

A TEST FOR SEXUAL SELECTION ON HYBRIDS OF TWO SYMPATRIC STICKLEBACKS

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Abstract.—In this study we assessed whether sexual selection against hybrids contributes to reproductive isolation between two sympatric stickleback species. The species are recently diverged and possibly in the final stages of speciation. Our aim was to find whether mating discrimination of the parental species selects against F₁ hybrids, and what conditions are necessary for such sexual selection to operate. We used conservative no-choice laboratory trials with reproductively naive, lab-reared fish to measure female mating preferences. Females exhibited ranked preferences, preferring in order: conspecific, hybrid, then heterospecific males. However, intermediate attractiveness does not necessarily imply selection against hybrids: two-way ANOVAs suggested that limnetic, benthic, and hybrid males were statistically equivalent when averaged across females. Thus, this experiment found no evidence for a hybrid mating disadvantage. Our interpretation is that if sexual selection against hybrids is present in the wild, then some factor that biases encounter rates between hybrids and parental species (e.g., habitat selection) is necessary to produce it.

Key words.—*Gasterosteus*, hybrid fitness, mating discrimination, reproductive isolation, sexual selection, speciation.

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Sexual selection has often been hypothesized as a major force promoting divergent mating preferences (e.g., West-Eberhard 1983). Despite theoretical work showing that divergent sexual selection can cause speciation (e.g., Lande 1981, 1982; Schluter and Price 1993) there has been little empirical work to explore whether such selection is operating in wild populations, and whether it is strong enough to produce reproductive isolation. Sexual selection may cause or aid speciation in a number of ways, but one common way may be through a disadvantage for hybrids when competing for mates (Fisher 1930). Most empirical studies of hybrids measure the cost of mismating by focussing on hybrid viability and mechanisms of natural selection rather than hybrid reproductive success (see e.g., Barton and Hewitt 1985; Coyne and Orr 1989; Harrison 1993). Yet, sexual selection against hybrids may also be important in speciation.

A mating disadvantage for hybrids may have one or more effects (Coyne and Orr 1989). The best known effect is classic reinforcement (Dobzhansky 1951), selection for greater prezygotic isolation between the parental types. A variation on classic reinforcement was suggested by Lande (1982) whereby selection against hybrids could trigger divergent “runaway” sexual selection. The type of selection on hybrids was likely envisioned as a viability disadvantage, but a mating disadvantage may possibly have the same effect. Classic reinforcement and divergent runaway sexual selection would each lead to greater reproductive isolation and potentially to speciation. But even if there is no evolutionary response to sexual selection against hybrids, a mating disadvantage may be a piece of the total selection against occasionally produced hybrids, and thus important in its own right for limiting gene flow during speciation. An impressive example is seen in wolf spiders whose interspecific F₁ hybrids are fully viable and fertile yet “behaviorally sterile,” and hence act as a strong barrier to gene flow (Stratton and Uetz 1986). Data exist in other studies to test for sexual selection against hy-

brids (e.g., Wood and Ringo 1980; Ahearn and Templeton 1989; Coyne 1993; Scott 1994), but to our knowledge have rarely been used for this purpose.

In this study we carried out an initial test of sexual selection against hybrids between two recently diverged sympatric stickleback species. Our aim was to find whether mating discrimination of the parental species selects against F₁ hybrids, and what conditions are necessary for such sexual selection to operate. Our findings suggest that some factor that biases encounter rates between hybrids and parental species (e.g., habitat selection) may be necessary for sexual selection to occur.

We use conservative criteria to assess whether divergent mating preferences lead to sexual selection against hybrids. Interspecific hybrids are often intermediate in morphology and behavior between parental species, and may also be of intermediate attractiveness as mates for the parental species. However, intermediate attractiveness does not immediately imply selection against hybrids; one must also assess the opportunity for interactions among hybrids and the parental species. If encounter rates among hybrids and parentals are in proportion to their frequencies in the wild then a hybrid that is of intermediate attractiveness to both parental species may obtain the same number of matings as a parental type that is preferred by its own type but least preferred by heterospecifics. That is, a hybrid may get a few matings from each parental species so that the total number of matings is the same on average as a parental individual. Sexual selection against hybrids can only be concluded if they get fewer matings on average than those obtained by both parental species.

Stickleback Species Pairs

Threespine sticklebacks (*Gasterosteus aculeatus* complex) are small fish common to coastal marine and fresh waters throughout the northern hemisphere (Bell and Foster 1994). In British Columbia, anadromous sticklebacks colonized

many low elevation coastal lakes and streams at the end of the Pleistocene (McPhail 1994). The great majority of these lakes contain a single species of stickleback, but several lakes on islands in the Strait of Georgia contain a sympatric species pair (McPhail 1984, 1992, 1993, 1994; Schluter and McPhail 1992). The species are recently diverged and possibly in the final stages of speciation. Each pair appears to have been independently derived (McPhail 1993; Taylor et al. in press), though they exhibit similar morphological and ecological divergence (Schluter and McPhail 1992). We refer to the species by their foraging habitats. "Limnetics" primarily exploit plankton, and "benthics" exploit mainly benthic prey in the littoral zone. We studied the pair from Paxton Lake, on Texada Island.

Male sticklebacks are the sole providers of parental care. In the spring, they acquire territories in the littoral region where they build nests, mate (sometimes with many females), and raise their offspring. In Paxton Lake, benthic males tend to build nests in areas of the freshwater alga, *Chara* sp., while limnetic males tend to nest in the open (McPhail 1994). The two microhabitats form a mosaic, and gravid females have a high probability of observing males of both species when searching for mates, so the species may be regarded as reproductively sympatric. F_1 hybrids currently make up approximately 1–2% of adult sticklebacks in Paxton Lake (McPhail 1992). Reproductive isolation in the wild is therefore incomplete.

Hybrids (F_1 s, F_2 s and backcrosses) between limnetics and benthics of Paxton Lake can be obtained by artificial fertilization (McPhail 1992; Hatfield 1995). F_1 hybrids are morphologically intermediate between the parental species (McPhail 1992; Hatfield 1995). Hybrid viability has been studied extensively in the lab, and there is no convincing evidence of F_1 or F_2 inferiority (McPhail 1992; Hatfield 1995), though there is some evidence of lower viability in backcrosses (Hatfield 1995). Lower foraging efficiency in the wild is the only known disadvantage for F_1 hybrids, but they are nevertheless viable in the wild (McPhail 1994; Hatfield 1995). In the experiments presented here we measured the success of male F_1 hybrids in attracting limnetic and benthic females as mates. Encounters between female hybrids and male hybrids are expected by chance to be rare in the wild and we therefore focused only on females of the parental species as potential mates.

METHODS

Experimental Crosses.—All fish used in these experiments were reared in the lab from gametes of wild-caught individuals (see Hatfield 1995). We made full-sib crosses in July–September 1991 and May–June 1992, and raised benthics (20 families), limnetics (17 families), and reciprocal F_1 hybrids (15 $L\text{♀} \times B\text{♂}$ families, 19 $B\text{♀} \times L\text{♂}$ families). All individuals were raised without nesting material, and out of view of the mating trials—they were reproductively naive, and used in only one trial. Fish were brought into reproductive condition by manipulation of temperature and light (Baggerman 1957; Hatfield 1995). Reproductive condition was maintained by constant temperature and light (18°–20° C; 16:8 L:D) typical of mating season in the wild for these species.

TABLE 1. Mean standard body lengths (mm) of males and sample sizes for the six combinations of mating trials ($n = 96$).

		Male					
		Limnetic		Hybrid		Benthic	
		n	\bar{x}	n	\bar{x}	n	\bar{x}
Female	Limnetic	20	46.1	17	48.7	15	48.5
	Benthic	14	49.2	16	50.4	14	48.1

Mating Tests.—To assess female attraction to males, we measured courtship latency times in "no-choice" mating trials. No-choice trials, in which a single male and female are allowed to interact, generally provide conservative estimates of mating preferences (e.g., Foote and Larkin 1988; Coyne 1993). We conducted experiments in July–October 1992 (57 trials) and in July 1993 (39 trials) when fish were just over one year old. Trials were carried out as fish came into condition, which allowed up to four trials per day. Trial types were interspersed to correct for possible differences in mating propensity through time. We conducted no trials between sibs.

We divided 100 L aquaria in two by an opaque barrier to make two mating arenas per tank. A single male was introduced to one side (assigned at random), given a tray of sand and plant material ("Java moss," *Vesicularia* sp.) for nesting, and visually isolated from other males. A solitary gravid female was isolated for 12 to 24 h, assigned at random to one type of trial, then placed in the tank and videotaped for 2 h. From the videotapes, we later extracted elapsed time to the onset of stereotypic female courtship behaviors (i.e., latency times). Timing began when the male started courting the female. Female mating behavior traces the following sequence: (1) orientation of body into a head up posture; (2) follow the male; (3) examine the nest by sticking snout in the nest opening; and (4) enter the nest to spawn. Both in the lab and in the wild females may break off courtships at any of these points (T. H. pers. obs.; see also Kynard 1978; Goldschmidt and Bakker 1990). The males we used were of approximately the same body size to control for female responses that correlate with male size (Nagel 1994). Mean body length of males and number of trials for each combination of male and female type are shown in Table 1.

All males courted the females vigorously. As a check on our assessment of whether gravid females were ready to mate, only females that responded with at least a head up were included in analyses. Once a female had given a head up response we interpreted a lack of further response as a measure of preference. Latency times of females refusing to follow, examine, or spawn were set to 2h, the length of the mating trials. All such females were therefore used in calculations of mean times and variances of follow, examine, or spawn behaviors. Elapsed times to onset of behaviors were \ln -transformed before statistical analysis.

A total of 33 F_1 hybrid males were used in the trials: 14 $B\text{♀} \times L\text{♂}$ and 19 $L\text{♀} \times B\text{♂}$. In the lab reciprocal F_1 crosses do not differ in morphology or survival (McPhail 1992; Hatfield 1995). We nevertheless checked whether males of each reciprocal cross elicit different limnetic or benthic female responses. Two sample t -tests on \ln -transformed latency

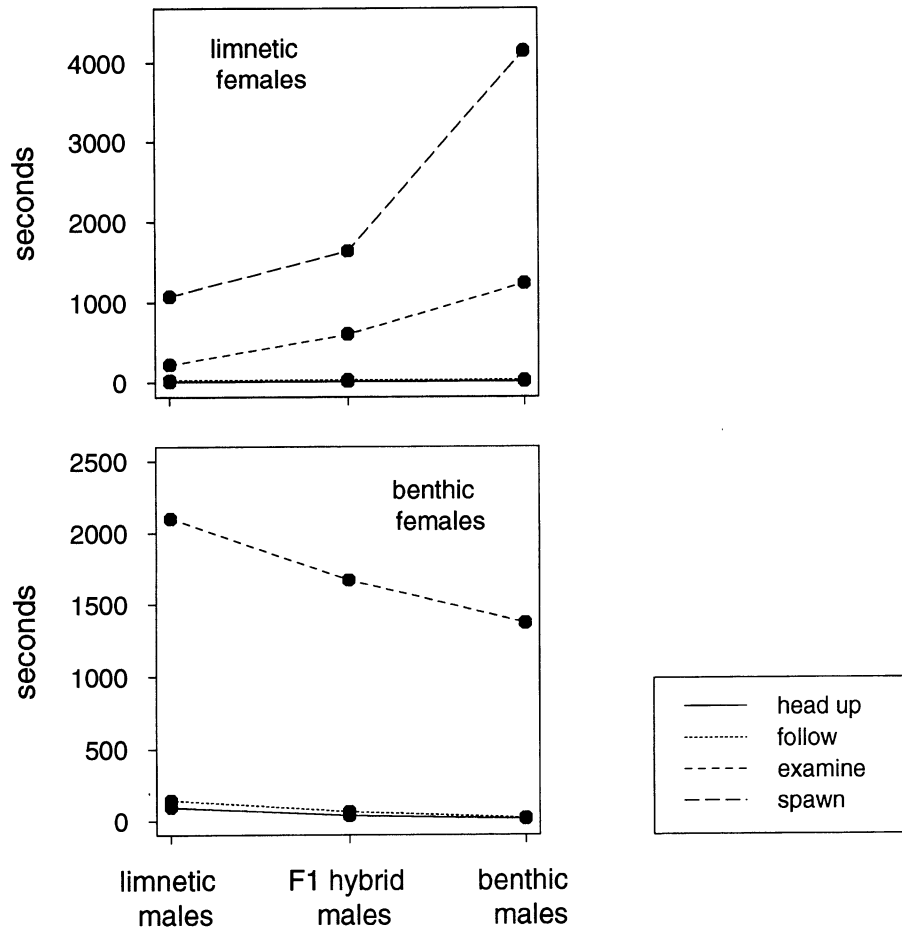


FIG. 1. Mean female response times to the three types of males. Hybrids elicit intermediate responses from both limnetic and benthic females.

times indicated that they did not elicit significantly different responses ($P > 0.35$ in all cases). We thus pooled all F_1 males before further analysis.

We used one-way ANOVAs with ordered expectations (Gaines and Rice 1990; Rice and Gaines 1994) to test whether females responded differently to conspecifics, hybrids, and heterospecifics. Ordered expectation ANOVAs are used when there are prior expectations of patterns in the data. The test is analogous to using one-tailed probabilities for a t -test and substantially improves power to detect a directional difference among means. These stickleback species mate assortatively (Nagel 1994), and prior behavioral and morphological analysis of hybrids (McPhail 1992; Schluter 1993; Hatfield 1995) suggest that attractiveness of hybrids should fall within the range delimited by attractiveness of the parental species. Thus, ordered expectations are appropriate for our analyses. The null expectation is that there would be no differences in attractiveness of conspecifics, hybrids, and heterospecifics. The alternative expectation was that females would exhibit courtship latency times in the following order: conspecific males < hybrid males < heterospecific males. We carried out Fisher's exact tests on the proportions of individuals exhibiting courtship responses. We used standard two-way ANOVAs to test for interactions between female

type and male type on female mating behavior, and to examine whether mating success of male types differed when averaged across females of the two types. Two-way ANOVAs could be performed only on the first three responses (head-up, follow, examine) because benthic females courted with, but did not spawn with, any of the males.

Note that intermediate attractiveness of hybrids does not in itself tell us about selection against hybrids. Selection against hybrids would occur if limnetic and/or benthic females find hybrid males more like heterospecifics than conspecifics in attractiveness. Such a finding could be drawn as a concave fitness set such as that for foraging success and growth rate in Schluter (1993, 1995). Thus, both one-way and two-way ANOVAs are necessary.

RESULTS

Both limnetic and benthic females readily distinguish among conspecific, hybrid, and heterospecific males (Fig. 1, Table 2). Four of seven one-way ANOVAs showed that mean response times of females differed significantly among conspecific, hybrid, and heterospecific males (Table 3). Weak discrimination was generally observed at the other stages (Fig. 1, Table 2). The ANOVAs suggest that hybrids elicit a

TABLE 2. Proportions of females that responded to courting males.

	Response	Limnetic males	Hybrid males	Benthic males	Fisher exact test
Limnetic females	head up	20/20	17/17	15/15	
	follow	20/20	17/17	15/15	
	examine	20/20	14/17	9/15	$P = 0.004$
	spawn	13/20	10/17	3/15	$P = 0.025$
Benthic females	head up	14/14	16/16	14/14	
	follow	13/14	16/16	14/14	
	examine	6/14	10/16	8/14	$P = 0.646$

response intermediate between that of the parental species males, but they do not distinguish between a response that is halfway between a conspecific and heterospecific male and a response that is closer to one type.

The stage of courtship at which differences in attractiveness were statistically significant was different for the two species of females. Limnetic females were most discriminating late in the courtship sequence (i.e., during nest examination and entry) whereas benthic females were most discriminating early in courtship (i.e., for head up and follow; Table 3).

Of females that responded to males with a head up, all but one (a benthic) also responded with a follow (Table 2), though fewer females responded with nest examination or entry. Proportions corroborate mean response time data for limnetics: females more readily court their own species than hybrids or heterospecifics. Fisher exact tests rejected the null model of no differences among group proportions in two of three tests (Table 2).

Two of the three two-way ANOVAs found statistically significant interactions between male type and female type (Table 4) supporting the view that limnetic and benthic females rank males differently. (The third was close to significant at $\alpha = 0.05$.) Limnetic and benthic females also differed significantly in their overall response to males because mean responses by limnetic females were faster than those by benthic females (see Fig. 1). The lack of significance of the male terms indicate that males were statistically equivalent when averaged across females. This suggests that even though there are significant differences among males in eliciting a response to limnetic or to benthic females (Tables 2, 3) when the responses are averaged over both species, hybrids obtain the same total response as both of the parental species males. Thus, this experiment found no evidence for hybrid disadvantage.

DISCUSSION

Paxton Lake limnetic and benthic females showed measurable differences in courtship times, which reflect prezygotic isolation between the species. They responded more often, and faster, to their own type than to hybrid and heterospecific males (Fig. 1, Table 2). Our results parallel studies by Ridgway and McPhail (1984) and Nagel (1994). They studied prezygotic isolation between several species pairs of sticklebacks (Enos Lake, Priest Lake, and Paxton Lake pairs) and found that benthics and limnetics in each of these lakes were well isolated by mating preferences.

TABLE 3. Female responses to courting males. P -values are from ordered expectations one-way ANOVAs on mean time (\ln seconds) for females to respond to courting males.

Response	Limnetic females	Benthic females
head up	$P = 0.424$	$P = 0.011$
follow	$P = 0.618$	$P = 0.011$
examine	$P = 0.003$	$P = 0.390$
spawn	$P = 0.021$	

Nevertheless, two-way ANOVAs showed that mean success of limnetic, benthic, and hybrid males was statistically equivalent when averaged across females. This suggests that despite their intermediate attractiveness, hybrid males may have reproductive success similar to that of pure-type males. Consequently, these lab results suggest no sexual selection against F_1 hybrid males.

The above conclusion, to be applicable in the wild, depends critically on two factors: (1) possible experimental artifacts; and (2) encounter rates between male and female types.

Benthic females courted with males and were differentially attracted early in courtship (Table 3), but their refusal to spawn within the allotted time and their generally slow responses (Fig. 1, Tables 2, 3) suggest that some caution may be necessary when extrapolating from our results to situations in the wild. Although we do not yet know whether these strong early responses are correlated with spawning success in this species, head-up behavior is highly correlated with spawning success in other *Gasterosteus aculeatus* populations (McLennan and McPhail 1990), and has been used as a measure of female preference in many other studies (e.g., Milinski and Bakker 1990, 1992; Bakker and Milinski 1991; McKinnon 1995). Thus, it seems likely that differential early responses by benthics reflect their true preferences.

The potential for biased encounters is suggested by divergent nesting sites (McPhail 1994; Hatfield 1995). Nests of limnetics and benthics in the wild are in different microhabitats: benthics under dense cover of algae, and limnetics in the open (McPhail 1994). These differences are not the result of current competition for nest sites. Lab-reared males when placed singly in enclosures in Paxton Lake with a choice of nesting habitat had strong preferences: 12 of 12 benthics nested in dense cover; seven of seven limnetics and 15 of 16 hybrids nested in the open or under sparse cover (Hatfield 1995). The strong similarity of hybrids to limnetics suggest that in the wild hybrid males may typically interact only with limnetic males and therefore possibly only with limnetic females.

TABLE 4. Two-way ANOVAs for female courtship responses. Each behavior represents a stage in the courtship sequence. Data are \ln -transformed times in seconds to exhibit the indicated behaviors by females.

	df	Head up		Follow		Examine nest	
		F	P	F	P	F	P
Female type	1	11.22	0.001	4.66	0.034	11.33	0.001
Male type	2	1.90	0.155	2.89	0.061	1.24	0.296
Female*male	2	3.42	0.037	2.63	0.077	3.40	0.038
Residuals	90						

Visitation rates to the two microhabitats by females remain to be studied. It seems likely that limnetic and benthic females would share nesting-habitat preferences of their males. If so, then hybrid males may be at a disadvantage if they encounter mainly limnetic females, which are less attracted to them than to limnetic males. Even though female mating preferences do not lead to sexual selection against hybrids in the lab, it is possible and perhaps likely that a hybrid mating disadvantage could arise as a consequence of habitat selection in the wild. Thus, ecological factors such as nesting-habitat preferences need to be considered in addition to mating preferences to predict patterns of mating success in sticklebacks. This may be true in other systems: hybrid mating success measured in the laboratory (e.g., Stratton and Uetz 1986; Krebs 1990; Price and Boake 1995) may be greater than that obtained in the wild when divergent ecologies of the parental species can bias encounter rates.

Nevertheless, in our no-choice trials many limnetic females eventually spawned with hybrid males (Table 2), which indicates only weak discrimination. It is possible that long duration no-choice mating trials may reduce discrimination (Scott 1994), or that preferences are stronger when females are given a choice of males (e.g., Foote and Larkin 1988), but our current evidence supports a conclusion of little or no sexual selection on hybrids in a laboratory setting. Our interpretation is that if sexual selection is present in the wild, then some factor that biases encounter rates between hybrids and parental species (e.g., habitat selection) is necessary to produce it.

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