

# Independent effects of familiarity and mating preferences for ornamental traits on mating decisions in guppies

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The avoidance of familiar individuals as mates can act to maximize the benefits of polyandry or might help to minimize inbreeding in small or highly philopatric populations. As previous mates are also familiar, the effects of familiarity and mating history can often be confounded. Here, we disentangle these effects on mating decisions in the guppy, *Poecilia reticulata*, and examine their influence on sexual selection. In 3 experiments, males and females were 1) able to mate, 2) had visual and olfactory contact, or 3) had visual contact only. Familiarity was successfully acquired via visual cues, and females were in all cases more likely to mate with unfamiliar than with familiar males, indicating that familiarity is a more important determinant of mating outcome than mating history. Males did not court unfamiliar females any more than familiar females and did not differentially allocate sperm. Familiarity did not alter the strength of sexual selection on male coloration: we found overall positive selection for bright, large males. Female preferences for unfamiliar males and ornamental traits may therefore be largely independent. *Key words*: mate choice, mating history, polymorphism, polyandry, sexual selection, sperm competition. [*Behav Ecol* 17:911–916 (2006)]

A number of adaptive forces influence the evolution of mating behavior, including direct benefits, additive genetic benefits conferred by a mate of high genetic quality, and nonadditive genetic benefits such as genetic compatibility and avoidance of inbreeding depression (Andersson 1994; Tregenza and Wedell 2000; Kokko et al. 2003). These forces can shape preferences for mates of a particular phenotype, the tendency to mate multiply within a given reproductive cycle, and the allocation of gametes and resources to a particular mating event. Considerable progress has been made in understanding the evolution of mating preferences and the sexual selection they impose (for reviews, see Andersson 1994; Kokko et al. 2003; Neff and Pitcher 2005). Mating decisions are also influenced by an individual's experience with previous mates and mating history (Jennions and Petrie 1997; Bateson and Healy 2005). However, less is known about how preferences and experience interact to influence mating success. Here we use guppies (*Poecilia reticulata*), a small live-bearing tropical freshwater fish, to test whether male and female mating decisions are influenced by whether they have previously mated with (i.e., mating history) and/or are otherwise familiar with (i.e., familiarity) a given potential mate. Our approach experimentally disentangles mating history and familiarity in an attempt to identify the factors responsible for the preferences male and female guppies have previously been shown to express for unfamiliar mates (Hughes et al. 1999; Kelley et al. 1999). We also measure mating preferences for ornamental traits and test whether the effects of familiarity and mating history alter the expression of mating preferences and the sexual selection they exert on these traits.

Familiarity and mating experience may influence female mating preferences and hence alter the strength of sexual selection on male ornamentation, a possibility that has not

been tested before. It is possible, for example, that the strength of female preferences for certain male traits may either be weakened or enhanced by the effects of experience on mating behavior. If males that are otherwise of average quality gain a mating advantage when they are unfamiliar to a female, preference for unfamiliar males will undermine sexual selection on signals of quality. However, with increasing experience of the variation in a pool of potential mates, females in many species have been shown to become choosier as they trade up on male quality (Gabor and Halliday 1997; Rosenqvist and Houde 1997; Pitcher et al. 2003). The consequent increase in choosiness is expected to impose stronger sexual selection on male ornamentation.

Female guppies choose mates on the basis of complex and highly variable color patterns comprising orange, iridescent, and black spots as well as on the basis of morphological traits such as tail fin size (Endler and Houde 1995; Houde 1997). These preferences impose complex multivariate sexual selection on the male traits concerned (Houde 1987; Blows et al. 2003). Previous work on guppies has revealed that experience can shape both male and female mating preferences. For example, female preferences for color patterns depend on pattern frequency, where rare patterns are generally preferred (Farr 1977; Hughes et al. 1999; Eakley and Houde 2004). Female mating decisions are also influenced by former mating experience (Rosenqvist and Houde 1997; Eakley and Houde 2004) and familiarity with coloration patterns (Hughes et al. 1999). Males, on the other hand, exhibit mating preferences for relatively large (Herdman et al. 2004) and unfamiliar females (Kelley et al. 1999).

Here we examine the effects of familiarity and previous mating experience on female sexual responsiveness and mating decisions as well as on male display behavior and sperm allocation. We also test whether familiarity influences the strength of sexual selection acting on male secondary sexual traits, expecting stronger selection when potential mates are familiar to the female. In behavioral trials, we investigated whether unfamiliar pairs mated more quickly than familiar pairs due to higher female responsiveness toward unfamiliar

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males (Hughes et al. 1999) and elevated display behavior in males (Kelley et al. 1999).

## METHODS

The guppies used in this experiment were aged between 10 and 14 months and were laboratory raised stock animals descended from wild-caught fish collected from Alligator Creek in Bowling Green National Park, 30 km south of Townsville, Queensland, in April 2002. We used virgin females that had been raised in tanks of 10–15 individuals until they were approximately 40 days old, sexed on the basis of the presence or absence of female egg spots, and separated into virgin cultures. The male cultures contained several females to ensure experience in courting behavior. All fish were fed fresh 1-day old brine shrimp (*Artemia* nauplius larvae) once a day throughout the experiment. Throughout the experiment, illumination was provided by 3 60-W daylight bulbs on a 12:12 h light:dark cycle.

### Experimental treatments

Three experiments were conducted to test the effects of 1) mating history, 2) a combination of chemical and visual familiarization, and 3) visual familiarity only on mate choice. Familiarization took place in 9-l glass tanks ( $28.5 \times 17 \times 19$  cm) divided into 2 equal compartments along the long axis by either a glass (Experiments 1 and 3) or glass and mesh (Experiment 2) divider. These tanks were wrapped with brown paper on 3 sides to exclude visual contact between animals in adjacent tanks.

#### Mating history

In each trial, a virgin female was housed in one side of a familiarization tank with a randomly assigned male. Each such pair was able to mate and was kept together in the same compartment for 21 days. After this period, the male was transferred to the second compartment, which allowed continued visual contact between the 2 fish but avoided possible uncontrolled matings after the female gave birth to her first brood ( $>22$  days after she first encountered the male). After the male was moved, the female was allowed a maximum of 4 weeks to give birth. If any of the 2 fish died or no brood was produced within this period, the pair was excluded ( $N = 13$ ). Each pair of familiarized male and female was allocated at random either to the familiar or unfamiliar treatment (25 “familiar” and “unfamiliar” trials were conducted, respectively). In the familiar treatment, behavioral trials (see below) were conducted on the paired female and male. In the unfamiliar treatment, the female was paired to a male from a different familiarization pair, and the male was assigned to another unfamiliar treatment. Therefore, unfamiliar males shared similar mating or familiarization histories, and any treatment effect must be due to the specific pairing of familiar or unfamiliar individuals.

#### Chemical and visual familiarization

In this experiment, the animals were not allowed to come into physical contact during familiarization. Males and females were assigned as above, but kept in separate enclosures, which were separated by a glass and mesh (bottom 4 cm) partition. This allowed the focal male and female in each replicate to become familiar with one another via both the visual and olfactory channels.  $N = 15$  per treatment.

#### Visual familiarization only

This experiment was identical to the one above, except that we allowed only visual communication between males and females by using sealed glass partitions between adjacent com-

partments. In this experiment, we conducted 15 trials in the familiar and unfamiliar treatment, respectively.

### Behavioral trials

The 150-l observation tanks were held at 26 °C (Via Aqua stainless 100W steel heaters with external temperature controller). The female was transferred into the mating arena on the evening of the day she gave birth to her first brood (Experiment 1) or on the evening of day 21 of the familiarization period (Experiments 2 and 3). Males and females were allowed to settle and acclimate in the observation tank the night before the trial but were separated by glass and visual shields until the beginning of the observations.

Behavior trials took place between 7 and 10 AM and were started 10 min after the lights came on. Time until mating and courtship details were recorded, and female responses to male courtship scored according to the protocol developed by Houde (1987, 1997). During courtship, males court females by displaying their ornamentation in a “sigmoid” posture while quivering. There is a stereotyped and well-characterized sequence of behaviors between display and any ensuing mating: the female glides toward the male and the 2 fish wheel in circles while the male attempts to insert his gonopodium (a modified anal fin that serves as an intromittent organ) into the female’s genital pore (Baerends et al. 1955; Houde 1997). Females can, however, break off the interaction at any time between the initial display and mating. In cases where the female did not respond at all to a male’s courtship display, the display was scored as “unsuccessful.” When females responded by at least gliding toward the male, the male’s display was recorded as “successful.” The proportion of successful displays to total displays defines the measure of male attractiveness (Houde 1997). Mating success was scored according to successful sperm transfer, which is evident by a series of male postcopulatory jerks (Liley 1966; Houde 1997).

### Measuring male sperm allocation

Twenty minutes after a successful mating, each female’s gonopore was flushed with saline solution to retrieve the male’s ejaculate and estimate the total number of sperm inseminated during the mating trial. To retrieve inseminated sperm, the female was anesthetized and placed ventral side up in a polystyrene “cradle” to expose her genital pore, which was flushed with 3 aliquots of 10  $\mu$ l of saline solution (0.9% NaCl) to retrieve all available sperm (Pilastro and Bisazza 1999). It has been previously shown that sperm transferred during a mating can be detected for up to 7 days (Matthews and Magurran 2000) but is most numerous for a few hours after the mating. Sperm from the previous mating is thus unlikely to have influenced our measures. To estimate the total number of sperm inseminated in each trial, we combined the 3 aliquots from each female and counted the sperm cells using an improved Neubauer hemocytometer. We also manually stripped each male after the mating trials to obtain all available sperm, using the methods described by Mathews et al. (1997). Sperm allocation was then estimated for number of sperm inseminated during the trial as a proportion of total sperm reserves.

### Measuring male color patterns

The males were anesthetized and photographed with color and size references for coloration analyses (Digital camera, Nikon Coolpix 990). Body area, tail area and surface area of carotenoid spots, sharp-edged black spots and lines, and fuzzy black and iridescent coloration were measured on the right body side of each fish. To control for effects of body size, we used relative area of coloration in all of our analyses.

The color tracing was accomplished with Measure Master version 3.44 (+), 1999 Leading Edge Pty Ltd, Adelaide, Australia.

### Statistical analyses

Statistical analyses were conducted using SPSS version 13.0 (SPSS Inc., USA). The data were checked for normality using normality plots, Kolmogorov–Smirnov and Shapiro–Wilk tests. All data except for the measures of sperm allocation were normally distributed and therefore used untransformed.

We used a 3-dimensional log-likelihood *G*-test of independence (Sokal and Rohlf 1995, p 689–708) to test whether the probability of a female mating with a male was independent of his familiarity to her or the type of familiarization treatment (i.e., experiment).

To test for differences in attractiveness between familiar and unfamiliar treatments and between experiments and for effects of mating success on attractiveness, we conducted univariate analysis of variance (ANOVA). We also used univariate ANOVA to test for differences in courtship behavior and sperm allocation between treatments and for differences between experiments. As none of the interaction effects in the analyses mentioned above were significant, they were removed from the final models and are not reported here.

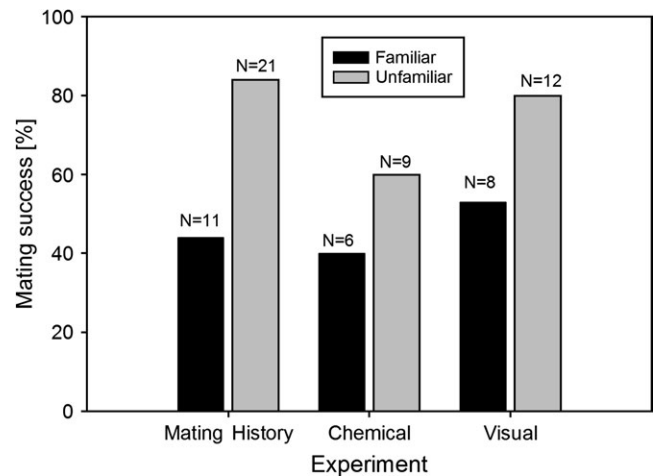
Univariate selection analyses of mating success on coloration were conducted using 6 linear and quadratic morphological and ornamental traits (body size, tail size, black, fuzzy black, orange, iridescent coloration). To allow comparison of selection among traits, we standardized these predictor variables to units of standard deviation (Lande and Arnold 1983). We used a sequential model building approach to estimate linear, quadratic, and correlational selection and to test for differences between familiar and unfamiliar treatments in these forms of selection (Chenoweth and Blows 2005). This approach uses partial *F*-tests to test whether each addition to the model significantly improves the overall fit (Bowerman and O'Connell 1994) and is outlined in more detail in Appendix A in Chenoweth and Blows (2005).

We first fitted a reduced model (1) that contained only the treatment, as fixed effect. We then compared this with a model including the linear terms (model 2) to test for significant linear selection. To test for differences in linear selection, we compared model 2 with a model (3), including the interactions between the linear terms and the treatment. Because there were no significant differences in linear selection, we tested for quadratic selection by comparing a model incorporating the quadratic terms (model 4) with model 2. To test for differences in quadratic selection, we compared model 4 with a model adding the quadratic term by treatment interactions (model 5). Because there were no significant differences in quadratic selection, we tested for correlational selection by comparing a model incorporating these terms (model 6) with model 4. To test for differences in correlational selection, we compared model 6 with a model adding the correlational gradient by treatment interactions (model 7).

## RESULTS

### Unfamiliar males are more likely to mate

The *G*-test of independence showed that whether a female mated with a male was not independent of familiarity and experiment ( $G_7 = 14.81$ ,  $P = 0.038$ ). Partitioning of this overall analysis showed that it was due to a significantly greater probability of a female mating with an unfamiliar male than with a familiar one ( $G_1 = 11.27$ ,  $P = 0.001$ , Figure 1). The type of familiarization treatment (i.e., experiment) had no effect on this probability ( $G_2 = 2.09$ ,  $P = 0.350$ ). On average, 75% of



**Figure 1**  
Influence of familiarity on the probability of mating in the 3 experiments.

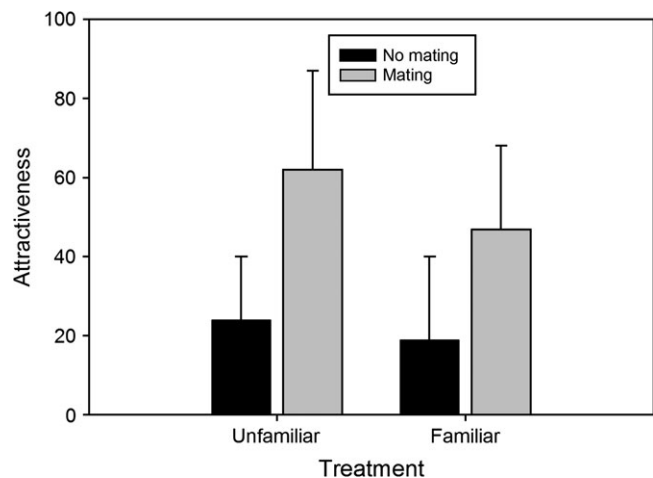
all trials with unfamiliar fish led to successful matings, whereas matings occurred in only 46% of the familiar trials (Figure 1). Despite the highly increased likelihood of successful mating in the unfamiliar treatment, pairs that did mate did not do so more rapidly when unfamiliar than when they were familiar to each other (Cox regression:  $\chi^2_3 = 4.52$ ,  $P = 0.210$ ).

### Unfamiliar males are more attractive to females

The proportion of positive responses (attractiveness) by females to male sigmoid courtship displays was significantly higher when the male was unfamiliar than when the male was familiar to female (ANOVA:  $F_{1,106} = 18.10$ ,  $P < 0.0001$ , Figure 2). This effect was not statistically different among experiments ( $F_{2,106} = 1.51$ ,  $P = 0.225$ ). We also found a strong effect of mating success on attractiveness ( $F_{1,107} = 51.68$ ,  $P < 0.0001$ , Figure 2).

### Sexual selection on male ornamentation

Female choice imposed marginally nonsignificant linear selection (model 2 vs. model 1, partial  $F_{6,102} = 2.01$ ,  $P = 0.070$ )



**Figure 2**  
Attractiveness (proportion of positive displays) in relation to mating success. Mated males within each treatment were more attractive than unmated males ( $F_{1,107} = 51.68$ ,  $P < 0.0001$ ).

Table 1

Selection analyses on the effect of mating success on a subset of male ornamental traits

	Unstandardized coefficients			
	$\beta$	Standard error	$t$	$P$
Linear terms				
Body size	<b>0.209</b>	0.063	3.297	0.001
Tail	0.064	0.054	1.185	0.240
Black	-0.106	0.061	-1.753	0.083
Fuzzy black	-0.047	0.095	-0.491	0.625
Orange	<b>0.143</b>	0.061	2.348	0.021
Iridescent	-0.015	0.067	-0.216	0.830
Quadratic terms				
Body size	-0.017	0.028	-0.601	0.550
Tail	-0.087	0.044	-1.978	0.051
Black	<b>0.131</b>	0.047	2.805	0.006
Fuzzy black	-0.004	0.038	-0.097	0.923
Orange	-0.067	0.052	-1.290	0.201
Iridescent	-0.018	0.036	-0.500	0.618

Significant selection gradients ( $\beta$ ) are given in bold.

irrespective of the treatment (model 3 vs. model 2, partial  $F_{6,96} = 0.35$ ,  $P = 0.908$ ). The strongest selection was for larger areas of orange and for larger bodied males (Table 1). Selection analysis also revealed significant quadratic selection (model 4 vs. model 2, partial  $F_{6,96} = 2.51$ ,  $P = 0.026$ ), due in large part to significant negative quadratic selection on the area of black (Table 1). There were no differences among treatments in quadratic selection (model 5 vs. model 4, partial  $F_{6,90} = 0.34$ ,  $P = 0.913$ ). There was no significant correlational selection (model 6 vs. model 4, partial  $F_{15,81} = 0.72$ ,  $P = 0.759$ ) and no differences among treatments in correlational selection (model 7 vs. model 6, partial  $F_{15,66} = 0.43$ ,  $P = 0.965$ ).

### Male courtship and sperm transfer

Male courtship behavior did not differ between trials in which the female was familiar or unfamiliar to male (ANOVA:  $F_{1,106} = 0.211$ ,  $P = 0.647$ ). Display rates differed significantly among the 3 experiments ( $F_{2,106} = 17.07$ ,  $P < 0.0001$ ); they were higher in the mating history experiments than in the other 2 experiments (Figure 3; Tukey's post hoc comparisons: Experiment 1 vs. Experiments 2 and 3,  $P < 0.0001$ , Experiment 2 vs. Experiment 3,  $P = 0.979$ ). Nevertheless, males transferred similar amounts of sperm to familiar and unfamiliar females (ANOVA:  $F_{1,52} = 0.169$ ,  $P = 0.683$ ), and the amount transferred did not differ between experiments ( $F_{2,52} = 2.28$ ,  $P = 0.113$ ).

### DISCUSSION

Familiarity strongly influences female mate choice in guppies. Females were more likely to mate with unfamiliar males and responded more positively to courtship performed by unfamiliar males. Moreover, this was simply a product of visual familiarity rather than previously having mated the familiar male. Males, however, did not alter their courtship or sperm allocation decisions under different familiarity scenarios. Contrary to our initial predictions, multivariate selection analysis revealed that the strong female preferences for unfamiliar males did not alter the strength or direction of sexual selection that female choice imposed on male ornamentation.

Previous work on guppies has shown that males bearing locally common color patterns are discriminated against (Farr

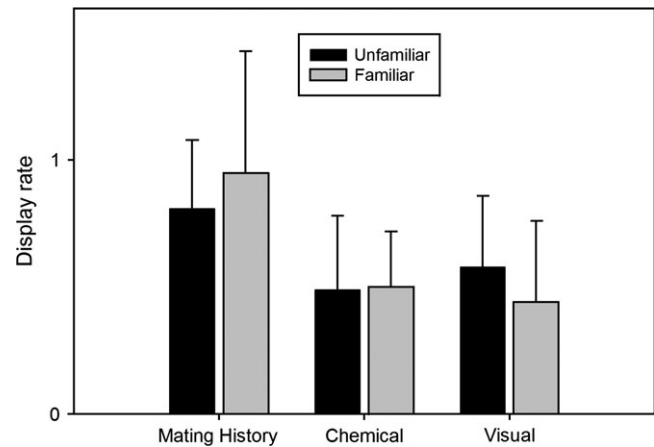


Figure 3

Differences in display rates in the 3 experiments. The treatment did not affect male courtship behavior, but males courted significantly more in the mating history experiment (ANOVA:  $F_{2,106} = 17.07$ ,  $P = 0.000$ ).

1977, 1980; Hughes et al. 1999) as are previous mates and males with similar color patterns to previous mates (Eakley and Houde 2004). The visual preference for unfamiliar males, whether they are previous mates or not, in our study may be at least partly responsible for these previously documented preferences for rare or novel male color patterns. Like these previously documented preferences, our results support a role for mate choice in generating negative frequency-dependent selection on male color patterns and thus, potentially, maintaining the extreme polymorphism in guppy color patterns. The adaptive reasons for why females prefer to mate with unfamiliar males remain less clear. Here we consider 2 nonexclusive possible benefits of such a preference: inbreeding avoidance and the benefits of polyandry.

Females that prefer to mate with unfamiliar individuals might benefit if this strategy reduces their chances of inbreeding. For example, if population structure is such that females are more likely to share a pool within a stream with related males, then preferring to mate with unfamiliar males may provide an effective mechanism favoring males that have recently migrated into the pool (such migration rates are reportedly low; Reznick et al. 1996), and these males are less likely to be close relatives of the female. In several species, recognition and avoidance of familiar individuals by either phenotype matching or imprinting (Pusey and Wolf 1996) helps to minimize the chance of offspring suffering from inbreeding depression. Experiments on naked mole rats (Clarke and Faulkes 1999), mandarin voles (Tai et al. 2000), and mountain voles (Berger et al. 1997) have also revealed strong female preferences for unfamiliar males, regardless of actual genetic relatedness.

An alternative adaptive reason to avoid unfamiliar males is the avoidance of previous mates because previous mates are likely to be familiar. Even if female guppies remember males that they have previously accepted as mates, sneak copulation is an important source of paternity (Houde 1997; Magurran 2005), and females may never know the identity of sneak mates. Thus, a female can be sure of mating with a new male by choosing an unfamiliar one. The benefits of polyandry are subject to intense, ongoing debate (Jennions and Petrie 2000). Higher offspring fitness in progeny from polyandrous versus single matings may arise via the inheritance of "good genes," avoidance of genetic incompatibility, and offspring heterozygosity. Polyandry and postcopulatory mate choice may therefore enable females to increase genetic diversity

among offspring and also decrease the likelihood of mating with genetically undesirable males, such as close relatives. Preference for unfamiliar mates has previously been shown in sequential mate choice experiments in the pseudoscorpion (*Cordyloderes scorpioides*, Zeh et al. 1998) and eastern mosquitofish (*Gambusia holbrooki*, McLaughlin and Bruce 2001).

We found that female mating preferences for unfamiliar males was due to familiarity rather than having mated with the male per se. If females had rejected previous mates and not discriminated against familiar males when no prior mating had occurred, this would have favored the idea that females are maximizing genetic benefits of polyandry other than inbreeding avoidance. Our finding that discrimination against familiar males was not exclusive to experiments with previous matings, however, leaves open the possibility that preferences for unfamiliar males might be favored because they facilitate inbreeding avoidance.

Male guppies did not discriminate between familiar and unfamiliar females in their courtship and sperm allocation "decisions." Although elevated courtship behavior toward unfamiliar females has previously been reported in a number of species (*Streptopelia risoria*, Erickson and Morris 1972; *Anolis sagrei*, Tokarz 1992; *P. reticulata*, Kelley et al. 1999), few studies have investigated whether males allocate sperm differentially toward familiar and unfamiliar females, which is likely to be due to the difficulties in retrieving ejaculates after insemination. Similar to our study, recent work on pseudoscorpions (Newcomer et al. 1999) has compared the number of sperm allocated toward previous and new mating partners and reported no effect of familiarity. Although males are expected to benefit by avoiding previous mating partners in favor of new ones (Wedell et al. 2002), such benefits will not apply if males perceive that only one female is available. Additionally, the males in our study had periods of several days to weeks without mating opportunity in all 3 experiments, which is likely to have influenced their willingness to mate. In a more natural setting where males are able to choose and discriminate among unfamiliar and familiar females, preferences for unfamiliar or new females might be measurable in both courtship behavior (as reported by Kelley et al. 1999) as well as sperm allocation.

Our analysis revealed significantly more courtship toward females with previous mating experience than toward virgin females. This may be due to high female sexual receptivity in this experiment because females that had previously mated had given birth the day before the trials. It has been shown before that female guppies are most responsive shortly after parturition (Houde 1997), and it is likely that males are able to chemically detect their mates' reproductive status (Crow and Liley 1979).

Until now there have been few studies examining the interacting effects of preferences for ornamentation and social factors, such as familiarity, on the sexual selection that results from mate choice. Patricelli et al. (2003) studied male mating success in satin bowerbirds (*Ptilonorhynchus violaceus*) and found that male attractiveness was more important than familiarity, but unfortunately, they reported no formal analysis of the interacting effects of familiarity and male attractiveness. In guppies, strong female preferences for colorful males have been shown in many studies (reviewed by Houde 1997). Our selection analysis revealed that females preferred large areas of orange coloration and large body size and smaller areas of black, consistent with previous studies on this population (Brooks and Endler 2001). As we found strong preference for unfamiliar males, we expected to find differences in the strength of sexual selection that females imposed on unfamiliar and familiar males. Preferred familiar males were expected to be bigger and have larger orange areas and less

black pigmentation than preferred unfamiliar males. Our analysis revealed no interaction between familiarity and the multivariate patterns of linear and quadratic selection. Contrary to our predictions, sexual selection was not altered by preferences for unfamiliar males. Although there is emerging evidence that mate choice decisions may depend strongly on the context (Bateson and Healy 2005), recently developed statistical approaches (Chenoweth and Blows 2005), such as the one we have adopted here, may provide a way forward to assessing the effects of a variety of ecological factors on the strength and pattern of sexual selection.

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