



Superior fighters make mediocre fathers in the Pacific blue-eye fish

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It is widely assumed that male competition and female choice select for elaboration of the same male traits and that fighting ability is synonymous with high quality in terms of benefits to females. Under these assumptions, females are expected to use the same traits that reflect fighting ability to choose the most dominant male, even if females are not privy to actual male–male interactions. Few studies, however, have explicitly investigated female choice in relation to male fighting ability. I conducted experiments separating the effects of male competition and female choice in a freshwater fish, the Pacific blue-eye, *Pseudomugil signifer*, to test whether females prefer dominant males and whether females obtain higher egg hatching success by being choosy. When females were precluded from witnessing agonistic encounters between two potential mates, they did not appear to use traits correlated with fighting ability to choose competitively superior males. However, even when females were privy to competition, witnessing male interactions did not induce a preference for dominant individuals. Lack of preference for superior fighters may be because there was no difference in hatching success between eggs guarded by dominant and subordinate males. Instead, females appeared to prefer males that spent a greater proportion of time engaged in courtship and, in so choosing, enjoyed higher egg hatching success. These results indicate that dominant males are not necessarily more attractive than subordinates nor do the former necessarily guarantee or deliver the kind of benefits that females may seek.

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It is generally assumed that male–male competition and female choice operate by mutually reinforcing one another and selecting for elaboration of the same male traits (Berglund et al. 1996). Signals important in a contest situation are also expected to serve as reliable cues in female choice because such traits are believed to convey accurate information about the overall condition of males as prospective mates (Candolin 1999; Berglund & Rosenqvist 2001). Indeed, superior fighting ability is often equated with high quality in terms of fitness gains to females (e.g. Bisazza et al. 1989; Montgomerie & Thornhill 1989; Alatalo et al. 1991; Kodric-Brown 1996). Because females maximize reproductive success by optimizing the quality of their mating partners (Qvarnström & Forsgren 1998), they are assumed to benefit by mating with dominant males. Certainly, across a suite of taxa, females are purported to derive a range of direct or indirect benefits by choosing to mate with dominant males (reviewed in Berglund et al. 1996) and females of some species are known to stage or incite competition,

presumably to ensure mating with the ‘best’ males (e.g. Cox & LeBoeuf 1977; Thornhill 1988; Montgomerie & Thornhill 1989; but see O’Connell & Cowlshaw 1994).

One potential problem, however, is that the two processes of sexual selection are often confounded in time and space. Although winners of male–male competition often enjoy higher mating success than losers, it may be difficult to determine accurately whether this mating bias actually reflects a female preference for dominant males. Furthermore, even if females are able to assess potential suitors accurately, there is no assurance that their preferences will be realized (Jennions & Petrie 1997; Kokko et al. 2003). Males, for example, may coerce females into mating with them (reviewed in Clutton-Brock & Parker 1995) or they may deny more attractive (but socially subordinate) males from holding territories needed for breeding (Andersson et al. 2002). In these instances, competition, rather than female choice, could operate to determine mating outcomes.

Mate choice in relation to male fighting ability may be less straightforward than traditionally assumed. It is becoming increasingly apparent that females do not always prefer to mate with dominant males. In terms of optimizing female fitness, mating with a superior competitor does

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not invariably mean that a given female will be mating with the 'best' male (Qvarnström & Forsgren 1998). Any benefits derived from mating with a male based on his fighting ability may, in fact, need to be balanced against other, potentially conflicting, components of female fitness (Kokko et al. 2003). For instance, dominance may reflect viability or genes conferring viability to offspring (Montgomerie & Thornhill 1989; Alatalo et al. 1991; but see Höjesjö et al. 2002), but if dominant males make average fathers (e.g. Forsgren 1997), a female may have to trade between direct and genetic viability benefits and, depending on context, could opt to choose good fathers over superior fighters. Furthermore, a male that is adept in competition may increase his own mating opportunities by excluding rivals and this may occur even if his actions reduce female fitness by decreasing her survival or fecundity (e.g. Holland & Rice 1998). Given these possibilities, there is no a priori reason why male competition and female choice have to be 'complementary' in their effects instead of selecting for different male traits or even work in opposing directions (e.g. Moore & Moore 1999; Andersson et al. 2002).

The Pacific blue-eye, *Pseudomugil signifer*, is an especially promising study subject for disentangling the mechanisms of male–male competition and female choice. Sexual selection is likely to be an important force shaping male morphology in this small (<6 cm), sexually dimorphic, freshwater fish found in streams across the east coast of Australia. Male blue-eyes are larger, more colourful and have longer fins than females. Males are also highly territorial and engage in spectacular fin-flashing displays during contests with rivals over the acquisition and defence of spawning sites (submerged logs, rocks, vegetation) close to the water's edge. Females move between territories, inspecting males along the way. Males play an active role in courting females (Wong & Jennions 2003) and will often swim over to display to passing females. If successful in his efforts, the female will follow the male to his territory and scatter her eggs among aquatic vegetation (Allen 1995). Males care for the eggs through defence of the spawning site. Blue-eyes are a highly amenable study species for behavioural work (Wong & Jennions 2003). They are popular aquarium fish and breeding protocols are well established (Allen 1995). Using the Pacific blue-eye, I set out to determine whether winners of male contests are also preferred by females. I also investigated whether female choice results in higher egg hatching success, a direct fitness benefit that appears to be especially important in guiding the mating decisions of female ectotherms in male guarding species (Møller & Jennions 2001).

METHODS

I collected 140 fish in March and August 2001 from Ross Creek in Townsville, Australia. The Pacific blue-eye is a common species throughout the east coast of Australia and is one of the most abundant freshwater/estuarine species in north Queensland (Pusey & Kennard 1996; Allen et al. 2002). In a survey of freshwater fish in the wet tropics, Pusey & Kennard (1996) found that *P. signifer* comprised 20% of their sample, making the species the second most

abundant in their census. The subsequent removal of 140 fish is therefore unlikely to have a significant or lasting impact on wild populations. Fish for my study were sampled using dip nets and bait traps and no permits were required under Queensland Fisheries regulations under my sampling regime. Animals were packed and freighted in accordance with International Air Transport Association Live Animal Regulations. Fish were imported into the Australian Capital Territory under permit pursuant to the Nature Conservation Act 1980. Males and females were kept in separate 300-litre aquaria (maximum 50 fish per tank) on a 12:12 h light:dark cycle and fed on a diet of manufactured fish flakes and daphnia. During the experiments, fish were fed daily. On days when observations were made, fish were fed after observations were completed. Each aquarium was connected to a wet/dry filtration system that provided mechanical and biological filtration. Temperature was held at a constant 25 °C. After the study, all fish were returned to the stock tanks for future research. I conducted two separate experiments.

Experiment 1

The first experiment had two specific aims. First, I tested whether male competition and female choice in Pacific blue-eyes select for elaboration of the same male traits (Berglund et al. 1996). If traits important in competition also play a role in signalling high quality, females should be able to use traits that are correlated with fighting ability to choose the most dominant males, even if females are denied the opportunity to view any direct competition between prospective suitors (cf. Candolin 1999; Berglund & Rosenqvist 2001). Second, I investigated whether females attain higher hatching success by mating with dominant males. It has been shown in at least one other fish (sand goby, *Pomatoschistus minutus*: Forsgren 1997) that dominant males are not better fathers than subordinates and, conceivably, there could be trade-offs made between investment in competition and parental care (Qvarnström & Forsgren 1998). A total of 30 trials were performed. The experiment itself consisted of four steps (Fig. 1).

Step 1: male–male competition

Two males were introduced into a 90-litre aquarium and were allowed to compete for a single spawning mop made from 80 strands of 40-cm-long green acrylic yarn (Fig. 1a). Males engage in two kinds of agonistic behaviours: lateral fin-flaring displays and chases. I defined the winner as the one that engaged in the most chases and fin flares over a 20-min period, 24 h after being introduced into the tank. This method of ascertaining winners of competition was consistent with the observation that one male (the dominant individual) would assert his position by taking possession of the entire aquarium. Male colour was given a score (e.g. Kodric-Brown 1996; Forsgren 1997) from 1 to 4. This score was based on the appearance and development of specific colour markings on the fins and bodies of the fish, with a score of 4 indicating maximal colour development (Table 1). After establishing the dominance relationship between the two males,

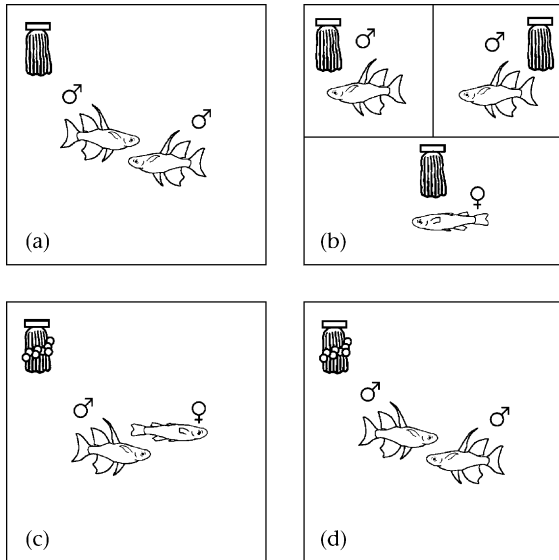


Figure 1. Experimental set-up. (a) Step 1: male–male competition; (b) step 2: female choice; (c) step 3: spawning; (d) step 4: egg hatching success.

I separated the fish and allowed them to rest for 24 h to control for the possible effect of competition on subsequent male behaviours. In a control study, I found no difference in the relative proportion of time spent courting by dominant and subordinate males before and 24 h after male–male competition (i.e. no order effect of competition on behaviour of dominant versus subordinate males; paired t test: $t_{13} = 0.10$, $N = 14$, $P = 0.93$).

Step 2: female choice

The following day, a female was given the opportunity to choose between the two males (Fig. 1b). I randomly assigned males to one of two compartments separated by an opaque divider in a mate choice tank. Each male was supplied with his own spawning mop. A female was

placed in a compartment separated from the males with a clear Plexiglas divider. A spawning mop was also placed in the female's compartment to provide refuge. The aquarium set-up prevented males from viewing one another but allowed the female to see both males. I conducted 120 spot samples over four 30-min sessions during a single day, with a minimum of 30 min between sessions. During a spot sample, a female was recorded as associating with a male if she had her body oriented unambiguously towards him while in front of his compartment. I anticipated that a female would spend more time in front of her preferred male, so I determined female preference from the number of times the female was associated with each male. I later validated this technique by comparing time to spawning between 'preferred' and 'nonpreferred' males (see below).

A number of studies have shown the importance of courtship as a cue in female choice (Andersson 1994). There are strong a priori reasons why this may also be the case in Pacific blue-eyes. Specifically, males play an active role in courtship of females (Wong & Jennions 2003) and strength of female preference for a particular male is correlated with how long he spends courting (Wong et al., in press). Accordingly, I calculated the proportion of time spent courting by scoring male behaviour (courting, swimming, foraging, stationary) when the female was in front of his compartment. After each session, a colour score was given to each male.

Step 3: spawning

Immediately after the completion of step 2, the female was paired randomly with either her preferred or non-preferred male and introduced into a tank containing a spawning mop that I subsequently inspected daily for eggs (Fig. 1c). After spawning, the female was removed and the number of eggs counted.

Step 4: egg hatching success

A randomly selected stock male (standard length = 33.23 ± 0.49 mm) was then introduced into the tank to act as a potential nest challenger and egg predator (Fig. 1d). Ten days later, I counted the embryos to compare the hatching success of eggs guarded by preferred and non-preferred males. After the experiment, I measured the weight, standard length and fin length of all test males. These traits and colour are often implicated as being important in male–male competition with dominant males usually being larger or more brightly coloured than subordinates (e.g. Forsgren 1997).

Experiment 2

The design of the first experiment deliberately precluded females from witnessing any fights between prospective mates. However, this information may be important under certain circumstances (e.g. if signals of fighting ability are unreliable: Candolin 1999; Berglund & Rosenqvist 2001). Consequently, I conducted a separate experiment to investigate whether being privy to male–male competition might induce a preference for

Table 1. Description of male colour scores

Score	Description
1	Light yellow dorsal, anal and caudal fins. Faint white edge on caudal fin tips with thin grey line on inside margin. Pelvic fins opaque. Pectoral fins clear
2	Faint white fore-edge on first dorsal fin. Grey fore-edge on second dorsal fin. Dorsal and ventral edges of caudal fin white with grey on inside margins. Pelvic fins opaque. Clear pectoral fin with grey line on inside margin of fore-edge.
3	Black patch at the base of first and second dorsal fins. Fore-edge of first dorsal fin lined in white. Second dorsal fin pale yellow with black outline within white margin. Anal fin pale yellow edged in black with white and black rays. Bright yellow caudal fin with dark yellow rays. Dorsal and ventral edge of caudal fin white with proximal black area. Cream-coloured pelvic fin with black edge. Fine white fore-edge on pelvic fin with strong black line on inside margin
4	Fin colours same as 3. Body darkens with scales edged in black

dominant males. On day 1, females were given the opportunity to choose between two randomly paired males assigned to the end compartments of a mate choice tank. The aquarium set-up and method for scoring female preferences and male behaviours were the same as in experiment 1. Immediately after determining female preference, however, I removed the opaque partition separating the two males, and allowed females in competition trials to view male–male interactions for 2 full days. At the end of the second day of competition, after scoring male behaviours on day 2 to determine which male was dominant (see step 1 in experiment 1), I again separated the males and restored the opaque partition. Female preferences were measured again the following day (day 4) using the same method as on day 1. I then determined whether females were consistent in their choice after having had the opportunity to witness male–male interactions by comparing them with control trials where females had been denied this opportunity. I conducted 40 trials (20 controls, 20 competitions). One of the control trials had to be excluded because the female failed to choose.

Statistical Analyses

Parametric tests were used unless the assumptions could not be satisfied. In those instances, nonparametric equivalents were used. For multiple comparisons of male traits, I applied a Bonferroni correction with the level of significance set at $P < 0.007$. Time to spawning in experiment 1 was used in a survival analysis to test the validity of female association preferences. Any pairings that did not result in spawning within 16 days were recorded as 'right censored'. I predicted that females paired with their 'preferred' male would spawn sooner. Tests are two tailed unless there were strong a priori reasons for invoking a one-tailed test, as in the case of courtship. Specifically, I predicted that preferred males would spend more time in courtship because males actively court females and strength of female preference is correlated strongly with courtship (Wong et al., in press). Data are presented as mean \pm SE.

Ethical Note

Male–male competition took the form of ritualized fin flaring displays and chases. Fish were monitored closely at

all times to ensure that no physical injuries were being inflicted. No actual contact was ever observed. Since competitive interactions may be stressful for the test subjects, the length of time that males were placed in a competitive environment was kept to a minimum and fish were separated immediately after observations were completed. The experiment was approved by the Australian National University Animal Experimentation Ethics Committee.

RESULTS

Experiment 1

Which traits predict the outcome of male–male competition?

Winners of male–male competition were generally larger and possessed longer fins than losers (Table 2) and were also more colourful (colour score: dominant: 2.5 ± 0.14 ; subordinate: 2.0 ± 0.14 ; Wilcoxon signed-ranks test: $Z = 2.98$, $N = 30$, $P = 0.003$).

Do females find dominance or traits correlated with dominance attractive?

There was no statistically significant difference in body size or fin length between preferred and nonpreferred males (Table 3). There was a trend for preferred males to be more colourful (colour score: preferred: 1.75 ± 0.12 ; nonpreferred: 1.55 ± 0.12 ; Wilcoxon signed-ranks test: $Z = -1.85$, $N = 30$, $P = 0.06$) but this effect was not significant after Bonferroni correction. Females did not always choose dominant males: 17 of 30 females chose the male that was subordinate in step 1 and 13 chose the male that was dominant (binomial test: $P = 0.58$).

Female blue-eyes were exercising choice during the trials as association preferences translated into actual mating preferences. Specifically, females paired with preferred males spawned sooner than those paired with nonpreferred males (mean preferred = 3.67 days, mean nonpreferred = 9 days; survival analysis: $\chi^2_1 = 6.14$, $P = 0.013$). Six of the 30 females tested failed to spawn (1/15 with preferred male, 5/15 with nonpreferred male).

I found a positive relation between female choice and male courtship, with preferred males courting, on average, 8% more than their nonpreferred counterparts per unit time when the female was choosing (one-sample t test: $t_{29} = 1.7$, $N = 30$, $P = 0.036$, one tailed; Fig. 2). The

Table 2. Paired t tests comparing male traits in dominant versus subordinate males

Trait	Dominant	Subordinate	t_{29}	P
Standard length (mm)	34.12 ± 0.34	31.48 ± 0.44	4.85	0.00002*
Weight (g)	0.82 ± 0.02	0.64 ± 0.03	4.22	0.0002*
Fin length (mm)				
First dorsal	16.04 ± 0.66	12.75 ± 0.83	2.91	0.006*
Second dorsal	12.36 ± 0.37	10.23 ± 0.39	3.72	0.0008*
Pectoral	7.71 ± 0.15	6.80 ± 0.19	3.86	0.0004*
Ventral	7.91 ± 0.28	6.63 ± 0.30	3.12	0.004*
Anal	12.27 ± 0.43	10.60 ± 0.43	2.75	0.01

*Significant after Bonferroni correction.

Table 3. Paired *t* tests comparing male traits in preferred versus nonpreferred males

Trait	Preferred	Nonpreferred	t_{29}	<i>P</i>
Standard length (mm)	32.93 ± 0.45	32.67 ± 0.47	0.36	0.72
Weight (g)	0.73 ± 0.03	0.73 ± 0.03	0.15	0.88
Fin length (mm)				
First dorsal	14.62 ± 0.70	14.18 ± 0.90	0.34	0.74
Second dorsal	11.50 ± 0.42	11.09 ± 0.43	0.59	0.56
Pectoral	7.28 ± 0.20	7.24 ± 0.18	0.14	0.89
Ventral	7.46 ± 0.27	7.08 ± 0.35	0.81	0.43
Anal	11.95 ± 0.43	10.92 ± 0.48	1.56	0.13

relation between the number of courtships and total time spent choosing was isometric (one-sample *t* test: $t_{28} = 0.84$, $P = 0.42$). Thus, the number of courtships per unit time did not increase with increasing time spent in front of a male, suggesting that males were not simply adjusting their behaviours and courting more in response to greater interest by females (i.e. feedback). There was no difference in the percentage of time spent courting between dominant and subordinate males (dominant: $21.6 \pm 4.5\%$; subordinate: $27.6 \pm 4.4\%$; paired *t* test: $t_{29} = -1.38$, $N = 30$, $P = 0.17$).

Egg hatching success

There was no statistically significant difference in hatching success between eggs guarded by dominant and subordinate males, although the latter tended to bring more eggs to hatching (dominant: $15.11 \pm 10.44\%$; subordinate: $29.80 \pm 8.78\%$; Mann–Whitney test: $U = 45.5$, $N_1 = 9$, $N_2 = 15$, $P = 0.11$; Fig. 3a). However, females paired with preferred males enjoyed a significantly higher hatching success than those paired with nonpreferred males (preferred: $37.50 \pm 9.95\%$; nonpreferred: $5.80 \pm 3.91\%$; $U = 30.5$, $N_1 = 14$, $N_2 = 10$, $P = 0.01$; Fig. 3b). Thus, females appeared to prefer males that delivered greater hatching success. There was no difference in the number of eggs spawned when females were paired with preferred and nonpreferred males (preferred: 5.21 ± 1.02 ; nonpreferred: 7.10 ± 2.61 ; $U = 67$, $N_1 = 14$, $N_2 = 10$, $P = 0.86$), nor was there a relation between the number of eggs laid and subsequent hatching success (Spearman correlation: $r_s = -0.25$, $N = 24$, $P = 0.23$).

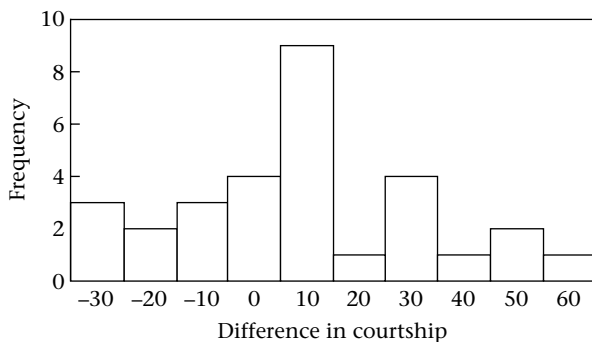


Figure 2. Difference in % time spent courting between preferred and nonpreferred male. A positive value indicates that the preferred male spent a greater percentage of his time in courtship than the nonpreferred male.

Experiment 2

Does witnessing male competition induce a preference for dominant males?

As in experiment 1, when males were allowed to interact with one another, larger individuals dominated their smaller opponents (in all cases, the larger of the two males won; binomial test: $P < 0.001$, one-tailed).

Larger (i.e. dominant) males were not significantly more preferred on day 1 (18/39 chose larger; binomial test: $P = 0.375$, one-tailed). At this stage, and consistent with the results of experiment 1, females in the competition trials had not yet been allowed to witness any agonistic encounters and there was no difference in preference for larger males between competition (8/20 chose larger) and control treatments (10/19 chose larger; Fisher's exact test: $P = 0.527$).

After being privy to competition on day 4, females showed repeatable preferences between days, with 74.4% of females choosing the same male on day 1 as on day 4 (29/39 consistent; binomial test: $P < 0.005$). There was no significant difference in consistency between the treatment and control trials (Fisher's exact test: $P = 0.27$) despite females now having had the opportunity to witness male–male interactions in the competition trials. When switching did occur in the competition treatment on day 4, it was not in favour of dominant males (four females switched to the dominant male, three to the subordinate).

Females did not 'fixate' on the male chosen on day 1: the percentage of time spent associating with this male decreased between days (day 1: $82.93 \pm 2.44\%$; day 4: $66.24 \pm 5.82\%$; paired *t* test: $t_{38} = 3.03$, $N = 39$, $P < 0.005$). The shift also does not appear to be a response to information gained as to fighting ability of the initially preferred male, as it made no difference whether the initial choice was for the subordinate or dominant male (mean decrease in percentage of time between days: subordinate: 24.84; dominant: 30.54; two-sample *t* test: $t_{18} = 0.27$, $N_1 = 12$, $N_2 = 8$, $P = 0.78$).

DISCUSSION

Contrary to the general assumption that dominance is attractive (Berglund et al. 1996), female blue-eyes did not prefer dominant males. Under the dual utility model (Berglund et al. 1996), traits important in competition are also expected to serve as reliable cues in female choice.

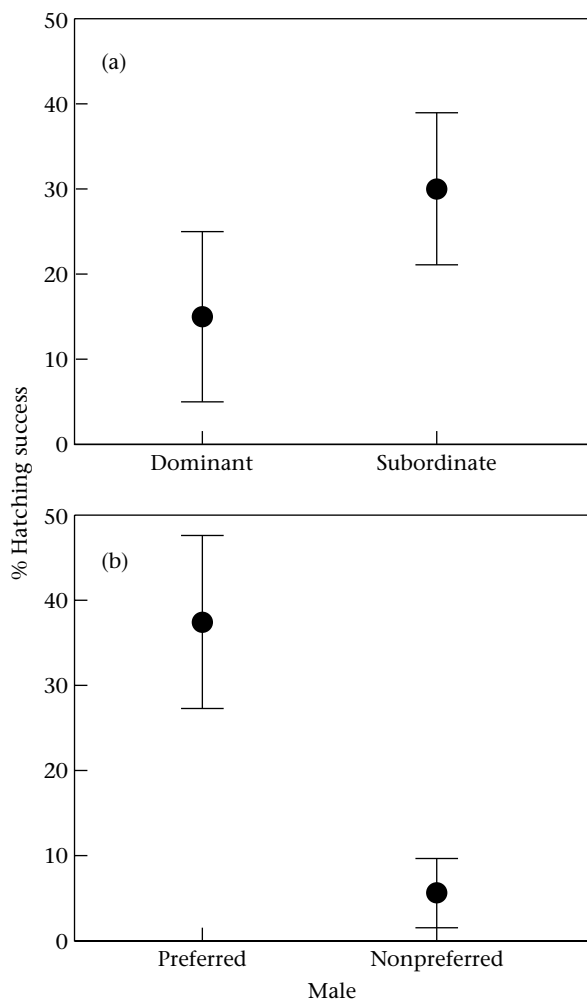


Figure 3. Mean hatching success \pm SE of eggs guarded by (a) dominant and subordinate males, (b) preferred and nonpreferred males.

Consequently, one would expect females to use these cues to discriminate in favour of males with greater potential as fighters. This was not the case. Experiment 1 showed that traits correlated with fighting ability do not appear to play a role in female choice. A possible exception might be colour, as preferred males tended to be more colourful than their nonpreferred counterparts. In my study, this marginally nonsignificant trend disappeared after Bonferroni correction, but I cannot discount the possibility that this negative result may be caused by low sample size (Jennions & Møller 2003). In any case, colour appears to be a plastic trait because more colourful males in competition were also large and dominant but this was not the case for preferred males.

Even when females were privy to competition this did not induce a preference for dominant males. In experiment 2, females were generally consistent in their choice although the strength of their overall preference for the initial male decreased from day 1 to day 4. However, this was the case irrespective of whether that male had been dominant or subordinate suggesting that competition did not subsequently make dominant males more attractive

than subordinates. My results suggest that females do not gain information from witnessing fights, as female choice did not appear to be based on fighting prowess. This is consistent with the prediction that competition may facilitate choice only if female preference is for a trait correlated with dominance (Candolin 1999; Kangas & Lindström 2001).

Female blue-eyes were choosy and achieved higher hatching success when they mated with preferred suitors. However, this benefit would not have been procured had females based their choice on male fighting ability, since dominant males made average fathers. My results are comparable with those of Forsgren (1997) who similarly found, in sand gobies, that females preferred good fathers over dominant males. More generally, the results are also consonant with the recent findings of Møller & Jennions (2001) who showed that hatching success may be an especially important direct fitness component for female ectotherms and one that could, conceivably, override any indirect benefits that may be gained by mating with dominant males.

Courtship might have been important in communicating paternal competence to females. Male blue-eyes play an active role in courting females (Wong & Jennions 2003) and our present results showed that the preferred male spent, on average, 8% more of his time in courtship when females were choosing. The role of courtship has consistently been implicated as an important cue in female choice. For example, in damselfish, *Stegastes partitus*, courtship signals mate quality by indicating the presence of large fat reserves (Knapp & Kovach 1991) and in fifteen-spined sticklebacks, *Spinachia spinachia*, body shaking during courtship reflects superior parental abilities (Östlund & Ahnesjö 1998).

Cues such as courtship may be relevant in signalling aspects of male quality that are important to females, even if paternal duties are limited to guarding. Male Pacific blue-eyes do not actively care for the eggs (e.g. by fanning) other than through defence of a spawning site. Territory defence requires considerable expenditure of time and energy (Sargent 1985). Independent of his abilities as a competitor, a male might cannibalize his own eggs (Okuda & Yanagisawa 1996), or defend his nest badly against other egg predators (Qvarnström & Forsgren 1998). Courtship may therefore be important in signalling male investment in activities that translate into actual fitness gains to females through higher hatching success.

An important caveat, however, is that male sexual advertisements do not always signal direct fitness benefits reliably (Kokko 1998; Møller & Jennions 2001). Courtship, for example, may depend on motivation and males may vary their efforts in response to competition (Candolin 1999). Also, in the field, dominant males may prevent other individuals from signalling their paternal competence accurately, thereby inducing a preference for dominant individuals. In this way, competition may even 'hamper' female choice (e.g. Kangas & Lindström 2001). Territory density may therefore be a relevant consideration in the field (Kangas & Lindström 2001).

The difference in hatching success between preferred and nonpreferred males was not due to more eggs being

deposited with the former. Increased hatching success is often correlated with brood size (e.g. Forsgren 1997). If females laid more eggs with preferred males, these males could be attaining higher hatching success independent of any effects of differences in male quality. However, I found no difference in the number of eggs laid between females paired with preferred and nonpreferred males based on the one day of laying. Furthermore, there was no correlation between the number of eggs laid and subsequent hatching success. It is conceivable that females paired with preferred and nonpreferred males may have invested differentially in the quality of the eggs (e.g. Kolm 2001). Unfortunately, I could not reliably measure egg quality in my experiment. In particular, the timing of allocation decisions is critical but is also difficult to determine (e.g. females may have already decided on a male in step 1 of the first experiment).

I was testing female preference for male phenotype, so I specifically controlled for resource quality by using artificial spawning mops. In the field, however, the quality of the resource might influence female choice, because territory quality may affect offspring survivorship as in, for example, bitterlings, *Rhodeus sericeus* (Candolin & Reynolds 2001). Dominant males may enjoy a mating advantage by monopolizing the best resources. In this way, competition may dictate the kinds of males that are available for mating, even if territory holders are potentially less attractive than floaters, as in red-collared widowbirds, *Euplectes ardens* (Andersson et al. 2002). The important point to note here is that female mating preferences may not necessarily be realized in the field but this does not negate the existence of such preferences (Kokko et al. 2003).

In blue-eyes, dominance and attractiveness are not necessarily synonymous. Traits such as body size, which are important in male–male competition, play no apparent role in female choice. Instead, females selected males capable of bringing more of their eggs to hatching. However, females would not have so benefited had they mated with males based on dominance per se. It is important to emphasize that dominant males are not necessarily bad for females as, in some cases, preferred males were also dominant and fighting ability may be correlated with other benefits (e.g. viability; but see Höjesjö et al. 2002). Rather, my results support the need for caution when generalizing about the way in which both processes of sexual selection are assumed to operate. Females do not always prefer dominant males nor is mating with males based on dominance a guarantee of maximal benefits to females.

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