Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence

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ABSTRACT

Costs of sexual traits are of central importance to the theory of sexual selection. To qualify as a cost in line with theoretical models, empirical studies must demonstrate that sexual traits cause negative effects on one component of fitness of the trait bearer. Moreover, it must be demonstrated that the costs are differential such that negative effects on fitness are more severe for individuals in poor condition than for individuals in good condition. However, in the current literature, there is confusion over what qualifies as a cost, and costs are often anticipated based on findings of increased expenditure. Consequently, it seems that the generally accepted notion that sexual traits are costly is in fact based almost exclusively on indirect evidence and that direct empirical evidence is very scarce.

Key words: differential cost, expenditure, fitness cost, immunocompetence, predation, sexual selection, survival, viability.

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I. INTRODUCTION

(1) Costs in the theory of sexual selection

In the contemporary literature concerning sexual selection it has been widely accepted that sexual traits that increase individual fitness must have some costs balancing their benefit. However, while concentrating carefully on the possible fitness benefits that individuals derive from exaggerated sexual traits (see e.g. Andersson, 1994; Johnstone, 1995; Møller and Alatalo, 1999), students of sexual selection have simultaneously introduced the concept of 'cost' with little consideration of what is actually required for a trait to be costly. Costs of sexual traits are of critical importance to our understanding of sexual selection because at some stage both currently favoured theories, the Fisherian self-reinforcing theory (Fisher, 1958; Lande, 1981; Kirkpatrick, 1982; Pomiankowski, Iwasa and Nee, 1991) and the indicator mechanism theory (Fisher, 1958; Williams, 1966; Zahavi, 1975, 1977; Andersson, 1982, 1986; Nur and Hasson, 1984; Pomiankowski, 1987; Grafen, 1990a, b; Iwasa, Pomiankowski and Nee, 1991; Johnstone and Grafen, 1992; Iwasa and Pomiankowski, 1994; Getty, 1998), require that sexual traits are costly. Furthermore, in the majority of models, costs have been explicitly described as having a negative influence on the fitness, and in particular on the survival, of the trait bearer (e.g. Andersson, 1982, 1986; Kirkpatrick, 1982; Nur and Hasson, 1984; Pomiankowski, 1987; Grafen, 1990a, b; Iwasa et al., 1991; Pomiankowski et al., 1991, but see Kodric-Brown and Brown, 1984). Therefore, if producing or maintaining sexual traits does not have a negative influence on the possessor's fitness it can not be inferred as being costly. If fitness is described simply as viability multiplied by reproductive success (although ultimately fitness can only be measured in terms of offspring produced in future generations), then, to count as an evolutionarily significant cost, an increase in the magnitude of sexual traits has to either increase mortality or decrease reproductive success. Here, it is imperative to make a distinction between expenditure and costs; traits may require expenditure of energy, time, etc. without being evolutionarily costly in terms of reduced future lifetime reproductive success. In the recent literature on the costs of sexual traits, definitions of cost have often been neglected and on many occasions the evidence for traits causing evolutionarily significant fitness costs is at best circumstantial.

(2) Costs in relation to indicator mechanism theory

Fisherian and indicator mechanism sexual selection models differ with respect to the importance of the costs of sexual traits. In Fisherian models, costs become important late when the exaggeration of the sexual trait is so large that natural selection prevents any further enlargement. In these models, the only requirement for costs is that they must reduce survival irrespective of phenotypic condition or genetic quality of individuals. By contrast, indicator mechanism has three main assumptions in which costs have a much more pronounced role (e.g. Grafen, 1990a; Johnstone and Grafen, 1992). Firstly, the production or maintenance of sexual traits must cause costs that reduce the fitness of their bearer. It is imperative that these costs increase in parallel with the increasing investment in the sexual trait. The second assumption, that sexual traits must be dependent on phenotypic and genotypic condition (Andersson, 1986; Grafen, 1990a; Rowe and Houle, 1996), does not itself incorporate costs but is directly linked to the third assumption that does: the marginal costs of sexual traits must be less for males in good condition than for males in poor condition (Grafen, 1990a; Rowe and Houle, 1996). In other words, there must be differential costs depending on the condition of the individuals. When the above conditions are met, sexual traits act as reliable indicators of overall genetic quality and become sexually selected exactly because they reduce one component of the fitness of their bearer. Recently, Getty (1998) argued that it is theoretically possible for there not only to be differential costs of traits on different quality males, but in addition there may also be differential benefits that could be realised through longer survival of better quality males.

Generally, costs that result from sexual traits may be divided into two classes depending on how the negative effect on fitness is manifest. If the trait has an immediate negative influence on the individual's fitness, as in the event of predation or parasitism, we may talk about direct costs. Conversely, if the negative influence on fitness is not immediate but rather arises through physiological effects such as increased energy expenditure or reduced immunocompetence we may talk about indirect or physiological costs.

Below, I will treat costs only in the light of the indicator mechanism of sexual selection. I will consider what is needed firstly for direct and secondly

for indirect costs to be evolutionarily significant costs of sexual traits.

II. DIRECT COSTS

(1) Predators and parasitoids

It is a common observation that, in locating their prey, predators and parasitoids exploit sexual traits (Table 1) (see also Burk, 1982; Lima and Dill, 1990; Sakaluk, 1990; Magnhagen, 1991; Verrell, 1991; Zuk and Kolluru, 1998). There is also some evidence that individuals are able to adjust their sexual traits in response to predation or parasitism risk (Spangler, 1984; Endler, 1987; Magurran and Segher, 1990; Magurran, 1991; Candolin, 1997, 1998; Kotiaho *et al.*, 1998*a*; Hedrick, 2000, see also Lima and Dill, 1990; Sakaluk, 1990), and that predation has shaped the evolution of sexual traits at the population level (Moodie, 1972; Farr, 1975; Endler, 1978, 1980, 1982; Tuttle and Ryan, 1981; Belwood and Morris, 1987; Zuk, Simmons and Cupp, 1993; Rotenberry *et al.*, 1996). These three lines of evidence could be taken as an indication that predation and parasitism have the potential to act as an evolutionarily significant cost on sexual traits.

However, before this potential is realised we need to consider if the costs that are manifest through predation or parasitism are able to fulfil the

Table 1. *Studies examining predation and parasitisim in relation to sexual traits*
(The columns give the study species, the type of cost i.e. predation or parasitism, type of trait, whether the study was a field or laboratory (Lab) study, whether the study was experimental (Exp), correlational (Corr) or observational (Obs) and the reference.)

Species	Cost type	Trait type	Field or lab	Study type	Reference
Birds					
Hirundo rustica	Predation	Morphology	Field	Corr	Møller and Nielsen (1997)
Fish					
Gasterosteus aculeatus	Predation	Colour	Lab	Exp	Moodie (1972)
Frogs/lizards					
Physalaemus pustulosus	Predation	Auditory	Field	Corr	Tuttle and Ryan (1981)
P. pustulosus	Predation	Auditory	Lab	Exp	Ryan *et al.* (1982)
P. pustulosus	Predation	Auditory	Field	Corr	Ryan *et al.* (1981)
Hyla boulengeri	Predation	Auditory	Lab & Field	Exp	Tuttle and Ryan (1981)
Leptodactylus pentadactylus	Predation	Auditory	Lab & Field	Exp	Tuttle and Ryan (1981)
Lacerta agilis	Predation	Colour	Field	Exp	Olsson (1993)
Insects/arthropods					
Amblycorypha uhleri	Predation	Auditory	Field	Obs	Walker (1964)
Anurogryllus celerinictus	Predation	Auditory	Field	Obs	Bell (1979)
Hygrolycosa rubrofasciata	Predation	Auditory	Lab	Corr	Kotiaho *et al.* (1998*a*)
Tettigonidae spp.	Predation	Auditory	Field	Exp	Belwood and Morris (1987)
Photuris spp.	Predation	Luminescence	Field	Exp	Lloyd and Wing (1983)
T. oceanicus	Predation	Auditory	Lab	Exp	Bailey and Haythornthwaite (1998)
T. oceanicus	Parasitism	Auditory	Field	Corr	Zuk *et al.* (1995*b*)
T. oceanicus	Parasitism	Auditory	Field	Corr	Zuk *et al.* (1998)
Ceratitis capitata	Predation	Olfactory	Field	Exp	Hendrichs and Hendrichs (1998)
C. capitata	Predation	Olfactory	Field	Exp	Hendrichs *et al.* (1994)
Gryllus integer	Parasitism	Auditory	Lab	Exp	Cade (1975)
G. integer	Parasitism	Auditory	Field	Exp	Cade (1981)
Gryllus spp.	Parasitism	Auditory	Field	Exp	Walker (1993)
Gryllus lineaticeps	Parasitism	Auditory	Lab	Exp	Wagner (1996)
Sciarasaga quadrata	Parasitism	Auditory	Field	Corr	Allen (1995)
Scapteriscus acletus	Parasitism	Auditory	Field	Exp	Mangold (1978)
Scapteriscus spp.	Parasitism	Auditory	Field	Exp	Fowler (1987)
Poecilimon spp.	Parasitism	Auditory	Field	Exp	Lehmann and Heller (1998)

assumptions of the indicator mechanism. For the present purposes, the differences between predation and parasitism through parasitoids are not important. Thus, predation and parasitism will be grouped together under the term predation. Let us consider signalling rate as an example of a sexual trait. The key assumption of indicator mechanisms is that sexual traits are condition dependent as well as costly, and most importantly that males in better condition are better able to bear the costs of increased signalling. In other words, individuals in better condition should have a lower cost/benefit ratio for a given rate of signalling. If the total signalling rate is held constant, then the only way that the condition of the signaller can affect the cost/benefit ratio is through changing the cost i.e. predation rate. If individuals in better phenotypic condition are better at escaping predation and signalling rate is positively dependent on condition, the condition-dependent escape rate would reduce the cost of signalling in males that are signalling the most, thus fulfilling the assumptions of indicator mechanism theory.

To date there is no empirical evidence that would fulfil these criteria and, in fact, these criteria have not been addressed in any empirical examination. Before these kinds of data are available it is impossible to draw conclusions concerning the potential for predation to be the condition-dependent differential cost that is required by the indicator models.

(2) Socially imposed or competitive costs

Another possible set of direct costs may be realised through socially imposed costs. This means costs that are mediated through incitement of increased aggression from competitors (Maynard Smith and Harper, 1988; Johnstone and Norris, 1993). Empirical evidence for increased aggression towards displaying males is not rare (e.g. Jones, 1966; Kodric-Brown, 1983; Peschke, 1987; McKaye, Louda and Stauffer, 1990; Simmons and Bailey, 1993; Borgia, 1995; Candolin, 1997; Kotiaho et al., 1999), but there is no direct evidence that increased levels of aggression from competitors cause evolutionarily significant costs for displaying males. Since aggression in animals rarely results in the death of one of the opponents (e.g. Huntingford and Turner, 1987), socially imposed costs may be more likely to be mediated either directly through decreased reproductive success, or indirectly through increased energy expenditure.

III. INDIRECT COSTS

(1) Energy expenditure

An increased energy expenditure or mass loss during the production or display of sexual traits is not in itself an indication that sexual traits are evolutionarily costly; it merely demonstrates that producing or displaying these traits requires energy. To show that energy expenditure on sexual traits poses significant fitness costs it must be demonstrated that this increased energy expenditure has a negative effect on individual fitness. This effect may arise through decreased survival or reduction in future reproductive success. However, if the energy expenditure of a sexual display can be compensated without negative effects on fitness, no matter how large the energy expenditure, it can not be considered to be an evolutionary meaningful cost. There are several studies demonstrating that the energy expenditure of sexual signalling and displays can be extensive, increasing the resting metabolic levels in some cases by more than two orders of magnitude (Table 2) (see also Ryan, 1988; Balmford, Thomas and Jones, 1993; Prestwich, 1994). However, there is evidence only from two organisms, barn swallows *Hirundo rustica* and drumming wolf spiders *Hygrolycosa rubrofasciata*, that increased energy expenditure results in evolutionarily significant costs i.e. reduces the survival of the individual (Møller, l989; Møller and de Lope 1994; Mappes et al., 1996; Saino, Bolzern and Møller, 1997a; Kotiaho et al., 1998b; Kotiaho, 2000). However, in barn swallows there is no evidence for (or against due to the low power of the test) an increased energy consumption of males with elongated tail streamers (Cuervo et al., 1996, see also Evans and Thomas, 1992) leading to uncertainty as to the basis for the mortality costs of the manipulated streamers.

An indirect energetic cost of sexual traits may arise in predatory species by making individuals more conspicuous to their own prey (Grether and Grey, 1996). Grether and Grey (1996) found evidence that in the rubyspot damselfly *Hetaerina americana* ornamental wing coloration reduces the prey capture success in males compared to non-ornamented females, and also in females that are manipulated to have ornaments compared to control females. Males that were manipulated to have larger colour spots suffered increased mortality compared to control males, which could be attributable to lower success in prey capture (Grether, 1997). These studies provide the first and only evidence for a

Table 2. *Studies examining energy expenditure in relation to sexual traits*
(The columns give the study species, type of trait, and reference.)

Species	Trait type	Ref.
Birds		
Centrocercus urophasianus	Display	Vehrencamp *et al.* (1989)
Gallinago media	Display	Höglund *et al.* (1992)
Nectarinia johnstoni	Ornament	Evans and Thomas (1992)
Frogs		
Hyla cinerea	Acoustic	Prestwich *et al.* (1989)
Hyla gratiosa	Acoustic	Prestwich *et al.* (1989)
Hyla microcephala	Acoustic	Wells and Taigen (1989)
Hyla squirella	Acoustic	Prestwich *et al.* (1989)
Hyla versicolor	Acoustic	Taigen and Wells (1985)
Hyperolius marmoratus	Acoustic	Grafe *et al.* (1992)
Hyperolius viridiflavus	Acoustic	Grafe *et al.* (1992)
Physalaemus pustulosus	Acoustic	Bucher *et al.* (1982)
Pseudacris crucifer	Acoustic	Taigen *et al.* (1985)
Insects/Arthropods		
Achroia grisella	Ultrasonic	Reinhold *et al.* (1998)
Anurogryllus arboreus	Acoustic	Prestwich and Walker (1981)
Anurogryllus muticus	Acoustic	Lee and Lower (1993)
Cystosoma saundersii	Acoustic	Mac Nally and Young (1981)
Euconocephalus nasutus	Acoustic	Stevens and Josephson (1977)
Gryllotalpa australis	Acoustic	Kavanagh (1987)
Hygrolycosa rubrofasciata	Acoustic	Kotiaho *et al.* (1998*b*)
Linyphila litigiosa	Display	Watson and Lighton (1994)
Neoconocephalus robustus	Acoustic	Stevens and Josephson (1977)
Oecanthus celerinictus	Acoustic	Prestwich and Walker (1981)
Oecanthus quadripunctatus	Acoustic	Prestwich and Walker (1981)
Requena verticalis	Acoustic	Bailey *et al.* (1993)
Teleogryllus commodus	Acoustic	Kavanagh (1987)

sexual trait to be costly in terms of reduced survival through conspicuousness to their own prey. However, this mechanism of costs may be operative in several other systems as well; the requirements being that the species is predatory and has conspicuous sexual traits that are exposed also during prey capture. When empirically pursuing this possible cost mechanism of sexual traits, care has to be taken not to infer costs from reduced prey capture efficiency alone. In the above damselfly system (Grether and Grey, 1996; Grether, 1997), the link, although indirect, between reduced prey capture success and increased mortality has been established.

(2) Immunocompetence

Recently, reduced immunocompetence has been raised as a potential cost of sexual traits (Folstad and Karter, 1992, see also Hamilton and Zuk, 1982).

Reduced efficiency of the immune system may be caused by the immunosuppressive effects of androgens or other self-regulating biochemicals that promote the expression of sexual traits (Grossman, 1985; Folstad and Karter, 1992). However, this new field of sexual selection research seems to be full of controversy: there is no consensus on the mechanisms that causally link the development or maintenance of sexual traits to the immune system (Møller, 1995; Owens and Short, 1995*a*, *b*; Sheldon and Verhulst, l996; Westneat and Birkhead, l998), there is disagreement over how the immunocompetence should be measured (Lochmiller, l995; Siva-Jothy 1995; Sheldon and Verhulst, 1996; Zuk and Johnsen, 1998), and an agreement upon formal definitions of the various terms is yet to be established (Skarstein, 1996). Generally, it has been assumed that maintaining appropriate immunocompetence is energetically demanding and therefore a compromise in resource allocation between immunocompetence

and sexual traits is unavoidable (Wedekind and Folstad, 1994; Westneat and Birkhead, 1998). However, instead of being caused by resource limitation, the latest development in this area points out that suppressed immunocompetence during stress (e.g. during development or display of sexual traits) may be an adaptation to avoid inappropriate immune responses to self (immunopathology) (Folstad and Skarstein, 1997; Hillgarth, Ramenofsky and Wingfield, 1997; Råberg et al., 1998; Westneat and Birkhead, 1998). Nevertheless, whatever the mechanisms are, for reduced immunocompetence to function as an evolutionary cost of sexual traits it must be shown explicitly that there is a reduction in fitness that results from the reduced efficiency of the immune system that in turn is caused by investment in or possession of sexual traits.

There are few studies that have found correlational evidence for the negative relationship between a magnitude of sexual trait and a measure of immunocompetence (Zuk, Johnsen and Maclarty, 1995 a; Møller, Kimball and Erritzøe, 1996; Salvador et al., 1996; Skarstein and Folstad, 1996; Saino et al., 1997 b). Recent evidence suggests that investing in sexual traits may be associated with reduction in some parts of immune defence, while other parts may remain uninfluenced (Zuk and Johnsen, 1998). There is also some experimental evidence from barn swallows Hirundo rustica suggesting that exaggerated sexual traits do indeed reduce the efficiency of immune defence (Saino and Møller, 1996; Saino et al., 1997 a). Furthermore, there is evidence that a positive association exists between the immune response after experimental challenge of the immune system and long-term survival (Saino et al., 1997 a). However, this evidence is not sufficient to show that there is a cost of reduced immunocompetence. Instead, it must be shown that there exists a causal link between reduced immunocompetence and reduced survival. Before these data are available reduced immunocompetence can not be considered to be costly in an evolutionarily meaningful way.

IV. DEVELOPMENTAL COSTS

Developmental costs may be mediated through time or energy expenditure on developing sexual traits, differential mortality during the development of sexual traits, or a combination of the two. It has also been suggested that in hemimetabolous insects mortality may be caused by physical hindrance

during moulting (Arnqvist, l994), but evidence for this is yet to be forthcoming. There is some evidence from dung beetles Onthophagus taurus (Hunt and Simmons, 1997) and water striders Gerris odontogaster (Arnqvist, 1994), that the increased development or moulting time of individuals with larger sexual traits renders them at a greater risk of predation. However, despite the evidence for a significant increase in time expenditure of developing larger sexual traits (e.g. Hunt and Simmons, 1997), the possible reduction in reproductive success resulting from this time expenditure has not been empirically demonstrated. Generally, the requirements derived in the above sections need to be fulfilled before developmental costs arising through energy or time expenditure or through predation can be inferred as being evolutionarily costly.

V. GENETIC COSTS

A recent study on guppies Poecilia reticulata suggests that males that bear genes for attractive traits may also bear genes that reduce other fitness components (Brooks, 2000, see also Etges, 1996; Wedell and Tregenza, 1999). In his study, Brooks (2000) found that there was a strong negative genetic correlation between male sexual attractiveness and offspring survival to maturity. Thus, a cost of attractive sexual traits may arise through the reduced survival of offspring. This avenue of costs may be supportive of indicator models of sexual selection only if there exists a positive genetic correlation between attractiveness and some other fitness component that negates the viability cost of attractiveness; so far there is no evidence for such counterbalancing genetic correlation (Brooks, 2000).

VI. DIFFERENTIAL COSTS

Even if we can demonstrate that a sexual trait directly causes an evolutionarily significant cost for the trait bearer, it is not enough. If we want to test the indicator mechanism of sexual selection, we must seek for differential costs. Differential costs are of vital importance because they ensure the honesty and evolutionary stability of sexual traits (Grafen, 1990 a; Johnstone, 1995). What is now needed are studies assessing whether the evolutionarily significant costs of a given sexual trait are smaller for individuals in good condition than they are for

individuals in poor condition. Because it may be expected that individuals in good condition have both large sexual traits and high survival, differential costs can not be revealed by correlations. Therefore, the best way to test for differential costs is experimental manipulation of both condition and sexual trait and then to study the interaction effect between trait and condition on survival.

There are only two studies that have tested for differential costs of traits. A study on barn swallows *Hirundo rustica* showed that increasing the length of the tail feathers of the males reduced their survival, but that naturally long-tailed males were better able to withstand the cost (Møller and de Lope, 1994). This study provides indirect evidence that in barn swallows tail length may cause differential costs for males. Direct evidence for differential costs was recently found in a drumming wolf spider *Hygrolycosa rubrofasciata* (Kotiaho, 2000). Simultaneous manipulation of sexual signalling rate and condition revealed a differential survival cost of signalling such that males manipulated to be in good condition survived better the increased signalling rate than males that were manipulated to be in poor condition.

VII. CONCLUSIONS AND PROSPECTS

Even in the most recent literature, costs are repeatedly mixed with expenditure and indirect costs are inferred as being direct evidence for costliness. In future empirical studies, extreme care should be taken that the real fitness costs are strictly separated from expenditure; while studies demonstrating that sexual traits cause expenditure are necessary and valuable, they should not be interpreted as providing direct evidence for the notion that sexual traits are costly in an evolutionarily meaningful way and in line with the theoretical requirements for costs. In addition, more attention should be paid in explicitly testing the assumptions of indicator mechanism of sexual selection, and in particular the assumption of differential costs.

(1) Plane of research

Comparative (e.g. Promislow, 1992; Promislow, Montgomerie and Martin, 1992; Owens and Bennett, 1994) or population-level (e.g. Endler, 1980, 1982; Belwood and Morris, 1987) studies are not useful in gaining empirical evidence for sexual traits being costly and costs being condition-de-

pendent in a way that the indicator mechanism of sexual selection requires. This is because the trade-off between trait size and survival occurs within individuals not across individuals or populations. Therefore, to test for the relevant costs of sexual traits in line with the indicator mechanism of sexual selection, research must be conducted at an individual level and not across populations or species. Furthermore, as condition-dependent costs can not be revealed by observational correlations (because high-quality individuals have both large sexual traits and high survival), experimental approaches that manipulate both sexual traits and condition simultaneously are needed. The best way to test whether traits are costly and condition-dependent is to study the interaction effect between trait and condition on survival. If simultaneous manipulations produce an interaction effect on survival such that the difference in survival between individuals with large sex traits and good or poor condition is greater than the survival difference between individuals with small sex traits and good or poor condition, it can be taken as strong empirical evidence for the indicator mechanism of sexual selection.

(2) Direct costs

In particular, the role of direct costs for the indicator mechanism needs further and more rigorous empirical testing. There are no empirical studies that have attempted to evaluate the importance of predation on the indicator mechanism within the assumptions of these models, and therefore whether predation can or cannot be an evolutionarily significant cost on sexual traits remains to be tested. These tests should focus on determining if success in predator avoidance is dependent on condition and thus if the cost is a differential cost. If future work proves these aspects to be true, predation may be seen as a significant evolutionary cost that fulfils the assumptions of the indicator mechanism.

(3) Indirect costs

There is ample evidence that sexual displays are energetically expensive but barely any that directly shows how this energy expenditure causes negative effects on fitness. While the need for more detailed energetic studies in relation to sexual traits is great, the need for relating the results from these studies directly to the real fitness costs is even greater.

A new area of research is currently focusing on the relationship between sexual traits and immuno-

competence. However, more data are needed firstly empirically to establish whether investment in sexual traits does reduce immunocompetence, and secondly, to determine if sexual traits can be evolutionarily costly through this reduction. It is imperative that students of this subject focus on the fitness effects of reduced immunocompetence that are mediated through investment in sexual traits. What is needed is a simultaneous manipulation of both immune defence and sexual traits coupled with an examination of the effects of different combinations of these two on survival. Such experimental tests would give us an insight into whether sexual traits may be evolutionarily costly through reduced immunocompetence.

(4) New avenues of research

Viability costs are the most often addressed, yet not the only possible avenue for fitness costs of sexual traits. Costs of sexual traits may also emerge through a reduction in future reproductive success (self-limiting sexual selection: Andersson, 1994). This approach to the costs of sexual selection is difficult and laborious to investigate empirically, since it requires measurements of lifetime reproductive success in relation to expression of natural and experimentally manipulated sexual traits. This possibly explains the lack of empirical studies examining the costs of sexual traits through reduced future reproductive success. Empirical studies aimed to determine costs mediated through reduced future reproductive success would be of great value to our understanding of costs of sexual traits.

An exciting new field of costs is emerging from the possibility that there are genetic costs through negative genetic correlations between the expression of sexual traits and survival. However, to function as a cost for indicator models of sexual selection there must be negating positive genetic correlations between trait expression and some other fitness component. This should be tested along with the negative effects.

Differential costs are vitally important for the theory of sexual selection through the indicator mechanism. However, currently there is almost no empirical work that has directly addressed differential costliness of sexual traits (but see Møller and de Lope, 1994; Kotiaho, 2000). This is an area that desperately needs more experimental research. Studies on this subject will be of great importance for our understanding of the costliness of sexual traits in line with modern theories of sexual selection.

A further advancement in the empirical study of costs would be an attempt to quantify the combined effect of different sources of costs. It is more than likely that sexual signalling may simultaneously attract costs from several different sources and studying one of these is not enough to reveal the whole picture. Increased predation risk, increased energy expenditure, decreased immunocompetence and decreased future reproductive success may work in concert to produce the overall evolutionarily significant cost on sexual traits. Thus, even if we do not find a negative effect on fitness while studying these possible avenues of costs individually, a study combining them could still find the expected negative effect.

To conclude, it is apparent from the sexual selection literature that a currently favoured paradigm is the notion that sexual traits are costly. However, there is little direct empirical evidence actually to verify this assumption. Lack of direct evidence is by no means a phenomenon unique to costliness of sexual traits. Indeed, the use of observational and correlational evidence and indirect measures of fitness in general are common also in many other fields of evolutionary and behavioural ecology (e.g. Reznick, 1992; Kempenaers and Sheldon, 1997; Sheldon, 2000). Two recent examples from fields closely related to sexual selection (Alatalo, Mappes and Elgar, 1997; Simmons *et al.*, 1999) call for caution in accepting the currently favoured paradigm too easily. Costs of sexual signalling are far from being self evident and with few exceptions the data do not provide direct general support for the assumption that sexual traits are costly in line with the indicator mechanism models of sexual selection.

VIII. ACKNOWLEDGEMENTS

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