to two feeding treatments. For 2 weeks, one group of males was fed twice a day on frozen chironomid larvae, whereas the other was food deprived. The lack of suitable nesting materials discouraged breeding behavior.

We randomly chose 30 well-fed and 30 poorly fed males and transferred them to individual 12-L flow-through aquaria kept under natural light conditions. Each aquar-

ium contained a “nesting dish” filled with sand and filamentous algae (*Cladophora* sp.) for nest construction and an artificial plant for hiding (Candolin 1997). Each male aquarium was placed in front of a larger aquarium (36-L) containing either three females or three males in good condition, with visual contact between the male and the three other fish. The three males were in breeding condition but could not build nests because of the lack of nesting material. The three females had spawned once and were developing the second batch of eggs, but they were not yet ready to spawn and did not stimulate the male to court. If a female ovulated and became ready to spawn, she was immediately replaced by another female.

One day after a male had completed nest building, he was sequentially exposed to two differently sized dummy females made out of clay and painted to look realistic. Dummy females were used to standardize female behavior and prevent differences in behavior from influencing male behavior. The dummy was kept in a Plexiglas cylinder (10 cm in diameter) and held in a head-up position, which indicates readiness to spawn, and placed 15 cm from the male’s nest. The cylinder was used to prevent the male from biting and destroying the dummy. The two dummies were 48 and 58 mm long (standard length), and several different dummy females were used. Half of the males were first exposed to the larger female, whereas the opposite order was used for the rest of the males. The interval between presenting the two females was 10 min. Male courtship behavior was recorded for 10 min by counting the number of leads to the nest (which are preceded by zigzag movements), which reflects male courtship intensity (Candolin and Voigt 1998). The time that the male spent courting the female and the time that he interacted with the three other fish in terms of attacks or by observing them—that is, directed toward them instead of toward the female—was recorded.

Courtship activity (number of leads) was normally distributed, and a repeated-measures ANOVA was used to analyze the data, with courtship activity directed to each of the two females as the repeated measure and male condition and sex ratio as the between-subjects factors. The within-subject contrasts indicate differences in preference for the two females, whereas between-subjects effects indicate differences in male courtship activity across females.

Results

Choosiness

Across all males, males preferred the larger female and courted her more vigorously (repeated-measures ANOVA, within-subject contrast: $F = 66.16$, $df = 1, 56$, $P < .001$). However, how male condition influenced choosiness de-

pendent on the sex ratio (repeated-measures ANOVA, within-subject contrast, interaction between female size, condition, and sex ratio: $F = 10.85$, $df = 1, 56$, $P = .002$). Under a female-biased sex ratio, condition had no statistically significant influence on choosiness (repeated-measures ANOVA, interaction between female size and condition: $F = 3.48$, $df = 1, 28$, $P = .073$), but when the sex ratio became male biased, poor-condition males became less selective while good-condition males continued to be selective (repeated-measures ANOVA separately for the two male condition groups, interaction between female size and sex ratio, poor-condition males: $F = 26.00$, $df = 1, 28$, $P < .001$; good condition males: $F = 0.23$, $df = 1, 28$, $P = .636$; fig. 1).

Courtship Activity

Males reduced their courtship activity under a male-biased sex ratio, but the reduction depended on condition; males in poor condition reduced their courtship activity to a larger extent than did good-condition males (repeated-measures ANOVA, between-subjects effects, interaction between condition and sex ratio: $F = 21.26$, $df = 1, 56$, $P < .001$; fig. 1). The reduction in courtship activity was due to male competition interfering with courtship. Under a male-biased sex ratio, males devoted time and attention to the competing males in the form of attacks and/or observations, resulting in a trade-off between courtship and fending off of observing competing males (depen-

dence of courtship time on time spent associated with the males, results for the small female presentation; $r^2 = 0.84$, $F = 314$, $df = 1, 58$, $P < .001$).

Discussion

Intensified male competition is predicted to reduce male mate choosiness both directly, since foregoing mating opportunities makes little sense when reproductive success is mate limited (Servedio and Lande 2006), and indirectly, since male-male competition induces choosiness in females, which in turn increases the cost of choice in males by reducing their mating opportunities (Kokko and Johnstone 2002). However, variation among males in competitive ability leads to variation in the cost of choice, which could cause variation in the strength or direction of mate preferences. This makes male mate choice more likely in a population (Fawcett and Johnstone 2003; Härdling and Kokko 2005) compared with a scenario in which male choosiness evolves irrespective of male competitive ability (Servedio and Lande 2006; Servedio 2007).

In support of these predictions, we found intensified male competition to induce variation in mate choosiness among threespine stickleback males. Under a female-biased sex ratio, when male competition was weak, all males were choosy independent of their condition and preferred larger, more fecund females. However, when perceived competition intensified through a switch from a female-biased to a male-biased sex ratio, only good-con-

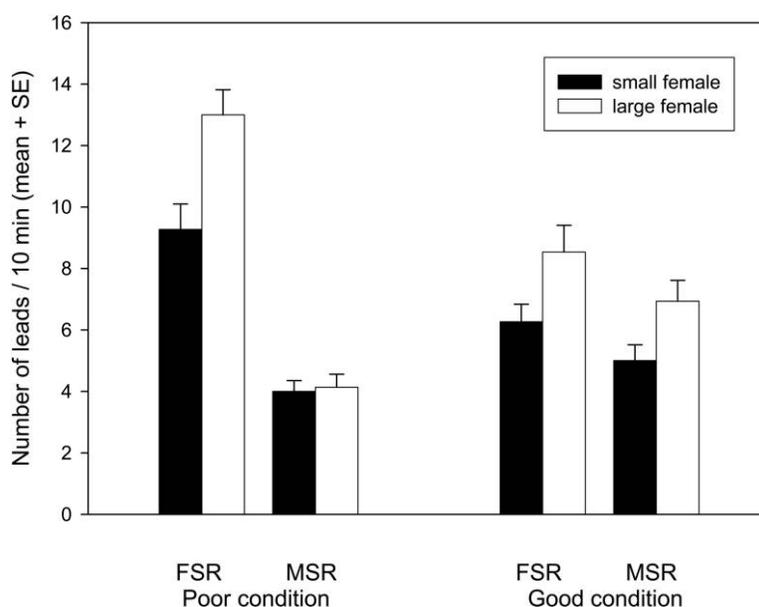


Figure 1: Courtship activity of condition-manipulated males toward sequentially presented small (*solid bars*) and large (*open bars*) females under a female-biased sex ratio (FSR) or a male-biased sex ratio (MSR).

dition males continued to be choosy while poor-condition males became indiscriminate. This was probably due to the cost of choice increasing more for poor-condition than for good-condition males when competition intensified as a result of their fewer mating opportunities when competing with good-condition males for females (Candolin 2000*b*).

Intensified male competition hence induced a divergence in the strength of choosiness. There was no indication of divergence in the direction of mate preferences, that is, assortative mating preferences. In a spider species, in contrast, selectivity and assortative mating increased when competition intensified (Bel-Venner et al. 2008). Why do males of different species then react differently to intensified competition, differentiating in either the direction or the strength of preferences? Which trajectory a male should choose depends on the cost of courtship, female selectivity, and the probability that courtship will result in mating. If courtship is costly and females prefer dominant males, or dominant males can take over the female, then subdominant males should preferentially court less attractive females. If courtship is less costly or females are indiscriminate and dominant males seldom take over females, then indiscriminate courtship should pay off.

In threespine sticklebacks, courtship is costly both energetically and in increasing the risk of predation on the male himself and on the eggs (Foster 1994, 1995), but the cost might be low compared with the risk of not mating at all, particularly for poor-condition males for which good-condition males reduce mate encounter rate (Candolin 2000*a*, 2000*b*; Candolin and Voigt 2001*a*). Moreover, females might prefer subdominant males when male interaction is prevented (Östlund Nilsson and Nilsson 2000), which would increase the benefit for subdominant males of courting attractive females when the opportunity arises. Thus, indiscriminate courtship may pay off for poor-condition, subdominant males.

So far, there are few examples of individual variation in male mate choosiness. In species where mating is costly to males but males are not mate limited, poor-condition males have been found to be choosier than good-condition males, due to their lower potential reproductive rate (Kvarnemo and Simmons 1998; Martel et al. 2008). However, in species where males are mate limited, poor-condition males, or small males, have been found to be less choosy than good-condition males (Poulin 1994; WearingWilde 1996; Lopez 1999) or large males (Amundsen and Forsgren 2003). This is due to their fewer mating opportunities, arising from their low success in mate attraction or male contest competition. These studies did not, however, investigate whether differential choosiness was adjusted to the intensity of competition.

Could the maintenance of choosiness in good-condition males under intense competition then have consequences for the direction and intensity of sexual selection on different traits? It could strengthen sexual selection on female traits, compared with the alternative scenario where all males become less choosy when competition intensifies (Servedio and Lande 2006). However, to determine the ultimate consequence of the maintenance of choosiness in dominant males, more information is needed on female mate preferences and choosiness under different degrees of competition. Choice behavior of female sticklebacks is condition dependent (Bakker et al. 1999) and influenced by time and energy constraints (Luttbeg et al. 2001). Intensified male competition could influence female mating opportunities and hence affect female mate choosiness. This could result in a complex interplay between condition-dependent male and female mate choosiness, adjusted to the social setting and the intensity of competition. Recently, the feedback between population dynamics and sexual selection has been stressed (Kokko and Rankin 2006), but the dependence of individual variation in choosiness on population structure has not been considered, although variation in mate preferences and mate choice behavior is acknowledged (Jennions and Petrie 1997). This study emphasizes the importance of considering individual variation in behavior and its dependence on population structure when investigating the feedback.

In summary, intensified male competition can lead to a differentiation in male choosiness in relation to dominance and condition, which could maintain male mate choosiness under intense male-male competition. The consequences this has for processes of sexual selection and the evolution of traits deserve further investigations.

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