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COMMENTARY

Do the elongated eye stalks of Diopsid flies facilitate rival assessment?

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Abstract The elongated eye span of male Diopsid flies is a sexually selected character that scales positively with body size. Previously, the duration of agonistic contests was found to increase as rival body size and eye span disparities decreased. Hence, along with its role in mate choice, eye span seems to facilitate mutual assessment of rival size. However, such results are also expected in the absence of rival assessment, when each individual persists according to its own size-dependent internal threshold. Here, we reanalyze these contests to distinguish between these two hypotheses using two measures of size: body length and eye span. Mutual assessment predicts that contest duration should increase with loser size and decrease with winner size. In contrast, our results were more consistent with self-assessment: We found a positive relationship between loser size and contest duration, whereas winner size did not affect contest duration. Thus, flies did not appear to assess the size of their rivals, indicating that the mutual assessment function of eye span elongation may be less important than previously suspected.

Keywords Self-assessment · Rival assessment · Fighting · Size · Armament · Stalk-eyed flies · Aggressive interactions

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Introduction

In agonistic interactions, large individuals are better able to inflict injuries, are less susceptible to injurious attacks, and enjoy higher social status than smaller individuals (Riechert 1998). Armaments such as horns and antlers may improve the efficacy and precision of rival assessment when incremental increases in body size are accompanied by greater incremental increases in armament size (Gould 1973; Gould 1974; Petrie 1988; Hongo 2006), a scaling pattern known as hyperallometry (Huxley 1932). Certain stereotyped postures that bring armaments into close proximity may further permit rivals to directly compare armament size. The elongated eye stalks of Diopsid flies (Diptera: Diopsidae) are among the better-known examples of such armaments (de la Motte and Burkhardt 1983). Eye span shows a close positive association with body size, as well as considerable interspecific variation (Baker and Wilkinson 2001). In sexually monomorphic species, both sexes bear short eye stalks that show modest length change in relation to body size (hypoallometry; Baker and Wilkinson 2001). In sexually dimorphic species, males bear much longer eyestalks than do females due to a more pronounced dependency of eye span on body size (i.e., hyperallometry; Baker and Wilkinson 2001). Large males with broad eye spans are able to exclude smaller rivals and also attract more females to their nocturnal roosting sites (Burkhardt and de la Motte 1987; Wilkinson et al. 1998). During agonistic interactions, flies approach their rivals head-on and align eyestalks with their rivals while rearing up and extending their front legs laterally. By comparing eye spans, rival males from sexually dimorphic species may determine relative size with great precision (Burkhardt and de la Motte 1983).

This hypothesis was tested in a study that examined the effect of size disparities on the outcome and duration of dyadic contests among male stalk-eyed flies (Panhuis and Wilkinson 1999). Game theory models of animal contests propose that as the degree of size disparity between opponents increases, rivals are able to gauge more readily which opponent is larger, and hence, both the maximal level of escalation and the duration of contests are predicted to decrease as size disparities increase (Maynard-Smith and Parker 1976; Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and Leimar 1983). In two sexually dimorphic species (*Cyrtodiopsis dalmanni* and *Cyrtodiopsis whitei*), contests were more often won by the larger individual of the dyad, and the mean duration of bouts of agonistic behavior decreased as the disparity in size increased. Furthermore, in these species, eye span predicted contest winner in more contests than did mass, body length, or thorax width. In *Cyrtodiopsis quinqueguttata*, a monomorphic species, winners did not differ in size from losers, and mean bout duration did not increase with size disparity. Using reciprocally selected lines of *C. dalmanni*, they were able to pair individuals of similar body size, but with large disparities in eye span. Despite the minimal differences in body size, individuals with wider eye spans won most of the contests. Taken together, these results prompted the conclusion that in males of sexually dimorphic species, eye span differences permit the assessment of rival size (Panhuis and Wilkinson 1999).

However, self-assessment—in which both individuals persist until the smaller individual reaches its persistence limit—could also cause contest duration to decrease as size disparities increase. The correlation between the size of the smaller contestant and size disparity creates a statistical relationship between contest duration and size disparity even when persistence is entirely determined by the size of the smaller contestant (Taylor and Elwood 2003). In the three species examined by Panhuis and Wilkinson (1999), for example, correlation coefficient between loser eye span and eye span disparity ranged from 0.75 to 0.96.

Hence, the goal of the present study is to re-evaluate the function of eye span elongation in Diopsid flies, by explicitly distinguishing between mutual assessment and self-assessment in the data set of Panhuis and Wilkinson (1999). When rivals rely on mutual assessment, contests should increase in duration as loser size increases and decrease in duration as winner size increases (Taylor and Elwood 2003). Mutual assessment further predicts that the regression coefficient of contest duration against size disparity and its coefficient of determination (R^2 value) should be greater than those given by regressing against loser size (Taylor and Elwood 2003). In contrast, the self-assessment hypothesis predicts that winner size will have no measurable effect on contest duration and that contest duration should increase as loser size increases (Taylor and Elwood 2003). Our analyses were designed to identify statistical predictors of contest duration to distinguish between self-assessment and mutual rival assessment (Taylor and Elwood 2003). We evaluated both eye span and body length as predictors in our analyses since eye span is the putative assessment cue, whereas body size may also serve as an assessment cue or could influence RHP (fighting ability).

To test the roles of rival assessment and self-assessment in each species, we first examined the effect of eye span and of body length of winners and of losers on contest duration in a series of bivariate regression analyses for each species separately. Due to the modest sample sizes and the collinearity of body size with eye span, multiple regression analyses were deemed inappropriate for this data. Furthermore, since winner and loser size were not correlated, simple regression coefficients provided an appropriate description of relationships between contestant size and contest duration.

In the first dimorphic species, *C. dalmanni*, the loser's eye span predicted contest duration, whereas the winner's eye span had no effect on contest duration (Electronic supplementary material, Table 1). Furthermore, the standardized β values indicate that eye span difference was not a better predictor of contest duration than was loser eye span. These results are inconsistent with mutual assessment and consistent with self-assessment. Body length showed qualitatively similar effects as eye span, but none of the predictors was statistically significant at the 0.05 level. In the second dimorphic species, *C. whitei*, loser size and winner size showed approximately equal and opposite β values, and winner–loser differences provided the best predictor of contest duration, but none of these predictors was statistically significant (Electronic supplementary material, Table 1). Therefore, results for this species do not conclusively support either hypothesis. In *C. quinqueguttata*, a species monomorphic for eye span dimorphism with both sexes bearing short eye stalks, none of the eye span variables significantly predicted contest duration. However, the loser's body length was a marginally significant predictor of contest duration, whereas the winner's body length did not affect contest duration (Electronic supplementary material, Table 1). Although suggestive of self-assessment, these results do not offer conclusive support to either hypothesis. Whereas body length differences were similar across the three species (Electronic supplementary material, Fig. 1a), compared with the other two species, eye span differences were very small in *C. quinqueguttata* (Electronic supplementary material, Fig. 1b).

In order to highlight the effect of eye span on contest behavior, *C. dalmanni* males of lines selected for a high eye span to body length ratio were pitted against males selected for a low eye span to body length ratio. In these contests, eye span differences were much larger than the differences in unselected *C. dalmanni* (Electronic supplementary material, Fig. 1b), and body size differences did not differ significantly from body size differences within dyads of unselected flies (Electronic supplementary material, Fig. 1c). None of the eye span and body size variables affected the duration of contests between *C. dalmanni* of the selected lines (Electronic supplementary material, Table 1), and hence, neither hypothesis was supported. Contest duration did not differ between selected line and unselected *C. dalmanni* (Electronic supplementary material, Fig. 1a; also see Panhuis and Wilkinson 1999).

Second, we modeled contest duration as ANCOVAs with species as the factor and a single size variable as a covariate. Size variables included loser eye span, winner eye span, loser body length, and winner body length. By combining all three species in one analysis, we increased our power to detect effects of the size variable, and using species as a covariate reduced the confounding effect of species on contest duration. In each of these ANCOVAs, the interaction term of species by size variable was not statistically significant, and hence, we did not include the interaction term in any of these models. The lack of significant interaction could represent similar effects of size variation on contest duration in all species. Alternatively, it may be attributed to the relatively restricted eye span variation represented in the monomorphic species (Panhuis and Wilkinson 1999). However, the species term was significant in each of these models (Electronic supplementary material, Table 2). For both eye span and body length, loser size, but not winner size, significantly predicted contest duration, and size difference was not a better predictor of contest duration than loser size, consistent with the hypothesis of self-assessment (Electronic supplementary material, Table 2).

Our reanalysis of Panhuis and Wilkinson's (1999) data set showed that neither winner eye span nor winner body size had a detectable effect on contest duration. In contrast, loser eye span or body length each exerted a significant effect on contest duration in some of our analyses. This pattern was predicted by the self-assessment hypothesis, whereas the rival assessment hypothesis predicted that winner size and loser size would exert effects equal in magnitude and opposite in sign to each other. Our reanalysis suggests that the role of eye span and its assessment in stalk-eyed fly contests is more limited than previously thought and that stalk-eyed flies may resolve some contests according to their own internally determined persistence thresholds.

Panhuis and Wilkinson (1999) presented additional arguments supporting the importance of eye span in mutual rival assessment in contests between males of the two sexually dimorphic species. However, these arguments are also open to alternative interpretations. In the two dimorphic species, in which male eye span is greater than body length, eye span predicted contest winner better than any other size measure (Panhuis and Wilkinson 1999). In contrast, none of the size measurements differed significantly between winners and losers of the monomorphic *C. quinqueguttata*, in which male eye span is considerably smaller than body length (Panhuis and Wilkinson 1999). As suggested previously, because all body size measures were tightly correlated and because winners and losers did not differ in residual eye span (correcting for body length), these results simply indicate a role for size in resolving contests between males of the two dimorphic species, but they do not show a role for eye span *independent* of body size (Panhuis and Wilkinson 1999). These results also suggested that, unlike the two dimorphic species, size is not a factor in contests among male *C. quinqueguttata* (Panhuis and Wilkinson 1999). However, given the somewhat smaller sample size (*C. quinqueguttata*: N=24, *T. dalmanni*: N=30, *C. whitei*: N=29) and the proportionately larger error expected in measuring the relatively small eye spans of males of the monomorphic species, the lack of size differences between winners and losers in *C. quinqueguttata* may also be attributed to insufficient statistical power. Counter to Panhuis and Wilkinson (1999), in our analysis, loser body length was a significant predictor of contest duration at the P=0.1 level in *C. quinqueguttata*, suggesting that size does exert an effect on contest behavior in this monomorphic species.

To isolate the effect of eye span independently of body size, flies from lines selected for broader eye span were pitted against flies selected for narrower eye span (Panhuis and Wilkinson 1999). In this group of contests, rivals were more closely matched for body length and exhibited a far greater disparity in eye span than in the previous contests. The individual with a residual eye span exceeding that of its rival won the majority of this group of contests, and hence, it was concluded that eye span could affect contest outcome independently of body size (Panhuis and Wilkinson 1999). We contend that this conclusion may not be robust because in most of these contests (19 of 29), one individual was larger in both body length and in eye span, whereas only a small number of contests (the remaining ten of 29) involved dyads with one rival having a longer body and the other having a broader eye span. To effectively compare the contribution of eye span differences and body size differences to winning contests, it is necessary to conduct additional contests in which one individual is larger in eye span, and his rival is larger in body length (Brandt 1999).

Conversely, setting up contests between males matched for eye span and mismatched for body size would highlight the role of body size independent of eye span.

If eye span differences are the primary determinant of contest duration, as suggested by the rival assessment hypothesis, then the duration of contests between selected line *C. dalmanni* should have been smaller than the duration of contests between unselected *C. dalmanni* because of a mean eye span disparity of nearly three-fold in contests among selected line flies. However, contest duration did not differ between these groups, indicating that contest duration is influenced by factors other than eye span differences, such as body length differences. However, in the contests between selected line males, the power to detect an effect of body length differences on contest duration is reduced because dyads were closely matched in body length (Brandt 1999).

Despite the lack of support for mutual rival assessment in the present data set, we do not exclude its possible importance in stalk-eyed fly agonistic interactions. First, the size disparities within the dyads examined in Panhuis and Wilkinson's (1999) study were moderate, to ensure high rates of fighting. However, this design reduces the power to detect effects of size disparities on contest duration. Conducting additional contests that include a broader range of size disparities will enhance the statistical power to detect such effects if they exist. Second, contests in laboratory arenas do not allow losers to depart and concede the resource to the winner after completing their assessment, as they are free to do in the field. In the laboratory, mutual assessment of rivals might occur in the first bout of agonistic behavior, or perhaps assessment occurs only in the most escalated of the bouts. If so, then the present analysis, which examines the mean duration of all the bouts, would obscure any pattern of mutual assessment in the earliest or in the most intense parts of the contest. Third, in addition to duration, it will be instructive to evaluate whether the maximal escalation in these contests increases as size disparities decrease, a pattern predicted by the mutual assessment hypothesis. Fourth, the dimensions of losers in this set of contests exhibited greater variability than the dimensions of winners, thereby increasing our ability to detect an effect of loser dimensions on contest duration. Finally, contests among stalk-eyed flies may be decided using some combination of self-assessment and mutual assessment, as reported in several recent studies (e.g., Morrell et al. 2005; e.g., Elias et al. 2008).

In summary, our reanalysis calls into question the role of eye span assessment in the resolution of contests among male stalk-eyed flies. However, we caution that further experiments are needed before we can ascertain the relative importance of mutual assessment and self-assessment in these contests, and whether eye span serves as an assessment cue.

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