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Do Female Three-Spined Sticklebacks Copy the Mate Choice of Others?

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A common assumption in evolutionary models of female mate choice is that mating preferences are genetically based and that females choose mates independently of the choices of other females in the population (reviewed in Andersson 1994; Ryan 1997). However, field observations (reviewed in Höglund and Alatalo 1995) have suggested and experimental studies (reviewed in Dugatkin 1996*a*) have confirmed that females, particularly in promiscuous and lekking species, may copy the choices of others under certain circumstances. A female is considered to have copied the mate choice of another female(s) if the probability of her choosing a specific male as a mate is increased specifically as a result of her observing other females previously choosing that same male (Wade and Pruett-Jones 1990; Pruett-Jones 1992; Dugatkin 1996*a*), rather than because of any change in that male's behavior due to his prior mating or proximity to females or because of any preference by females for certain sites irrespective of the male or to aggregate with other females (Dugatkin 1992, 1996*a;* Pruett-Jones 1992).

Potential fitness benefits of copying accruing to females include information gained from other individuals that might know more about prospective mates, increased accuracy with which females discriminate male quality, and reduction of the costs of mate assessment and choice. By copying, however, an individual risks mating with a recently mated male with depleted sperm supply or one of relatively poor quality due to discrimination errors made by the female(s) copied (Gibson and Höglund 1992; Dugatkin 1996*a*). To our knowledge, currently no empirical data are available on the benefits or costs of such copying behavior. Nonetheless, mate-choice copying can be viewed as a facultative alternative to independent mate choice. Theoretical models have shown that copying may evolve and be maintained in a population through either direct (Losey et al. 1986; Pruett-Jones 1992; Kirkpatrick and Dugatkin 1994; Laland 1994; Dugatkin and Höglund 1995) or indirect (Servedio and Kirkpatrick 1996) selection on females. Copying, like independent mate choice, increases the variance of male mating success in a population and thus the opportunity for sexual selection (Wade and Pruett-Jones 1990).

In several species of polygynous fish (reviewed in Pruett-Jones 1992; Jamieson 1995; Dugatkin 1996*a*), including the three-spined stickleback, *Gasterosteus aculeatus* (Ridley and Rechten 1981; Jamieson and Colgan 1989; Belles-Isles et al. 1990; Goldschmidt et al. 1993), females prefer to mate with males whose nests contain eggs obtained from prior matings. Although previously attributed to copying (Goldschmidt et al. 1993), it remains uncertain whether this phenomenon is due to actual mate-choice copying (as defined earlier), as females apparently did not directly observe the mate choice of others in these studies. Alternatively, females may be attracted to nests already containing eggs because the males that defend such nests have been chosen previously by other females (Jamieson 1995; Dugatkin 1996*a*), provide more parental care (Sargent 1988), may court more vigorously (Jamieson and Colgan 1989), or may be more colorful (Jamieson and Colgan 1989) and/or because predation risk on their own eggs would be diluted by the presence of other females' eggs in the nest (Jamieson 1995; Forsgren et al. 1996). If females prefer males with eggs already in their nest for reasons of mate choice, then they may copy other females' mate choice whenever directly observed. Here, we experimentally investigated whether female three-spined sticklebacks copy the apparent mate choice of another female when given the behavioral opportunity to do so, while controlling for other factors that could potentially bias female choice, such as the

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presence of eggs in a male's nest and differential male coloration and courtship behavior.

The three-spined stickleback is a polygynous species with external fertilization and paternal care (Wootton 1976; Rowland 1994; Whoriskey and FitzGerald 1994). During the reproductive season, males develop nuptial coloration (red underside, blue iris, and bluish dorsolateral surfaces) and compete for territories, in which they build a small algal nest on the substratum. Territorial males attempt to attract females to spawn in their nest with elaborate courtship displays, including the conspicuous "zig-zag dance" (Wootton 1976; Rowland 1994; Whoriskey and FitzGerald 1994). Males vary widely in their body coloration, courtship behavior, and mating success within populations (reviewed in Rowland 1994; Whoriskey and FitzGerald 1994). Depending on the population, females tend to prefer males that are more brightly colored, court more vigorously, and/or already possess eggs in their nest (reviewed in Bakker and Milinski 1993; Rowland 1994; Whoriskey and FitzGerald 1994). Individual females may sequentially visit and assess a number of territorial males before spawning in the nest of a particular male (Kynard 1978; Bakker and Milinski 1991; Milinski and Bakker 1992). Female three-spined sticklebacks likely have opportunities to observe the mate choices of other females in natural populations, as they commonly shoal during the reproductive season (Whoriskey and FitzGerald 1994), sometimes visit territorial males in pairs (Wootton 1976), and, particularly in high-density populations, may simultaneously view several adjacent nesting and courting males (Kynard 1978; FitzGerald 1983; Whoriskey and FitzGerald 1994).

Methods

We collected, using a beach seine, adult marine three-spined sticklebacks from salt-marsh tide pools and a nearby beach site in Baie Verte, New Brunswick, Canada (46°01′ N, 64°05′ W), during their reproductive season (May–July) in 1996 and 1997. In the laboratory, the males were held in a large fiberglass tank (200 cm × 200 cm × 54 cm, L × W × H) in the continuous presence of at least 40 gravid and sexually receptive females, which were held separately in a meshed container (67 cm × 67 cm × 40 cm) located in this tank. Males and females could view and court each other across the meshed walls of this container but were not allowed to interact directly. The males were provided with clay pots, petri dishes, and filamentous green algae (*Enteromorpha intestinalis*) as nesting materials. The holding tank contained continuously filtered brackish water (10‰–12‰, 17°–19°C) and was exposed to a 16L : 8D illumination regime. Light was provided by Sun-Glo fluorescent tubes (R. C. Hagen Ltd., Montreal), which simulate the energy spectrum of sunlight. These conditions approximate summer conditions at the field sites where the fish were collected. Fish were fed ad lib. several times daily with commercially available freeze-dried krill, supplemented with frozen brine shrimp and freeze-dried chironomids.

Males that exhibited nest-building behavior (see Wootton 1976; Rowland 1994) in the large holding tank were measured (standard length), wet weighed, and transferred individually to glass aquaria (31 cm × 13 cm × 20 cm), in which they were allowed to complete a nest in a sand-filled petri dish with a standardized amount (mean ± SE; 1.59 ± 0.04 g) of filamentous algae. These aquaria were exposed to the same conditions as the larger holding tank. Males in adjacent aquaria could see each other. Nesting males were stimulated individually with a gravid female contained in a 1-L glass beaker, which they typically courted, for 15 min once daily until needed in experiments (see below). This procedure accelerated nest building and ensured long-term maintenance of their sexual motivation and nuptial coloration (see McLennan and McPhail 1990; Milinski and Bakker 1990). Before a male was transferred to the experimental mate-choice apparatus (described below), his nuptial coloration was scored while still in his home aquarium immediately following the presentation of the female in a beaker. We compared the nuptial color of individual males to color photographs of 10 male sticklebacks that represented the natural range of male nuptial coloration in our study population. The photographs were arranged in order (from 1 to 10) of gradually increasing amount and intensity of nuptial colors, with a score of 1 denoting a male with only weakly blue eyes and no red coloration ("dullest" male) and a score of 10 a male with bright red color, extending from his mouth, along the abdomen, to the caudal peduncle, blue eyes, and bluish dorsolateral surfaces ("brightest" male). This color-scoring system is similar to one used by Milinski and Bakker (1990). Two persons (including one of us, K.J.P.-M.) scored the body coloration of individual males using this 10-point scale. Their independent color scores were highly concordant (Spearman rank correlation, $r_s = 0.93$, df = 82, $P < .001$) and were averaged for each male. None of the males used in the current study had any visible external parasites, which are known to adversely affect their nuptial colors (Milinski and Bakker 1990).

We experimentally determined the mating preference of individual female sticklebacks using a binary mate-choice apparatus (fig. 1), similar to the one used by Schlupp et al. (1994). The apparatus consisted of a Plexiglas aquarium (155 cm × 42 cm × 37 cm) divided into five compartments. A clear, perforated Plexiglas partition was placed 20 cm from each of the end walls, thus creat-

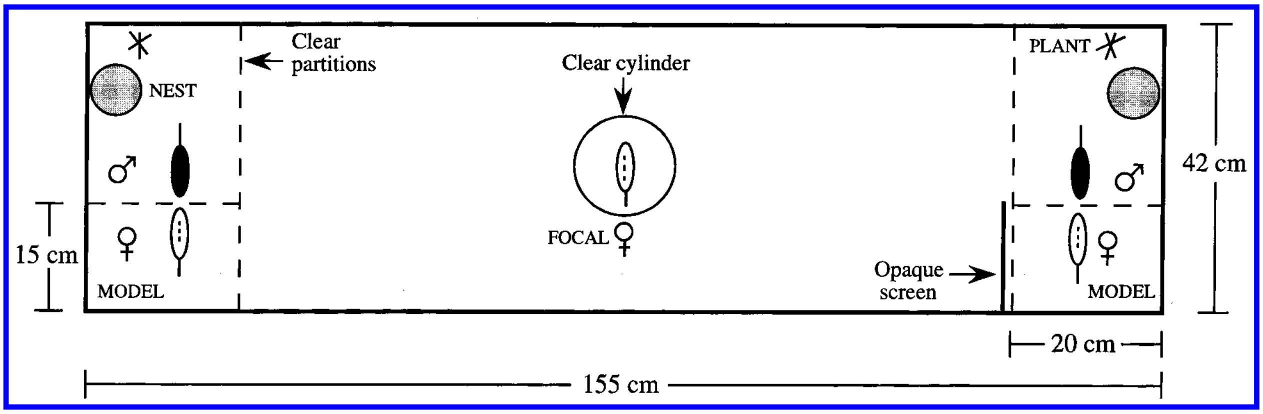

Figure 1: Top view of the experimental aquarium. It consisted of a central mate-choice arena, containing a single test female (the "focal" female) and two similar end compartments, each containing one stimulus male and one "model" female, separated by a clear Plexiglas partition. The end compartments housing the stimulus males contained their algal nest and a plastic aquatic plant, as shown. A fixed opaque Plexiglas screen blocked the focal female's view of one of the model females (i.e., the hidden model). During the initial acclimatization period, the focal female's view into both end compartments would be blocked by removable, opaque Plexiglas partitions (not shown). The focal female was temporarily held in a clear Plexiglas cylinder located in the center of the aquarium during the initial fish-viewing period.

ing two end compartments (20 cm × 42 cm × 37 cm) and a central choice arena (115 cm × 42 cm × 37 cm). The end compartments were further divided into two unequal sections with an additional clear, perforated Plexiglas partition. The bottom of each end compartment was covered with silica sand (2.5 cm deep), and the larger (20 cm × 27 cm × 37 cm) of its two sections was furnished with a water filter (located in the back corner) and a plastic aquatic plant (anchored to the bottom) adjacent to the filter along the back wall. A removable opaque Plexiglas partition was placed directly in front of each end compartment. The end and back walls and the bottom of the tank were covered externally with tan paper to provide a uniform background and to reduce external disturbances. The front wall was covered with a cardboard blind, equipped with a narrow screened opening through which fish behavior could be observed. The environmental conditions were similar to those of the holding tanks.

Our experimental protocol generally followed the one used by Dugatkin (1992) for ascertaining the occurrence of mate-choice copying. Female sticklebacks were allowed individually to "choose" between two sexually active (but nonparental) stimulus males as potential mates, each located in the larger section of the separate compartment at either end of the experimental aquarium (fig. 1). In any given trial, the paired males were matched for both standard length (mean ± SE; 51.8 ± 0.6 mm vs. 51.7 ± 0.6 mm; two-tailed paired t-test, $t = 1.04$, df $= 34$, $P > .30$) and color score (3.85 ± 0.36 vs. 3.81 ± 0.38; $t = 0.22$, df $= 34$, $P > .80$) as closely as possible. The males, with their nests (which did not contain any eggs), were transferred to their respective end compartments (predetermined at random) the day before a trial and were allowed to acclimatize overnight. The next morning, a gravid female (i.e., "model" female) was placed in the smaller section of the end compartment adjacent to each male. Both males could thus interact behaviorally with a female nearby (they mutually courted each other). Following Schlupp et al. (1994), we introduced a model female near each male to minimize potential differences in the activity level, including courtship behavior, of the males when they were initially viewed at a distance by the test female (see below). With the opaque partitions lowered, a sexually receptive gravid female (i.e., "focal" female) was then placed in the larger central choice arena and allowed to swim freely for 30 min. In each trial, the two model females were matched for both body length (53.5 ± 0.9 mm vs. 53.7 ± 0.9 mm; $t = 0.92$, df $= 34$, $P > .35$) and relative abdominal distensions (gravid state, determined by visual inspection) and were also similarly matched with the focal female (54.2 ± 0.9 mm).

Following this acclimation period, the focal female was gently dipnetted and transferred into a clear Plexiglas cylinder (16 cm diameter) in the center of the tank, and the opaque partitions were raised, thus allowing her to view the other fish in the tank for 10 min. During this period, the focal female's view of one of the two model females (predetermined at random) was blocked by an opaque Plexiglas screen (fig. 1). Therefore, the female could observe one male courting a visible model and the other male apparently alone (i.e., model hidden), which thus simulated mate choice by the visible model female for the male near her. After the 10-min viewing period, the model females were removed, and the focal female was released from the cylinder and allowed to choose between the two males as potential mates for 10 min. We recorded concurrently which of the two stimulus males the focal female visited first (= approach, while in the head-up posture, within 5 cm of the male's compartment), the number of visits to each male, the total time the focal female spent displaying in the sexual head-up posture (sensu Wootton 1976; Rowland 1994) toward each male, and the number of zig-zag courtship displays (sensu Wootton 1976; Rowland 1994) performed by each male.

If a focal female displayed >55% of her total head-up posture time toward one of the males, we considered her to have "preferred" that particular male. By this criterion, a preference for a particular male was shown only if the times spent in the head-up posture by the focal female directed at each male differed by at least 10%. Time spent in the head-up posture near a male is known to correlate strongly with actual choice of mate when mating is allowed in the three-spined stickleback (McLennan and McPhail 1990), and it is consequently used here as an indicator of female mate choice. If a focal female preferred the male that she had previously observed courting the visible model female, we considered this consistent with mate-choice copying behavior. We conducted 35 such mate-choice copying trials, each with a different focal female and different stimulus males. Because of the limited availability of receptive females of similar size, some of the model females were reused (as models only) in subsequent trials.

We used the paired *t*-test (Zar 1974) to compare the behavior (i.e., frequency of visits, time spent in head-up posture) of focal females toward paired stimulus males presented and to compare the courtship rates of paired males. Data on these behaviors were normalized by $\log_{10}(X + 1)$ transformation prior to statistical analysis. We also used the normal approximation to the binomial test for large samples (Zar 1974) to compare the numbers of focal females that preferred either male in a matched pair against frequencies expected by chance. The power of these statistical tests was determined separately using power analysis (Cohen 1988).

Results

All focal females ($N = 35$) exhibited a mating preference (as defined earlier) for one of the two simultaneously presented males, which did not differ significantly in their courtship rate (7.8 ± 2.5 zig-zag displays/10 min for the male near the visible model vs. 12.1 ± 5.5 for the male near the hidden model; two-tailed paired t-test, $t = 0.071$, df = 34, $P > .90$) or in their body length and nuptial color score (as noted earlier). However, the females chose randomly between the paired males. The particular male in a matched pair that was first visited and sexually displayed to by the focal females, following the model viewing period, was not different from that expected by chance (fig. 2*A;* one-tailed normal approximation to the binomial test, $Z = 0.68$, df = 34, $P > .25$). For all but one of the 35 females tested, the male that was first visited by a female was the same male she spent most of her subsequent time sexually displaying to. Moreover, the females did not visit any more frequently (fig. 2*B;* one-tailed paired *t*-test, power = 0.84, $t = 0.56$, df = 34, $P > .30$) the male that had previously been observed near the visible model female or spend any more time displaying the sexual head-up posture to him (fig. 2*C;* one-tailed paired *t*-test, power = 0.91 $t = 0.41$, df = 34, $P > .50$) than the other male that they had not previously observed interacting with a female. Based on the latter sexual posture time data, 22 of the 35 focal females (62.9%) were categorized as having preferred the male that they had previously observed being courted by another female (the visible model), whereas 13 (37.1%) females preferred the other male; these frequencies are not significantly different from those expected by chance ($Z = 1.40$, df = 34, $P > .08$, power = 0.46).

Discussion

In the current study, the paired stimulus males that were presented to individual females as potential mates had similar body lengths, nuptial colors, parental status, courtship behavior rates, nests, and territory sizes. These circumstances should promote mate-choice copying (see Dugatkin 1996*a*), if it occurs at all, since females might experience difficulty in making an independent choice between phenotypically similar males and thus may rely on the apparent choice of others. Despite such favorable conditions, only 62.9% of our focal females showed a mating preference for the male that they had previously observed being courted by another female; this proportion is marginally nonsignificant. In a similar study on marine three-spined sticklebacks from Long Island, New York, J. Jenkins and W. J. Rowland (unpublished data) obtained results similar to ours. Their focal females did not visit first the male that they had previously observed interacting with other live females any more frequently (15 of 24 females, $P = .154$) than the other male with no females nearby, but they did spend marginally ($P = .072$) more time visiting the former male. Although our findings, and those of Jenkins and Rowland, do not comprise evidence for mate-choice copying behavior in female three-spined sticklebacks, one might argue that these results are sufficiently suggestive of a tendency to mate-

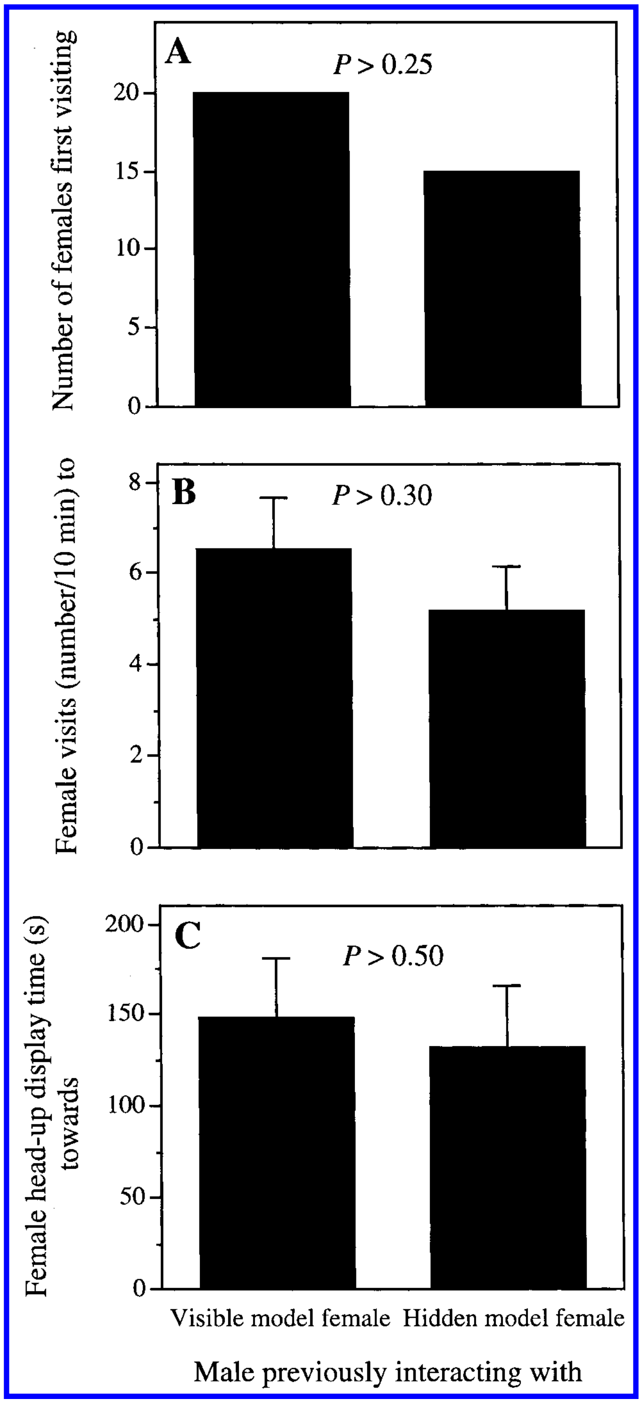

Figure 2: Number of focal female three-spined sticklebacks ($N = 35$) first visiting either stimulus males (*A*), mean (+ SE) number of female visits per 10 min to either males (*B*), and female time spent in the head-up sexual posture near either male (*C*). One of the paired males was previously observed by the focal female to interact with a visible model female, whereas the other male interacted with a model female hidden from the view of the focal female. Also shown are *P* values for the paired comparisons.

choice copy to warrant further investigation of this phenomenon in this species.

Experimental evidence for mate-choice copying available to date is almost exclusively for promiscuous and lekking species with internal fertilization and lack of paternal care, such as the guppy, *Poecilia reticulata* (Dugatkin 1992, 1996*b;* Dugatkin and Godin 1992, 1993; Briggs et al. 1996); Japanese medaka, *Oryzias latipes* (Grant and Green 1996); sailfin molly, *Poecilia latipinna* (Schlupp et al. 1994; Schlupp and Ryan 1997); and black grouse, *Tetrao tetrix* (Höglund et al. 1995; but for exceptions, see Clutton-Brock and McComb 1993; Brooks 1996). In comparison, the three-spined stickleback (the current study; J. Jenkins and W. J. Rowland, unpublished data) and the sand goby, *Pomatoschistus minutus* (Forsgren et al. 1996), both polygynous fish species with external fertilization and paternal care, apparently do not mate-choice copy. The benefits and costs to females of copying may vary, in a still unknown manner, depending on a species' breeding system (sensu Reynolds 1996), the particular population, and/or the tactics females use to assess potential mates. Therefore, mate-choice copying in the three-spined stickleback may be somehow constrained or otherwise more costly than direct independent mate assessment based on differences among males in their body coloration, courtship behavior, and/or nest quality (see Rowland 1994; Whoriskey and FitzGerald 1994), and it was consequently not expressed in the current study. Clearly, more research elucidating the relationships between copying tendency, breeding system, and female mate-assessment tactics is required.

If our experimental results and conclusion here are robust and relevant to a natural context, then the observed phenomenon that female three-spined sticklebacks prefer to spawn in the nest of males that already contain eggs (Ridley and Rechten 1981; Jamieson and Colgan 1989; Belles-Isles et al. 1990; Goldschmidt et al. 1993) cannot be attributed to behavioral mate-choice copying per se. A previously proposed alternative adaptive explanation for this phenomenon is that female sticklebacks prefer such males because the survival of their eggs is maximized, through dilution of predation risk on their eggs and/or greater care of their eggs by the parental male, in doing so (reviewed in Jamieson 1995; Forsgren et al. 1996). Females may assess the presence or absence of eggs in a male's nest directly by nosing at the nest's entrance or entering the nest (Kynard 1978; Belles-Isles et al. 1990; Goldschmidt et al. 1993) or indirectly through changes in the courtship behavior of males that already care for eggs (Jamieson and Colgan 1989, but see Goldschmidt et al. 1993).

Notwithstanding the aforementioned, female three-spined sticklebacks may copy the mate choice of others when given the opportunity to do so, but we failed to reject the null hypothesis of no copying (i.e., no preference for either male or a preference for the male not previously observed near a model female) in the current study for at least three possible reasons.

First, females in our study population may not discriminate among available males as potential mates and consequently would not be expected to mate-choice copy. This is not likely, however, as female sticklebacks from this population have been shown experimentally to discriminate among potential mates based at least on differences in their nuptial coloration and courtship behavior (J.-G. J. Godin and A. J. MacAulay, unpublished data).

Second, although our measure of female mating preference (i.e., time spent in the sexual head-up posture near a male) is known to be a good predictor of actual mate choice in the three-spined stickleback (McLennan and McPhail 1990) and has been used previously in other mate-choice studies on this species (e.g., McLennan and McPhail 1990; Milinski and Bakker 1990; Bakker and Milinski 1991), it is nonetheless possible that our experimental design and apparatus did not allow focal females to accurately express their preference because they did not have direct access to the males or their nest (as they were separated by clear, perforated Plexiglas partitions). Evidence indicates that female three-spined sticklebacks require direct interactions with males and direct assessment of the content of their nests before deciding to enter and spawn in the nest of a particular male (Kynard 1978; Belles-Isles et al. 1990; Goldschmidt et al. 1993; Rowland 1994). This possibility seems unlikely because the particular male to which a focal female was initially attracted and visited (immediately following the model viewing period) was typically the same male she spent most of her subsequent time sexually displaying to, and because female sticklebacks from our study population have been shown to exhibit mate choice based on differences in male body coloration, in the absence of any model female, in the same experimental aquarium described herein (J.-G. J. Godin, unpublished data).

Third, our statistical tests may not have had sufficient power to reject the null hypothesis of no copying, if in fact it is false and should be rejected (see Cohen 1988). However, the power of the statistical tests applied (at the stringent $\alpha = 0.05$ criterion) to our mating preference data ranged from moderate (0.46) to very high (0.98) levels, depending on the dependent variable considered. This means that the likelihood of incorrectly concluding that female sticklebacks did not mate-choice copy (i.e., of making a Type II error) in our study is moderate to very low. Therefore, we are reasonably confident in making this conclusion.

Other than the unpublished study of J. Jenkins and W. J. Rowland (described earlier), the current study represents the only controlled experimental test of behavioral mate-choice copying (sensu Pruett-Jones 1992; Dugatkin 1996*a*) in the three-spined stickleback to date. Contrary to expectation if females mate-choice copied, we found that female three-spined sticklebacks did not significantly prefer a male that they had previously seen courting another female over another male, when differences in nuptial coloration, body size, nest quality, parental status, territory size, and courtship behavior between the males were controlled for. Based on these findings, we tentatively conclude that female three-spined sticklebacks do not base their mate-choice decisions on the (directly observed) apparent mate choice of others. Whether mate-choice copying behavior would have been revealed in the current study if female sticklebacks had been given complete access to the males and their nests remains to be ascertained.

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