FORUM

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The value of titration experiments: a reply to Moody et al. (1996)

Behavioural ecology has been remarkably successful as a discipline, in part because much of the theory that has been developed is readily testable through manipulative experiments in the laboratory and the field. Although the preferred currency for most theories is fitness, it has usually been possible to incorporate modifications or simplifying assumptions that allow the use of more readily observed, surrogate measures of fitness. Admittedly this does require some compromise, but in the grand tradition of behavioural ecology this trade-off is easy to solve: the benefits outweigh the costs.

Moody et al. (1996) (henceforth referred to as MHM), explored the role that risk dilution will have on the results of experiments that investigate predation risk – foraging trade-offs. Assuming that the probability of being killed by a predator is inversely related to the number of animals feeding at a site, they developed a model that incorporates risk dilution into ideal free distributions (IFDs) under predation risk. Due to risk dilution, their model suggests that patch choice decisions will be affected not only by the presence of predators and relative food availability, but also by the total number of animals. Their suggestions are very useful in advancing our theoretical understanding of this problem. However, we disagree with their critical assessment of the use of the IFDs as an experimental tool to quantify decisions involving conflicting demands.

In 1989, Abrahams and Dill (henceforth referred to as AD) published a paper that described an experimental technique that could be used to quantify the energetic equivalence of the risk of predation and, more importantly, presented the results of experiments that tested its

validity. The approach is based upon a continuous-input IFD. With this type of IFD, when food is the only parameter that describes patch quality, the spatial distribution of the foragers will match the spatial distribution of their food. A large number of authors have demonstrated that under experimental conditions, animals closely conform to an IFD (for a review see Milinski and Parker 1991). Incorporation of an additional patch parameter (i.e. the risk of predation) should result in a change in the spatial distribution of animals that reflects the relative change in patch quality. Differences in individual intake rates will then provide a measure of the assessed value of this parameter from the animals' perspective, and can be determined empirically. This approach describes our first experiment. Our second experiment then tested a prediction (derived from the results of the first experiment) concerning how much additional food must be added to the dangerous patch in order for the foragers to consider it equivalent to the safe patch. To make this prediction, we assumed a linear relationship between energy and fitness. This was not intended to describe the actual relationship between these two parameters, but to make it possible to interpret deviations in the spatial distribution with respect to the relationship between energy and fitness. For example, if more animals than we predicted used the dangerous location after the addition of extra food, then we concluded that the fitness benefits of the patch increased by more than the manipulated energy benefits. Conversely, if the addition of extra food resulted in fewer animals than predicted using the dangerous location, then we concluded that the fitness benefits of the patch increased by less than the manipulated energy benefits. These experiments demonstrated that even with the linearity assumption, we could fairly accurately predict the amount of additional food that must be added to a dangerous patch to offset the risk of predation.

MHM were critical of this approach for three reasons: (1) our calculations did not incorporate risk dilution; (2) the relationship between fitness and energy should have no influence on the calculations necessary to

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determine the energetic equivalence of predation risk, and (3) we did not incorporate how changes in the energetic state of the animal would affect the food necessary to offset the risk of predation.

MHM are correct that risk dilution was not explicitly incorporated into our calculations. In our experiments, we sought to return the fish to an approximately even distribution after quantifying the impact of predation risk. We assumed that the effect of predation risk would not change between the two experiments, allowing us to use the results of experiment 1 to calculate the amount of food necessary to offset the effect of predation risk on patch choice in experiment 2. As we sought to increase the number of animals feeding in the presence of a predator, risk dilution should manifest itself in more fish than predicted using the dangerous feeder after the addition of extra food. This is because the effect of predation risk should be diminished by the larger number of individuals now using the dangerous location and should reduce the amount of food necessary to offset the risk of predation. Since this result was not generally observed, we conclude that there is no evidence from our data to support the contention that risk dilution had a signicant influence in our experiments.

MHM's second criticism is that the precise relationship between energy and fitness should have no influence upon the calculation of the energetic equivalence of predation risk. They note that analysis of their model results in the exclusion of all parameters concerning the relationship between energy and fitness, making it unlikely that our calculations represent an energetic equivalence of the risk of predation. We disagree with their conclusion for two reasons. First, since they have excluded the relationship between energy and fitness from their equations, it suggests that the relationship between energy and fitness is irrelevant to their model. If so, then we fail to understand why we should be criticized for employing *any* function relating energy to fitness.

Second, MHM and AD have both addressed a common problem, but have done so from a different perspective. We have used an IFD where patch quality is determined only by the fitness benefits of food and the fitness cost of risking exposure to a predator. When an animal risks exposure to a predator, it does so by increasing the rate of energy acquisition beyond that which could be obtained in safety. For this reason, we believe that the correct approach for calculating the energetic equivalence of predation risk is to first determine the fitness value associated with the absolute feeding rate in the presence of the predator. We must then determine the fitness value associated with the absolute feeding rate in safety. The energetic equivalence of risk can then be calculated from the difference in the two fitness values. We do not believe that it is appropriate to calculate the energetic equivalence of predation risk by simply calculating the fitness equivalent of the difference in feeding rates as this ignores the relationship between energy and fitness. For details on our methodology, see Fig. 2 in Abrahams and Dill (1989). MHM assume a state-dependent IFD so that both age and energetic state affect perceived habitat quality in addition to the amount of food available and the probability of being killed by a predator. Therefore, manipulating environmental variables is not assumed to have the same influence on all individuals. Those that are older will incur relatively less of a cost associated with the risk of predation. Variation in the energetic state of the foragers will also influence the relative benefits associated with changes in feeding rate in the safe and dangerous patches. The necessary approach captures more of the detail associated with an animal's life history characteristics, but requires a very detailed study to obtain such information.

The final criticism by MHM is related to our previous comments, in that we did not take into account the changing energetic state of the animal. We did not explicitly do this, although this issue can be addressed from our data. Experiments for both sexes were conducted at three different feeding rates. Presumably, altering the feeding rate should change the rate at which energetic state changes and therefore we should expect this manipulation to affect our ability to offset risk. For female guppies, there was no major effect: the ability to offset predation risk was not strongly influenced by diet level. For male guppies, on the other hand, there was an effect: at the highest diet levels, they chose to feed only in the safe patch. Whether this result was due to changes in energetic state or to non-linearities in the energy-fitness relationship is impossible to determine.

In concluding their paper, MHM state that, ''Our analysis of the work of Abrahams and Dill (1989) shows that their model fails to find the energetic equivalence of predation risk whenever there is dilution of risk.'' They then go on to prescribe research programs that use lifetime reproductive success as the preferred currency for investigating decisions involving the risk of predation. In reaching their conclusion, we believe that MHM have unfairly criticized the approach of AD, particularly by ignoring the experimental support for it. While their model is based upon sound reasoning, it requires considerably more effort to obtain the data required to estimate its parameters. Furthermore, MHM have provided no evidence that their model will provide a better explanation of existing data. Given this, we do not believe that the potential benefits associated with MHM's recommendations justify the considerable cost.

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