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## Copying and the repeatability of mate choice

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**Abstract** Models of sexual selection by female choice require heritable variation in female mating preferences in order for sexual selection to operate. However, recent theoretical work shows that female preferences which are transmitted non-genetically can result in exaggeration of male ornamentation. Guppies exhibit both mate copying and considerable heritable variation in female preferences. I studied the importance of these phenomena by measuring repeatability of female mate choice, which acts as an estimate of the upper limit to which a feature may be heritable, and the incidence of mate choice reversal in paired-trial binary mate choice experiments. Mate choice was significantly repeatable except in the treatment where females were given the opportunity to copy a female that contradicted their original choice. Apart from this, I found no evidence that females copy the mate choice of others. The differences between males in ornamentation had no effect on the consistency of female mate choice or the probability that they would reverse their original choice decision (in both controls and the copying experiment). The interval between choice trials did not influence repeatability significantly, indicating that the independence of choice decisions is not related to the time interval between them.

**Key words** Mate choice · Mate copying · Ornaments · Repeatability · Guppy

### Introduction

Despite the popularity of sexual selection, and particularly female mate choice, as a field of study (see

Andersson 1994 for a thorough overview), the inheritance and ontogeny of female mating preferences are still poorly understood. Models of female choice have traditionally treated female preferences as characters that are entirely determined by genes (Lande 1981; Grafen 1990a, b). Whilst this served to simplify some difficult questions regarding how male displays and female preferences for those displays might evolve, we still lack insight as to how female preferences are inherited and how they are shaped during growth. Recently, the forces influencing female mating behaviour and preferences have begun to receive more attention (see Rosenqvist and Berglund 1992). In particular, the genetic basis for female preferences (Majerus et al. 1982, 1986; Bakker 1993; Houde 1994; Wilkinson and Riello 1994) and the effects of female experience in sampling males (Janetos 1980; Brown 1981; Bakker and Milinski 1991), imprinting on early experiences (ten Cate and Bateson 1988, 1989), and using information about the choices made by other females when choosing mates (Losey et al. 1986; Wade and Pruett-Jones 1990; Gibson and Höglund 1992; Kirkpatrick and Dugatkin 1994; Laland 1994) have enjoyed increased theoretical and empirical attention.

In this paper I address two processes fundamental to the way preferences evolve in populations and develop within individual females: (i) the repeatability of choice behaviour, which is an indicator of the heritability of mating preferences, and (ii) the importance of mate copying, by which mating preferences can be transmitted culturally rather than genetically. This paper therefore represents a first attempt at trying to understand the relative contributions of genetic and cultural determinants to female choice behaviour in a single species (*Poecilia reticulata*).

Despite the importance of additive genetic variation in female mating preferences to most models of sexual selection (Lande 1981; Grafen 1990a, b; Pomiankowski et al. 1991; Iwasa et al. 1991) only a handful of experiments have shown evidence for this (Majerus et al. 1982,

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1986; Moore 1989, 1990; Bakker 1993; Houde 1994; Wilkinson and Riello 1994). The repeatability of a behavioural trait such as a mating preference describes the contribution of within-individual variability in the trait (which obviously cannot be heritable) to the total variability within the population (Boake 1989). Therefore repeatability estimates an upper limit of the extent to which a trait can be heritable (Falconer 1989; Boake 1989). In fact, repeatability is thought to overestimate heritability (Boake 1989). This may be because not all between-individual variability is the result of heritable differences between females, because social and developmental differences between females are not factored out. Also, within-individual variability may be underestimated if trials conducted on the same female within the time constraints of a normal experiment are nonindependent. This may occur if a female's preference expression is influenced by factors such as her condition and recent experience (Bakker and Milinski 1991; Brooks and Caithness 1995c). In this paper I test the influence of the interval between mate choice trials on the measurable repeatability of female preference by varying the time interval between choice trials in different treatments. I also examine the effects of one social phenomenon, the opportunity to copy the mate choice of others, on repeatability.

Mate copying is a form of nonindependent choice which occurs if the probability of a female choosing a particular male increases if he has already been chosen by other females and decreases if he has not (Pruett-Jones 1992). Apparent copying behaviour has been documented in several taxa (see Gibson and Höglund 1992 for a review), but only in guppies have alternative explanations such as a female grouping behaviour been effectively controlled out (Dugatkin 1992). Female guppies will even reverse their original choice of males in binary mate-choice trials to copy the choice of another female (Dugatkin and Godin 1992, 1993).

The possibility that there is a cultural component to the transmission of mating preferences has important evolutionary consequences. Copying is likely to result in an increased variance in male mating success (Wade and Pruett-Jones 1990), and therefore increased opportunity for sexual selection (Wade 1979). Furthermore, the spread of a preference is likely to be faster than under strictly vertical (genetic) inheritance because preferences can also be transmitted diagonally or horizontally (Kirkpatrick and Dugatkin 1994; Laland 1994). This may result in more rapid exaggeration or fixation of the male ornament on which the preference is based than is the case with preferences that are only inherited genetically (Laland 1994), and even the loss of all but the (initially) most common male traits and female preferences (Kirkpatrick and Dugatkin 1994; but see Findlay et al. 1989).

The effects of ornamentation on repeatability of choice and the operation of mate copying have not been examined previously. A functional explanation for

copying is that it reduces costs associated with the time taken to assess males and that some females are poorer at discriminating between males than others (Dugatkin and Godin 1993; but see Gibson et al. 1991), and that it is these females who have most to gain from copying. In a mixed copying/independent choice strategy, there may be a tradeoff for females between following their own choice decision and copying others when the two are contradictory. I therefore asked whether copying is stronger or weaker than independent choice, and whether the similarity of the ornamentation of males (in a binary choice trial) contributes to a female's decision to copy or stick with her original choice. When males are most similar, choice is expected to be at its least repeatable and copying is expected to be common.

Guppies are well suited to attempts to resolve the repeatability of female mating behaviour, and the effects of copying on the outcome of choice decisions, for several reasons. They are something of a model organism in studies of sexual selection due to their highly promiscuous, non-resource-based mating system and the importance of female choice to paternity. Female choice is responsible for the evolution and maintenance of several of the ornaments borne by male guppies including orange (carotenoid) pigment (Houde 1987; Kodric-Brown 1985, 1989; Brooks and Caithness 1995a), black (melanin) pigment (Endler and Houde 1995; Brooks and Caithness 1995b; Brooks 1996) iridescent (structural) pigments (Kodric-Brown 1985; Endler and Houde 1995) exaggerated fins (Bischoff et al. 1985) and enlarged body size (Reynolds and Gross 1992; Endler and Houde 1995). There is evidence from selection experiments that there is additive genetic variation in (at least) the female preference for orange spots on males (Houde 1994; but see Breden and Hornaday 1994). Studies on guppies have produced the best evidence yet for the joint evolution of female preferences and male ornaments within populations (Breden and Stoner 1987; Houde 1988; Stoner and Breden 1988; Houde and Endler 1990; Endler and Houde 1995).

To date, the best experimental evidence for female mate copying has been obtained using guppies (Dugatkin 1992; Dugatkin and Godin 1992, 1993). However, Kirkpatrick and Dugatkin (1994) argued that widespread copying is unlikely to favour the origin or maintenance of multiple sexual ornaments, but will rather favour the most common male ornament at the expense of others. The multiple ornaments borne by male guppies contradict this prediction, such that Kirkpatrick and Dugatkin were forced to invoke some unidentified form of selection as the agent favouring multiple ornaments in opposition to the effects of mate copying.

Virgin female guppies from the population I used in this study are able to exercise their mating preference for more orange males (Brooks and Caithness 1995c). This precludes the possibility that female mating

preferences are transmitted entirely by culture as in the models by Laland (1994) and Kirkpatrick and Dugatkin (1994). However, I have also shown that a female's previous experience of males is important to her choice decisions (Brooks and Caithness 1995c) in that a female adjusts her response to a male based on her experience of the level of ornamentation in the population.

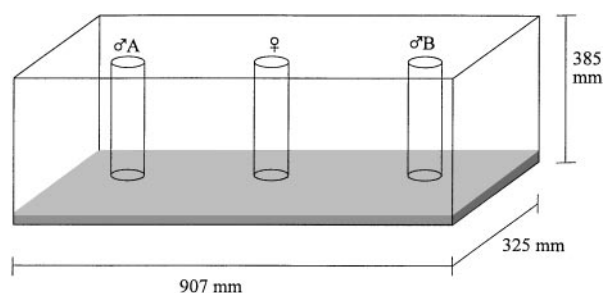
I have therefore attempted, in this paper, to understand the extent to which female mating preferences could be heritable by quantifying the repeatability of a female's choice between two males. I have further examined some aspects of copying behaviour in order to understand if female preferences could be, at least partially, culturally transmitted. Lastly, I have looked at how male ornamentation is related to the repeatability of choice and the likelihood of mate copying.

## Methods

The guppies used in this study were collected from a feral population in Durban, South Africa (see Brooks and Caithness 1995a for more on the population history). Males and females were separated into single-sex cultures as soon as individuals could be sexed (when the female gravid spot or the male gonopodium became visible). Therefore, both males and females were sexually inexperienced.

### Choice trials

This study comprised four treatments. In each treatment two choice trials were conducted, using one female and two males. Choice trials were conducted in a 100-l aquarium as shown in Fig. 1. I placed a (randomly chosen) male in each of two "end" glass tubes (all tubes diameter = 90 mm) and a (randomly chosen) female (the "focal" female, after Dugatkin 1992) in the central glass tube. After 10 min, I slowly lifted the central tube by hand in a direct vertical line (to prevent experimenter bias) until the female swam clear, and then placed the tube gently down in the tank again. In 38 trials, I noted the direction the female initially swam in, in order to compare this with the eventual outcome of the trial. The female did not



**Fig. 1** The aquarium used in choice trials. Background and bottom colour were standardised by placing 2 cm of fine light brown river sand on the *bottom* of the tank and tan paper on three sides (the *long side* facing the observer was left clear). Three open-ended *glass tubes* 90 mm in diameter and 350 mm in length were placed in the longitudinal midline of the tank. The *tube* (♀) which contained the focal female was in the centre of the tank, with *tubes* bearing males (♂A and ♂B) 290 mm away (centre to centre)

swim to the side bearing the eventual winner of the trial significantly more often than to the other side ( $G = 0.747$  d.f. = 1, n.s.). The female was watched for 10 min, and the time spent within two body lengths (horizontally) of each male's tube and within 3 cm (vertically) of the male in that tube was recorded. Vertical distances were estimated from graduations every 3 cm (vertically) on the tubes. Three sets of such graduations were etched at 120° intervals around the tubes. Similar measures of female choice behaviour have been used before, and shown to accurately predict success in mating encounters (Kodric-Brown 1985).

For each treatment, I swapped the side of the tank that males were in between trials in half of the replicates, and left males in the same tubes in the other half. There was no significant side preference either generally or within males. The time between choice trials varied between treatments. In treatment 1 ("2-day") 48 h elapsed between choice trials. In treatment 2 ("copying") the second choice trial from the 2-day treatment made up the first part of the treatment, and the second trial followed 30 min later. The difference between this and the other treatments was that during the first 8 min of the 10-min "viewing time" (when the focal female was confined to her tube) a second, "model" female was placed in a (similar) glass tube adjacent to the male that had "lost" the first trial. I removed the model female and her tube after 8 min and 2 min later released the focal female to swim freely for 10 min during which I documented the time she spent near each male. The model female was larger than any of the focal females used in the experiment (model = 36.66 mm, focal = 20.48–32.54 mm total body length), as a female is more likely to copy a larger (and thus older) female than one smaller than herself (Dugatkin and Godin 1993).

I used the same male pairs in treatment 3 ("30-minutes"), in which 30 min elapsed between choice trials, between 10 and 30 days after treatments 1 and 2. Whilst in treatments 1 and 2 I used the same female with a given male pair, I used a different focal female in the 30-min treatment for a given pair of males than in the first two. I then used yet another different female in treatment 4 ("1-day"), in which 24 h passed between the first and second choice trial. For the first two treatments 40 replicates were performed, but unfortunately, during the period between the first two and the last two treatments, many of the males contracted fin-rot or died. If a male had visible fin-rot, I did not use him in a trial in case females avoided him to prevent contracting the infection themselves, thereby influencing the outcome of the trials. Therefore of the original 40 pairs of males used in the first two treatments, only 24 remained intact; 12 healthy fish from the 16 "broken" pairs were arbitrarily paired up to make up the sample for these two trials to 30 pairs.

The design of this experiment is therefore similar, except for superficial differences in choice tank design, to other experiments investigating female choice (Bischoff et al. 1985; Kodric-Brown 1985) and in particular repeatability of female choice (Godin and Dugatkin 1995) and female copying (Dugatkin 1992; Dugatkin and Godin 1992, 1993) in guppies.

### Measuring male ornamentation

I measured ornamentation by taking slide photographs of male fishes under tungsten lighting and then tracing the projected slides onto white A3 paper, including part of a section of plastic ruler which I included in the photographs for calibration. This enabled me to measure the area of each fish's body and of each colour patch using a grid of squares. The orangeness of each male was estimated visually using Munsell colour chips. The hue, value and chroma of the colour chip that most closely resembled each colour patch was noted. In analysis, all three colour dimensions were used, and in addition an "orangeness" variable was constructed by scoring hue from 1 (2.5 Y) to 6 (10 R) and multiplying this by chroma. This did not provide substantially different results from those obtained for the separate colour dimensions, and is therefore the only colour measure presented.

## Statistical analysis

I analysed data using Statistica for Windows (v. 4.5, Statistica Inc., 1993) statistical software. I tested all variables for normality using Lilliefors' test, and used angular transformation (Sokal and Rohlf 1981) before using proportional data in parametric tests. Where normality or other assumptions of parametric tests were not satisfied, I used non-parametric tests.

I estimated repeatability after Falconer (1989), Lessels and Boag (1987) and Boake (1989), using a one-way analysis of variance (ANOVA) to partition the total variance in female choice of one (randomly chosen) male in a pair over the other into the added variance due to differences between females ( $S_A^2$ ) and the variance within individuals ( $S^2$  or error variance). The ratio of between-individual variance ( $S_A^2$ ) to total phenotypic variance ( $S^2 + S_A^2$ ) is equivalent to  $r$ , the coefficient of intra-class correlation, which is a measure of repeatability. I used the method of Becker (1984) to calculate the standard error of the repeatability measure. I compared the repeatabilities of different pairs of treatments using the method of Zar (1984) for comparing correlation coefficients.

I used the  $G$ -test (Sokal and Rohlf 1981) to compare the ratio of females reversing to those remaining consistent in their "decision" between trials with different models of choice. I compared all treatments with a model of no choice (half the females switch their preference and half are consistent). I also compared the ratios obtained in the copying treatment with the ratios observed in the 2-day treatment (in which the same female was used with each pair of males) and in the 30-min treatment (in which the same time elapsed between choice trials).

To compare the increase in proportion of time a female spent with the loser of the first trial in the first and second trials of a treatment, I used paired-sample Student's  $t$ -tests.

I used a Mann-Whitney  $U$ -test to compare the magnitudes of the difference in various secondary sex characters between the two males for replicates in which the female reversed her choice versus those in which she chose the same male in both trials. Lastly, I estimated the correlation between the above differences and the absolute change in the measure of female preference in a replicate using Spearman's rank-order correlation coefficient.

Where tables of results are presented, I have used the sequential Bonferroni readjustment (Rice 1989) to correct the 0.05  $\alpha$ -level of acceptance for the number of tests performed.

## Results

The repeatability with which a female chooses one male over the other is significantly greater than zero in all treatments except the copying treatment (Table 1). None of the repeatability estimates differed significantly from any of the others, the largest difference being between the 2-day and copying treatments ( $Z = 1.34$ ,  $\sigma = 0.232$ , 1-tailed  $P = 0.090$ ).

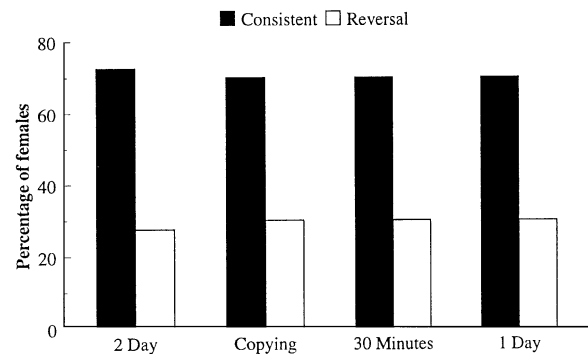
**Table 1** Results of one-way ANOVAs of the proportion of time a female spends with one (randomly picked) male in a binary choice trial, and the repeatability estimate and standard error thereof for each of the four treatments

Treatment	Source of variation	SS	df	ANOVA			Repeatability	
				MS	$F$	$P$	$r$	SE
2-Day	Between females	6.499	39	0.169	2.088	0.011	0.352	0.052
	Within females	3.191	40	0.080				
Copying	Between females	4.321	39	0.111	1.114	0.367	0.056	0.012
	Within females	3.977	40	0.099				
30-Min	Between females	5.199	29	0.179	2.057	0.027	0.346	0.059
	Within females	2.614	30	0.087				
1-Day	Between females	3.899	29	0.134	1.924	0.040	0.315	0.050
	Within females	2.096	30	0.070				

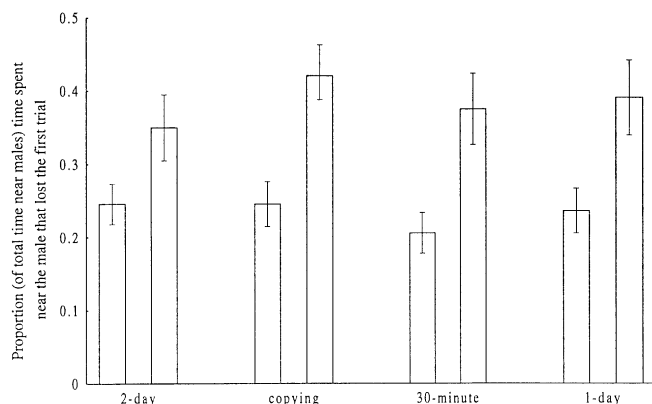
In all four treatments, females chose the same male significantly more often than expected under a random model of choice (Fig. 2). Furthermore, in the copying treatment, the relative frequencies of consistency and reversal did not differ significantly from those observed in the 2-day treatment or the 30-min treatment, as predicted if females reverse their choice due to copying. Whilst females did not copy the "model" female, they did not avoid copying her either.

Although females did not reverse their preference in the copying treatment, the proportion of the total time near males that they spent with the male that had been near the model female (as opposed to their originally preferred male) increased (Fig. 3). However, significant increases in time spent with the loser of the first choice trial also occurred from the first to the second trial in all three of the other treatments (Fig. 3). The increase from part one to part two was not significantly greater in the copying treatment than in the 2-day treatment (paired-sample  $t = 0.076$ ,  $df = 39$ , n.s.).

Males in trials where females reversed their choice decisions were neither more nor less similar to one



**Fig. 2** The percentage of focal females choosing the same male (consistent) and reversing their choice (reversal) between the first and second trial in each experiment. In all four treatments, significantly more females consistently prefer the same male than change their choice of male. This consistency is significantly different from a random model of choice for all experiments (2-day  $G_{adj} = 8.295$ ,  $df = 1$ ,  $P < 0.01$ ; copying  $G_{adj} = 6.501$ ,  $df = 1$ ,  $P < 0.02$ ; 30-min  $G_{adj} = 4.857$ ,  $df = 1$ ,  $P < 0.05$ ; 1-day  $G_{adj} = 4.857$ ,  $df = 1$ ,  $P < 0.05$ ). The number of females reversing their choice in the copying treatment did not differ significantly from the pattern shown in the 2-day treatment ( $G_{adj} = 0.625$ ,  $df = 1$ , n.s.) or the 30-min treatment ( $G_{adj} = 0.063$ ,  $df = 1$ , n.s.)



**Fig. 3** The proportion (of the total time a female spent near both males) time that a female spent with the loser of the first trial of each treatment in the first (*left bar*) and second (*right bar*) trials of that treatment. Differences are all significant (2-day: paired-sample  $t = 1.893$ ,  $df = 39$ , 1-tailed  $P = 0.033$ ; copying:  $t = 4.076$ ,  $df = 39$ ,  $P = 0.000$ ; 30-min:  $t = 3.219$ ,  $df = 29$ ,  $P = 0.002$ ; 1-day:  $t = 2.566$ ,  $df = 29$ ,  $P = 0.008$ )

another than in trials when females remained consistent in any of the potential cues measured (Table 2). Similarly, the absolute value of the change in female preference between trials did not relate consistently to any of the potential cues (Table 3).

The possibility that the model female influences the outcome of behaviour trials because females are more likely to investigate the male she was “with” first than

**Table 2** Results of Mann-Whitney  $U$ -tests in which the absolute value of the difference between males in each potential cue was compared for trials in which females reversed their choice versus those in which females chose the same male both times. None of the differences are significant after the sequential Bonferroni adjustment

	$U$	$Z_{adj}$	1-tailed $P$	
	2-Day	Copying	30-Min	1-Day
Body size	75 (1.044) > 0.1	85 (0.316) > 0.1	47 (1.415) > 0.05	36 (2.038) 0.028
Orange area	76 (1.001) > 0.1	83 (0.406) > 0.1	61 (0.623) > 0.1	46 (1.472) > 0.05
Orangeness	100 (0.924) > 0.1	104 (0.497) > 0.1	84 (0.456) > 0.1	79.5 (0.684) > 0.1
Black area	91 (0.348) > 0.1	69 (1.04) > 0.1	68 (0.226) > 0.1	64 (0.453) > 0.1
White area	97 (0.087) > 0.1	85 (0.316) > 0.1	55 (0.963) > 0.1	59 (0.736) > 0.1
Pattern complexity	96 (0.131) > 0.1	87 (0.203) > 0.1	55 (0.963) > 0.1	62 (0.567) > 0.1

**Table 3** Correlations of the absolute value of the difference between males in each potential cue with the absolute value of the difference between preference for one (randomly chosen) of the males in the first and second parts of the treatment

	$r_s$	$(n)$	$P$	
	2-Day	Copying	30-Min	1-Day
Body size	-0.030 (30) > 0.1	0.071 (30) > 0.1	-0.244 (19) > 0.1	-0.483 (19) 0.02
Orange area	-0.424 (30) 0.01	-0.069 (30) > 0.1	-0.054 (19) > 0.1	-0.123 (19) > 0.1
Orangeness	0.172 (34) > 0.1	0.095 (34) > 0.1	-0.037 (28) > 0.1	0.217 (28) > 0.1
Black area	-0.083 (30) > 0.1	0.210 (30) > 0.1	0.000 (19) > 0.1	0.269 (19) > 0.1
White area	-0.322 (30) 0.04	-0.107 (30) > 0.1	-0.022 (19) > 0.1	0.211 (19) > 0.1
Pattern complexity	0.301 (30) 0.05	-0.262 (30) > 0.05	0.043 (19) > 0.1	0.153 (19) > 0.1

they are the other male is refuted as the focal female went first to the side where the model female was only 16 times out of 40 ( $G_{adj} = 1.161$ ,  $df = 1$ ,  $P > 0.1$ ).

## Discussion

I have shown that not only do females prefer the same male significantly more often than they reverse their choice decision, but that the variability between females in their mating behaviour is significantly greater than the within female variability (except in the copying treatment). The repeatability of a female’s preference for one male over another is the maximum to which a female preference for any particular male trait may be heritable, because it is unlikely that, even in the simplest mate choice systems, one factor (the cue) alone is the only determinant of a female’s response to a male. The repeatabilities obtained in this study are higher than the non-significant values for preferences for specific ornaments in flour beetles ( $r = 0.0$ , Boake 1989) and barn swallows ( $r = 0.152$ – $0.241$ , Barbura 1992), but not as great as those obtained in sticklebacks ( $r = 0.65$ , Bakker 1993) and, interestingly, another study of barn swallows ( $r = 0.57$ , Møller 1994). The repeatability measures that I obtained in this study are lower than the repeatability of female guppies’ preference for brighter males ( $r = 0.577 \pm 0.107$ ; Quaré river, Trinidad) reported by Godin and Dugatkin (1995), but not significantly so (compared with the 2-day trial:

$Z = 0.125$ ,  $\sigma = 2.32$ , 2-tailed  $P = 0.216$ ) except for the copying treatment ( $Z = 0.259$ ,  $\sigma = 2.32$ , 2-tailed  $P = 0.011$ ). Therefore in this population, as in some others, female choice behaviour shows significant repeatability, a result necessary but not sufficient to claim that additive genetic variation for female mate preferences is present in the population.

Repeatability of mate choice behaviour is reduced when a female observes another female contradicting her mate choice decision. The negative effect on repeatability that was seen in the copying treatment is not necessarily the same as the effect expected in a wild situation. This is because, if females in a population share similar preferences, copying is more likely to corroborate a female's independent decision than contradict it. I therefore predict that if there is copying and it has any effect on repeatability in the wild, it increases repeatability rather than decreasing it as seen in this study. This prediction remains to be tested.

The time between choice trials does not appear to influence the repeatability of choice. The slightly (but not significantly) lower repeatability in the 30-min and 1-day treatments than in the 2-day treatment may well be due to the reduced sample in the former treatments due to illness and death of fishes. This lends credibility to measures of repeatability in which the repeated measures are separated by a relatively short time interval, such as that obtained by Godin and Dugatkin (1995). However, the time intervals used in this study are all relatively short, and certainly several orders of magnitude smaller than a female's reproductive lifespan. I suggest that repeatabilities should be estimated using longer intervals between measures before firm conclusions are drawn in this regard.

Ironically, whilst the copying treatment shows such low repeatability, there is no direct support for any claim that females in this population copy the mate choice of others. Females do not reverse their choice decision when faced with a female that chooses another male, as shown by Dugatkin and Godin (1992, 1993) in a wild Trinidadian guppy population. Similarly, although females in the copying treatment pay relatively more attention to the male that they had observed with the "model" female, this increase is not significantly larger than the increase in attention paid to the "loser" of the first trial in other treatments. If copying does occur, it is certainly much weaker than independent mate choice. The predominance of individual mate choice over copying (if it occurs) may be due to the fact that I did not match male pairs for similarity in size and colouration as was the case in experiments where females did copy one another (Dugatkin 1992; Dugatkin and Godin 1992, 1993). If this is the reason for our failure to find strong evidence for copying, it may be true that previous studies overestimated the importance and strength of imitative behaviour in determining the outcome of female mating decisions. This would favour the hypothesis that copying is an important aid to females having trouble discriminating

between males on the basis of their ornamentation (see Gibson and Höglund 1992 for a fuller treatment of this hypothesis and its alternatives).

The above explanation is unsubstantiated, however, as males in all treatments, including the copying treatment, in replicates where females reversed their choice decision were no more or less similar to one another than in replicates where females chose the same male twice. Likewise, the change in female behaviour was not significantly correlated with the difference in male ornamentation. These two types of analysis were used because they were expected to reflect the "certainty" with which a female chooses a male. If males do not differ a great deal in the cues that a female uses for choice, and we know that the females in this population use at least orange (Brooks and Caithness 1995a) and black (Brooks and Caithness 1995b; Brooks 1996), I predicted there would be larger changes in preference scores and a higher incidence of choice decision reversal than if the males are extremely different. This is because the chances of receiver error and failure to discriminate effectively (Schluter and Price 1993) are higher if the males on offer are similar than if they are very different. It seems that within-female variability in mate choice behaviour cannot be explained by receiver error or inability to effectively discriminate between males.

Kirkpatrick and Dugatkin (1994) argue that the nature of sexual selection, if copying is widespread, will not favour the evolution or maintenance of more than one ornament, as only the most common ornament will be selected for. The apparent lack (or extreme weakness) of mate copying in this population allows for the possibility that female choice is the agent selecting for the multiple ornaments of male guppies in this population (see Brooks and Caithness 1995a, b; Brooks 1996).

Since Fisher (1930) it has been accepted that female preferences evolve (and coevolve with male ornamentation) genetically. It seems possible from recent models (Laland 1994; Kirkpatrick and Dugatkin 1994) that similar results could be obtained even if the female preferences were inherited in a strictly cultural fashion. At this point, the evidence points to a role for both genetic inheritance and experience (see also Brooks and Caithness 1995c) but not cultural determination, in shaping female choice behaviour in this guppy population.

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