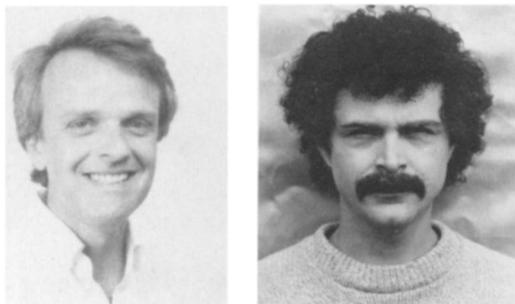


Mad River Sculpins: Just Another Fish Story?

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Female animal mating preferences have played an important role in the evolution and maintenance of mating systems because females generally make greater investments in reproduction than do males (Darwin 1871; Fisher 1958; Orians 1969; Emlen and Oring 1977; Wittenberger 1981). Females are thus thought to be the more prudent sex, and a large body of theory has developed to account for the factors that alter or influence the kinds of choices that females make. If female mate choice is important evolutionarily, then we may be able to understand why a particular species breeds in the way it does by identifying the factors that influence female preferences. For the past several years, we have been attempting to unravel the factors that influence the mating preferences of female mottled sculpins, a small North American fish. Our findings suggest that female mate preferences are influenced by at least four major factors, and that the relative importance of these factors changes through time. The type of choice that a female makes thus depends on the time of breeding.

Mottled sculpins are polygynous: in each year, a male may spawn with more than one female whereas females only spawn once. The breeding biology of this species is not complicated. Generally, a male takes up residence under a rock, or in some other naturally occurring crevice on the stream bed. Gravid females approach a male and are courted. During courtship the male will spread and fan his anterior or pectoral fins, which are greatly enlarged in this species (Plate 1). The male may also spread his opercular plates (the large flat bony structure that cover the gills). He may gape at the female, and in certain instances he may take the female's entire head into his mouth. Should the female spawn with the male, she will turn over and deposit her eggs on the ceiling of the grotto occupied by the



A very large adult male sculpin from Thompson Creek (Gallatin River, Montana).

male. The female then leaves. The male courts and spawns other females, and ultimately is left with all the eggs until they hatch. Usually, the male remains with the newly hatched fry for about two weeks.

This brief summary of the breeding biology of sculpins suggests that females might make choices among males on the basis of the quality of the nest occupied by the male or on the qualities of the male. Nest site qualities might be important to females because the eggs and fry remain and develop in the nest for nearly two months. Male characteristics might also be important since the male remains with the female's progeny for a prolonged period of time, and he is solely responsible for the care of the young.

In our initial studies of this species we manipulated nest site quality by placing slate tiles of different sizes in our stream (Downhower and Brown 1980). By scattering the tiles haphazardly in the stream, we precluded any physical factor other than size from being a unique characteristic of a set of tiles. Males readily occupied our sites and females spawned with them. In the past four years we have recorded the spawning preferences of over 2,000 females. At no time has the sizes of males or the success of those males been different from that of males occupying natural spawning sites in the same area.

We conducted two experiments in which we seeded our stream with tiles of different sizes. In both those

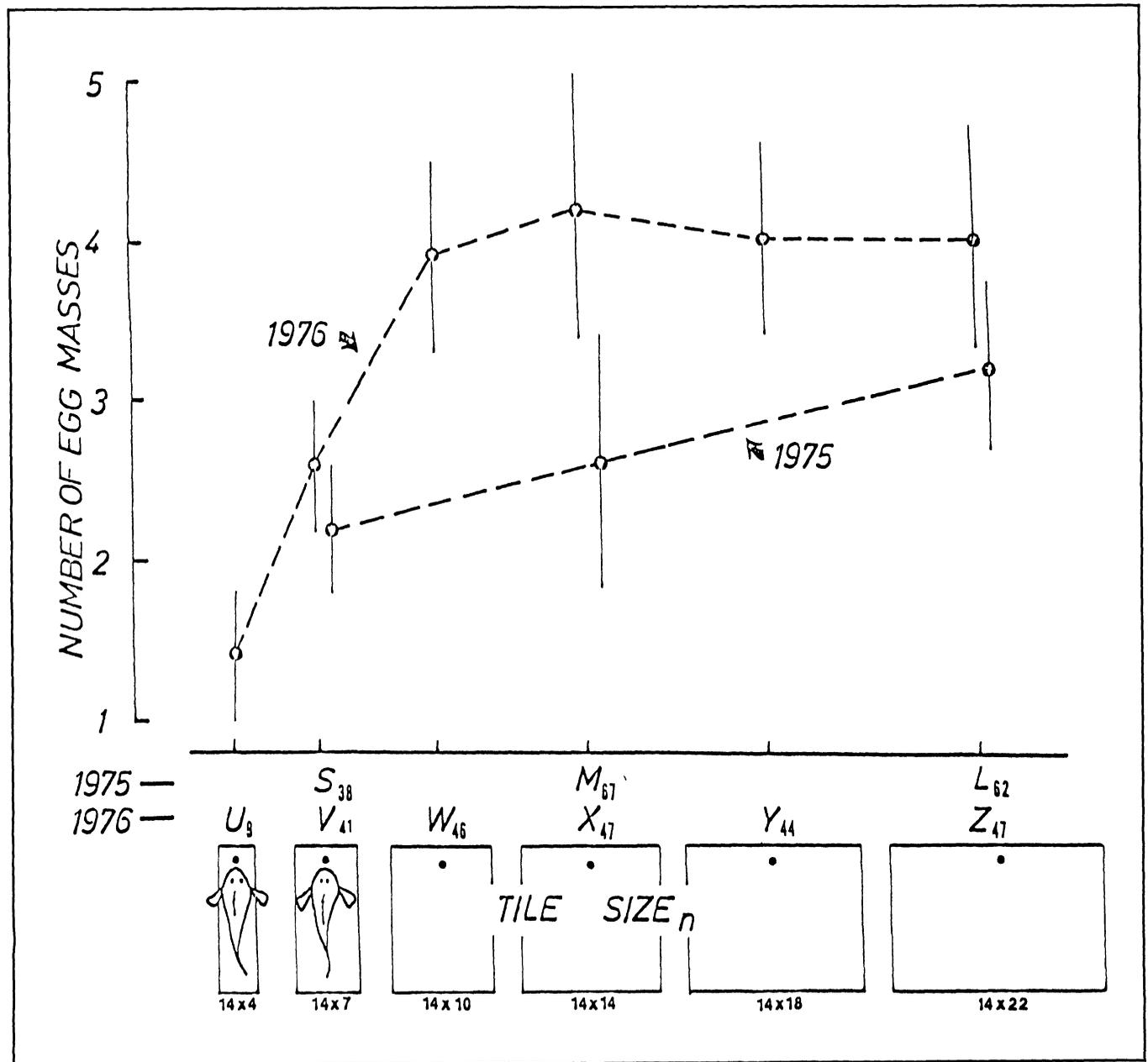


FIGURE 1. Breeding site size and courtship success of adult male sculpins. A scale drawing of the breeding sites used, together with an average sized male from 1976 is provided at bottom of the figure. Tile sizes S, M, and L were used in 1975, and U, V, W, X, Y, and Z were used in 1976. Males occupying larger breeding sites mated with more females than those at smaller breeding sites. Sample sizes for each tile size are given as subscripts, and means are bounded by two standard errors.

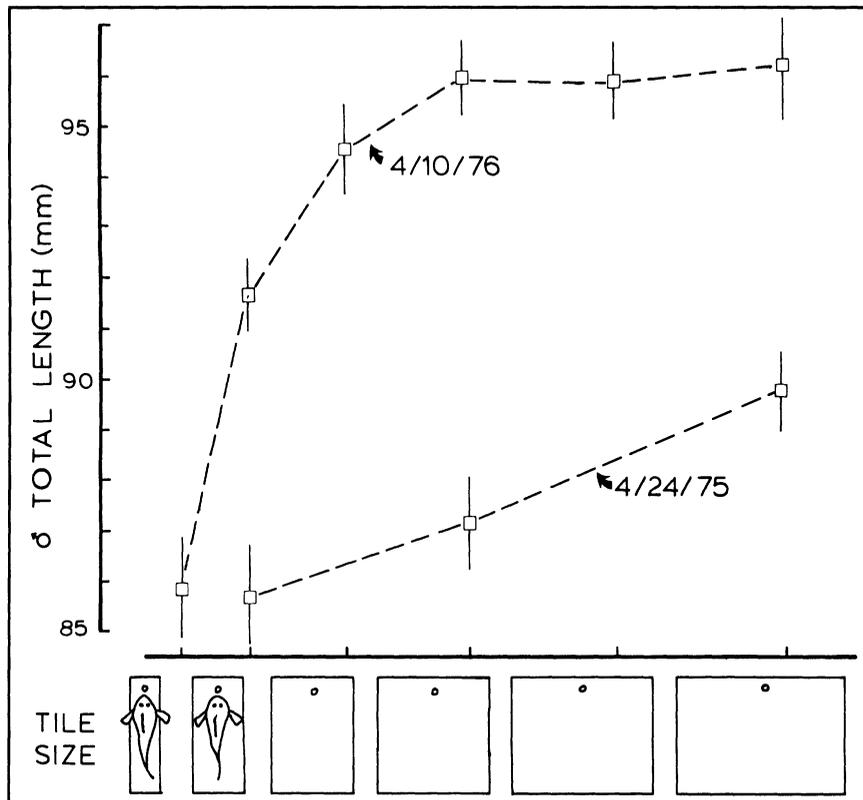


FIGURE 2. Male size as a function of breeding site size in 1975 and 1976. Larger males were captured at larger breeding sites, while smaller males tended to occupy smaller breeding sites.

years the number of egg masses fertilized by a male was higher for males occupying the larger tiles. However, larger males also occupied larger tiles. Thus, both site quality and male quality appeared to be involved in the choices made by females. However, this is not the case: when the data were analyzed more carefully, it became clear that the influence of site quality was a reflection of the sizes of the males occupying the site and not a preference on the part of females. The effect of tile size is what is termed a spurious correlation. Such relationships are common in biological studies. For example, the rates at which male field crickets call is dependent on temperature; the tempo of the call is faster when it is warm. It would be a mistake, however, to conclude that male crickets are giving weather reports. In a similar fashion, female sculpins appear to be more interested in the male than the place in which he resides.

Female preference for large males was rewarded by increased survival of eggs deposited with larger males: larger males appear to make better parents. Thus, in evolutionary terms there was a selective advantage for females that bred with larger males. However, our studies have indicated that the largest males are not always more successful than small males in attracting females, and in fact they may obtain fewer spawnings than medium-sized males. In addition, we were able to collect data that suggested that females breeding late in the season were actually avoiding most males! Thus, although there was a selective advantage in breeding with larger males, not all females did so, and large

males were not uniformly successful (Downhower, *et al.*, 1983). Why was this so?

It turned out that male size was not the only influence on female reproductive success. Survival of egg masses deposited late in the spawning season was lower than that of egg masses deposited early. Therefore, the timing of reproduction also influenced female reproductive success.

Incorporating a time element into our understanding of female behavior was troublesome until we realized that time could have the following meaning for sculpins. Consider the fate of an egg mass deposited with a male, who has yet to spawn. That egg mass might be the *first* of several egg masses fertilized by a male. Alternatively it might be the *only* egg mass the male obtained. Consider, further, the fate of an egg mass deposited with a male who is already guarding one or more egg masses. This egg mass might represent the *last* eggs fertilized by a male, or it might be one of several additional egg masses to be fertilized—a *middle* egg mass. The survival of an egg mass depends on whether it is the *last* egg mass, an *only* egg mass, or a *first* or *middle* egg mass. Only 50% of the egg masses that were *last* survived; only 35% of the *only* egg masses survived, whereas 75% of the *firsts* and *middles* survived. When we recalculated the average survivorship of egg masses at various sites using these survivorship estimates, the correspondence between the two curves were extraordinarily close (fig. 3). Thus, female reproductive success was determined by when she spawned in that sequence of egg masses that a par-

ticular male fertilized. Further, we found that the probability of being the *only* female to spawn with a male did not change during the spawning season, whereas the likelihood that a female would be the *last* to spawn with a male increased during the spawning season. Time was thereby reduced to position in a sequence, and time was further reduced to simple avoidance of being *last*.

When we focused on how a female might reduce the likelihood that she would be the *last* to spawn with a male, it became intuitively clear that the simplest tactic would be to spawn as early as possible. Since female sculpins spawn only once, the probability of being *last* becomes a function of the number of females who remain to spawn. That probability must increase through time since more and more females have already spawned and fewer and fewer remain to spawn. We suspect that the high degree of synchrony in spawning that these animals evidence is in no small way related to the selective advantages of being *first*.

Synchronous spawning raised yet another series of problems, because synchronous spawning inevitably led to situations in which a male was confronted with more than one female. Males could therefore choose which female they would spawn with first. This was no small fraction of males, for at peak spawning 30% of the males who were courting females had two or more females present at their sites. Our aquarium studies of male mate preferences indicate that males court large and small females with equal vigor when no other female is present. However, when a male has a choice between females of different sizes, he courts the larger female and generally ignores the smaller. Again there is a reproductive advantage associated with this behavior: large females carry more eggs than smaller females. For females the results of males' preferences are mixed: large females are almost assured of being able to breed first—should two females be present—whereas small females will breed later. Late breeding, as we have seen increased the probability of being the last female to spawn with a male which reduces the reproductive success of those females.

Male preferences as well as physiological factors establish a queuing that is dependent on the size of the female, and this works to the advantage of large females and to the disadvantage of small females. However, these effects do not account for reduced reproductive success associated with larger males, nor do they account for the observation that late spawning (i.e., small) females seemingly avoid larger males.

The clues to the other factors influencing female preferences were derived from our work on parental care. Careful analysis of our field data indicated that mortality rates of eggs at sites that were abandoned by a male were on the order of 50% per 48 hours. At sites where the male was present loss rates were on

the order of 10% per 48 hours, and these rates of loss were dependent on the size of the male. Lower loss rates occurred at the sites occupied by larger males. Thus the presence of males decreased the losses of eggs, but some loss still occurred. To determine what causes of loss were, we removed the male from his site and then enclosed the site in a wire cage. By varying the mesh size of such cages, we were able to exclude predators of different sizes. The smallest mesh size excluded everything.

The primary predators on sculpin eggs appear to be other sculpins. Both adult males and adult females were captured. However, females were far more likely to be engorged on eggs than males. Our studies on energetics of sculpins indicate that a female loses 30-50% of her total lipids and protein in the form of eggs. The post-spawning period is physiologically most critical for females, and it is not surprising that they attempt to prey on the eggs that males guard.

Since males appear to defend the spawning site against intruders which are often female sculpins, it is in the best interest of a female to choose a mate who is larger than she is (also see Rohwer 1978). Thus female preferences for larger mates, and predation on eggs by females insures that males will be the larger sex.

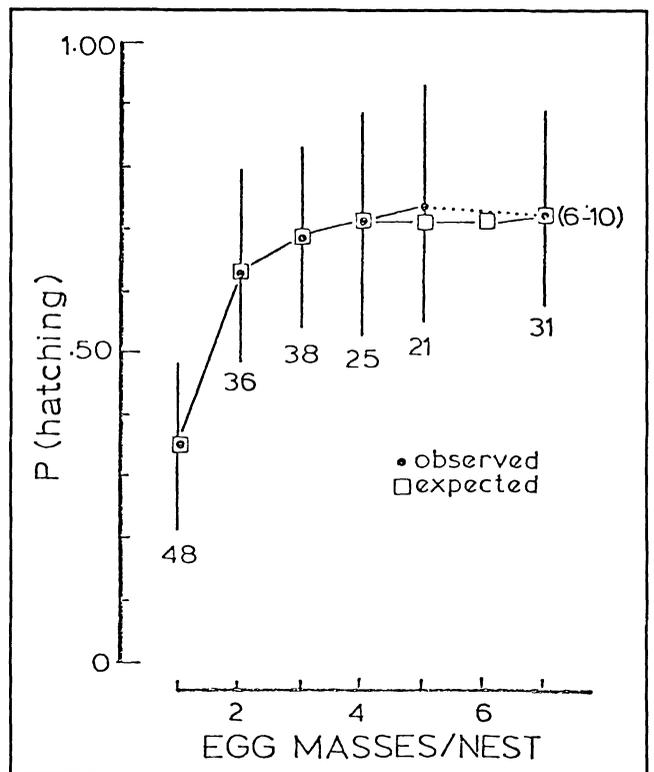
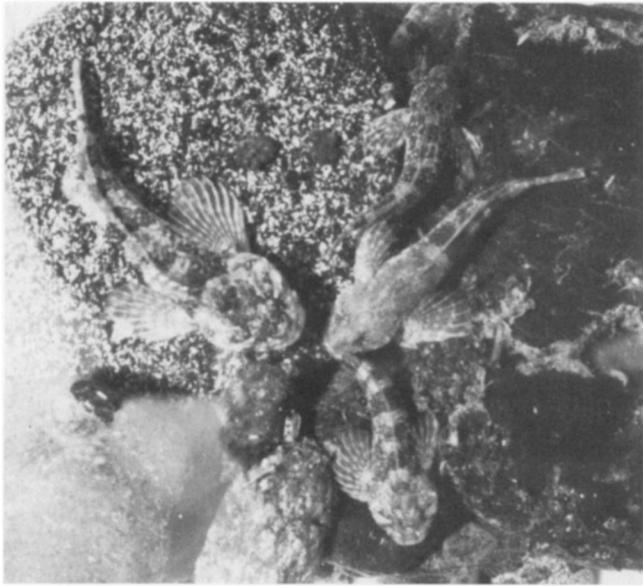


FIGURE 3. Egg mass survival as a function of the number of masses present in a male's nest. Solid circles represent the observed survival probabilities. Open squares represent the survival probabilities expected on the basis of differences between *only*, *first*, *middle*, and *last* egg masses. For example, the expected survival probability for an egg in a nest of two masses was calculated as the average of one *first* and one *last* mass. The number of masses associated with each point is given, and observed proportions are bounded by 95% confidence limits.



As the shape of this male's head suggests, sculpins are voracious predators, frequently cannibalizing any individual small enough to be gulped. Natural cannibalism has been observed in the wild on several occasions.

Loss rates of eggs were also dependent on male size—fewer losses were recorded for large males. Indirect evidence, from studies on other fish with similar breeding habits, indicate that the resident male himself may be sustaining himself by feeding on some of the eggs he guards. Males of this species do lose weight during the breeding season, but weight losses are relatively smaller for large males (Downhower 1976). Thus, if there is a critical weight loss which males cannot tolerate, then small males are the first to reach it. Guarding of eggs is energetically costly, and males may pay part of that cost by eating some of the eggs they guard. However, if some other food item is available then they may eat it.

Sculpins do not discriminate greatly among prey items. A sculpin can and will eat any acceptable item that it can ingest. Some of these prey items are other sculpins. In fact, a sculpin can and will eat any other sculpin who is 40 mm or shorter than it is. As the spawning season progresses smaller and smaller females breed. The first females to spawn are so large, relative to males, that it is unlikely that a male could eat them. By mid-spawning there are females in the population of breeders who are small enough to be eaten by the larger males. Thus larger males are likely to be avoided by these females. Avoidance is most pronounced at the end of the spawning season when the smallest females breed because there are many males who could prey on them and those males have already lost some of their energy reserves in the guarding process.

The result of predation by males is to increase the risks associated with being *last* and to reduce the



Although this sculpin has the body shape of a gravid female, it is actually an adult male—with gut and abdomen engorged with stolen eggs. Egg cannibalism is a common occurrence, females eating eggs more often than males. Protecting a nest from marauders is one of the guardian male's chief duties.

number of spawnings the largest males receive. Thus predation by females on the eggs of other females would seem to insure that males will be bigger than females, and male deterrence of such predation will preclude males from being too much bigger than females.

The mate choices that female sculpins make change during the course of the spawning season. Initial preferences for larger males are compromised by costs associated with when a female spawns. These in turn are modified by male preferences for larger females. Female investments in reproduction place females in a physiologically precarious state, leading to female predation on eggs. Males that could successfully deter such predation would necessarily be larger than females, and at their largest they themselves become predators on females. Thus, late-breeding females must avoid large males lest they go one step too far and turn an advantage into a fatal mistake.

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(Continued on p. 354)

to test the feeding response of a sea anemone.

Additional Activities

Observe the discharge of nematocysts through a compound microscope. Is the discharge of nematocysts always linked to feeding response? Do all tentacles discharge nematocysts? The color of the anemone can be changed with food color. This color change will last for perhaps a month. Can you devise a method for doing this that would allow you to observe the distribution of ingested food in anemones?

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Mad River Sculpins

. . . from p. 324

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