

# Alternative phenotypes and sexual selection: can dichotomous handicaps honestly signal quality?

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Considerable theoretical and empirical effort has been focused on the potential of continuously variable sexual traits to honestly indicate male quality, but relatively little effort has been devoted to a similar evolutionary role for dimorphic traits. Male dimorphisms, associated with conditionally expressed alternative reproductive tactics, represent extreme phenotypic plasticity. Evidence suggests that considerable heritable variation exists in the 'liability' underlying many threshold traits; if this liability is correlated with the genetic quality of males, dimorphic traits have the potential to be reliable indicators. We investigated the genetic architecture of phenotypically plastic morph expression in the context of condition-dependent signalling theory. Male morph in the mite *Sancassania berlesei* is condition dependent: 'fighters' armed with thickened and sharp third pairs of legs emerge from heavier nymphs than unarmoured 'scramblers'. We selected on male morph in three replicate 'fighter' and 'scrambler' lines and recorded a significant response to selection over seven generations; this was due to a shift in the threshold reaction norm but the lines showed no correlated response in condition. This is inconsistent with models predicting a substantial genetic correlation between condition and sexual trait expression. We discuss why dimorphic sexual traits may show more condition-independent genetic variance than continuous sexual traits.

**Keywords:** lek paradox; genic capture; condition dependence; threshold polyphenism

## 1. INTRODUCTION

If mate choice is to bring genetic benefits to the choosing sex, either in terms of increased reproductive success of progeny (Fisher 1958) or better viability (Zahavi 1975), some mechanism has to maintain significant additive genetic variance for the trait subject to mating preferences (reviewed in Kokko *et al.* 2002). Andersson (1982, 1986) proposed that sufficient genetic variance could be maintained if costly sexual traits depend on an individual's condition. Condition itself is the individual's ability to acquire resources (Rowe & Houle 1996) and is likely to be influenced by many genes throughout the genome (Andersson 1982, 1986; Houle 1992). Through their condition dependence, sexual traits are thought to capture variation in the many genes affecting condition ('genic capture'; Andersson 1982, 1986; Iwasa *et al.* 1991; Iwasa & Pomiankowski 1994; Rowe & Houle 1996). Genic capture is not limited to traits that serve a signal function, rather the process requires only that traits are condition dependent and that there is genetic variance for condition (Rowe & Houle 1996). Although there is abundant evidence for condition dependence of sexual traits (reviewed in Andersson 1994; Johnstone 1995; Kotiaho 2000), a stringent test requires demonstration of a positive genetic correlation between condition and sexually selected trait expression. In the only study we are aware of so far, such a correlation was demonstrated between courtship rate and condition in the dung beetle *Onthophagus taurus* (Kotiaho *et al.* 2001). Here, we selected for a sexual trait in the mite *Sancassania berlesei* (Acari: Astigmata: Acaridae) and we

evaluated a correlated response in pre-adult body mass, a trait likely to reflect condition *sensu* Rowe & Houle (1996).

Sexual traits are often expressed discontinuously (Radwan 1995, 2001; Alcock 1996; Heinze *et al.* 1998; Greeff & Ferguson 1999) or bimodally (Emlen 1994; Tomkins 1999) such that alternative morphs can be defined within one sex (Gross 1996; Shuster & Wade 2003; West-Eberhard 2003). Recently, West-Eberhard (2003) has argued convincingly that alternative phenotypes may be crucial to the evolution of many adaptations, as they allow the acquisition and selective fine-tuning of novel life-history traits while maintaining an existing alternative (West-Eberhard 2003). In the context of sexual selection, Emlen (1996) suggested that costly sexual traits with threshold expression can become fixed in a population more easily than traits that are linearly dependent on condition. This is because under the strong mating bias created by sexual selection, males of intermediate quality have little chance to reproduce and threshold expression allows them to avoid the cost of producing extravagant ornaments. Many such dimorphic traits are threshold traits, i.e. quantitative traits with threshold expression (Roff 1996). The quantitative trait loci influencing threshold traits determine 'liability', a continuously distributed variable that underlies morph expression, so that expression depends on whether the value of liability is above or below the threshold (Falconer & Mackay 1996).

Males of the mite *S. berlesei* are dimorphic, with the fighter morph expressing thickened and sharply terminated legs that are used as a weapon in intrasexual contests. Expression of this trait depends on population size, which is perceived through airborne substances emanating from colonies. High concentrations of these substances suppress fighter morph expression (Timms *et al.* 1980;

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Radwan *et al.* 2002). This appears to be adaptive because the benefits of fighter behaviour can be best realized when small population size allows fighters to exterminate rival males and monopolize females; this is impossible in large populations in which fighters survive on average less well than scramblers (Radwan 1993a). However, expression of armoured legs also depends on the weight of the pre-adult tritonymph (measured at the quiescent phase before adult eclosion), with fighter males emerging from heavier quiescent tritonymphs. In the context of threshold trait evolution the weight of quiescent tritonymphs is likely to be equivalent to the notion of 'liability' (*sensu* Falconer & Mackay 1996).

Within the framework of Rowe & Houle's (1996) 'genic capture' model of condition-dependent sexual trait expression, we measured 'condition' as quiescent tritonymph weight (QTW). We used QTW for our estimate of condition because it is the point at which all resources for determining adult size have been acquired. Furthermore, as fighters do not take any longer to develop than scramblers, but are heavier as quiescent tritonymphs (Radwan *et al.* 2002), greater QTW is likely to reflect individual efficiency in acquiring resources, i.e. condition (Houle 1991; Rowe & Houle 1996).

Previous data show that for nymphs of the same QTW fighter males emerge at a lower adult weight than scramblers (Radwan *et al.* 2002); hence expression of the fighter phenotype appears to carry a cost. This size cost is likely to be evolutionarily significant given that there is a positive correlation between male fighter size and fitness measured as both mating success and probability of being killed (Ł. Michalczyk, J. Radwan, N. R. LeBas and J. L. Tomkins, unpublished data).

Selection for continuously expressed traits results in changes in trait value. In the case of dimorphic traits, we observe a change in proportion of individuals expressing the trait. The response to selection on threshold traits might result either from changes in frequencies of genes determining liability or genes affecting the position of the threshold (Fairbairn & Yadlowski 1997). Therefore, provided we obtained a significant response to selection on the male sexual trait (thickened legs) in our selection experiment, we could have three possible outcomes:

- (i) a correlated response in male condition, with no change in the switch point specifying the condition at which males are more likely to express fighter phenotypes;
- (ii) no response in condition, but a change in switch point; or
- (iii) a significant correlated response in condition, with simultaneous change of switch point.

Our results are consistent with the second possibility, indicating that the genetic variation in the expression of the sexually selected trait is mostly independent of genetic variance in condition.

## 2. MATERIAL AND METHODS

The population was obtained from the University of Stirling, UK, in 2001. It was originally collected from poultry litter near Stirling, Scotland, in 1998. Since 2001, it was mass cultured in

50 ml vials with *ad libitum* powdered yeast and wheatgerm (3 : 1) and plugged with dense cotton wool. The culture was kept in a desiccator at more than 90% relative humidity buffered by KOH solution ( $153 \text{ g l}^{-1} \text{ H}_2\text{O}$ ).

As the expression of fighter morph is progressively suppressed with increasing density (Radwan 1993b; Radwan *et al.* 2002), we first determined the density at which both morphs can be obtained in approximately equal proportions. Mites were reared in 2.5 cm diameter, 2 cm high universal plastic vial tops with a base of plaster, with powdered charcoal admixture used to darken the substrate. The top of the vial was pierced and had a 5 mm hole plugged with cotton wool. Three replicates of increasing density of first instar larvae (10, 20, 30, 40, etc. to 100) were placed into vials and the morph ratio recorded. The density that gave both male morphs in all three replicates, and thus made selection on male morph feasible, was 20 larvae provided with five balls of Allison's dried yeast. The food was not a limiting factor in this setting, but standardization was made to ensure a similar pheromone concentration absorbed in the food. This density yielded 24% fighters and 75% scambler males.

Selection was carried out in three replicates in both directions (fighter selection and scambler selection). From larvae onwards, a quiescent stage precedes the emergence of each consecutive instar: protonymph, tritonymph and adult; the quiescent stage only lasts a few hours, this allows good control over age at isolation. Selection started from the isolation of 1800 quiescent larvae, these were placed in groups of 20 into 2.5 cm vials and provided with five balls of yeast. The vials were randomly distributed between up and down lines, 15 vials per each of the replicate lines. Another set of 1800 larvae was isolated to 0.8 cm diameter vials to provide about 150 virgin females per line. Five days after isolation of larvae, newly emerged males were scored for morph, and males of the selected morph were collected from each vial and mated to virgin females on consecutive days. Each male was mated with up to five females, depending on the ratio of males of the selected morph to virgin females available. Females were then placed in a 9 cm Petri dish with plaster substrate to oviposit and provided with powdered yeast. After 2–3 days, 20 quiescent larvae were isolated to 15 2.5 cm vials, along with 300 individually isolated larvae per line to provide virgin females. The procedure was repeated for seven generations.

We tested whether there had been a correlated response in QTW to selection on male morph. To do this we reared the final generation in isolation from first instar through to adulthood. To isolate larvae, females were allowed to lay eggs on Petri dishes with *ad libitum* food as for the experiment. The same numbers of females were placed on the Petri dishes for each line; hence there was no systematic bias in competitive environment in favour of either up or down lines. After 3 days (allowing eggs to hatch), isolation of first instar larvae began and was performed on three consecutive days; 35 larvae per line per day were isolated into 0.8 cm diameter vials and reared to adulthood. Individual isolation avoids the effects of common rearing environment confounding differences in QTW between lines and selection regimens. A total of 105 quiescent larvae per line were isolated. Four days after isolation, and twice daily following, the vials were checked for nymphs reaching the quiescent tritonymph stage. Quiescent tritonymphs were removed and weighed on a Sartorius Supermicro balance to 0.0001 mg. QTW measured in this way is known to be highly repeatable (Radwan *et al.* 2002).

Table 1. ANOVA with QTW as the dependent variable, morph and selection direction as main effects, replicate nested within selection and day of larvae isolation as a random factor. (Non-significant ( $p > 0.15$ ) interactions were discarded sequentially from the model.)

source	d.f.	mean square	<i>F</i>	<i>p</i>
morph	1	359335	30.23	< 0.001
selection	1	9021	0.27	0.642
replicate (selection)	4	19746	1.66	0.158
day	2	211511	7.50	0.118
selection × day	2	28138	2.37	0.095
residual	340	11885		

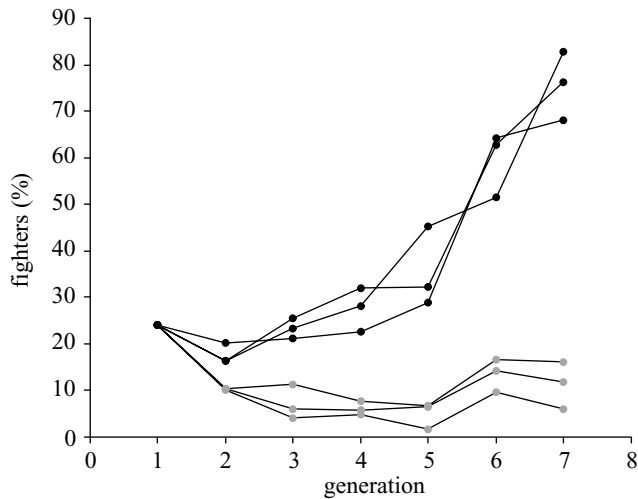


Figure 1. Response to selection on male morph. Black circles, fighter selection lines; grey circles, scrambler selection lines.

### 3. RESULTS

After seven generations of selection, the proportions of fighters in fighter-selected lines were 0.68, 0.76, 0.83, and in the scrambler-selected lines 0.16, 0.06 and 0.12 (figure 1). The divergence was highly significant ( $t_4 = 12.3$ ,  $p = 0.0002$ ). The realized heritabilities were calculated according to the liability model (Falconer & Mackay 1996) as cumulative response to selection divided by cumulative selection differential (divided by 2 to take into account that only males were selected). In the fighter lines, the heritabilities were 0.40, 1.6 and 0.74, with a mean of 0.92, and in the scrambler lines 0.32, 0.40 and 0.48, with a mean of 0.40.

When reared in isolation after seven generations of selection, the proportions of fighters in fighter-selected lines were 0.98, 0.87 and 1.00, and in scrambler-selected lines 0.81, 0.63 and 0.71. This was significantly more than in larvae reared in groups of 20 (paired  $t$ -test,  $t_4 = 4.19$ ,  $p = 0.009$ ), confirming suppressive effect of colony chemicals (Radwan *et al.* 2002). However, the proportion of fighters was still significantly higher in fighter-selected lines ( $t_4 = 3.59$ ,  $p = 0.022$ ).

Although males that emerged into fighters were on average heavier at the tritonymphal stage than those that emerged into scambblers, selection lines did not differ in QTW (table 1, figure 2). Thus, there was no evidence for a correlated response in QTW.

Logistic regression was used to detect the divergence between selected lines in the threshold of the fighter phenotype on tritonymph weight. The basic model was a logistic regression with male morph as the dependent variable and tritonymph weight as a covariate, and confirmed results from analysis of variance in that condition dependence was evident ( $\chi^2 = 29.62$ , d.f. = 1,  $p < 0.001$ ). The addition of selection direction as a factor in the model significantly improved the model fit ( $\chi^2 = 38.294$ , d.f. = 1,  $p < 0.001$ ), but the addition of selection line replicate did not ( $\chi^2 = 2.54$ , d.f. = 4,  $p > 0.5$ ). Hence, the threshold, which can be envisaged as a weight at which a tritonymph has a 50% probability of becoming either morph, differed between selection regimens (figure 3).

### 4. DISCUSSION

*Sancassania berlessei* responded to selection on male morph, and male morph was condition dependent, i.e. fighters emerged from heavier tritonymphs (table 1). This latter result is consistent with the data previously obtained from another population of *S. berlessei* (Radwan *et al.* 2002). Nevertheless, there was no correlated response in QTW to selection on male morph. Thus, the observed response to selection (increasing and decreasing fighter ratio) was probably the result of a change in the genetically determined position of the QTW threshold at which the fighter morph is expressed. This was confirmed by logistic regression analysis which indicated that the up and down lines differed in the reaction norm of morph expression on QTW (figure 3). This shows that genetic variance influencing the expression of the sexually selected thickened legs in *S. berlessei* is mostly independent of condition (measured as QTW). Genetic variance for the threshold of response to cues inducing phenotypically plastic alternative phenotypes has previously been documented in contexts other than sexual selection, e.g. in predator-induced defences (Hazel & West 1982) or migratory polymorphism (Knülle 1991, 2003; Fairbairn & Yadlowski 1997).

In a population of the same origin, we have found a positive correlation between father QTW and proportion of fighters in their progeny (Tomkins *et al.* 2004), which indicates that morph and QTW are to some degree genetically correlated. However, this does not necessarily conflict with the results of the present study, as we also found a highly significant correlation between father and son morph that was independent of QTW (Tomkins *et al.* 2004). This is indicative of large genetic variance for the threshold and therefore consistent with the results of the

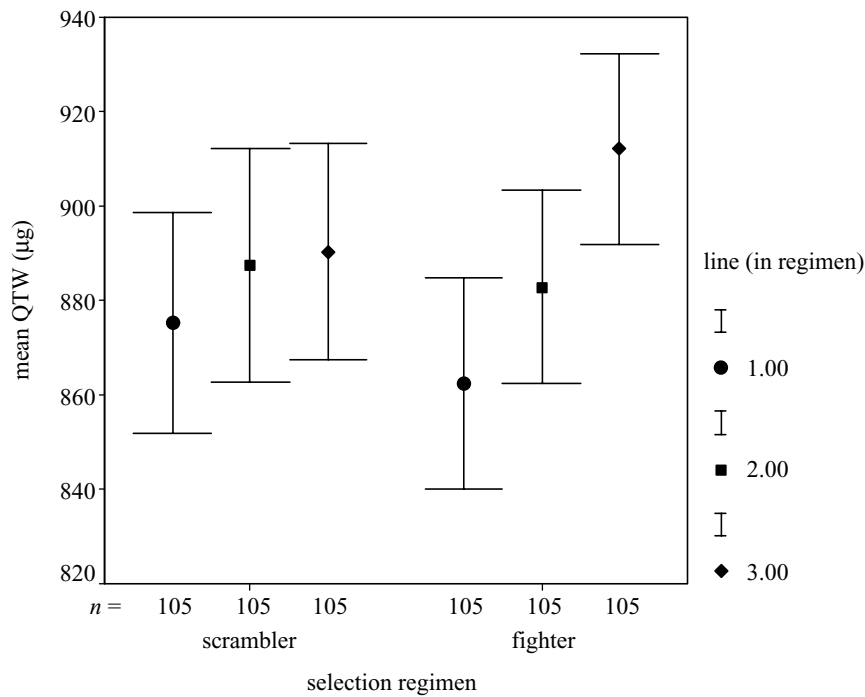


Figure 2. Mean QTWs of males from three selection lines in each of two regimens, demonstrating that there was no significant correlated response to selection. Vertical lines show s.e.m.

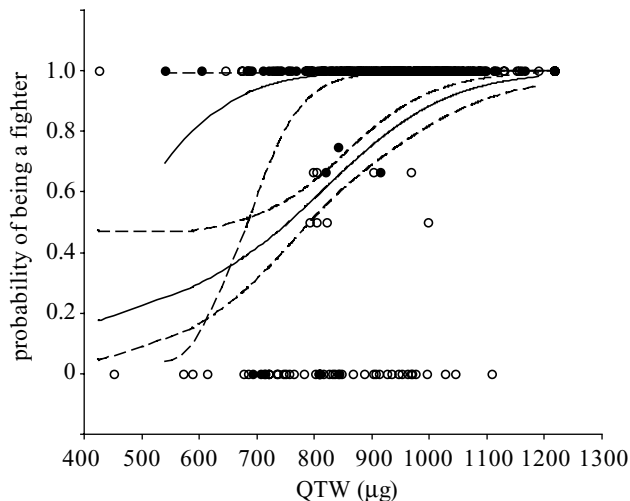


Figure 3. Cubic splines (solid lines)  $\pm 95\%$  CI (dashed lines) from 500 iterations showing the outcome of selection on the expression of the fighter phenotype. The threshold in the scrambler selected lines (open circles and lower spline) is at a higher QTW than the fighter selected lines (filled circles and upper spline). Splines were calculated using GLMSWIN 10 (Schluter 1998).

selection experiment reported here; if the selected trait has a large additive genetic variance that is independent of condition, any correlated response in condition will be weak and difficult to detect.

In the horn-dimorphic beetle *Onthophagus acuminatus*, Emlen (1996) recorded a significant response to selection for the scaling relationship between horn length and body size. Emlen (1996) concluded that genetic variance affecting horn expression was mostly caused by variation in the position of the threshold. The selection imposed was for relative horn length and so was directly selecting on

variance in horn expression that was largely independent of body size. Nevertheless there was a correlated response in body size in one direction, suggesting some genetic correlation between horn size and body size (Emlen 1996). The genetic correlation between body size and horn length in another dung beetle, *Onthophagus taurus*, is significant (Kotiaho *et al.* 2001), suggesting that indeed the low/absent correlated responses in body size in the experiment of Emlen (1996) were because he managed to select mainly on the threshold. We were not selecting on the threshold *per se* in our experiment but rather were selecting all individuals of one morph or the other. Therefore, all things being equal, the type of selection we imposed would be more likely to lead to a correlated response in QTW—that it did not, despite dramatic shifts in threshold, further suggests that the genetic variance in threshold is large whereas its correlation with QTW is small.

The validity of using a threshold trait to investigate condition-dependent signalling depends on the relationship between the underlying 'liability' and condition. Body size in dung beetles is likely to be tightly correlated to liability as the switches that determine hormonal control of horn length depend on the weight of the larva during a critical period of development (Emlen & Nijhout 1999, 2001). Nevertheless, body size is largely determined by the size of the brood mass provided by the female, and not the resource acquisition ability of the individual; consequently body size in dung beetles is not a good measure of condition, *sensu* Rowe & Houle (1996). QTW in *S. berlessei* does provide a good reflection of the individual's ability to acquire resources and is therefore a more accurate reflection of condition than size measures in dung beetles. Thus, our results appear to go against the prediction of the genic capture model of sexual selection (Rowe & Houle 1996) as this model relies on a very high genetic

correlation between condition and the expression of the condition-dependent traits (Rowe & Houle 1996; Kotiaho *et al.* 2001). The simple criteria from which genic capture should evolve (condition dependence and genetic variance in condition) mean that a signalling function to the trait is not a necessary prerequisite for a correlation between genetic quality (measured as the load of deleterious mutations) and trait expression (Rowe & Houle 1996). Whether the thickened legs of *S. berlessei* are used for sexual signalling purposes has not been investigated. Nevertheless, weapons can evolve signalling function through condition dependence (Berglund *et al.* 1996). However, if the expression of dimorphic traits depends little on genetic quality, the evolution of these traits as reliable indicators of quality is unlikely.

Our results raise the question as to what maintains the apparently large levels of genetic variance for the threshold in this species and why the genetic correlation with condition is low in this phenotypically condition-dependent trait. The maintenance of genetic variance for threshold traits probably has several sources. Threshold traits allow for the maintenance of more genetic variation under directional selection than continuously distributed traits (Roff 1996; West-Eberhard 2003). This is because under directional selection for a morph, the selection intensity necessarily declines as the population responds to selection and the heritability can be restored (Roff 1996). Even when selection has removed the phenotypic expression of one morph, selection is unable to erode the genetic variation for the threshold trait completely as it remains hidden from selection (Roff 1996). Furthermore, high levels of genetic variance for thresholds themselves are perhaps to be expected, particularly as selection on the threshold is not exerted equally on all individuals. Game theory models predict that thresholds occur because the fitness returns from adopting alternative tactics change with status (Hazel *et al.* 1990). To have a threshold, fitness functions must necessarily intersect—a point at which there will be equal fitness for both tactics (Gross 1996). At this threshold it is perhaps paradoxical that selection is weakest; nevertheless it ensures that under all but the most intense status-dependent selection, large amounts of genetic variance for the exact position of the threshold are likely to be maintained (Tomkins 1999; see also West-Eberhard 2003). An additional peculiarity of selection on threshold traits is that the further from the threshold that an individual develops, the less important the precision of its developmental algorithm is, i.e. fine-scale selection on the threshold is exerted only on individuals that develop close to the threshold. Potentially therefore, the threshold expressed by most individuals may escape selection entirely, protecting the genetic variation of the threshold (Roff 1996). In *S. berlessei* the threshold is not only dependent on males' QTW but also on colony size, hence thresholds shift as population density increases (Radwan *et al.* 2002; Tomkins *et al.* 2004) to the extent that population growth will remove the expression of fighters almost completely over a few generations. Even within a male's lifetime, as the density increases through the recruitment of offspring to adulthood, males that adopted fighter tactics as a result of the low-density conditions in their larval period will find themselves in populations where they would be better off as scramblers. Hence, in *S. berlessei*

selection at the threshold is likely to be both shifting and periodic, perhaps maintaining the high genetic variance detected in this and other studies (Tomkins *et al.* 2004).

Previous analysis of morph determination in a different population of *S. berlessei* did not find a significant heritability of male morph (Radwan 1995), but confirmed previous findings that rearing in groups suppresses expression of the fighter morph (Timms *et al.* 1981; Radwan 1993a). In the present study, we have also found that the proportion of fighters obtained from isolated larvae is significantly higher than from larvae reared in groups. However, we found high realized heritabilities of male morphs. Similarly, the data for another male dimorphic acarid, the bulb mite, *Rhizoglyphus robini*, obtained from two different populations (Radwan 1995, 2003) show substantial inter-population variation in heritabilities, although both studies did detect significant heritabilities of male morph under the liability model. The causes of this inter-population variation remain to be investigated.

Emlen (1996) suggested that costly sexual ornaments with threshold expression can become fixed in a population more easily than traits that are linearly dependent on condition. However, if sexual traits are to be used as indicators of genetic quality, one also needs to consider their reliability. If most of the genetic variance in a sexually selected trait arises because of its dependence on condition, then such indicators will be reliable (Rowe & Houle 1996). If, conversely, a sexual trait maintains a lot of variance that is independent of condition, such traits might be very poor indicators of genetic quality. As we discussed earlier, there are several reasons why there may be more genetic variance for threshold traits than for continuous traits (Emlen 1996; West-Eberhard 2003). These processes are likely to maintain substantial genetic variance in discontinuous traits that is independent of condition, a conclusion supported by our results. The suggestion of Emlen (1996) that costly traits are more likely to be maintained when they show threshold expression might apply to weapons used in intrasexual competition. However, such traits are unlikely to be subject to mate choice for indirect benefits if, as we found, they are unreliable indicators of genetic quality, even when phenotypic condition dependence suggests otherwise. More research is needed to confirm the generality of this finding.

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