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Estimating condition: pitfalls of using weight as a fitness correlate

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Condition dependence of traits is vital to our understanding of sexual selection (Andersson, 1994). Many theoretical studies have used condition as a parameter; for example, Rowe and Houle (1996) used condition as an internal property of the individual that accounts for a large proportion of fitness. This is analogous to the use of state in state-dependent models (Clark and Mangel, 2000). However, as pointed out by Kotiaho *et al.* (2001), this is difficult if not impossible to measure. Brommer (2000) concluded: 'individuals making decisions on the basis of their state, begs the question what state actually stands for in real-life scenarios'. Therefore, predictions of such models are extremely difficult to test empirically.

Despite the body of theory on condition, there is no single definition of condition applicable to real-life scenarios. Many studies have used measurements of fresh weight in one way or another to estimate individual condition. Besides the statistical difficulties of incorporating size (e.g. Garcia-Berthouz, 2001; Green, 2001; Darlington and Smulders, 2001), there is still the basic question of what fresh weight tells us about condition. It is clear that, for several reasons, most studies in behaviour and ecology can rely only on measurements of weight as indicators for condition. Methods of obtaining more accurate indicators of condition often include destructive sampling.

There are three levels to the problem of what is condition and how to measure it: (i) establishment of a sound definition of condition for use in theoretical studies; (ii) the laying down of guidelines of how to measure condition in real-life scenarios; and (iii) the investigation of which measurements are useful and easy to obtain as correlates of condition. We confine our contribution mainly to (ii) and (iii). The major aim of this commentary is to highlight the shortcomings of weight as a measurement of condition.

However, to clarify our aim and attempt not to shy away from (i), we use the following definition as background: 'condition is the status of physiological reserves which are essential and available for the (behavioural) trait under study in the appropriate time frame'.

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A good example of this definition is given by Plaistow and Siva-Jothy (1996), who showed that thorax fat content is an important determinant for mating success in calopterygid dragonflies, thereby being a condition-dependent determinant of fitness as well. Fat reserves in these species are needed to sustain escalated fights. If, for example, the fat metabolism is disrupted by an infection, condition is weakened and the ability to win escalated fights is lowered (for vertebrate examples of fat storage and condition, see Gentle and Gosler, 2001; Thomas and Cuthill, 2002, and references therein).

The correlation between certain physiological parameters, which are closely related to condition, and fresh weight is most likely to be sex- and stage-dependent. Furthermore, for some physiological parameters, fresh weight is a poor predictor. To illustrate these problems, we used a data set of dragonflies (*Coenagrion puella*). The parameters we obtained, which are known to be related to condition, were fresh weight, dry weight, fat content and muscle mass. All data were gathered using well-established protocols (Marden, 1989; Plaistow and Siva-Jothy, 1996; the full data set will appear in a separate publication).

The question we asked is: 'Can fresh weight be used as a surrogate for condition?' We approached this by using fresh weight as a predictor for fat content, dry weight, muscle mass and head width, the latter being an indicator of size.

Fresh weight is probably the most common predictor for condition in ecological studies in general (Corbet, 1999; Green, 2001). It has been shown to be related to parasite-mediated mortality (Braune and Rolff, 2001). Fat as well as muscle mass have been shown to be related to condition and fitness (e.g. Marden, 1989; Plaistow and Siva-Jothy, 1996; Siva-Jothy and Plaistow, 1999). According to Wigglesworth (1966), 'fat is the chief form in which energy is stored' in insects. Dry weight is usually assumed to be a much more accurate measure of condition than fresh weight.

The adults in our experiment emerged in the laboratory and were between 3 and 24 h old. The larvae had already left the water for emergence. So the two groups only differed by a few hours of age around emergence. But they were separated by the dramatic niche shift they undergo during emergence, which is a crucial time for physiological reorganization (Corbet, 1999; Plaistow and Siva-Jothy, 1999).

We ran a full model to explore the influence of sex and stage on the relationships between fresh weight and fat, dry weight, muscle mass and head width, respectively. Sex and stage were significant factors in all four models. Here we give only the highest significant order results from the four separate analyses of covariance (fat: sex, $F_{1,157} = 6.0$, $P = 0.0155$; stage, $F_{1,157} = 18.3$, $P < 0.0001$; dry weight: fresh weight × sex, $F_{1,154} = 7.8$, $P = 0.0058$; fresh weight × stage, $F_{1,154} = 12.0$, $P = 0.0007$; muscle mass: fresh weight × sex × stage, $F_{1,153} = 7.9$, $P = 0.0057$; head width: fresh weight × sex, $F_{1,155} = 5.2$, $P = 0.0247$; fresh weight × age, $F_{1,155} = 20.0$, $P < 0.0001$). The results clearly show that the predictive value of fresh weight is sex- and stage-dependent.

Subsequently, we performed separate linear regressions to determine whether fresh weight predicts the other parameters successfully. Males and females and larvae and adults were analysed separately, because of the gender and stage differences. We do not present multiple regressions using fresh weight and head width as explanatory variables, as head width failed to have any explanatory power in any of the models [$P > 0.25$ in all models; head width was used as a correlate for size and entered as a covariate following the suggestions of Garcia-Berthouz (2001) and Green (2001)].

As shown in Table 1, fresh weight significantly explains all four response variables in newly emerged females. However, in newly emerged males, only dry weight and muscle mass

Table 1. Fresh weight used to predict four parameters related to condition in the damselfly *Coenagrion puella*

	Females				Males			
	Adult ($n = 15$)		Larva ($n = 62$)		Adult ($n = 15$)		Larva ($n = 69$)	
	R^2	P	R^2	P	R^2	P	R^2	P
Fat	0.300	0.033	0.043	0.104	0.060	0.42	0.091	0.012
Dry weight	0.608	0.000	0.441	> 0.0001	0.456	0.005	0.072	0.025
Muscle mass	0.375	0.009	0.470	> 0.0001	0.580	0.001	0.016	0.301
Head width	0.420	0.005	0.332	> 0.0001	0.050	0.298	0.017	0.289

Note: The variables were log-transformed before analysis to fulfil assumptions of normality of errors and/or to account for allometric relationships. All relationships reported are positive.

Table 2. Dry weight used to predict the physiological parameters from Table 1

	Females				Males			
	Adult ($n = 15$)		Larva ($n = 62$)		Adult ($n = 15$)		Larva ($n = 69$)	
	R^2	P	R^2	P	R^2	P	R^2	P
Fat	0.598	< 0.001	0.353	< 0.001	0.404	0.015	0.281	< 0.001
Muscle mass	0.456	< 0.001	0.781	< 0.001	0.646	< 0.001	0.747	< 0.001

Note: Dry weight is a reliable indicator for condition-related physiological traits.

can be sufficiently explained by fresh weight. By contrast, in male larvae, fresh weight predicts fat content and dry weight, whereas in female larvae, only fat content is not predicted by fresh weight. However, even though fresh weight predicts the other traits in 11 of 16 cases shown in Table 1, it is noteworthy that fresh weight usually explains less than 50% of the variance.

By contrast, using dry weight, a measurement preferred by physiologists, is far more accurate. Dry weight as an explanatory variable explains the other two physiological traits, muscle mass and fat content, significantly in all cases (Table 2). Furthermore, the amount of variance explained is higher in each case (Tables 1 and 2). Hence, in the data set presented here, using fresh weight as a surrogate for condition would actually be misleading. Whereas the significant relationships are supported, the non-significant ones are disproved. This means that inferring from significant results using fresh weight as a surrogate measurement will give a conservative estimate. However, if fresh weight does not explain other condition-related traits, no information can be gained. For instance, if no correlation between fresh weight and survival is detected, it does not mean that condition and survival are not correlated. In dragonflies, size and weight at emergence decline over the season. The condition of males is determined by fat reserves (Plaistow and Siva-Jothy, 1996), not body weight *per se*, with younger males having more fat reserves. However, they are presumably lighter and smaller as they emerged later than older conspecifics. The use of weight alone as a surrogate

for fitness will fail to include fat reserves, a factor known to be important, and lead to possible errors in the estimation of condition.

This data set underlines the suggestion that relations between certain potential correlates of condition are sex- and stage-dependent. In the case of the damselflies, there is some evidence that fat is a good indicator for condition due to its link with mating success (Plaistow and Siva-Jothy, 1996) and parasite abundance (Siva-Jothy and Plaistow, 1999). Still, the link between fresh weight and fitness occurs by natural selection in coenagrionid damselflies. Parasite-mediated mortality is lower in animals of higher weight per body size (Braune and Rolff, 2001), but weight at emergence does not translate into reproductive output (Richardson and Baker, 1997).

In conclusion, physiological parameters related to condition cannot always be predicted by fresh weight. Furthermore, their predictive value is stage- as well as sex-dependent, as shown here using dragonflies as an example. We suggest, therefore, that for the successful study of condition-dependent traits, it is obligatory to understand the relationship between fresh weight and physiological parameters directly related to condition. It will often be necessary to establish such physiological correlates in the species under study before one uses fresh weight as a condition indicator (or even fitness surrogate). Furthermore, to test models that use condition as a parameter, theoreticians should be more precise about the defintion of condition: it has to be measurable. An unspecific definition of condition also gives rise to speculation of physiological trade-offs, for which there is very scant empirical support. A definition using a general pool of resources is only useful if mechanistic links between traits in conflict can be shown (Zera and Harshman, 2001).

Finally, we hope we can start a debate on the use of the term 'condition'. Theoreticians need to be more precise about what they mean by condition if certain model predictions are to become testable. Empiricists, on the other hand, should try to identify physiological correlates of, for example, survivorship that are meaningful in the life-history context of the organism and question studied.

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