Review Paper

Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis?

Samuel Cotton[1], Kevin Fowler[1] and Andrew Pomiankowski[1,2*]

[1]*The Galton Laboratory, Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK*
[2]*Collegium Budapest, Szentháromság utca 2, H-1014 Budapest, Hungary*

The handicap hypothesis of sexual selection predicts that sexual ornaments have evolved heightened condition-dependent expression. The prediction has only recently been subject to experimental investigation. Many of the experiments are of limited value as they: (i) fail to compare condition dependence in sexual ornaments with suitable non-sexual trait controls; (ii) do not adequately account for body size variation; and (iii) typically consider no stress and extreme stress manipulations rather than a range of stresses similar to those experienced in nature. There is also a dearth of experimental studies investigating the genetic basis of condition dependence. Despite the common claim that sexual ornaments are condition-dependent, the unexpected conclusion from our literature review is that there is little support from well-designed experiments.

Keywords: condition; condition dependence; handicap; ornament; sexual selection

1. INTRODUCTION

The handicap hypothesis of sexual selection has increasingly come to dominate discussions about the evolution of exaggerated sexual ornaments (Andersson 1994). It predicts that female preferences have evolved for exaggerated sexual ornaments which signal male genetic quality. Male sexual traits have coevolved with female preference to be larger, and so more costly. One of the key predictions made by the handicap hypothesis is heightened condition-dependent expression of sexual ornaments (Pomiankowski 1987; Grafen 1990; Iwasa & Pomiankowski 1994). Males in good genetic condition are assumed to signal their quality through greater sexual trait size or more vigorous display. Males in worse condition are unable to do this because of the viability costs associated with such extravagance. The same logic applies when male quality varies owing to environmental conditions and this affects fertility, parenting or some other directly important reproductive ability (Iwasa & Pomiankowski 1999). So sexual trait condition dependence can evolve to signal male genetic or environmental quality, or both.

It is widely assumed that condition dependence is a common feature of sexual traits. This is backed by previous reviews that list many examples of ornament size and courtship performance being positively correlated with measures of condition (Andersson 1994; Johnstone 1995). However, the bulk of the evidence reported in these reviews is just correlational. These are indicative of an underlying causal relationship but correlation is not cause. There is a need for experimental studies to confirm that sexual ornaments have strong condition-dependent expression. In addition, surprisingly few studies in these older reviews report null or negative relationships between ornaments and condition. This gives the impression of publication or study bias.

Over the past decade there has been an increasing use of experimental techniques to investigate condition dependence. In this paper, we assess the current state of experimental evidence and ask whether, like the correlational data, the experimental results stack up in support of the condition-dependent sexual trait hypothesis. A second aim of this review is to set out the criteria needed for carrying out a rigorous study. We show that improvements in understanding are limited by deficiencies in experimental design. This leads on to suggestions as to where further investigation needs to be directed.

2. HANDICAP THEORY

In this section, we outline the theory behind condition-dependent signalling. Theoretical investigation of handicap models has been performed using major gene (Pomiankowski 1987), game theory (Grafen 1990) and quantitative genetics models (Iwasa *et al.* 1991). Here, we concentrate on a simple quantitative genetic treatment, which sets out the major predictions of the handicap hypothesis (for more details see Iwasa *et al.* (1991) and Iwasa & Pomiankowski (1994, 1999)). Let s be the size of a male sexual ornament used by females in their mate choice,

$$s = t + t'v. \tag{2.1}$$

Ornament size is determined by a condition-independent (t) and a condition-dependent ($t'v$) part. The model assumes a linear relationship between ornament size and male additive genetic quality or condition (v). This is mediated by t', the degree of condition dependence. In the simplest case we ignore environmental variation

Proc. R. Soc. Lond. B (2004) **271**, 771–783
DOI 10.1098/rspb.2004.2688

771

[*]Author for correspondence (ucbhpom@ucl.ac.uk).

assuming that it has a mean effect of zero on the sexual ornament. The basic assumption of the handicap hypothesis is that the cost of the ornament varies with male quality,

$$\text{cost} = \frac{c}{1 + kv} s^2. \quad (2.2)$$

For simplicity we set the natural selection optimum ornament size to $s = 0$, with survival chances declining symmetrically around this optimum. The rate of decline is set by the cost coefficient (c). Survival chances also depend on male quality (v). They decline more quickly for lower-quality individuals at a rate that reflects the cost differential (k). If k is large, lower-quality individuals (i.e. lower v) pay higher costs for larger sexual ornaments, whereas if $k = 0$, male quality has no effect on survival chances. Given that females prefer to mate with larger ornamented males, equilibrium conditions can be derived for the size of the male ornament (Iwasa & Pomiankowski 1994, 1999). Of relevance here, we can specify the relative condition dependence of the male ornament,

$$\frac{\bar{t}'}{\bar{t}} = k, \quad (2.3)$$

where $\bar{t}$ and $\bar{t}'$ are the mean trait values. This shows that as the cost differential k increases, so does the mean condition dependence of the sexual ornament ($\bar{t}'$).

A previous interpretation of this result (Iwasa & Pomiankowski 1994) was that the cost differential was $k = 0$ under Fisher's runaway process (Fisher 1930), and there would therefore be no condition dependence (i.e. $\bar{t}' = 0$) in ornaments that did not signal good viability genes. This ignores the fact that most traits to some extent show condition-dependent expression. This is obvious when body size is closely associated with fitness, and many traits scale with body size. A better interpretation is that Fisher's runaway does not assume any greater cost differential in the ornament than seen in other traits, so there is no expectation of heightened condition dependence in sexual ornaments that only signal attractiveness genes. By contrast, the handicap hypothesis assumes greater differential costs, and so predicts heightened condition dependence in sexual ornaments compared with other traits.

In equation (2.2) we assume that there is genetic variation in male quality. We can also consider environmental quality variation (e) between males. For instance, individuals may differ in the food and resources available during development or in adult life. Given that we expect that the cost equation has the same dependency on environmental quality as it does on genetic quality, we can simply substitute e for v in equation (2.2), and then equation (2.3) still holds. So the handicap hypothesis predicts that sexual ornament condition dependence should occur with environmental quality variation just as it does with genetic quality variation. This is important because environmental variation in quality may be high under natural conditions, or because the experimenter creates large differences in environmental conditions so as to investigate condition dependence.

3. WHAT IS CONDITION?

The theoretical position set out above views condition (or quality) as a trait closely related to viability (Iwasa *et al.* 1991; Iwasa & Pomiankowski 1994). Condition has the property that higher values confer greater fitness, and it can have genetic (v) and environmental (e) components (Iwasa & Pomiankowski 1999). This simplistic view does not specify how condition is related to quantities that can be easily measured by field and experimental biologists. Here, we briefly discuss various approaches to this question.

Measures of condition have been used for a long time as a general gauge of individual nutritional state, resources, energy reserves and health in a variety of biological contexts (Bolger & Connelly 1989; Rowe & Houle 1996). Typical indexes attempt to control for body size by taking simple ratios (mass divided by the cube of body size), slope-adjusted ratios (slope of log(body mass) on log(body size)) or residuals (Jakob *et al.* 1996). All of these indexes have been criticized, largely because the true relationship between the two variables is unknown *a priori*, and each method introduces assumptions that may not be biologically or statistically justified (see Jakob *et al.* 1996; Kotiaho 1999; Packard & Boardman 1999; Green 2000; Darlington & Smulders 2001; García-Bertou 2001). To confound matters, there is no assurance that fresh weight is always a good indicator of fat reserves, or that fat reserves are a good indicator of fitness. For example, Rolff & Joop (2002) report that fresh weight in a dragonfly was a poor predictor of other fitness traits such as fat content, dry weight and muscle mass, and Ekman & Lilliendahl (1993) and Gosler (1996) found that fat storage was negatively correlated with social dominance in tits.

It is clear that size and energy reserves often play an important role in determining fitness. However, the idea that a higher condition index equates to greater fitness is too simplistic. In some species, at some life-history stages, in some environments, for some types of condition, these indexes may be strongly correlated with major components of fitness. Nonetheless, there is no reason to believe that this will always be the case. The ease of measuring condition indices has resulted in a plethora of studies reporting a positive correlation between 'condition' and sexual ornament size (Andersson 1994; Johnstone 1995). But these relationships provide only weak evidence for condition dependence in the absence of experimental verification.

4. EXPERIMENTAL STUDIES OF CONDITION DEPENDENCE

Before reviewing the literature, we consider how to carry out a rigorous experimental study of condition dependence. There are three main areas of concern.

(a) *Comparison of traits*

Statements about the condition dependence of sexual traits are of little value unless they refer to other traits against which ornaments can be compared; bluntly, 'no controls, no conclusions' (Crawley 1993, p. 58). In particular, it is vital to contrast condition-dependent expression in sexual ornaments with that seen in other

non-sexually selected traits. Comparisons have been made using the homologous trait in females (if present), on the assumption that condition dependence of the female trait approximates that of the ancestral unexaggerated state. Comparisons to male non-sexual traits are useful to make sure that differences in condition dependence are trait specific (sexual versus non-sexual) not sex specific. Comparisons have also been made among sexual traits, when males have several ornamental traits or behaviours, to test whether those subject to stronger mate preference have higher condition dependence.

In all cases the prediction is that ornaments will have greater condition dependence than other traits, and this difference should increase as ornaments become more exaggerated. This requirement for a comparative approach to studying condition dependence is not new. Zuk *et al.* (1990) 'measured several non-ornamental characters to test that … [parasite-induced stress] …should exert a *greater* effect on ornamental than non-ornamental traits, and that female choice should be focused specifically on male traits that best reveal information about male health' (p. 236; emphasis ours). However, there are still far too many studies that simply report condition dependence just for a single sexual trait.

(b) *Control of body size*

The need to compare sexual and non-sexual traits arises from the fact that many, if not all, traits show some degree of condition-dependent expression. Likewise, many, if not all, traits show some degree of allometric scaling with body size. So removing the effect of body size is an important step in comparing sexual and non-sexual traits. In addition, the importance of body size scaling may reveal whether ornaments primarily signal body size or some other components of condition. Sexual ornaments may just be exaggerated representations of body size, in which case demonstrating heightened condition dependence of absolute ornament size is sufficient. Alternatively, ornament expression may reflect a wider range of condition factors, and then we expect part of the ornament's condition dependence to be independent of body size. The need to control for and determine the importance of body size scaling has been under-appreciated literature on condition dependence.

To control for body size in the comparison of sexual and non-sexual traits one needs to know *a priori* how each trait scales with body size so that the covariance between each trait and body size can be appropriately removed. A common approach is to use relative trait size (individual trait size divided by body size) or trait size as a percentage of body size. But this is problematic if scaling deviates from isometry, as the covariance with body size will persist (Packard & Boardman 1999) and condition dependence may arise as an artefact. Residuals derived from the regression of trait size on body size have also been used, but this procedure has been the subject of recent criticism (Kotiaho 1999; Green 2000; Darlington & Smulders 2001; García-Bertou 2001). A preferable approach is to express trait size as a function of body size and statistically account for it as a covariate in general linear models, which avoids the drawbacks associated with relative and residual measures (Darlington & Smulders 2001; García-Bertou 2001).

(c) *Experimental manipulation of condition*

Most experimental studies have used variation in environmental quality rather than in genetic quality to assess condition dependence of sexual ornaments. This is because accurate control over environmental quality can usually easily be achieved under laboratory conditions. By contrast, it is hard to estimate genetic quality *a priori* or to set up distinct categories of genetic quality (but see § 6). Typically, two levels of environmental stress have been used, for example: food versus no food or unparasitized versus parasitized. Usually this allows low and high condition to be assigned unambiguously to the different stress levels.

In many cases, this approach has been sufficient to demonstrate a change in ornament size with condition. However, the use of only two groups is often problematic. First, the stress categories used may be unrelated to those experienced under natural conditions. In most cases, the range of stress experienced under natural conditions is not known with any degree of accuracy. But, truly unstressed animals are probably little more than laboratory artefacts, and many stressed groups are often exposed to environments at the extreme or beyond those to which they are adapted. This means that the choice of stress treatments is crucial. If there is little difference between the two groups, there may be insufficient power to detect condition dependence, with the risk of declaring a false negative. If the two groups are exposed to extremely benign and extremely harsh stresses, then a response to treatment may be condition-dependent, but biologically unrealistic if the treatment range falls outside that found in nature. In this case one risks declaring a false positive.

One straightforward solution to these problems is to examine a much broader set of stress classes. Although this has the cost of increasing sample size, it allows condition-dependent expression of sexual traits to be more accurately assessed. It increases the chances of detecting condition dependence and gives a much better ability to bring out whether sexual traits have heightened condition dependence. A related problem concerns timing. Stress can be applied continuously or at one point during development. These different approaches tend to be appropriate for considering different questions. Animals are likely to have an adaptive response to continuous stress if this is a frequent occurrence in nature. So continuous stress experiments are likely to reveal the nature of this adaptive response to stress. By contrast, brief stress shocks (e.g. an extreme temperature) are less predictable events, and may be useful for finding which parts of development are sensitive to environmental stress.

5. METHODS

We surveyed published literature, restricting our compilation to experimental tests of sexual ornament condition dependence performed using controlled variation of environmental or genetic factors. We used Johnstone (1995) to obtain references for literature published before 1995, and searched an electronic database (Web of Knowledge: http://www.wok.mimas.ac.uk) for relevant recent articles. We also consulted the reference lists of these papers to identify additional studies. Although not exhaustive, the review is large and represents the state of contemporary literature. In the survey we do not discuss correlations between

ornaments and components of fitness as these relationships are beyond the scope of this paper and have been subject of two recent reviews (Møller & Alatalo 1999; Jennions *et al.* 2001).

For each study we inferred an ordinal scale of condition using experimental groups and noted the type and number of treatments. We looked for comparisons between the response of sexual and non-sexual traits to treatment so as to test the hypothesis that the condition dependence of ornaments is greater than that of other traits. Control traits were defined as such if they were similar in kind to ornamental traits and were of the same dimensions (where appropriate). For example, behavioural displays were not compared with non-sexual morphological traits. We also looked to see if traits had been compared after the influence of body size had been removed, and whether an effort had been made to investigate the genetic basis of condition dependence. Finally, we note that our scale of condition was, in many cases, different to that of the original author(s) because we did not use indexes of condition, and so some of our conclusions differ from those reported in the source paper (e.g. Frischknecht 1993; Birkhead *et al.* 1998).

6. RESULTS

(a) *General findings*

Our review of the experimental literature comprised 55 studies covering 33 species in 25 genera from a wide range of vertebrate and invertebrate taxa (table 1). Seven studies measured the effect of an environmental stress on two sexual characters, and five studies used two or more methods to investigate the condition dependence of sexual traits. A variety of different stresses were used, including food quantity and quality, parasite infection and brood manipulation. Out of these studies (65 experiments in total), 49 report that sexual ornaments were condition-dependent; that is, the sexual trait showed decreased size in response to experimentally increased stress. Fourteen sexual ornaments were not condition-dependent under this definition.

Most studies (40 out of 65) employed only two stress treatments, often limiting the analysis to a simple comparison of apparently 'stressful' and 'non-stressful' conditions. This procedure was sufficient to reveal sensitivity in the sexual trait in several species (table 1). However, negative results are harder to interpret. It is noteworthy that most (12 out of 14) of the studies that failed to find a condition-dependent response used only two treatments. To firmly establish that traits are not condition-dependent requires investigation of a wider range of stress levels and even different types of stress.

Only 20 studies compared the response of the sexual ornament with a suitable control trait. Out of these, 15 studies confirmed that the sexual trait exhibited heightened sensitivity to stress in two species of cricket (Wagner & Hoback 1999; Holzer *et al.* 2003; Scheuber *et al.* 2003*a,b*), two stalk-eyed fly species (David *et al.* 1998, 2000; Knell *et al.* 1999), wolf spiders (Kotiaho 2000), guppy fish (Sheridan & Pomiankowski 1997; Grether 2000), two species of finch (Hill & Brawner 1998; Hill 2000; McGraw & Hill 2000), the brown-headed cowbird (McGraw *et al.* 2002) and red jungle fowl (Zuk *et al.* 1990). Sexual traits that failed to show heightened condition dependence include components of courtship song in *Gryllus* crickets (Gray & Eckhardt 2001), male genital

traits in water striders (Arnqvist & Thornhill 1998) and bill colour in zebra finches (Burley *et al.* 1992). In other studies, non-sexual trait expression was ignored.

About half (37 out of 64) of the studies made appropriate adjustments for body size variation. This lack of control is worrying because correlated change of traits with body size could account for a large part of the condition-dependent response observed. This adjustment is unlikely to be important for some traits like colour and behaviour, which are not expected to covary with body size. This is often assumed; it would be better if it were demonstrated (e.g. Kotiaho 2002; Scheuber *et al.* 2003*a*).

Surprisingly, studies using genetic information are rare (table 1), despite the importance of genes in the proposed function of sexual ornaments. Several studies used a split brood design, in which brothers were either stressed or unstressed (seven studies), simply as a control for genetic effects. Two studies used inbreeding as a form of genetic stress (Sheridan & Pomiankowski 1997; Van Oosterhout *et al.* 2003). Of greater interest, a few studies used pedigree information to investigate elements of the handicap hypothesis. In dung beetles, manipulation of environmental quality revealed that courtship is condition-dependent as adult males kept on excess dung had higher courtship display rates than males experimentally deprived of dung (Kotiaho *et al.* 2001; Kotiaho 2002). Kotiaho *et al.* (2001) also used a half-sib design to show that display rate was genetically correlated to offspring residual mass (a measure of condition). Unfortunately, no comparisons with non-sexual behaviour were made. A different point was investigated by comparing half- and full-sib stalk-eyed fly families under a range of food stresses (David *et al.* 2000). This revealed genetic variation underlying condition-dependent expression of the male sexual ornament; some families produced large male eyespan under all conditions, whereas others showed a consistent decline in male eyespan as stress increased. However, an experiment using waxmoths by Jia *et al.* (2000) found that different genotypes (lines artificially selected for high or low values of two sexual traits) predominantly showed crossing-over of reaction-norms between control and non-standard environments (i.e. line ranks tended to be reversed in the non-standard treatments). This suggests that genetic specialization and trade-offs dominate sexual trait expression rather than condition-dependent quality variation. However, these findings are difficult to interpret from the perspective of condition dependence, as it is unclear whether the non-standard environments were more or less stressful than the standard rearing procedure.

To clarify the current state of experimental work, we discuss in greater detail the seven taxa in which there is good evidence for heightened condition dependence of sexual ornaments. The experiments are not without problems, so an objective is to show where more work is needed. For instance, few studies have taken into account body size covariation, examined more than two levels or different types of stress, and investigated the genetic basis of condition dependence.

(b) *Crickets*

Male crickets produce long-range calling song to attract females and short-range courtship song to persuade attracted females to mate (Alexander 1961).

Table 1. Experimental investigations into the condition dependence of sexual traits.

(CD, condition dependence. Stress: *n*, number of stresses; A, diet (quantity); B, diet (quality); C, density; D, temperature; E, photoperiod; F, carotenoid availability (diet otherwise constant across treatments); G, parasites; H, inbreeding (genetic stress); I, exercise; J, brood size manipulations; K, reproductive effort; L, predictability of food supply. Genetic design: SB, split brood; HS, half-sib; PO, parent/offspring; FS, full-sib; AS, artificial selection; BIP, bi-parental progenies; F/MS, father on mid-son; IPV, inter-population variation when reared under standard conditions; IB, inbreeding. Genetic effect: G, genotype effect; G×E, genotype × environment interaction.)

species		sexual trait	control trait	sexual trait CD	control trait CD	sexual trait CD > control trait CD	controlled for body size	stress (*n*)	genetic design	genetic effect	reference
insects, arachnids and crustaceans											
cricket	*Gryllus campestris*	calling song	song components	✓	×	✓[a]	✓[b]	A (2)	×	—	Holzer et al. (2003)
	G. campestris	calling song	song components	✓	×	✓[a]	✓[c]	A (3)	✓(SB)	—	Scheuber et al. (2003a)
	G. campestris	calling song/harp size	song components	✓	×	✓[a]	✓[d]	B (2)	✓(FS)	✓(G)	Scheuber et al. (2003b)
	G. lineaticeps	calling song	song components	✓	×	✓[a]	×	B (2)	✓(SB)	—	Wagner & Hoback (1999)
	G. lineaticeps	courtship song	×	×	—	—	×	B (2)	✓(SB)	—	Wagner & Reiser (2000)
	G. texensis	courtship song	song components	×	×	×	×	B (2)	×	—	Gray & Eckhardt (2001)
damselfly	*Mnais costalis*	wing pigmentation	×	✓	—	—	×	A (2)	×	—	Hooper et al. (1999)
dung beetle	*Onthophagus taurus*	courtship rate	×	✓	—	—	✓[b]	A (2)	✓(HS)	✓(G)	Kotiaho et al. (2001)
	O. taurus	horn length	×	✓	—	?	✓[f]	A (4)	×	—	Hunt & Simmons (1997)
	O. acuminatus	horn length	×	✓	—	?	✓[f]	A (2)	✓(PO)	×(G)	Emlen (1994)
	O. taurus, O. binodis, O. australis	courtship rate	×	✓	—	—	✓[c,d]	A (2)	×	—	Kotiaho (2002)
fruitfly	*Drosophila grimshawi*	courtship display	×	✓	—	—	×	B (2)	×	—	Droney (1996)
grain beetle	*Tenebrio molitor*	pheromone	×	✓	—	—	×	A (2)	×	—	Rantala et al. (2003)
stalk-eyed fly	*Cyrtodiopsis dalmanni*	eyespan	female eyespan	✓	×	✓	✓[d]	A,C (5)	×	—	David et al. (1998)
	C. dalmanni	eyespan	wing, female eyespan	✓	×	✓	✓[g]	B (3)	✓(HS,FS)	✓(G×E)	David et al. (2000)
	Diasemopsis aethiopica	eyespan	female eyespan	✓	✓	✓	✓[d]	B (2)	×	—	Knell et al. (1999)
water strider	*Gerris incognitus*	genitalia	morphological traits	✓	✓	×	×	A,B (2)	✓(FS,BIP)	✓(G)	Arnqvist & Thornhill (1998)

(Continued.)

Table 1. (*Continued.*)

species		sexual trait	control trait	sexual trait CD	control trait CD	sexual trait CD > control trait CD	controlled for body size	stress (*n*)	genetic design	genetic effect	reference
waxmoth	*Achroia grisella*	acoustic signal rate	×	?[h]	—	—	×	A,B,C,D,E (6)	✓(AS)	✓(G×E)	Jia *et al.* (2000)
		acoustic peak amplitude	×	?[h]	—	—	×	A,B,C,D (4)	✓(AS)	✓(G)	
wolf spider	*Hygrolycosa rubrofasciata*	drumming rate	×	✓	—	—	✓[b]	A (3)	×	—	Mappes *et al.* (1996)
	H. rubrofasciata	drumming rate (female present)	drumming rate (female absent)	✓	✓	✓	✓[b]	A (3)	×	—	Kotiaho (2000)
fiddler crab	*Uca beebei*	mud pillar building	×	✓	—	—	×	A (2)	×	—	Backwell *et al.* (1995)
	U. annulipes	claw waving	×	✓	—	—	×	A (3)	×	—	Jennions & Backwell (1998)
	U. lactea	semidome building	×	✓	—	—	✓[c]	A (3)	×	—	Kim & Choe (2003)
		claw waving	×	✓	—	—	✓[c]	A (3)	×	—	
fish and amphibians											
guppy	*Poecilia reticulata*	carotenoid pigmentation	×	✓	—	—	✓[i]	F (2)	✓(SB)	✓(G)	Kodric-Brown (1989)
	P. reticulata	carotenoid pigmentation	×	✓	—	—	✓[b]	G (2)	✓(SB)	—	Houde & Torio (1992)
	P. reticulata	carotenoid pigmentation	morphological traits, melanin pigmentation	✓	×	✓	✓[j]	H (2)	✓(IB)	✓(G)	Sheridan & Pomiankowski (1997)
	P. reticulata	carotenoid pigmentation	morphological traits, other pigmentation	✓	×	✓	✓[g]	F (3)	✓(IPV,FS)	✓(G×E)	Grether (2000)
	P. reticulata	carotenoid pigmentation courtship display	melanin pigmentation	✓	✓	—	✓[i]	H (3)	✓(IB)	—	Van Oosterhout *et al.* (2003)
three-spined stickleback	*Gasterosteus aculeatus*	carotenoid pigmentation	×	✓	—	—	×	H (3)	✓(IB)	—	Milinski & Bakker (1990)
			×	✓	—	—	×	G (2)	×	—	
	G. aculeatus	carotenoid pigmentation	×	×	—	—	✓[i]	A (2)	×	—	Candolin (1999)
	G. aculeatus	carotenoid pigmentation	×	×	—	—	✓[k]	A (2)	×	—	Candolin (2000)
	G. aculeatus	carotenoid pigmentation	blue eye pigmentation	×	—	—	✓[d]	A (5)	×	—	Frischknecht (1993)
smooth newt	*Triturus vulgaris*	dorsal crest	×	✓	—	—	×	A (2)	×	—	Green (1991)

(*Continued.*)

Table 1. (*Continued.*)

species	sexual trait	control trait	sexual trait CD	control trait CD	sexual trait CD > control trait CD	controlled for body size	stress (*n*)	genetic design	genetic effect	reference
birds										
american goldfinch *Carduelis tristis*	carotenoid pigmentation	melanin pigmentation	✓	×	✓	✓i	G (2)	×	—	McGraw & Hill (2000)
barn swallow *Hirundo rustica*	tail length	×	✓	—	—	✓b	G (3)	×	—	Møller (1991)
brown-headed cowbird *Molothrus ater*	iridescent plumage	melanin pigmentation	✓	×	✓	✓i	A (2)	×	—	McGraw *et al.* (2002)
collared flycatcher *Ficedula albicollis*	forehead patch	×	✓	—	—	×	J (5)	×	—	Gustafsson *et al.* (1995)
F. albicollis	forehead patch	×	✓	—	—	✓b	K (5), J (3)	✓(F/MS)	✓(G×E)	Qvarnström (1999)
european starling *Sturnus vulgaris*	song	×	✓	—	—	×	L (2)	×	—	Buchanan *et al.* (2003)
house finch *Carpodacus mexicanus*	carotenoid pigmentation	×	✓	—	—	×	F (3)	×	—	Hill (1990)
C. mexicanus	carotenoid pigmentation	×	✓	—	—	×	F (2/3)	×	—	Hill (1992)
C. mexicanus	carotenoid pigmentation	×	✓	—	—	×	F (2/3)	✓(IPV)	✓(G)	Hill (1993)
C. mexicanus	carotenoid pigmentation	melanin pigmentation	✓	×	✓	×	G (2)	×	—	Hill & Brawner (1998)
C. mexicanus	carotenoid pigmentation	×	✓	—	—	✓i	G (4)	×	—	Brawner *et al.* (2000)
C. mexicanus	carotenoid pigmentation	melanin pigmentation	✓	×	✓	×	A + F (5)	×	—	Hill (2000)
house sparrow *Passer domesticus*	melanin pigmentation	×	×	—	—	×	B (2)	×	—	Gonzalez *et al.* (1999)
P. domesticus	melanin pigmentation	×	✓	—	—	✓b	J (5)	×	—	Griffith (2000)
P. domesticus	melanin pigmentation	×	×	—	—	✓i	A (2)	×	—	McGraw *et al.* (2002)
mallard *Anas platyrhynchos*	display activity	×	✓	—	—	✓i	A (2)	×	—	Holmberg *et al.* (1989)
red jungle fowl *Gallus gallus*	plumage status		×	—	—	✓i	A (2)	×	—	Zuk *et al.* (1990)
Gallus gallus	plumage and comb characteristics	tarsus length, bill size, saddle feathers	✓	×	✓	×	G (2)	×	—	Zuk *et al.* (1990)

(*Continued.*)

Table 1. (*Continued.*)

species	sexual trait	control trait	sexual trait CD	control trait CD	sexual trait CD > control trait CD	controlled for body size	stress (n)	genetic design	genetic effect	reference
ring-necked pheasant *Phasianus colchicus*	wattle	×	✓	—	—	✓[d]	B (2)[l]	×	—	Ohlsson *et al.* (2002)
zebra finch *Taeniopygia guttata*	spurs	×	×	—	—	✓[d]	B (2)[l]	×	—	Burley *et al.* (1992)
	bill colour	female bill colour	✓	✓	×	✓[b]	B (2)[m]	×	—	
T. guttata	bill colour	×	×	—	—	✓[b]	B (2)	×	—	Blount *et al.* (2003a)
T. guttata		×	✓	—	—	×	C (2)	×	—	Blount *et al.* (2003b)
T. guttata	bill colour	×	✓	—	—	✓[b]	F (2)	×	—	Birkhead *et al.* (1998)
T. guttata		×	×	—	—	✓[i]	B (2)	×	—	
	bill colour	×	×	—	—	×	B + I (2)	✓(SB)	—	
	song rate	×	×	—	—	×	B + I (2)	✓(SB)	—	
mammals										
red deer *Cervus elaphus*	antlers	×	✓	—	—	×	A (2)	×	—	Suttie (1980) (cited in Andersson 1994)

[a] Some parameters of calling song show condition dependence with specific stresses whereas others do not. This suggests that different components of the sexual trait show heightened condition dependence under some circumstances.
[b] Repeated measures.
[c] No correlation with body size.
[d] Body size included as a covariate.
[e] Horn length shows sigmoidal allometry unlike other traits which is interpreted as elevated condition dependence, but horns are thought to be weapons rather than sexual ornaments (Kotiaho 2002), and under frequency-dependent rather than sexual selection (Moczek & Emlen 2000).
[f] Via allometry (see footnote e).
[g] Trait size divided by body size.
[h] Evidence unclear (see text).
[i] No size difference between treatments.
[j] Percentage coverage.
[k] Residuals from regression of ornament on body size.
[l] Two treatments applied either in early or late growth periods.
[m] Wild versus supplemented aviary birds.

Scheuber *et al.* (2003*a*) experimentally investigated the condition dependence of calling song in *Gryllus campestris*. They found that the frequency of calling and the chirp rate declined as adult dietary stress increased. However, treatment had no effect on other song characteristics (chirp duration, syllable number, chirp intensity and carrier frequency). Likewise, in an experimental field study, *G. campestris* males with an augmented food supply called more frequently than a group of control males (Holzer *et al.* 2003). Again, no effect of treatment was found on any other song characteristic. Comparable effects of adult dietary stress have been reported in the calling song of a congener, *G. lineaticeps* (Wagner & Hoback 1999). Scheuber *et al.* (2003*b*) also examined the effect of nymphal stress on calling song in *G. campestris*. Individuals reared on a poor nymphal diet suffered a disproportionate reduction in the stridulatory harp area, and produced a calling song with a higher carrier frequency when adults. These males were less attractive, as females prefer low-frequency calls. Nymphal stress did not affect any other song characteristic.

Courtship song has been investigated in *G. texensis* (Gray & Eckhardt 2001). Food treatment in nymphs and adults had no effect for any of the three courtship song parameters measured (interphase interval, chirp rate and the number of low-frequency chirps). Courtship song was also insensitive to adult dietary stress in *G. lineaticeps*, although only chirp rate was measured (Wagner & Reiser 2000).

The acoustic signals of male crickets are complex multi-component traits. Calling song was condition-dependent, whereas courtship song was not. Only certain elements of the calling song showed condition dependence and the timing of stress (nymphal versus adult) affected different components. The strength of these studies lies in the use of multiple elements of a sexual trait to identify those that are strongly condition-dependent against non-responding 'controls'.

(c) *Stalk-eyed flies*

Stalk-eyed flies, as their name suggests, have their eyes laterally displaced from the head on eye-stalks. Both sexes possess this trait, but in many species male eyespan is much greater than that of females. Sexual dimorphism is maintained through sexual selection as females prefer to mate with large eyespan males (Wilkinson & Reillo 1994; Hingle *et al.* 2001) and large eyespan males are more successful in intrasexual contests (Panhuis & Wilkinson 1999).

The main stalk-eyed fly species examined is the highly dimorphic *Cyrtodiopsis dalmanni*. Five levels of food stress were investigated in two populations by decreasing the amount of food given to a set number of eggs (David *et al.* 1998). In each population, male eyespan was significantly more sensitive to changes in larval density than female eyespan (David *et al.* 1998). This greater decrease in male eyespan persisted when relative trait size was investigated and when body size (wing size) was introduced as a control variable in a general linear model. Male eyespan condition dependence remained strong after control for body size, whereas female eyespan condition dependence was almost entirely accounted for by changes in body size. A similar result was found in another dimorphic diopsid,

Diasemopsis aethiopica (Knell *et al.* 1999). In this study, appropriate control for body size was made but only two larval food stress levels were investigated.

A further study in *C. dalmanni* showed that there was genetic variation underlying the response of male eyespan to food stress (David *et al.* 2000). This experiment used a full- and half-sib design, exposing larvae to three food quality types. Some genotypes maintained large male eyespan under all environments, whereas others became progressively smaller as stress increased. This pattern persisted when body size variation was controlled for using relative trait values. However, female eyespan and wing length in both sexes showed no or little genetic condition-dependent response once body size had been controlled for.

It was also noted that the sexual trait amplified differences between genotypes under stressful environmental conditions, even though the mean trait size declined (David *et al.* 2000). Again this pattern persisted using relative trait values. Non-sexual control traits, female eyespan and wing length in both sexes, did not show any change in genetic variation across environments.

(d) *Wolf spiders*

Male wolf spiders (*Hygrolycosa rubrofasciata*) court females by drumming dry leaves with their abdomen, and females mate preferentially with males drumming at the highest rate (Parri *et al.* 1997). Kotiaho (2000) investigated the condition dependence of drumming rate by keeping males on three food (quantity) regimes in both the presence and absence of females. The male sexual trait was therefore assayed under conditions when it had little sexual signalling value (females absent) and when it had high sexual signalling value (females present). All males increased their drumming rate when females were present. However, there was a disproportionate increase in drumming among males reared on better food. Thus drumming rate in male *H. rubrofasciata* shows heightened condition dependence; when used, its signalling function is elevated. Note that this experimental design cleverly allowed the sexual trait to act as its own control in the absence of females.

(e) *Guppy*

Sheridan & Pomiankowski (1997) used inbreeding to generate genetic stress in two populations (Paria and Aripo) of male Trinidadian guppies (*Poecilia reticulata*). Males from the Paria population have bright carotenoid coloration and Paria females show strong preference for this trait (Houde 1988*a*; Houde & Endler 1990). Aripo females do not prefer males with high carotenoid coloration, and Aripo males are less ornamented (with respect to carotenoid coloration) than Paria males (Houde 1988*b*).

Replicate inbred and control lines were created for each population (Sheridan & Pomiankowski 1997). Inbreeding had little effect on morphological characters from either population. The sexual trait in Paria males, carotenoid coloration, was significantly reduced in inbred relative to control lines and this difference persisted after controlling for body size. There was no difference between inbred and control lines in two coloration traits that are thought to be of lesser importance in mate choice: melanin pigmentation

and the number of pigment spots (Houde 1988*a*; Houde & Endler 1990). The sexual trait was thus more sensitive to moderate genetic stress than non-sexual traits. By contrast, inbred Aripo males did not differ from controls in the amount of carotenoid coloration, but inbred males had reduced melanin and spot numbers. Whether these latter two traits serve as sexual attractants in the Aripo population is not known (Houde 1988*b*).

Similar results have recently been reported for another population of guppies from the Tacarigua river in Trinidad (Van Oosterhout *et al.* 2003). The area of male carotenoid and melanin coloration, and the frequency of male courtship sigmoid displays showed strong inbreeding depression after two generations of inbreeding. Unfortunately no outbred controls were bred to test for the effect of laboratory rearing. In addition, no comparisons were made between traits, so it is not possible to conclude that there is heightened sexual trait condition dependence.

In another study on Trinidadian guppies, Grether (2000) manipulated dietary carotenoid levels and examined the response of male pigmentation in several different populations. After controlling for body size, several measures of male carotenoid coloration responded to diet, whereas other pigmentation did not. As carotenoid coloration is important in sexual attraction, this study shows that the sexual traits were more sensitive to dietary treatment than other pigments. Importantly, males from different populations reacted more or less strongly to the dietary treatment, suggesting genetic variation in the response. However, the diets differed only in carotenoid content. So although this study demonstrates heightened carotenoid-dependent expression in carotenoid-based coloration, it remains unclear how this relates to condition. Similar carotenoid-limited findings also have been reported in another guppy experiment (Kodric-Brown 1989; Hill 1992, 1993; Blount *et al.* 2003*a*).

(f) Finches and cowbirds

Hill (2000) found that food stress modulated the ability of male house finches (*Carpodacus mexicanus*) to process different carotenoids from the diet into plumage coloration. Males were collected as juveniles from the wild and subjected them to high or low food, with abundant or restricted carotenoid content (2×2 design). In general, males on poor diets were less able to convert dietary carotenoids into colourful ornaments. By contrast, diet had no discernible effect on the deposition of melanin pigmentation in tail feathers. Likewise, nutritionally deprived male brown-headed cowbirds (*Molothrus ater*) grew significantly less green, less saturated and less bright iridescent plumage than did birds fed *ad libitum*, but this treatment had no effect on melanin pigmentation (McGraw *et al.* 2002).

In another study using house finches, Hill & Brawner (1998) investigated the effect of parasitism on carotenoid coloration. They found that juvenile males experimentally infected with a modest level of coccidians (*Isospora* species and/or *Mycoplasma gallicepticum*) developed plumage that was less red and had less saturated carotenoid coloration than juveniles treated that had sub-clinical infections. Again, there was no effect of infection status on melanin pigmentation in tail feathers. Similar experimental findings have been reported for the expression of carotenoid

and melanin pigmentation in parasitized and unparasitized male American goldfinches, *Carduelis tristis* (McGraw & Hill 2000). Together these studies provide good evidence for heightened condition dependence of carotenoid/iridescent pigmentation compared with melanin pigmentation.

(g) Red jungle fowl

Male jungle fowl (*Gallus gallus*) possess several secondary sexual traits that are attractive to females, such as elongated and ornamental feathers and coloured facial features (comb and iris). Zuk *et al.* (1990) experimentally divided chicks into two groups and administered a dose of the intestinal roundworm *Ascaridia galli* to one group (at a naturally occurring magnitude). At maturity, a suite of sexual and non-sexual male traits were measured and canonical discriminant analysis was applied to each set of traits to see if group membership (i.e. parasitized or control) could be predicted using several characters simultaneously. Control males, in general, had more exaggerated and elaborate ornamental plumage and brighter sexual coloration than parasitized males. However, the same analysis performed on a set of non-sexual traits (tarsus length, bill length, bill width, length of saddle feathers) showed no significant separation for parasitized and control roosters. The presence of roundworm therefore had a disproportionate effect on ornamental traits.

7. DISCUSSION AND FUTURE DIRECTIONS

Despite the common claim that ornaments are condition-dependent, the unexpected conclusion from our literature review is that there is little support from well-designed experiments. Based on the minimum criterion that sexual traits were shown to be more sensitive to stress than non-sexual traits, only experiments in 10 species support this claim: two cricket species, two stalk-eyed fly species, wolf spiders, guppies, two species of finch, brown-headed cowbirds and red jungle fowl (Zuk *et al.* 1990; Sheridan & Pomiankowski 1997; David *et al.* 1998, 2000; Hill & Brawner 1998; Knell *et al.* 1999; Wagner & Hoback 1999; Hill 2000; Kotiaho 2000; McGraw & Hill 2000; McGraw *et al.* 2002; Holzer et al. 2003; Scheuber *et al.* 2003*a*,*b*). We do not conclude that condition dependence is rare; rather that good experimental support is lacking in most of the species studied. More rigorous studies are needed to fully test the prediction of *heightened* condition dependence in sexual ornaments made by the handicap hypothesis.

There are several key elements that need to be addressed in an experimental study. First, the response of the male sexual trait needs to be assessed relative to traits under weaker or no sexual selection. The latter could be the homologous trait in females, or other traits in the male that do not have signalling functions. A possible additional comparison is within or between ornaments, as different elements of courtship display may have evolved to signal different characteristics (Møller & Pomiankowski 1993; Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994). Temporal comparisons of sexual trait condition dependence can also be made when the value of the signal differs over time (e.g. Kotiaho 2000). Second, proper account of body size scaling needs to be undertaken as

most traits scale with body size. This is important not just for the proper comparison of sexual ornaments and non-sexual traits. It is also informative in establishing whether sexual ornaments signal something other than body size. Third, a suitable number of stresses need to be examined (three to five is usually sufficient), within the normal range experienced under natural conditions. It is not enough to compare extreme stress and no stress. It is also useful to investigate several types of environmental stress or stress applied at different times during development, which are likely to be relevant to the species under study. Unfortunately, few studies satisfy all of these conditions.

How is this field of investigation likely to develop over the next decade? One area that needs far more development is the study of the genetic basis of condition-dependent expression. If exaggerated sexual ornaments signal male genetic quality, we expect a genetic basis to condition dependence. In particular, we expect males with higher-quality genotypes to have larger sexual ornaments. This can be tested directly, where there is independent evidence that different genotypes vary in fitness or in major components of fitness. For example, experimental manipulation of mutation load would be expected to induce greater changes in sexual traits relative to non-sexual traits when compared with a control group reared under the same environment. Indirect tests are also possible by searching for genetic variation in condition dependence. In addition, the interaction between environmental and genetic variation is important. Condition, like other life-history traits, is expected to exhibit a large component of environmental variance (Price & Schluter 1991; Houle 1992). As a result of heightened condition-dependent expression, ornaments are also expected to possess large components of environmental variance. This means that genotype by environment interactions are crucial for our understanding of sexual traits, as they determine whether ornaments signal heritable properties. The handicap hypothesis predicts that males with high genetic quality should do well in all environments, and their advantage in terms of ornament size should be amplified under harsh environmental conditions, as these increase the differential costs of signalling. Alternatively, the genetic variation underlying sexual ornament size may reflect local adaptation to particular environmental conditions. So far, one experimental study supports each of these possibilities (David *et al.* 2000; Jia *et al.* 2000), but more are required to examine their generality.

Related to these points is the need for an understanding of the actual genes and other proximate mechanisms involved in determining condition dependence. We would like to know which aspects of condition are being signalled, and whether the underlying mechanisms involved in signalling are organism specific or general across taxa. It will also be important to understand how the gene networks underlying ornament expression evolve for it to signal condition

In this review, we have emphasized the need for experimental studies. But conversely these need to relate back to behaviour in the field. It is often unclear whether the environmental stresses investigated are relevant to the natural ecology of the species involved. The best evidence on this should come from long-term field studies, like that of the collared flycatcher, where brood manipulation has been used to measure how environmental stress affects the expression of the white forehead patch (Gustafsson *et al.* 1995; Qvarnström 1999).

Another area that seems ripe for investigation is the evolutionary pattern of condition dependence. In groups with many species, it should be possible to test for ecological and reproductive correlates of increased condition dependence in sexual traits. For example, the extensive changes in stalk-eyed fly eyespan exaggeration or in guppy fish coloration and concomitant changes in female mate preferences (Houde & Endler 1990; Wilkinson & Dodson 1997; Baker & Wilkinson 2001) are predicted to be linked to alterations in sexual trait condition dependence. Accordingly, phylogenetic tests should be designed to detect an evolved change in condition dependence rather than its existence *per se*. This kind of comparative analysis has not yet, to our knowledge, been attempted.

REFERENCES

Alexander, R. D. 1961 Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour* **17**, 130–223.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Arnqvist, G. & Thornhill, R. 1998 Evolution of animal genitalia: patterns of phenotypic and genotypic variation and condition dependence of genital and non-genital morphology in water strider (Heteroptera: Gerridae: Insecta). *Genet. Res. Camb.* **71**, 192–212.

Backwell, P. R. Y., Jennions, M. D., Christy, J. H. & Schober, U. 1995 Pillar-building in the fiddler crab *Uca beebei*: evidence for a condition-dependent ornament. *Behav. Ecol. Sociobiol.* **36**, 185–192.

Baker, R. H. & Wilkinson, G. S. 2001 Phylogenetic analysis of sexual dimorphism and eyespan allometry in stalk-eyed flies (Diopsidae). *Evolution* **55**, 1373–1385.

Birkhead, T. R., Fletcher, F. & Pellatt, E. J. 1998 Sexual selection in the zebra finch *Taeniopygia guttata*: condition, sex traits and immune capacity. *Behav. Ecol. Sociobiol.* **44**, 179–191.

Blount, J. D., Metcalfe, N. B., Birkhead, T. R. & Surai, P. F. 2003*a* Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science* **300**, 125–127.

Blount, J. D., Metcalfe, N. B., Arnold, K. E., Surai, P. F., Devevey, G. L. & Monaghan, P. 2003*b* Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. *Proc. R. Soc. Lond.* B **270**, 1691–1696. (DOI 10.1098/rspb.2003.2411.)

Bolger, T. & Connelly, P. L. 1989 The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* **34**, 171–182.

Brawner III, W. R., Hill, G. E. & Sundermann, C. A. 2000 Effects of coccidial and mycoplasmal infections on carotenoid-based plumage pigmentation in male house finches. *Auk* **117**, 952–963.

Buchanan, K. L., Spencer, K. A., Goldsmith, A. R. & Catchpole, C. K. 2003 Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). *Proc. R. Soc. Lond.* B **270**, 1149–1156. (DOI 10.1098/rspb.2003.2330.)

Burley, N. T., Price, D. K. & Zann, R. A. 1992 Bill color, reproduction and condition effects in wild and domesticated zebra finches. *Auk* **109**, 13–23.

Candolin, U. 1999 The relationship between signal quality and physical condition: is sexual signalling honest in the three-spined stickleback? *Anim. Behav.* **58**, 1261–1267.

Candolin, U. 2000 Increased signalling effort when survival prospects decrease: male–male competition ensures honesty. *Anim. Behav.* **60**, 417–422.

Crawley, M. J. 1993 *GLIM for ecologists*. Oxford: Blackwell Scientific Publications.

Darlington, R. B. & Smulders, T. V. 2001 Problems with residual analysis. *Anim. Behav.* **62**, 599–602.

David, P., Hingle, A., Greig, D., Rutherford, A., Pomiankowski, A. & Fowler, K. 1998 Male sexual ornament size but not asymmetry reflects condition in stalk-eyed flies. *Proc. R. Soc. Lond.* B **265**, 2211–2216. (DOI 10.1098/rspb.1998.0561.)

David, P., Bjorksten, T., Fowler, K. & Pomiankowski, A. 2000 Condition-dependent signalling of genetic variation in stalk-eyed flies. *Nature* **406**, 186–188.

Droney, D. C. 1996 Environmental influences on male court-ship and implications for female choice in a lekking Hawaiian *Drosophila*. *Anim. Behav.* **51**, 821–830.

Ekman, J. B. & Lilliendahl, K. 1993 Using priority of food access: fattening strategies in dominance-structured willow tits (*Parus montanus*). *Behav. Ecol.* **4**, 232–238.

Emlen, D. J. 1994 Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. R. Soc. Lond.* B **256**, 131–136.

Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford University Press.

Frischknecht, M. 1993 The breeding coloration of male three-spined sticklebacks (*Gasterosteus aculeatus*) as an indicator of energy investment in vigour. *Evol. Ecol.* **7**, 439–450.

García-Bertou, E. 2001 On the misuse of residuals in ecology: testing regression residuals versus the analysis of covariance. *J. Anim. Ecol.* **70**, 708–711.

Gonzalez, G., Sorci, G., Møller, A. P., Ninni, P., Haussy, C. & De Lope, F. 1999 Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *J. Anim. Ecol.* **68**, 1225–1234.

Gosler, A. G. 1996 Environmental and social determinants of winter fat storage in the great tit *Parus major*. *J. Anim. Ecol.* **65**, 1–17.

Grafen, A. 1990 Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* **144**, 473–516.

Gray, D. A. & Eckhardt, G. 2001 Is cricket courtship song condition-dependent? *Anim. Behav.* **62**, 871–877.

Green, A. J. 1991 Large male crests, an honest indicator of condition, are preferred by female smooth newts, *Triturus vulgaris* (Salamandridae) at the spermatophore transfer stage. *Anim. Behav.* **41**, 367–369.

Green, A. J. 2000 Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* **82**, 1473–1483.

Grether, G. F. 2000 Carotenoid limitation and mate prefer-ence evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution* **54**, 1712–1724.

Griffith, S. C. 2000 A trade-off between reproduction and a condition-dependent sexually selected ornament in the house sparrow *Passer domesticus*. *Proc. R. Soc. Lond.* B **267**, 1115–1119. (DOI 10.1098/rspb.2000.1116.)

Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995 Trade-offs between life-history traits and a secondary sexual charac-ter in male collared flycatchers. *Nature* **375**, 311–313.

Hill, G. E. 1990 Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* **40**, 563–572.

Hill, G. E. 1992 Proximate basis of variation in carotenoid pig-mentation in male house finches. *Auk* **109**, 1–12.

Hill, G. E. 1993 Geographic variation in the carotenoid plu-mage pigmentation of male house finches (*Carpodacus mexicanus*). *Biol. J. Linn. Soc.* **49**, 63–86.

Hill, G. E. 2000 Energetic constraints on expression of carotenoid-based plumage coloration. *J. Avian Biol.* **31**, 559–566.

Hill, G. E. & Brawner III, W. R. 1998 Melanin-based plumage coloration in the house finch is unaffected by coccidial infec-tion. *Proc. R. Soc. Lond.* B **265**, 1105–1109. (DOI 10.1098/rspb.1998.0405.)

Hingle, A., Fowler, K. & Pomiankowski, A. 2001 Size-dependent mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Anim. Behav.* **61**, 589–595.

Holmberg, K., Edsman, L. & Klint, T. 1989 Female prefer-ences and male attributes in mallard ducks *Anas platyrhynchos*. *Anim. Behav.* **38**, 1–7.

Holzer, B., Jacot, A. & Brinkhof, M. W. G. 2003 Condition-dependent signalling affects male sexual attractiveness in field crickets, *Gryllus campestris*. *Behav. Ecol.* **14**, 353–359.

Hooper, R. E., Tsubaki, Y. & Siva-Jothy, M. T. 1999 Expression of a costly, plastic secondary sexual trait is corre-lated with age and condition in a damselfly with two male morphs. *Physiol. Entomol.* **24**, 364–369.

Houde, A. E. 1988*a* Genetic difference in female choice between two guppy populations. *Anim. Behav.* **36**, 510–516.

Houde, A. E. 1988*b* The effects of female choice and male–male competition on the mating success of male guppies. *Anim. Behav.* **36**, 888–896.

Houde, A. E. & Endler, J. A. 1990 Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. *Science* **248**, 1405–1408.

Houde, A. E. & Torio, A. J. 1992 Effect of parasitic infection on male color pattern and female choice in guppies. *Behav. Ecol.* **3**, 346–351.

Houle, D. 1992 Comparing evolvability and variability of quantitative traits. *Genetics* **130**, 195–204.

Hunt, J. & Simmons, L. W. 1997 Patterns of fluctuating asym-metry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behav. Ecol. Sociobiol.* **41**, 109–114.

Iwasa, Y. & Pomiankowski, A. 1994 The evolution of mate preferences for multiple handicaps. *Evolution* **48**, 853–867.

Iwasa, Y. & Pomiankowski, A. 1999 Good parent and good genes models of handicap evolution. *J. Theor. Biol.* **200**, 97–109.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991 The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution* **45**, 1431–1442.

Jakob, E. M., Marshall, S. D. & Utez, G. W. 1996 Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67.

Jennions, M. D. & Backwell, P. R. Y. 1998 Variation in court-ship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behav. Ecol.* **9**, 605–611.

Jennions, M. D., Møller, A. P. & Petrie, M. 2001 Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* **76**, 3–36.

Jia, F. Y., Greenfield, M. D. & Collins, R. D. 2000 Genetic variance of sexually selected traits in waxmoths: mainte-nance by genotype × environment interaction. *Evolution* **54**, 953–967.

Johnstone, R. A. 1995 Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol. Rev.* **70**, 1–65.

Kim, T. W. & Choe, J. C. 2003 The effect of food availability on the semilunar courtship rhythm in the fiddler crab *Uca lactea* (de Hann) (Brachyura: Ocypodidae). *Behav. Ecol. Sociobiol.* **54**, 210–217.

Knell, R. J., Fruhauf, A. & Norris, K. A. 1999 Conditional expression of a sexually selected trait in the stalk-eyed fly *Diasemopsis aethiopica*. *Ecol. Entomol.* **24**, 323–328.

Kodric-Brown, A. 1989 Dietary carotenoids and male mating success in the guppy: an environmental component to female mate choice. *Behav. Ecol. Sociobiol.* **225**, 393–401.

Kotiaho, J. S. 1999 Estimating fitness: a comparison of body condition indices revisited. *Oikos* **87**, 399–400.

Kotiaho, J. S. 2000 Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behav. Ecol. Sociobiol.* **48**, 188–194.

Kotiaho, J. S. 2002 Sexual selection and condition dependence of courtship display in three species of horned dung beetles. *Behav. Ecol.* **13**, 791–799.

Kotiaho, J. S., Simmons, L. W. & Tomkins, J. L. 2001 Towards a resolution of the lek paradox. *Nature* **410**, 684–686.

McGraw, K. J. & Hill, G. E. 2000 Differential effects of endo-parasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proc. R. Soc. Lond.* B **267**, 1525–1531. (DOI 10.1098/rspb.2000.1174.)

McGraw, K. J., Mckillop, E. A., Dale, J. & Hauber, M. E. 2002 Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* **205**, 3747–3755.

Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. 1996 Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proc. R. Soc. Lond.* B **263**, 785–789.

Milinski, M. & Bakker, T. C. M. 1990 Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**, 330–333.

Moczek, A. P. & Emlen, D. J. 2000 Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? *Anim. Behav.* **59**, 459–466.

Møller, A. P. 1991 Sexual selection in the monogamous barn swallow (*Hirundo rustica*). I. Determinants of tail ornament size. *Evolution* **45**, 1833–1836.

Møller, A. P. & Alatalo, R. V. 1999 Good-genes effects in sexual selection. *Proc. R. Soc. Lond.* B **266**, 85–91. (DOI 10.1098/rspb.1999.0607.)

Møller, A. P. & Pomiankowski, A. 1993 Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167–176.

Ohlsson, T., Smith, H. G., Råberg, L. & Hasselquist, D. 2002 Pheasant sexual ornaments reflect nutritional condition during early growth. *Proc. R. Soc. Lond.* B **269**, 21–27. (DOI 10.1098/rspb.2001.1848.)

Packard, G. C. & Boardman, T. J. 1999 The use of percentages and size specific indices to normalise physiological data for variation in body size: wasted time, wasted effort? *Comp. Biochem. Physiol.* A **122**, 37–44.

Panhuis, T. M. & Wilkinson, G. S. 1999 Exaggerated eyespan influences male contest outcome in stalk-eyed flies. *Behav. Ecol. Sociobiol.* **46**, 221–227.

Parri, S., Alatalo, R. V., Kotiaho, J. & Mappes, J. 1997 Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. *Anim. Behav.* **53**, 305–312.

Pomiankowski, A. 1987 Sexual selection: the handicap principle does work—sometimes. *Proc. R. Soc. Lond.* B **231**, 123–145.

Pomiankowski, A. & Iwasa, Y. 1993 Evolution of multiple sexual preferences by Fisher's process of sexual selection. *Proc. R. Soc. Lond.* B **253**, 173–181.

Price, T. & Schluter, D. 1991 On the low heritability of life-history traits. *Evolution* **45**, 853–861.

Qvarnström, A. 1999 Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution* **53**, 1564–1572.

Rantala, M. J., Kortet, R., Kotiaho, J. S., Vainikka, A. & Suhonen, J. 2003 Condition dependence of pheromones and immune function in the grain beetle *Tenebrio molitor*. *Funct. Ecol.* **17**, 534–540.

Rolff, J. & Joop, G. 2002 Estimating condition: pitfalls of using weight as a fitness correlate. *Evol. Ecol. Res.* **4**, 931–935.

Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond.* B **263**, 1415–1421.

Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003a Condition-dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris*. *Anim. Behav.* **65**, 721–727.

Scheuber, H., Jacot, A. & Brinkhof, M. W. G. 2003b The effect of past condition on a multicomponent sexual signal. *Proc. R. Soc. Lond.* B **270**, 1779–1784. (DOI 10.1098/rspb.2003.2449.)

Sheridan, L. & Pomiankowski, A. 1997 Fluctuating asymmetry, spot asymmetry and inbreeding depression in the sexual coloration of male guppy fish. *Heredity* **79**, 515–523.

Van Oosterhout, C., Trigg, R. E., Carvalho, G. R., Magurran, A. E. & Hauser, L. 2003 Inbreeding depression and genetic load of sexually selected traits: how the guppy lost its spots. *J. Evol. Biol.* **16**, 273–281.

Wagner, W. E. & Hoback, W. W. 1999 Nutritional effects on male calling behaviour in the variable field cricket. *Anim. Behav.* **57**, 89–95.

Wagner, W. E. & Reiser, M. G. 2000 The importance of calling song and courtship song in female mate choice in the variable field cricket. *Anim. Behav.* **59**, 1219–1226.

Wilkinson, G. S. & Dodson, G. N. 1997 Function and evolution of antlers and eye stalks in flies. In *The evolution of mating systems in insects and arachnids* (ed. J. Choe & B. Crespi), pp. 310–328. Cambridge University Press.

Wilkinson, G. S. & Reillo, P. R. 1994 Female preference response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc. R. Soc. Lond.* B **255**, 1–6.

Zuk, M., Thornhill, R., Ligon, J. D. & Johnson, K. 1990 Parasites and mate choice in red jungle fowl. *Am. Zool.* **30**, 235–244.