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FORUM

When size is not everything: determining the relative importance of two asymmetries influencing contest outcome

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Studies of fighting behaviour in fish have repeatedly shown that the larger contestant in pairwise contests is much more likely to win than is the smaller contestant, even when the difference in size is subtle (Turner & Huntingford 1986; Enquist et al. 1990; Ribowski & Franck 1993). Body size is an important asymmetry in determining contest outcome across a wide range of taxa, because larger contestants are physically stronger and thus can inflict more damage upon their opponents (Maynard Smith 1982; Riechert 1998). Yet in a study of contests staged between male cichlid fish *Tilapia zillii*, Neat et al. (1998) found that larger contestants won only 58% of all contests. They found a much better predictor of contest outcome: contestants with relatively larger testes won 88% of all contests. Based on *P* values obtained from a multiple logistic regression analysis, they concluded that relative testes weight was a good predictor of fight outcome while relative body weight was not.

Here I argue three points. (1) Neat et al. have misinterpreted the results of their experiment, having based their conclusion upon statistical significance (*P* values). In contrast, comparing the regression coefficients reveals that, compared with testes weight, relative body weight may be less important, as important, or even many times more important in predicting contest outcome. Thus, while Neat et al. have demonstrated that relative testes weight plays a role in determining contest outcome, their data do not support the conclusion that relative body weight bears little influence on contest outcome. (2) Neat et al.'s experiment was predisposed to reveal an effect of testes size, but far less likely to reveal an effect of body size, on contest outcome. Their study had very low statistical power for detecting the effect of body size, because contestants were paired such that their body size was roughly similar, while the size of their testes was free to vary. Similarly, the surprisingly low percentage of pairwise contests won by the larger contestant is simply a consequence of this aspect of the experimental design. By contrast, earlier studies consistently revealed effects of body size on contest outcome because they were designed such that body size was the only substantial asymmetry among contestants. (3) To design experiments that efficiently compare the relative importance of two traits in determining contest outcome, one should maintain substantial levels of asymmetry in both traits of interest, thereby ensuring high power to detect the effects of both traits. Conversely, when the goal is to establish whether a single trait may play a role in determining the outcome of aggressive interactions, it is more efficient to design an experiment that minimizes asymmetries in all variables other than the variable of interest.

Neat et al. based their conclusion that relative testes weight was a good predictor of contest outcome, while relative body weight was not, upon a multiple logistic regression analysis (Table 1 in Neat et al. 1998), which yielded a significant *P* value (<0.05) for relative testes weight but not for relative body weight (<0.1). However, the *P* value is not an appropriate metric for gauging the magnitude of an effect that an independent variable has on a dependent variable. The *P* value quantifies the probability of obtaining a given regression line assuming the null hypothesis is correct, that is, assuming the dependent variable varies at random with respect to the independent variable. It is the regression coefficient that quantifies the effect of an independent variable on the dependent variable. The regression coefficients of the two independent variables in Neat et al.'s analysis are strictly comparable because each is expressed as the log of the ratio of the two contestants' sizes (Enquist & Leimar 1983; Neat et al. 1998).

A comparison of the regression coefficients in Neat et al.'s analysis shows that one cannot exclude the

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possibility that relative body weight is important in determining contest outcome. The regression coefficient for relative body weight was 22.33 ± 12.68, and that for relative testes weight was 8.69 ± 3.65 (see Table 1 in Neat et al. 1998). The 95% confidence intervals for the regression coefficients range from -3.41 to $+48.07$ for relative body weight and from $+1.28$ to $+16.10$ for relative testes weight. Based on this analysis, one cannot decide whether relative body weight is less important than, as important as or more important than relative testes weight in predicting contest outcome.

Why were *P* values significant for relative testes weight but not for relative body weight in Neat et al.'s study? The answer to this question lies in the design of their experiment, in which pairs of fish were closely matched for body weight, but not for relative testes weight. The range of variation in body weight in this sample was seven-fold (20–140 g), yet contestants were paired such that the largest weight advantage was 35%. However, the gonadosomatic index (defined as $100 \times$ testes weight/body weight) of fish in this study varied over 60-fold (0.01–0.61%), and was free to vary within a pair because it was unknown prior to pairing the contestants. The statistical power of a test to detect the effect of an asymmetry is an increasing function of the magnitude of that asymmetry. Consequently Neat et al.'s experimental design achieved high statistical power for detecting the effects of relative testes weight but low statistical power for detecting the effects of relative body weight. Thus, their experimental design stacked the odds in favour of detecting a statistically significant effect of relative testes weight, and against detecting an effect of relative body weight.

Why did larger fish win such a small percentage of the contests in Neat et al.'s study? How could this result be consistent with the results of some earlier studies, in which larger fish won over 90% of the contests, even when contestants were similar in size? The difference between the experimental designs of Neat et al.'s study and of earlier studies can easily account for this discrepancy. Earlier studies were designed to eliminate all asymmetries between contestants except the asymmetry in body size. Such a design maximizes the power of the statistical test to detect the effect of body size by reducing the error variance. These earlier studies were not directly concerned with studying the effects of gonadal state on fighting, nor did they aim to eliminate asymmetries in gonadal state per se. However, by carefully controlling the subject's social experience, these earlier studies may have achieved just that. Subjects in two studies were reared in isolation (Turner & Huntingford 1986; Enquist et al. 1990), while those in a third were matched for social status (Ribowski & Franck 1993). By minimizing all asymmetries other than body size, these earlier studies demonstrated consistent advantages of larger fish over their smaller opponents, even when size differences were slight. By contrast Neat et al.'s study examined simultaneously the effects of two asymmetries: body size and testes size, reducing the power of the experiment to detect the effect of body size. The power of the experiment to detect the effect of body size was further reduced as a consequence of pairing contestants that were roughly equal in body size, but were substantially asymmetrical in testes size. Thus it should not be surprising to find the effect of body size on contest outcome was rather cryptic in Neat et al.'s study.

An efficient experimental design for detecting the effects of two traits and for comparing their relative importance in determining contest outcome must ensure substantial levels of asymmetry in both traits of interest. Such an experimental design maintains adequate power for detecting the effects of both traits. An alternative experimental design is efficient for detecting the effect of a single trait. In this design, asymmetry in the trait of interest is enhanced, while asymmetries in all other traits are minimized. Clearly, distinct goals are served by each of these designs. Hence, the goal of a study dictates the choice between these two experimental designs. Intermediate experimental designs, such as Neat et al.'s, are less efficient for either of these goals. Selecting an efficient experimental design will enhance the quality of inference that one may draw from an experiment, and can also be used to reduce the sample size needed to obtain statistically significant results, with favourable consequences both for economic costs and animal welfare.

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