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# Switching assessment strategy during a contest: fighting in killifish *Kryptolebias marmoratus*

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To determine whether animals assess each other's fighting ability in contests, researchers usually regress contest duration over the sizes of the contestants. The predominant trend in recent studies is for the contest duration to correlate positively with the size of the smaller opponent but to have no obvious relationship with the size of the larger opponent. This indicates that animals make contest decisions based on their own abilities ('self assessment') and displaces the once-popular belief that they assess their opponents ('mutual assessment'). These tests, however, are based on the implicit but never stated assumption that animals adopt only one assessment approach throughout an entire contest. By examining the contest behaviours of a killifish, we show that (1) the fish adopt mutual assessment at earlier stages when deciding whether to escalate the contest from the mutual display to the attack phase and (2) once a contest is escalated, the fish switch to self assessment to decide how long to escalate. Our results show that individuals may adopt multiple assessment approaches in one contest; contest behaviours in different stages (where applicable) of a contest should be analysed separately to better elucidate animal contest assessment strategies.



*Keywords*: animal contests; decision making; fighting ability; killifish; *Kryptolebias marmoratus*; mutual assessment; self assessment

Fighting for limited resources is costly in terms of expenditures of time and energy (Neat et al. 1998), and risks of physical injuries (Austad 1983; Neat et al. 1998) and predation (Brick 1999). It is advantageous for animals in contests to assess each other's fighting ability and retreat immediately to avoid unnecessary risk if they decide that they are unlikely to win ('mutual assessment'). Body and weapon size are often good surrogate measurements for fighting ability (Hsu et al. 2006). Contest duration, the most frequently examined behaviour, is expected to be inversely correlated with size difference because an animal can detect and act on a large difference more quickly than on a small difference (Maynard Smith & Parker 1976; Enquist & Leimar 1983). Significant negative relations between contest duration and size disparity in empirical studies had long been regarded supporting evidence for mutual assessment in animal contests (e.g. Austad 1983; Rosenberg & Enquist 1991; Hack 1997). Recent studies, however, have shown that the primary relationship is between the contest duration and the size of the smaller animal (e.g. Taylor et al. 2001b; Jennings et al. 2004; Prenter et al. 2006; but see Kemp et al. 2006): the inverse relationship with size disparity is merely a by-product of this (Taylor & Elwood 2003). These studies indicate that animals make contest decisions based on their own abilities ('self assessment') and have cast reasonable doubt on the once-popular belief that they assess their opponents.

There are two predominant self assessment models: energetic war of attrition (Mesterton-Gibbons et al. 1996; Payne & Pagel 1997) and cumulative assessment (Payne 1998). Energetic war of attrition proposes that an individual's persistence in a contest depends entirely on its energy reserve and not on assessment of its opponent's ability. Contest duration should have a strong positive relationship with the size of the smaller contestant but a weaker or even insignificant positive relationship with the size of the larger contestant because the smaller contestant is likely to retreat first (Taylor & Elwood 2003). And, if two rivals in a contest are matched in size, contest duration should correlate positively with the size of the contest

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pair, which is not expected of mutual assessment. Cumulative assessment takes into account not only the energetic costs but also the physical costs inflicted by the opponent. It proposes that an individual enters a contest with a cost threshold that it will endure depending on its own body condition but independent of its rival. None the less, a rival capable of inflicting damage more quickly will cause the individual to reach its cost threshold and retreat sooner. Cumulative assessment, hence, predicts contest duration to correlate positively with the size of the smaller opponent and negatively with the size of the larger opponent, the same as the mutual assessment model. But cumulative assessment makes this prediction only for contests that involve physical fights (Payne 1998) whereas mutual assessment also applies to contests that to resolve with nondangerous interactions.

Other than contest duration, contest intensity is often examined when testing different assessment models (e.g. Taylor et al. 2001b; Jennings et al. 2004; Stuart-Fox 2006). Total contest duration and maximum contest intensity are overall measures of a contest. Using them to test between different assessment models requires the implicit but never stated assumption that animals adopt only one assessment approach throughout an entire contest. Researchers therefore have been striving to identify one global assessment strategy for their study animals. None the less, although most of the studies (other than Jennings et al. 2005) reached a conclusion on a global assessment strategy most consistent with the behaviour patterns of their study animals, many noted that the best fit strategy could not account for all contest characteristics observed (e.g. Pratt et al. 2003; Stuart-Fox 2006; Briffa 2008). In fiddler crabs (Morrell et al. 2005), although escalation duration was best explained by the cumulative assessment model, fights were size assortative (intruders tended to fight residents that were of a similar size to themselves), which led the authors to suggest that the opponents might have mutually assessed each other prior to determining whether to engage in contest interactions. All these results indicate that animals may adopt multiple assessment strategies and switch between different strategies during a contest.

The objective of our study was to examine whether *Kryptolebias marmoratus*, a killifish, switch assessment strategies during a contest. To do this we tried to determine assessment strategy first from analysing the overall contest duration and second from examining behaviour in different stages of contests, comparing the conclusions reached from the two approaches.

The contest behaviours of *K. marmoratus* have been described by Hsu & Wolf (1999, 2001). At the start of the contest, the fish usually move towards each other, often with gill covers erected (opercular flare displays). After a few bouts of mutual displays, one fish sometimes retreats and the contest is resolved in favour of the other. If not, one fish usually launches a first attack. Sometimes the fish receiving the first attack retreats, and the contest is resolved as before; sometimes the fish being attacked fights back, and the contest is escalated.

We first considered the models' predictions for the effect of size on the likelihood of a contest being resolved with only mutual displays. With no physical damage at this stage of a contest, the cumulative assessment model is not relevant. Both other models predict the likelihood to correlate negatively with the size of the smaller opponent, but they make different predictions with respect to the larger opponent: the energetic war of attrition model predicts a small negative correlation (the larger fish is less likely to give up) and the mutual assessment model predicts a positive correlation (the smaller fish is more likely to retreat when faced with a larger opponent). Contests not resolved after display only may be resolved at the first attack. Because little or no physical damage occurs at this stage, the arguments are the same but relate to the attacker/receiver of the attack rather than to the larger and smaller fish. For escalated contests, we examined the size effects on the duration of escalation. Physical damage was possible in escalation so all three models apply. Their predictions regarding the effect of size on the duration of the escalation stage are the same as their predictions on the total contest duration. All these predictions are summarized in Table 1.

## METHODS

### Study Species and Types of Contests

The mangrove killifish, *K. marmoratus*, formerly *Rivulus marmoratus* (Costa 2004), is an internally self-fertilizing hermaphroditic fish (Taylor et al. 2001a). It is capable of producing fertilized eggs all year round and does not have obvious oviposition cycles (Harrington 1963). Most populations of this fish exist in nature as isogenic, homozygous strains, although outcrossing heterozygous populations have been discovered in Twin Cays, Belize (Taylor et al. 2001a). *Kryptolebias marmoratus* has an epidermal capillary bed (Grizzle & Thiyagarajah 1987) which enables the fish to respire through air, be semiterrestrial and travel between locations by flipping or slithering through wet pebbles and mud (e.g. Davis et al. 1990; Taylor 1990). Some emersion might be obligatory for the fish as completely submerged traps often contained dead individuals (Davis et al. 1990). In their natural environment, they are often found to hide under damp cover (e.g. logs, mangrove leaves) or to live in the burrows of land crabs (Davis et al. 1990; Taylor 1990).

This study used individuals of five strains of *K. marmoratus* from various geographical areas (DAN2K: Dangria, Belize, collected in 2000; HON9: Utila, Honduras, collected in 1997; RHL: San Salvador, Bahamas, collected in 2001; SLC8E: St. Lucie County, Florida, U.S.A., collected in 1995; VOL: Daytona Beach, Florida, U.S.A., collected in 1995) which were the F2–F5 of the fish originally collected from the field by Dr. D. Scott Taylor, (Florida, U.S.A.). Fish were isolated within a week of hatching and kept alone in a $10 \times 10 \times 10$ cm translucent polypropylene plastic maintenance container filled with 400–500 ml of approximately 25 ppt synthetic sea water (Instant Ocean powder) and labelled with a unique code for individual identification. For each container, we drilled four holes in the lid and one hole close to the upper edges