Male competition is disruptive to courtship in the Pacific blue-eye

B. B. M. WONG

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

The present study examined the effects of competition on male courtship in the Pacific blue-eye *Pseudomugil signifer*, a species of fish where females have previously been shown to use courtship, but not male fighting prowess, as an important mate choice cue. Courtship bouts directed to a stimulus female were shortest when two males were allowed to freely interact (contact treatment) and longest when there was only one male (non-interaction). Courtship length in trials where one of two males was confined to a clear cylinder (visual) was intermediate between the other two treatments. Courtship in visual and contact treatments was constantly disrupted. The percentage of interrupted courtships was higher for the contact compared to visual treatment where aggressive interactions were also longer in duration and took place more frequently. Within contact trials, dominant males courted longer than subordinates despite both males experiencing comparable rates of courtship disruption. These results suggest that male-male competition can have important implications for adaptive female choice particularly in circumstances where the benefits being sought by females are unrelated to male fighting ability. © 2004 The Fisheries Society of the British Isles

Key words: courtship disruption; male-male competition; mate choice; sexual selection.

INTRODUCTION

Males generally compete for mating opportunities and this can have important consequences for female fitness. Many studies suggest that competition can benefit the choosing sex (Montgomerie & Thornhill, 1989; Howard *et al.*, 1998; Candolin, 1999, 2000; Berglund & Rosenqvist, 2001; Pizzari, 2001), bolstering the traditional view that competition and mate choice operate to mutually reinforce each other (Berglund *et al.*, 1996; Wiley & Poston, 1996). For example, in numerous species, signals of fighting ability also function as important cues in female choice (Berglund *et al.*, 1996). In such instances, competition can facilitate choice by compelling the competing sex to signal their condition honestly to avoid the high cost of deception if condition is ever challenged in combat (Candolin, 1999, 2000). In this regard, females have

---

Present address: Boston University Marine Program, 7 MBL Street, Woods Hole, MA 02543, U.S.A. Tel.: +1 508 289 7430; fax: +1 508 289 7413; email: bobwong@bu.edu

even been shown to deliberately manipulate male sexual behaviours by staging or inciting competition to ensure mating with winners of competition (Cox & Le Boeuf, 1977; Montgomerie & Thornhill, 1989; Semple, 1998; Pizzari, 2001). Although such studies intimate that competition should facilitate mate choice, the generality of this assumption has, surprisingly, been subject to few empirical tests (Candolin, 1999, 2000; Berglund & Rosenqvist, 2001; Kangas & Lindström, 2001).

Competition may not always be beneficial to females and, under some circumstances, may even hamper mate choice. Conflicts of interest often exist between the sexes when it comes to optimizing reproductive success (Moore *et al.*, 2001; Blankenhorn *et al.*, 2002; Pitnick & García-González, 2002; Chapman *et al.*, 2003), and just because female have preferences does not mean that they are always realized (Jennions & Petrie, 1997; Kokko *et al.*, 2003). Competition may, for instance, impinge on male signalling and negatively affect a female's ability to properly assess prospective mates as in hylid frogs, where important components of a male's advertisement call are obscured by other calls in the chorus (Wollerman, 1999). Similarly, deliberate interference may prevent females from mating with their preferred mate (Lanctot *et al.*, 1998) and stop more attractive suitors from displaying (Howard *et al.*, 1997). Although winners of competition often enjoy higher reproductive success, evidence suggests that females do not always prefer, or indeed benefit from, mating with winners of competition (Qvarnström & Forsgren, 1998; Moore & Moore, 1999; Andersson *et al.*, 2002; López *et al.*, 2002; Wong, 2004). If dominance does not correlate with male quality in terms of the fitness gains being sought by females, competition could, potentially, hamper mate choice (Candolin, 1999; Kangas & Lindström, 2001). Such a possibility exists in the Pacific blue-eye *Pseudomugil signifer* Kner, a freshwater fish from eastern Australia.

Female Pacific blue-eyes do not choose males based on their fighting prowess (Wong, 2004). This is because dominant males make average fathers: winners of male contests are no better at bringing a female's eggs to the hatching stage than losers. Male Pacific blue-eyes actively court females (Wong & Jennions, 2003) and, in previous experiments, females were found to prefer males that spend a greater proportion of time in courtship (Wong, 2004; Wong *et al.*, 2004). Although male Pacific blue-eyes do not actively care for the eggs other than through defence of the spawning site, courtship in Pacific blue-eyes, in common with other species of fishes (Knapp & Kovach, 1991; Östlund & Ahnesjö, 1998), appears to be important in signalling fitness gains to females in the form of higher egg hatching success (Wong, 2004). A previous experiment also showed that witnessing competition between rival males does not subsequently induce a female preference for superior fighters (Wong, 2004) in contrast to the study by Berglund & Rosenqvist (2001), consistent with the prediction that competition will only facilitate choice if female preference is for a trait (or traits) correlated with dominance (Candolin, 1999; Kangas & Lindström, 2001). Instead, it was suggested that competition may possibly hamper choice in Pacific blue-eyes (Wong, 2004). This is because male Pacific blue-eyes frequently engage in agonistic encounters in the field and courtship displays are often interrupted due to intrusion by other males (pers. obs.). Because of the importance of courtship as a cue, competing males may prevent

each other from signalling their quality accurately to females through disruption of one another's displays.

The aim of the present study was to examine the effects of male-male competition on courtship in Pacific blue-eyes by comparing the frequency and duration of aggressive interactions and courtship activity after manipulating the opportunity for male-male competition. It was predicted that courtship bouts directed towards females should be longer in the absence of competition. In treatments where males are able to interact, it was expected that courtship activity will be reduced due to male-male competition. Winners of competition, however, were also expected to court longer than losers because the former is likely to suppress courtship of the latter (Kangas & Lindström, 2001).

MATERIALS AND METHODS

Fish were collected in March and August 2001 from Ross Creek (19°27′ S; 146°36′ E), Townsville, Australia. Males and females were kept in six separate 300 l aquaria (50 fish per tank) on a 12L : 12D photoperiod and fed on a diet of manufactured fish flakes and live *Daphnia*. 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.

Experimental aquaria measured $90 \times 60 \times 60$ cm. Each tank was provided with two spawning mops to serve as spawning substrata, each made from 80 strands of 40 cm long green acrylic yarn as in Wong (2004). Three treatments were used in order to vary the extent of male-male competition in the experimental aquaria. In non-interaction trials, only a single male was added to the aquarium. In visual trials, two males were placed in the same aquarium but one male was chosen randomly and confined to a clear cylinder (20 cm diameter $\times$ 60 cm high) located at one end of the tank. In contact trials, two males were introduced directly into the same aquarium and were free to interact. A gravid female was introduced into each aquarium after the males were given 24 h to acclimate. Males and females measured a mean ± S.D. standard length (L_S) of 33.0 ± 3.2 and 31.3 ± 2.6 mm respectively with no significant difference in the L_S of males (Kruskal–Wallis test, $n = 15$, 30, 30, $P = 0.45$) or females (Kruskal–Wallis test, $P = 0.3$) among treatments. There was no difference in size between the paired males in the two competition treatments (Mann–Whitney U-test, $n_1 = n_2 = 15$, $P = 0.55$).

For each tank, behavioural observations were conducted 24 h after females were introduced to their aquarium. This was to ensure that all individuals were acclimated to their surroundings (Wong, 2004). Behavioural observations were carried out over a 20 min period. During this time, the frequency and duration of any agonistic encounters were recorded. In contact trials, individual differences in body size and fin length were used to help distinguish between the two males. Aggressive interactions in Pacific blue-eyes take two forms: lateral fin flaring displays and chases (Wong, 2004). The frequency and duration of courtship activity was also recorded, along with information on who was directing these behaviours and whether or not a display was interrupted by the other male in the tank. A display was defined as being interrupted when a male stopped his courtship of a female and immediately engaged in agonistic behaviours with the other male in the tank (Kangas & Lindström, 2001). Any spawnings that took place during the observation session were also noted.

In contact trials, it was possible to ascertain which of the two males was dominant (Wong, 2004). The dominant male was defined as the one who engaged in the most chases and fin-flaring displays towards the other male over the 20 min observation period (Wong, 2004). From this, the duration of uninterrupted courtship bouts were calculated for dominant and subordinate individuals. Any difference between the two groups in the proportion of courtship displays that were interrupted was also calculated.

All tests were two-tailed unless indicated otherwise.

RESULTS

MALE–MALE INTERACTIONS

Aggressive interactions were common in the two treatments where males were able to interact (*i.e.* visual and contact treatments). Aggressive interactions occurred more frequently during the contact compared to visual treatments [contact $= 25 \cdot 2 \pm 4 \cdot 9$, visual $= 4 \cdot 7 \pm 2 \cdot 1$ (mean $\pm$ s.e.); Mann–Whitney *U*-test, $n_1 = n_2 = 15$, $P < 0 \cdot 001$]. When aggressive interactions occurred, they were also longer in duration in the contact treatment [contact $= 2 \cdot 9 \pm 0 \cdot 6$ s, visual $= 1 \cdot 6 \pm 0 \cdot 5$ s (mean $\pm$ s.e.); Mann–Whitney *U*-test, $n_1 = n_2 = 15$, $P = 0 \cdot 028$]. These differences were due to the fact that males in the contact treatment were able to chase one another as well as fin flare whereas aggressive encounters in the visual treatment were restricted to fin flaring. A comparison of fin flares between visual and contact treatments revealed no significant difference in either the number of displays that took place (Mann–Whitney *U*-test, $n_1 = n_2 = 15$, $P = 0 \cdot 43$) nor the average length of display (Mann–Whitney *U*-test, $n = 10$, 11, $P = 0 \cdot 86$).

COURTSHIP

There was a significant difference in the average length of uninterrupted courtship bouts among the three treatments (Kruskal–Wallis test, $n = 45$, $P = 0 \cdot 02$). Courtship bouts were longest in the non-interaction treatment and shortest in the contact treatment (Fig. 1). Multiple comparisons among the three
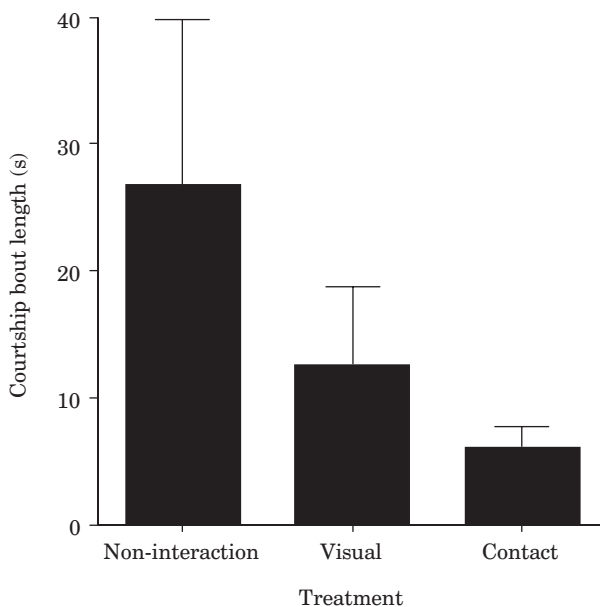

Fig. 1. The mean + s.e. length of uninterrupted courtship bouts of Pacific blue-eye under non-interaction (control) and interaction (visual and contact treatments). All courtships have been combined.

treatment groups (Siegel & Castellan, 1988) revealed that the only significant difference was between the non-interaction and contact treatments ($P < 0.05$).

Courtship in both interaction treatments was frequently interrupted by competition (Fig. 2). Moreover, the percentage of interrupted courtships was significantly higher in the contact compared to visual treatments [contact $= 32.2 \pm 7.8\%$, visual $= 4.3 \pm 2.6\%$ (mean $\pm$ s.e.); Mann–Whitney U-test, $n_1 = n_2 = 15$, $P = 0.001$].

In 86·7% of the contact trials (13 of 15), larger individuals dominated smaller opponents (binomial test, one-tailed $P = 0.0035$). Dominant males courted longer than their opponents (dominant $= 6.3 \pm 1.8$ s, subordinate $= 1.2 \pm 0.4$ s; Wilcoxon's signed ranks test, $n = 15$, $P = 0.009$). Dominant males were not simply courting more because they were larger and larger males court more. If this had been the case there should have been a positive relationship between the length of uninterrupted courtship bouts and L_S in the non-interaction treatment. There was no such relationship (Spearman's correlation, $n = 15$, $P = 0.90$; Wong, 2004). The subordinate male failed to court in two of the trials. Of the remaining 13 trials, dominant males were just as likely to have their courtship disrupted as subordinates (dominant $= 33.6 \pm 8.4\%$, subordinate $= 38.6 \pm 10.9\%$; Wilcoxon's signed ranks test, $n = 13$, $P = 0.81$).

SPAWNING

Eight of 45 females spawned during the observation period, four in the non-interaction treatment and two in each of the interaction treatments. The average length of uninterrupted courtship received by females that spawned was
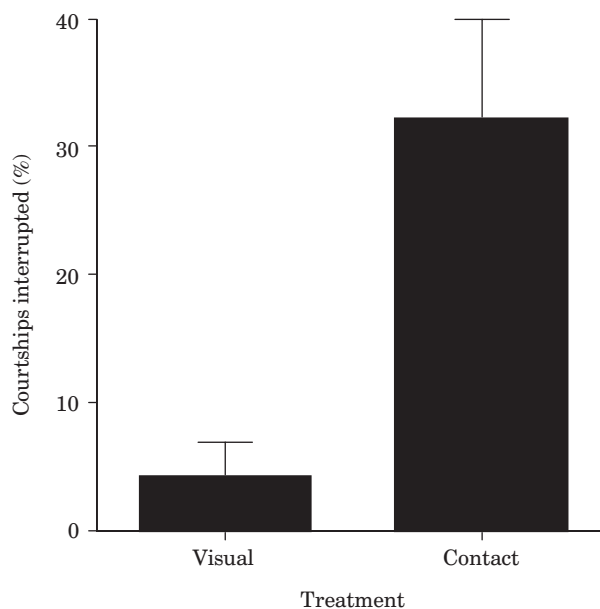

FIG. 2. The mean $+$ s.e. percentage of courtships disrupted of Pacific blue-eye under visual and contact treatments.

significantly higher than for those that did not (spawn $= 60\cdot5 \pm 22\cdot6$ s, $n = 8$; no spawn $= 5\cdot2 \pm 0\cdot6$ s, $n = 37$; Mann–Whitney U-test, $P < 0\cdot001$). This result, however, included courtship bouts that also contained actual spawning activity (*e.g.* positioning and laying eggs). Nonetheless, even when such bouts were excluded from analysis, the results were still significant (spawn $= 34\cdot4 \pm 10\cdot1$ s; Mann–Whitney U-test, $P < 0\cdot001$).

DISCUSSION

Competition has important implications for male courtship in the Pacific blue-eye. In the current experiment, males in the non-interaction treatment engaged in longer courtship bouts compared to those in the interaction treatments. These results are comparable with those reported in sand gobies *Pomatoschistus minutus* (Pallas) where the possibility for physical and visual interaction between rivals also made long courtship bouts unlikely (Kangas & Lindström, 2001). It is likely that time spent in competition may also impinge on time that could be spent interacting with females as in mosquito fish *Gambusia holbrooki* Girard where males experienced fewer mating opportunities when preoccupied with preventing other males from mating (Pilastro *et al.*, 2003). Indeed, when male Pacific blue-eyes did court, courtship displays were often disrupted by aggressive interactions. The percentage of disrupted courtships was greater in the contact than visual treatment due to direct interference in the former. In the field, fish densities and distance between territories is likely to dictate the extent to which courtships are disrupted (Lanctot *et al.*, 1998; Kangas & Lindström, 2001). No information presently exists regarding the effects of territory density or population sizes on courtship disruption in Pacific blue-eyes. Males have, however, on occasion, been observed interfering with the courtship of territory holders in the field (pers. obs.).

In the contact treatment, although dominant males and their subordinate rivals both experienced similar rates of courtship disruption, uninterrupted courtship bouts of the former were significantly longer than subordinates. Courtship activity in Pacific blue-eyes has an important bearing on male mating success. In a previous experiment, female Pacific blue-eyes were shown not to prefer males based on their fighting ability or traits correlated with fighting prowess (Wong, 2004). Instead, females chose males that spent a greater proportion of time in courtship and, in so doing, benefited through higher egg hatching success (Wong, 2004). Importantly, in the context of egg hatching success, when competition was controlled, courtship did not correlate with fighting ability: preferred males that courted more were not necessarily successful in competition (Wong, 2004). This contrasts with the results reported here where males that courted more under a competitive setting were also dominant.

The present findings, considered in concert with previous results (Wong, 2004), have interesting implications for how the two processes of sexual selection interacts in the Pacific blue-eye. In a competitive setting, male-male interactions results in dominant males displaying more to females. This, in turn, can induce a 'preference' for dominant males. Would this be beneficial or detrimental to females? It is certainly conceivable that females might gain indirect benefits by mating with superior fighters (*e.g.* inheritance of fighting prowess by her sons) so

the possibility exists that, by choosing males that court more in a competitive setting, females may actually be preferring dominant males. Alternatively, in common with other male guarding ectotherms (Møller & Jennions, 2001) if direct benefits (*e.g.* hatching success) are more important for female Pacific blue-eyes than any possible indirect gains, dominant males could potentially prevent 'better' subordinates (in terms of parenting abilities) from conveying their quality accurately to females. In so doing, it is conceivable competition might, in some situations, hamper female choice. This suggestion is based on the findings of Wong (2004) which showed that success in competition had no bearing on paternal abilities because dominant males, in fact, made average fathers.

The possibility that competition might hamper choice is consistent with results reported in other species where females do not prefer dominant males. Female tiger salamanders *Ambystoma tigrinum tigrinum* (Green), for example, prefer males with long tails, a trait that confers no competitive advantage during male fights (Howard *et al.*, 1997). Large body size, however, is important during male contest and larger, competitively superior male tiger salamanders hamper choice by interrupting the courtship of preferred (subordinate) suitors. Similarly, male sand gobies interfered with one another's courtship (Kangas & Lindström, 2001). This, in turn, impeded female assessment of mates because, like Pacific blue-eyes, female sand gobies use courtship as a cue to select males with superior parental abilities, a quality that is also unrelated to male fighting ability (Forsgren, 1997).

Such results provide an interesting comparison with studies where competition has been shown to facilitate choice. Female three-spined sticklebacks *Gasterosteus aculeatus* L., for instance, use the intensity of the male's red throat colouration as a cue in selecting males that are able to deliver superior parental care (Candolin, 1999). In this case dominant males are also better fathers and competition facilitates mate choice because the same signal used in female choice is also involved in signalling fighting ability (Candolin, 1999, 2000). Thus, competition ensures signal honesty by preventing poor quality subordinate males from signalling their condition dishonestly to females. Similarly in sex role reversed pipefish *Syngnathus typhle* L. 'choosy' males used signals displayed by competing females during contests to select their mates because these are also more reliable signals of mate quality (Berglund & Rosenqvist, 2001).

Traditionally, the two main components of sexual selection have been viewed as forces that operate by mutually reinforcing one another (Berglund *et al.*, 1996; Wiley & Poston, 1996). As a consequence, it seems logical to assume that competition ought to facilitate mate choice. But is this always the case? The question of whether mate choice is helped or hindered by competition may depend, in part, on whether superior fighting ability also reflects the kind of benefits that females seek. Future studies may wish to explore the generality of this assertion in other taxa.

References

Andersson, S., Pryke, S. R., Ornborg, J., Lawes, M. J. & Andersson, M. (2002). Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist* **160,** 683–691.

Berglund, A. & Rosenqvist, G. (2001). Male pipefish prefer dominant over attractive females. *Behavioral Ecology* **12,** 402–406.

Berglund, A., Bisazza, A. & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* **58,** 385–399.

Blankenhorn, W. U., Hosken, D. J., Martin, O. Y., Reim, C., Teuschl, Y. & Ward, P. I. (2002). The costs of copulating in the dung fly *Sepsis cynipsea. Behavioral Ecology* **13,** 353–358.

Candolin, U. (1999). Male-male competition facilitates female choice in sticklebacks. *Proceedings of the Royal Society of London, Series B* **266,** 785–789.

Candolin, U. (2000). Male-male competition ensures honest signaling of male parental ability in the three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* **49,** 57–61.

Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. (2003). Sexual conflict. *Trends in Ecology and Evolution* **18,** 41–47.

Cox, C. R. & Le Boeuf, B. J. (1977). Female incitation of male competition: a mechanism in sexual selection. *American Naturalist* **111,** 317–335.

Forsgren, E. (1997). Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society of London, Series B* **264,** 1283–1286.

Howard, R. D., Moorman, R. S. & Whiteman, H. H. (1997). Differential effects of mate competition and mate choice on eastern tiger salamanders. *Animal Behaviour* **53,** 1345–1356.

Howard, R. D., Martens, R. S., Innis, S. A., Drnevich, J. M. & Hale, J. (1998). Mate choice and mate competition influence male body size in Japanese medaka. *Animal Behaviour* **55,** 1151–1163.

Jennions, M. D. & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society* **72,** 283–327.

Kangas, N. & Lindström, K. (2001). Male interactions and female mate choice in the sand goby, *Pomatoschistus minutus. Animal Behaviour* **61,** 425–430.

Knapp, R. A. & Kovach, J. T. (1991). Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus. Behavioral Ecology* **2,** 295–300.

Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London, Series B* **270,** 653–664.

Lanctot, R. B., Weatherhead, P. J., Kempenaers, B. & Scribner, K. T. (1998). Male traits, mating tactics and reproductive success in the buff-breasted sandpiper, *Tryngites subruficollis. Animal Behaviour* **56,** 419–432.

López, P., Muñoz, A. & Martín, J. (2002). Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola. Behavioral Ecology and Sociobiology* **52,** 342–347.

Møller, A. P. & Jennions, M. D. (2001). How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88,** 401–415.

Montgomerie, R. & Thornhill, R. (1989). Fertility advertisement in birds: a means of inciting male-male competition? *Ethology* **81,** 209–220.

Moore, A. J. & Moore, P. J. (1999). Balancing sexual selection through opposing mate choice and male competition. *Proceedings of the Royal Society of London, Series B* **266,** 711–716.

Moore, A. J., Gowaty, P. A., Wallin, W. G. & Moore, P. J. (2001). Sexual conflict and the evolution of female mate choice and male social dominance. *Proceedings of the Royal Society of London, Series B* **268,** 517–523.

Östlund, S. & Ahnesjö, I. (1998). Female fifteen-spined sticklebacks prefer better fathers. *Animal Behaviour* **56,** 1177–1183.

Pilastro, A., Benetton, S. & Bisazza, A. (2003). Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish *Gambusia holbrooki*. *Animal Behaviour* **65,** 1161–1167.

Pitnick, S. & García-González, F. (2002). Harm to female increases with male body size in *Drosophila melanogaster*. *Proceedings of the Royal Society of London, Series B* **269,** 1821–1828.

Pizzari, T. (2001). Indirect partner choice through manipulation of male behaviour by female fowl, *Gallus gallus domesticus. Proceedings of the Royal Society of London, Series B* **268,** 181–186.

Qvarnström, A. & Forsgren, E. (1998). Should females prefer dominant males? *Trends in Ecology and Evolution* **13,** 498–501.

Semple, S. (1998). The function of copulation calls in the Barbary macaque (*Macaca sylvanus*). *Proceedings of the Royal Society of London, Series B* **265,** 287–291.

Siegel, S. & Castellan, N. J., Jr. (1988). *Nonparametric Statistics for the Behavioral Sciences.* New York: McGraw-Hill.

Wiley, R. H. & Poston, J. (1996). Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50,** 1371–1381.

Wollerman, L. (1999). Acoustic interference limits call detection in a neotropical frog *Hyla ebraccata. Animal Behaviour* **57,** 529–536.

Wong, B. B. M. (2004). Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Animal Behaviour* **67,** 583–590.

Wong, B. B. M. & Jennions, M. D. (2003). Costs influence male mate choice in a freshwater fish. *Proceedings of the Royal Society of London B (Supplement), Biology Letters* **270,** s36–s38.

Wong, B. B. M., Keogh, J. S. & Jennions, M. D. (2004). Mate recognition in a freshwater fish: geographic distance, genetic differentiation, and variation in female preference for local over foreign males. *Journal of Evolutionary Biology* **17,** 701–708.