

Costs influence male mate choice in a freshwater fish

Bob B. M. Wong* and Michael D. Jennions

School of Botany and Zoology, Australian National University, Canberra, 0200 ACT, Australia

* Author for correspondence (bob.wong@anu.edu.au).

Recd 06.01.03; Acctptd 29.01.03; Online 06.03.03

It is well known that female mate choice decisions depend on the direct costs of choosing (either because of search costs or male-imposed costs). Far less is known about how direct fitness costs affect male mate choice. We conducted an experiment to investigate male mate choice in a fish, the Pacific blue-eye (*Pseudomugil signifer*). Preferred females were larger, probably because larger females are also more fecund. Males, however, were consistent in their choice of female only when the costs of associating with prospective mates were equal. By contrast, males were far less consistent in their choice when made to swim against a current to remain with their initially preferred mate. Our results suggest that males may also respond adaptively to changes in the costs of choosing.

Keywords: Pacific blue-eye; *Pseudomugil signifer*; fecundity; sexual selection

1. INTRODUCTION

Mate choice can be a costly undertaking involving considerable expenditure of time and energy (Milinski & Bakker 1992), and an increase in an individual's vulnerability to predators (Gibson & Langen 1996). These costs, in turn, may affect the rules choosy individuals use to discriminate among potential mates (Kokko *et al.* 2003). Theory predicts that individuals should become less choosy as search costs increase (Real 1990; Crowley *et al.* 1991) and empirical support for this prediction appears widespread for choosy females (reviewed in Jennions & Petrie 1997). Greater direct fitness costs associated with choosing one mate over another (Pocklington & Dill 1995) can also have important implications in understanding how shifting costs influence mating dynamics. We are, however, at present unaware of any studies that have directly investigated behavioural plasticity in mate choice when males must trade-off higher direct costs to choose a more attractive female against reduced costs of associating with a less attractive mate.

The effect of direct fitness costs on investment in discriminating among potential mates is important for *both* sexes. Females are typically the choosier sex but, under certain conditions, males also gain from mate choice (Kokko & Johnstone 2002). In many taxa, owing to strong size–fecundity relationships, females vary greatly in reproductive value and males preferentially court larger, more fecund females (Katvala & Kaitala 2001). Males are more likely to be choosy if energetic and temporal constraints limit their mating opportunities. For example, a major cost of male mate choice is related to courtship, which can

be energetically expensive (Judge & Brooks 2001), and risky in terms of attracting predators (reviewed in Kotiaho 2001). Similarly, costs relating to sperm production (Galvani & Johnstone 1998) or mating resources can limit male reproduction resulting in strategic allocation of mating effort and cryptic male choice (Engqvist & Sauer 2001; Wedell *et al.* 2002). Thus, as with females, one expects male choosiness to vary depending on costs associated with mate discrimination. Despite this, few studies have considered how the costs of searching for or courting specific females affect male mate choice strategies.

Here, we examine whether male Pacific blue-eye fish (*Pseudomugil signifer*) are consistent in their choice of mates when the costs of associating with a 'preferred' female are increased by forcing the male to swim against a water current if he wishes to continue to court this female.

2. MATERIAL AND METHODS

(a) Study species

The Pacific blue-eye is a small (3–4 cm), sexually dimorphic freshwater fish from eastern Australia. The males are brightly coloured and possess spectacular fin ornaments that are displayed during courtship and agonistic encounters. Male blue-eyes guard and maintain territories (submerged logs, rocks) close to the riverbank. Females swim along the river's edge inspecting males along the way. Typically, males court females and females discriminate among males. Male choice may, however, also be important as female fecundity increases with standard length (Pearson's correlation: $r = 0.42$, $p = 0.021$, $n = 24$). The species breeds year round.

We collected fishes from the Johnstone River near Innisfail (a velocity 30 cm below surface of $0.4\text{--}3.0\text{ m s}^{-1}$). The sexes were housed separately in 300 l aquaria on a 12 L : 12 D cycle at 25 °C and fed fish flakes and daphnia.

(b) Experimental procedure

The experiments were conducted in an aquarium divided into three compartments (figure 1). The two smaller compartments were separated by an opaque divider and each housed a female during trials. The larger compartment housed the test male. The glass divider between the large and two smaller compartments allowed the male to see both females. One aquarium pump was positioned on either side of the main compartment immediately in front of each female compartment. Both pumps faced one another. A 5 cm portion of the opaque partition extended into the large compartment to prevent flow in front of one compartment reaching the other.

In each trial, females were randomly selected and assigned to one of the small compartments and allowed to acclimate for more than 5 min. The test male was then placed into a clear cylinder (10 cm in diameter) in the large compartment positioned 50 cm in front of the female compartments. After 5 min the tube was slowly lifted until the male swam clear. A trial comprised two 15 min sessions with a 5 min interval. In session 1, neither water pump was active and the male paid equal costs to associate with each female. In session 2, the pump in front of the initially preferred female was activated in treatment trials so that the male had to swim against a current (30 cm s^{-1}) if he was to continue courting this female. In control trials, the pump was not activated in session 2 so the male did not pay a greater cost to continue associating with the initially preferred female.

In each session male association preference was measured by conducting focal samples every 30 s. Association preferences in blue-eyes translate into actual mating preferences (B. B. M. Wong, unpublished data). During focal samples a male was only deemed to be associating with a female if he was within 5 cm of her compartment with his body oriented unambiguously towards her. We defined the preferred female in session 1 as the one with whom the male spent more time.

We invoked two criteria to exclude unresponsive or indiscriminate males as follows.

- (i) We excluded males that spent less than 33% of a session associating with females. These males appeared to be sexually less responsive.
- (ii) We excluded males that spent less than 70% of their association time with a single female.

Hence, any male that switched females between sessions went from spending at least 70% of his association time with female A to at least 70% with female B. We thus excluded eight males (four control and four treatment males) from our analyses, but inclusion of these males did not change our findings (see § 3).

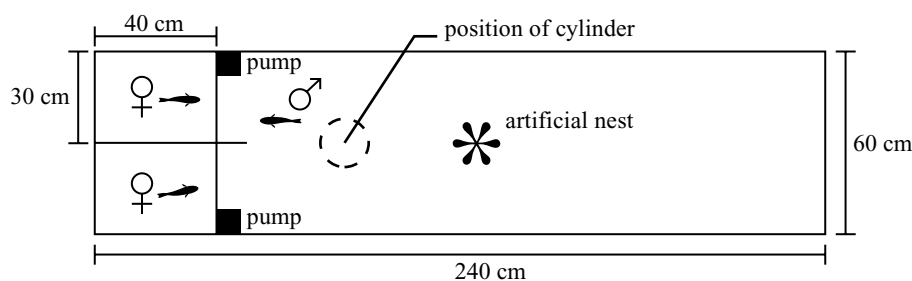


Figure 1. Tank design. (See text for details.)

(c) Statistical analyses

We expected males to be more consistent in their choice of female in the control rather than water treatment owing to the energetic costs of associating with the previously preferred female in session 2 (Milinski & Bakker 1992). We also predicted that males would prefer larger, more fecund, females (Houde 1997). Given these hypotheses, all tests are one-tailed unless otherwise stated. Power is the likelihood of detecting a medium strength effect with $\alpha = 0.05$ (two-tailed) (Cohen 1988).

3. RESULTS

In the first session, the preferred female was significantly larger than the other female (mean preferred $SL \pm s.e. = 30.0 \pm 0.5$ mm, non-preferred = 28.7 ± 0.4 mm; paired t -test: $t = 1.747$, $n = 34$ pairs, $p = 0.045$). There was no side bias. In session 1, 53% of males (18 out of 34) preferred the female in the left-hand compartment (binomial, $p = 0.432$; power, 45%).

In total, 64.7% of males chose the same female in both sessions. There was, however, a significant difference between treatment and control trials (Fisher's exact test: $p = 0.035$). In the control, 14 out of 17 males chose the same female in both sessions (binomial test: $p = 0.006$). By contrast, only 8 out of 17 males in the water current treatment displayed a consistent choice (binomial test: $p = 0.5$). These analyses excluded eight males whose degree of responsiveness and strength of choosiness did not meet our most stringent criteria. Even if these males are included in the analysis, however, the results are still significant: 17 out of 21 and 10 out of 21 males remaining consistent in control and treatment trials, respectively (Fisher's exact test: $p = 0.026$).

Although unlikely, we considered the possibility that males may have switched sides in treatment trials owing to the noise of the pump or the sudden increase in water flow. We therefore conducted a second experiment and compared the consistency of male choice between the control and treatment trials in which both pumps were activated in session 2. We found no difference in consistency of male choice between these new trials (13 out of 14 males consistent) and controls (10 out of 12 consistent) (Fisher's exact test: $p = 0.58$). Thus, we conclude that the activation of the pump *per se* is not responsible for the increase in mate switching between trials in the water treatment in the first experiment.

4. DISCUSSION

Our study shows that costs can affect male mate choice in Pacific blue-eyes. In common with other studies (reviewed in Houde 1997), males preferred larger females, probably because they are also more fecund. However, males were consistent in their choice only when the costs

of associating with prospective mates were equal. Males were more likely to switch their choice of mates between sessions if forced to swim against a current to be with their initially preferred mate (when the alternative is to switch over to courting the other female in still water). This is probably owing to the associated increase in the demands of swimming imposed by the current (Milinski & Bakker 1992).

Our findings are concordant with theoretical predictions and empirical studies of how general search costs influence mate choice in females. For example, female sticklebacks (*Gasterosteus aculeatus*) more readily accept an otherwise less attractive mate when forced to expend more energy swimming against a current (Milinski & Bakker 1992). Only a few studies (Hedrick & Dill 1993), however, have investigated mate choice plasticity when individuals must directly trade-off approaching a more attractive individual against the higher direct costs associated with choosing such an individual. This is a biologically meaningful question because some females may occur in more risky or energetically costly habitat, or are more likely to mate multiply and generate sperm competition (Wedell *et al.* 2002). We found approximately half the males changed their preference to the less costly alternative when forced to swim against a current to remain with the initial female. This suggests that males may invest differently with regard to the quality of their female mating partners as shown, for example, in scorpionflies (*Panorpa cognata*; Engqvist & Sauer 2001).

One potential criticism of our study is that association preferences may not reflect actual mating preferences. For example, males may have associated with a female because they were exhibiting schooling behaviour. We do not believe this was the case for the three following reasons.

- (i) Association preferences translate into actual mate choice in several fish species (Forsgren 1992), including blue-eyes (B. B. M. Wong, unpublished data).
- (ii) Male preference for large females is consistent with studies where mate choice has been demonstrated (Houde 1997).
- (iii) If males were merely schooling we would expect all of the males in the water current treatment to switch position and associate with the female in the less turbulent environment. Instead, half the males fought the current to stay with the initially preferred female.

So why have so few studies previously considered how costs affect male mate choice? This may be related to differences in the perceived benefits gained by males and

females through mate choice. In many species the benefits of female choice are assumed to be primarily genetic and these genetic benefits are thought to be small (Kirkpatrick & Barton 1997). Thus, females should be sensitive to any change in the direct costs of choosiness that decrease their potential lifetime reproductive output (Jennions & Petrie 1997). By contrast, because male choosiness often appears to be for direct fitness gains (e.g. mating with more fecund females, or those where confidence of paternity is higher) we might expect males to be less sensitive to small changes in the costs of choosing. Our study highlights the need to pay closer attention to how costs affect male mate choice. Despite apparent sexual differences in the benefits of being choosy, our study suggests males also respond adaptively to changes in the costs of choosing.

Acknowledgements

The authors thank D. Chapple, S. Downes, S. Keogh, R. Magrath and reviewers for comments; and D. Keating, D. McGlashan, A. Hooper, fish collectors and landholders for help. Financial support was received from the Seaworld Research and Rescue Foundation, the Joyce W. Vickery Fund, the Ethyl Mary Read Fund and the Australian Geographic Society.

Cohen, J. 1988 *Statistical power analysis for the behavioural sciences*, 2nd edn. Hillsdale, NJ: Lawrence Erlbaum Associates.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohn, S. L., Sih, A. S. & Sargent, C. R. 1991 Mate density, predation risk and the seasonal sequence of mate choices: a dynamic game. *Am. Nat.* **137**, 567–596.

Engqvist, L. & Sauer, K. P. 2001 Strategic male mating effort and cryptic male choice in a scorpionfly. *Proc. R. Soc. Lond. B* **268**, 729–735. (DOI 10.1098/rspb.2000.1423.)

Forsgren, E. 1992 Predation risk affects mate choice in a gobiid fish. *Am. Nat.* **140**, 1041–1049.

Galvani, A. & Johnstone, R. A. 1998 Sperm allocation in an uncertain world. *Behav. Ecol. Sociobiol.* **44**, 161–168.

Gibson, R. M. & Langen, T. A. 1996 How do animals choose their mates? *Trends. Ecol. Evol.* **11**, 468–470.

Hedrick, A. V. & Dill, L. M. 1993 Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* **53**, 1103–1117.

Houde, A. E. 1997 *Sex, color and mate choice in guppies*. Princeton University Press.

Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**, 283–327.

Judge, K. A. & Brooks, R. J. 2001 Chorus participation by male bullfrogs, *Rana catesbeiana*: a test of the energetic constraint hypothesis. *Anim. Behav.* **62**, 849–861.

Katvala, M. & Kaitala, A. 2001 Male choice for current female fecundity in a polyandrous egg-carrying bug. *Anim. Behav.* **62**, 133–137.

Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286.

Kokko, H. & Johnstone, R. A. 2002 Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Phil. Trans. R. Soc. Lond. B* **357**, 319–330. (DOI 10.1098/rstb.2001.0926.)

Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. 2003 The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B* **270**, 653–664. (DOI 10.1098/rspb.2002.2235.)

Kotiaho, J. S. 2001 Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biol. Rev.* **76**, 365–376.

Milinski, M. & Bakker, T. C. M. 1992 Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proc. R. Soc. Lond. B* **250**, 229–233.

Pocklington, R. & Dill, L. M. 1995 Predation on females or males: who pays for bright male traits? *Anim. Behav.* **49**, 1122–1124.

Real, L. 1990 Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.* **136**, 376–404.

Wedell, N., Gage, M. J. G. & Parker, G. A. 2002 Sperm competition, male prudence and sperm-limited females. *Trends Ecol. Evol.* **17**, 313–320.