Large body size for winning and large swords for winning quickly in swordtail males, *Xiphophorus helleri*

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(Received 18 July 2007; initial acceptance 17 September 2007; final acceptance 25 December 2007; published online 16 April 2008; MS. number: 9460)

Contestants can either assess their own resource-holding potential relative to their opponent (mutual assessment) or rely solely on the assessment of their own fighting ability (self-assessment). To discriminate between these possibilities, we staged dyadic territorial contests between ‘size-matched’ male swordtails. These contests consist of a combination of ritualized displays and direct fighting. Although size differences were small, winners were larger than losers and smaller fish tended to be winners only when the size difference was negligible. Body size, however, did not influence contest duration and there was no increase in contest duration with mean body size; thus, there is no support for self-assessment in these animals. We also examined the effects of the sword, which comprises a sexually selected extension used in female choice that reduces swimming efficiency but increases acceleration. The length of the sword (adjusted for body size) did not differ between winners and losers; however, losers conceded earlier if the opponent had a large sword for its body size but this decision was independent of the loser’s own sword length. Losers thus assessed the swords of winners, which precludes self-assessment; however, because winners appeared not to assess the swords of losers, this does not fully support the idea of mutual assessment.

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Keywords: honest signal; male–male contest; mutual assessment; self-assessment; swordtail fish; *Xiphophorus helleri*

Animal contests are usually settled on the basis of asymmetries in fighting ability or resource-holding potential (RHP; reviewed in Huntingford & Turner 1987; Andersson 1994; Riechert 1998; Briffa & Sneddon 2007), resource value (e.g. Cross et al. 2006) and resource ownership (Olsson & Shine 2000). Previous experience (reviewed in Hsu et al. 2006), injuries (Taylor & Jackson 2003), metabolic costs and/or constraints (reviewed in Briffa & Sneddon 2007) and hunger (Stocker & Huber 2001) may influence contest outcome. Selection is expected to favour individuals that gather accurate information about the costs and benefits of conflict (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981). Contestants with information about their own RHP are expected to benefit if they can also assess the ability of their opponents. Such ‘mutual assessment’ allows rivals to obtain a reliable estimate of differences in ability between themselves and their opponent. They can then use this information in deciding whether to continue fighting. Alternatively, contestants may rely solely on an estimate of their own RHP, persisting in contests in accordance with their own fighting ability (‘self-assessment’ or ‘own size assessment’; e.g. Taylor & Elwood 2003), and not in accordance with their relative RHP. In both cases, the loser’s decision to give up determines the duration of the contest.

A negative relation is commonly found between the relative size of the contestants and the cost (duration, physiological change or number of specific signals) of a contest and this trend has historically been considered as support for the hypothesis of mutual assessment.
However, self-assessment may also produce this relation (Taylor & Elwood 2003). These two hypotheses may be distinguished by two main methods. First, in random pairings, the relation between the winner's size and the costs of the contest is expected to be positive in self-assessment but negative for mutual assessment (Taylor et al. 2001; Taylor & Elwood 2003). Second, large size-matched pairs are expected to incur greater costs than small size-matched pairs in self-assessment but not in mutual assessment (Taylor & Elwood 2003).

We investigated the mode of assessment and contest resolution in swordtail fish (Poeciliidae). Competitive interactions between males are well documented (e.g. Francis 1983; Franck & Ribowski 1987, 1989; Beaugrand et al. 1991, 1996), comprising a series of escalating activities (see Franck & Ribowski 1989) from a form of lateral inspection and display to biting, nipping and mouth wrestling. Previous work has largely focused on factors influencing contest outcome although, as with much research on contests (Taylor & Elwood 2003), until recently the prospect of self-assessment has been largely ignored. Body size, sword length, previous experience (but see Earley & Dugatkin 2002) and prior residency have all been reported to affect (either individually or in combination) contest outcome in swordtails (Hemins 1966; Franck & Hendricks 1973; Franck & Ribowski 1987, 1989; Beaugrand & Beaugrand 1991; Beaugrand et al. 1991, 1996; Beaugrand 1997; Benson & Basolo 2006).

The ‘sword’ in these fish comprises a set of multi-coloured fin rays extending well beyond the caudal margin (Benson & Basolo 2006). Large swords confer an advantage in attracting females (Basolo 1990; Basolo & Trainor 2002) but at a cost to the bearer in terms of predation risk (Basolo & Wagner 2004) and increased energy expenditure in sustained swimming (Basolo & Alcaraz 2003). However, large swords enhance the fast-start swimming response that, in contradiction to the above, should increase ability to escape from predators (Royle et al. 2006). Because fights are generally energetically demanding (Briffa & Sneddon 2007), it is possible that males would suffer a cost of long swords in contests. However, Benson & Basolo (2006) found that variation in natural sword length did not influence the outcome of fights. When artificial swords of equal size were attached to fish but painted to appear different, males with the apparently larger swords were more likely to win (Benson & Basolo 2006). In this case the cost of the apparently large and small swords would have been the same because they would have had the same hydrodynamic effect. We explored how variation in sword length influences fight outcome and fight duration and whether that might help distinguish between self- and mutual assessment. By examining contests between size-matched rivals, we should be better able to investigate the effects of sword length on contests.

If longer swords impose a cost in contests, then for self-assessment we predicted that losers would have longer swords for their body size than winners and that the longer the sword the sooner the animal should give up. For mutual assessment we predicted that relative sword length would be a determinant of contest duration with swift resolution occurring when the winners have swords that are much shorter than those of losers.

Alternatively, the sword might confer an advantage (Benson & Basolo 2006) and this could be for two reasons. First, the sword might specifically enhance the ability to fight (e.g. by increasing stability during slow movements) and either self-assessment or mutual assessment could occur. Second, it might be a signal to the opponent that the bearer is in good condition and therefore a good fighter, but without specifically enhancing fighting ability, that is, it might be a badge (e.g. Rohwer 1975; reviewed in Searcy & Nowicki 2005; but see Royle et al. 2005). In this case the sword can only be used to influence the motivation of the opponent and that implies mutual assessment. Thus if the relation between sword length and contest duration indicates self-assessment, it would also indicate that the sword confers an advantage in RHP. If this relation indicates mutual assessment, the sword could either increase RHP or be a signal of quality.

**METHODS**

**General Methods**

Swordtail males were obtained from a local supplier (Grosvener Tropicals, Belfast, U.K.) and kept in mixed-sex groups in laboratory aquaria ranging in size from 54 to 90 litres. Tanks were equipped with chemical and biological filtration, substantial aeration and a gravel substrate to a depth of 6 cm with plants as refuges. Temperature was maintained between 25 and 27°C and pH between 7 and 8, with a 12:12 h light:dark cycle. Fish were fed Tetra-Min flake food (Tetra GmbH, Melle, Germany) twice daily, and bloodworm (red mosquito larvae, San Francisco Bay Brand, Newark, California, U.S.A.) once a day. Two groups of males were maintained separately with females. Allowing males to be exposed to females reduced the risk of inappropriate responses to conspecifics (Franck & Hendricks 1973) and was expected to promote competition between males.

Our basic methodology followed that of Earley et al. (2005). We removed males from holding tanks, transferred them to individual 8-litre screened-off, isolation tanks for 48 h, and then placed them in experimental aquaria for a 16 h acclimation period. This gives a total period of 64 h without social interaction to mitigate the behavioural effects of prior experience of winning and losing that may persist for at least 24 h in *X. helleri* (Franck & Ribowski 1987). Experimental aquaria consisted of a 20-litre tank divided in half by an opaque, removable, corrugated plastic partition. The partition was removed at the start of an observation. All pairs were novel and matched by eye, resulting in a mean size difference of 5.83% body length. This resulted in a strong correlation between the size of the larger and smaller opponents in the dyads (Pearson correlation: $r_{29} = 0.86$, $P < 0.0001$), but a weaker relation between the swords of the contestants ($r_{29} = 0.41$, $P = 0.021$). Each male of the pair was from a different stock tank. Experimental tanks, isolation tanks, stock tanks and subjects in experimental tanks were visually isolated from one another, thereby
eliminating the possibility of gaining information by ‘eavesdropping’ (Earley & Dugatkin 2002).

Determining the point in the interaction at which the contest is over and the outcome is decided is key to our analysis. We defined the decision time (end of a contest) as the initiation of chasing. The initiation of chasing by one contestant and rapid retreat by the other denotes the point when contest roles are decided (fixed; see Benson & Basolo 2006). Contest duration was determined as the interval between the start of the interaction and the initiation of chasing behaviour.

Morphological Measurements

Immediately after observation, we removed both fish from the experimental tanks using a hand net and killed them with a lethal dose of the anaesthetic MS222. We measured males with digital callipers (Moore & Wright model no. M&W3412280B). For each fish we measured body length (mm) from the anterior of the head to the base of the caudal fin along the mid line, body (flank) height (mm) from gonopore to base of dorsal fin, and sword length (mm) from the proximal margin of the caudal fin to the distal tip of the sword. We estimated the body surface area as the area of an ellipse (area = \( \pi \times (a \times b) \), where \( a \) is the length of the major axis/2, i.e. body length/2, and \( b \) = the length of the minor axis/2, i.e. body (flank) height/2) as a measure of body size that is independent of the sword length.

Statistical Analyses

Two-tailed summary statistics are presented as mean ± SE. For analyses we used JMP version 5 for Macintosh (SAS Institute Inc., Cary, NC, U.S.A.). Prior to carrying out tests, we checked the normality of data by visual examination of distributions and by a Shapiro–Wilks W test. Non-normally distributed data were log transformed before parametric analyses were done. Body size and sword length in winners and losers were compared in paired t tests. We also examined how size and sword length predicted outcome in a multivariate logistic regression. Univariate and multivariate regression analyses were used to examine relations between contest cost (duration and intensity, i.e. level of contest escalation) and RHP (fighting ability).

Ethical Note

In nature, swordtail males defend home ranges aggressively against other males (Franck & Ribowski 1993; Franck et al. 1998). While it was our intention to intervene should levels of aggression become so severe as to result in physical injury, this was not necessary. We did not detect any wounds or mortality as a result of observed aggressive behaviour in test subjects. Males were always free to escape an aggressor by swimming away to another area of the tank. All aspects of the research were covered by a U.K. Home Office project licence and conducted by an experienced personal licence holder. Subject males were killed after observation to provide data for another study.

RESULTS

Thirty-seven male–male contests were observed. However, data on contest duration are available for only 31 dyads, as chasing did not occur in six pairings (i.e. the contest was not resolved before termination of observation, 1 h). Mean contest duration ± SE was 1000.27 ± 122.09 s (range 155.2–2951.7 s). Sword length was weakly correlated with body length (Pearson correlation: \( r_{60} = 0.261 \), \( P = 0.040 \)), but not with body height (\( r_{60} = 0.020 \), \( P = 0.880 \)) or body surface area (\( r_{60} = 0.139 \), \( P = 0.283 \)). Winning males had longer and taller bodies, and consequently greater body surface area than losers (Table 1). However, we found no statistical differences between winners and losers with regard to absolute sword length or residuals of sword length against body size (size-corrected sword length). We therefore used body surface area as a measure of body size in further analyses.

A multivariate logistic regression examined which variables predicted outcome in these contests when examined in combination. An overall model including body size for the larger and smaller animal and body size-corrected sword length for each male (residuals) was not significant (\( U = 0.21, N = 31, X^2 = 7.26, P = 0.108 \)), although the size of the larger (likelihood ratio test: \( G_1 = 4.84, P = 0.028 \), \( B = -12.49 \)) and smaller male (\( G_1 = 5.96, P = 0.015, B = 13.57 \)) had equal and opposite effects on the probability that the larger contestant won. Body size-corrected sword length did not predict contest outcome (larger male: \( G_1 = 0.46, P = 0.499, B = -0.08 \); smaller male: \( G_1 = 0.34, P = 0.562, B = -0.09 \)). To examine the effects of body size difference on the probability of the larger fish winning, we repeated the analysis but used body size difference instead of the individual sizes. The overall model was marginally nonsignificant (overall model: \( U = 0.21, N = 31, X^2 = 7.26P = 0.064 \)). However, size difference predicted outcome in terms of whether or not the larger contestant won (\( G_1 = 5.64, P = 0.018, B = 2.31 \)).

Table 1. Comparison of morphological measurements between winners and losers in contests between male swordtails, X. helleri, matched for size

<table>
<thead>
<tr>
<th>Loser</th>
<th>Winner</th>
<th>( t_{50} )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length (mm)</td>
<td>44.85±1.09</td>
<td>46.84±1.01</td>
<td>−3.22</td>
</tr>
<tr>
<td>Body height (mm)</td>
<td>13.38±0.36</td>
<td>14.06±0.35</td>
<td>−2.98</td>
</tr>
<tr>
<td>Surface area (mm(^2))</td>
<td>478.92±24.02</td>
<td>523.50±22.71</td>
<td>−3.58</td>
</tr>
<tr>
<td>Sword length (mm)</td>
<td>31.30±1.08</td>
<td>29.92±0.89</td>
<td>0.69</td>
</tr>
<tr>
<td>Size-corrected sword length (mm)</td>
<td>0.02±0.04</td>
<td>−0.02±0.03</td>
<td>0.88</td>
</tr>
</tbody>
</table>

Means ± SE for raw (untransformed) data are presented; paired t tests were conducted on transformed data (see text for details of calculations).
Body size-corrected sword length for winners was negatively related to contest duration (Fig. 1). Body size-corrected sword length for losers was not related to contest duration (larger male: $G_1 = 0.42, P = 0.518, B = -0.07$; smaller male: $G_1 = 0.59, P = 0.443, B = -0.11$). Thus, body size but not sword length influenced the outcome of fights.

**RHP, Contest Duration and Escalation**

We carried out a multivariate regression on log contest duration with body size and body size-corrected sword length for winners and losers. The overall model was not significant ($N = 31, F_{4,30} = 2.23, R^2 = 0.256, P = 0.093$). However, size-corrected sword length for winners was negatively related to contest duration ($F_{1,30} = 6.65, \beta = -2.30, P = 0.016$) but no other variable was significant (body size winners: $F_{1,30} = 0.93, P = 0.344$; body size losers: $F_{1,30} = 0.37, P = 0.548$; sword length losers: $F_{1,30} = 0.41, P = 0.526$). Sequential stepwise removal of the least significant variable did not improve the model markedly. This multivariate model was not far removed from the univariate regression of body size-corrected sword length for winners versus log contest duration ($N = 31, F_{1,30} = 7.02, R^2 = 0.195, \beta = -2.01, P = 0.013$; Fig. 1). Body size-corrected sword length for losers was not related to log contest duration ($F_{1,30} = 0.99, \beta = -0.55, P = 0.328$). Furthermore, the difference between winners and losers in body size-corrected sword length was not related to contest duration ($N = 31, F_{1,30} = 0.34, R^2 = 0.012, \beta = -0.29, P = 0.566$). Similarly, the difference in body size between winners and losers was not related to contest duration ($N = 31, F_{1,30} = 0.54, R^2 = 0.018, \beta = -0.13, P = 0.468$). Thus, only body size-corrected sword length of the winner influenced duration of the contest.

A specific prediction of the self-assessment model is that contest duration should increase with increasing mean contestant size when rivals are matched for size (Taylor et al. 2001; Taylor & Elwood 2003); however, when this was included in the multivariate regression model, contest duration did not change with mean contestant body size ($F_{1,30} = 1.25, \beta = 53.13, P = 0.274$).

The probability that a fight escalated to mutual biting was not influenced by the body size or sword length (corrected for body size) of winners and losers ($U = 0.074, N = 31, \chi^2 = 3.00, P = 0.559$). Having excluded those fights that were resolved after mutual biting, the probability of further escalation to mouth wrestling was also not related to the body size or sword length ($U = 0.078, N = 20, \chi^2 = 2.10, P = 0.718$). We repeated the analysis of the probability of escalation to mouth wrestling, for all contests, but again the probability that a contest escalated to mouth wrestling was not affected by size or sword length ($U = 0.054, N = 31, \chi^2 = 2.22, P = 0.700$). Substituting body size difference or difference in sword length did not improve the models.

**DISCUSSION**

Contest outcome was dependent on male size, with winners being greater in length, height and surface area. Such a size advantage is a common feature of animal contests (reviewed in Huntingford & Turner 1987; Andersson 1994; Riechert 1998; Briffa & Sneddon 2007), including those of swordtails (Beaugrand & Zayan 1985; Beaugrand et al. 1991, 1996; Ribowski & Franck 1993; Moretz 2003; Benson & Basolo 2006). Body size may affect outcome by either self-assessment or mutual assessment. To distinguish between these possibilities, we examined whether contest duration increased with mean contestant size, as predicted by the self-assessment model (Taylor & Elwood 2003) but found no significant effect and hence no evidence of self-assessment. The self-assessment model has been found to apply to various species including fiddler crabs, *Uca mjoeberti* (Morrell et al. 2005), amphipods, *Gammarus pulex* (Prenter et al. 2006), jumping spiders, *Plexippus paykulli* (Taylor et al. 2001), tree wetas, *Hemideina crassidens* (Kelly 2006), dwarf chameleons, *Bradypodion punillum* (Stuart-Fox 2006) and fallow deer, *Dama dama* (Jennings et al. 2004). Because our fish had been size matched, we could not use the regressions between individual body sizes and contest duration to discriminate further between self-assessment and mutual assessment models (Taylor & Elwood 2003).

Body size, however, does not provide complete information about fighting ability in swordtails, as smaller contestants can still win contests (Franck & Ribowski 1989) and 25.8% did so in the present study. We explored factors that affect contest outcome in combination by multivariate logistic regression. This indicated that the greater the size difference the more likely the larger fish won. This occurred despite the small variation in size difference and again indicates the importance of body size on outcome. There was, however, no indication of an effect of sword length. This agrees with Benson & Basolo (2006) who noted a body size effect but failed to find an
effect of absolute natural sword length on fight outcome. However, it does not agree with their finding that false swords, painted to appear different sizes, influenced outcome. From our data on outcome it seems that natural swords neither enhance nor reduce the chances of victory in these contests.

Numerous studies have shown that a key predictor of contest duration is the size difference between the contestants. Regardless of whether mutual or self-assessment occurs, fights are expected to be short when the size difference is large and this has been repeatedly found in a wide variety of species (reviewed in Taylor & Elwood 2003). However, in the present study the low variance in size difference caused by our attempt to size match resulted in this relation between size difference and contest duration being nonsignificant. However, the sword of the winner had a marked effect on the timing of the giving-up decision of the loser because fights were shorter when the winner had a long sword relative to body size (Fig. 1). Having a large sword relative to the body size thus appears to be advantageous in winning quickly.

We sought to distinguish between the possibilities that the sword directly affects fighting ability or that it is an honest indicator of condition and hence of fighting ability. The former seems unlikely because it is not used as a weapon and because there are hydrodynamic costs of bearing a long sword (Basolo & Alcaraz 2003; Basolo & Wagner 2004). It seems more likely that the sword acts as an honest signal of condition or fighting ability that allows faster decisions from losers. We presume it is honest because of the hydrodynamic costs shown previously (Basolo & Alcaraz 2003) and a long sword seems to increase predation risk (Basolo & Wagner 2004; see also Rosenthal et al. 2001). However, longer swords are associated with increased ability in fast-start swimming (Royle et al. 2006), so they may be an indicator of, and potentially enhance, fighting ability. Benson & Basolo (2006) noted that males with larger apparent swords were more likely to win even though the actual swords were the same in the two contestants. Thus the hydrodynamic effects must have been the same, and the fighting ability could not have been influenced; the loser must therefore have been responding to a signal of quality. Furthermore, we would have predicted that if the sword confers a physical advantage then winners with large swords would be more likely to escalate the contest and bring about swift resolution by that tactic. However, our data did not support this prediction concerning escalation and we conclude that the sword is a signal of condition rather than being a feature that enhances fighting ability.

If the loser gathered information about the condition of the winner via the size of the winner’s sword then this would preclude the self-assessment model of conflict resolution (Taylor & Elwood 2003). Mutual assessment, however, predicts that the sword of the loser and relative sword length should have effects but this was not found. Losers gathered information about the eventual winner but that information seemed not to be used in relation to the loser’s own sword. Furthermore, there was no indication that the winner gathered information about the loser with respect to swords. Thus, while the data preclude self-assessment, they do not fit the expected pattern of mutual assessment with respect to swords. This appears to be a case of asymmetry in information use that has been seen when animals take different positional roles in fights (Briffa & Elwood 2005).

An alternative to the explanation that sword length represents an honest signal of condition might involve the social inhibition of maturation found in related platyfish, Xiphophorus variatus (Borowsky 1973, 1978). The sword may indicate the time since release from inhibition and maturation. If this in turn indicates fighting experience, then males could be assessing the experience of their opponents in contests via assessment of their sword. However, the consequences of this inhibition are unclear and this idea does not sit well with the compensatory growth also known to occur in this species (Royle et al. 2006).

It may seem odd that a feature such as sword length can alter tactical decisions such as the time afforded to the contest and yet does not alter the outcome to a significant degree. In this respect our study is similar to those that have shown altered tactics that resulted in only marginal and nonsignificant shifts in probability of victory (e.g. Dugatkin & Ohlsen 1990; Arnott & Elwood 2007; see also Magnhagen 2006 in which information about an opponent available through eavesdropping did not increase the probability of winning a nest site, but did decrease the level of aggression in contests in common gobies, Pomatoschistus microps). In the present study, the main decision about giving up might have been based on body size and reinforced by the eventual loser attending to information gathered about the sword of the winner. A loser that perceives a long sword may thus take this as confirmation of its inferiority whereas a loser that perceives a short sword on a large fish may not be so sure about being inferior and continues to interact for a while. There is a benefit to the winner in having the long sword, however, not because it enhances the probability of victory but because the winner does not have to fight for as long. Presumably, however, a shift in contest duration will have some effect on outcome but that effect may be too small to determine easily through experimentation.

Acknowledgments

We are grateful to Ryan Earley, Mark Briffa and Gareth Arnott for discussion and comments on the manuscript. Funding was provided by a grant from the U.K. Biotechnology and Biological Sciences Research Council (Research Grant S20306 to R.W.E. and J.P.). We thank Gillian Riddell, Stuart Barr and Gareth Arnott for their assistance in maintaining the fish.

References


