Females prefer athletes, males fear the disadvantaged: different signals used in female choice and male competition have varied consequences

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The most commonly assumed cost for exaggerated male ornamentation is increased predation pressure owing to decreased locomotor performance or increased conspicuousness to predators. Despite its intuitive basis, the locomotor costs of male ornamentation are not well established. We tested the hypothesis that multiple male signals that are used independently during female choice and male competition could lead to varied locomotor costs. Multiple signals with varied costs could provide a more detailed indicator of overall male quality, as only the highest-quality individuals could support all costs. To test this idea, we investigated the burst locomotor consequences of multiple ornaments for males of the pacific blue-eye (*Pseudomugil signifer*). We evaluated five competing models relating body size, ornament size and performance traits to field measures of dominance and attractiveness. Non-propulsive male fin ornaments used during male competition were different from those used in female choice. First dorsal fin length was the most important predictor of male attractiveness, while dominance was only associated with anal fin length. Furthermore, first dorsal fin length was positively correlated with swim speed, while anal fin length was negatively associated with speed. Our study shows that multiple male signals that are used independently during male competition and female choice also differ in their associated costs. This provides a mechanism for understanding why locomotor costs for exaggerated male ornamentation are not often empirically demonstrated.

Keywords: burst swimming; locomotor costs; signals; ornaments; performance

1. INTRODUCTION

The elaborate ornamentation exhibited by males of many species can evolve because of the benefits accrued from increased access to mates either during male–male competition or female choice. These benefits are predicted to be counterbalanced by costs inherent in the production or possession of these traits (Andersson 1994). Costs to the individual occur via decreases in survival or increases in the energetic requirements associated with their maintenance (Møller 1989; Barbosa & Møller 1999; Kotiaho 2001; Basolo & Alcaraz 2003). This balance between the benefits received via sexual selection and the costs imposed through natural selection is the dominant mechanism thought to shape the evolution of male sexually selected traits (Andersson 1994). The most intuitive and commonly assumed cost for male ornamentation is increased predation pressure resulting from either increased conspicuousness to predators or decreased locomotor function (Rosenthal *et al.* 2001; Walker *et al.* 2005; for reviews, see also Lailvaux & Irschick 2006; Oufiero & Garland 2007). Simple consideration of the elaborate tail ornamentation of male peacocks emphasizes the logical basis of these presumed locomotor costs.

However, despite its intuitive basis, the influence of male ornamentation on locomotor function is not well established and the evidence is often mixed (Ryan 1988; Basolo & Alcaraz 2003; Royle *et al.* 2006; Wilson *et al.* 2009; but for other associated costs see Møller 1989; Kotiaho 2001; Karino *et al.* 2006).

The most convincing and widely reported evidence demonstrating the negative effects of male ornamentation on locomotor function is largely based on theoretical studies rather than direct empirical evidence. Using models of flight behaviour, Barbosa & Møller (1999) demonstrated that male barn swallows with longer tail feathers have increased drag during flight and decreased foraging efficiency. The potential locomotor costs of exaggerated male ornamentation should be even more pronounced for aquatic organisms, owing to the greater viscosity and drag of the surrounding fluid. However, evidence for a pronounced locomotor cost for male ornamentation from studies of fish is also varied (Ryan 1988; Basolo & Alcaraz 2003; Royle *et al.* 2006). No effect of natural variation in sword length on swimming endurance was observed for male *Xiphophorus nigrensis* (Ryan 1988), while sword length was positively associated with burst swimming performance for male *Xiphophorus helleri* (Royle *et al.* 2006).

Three hypotheses (not mutually exclusive) could help explain the limited empirical support for these predicted locomotor costs. First, as suggested by the lack of strong empirical support, greater exaggeration of male

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ornamentation may not actually be commonly associated with reductions in locomotor function. Second, high-quality males may possess compensatory traits that increase locomotor function and mask the detection of the predicted locomotor costs (Møller 1996; Oufiero & Garland 2007). The third hypothesis is based on the implications of recent studies that reveal female choice and male competition can act independently on different male ornament traits. Multiple signals are used by the males of many organisms and can provide a more detailed indicator of overall male quality than just a single cue, as only the highest-quality individuals are able to perform well across all tasks (Candolin 2005; Meyers *et al.* 2006). For example, Candolin (2005) showed in the water boatman (*Sigara falleni*) that condition-dependent traits used during female choice were determined at different life-history stages from those used during male–male competition. Only individuals in good condition throughout both developmental stages can compete with males and successfully attract females. Different male ornament traits that also vary in their associated costs (e.g. greater energetic, predator detection, locomotor and other costs) could also potentially provide a more robust test of an individual male's quality. This hypothesis predicts that different male ornament traits that are used as independent signals by males and females could also vary in their locomotor consequences. Thus, only high-quality males could bear traits that have multiple independent costs. To test this idea, we investigated both the consequences of multiple ornaments in the pacific blue-eye (*Pseudomugil signifer*) for burst locomotion and whether these signals are used differently during male–male competition and female choice.

The pacific blue-eye is a small egg-laying highly sexually dimorphic fish native to eastern Australia and has been extensively used as a model species for studies of sexual selection (Wong & Jennions 2003; Wong 2004a,b). Males possess highly exaggerated non-propulsive fin extensions on the first and second dorsal and anal fins that are used during spectacular fin-flashing displays at passing females and rival males. Males are highly aggressive and establish small territories close to the water's edge, while females move in small groups and inspect the males and their territories. Importantly, previous studies suggest that ornament traits that are used during male competition do not appear to predict female choice (Wong 2004b), suggesting this species is ideal for work on varied ornament signals and their consequences for burst locomotion. We evaluated five competing models relating body size, ornament size and performance traits to field measures of dominance and attractiveness using the statistical approach advocated by Oufiero & Garland (2007; following Arnold 1983). We predicted that different male ornaments that are independently associated with dominance and attractiveness would also differ in their consequences for burst locomotion.

2. MATERIAL AND METHODS

We examined the territorial and mating behaviour of male *P. signifer* in a large slow-flowing pool (50 × 10 m) near the upper reaches of Bouloumba Creek in southeast Queensland. We recorded the morphometrics, ornamentation, burst

swimming performance, dominance and attractiveness of 40 individual males.

All behavioural observations were conducted between 9.00 and 13.00 during full sun exposure and peak territorial activity. Observations for each male were preceded by a 5 min initial assessment to ensure that each focal male maintained a territory. The total number of displays to rival males, number of wins against rival males (opponent male would swim away), number of losses (focal male would swim away from opponent after mutual display), number of displays to passing females and total number of females inspecting a male by entering the male's territory were recorded over a 10 min period. Males were then captured using a large aquarium net (20 × 20 cm). Total territory size was estimated using 1 × 1 m quadrats with 0.05 × 0.05 m divisions (0.0025 m² squares) to measure the total number of squares each individual fish inhabited during the observation period.

Male attractiveness was defined as the total number of visitations by females, and a dominance score was derived for each male from the following equation:

$$\text{dominance} = \left(\frac{W - L}{E} \right) + \left(\frac{E}{\max(E)} \right) + \left(\frac{W}{\max(W)} \right),$$

where W is the number of male–male contests won, L is the number lost, E is the total number of encounters with rival males ($W + L$), $\max(E)$ is the highest number of encounters observed for any of the focal males and $\max(W)$ is the highest number of wins observed for any of the focal males.

Burst swimming performance was assessed by filming five startle responses for each individual with a high-speed digital camera. Swimming responses were elicited by placing fish into the centre of a swimming arena (0.2 × 0.2 × 0.1 m deep) and tapping the side of the tank. Swimming sequences were filmed at 200 Hz (Redlake Imaging Corporation, USA) by recording the image off a mirror that was suspended at 45° above the aquarium. The accompanying software package was used for analysis of the first 100 ms of a startle response following the initial C-start. Escape responses consisted of an initial bending of the body into a C-configuration (stage 1) followed by a contralateral contraction of the body (stage 2) and then several propulsive strokes (stage 3; Domenici & Blake 1997). Sequences were replayed frame-by-frame and the start of the analysis was taken as the end of the first half tail beat immediately after the initial C-start (stage 1). As such, we analysed swimming during stages 2 and 3 of each individual's burst response. During analyses, the centre region of the head (i.e. between the eyes) was digitized as this was the easiest and most consistent point of reference and there was no detectable effect of lateral movement on performance.

We calculated maximum instantaneous swimming velocity ($U_{\max}$), maximum instantaneous acceleration ($A_{\max}$) and the stride velocity averaged over a full stride (U_S) from each response. Instantaneous measures of velocity were calculated by differentiating distance data that were previously subjected to a three-point moving average filter (Wilson & Franklin 1999), where each datum point is derived from the average of three successive raw distance measurements. Instantaneous measures of acceleration were calculated by differentiating the velocity data. Measures of velocity averaged over a stride (U_S) were also calculated over the full stride immediately following stage 1 (i.e. throughout the second and third half tail beat). We analysed all five trials for each individual and took all three performance traits

Figure 1. (a) Model A, (b) model B, (c) model C, (d) model D and (e) model E. Five path models showing predicted relationships among morphology (body length and ornamentation), burst swimming performance, attractiveness and dominance for males of the pacific blue-eye (*P. signifer*).

from the one swim that produced the highest instantaneous velocity. Thus, $U_{\max}$ was defined as the peak instantaneous velocity attained by an individual in any of the five swims, while $A_{\max}$ was the peak acceleration and U_S was the stride velocity taken from this same swim. All performance traits were positively correlated, and the first axis from a principal components analysis of all swimming traits described greater than 90 per cent of the variation. Thus, this first axis was deemed a suitable measure of overall burst swimming performance (U_P) for each individual. All subsequent analyses were conducted using U_P .

Body and fin morphometrics were determined for each male from lateral images captured with a Panasonic digital camera and analysed with morphometric software (SIGMA-SCAN 5.0). Fish were anaesthetized at 5°C and then photographed in a lateral position. Seven different morphological measures were taken from each photo: standard length, total length, maximum body depth, ornament length of the first and second dorsal fins, anal fin ornament length and caudal fin length. We used three independent measures (first dorsal, second dorsal and anal fins) of ornamentation for subsequent path analyses.

We evaluated five competing models relating morphological and performance traits to dominance and attractiveness (figure 1). Models were fitted by path analyses conducted

with AMOS 5.0 (SPSS Inc., Chicago, IL, USA). After fitting each model, we calculated the second-order Akaike information criterion (see equation in the electronic supplementary material) and the weights were used to assess which model was most likely to be correct. Correlations between measures of dominance and attractiveness were performed using Pearson's product moment correlation. Statistical significance was taken at the level of $p < 0.05$ and data are presented as means $\pm$ s.e.

3. RESULTS

We found substantial variation in body dimensions and fin ornamentation among male *P. signifer* (table 1). $U_{\max}$ of male *P. signifer* was unaffected by total body length ($r^2 = 0.02$; $p > 0.05$; $n = 40$) and averaged $1.17 \pm 0.03 \text{ m s}^{-1}$ (table 1). Although these represent high body-length-specific swim speeds, these are similar values to other species when the allometry of swim speed is considered (Domenici & Blake 1997).

Each male–male interaction typically resulted in mutual lateral fin displays by both rival males that lasted about 1–2 s. However, on several occasions, male–male signalling escalated to extended fights that involved both signalling and biting. We observed up to 50 flared fin

Table 1. Body and fin ornamentation dimensions and maximum burst swimming speed for the 40 male pacific blue-eyes (*P. signifer*) used in this study.

parameter	average $\pm$ s.e.	range
total length (mm)	28.23 $\pm$ 0.36	24.66–33.59
standard length (mm)	24.37 $\pm$ 0.31	21.02–29.02
maximum body depth (mm)	5.93 $\pm$ 0.09	5.00–7.31
first dorsal fin (mm)	7.06 $\pm$ 0.31	3.31–14.35
second dorsal fin (mm)	5.59 $\pm$ 0.18	3.59–7.29
anal fin length (mm)	5.84 $\pm$ 0.16	3.90–7.84
caudal fin length (mm)	5.93 $\pm$ 0.09	4.91–7.40
max. instantaneous speed (m s ⁻¹)	1.17 $\pm$ 0.03	0.82–1.69
max. stride speed (m s ⁻¹)	0.89 $\pm$ 0.03	0.51–1.21
max. acceleration (m s ⁻²)	22.1 $\pm$ 2.5	11.9–28.8

displays directed towards rival males, with an average of 16.1 ± 2.0 displays per individual over the 10 min observation period. The average number of aggressive interactions that resulted in focal males chasing away rival males was 25.8 ± 3.5 (0–97). In contrast, focal males, which all occupied a territory, were chased away by rival males and lost on average 8.6 ± 2.2 bouts. Estimated territory size for individual males was 0.76 ± 0.09 m², ranging from 0.07 to 2.7 m². We found female *P. signifer* usually associated with other females in the deeper water just beyond the shallow territories of the males. Females regularly ventured towards the shallower regions to inspect both the displaying males and their territories. Males were visited on average on 28.6 ± 2.5 occasions by females during the observation period, with one male visited on 81 separate occasions. Although some females undoubtedly revisited individual males and values are not independent female visitations, it allowed a relative measure of female attention given towards each male. Male dominance was highly positively correlated with scores of attractiveness ($n = 40$, $r_p = 0.63$; $p < 0.0001$; figure 2).

Of the models described in figure 1, model E was more than 99 per cent likely to provide the best description of the data (table S2 in the electronic supplementary material; figure 3). Using the simplified model E, after removal of non-significant correlations from the model, we found dominance was largely determined by anal fin ornamentation ($p < 0.001$), while attractiveness was determined by first dorsal ornamentation ($p < 0.001$). U_p was negatively associated with anal fin ornamentation ($p < 0.001$), but positively associated with first dorsal ornamentation ($p < 0.001$).

4. DISCUSSION

Our study shows that multiple male signals that are used independently during male–male competition and female choice can also differ in their associated costs. The first dorsal fin of male *P. signifer* was highly positively associated with burst swimming speed, while the anal fin was negatively associated with burst swim speed. First dorsal fin length of male *P. signifer* was the most important predictor of field measures of male attractiveness, while dominance was only associated with anal fin length. Wong (2004b) also found that female preference in

Figure 2. The relationship between measures of attractiveness (number of female visitations) and dominance (§2) recorded for 40 male pacific blue-eyes (*P. signifer*; $n = 40$, $r_p = 0.63$; $p < 0.0001$).

P. signifer is not directed towards the same male attributes that predict dominance. Candolin (2005) showed that multiple cues can provide a more complete picture of overall male quality than a single cue reflecting condition. As such, multiple signals that differ in the types of associated costs or consequences could also provide a more complete indicator of male quality. This provides a mechanism for understanding why locomotor costs for exaggerated male ornamentation are not often empirically demonstrated.

The maintenance of the reliability of sexual signals as indicators of male quality is predicted to occur via either performance-based signalling or through the costs imposed by the production or maintenance of the signals (Maynard Smith & Harper 2003). We found a complex relationship between ornamentation and burst swimming performance for male *P. signifer*. Although the first dorsal fin length was positively correlated with burst speed, it is unlikely the fin could provide any possible propulsive benefits as the extended filaments are not rigid and trail behind the upper body. Instead, it is likely that these faster swim speeds may be due to an associated correlation between condition or physical fitness and relative first dorsal fin ornamentation. Such a correlation provides a clear and reliable signal for assessing a male's physical quality, but how the reliability of this signal is maintained is not evident. Similarly, Royle *et al.* (2006) found that male green swordtails with the longest sexual ornaments ('swords') have the greatest burst swimming speed. In contrast, the anal fin ornaments of male *P. signifer* were negatively correlated with burst escape swim speed, providing support for the predicted hydrodynamic costs of increased ornamentation. The anal fin ornaments remain unextended and trail behind the lower body of the fish during burst swimming and could increase drag coefficients that reduce locomotor function.

We found field measures of dominance for male *P. signifer* were highly correlated with male attractiveness. In contrast, a previous study of *P. signifer* in the laboratory found more dominant males were not necessarily preferred by females (Wong 2004b). Differences between these studies may be due to our analyses being conducted *in situ* in the field environment, where male–male competition can also potentially hamper female choice by

Figure 3. The best path model explaining morphological and performance relationships with attractiveness and dominance after removal of non-significant correlations from model E (figure 1e). Significant correlations were detected at the level of $**p < 0.001$.

excluding males from access to high-quality territories (Wong & Candolin 2005). Female visitation rates in our study were a product of both the males' physical attributes and the resources guarded within their territory. Thus, the ability of dominant males to maintain a territory with desirable characteristics for egg rearing may explain the close correlation between male dominance and attractiveness scores. We also found no direct relationship between maximum swimming speed and measures of either dominance or attractiveness for male *P. signifer*.

Our analysis of the costs of a putative sexually selected trait (relative ornamentation) does not explicitly consider any compensatory mechanisms that may mask the detection of these costs at the whole-performance level (Møller 1996; Oufiero & Garland 2007) and even lead to positive correlations between ornamentation and locomotion (as per the first dorsal fin of *P. signifer*). An interspecific comparative study of birds by Balmford *et al.* (1994) provides evidence for such compensatory traits, as species with elongated male tails have also evolved increased wing-spans. It is feasible that the absence of any detected costs of the second dorsal fin for male *P. signifer* and positive correlations for the first dorsal fin may be due to associated compensatory traits that improve performance, as suggested by Oufiero & Garland (2007). It is also possible that there may be other locomotor costs associated with the exaggerated fin ornamentation of male *P. signifer* that were not detected in our study. We captured only a single measure of locomotor function (burst swimming), and other measures of locomotor performance, such as steady swimming and agility, may have revealed different locomotor consequences. For example, previous studies of steady swimming in the swordtail *Xiphophorus montezumae* revealed males that possessed long swords had greater metabolic costs during both routine and courtship swimming than males with shortened swords (Basolo & Alcaraz 2003). In contrast, males of the green swordtail *X. helleri* possessing long swords had greater burst swimming speeds than males with small swords (Royle *et al.* 2006). Like previous analyses of the locomotor costs of male sexual ornaments, we found a complex relationship between ornamentation and burst swimming performance for male *P. signifer*. We provide data showing that male signals that are used independently during male competition and female choice also differ in their associated consequences for burst locomotion.

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