

Male mate choice in fishes

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Abstract. Selection generally favours male competition for females, and female mate choice of males. If, however, females vary in quality, and if males are limited in the maximum number of females with which they can mate, then selection should also favour male mate choice. We report on male mate choice in two species of fishes with different mating systems: the threespine stickleback, which has male parental care, and the coho salmon, which has female parental care. In both species, males allocated their mating effort in direct proportion to female quality.

Darwin's (1871) theory of sexual selection has been powerful in explaining the stereotyped roles of the two sexes in animals. Generally, males are selected to maximize their reproductive success quantitatively, by mating with as many females as possible, whereas females are selected to maximize their reproductive success qualitatively, by choosing mates that will contribute the best resources, genes, or both to their offspring (Bateman 1948; Trivers 1972; Williams 1975). However, if females vary in quality (e.g. fecundity, egg size, ability to provide parental care), and if males are limited in the maximum number of females with which they can mate (e.g. see Nakatsuru & Kramer 1982), then natural selection should favour males choosing those females that will yield them the highest reproductive success (Williams 1975; Parker 1983; Ridley 1983).

Until recently, the phenomenon of male mate choice has been largely overlooked. We know that for some species in which female fecundity increases with body size (e.g. fishes: Bagenal & Braum 1978; insects: Thornhill & Alcock 1983), males prefer the largest and most fecund female (e.g. Downhower & Brown 1981; Gwynne 1981, 1984; Loiselle 1982; Rowland 1982). We also know that males of some species adjust their mating behaviour subject to the level of male competition. These males distribute themselves in an 'ideal free distribution', which is in direct proportion to the probability of obtaining a mate devalued by male competition (Parker 1970, 1974; Davies & Halliday 1979). What has not been shown, however, is whether males assess the relative quality of each

available female in their attempts to maximize reproductive success. For example, if males are behaving so as to maximize their overall rate of return on investments in mating (e.g. Loiselle 1982; Ridley 1983), and if to maximize this rate of return, males must distribute their mating effort over more than one female (i.e. non-exclusive choice), then males should distribute their mating effort among available females in direct proportion to female quality (e.g. Staddon 1983).

Our study was conducted on two species of fish: the threespine stickleback (*Gasterosteus aculeatus*), and the coho salmon (*Oncorhynchus kisutch*). With threespine sticklebacks we investigated how a territorial male divided his courtship over two females that differed in fecundity, and asked whether these males assess the relative quality of each available female. With coho salmon we investigated how males distributed themselves spatially among a smaller number of breeding females, and asked whether such males assess the relative qualities of the available females discounted by male competition.

STICKLEBACK EXPERIMENT

The threespine stickleback is characterized by males that aggregate in shallow water, compete for territories, build nests, spawn, and care for the developing eggs and newly hatched fry. A single male may spawn with several females, and usually cares for several clutches simultaneously (Wootton 1976). Because of synchrony on the spawning grounds, males may be faced simultaneously with several receptive females (Kynard 1978), and thus have to make choices.

We considered the simple case of a single male

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confronted with two females as potential mates. A male should court the larger female first, because he should gain more fecundity per unit courtship by spawning with the larger female. If, however, the female does not respond to the male's courtship, then, after some critical point, the male should redirect his courtship to the smaller female. This should occur because, as a male courts a female, his expected rate of return on investment declines; that is, his costs of courtship continually increase while female fecundity remains fixed. Thus, as the male continues to court the larger female, his expected rate of return may fall below that for courting the smaller female, whereupon he should switch and court the smaller female. Similarly, as the male courts the smaller female, his expected rate of return on courtship declines, and may fall so low as to make it profitable to switch back to courting the larger female again. As this process is repeated, the male should be observed to divide his courtship between the two females, in direct proportion to their difference in fecundity, assuming that female receptivity is independent of fecundity.

Methods

The stickleback experiment was conducted at the State University of New York at Stony Brook during April 1981. See Sargent & Gebler (1980) for fish-collecting and handling procedures. To test our prediction on male mate choice, nesting male threespine sticklebacks were presented with a series of pairs of gravid, receptive females. Each female within a pair was confined in a separate glass jar to prevent spawning.

Six males were presented with the same series of nine pairs of gravid, receptive females. Each male had a nest under a clay flowerpot in the centre of a $120 \times 26 \times 60\text{-cm}^3$ aquarium. Before presentation, each female within a pair was weighed and enclosed in a glass jar. The male was chased into his flowerpot, and the two jars were lowered simultaneously to opposite ends of the aquarium; the end of the aquarium that received the larger female was chosen randomly for each trial. As soon as the male emerged from his flowerpot, he began courting the females. A trial lasted 10 min, which is four times the length of the average courtship that results in spawning between a solitary male and an unrestrained female (Sargent 1981). We were not concerned with the dynamics of a male's switching behaviour, but rather with the net outcome of his

switching behaviour. Thus, for each trial we recorded which female was courted first, and the total number of zig-zags (courtship displays) directed to each female.

Female fecundity was estimated from the following regression equation, which was obtained from an independent sample of females: $Y = 198.6X - 328.9$ ($P < 0.001$, $N = 34$), where Y is the number of eggs and X is body weight in grams. To determine if males assess the quality of both females within a pair, we compared the magnitude of a male's preference for the larger female with the proportion of total eggs at stake in the larger female. We considered three possible outcomes: (1) males court females at random; (2) males court only the larger female; or (3) males court the two females in direct proportion to their difference in fecundity.

Results

Male sticklebacks courted both the large and small female within a pair; however, they courted the larger female first 67% of the time ($G = 6.0$, $N = 54$, $P < 0.025$). Using a repeated measures single classification analysis of variance (Winer 1971), we found that the proportion of courtship directed to the larger female within a pair increased linearly with the proportion of eggs present in the

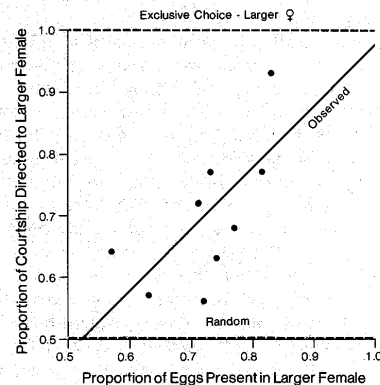


Figure 1. Mate choice by male threespine sticklebacks. The observed distribution of points is compared with that predicted by exclusive choice for the larger female, and by random mating. The trend is significant and positive ($Y = 1.00X - 0.02$, $P < 0.01$, one-tailed).

larger female ($F=4.30$, $df=1,40$, $P<0.05$). Furthermore, the proportion of courtship directed to the larger female within a pair, averaged over the six males, approximately equalled the proportion of fecundity at stake in the larger female (Fig. 1).

SALMON EXPERIMENT

Unlike the threespine stickleback, the coho salmon is a semelparous species in which a female competes for a territory, excavates a nest, spawns, buries her eggs, and guards the eggs until her death. Because larger females provide better parental care than smaller ones, they have relatively higher reproductive success than would be predicted by fecundity alone (van den Berghe 1984; van den Berghe & Gross 1984).

At any point during the breeding season, there are fewer females digging nests than there are males trying to obtain mates. As a female prepares to spawn, she is joined by one, or usually an aggregation of males who compete to fertilize her eggs. Males move back and forth among females who are preparing to spawn; however, only the males within an aggregation participate in fertilizing a female's eggs (Gross 1984).

To test whether or not males, in their choice of spawning aggregation, assess female quality devalued by male competition, we borrowed a model from habitat-selection theory: the 'ideal free distribution' (Fretwell & Lucas 1970; Fretwell 1972). If males are free to enter and leave any aggregation, and if males within an aggregation have equal access to the female when she spawns, then males should distribute themselves among aggregations so that the expected number of offspring per male is equal for all males in the population. In other words, average reproductive success per male within aggregations should be equal among aggregations.

Male coho salmon within an aggregation, however, may not all have equal access to the spawning female. For example, in chum salmon (*Oncorhynchus keta*) the male closest to the female is the first to fertilize the eggs, and thus sires most of the offspring (Schroeder 1982); presumably similar processes operate in coho salmon (Gross 1984, 1985).

Let us assume that males compete to gain access to females, and that the earlier a male joins an aggregation the better his chances of fertilizing a

female's eggs (for males of the same body size). Habitat-selection theory then predicts that the average reproductive success per male within an aggregation will increase with female reproductive success among aggregations (e.g. see Fretwell 1972). In other words, as female reproductive success increases, the size of a male aggregation increases, but at a lower rate than that predicted by the ideal free distribution. This distribution is called a 'despotic distribution' (Fretwell 1972).

Methods

Male mate choice in the coho salmon was studied in Deer Creek, Jr, a small tributary of the Skykomish River in Washington State, during the autumn and winter of 1981 and 1982. See van den Berghe & Gross (1984) for a description of the study site and fish-handling procedures. The study population consisted of 142 males and 83 females in 1981, and of 96 males and 78 females in 1982. In both years these fish had approximately 90 m² of available spawning substrate. Male aggregation size versus female reproductive success was recorded for 22 females in 1981, and for 12 females in 1982. A female's reproductive success, or the number of her progeny that survive to reproduce (i.e. recruits), depends on fecundity, egg size and quality of parental care, which all increase with body size (van den Berghe 1984). Therefore, we estimated each female's reproductive success from her body size using the following quadratic regression equations obtained from data in van den Berghe (1984): for 1981, $Y=112-5.07X+0.06X^2$ ($N=11$, $R^2=0.97$, $P<0.01$); for 1982, $Y=147-6.57X+0.07X^2$ ($N=10$, $R^2=0.96$, $P<0.01$), where Y is female reproductive success in recruits and X is female fork length in cm.

If we assume that males distribute themselves among females (over space and time) so as to maximize their overall rate of return on investments in mating, and if we assume that our samples of females and their attendant males are drawn at random from the whole population, then we can compute an expected ideal free distribution of males per female for each year. We considered three possible outcomes: (1) males join aggregations at random; (2) males distribute themselves among females in an ideal free distribution; or (3) males distribute themselves among females in a despotic distribution.

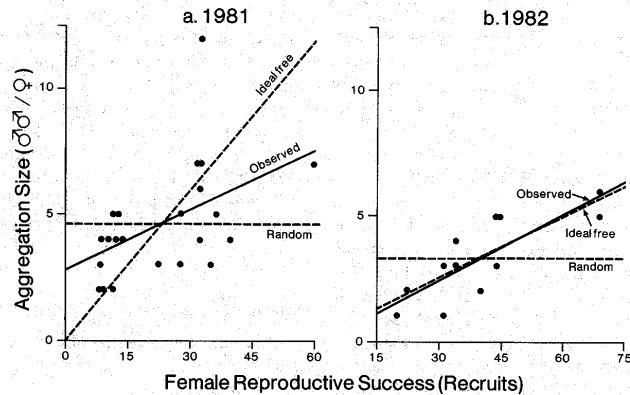


Figure 2. Mate choice by male coho salmon. The distribution of points is compared with that predicted from a random mate choice model and from an ideal free distribution.

Results

The results are summarized in Fig. 2. In 1981 the number of males per female increased with expected female reproductive success ($r=0.49$, $P<0.02$, one-tailed), but at a significantly lower rate than that predicted by the ideal free distribution ($t=2.50$, $P<0.02$, two-tailed, Fig. 2a). Furthermore, in that year, the expected reproductive success per male within aggregations increased with expected female reproductive success among aggregations ($r=0.70$, $P<0.001$), as predicted by a despotic distribution. During 1982, however, male aggregation size increased with expected female reproductive success ($r=0.80$, $P<0.001$, one-tailed) in approximate agreement with the ideal free distribution ($t=0.73$, $P>0.40$, two-tailed, Fig. 2b). Furthermore, the expected reproductive success per male within aggregations was not significantly correlated with expected female reproductive success among aggregations ($r=-0.20$, $P>0.50$), as predicted by the ideal free distribution.

DISCUSSION

Male fishes in two different mating systems appeared to assess relative quality among females. In the threespine stickleback, males divided their courtship between females and approximately matched the females' expected fecundities. Thus the male sticklebacks adjusted their mating beha-

viour according to female quality. One might question whether these males were responding to female quality per se, or perhaps were simply responding directly to the size of the stimulus value (e.g. body size) of each female.

This question was answered by Rowland (1982) who presented male sticklebacks (from the same population that we studied) with two female dummies of different sizes. When the dummies were presented simultaneously the males courted both of them, but showed a significant tendency to court the larger one. When the dummies were presented sequentially (one at a time), however, both received approximately the same amount of male courtship. Thus, it appears that sticklebacks evaluate the relative quality of each available female rather than female size.

The magnitude of such male mate choice in the field should increase with increasing variance in female quality, and with decreasing costs of searching for (and of rejecting) mates (Parker 1983). Although active male courtship displays and competition for females, along with female mate choice of males, appear typical for threespine sticklebacks (McPhail 1969; Semler 1971; Hay & McPhail 1975; Sargent & Gebler 1980; Sargent 1982), in certain populations females initiate courtships toward the end of the breeding season (Kynard 1978; R.C.S., personal observation), or throughout the breeding season (Pressley 1981; J.D. McPhail, personal communication). The study of such populations,

which have females competing for males and male mate choice (e.g. Li & Owings 1978), will provide valuable tests of sexual selection theory.

In coho salmon, males distributed themselves among females in direct proportion to female quality, which was devalued by male competition. In 1982, the distribution of males among females was approximately ideal free; however, in 1981 the male distribution was not ideal free, but was despotic. Interestingly enough, both the proportion of males in the population and the total population size were lower in 1982. Thus, the effects of male competition (despotism) may have been lower in 1982, which could explain the tendency toward an 'ideal free distribution' in that year. We would expect that departures from an ideal free distribution would increase with increasing levels of male competition, with for example, an increasing proportion of males in the population, increasing population density, or decreasing synchrony in the timing of female reproduction.

In summary, males of both species of fishes not only discriminated the largest available female, but appeared to assess the quality of each available female. This ability to respond to variance in female quality may have important implications for sexual selection in both sexes of fishes.

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