Review

Compensatory traits and the evolution of male ornaments

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Summary

How ornaments that are used during mate choice and rival assessment remain reliable has been a source of contention for many years. Such signals are hypothesized to be costly (i.e., 'handicaps'), but empirical studies testing for costs of sexually selected ornaments are equivocal at best, contradictory at worst. We review recent studies finding compensation for sexually selected ornaments, in both intra- and inter-specific studies, suggesting that other traits evolve to mitigate costs of ornaments. We synthesize these studies to elucidate the role of compensatory traits in the evolution of reliable ornaments and explain how selection to reduce ornament costs may influence aspects of the phenotype that are not subjected to direct sexual selection and may obscure our ability to directly measure ornament costs. Both intra-specific studies and comparative studies in a phylogenetic framework are important for our understanding of how the costs of signals may be reduced by compensation, but each approach answers different questions about ornament evolution. We also elaborate on a general theoretical model that can be useful when testing for costs of ornaments in correlational and experimental studies. We recommend that future investigators should consider compensatory traits when testing for ornament costs, especially when manipulating ornamentation.

Keywords: compensation, costs, performance, signals.

1. Introduction

One of the most elusive questions in animal behaviour is how ornaments and armaments used during mate choice and rival assessment remain reliable over evolutionary time. The prevailing hypothesis is that such signals

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are costly to their bearers (i.e., 'handicaps'). However, empirical studies that seek to find costs of sexually selected traits are equivocal at best, contradictory at worst. We highlight recent work showing that the evolution of compensatory traits may obscure the detection of signal costs, and we propose new ways of testing for costs of ornaments and armaments by taking these compensatory traits into account. Whereas the distinction between ornaments, armaments and weapons has been made in the literature (e.g., Berglund et al., 1996), many structures may serve multiple functions, so we refer simply to 'ornaments' throughout for simplicity. Many of the patterns and concepts we discuss in this review apply to the evolution of exaggerated male armaments and weapons, especially those that are enlarged structures (see Emlen, 2008), in a manner similar to ornaments.

In this paper we have three main objectives. First, we explain what compensatory traits are and how the evolution of reliable ornaments may influence the evolution of other aspects of the phenotype. We consider a paradigm used by evolutionary biologists and functional morphologists to elucidate how sexual selection on ornaments may have far-reaching effects on the phenotype via indirect selection on other traits. Second, we provide examples of compensation for exaggerated ornaments studied within species, as well as studies of compensation in an inter-species comparative framework. We highlight the utility of both approaches, since each answers different questions about the evolution of ornaments. Finally, we elaborate on a general model that can be useful when testing for costs of ornaments in correlational and experimental studies.

2. Costs and the reliability of ornaments

There are two general explanations for how ornaments used during rival assessment and mate choice remain reliability over evolutionary time: indices and handicaps. An 'index' is a signal whose intensity is physically constrained by the trait(s) that it advertises so that deception is impossible (Taylor et al., 2000; Maynard Smith & Harper, 2003; Lappin et al., 2006), whereas 'handicaps' are signals that are costly to the sender (Zahavi, 1975). Costs of signals are generally categorized as either receiver-independent or receiver-dependent based on whether the cost is imposed upon the sender by the intended receiver or by other internal or external factors (e.g., predators, developmental costs). Receiver-independent costs result from the development, production, or maintenance of the signal, whereas receiver-dependent costs depend on the response of receivers and entail either increased vulnerability to or increased retaliation from intended receivers (Vehrencamp, 2000; Searcy & Nowicki, 2005). That elaborate secondary sexual characteristics are costly to produce or maintain is central to all recent theoretical models of sexual selection (Kotiaho, 2001), including variations on Fisherian self-reinforcing theory (e.g., Fisher, 1958; Lande, 1981; Kirkpatrick, 1982; Pomiankowski et al., 1991; Takahashi, 1997) and indicator mechanism theory (e.g., Zahavi, 1975; Pomiankowski, 1987; Iwasa et al., 1991; Iwasa & Pomiankowski, 1994; Getty, 1998); however, the manner in which to test for costs remains controversial (Getty, 1998, 2006). This controversy is beyond the scope of our paper, but we briefly mention some important points with regard to how costs should be studied. In general, signal reliability can evolve when the fitness cost-to-benefit ratio of a signal is lower for a signaller that is of high quality compared to lower-quality signallers (Grafen, 1990), but with the realization that fitness is a multiplicative function of viability and fecundity (Getty, 1998, 2006), such that these two components of fitness can trade-off in terms of resource allocation (i.e., investment in signal intensity versus traits enhancing viability; Lailvaux et al., 2010). This latter point is important when one considers the importance of ornament costs to signal reliability and how individuals may reduce those costs. However, in the signalling literature many studies focus solely on absolute costs of a signal or, in very rare cases, costs relative to male quality (as emphasized by Getty, 1998; Kotiaho, 2001; Getty, 2006; Murai et al., 2009). Because compensatory traits co-evolve with ornaments, compensatory traits may obscure the true costs of bearing an ornament and, as a consequence, we propose that simply testing for bivariate relationships between signal intensity and some proxy for fitness (e.g., performance, survival) is an incomplete approach and can lead to inconclusive or misleading results.

3. Ornaments and performance

Evolutionary biologists have long appreciated that selection operates on the integrated functional manifestations of morphological and physiological traits; that is, selection acts on how well animals perform in nature (Figure 1)

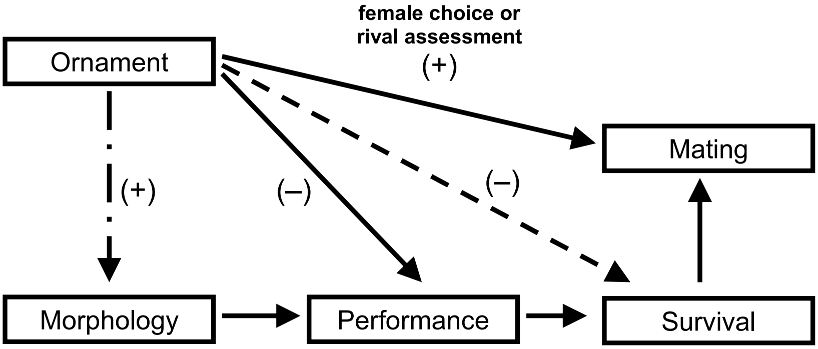

Figure 1. Schematic representation of Arnold's (1983) paradigm modified to incorporate ornaments and compensatory traits. Arnold's (1983) original model proposed that selection operates on performance traits, which are constrained by underlying morphological traits. The response to selection changes the morphological traits, but indirectly via selection on the functional manifestation of morphology: performance. Ornaments used during rival assessment or female choice (i.e., direct selection on morphology, not performance) may result in decreased performance, with an indirect result on survival (dashed line). The evolution of compensatory traits (i.e., increased performance to alleviate costs of the ornament) results in an indirect influence (dashed-dotted line) on the morphological trait(s) underlying the performance trait. Multiple morphological traits typically underlie any given performance trait such that the indirect morphological response(s) to sexual selection on the ornament will depend on how those same morphological traits impact fitness via their effects on other performance traits, as well as the presence of any genetic correlations among traits and the intensity of selection on performance. We note that an arrow can also be drawn directly from performance to mating success (see Husak & Fox, 2008; Byers et al., 2010 and references therein), but our conclusions remain the same, and for aesthetic reasons we only place an arrow from performance to survival.

(Bartholomew, 1958; Huey & Stevenson, 1979; Arnold, 1983; Pough, 1989; Irschick & Garland, 2001; Irschick et al., 2008). 'Performance' is generally defined by functional morphologists as an organism's ability to accomplish an ecologically relevant task (Bennett & Huey, 1990; Lailvaux & Irschick, 2006; Husak et al., 2009), and represents how the morphology of organisms (including biochemical, physiological, and gross morphological traits in general; Arnold, 1983) interacts with the environment. Since performance traits are the functional manifestations of integrated morphological and physiological traits, the response to selection on performance is seen in evolutionary changes to those lower-level traits (Arnold, 1983). Recent studies have revealed the fitness advantages afforded to better performers in terms of survival and mating success (reviewed in Irschick et al., 2008), yet despite the empirical support for this paradigm (i.e., better performance enhances fitness), sexual selection on ornaments represents an exception. Direct selection on morphology, via female choice of an ornament or use of an ornament to assess rivals, can indirectly drive the evolution of performance and its underlying morphology when the ornament is detrimental to performance (Figure 1). That is, sexual selection favors increased ornament size, which may decrease performance capacity, which may increase selection intensity on performance, thus altering the underlying traits constraining performance (Figure 1). Depending on the nature of the ornament, ornaments may negatively affect individual performance capacity, either directly or indirectly. This possibility has important ramifications for those who study the evolution of performance and its underlying proximate basis, as well as those who study the evolution of sexually selected ornaments and other sexual signals.

Perhaps the most often studied maintenance cost of ornaments is that of decreased locomotor performance (Oufiero & Garland, 2007). Ornaments, in general, are structural features of an organism (e.g., exaggerated appendages, colour patches, horns) that can have either a direct impact on performance (e.g., tail length may affect flight performance), no direct impact on performance (e.g., a colour patch will not physically make an individual run slower), or indirect impacts on performance over evolutionary time (e.g., increased conspicuousness from a colour patch may result in selection for better escape ability). A substantial decrease in locomotor performance is likely to have negative impacts on the ability of animals to effectively escape predators, forage, and interact with conspecifics (Irschick & Garland, 2001; Husak, 2006; Husak & Fox, 2006). In some cases, ornaments have been shown to reduce locomotion of males in some species, yet this relationship is absent in other species where decrements are expected. For example, gonopodium length was found to be negatively associated with the ‘c-start’ escape response in *Gambusia* fishes (Domenici & Blake, 1997; Langerhans et al., 2005). However, the extravagant tail morphology of male guppies (*Poecilia reticulata*) was unrelated to swimming speed (Nicoletto, 1991). Similarly, there was no relationship between sword length and swimming endurance in the swordtail fish *Xiphophorus nigrensis* (Ryan, 1988). Surprisingly, male *X. helleri* with longer swords were found to have faster escape performance (Royle et al., 2006). Among males of the Australian slender crayfish (*Cherax dispar*), there is a negative relationship between chelae size and escape swimming speed among males (Wilson et al., 2009). In sand fiddler crabs (*Uca pugilator*), increased claw size diminished the locomotor endurance of males, but did not reduce maximal sprint speed (Allen & Levinton, 2007). Although issues related to sample size and the nature of the study (e.g., correlational versus experimental) can complicate interpretation and inference, the surprising and seemingly ambiguous results of many studies makes it clear that testing for costs of ornaments, or signals in general, is not as straightforward as looking for a simple relationship between ornament size and locomotion or even an average reduction in locomotion after experimental increase of an ornament.

4. Compensatory traits

Although ornaments are typically under the influence of sexual selection, either through male–male competition or female choice, natural selection works on the integrated phenotype of individuals (Arnold, 1983; Lande & Arnold, 1983; Møller et al., 1995a; Cornwallis & Uller, 2010). Natural selection may limit elaboration and exaggeration of ornaments (reviewed in Andersson, 1994; Kotiaho, 2001), but it is unlikely to do so only by selecting against those individuals with larger or more exaggerated signals. Instead, there may also be selection on traits that reduce the negative effects of sexually selected traits, including ornaments; specifically, there may be correlated selection for compensatory traits (Kirkpatrick, 1987; Møller, 1996; Jennions et al., 2001; Tomkins et al., 2005; Oufiero & Garland, 2007; Swallow et al., 2009; Figure 1). Compensation may come in the form of novel or modified structures, physiology, behavior, or performance (DeWitt et al., 1999; Husak & Fox, 2006). Such traits have important implications for how we view the evolution of reliable signals, though this issue has received little attention, especially in theoretical models of signal evolution. In essence, a population may be viewed as being in a state of equilibrium where the cost of the ornament has been balanced by the evolution of compensatory traits and the current phenotype represents an ‘optimum’ balance between the benefits of the ornament (increased mating success) and the costs (reduced survival) in that given selective environment. In environments where there is highly fluctuating sexual selection or natural selection pressure, the balance may shift considerably over time (Cornwallis & Uller, 2010). Without considering compensatory traits, one may obtain spurious correlations between ornament size and performance or survival. Indeed, ignoring potential compensatory traits may mask the negative effects of an ornament or create the illusion that an ornament enhances performance (Jennions et al., 2001; Oufiero & Garland, 2007).

Oufiero & Garland (2007) used simulated data for 57 species of swordtail fishes (genus *Xiphophorus*) to illustrate how compensatory traits can complicate tests of signal costs. In their simulation, the length of the sword (an ornament) on the caudal fin was positively related to body length, as was swimming endurance and the mass of the heart's ventricle (a compensatory trait). Path analysis that included these variables, but excluded ventricle mass, resulted in a path model indicating positive relationships between body length, sword length and swimming endurance, thus suggesting the counter-intuitive notion that sword length may increase endurance capacity. However, performing the same analysis, but including ventricle mass, the compensatory trait, resulted in a path model clearly showing a negative effect of sword length on swimming endurance, as well as the positive compensatory relationship between ventricle mass and endurance. In this hypothetical example, ignoring a compensatory trait led to an incorrect and illogical conclusion. They concluded that investigators in the future should use appropriate statistical methods when dealing with multiple variables that are likely intercorrelated and consider the complicating effects of compensatory traits. Below we discuss empirical examples of compensation for ornaments studied from both an intra-specific and a comparative inter-specific perspective.

4.1. Intra-specific examples of compensation

Intra-specific studies can be useful for testing the fitness costs and benefits to individuals of having smaller or larger ornaments relative to their compensatory abilities, thus allowing one to quantify the strength of selection on ornaments and correlated selection on compensatory traits. Empirical examples of compensation to date are largely those related to how ornaments affect flight performance, but the simulated example explored by Oufiero & Garland (2007) discussed above emphasizes the likely widespread presence of compensatory traits in a diverse array of animal taxa. We hope future work will consider other kinds of ornaments that may have different direct effects on performance traits other than flight (e.g., terrestrial locomotion or swimming), indirect evolutionary effects on performance (e.g., colour patches), or ornaments that are compensated for in other ways (e.g., through novel structures or behaviour; see Møller et al., 2006).

Among bird species, elongated tail ornaments increase drag, which may hinder flight performance (Thomas, 1993). To apparently alleviate the aerodynamic costs of elongated tails used by male birds as ornaments, numerous species have evolved larger wings than females, and within males, individuals with larger tail ornaments have larger wings. In barn swallows (*Hirundo rustica*), males have greater wing spans, wing areas, and aspect ratios and reduced wing loading compared to females in several populations (Møller et al., 1995a). Further, the outermost tail feathers which make up the ornament are not just exaggerated versions of shorter feathers; instead, males reduce drag of their ornamental tail feathers with morphological modifications compared to females: the outermost feathers are narrower at the tips in males compared to females. In addition, tail length was positively related to wing length, wing span, and wing area among males, but aspect ratio and wing loading were unrelated to tail length. These findings suggest that wing size more than shape is used to compensate for tail ornaments in male barn swallows. Møller et al. (1995a) also examined population variation in wing and tail morphology of barn swallows, finding that sexual dimorphism in tail length was positively correlated with dimorphism in wing length across populations. Similar results have been found in other bird species. In scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*), the elevated moment of inertia and increased drag caused by increased tail length is apparently offset by increased wing span, which increases power generation during flight. (Evans & Hatchwell, 1992; Evans & Thomas, 1992). Tail ornament length and wing length was also found to be positively related in the long-tailed widowbird (*Euplectes progne*; Craig, 1989) and Jackson's widowbird (*E. jacksoni*; Andersson, 1992), presumably to compensate for reduced flight performance.

An interesting example of compensation for an ornament that is not even part of the body of the male bearing it is the case of male black wheatears (*Oenanthe leucura*) that carry stones (up to several hundred total over multiple trips!) to females that are in cavities within cliffs and caves (Moreno et al., 1994; Soler et al., 1996, 1999). Females mated to males that carry more stones have higher fecundity compared to males that carry fewer stones (Moreno et al., 1994; Soler et al., 1996). Males have greater wing area and lower wing loading compared to females, and both the number and mass of stones carried by males are inversely related to wing loading (Møller et al., 1995b). Further, experimental removal of two primary feathers of the wings resulted in decreased stone-carrying ability compared to control groups, but males with initially large wing areas were affected least by the experimental treatment (Møller et al., 1995b). These results suggest that a large wing area and low wing loading have evolved to offset the costs associated with stone carrying, emphasizing that selection may be strong to reduce costs of sexual displays even when they are not part of the body per se (e.g., Schaedelin & Taborsky, 2009).

In the earwig *Forficula auricularia*, posterior forceps are used during fights between males and are under the influence of sexual selection for increased mating success (Tomkins et al., 2005). There is a positive relationship between relative forceps size and relative elytra length (a proxy for wing length) in males, which was proposed to be due to compensation for the burden of a sexually selected trait, the forceps (Tomkins et al., 2005). The authors suggested that the two traits have become developmentally integrated, most likely from a history of correlated selection. In the same study, Tomkins et al. (2005) found a negative relationship between elytra length and horn size in the dung beetle *Onthophagus taurus*, presumably because there is a trade-off between the sexually selected trait (the horn) and other traits for allocation of resources during development. This result is consistent with other work on dung beetle traits that are adjacent to each other and compete for resources during development (e.g., Emlen, 2001; see also Knell et al., 2004; but see Hunt et al., 1999). It is also worth noting that for both species there were positive relationships between the relative size of the sexually selected traits and relative limb dimensions (hind-femur length and forceps length in earwigs; fore-tibia length and horn length in dung beetles), presumably also for compensatory purposes (Tomkins et al., 2005).

Stalk-eyed flies (Diopsidae) are a family of flies characterized by having their eyes displaced laterally on long peduncles, or stalks. The family includes species that are sexually dimorphic for eye stalk length, where males have considerably larger eye spans than females, and those that are monomorphic, where males and females do not differ in eye span (Wilkinson & Dodson, 1997; Baker & Wilkinson, 2001). The exaggerated eye span in dimorphic species is under the influence of sexual selection via both female choice (Burkhardt & de la Motte, 1988; Wilkinson & Reillo, 1994; Wilkinson et al., 1998) and male–male competition (Burkhardt & de la Motte, 1985; Panhuis & Wilkinson, 1999). Eye span of males in monomorphic species does not appear to be sexually selected (Wilkinson et al., 1998;

Panhuis & Wilkinson, 1999), and may be closer to an optimum size from natural selection, as is predicted for females (Worthington & Swallow, 2010). Although greater eye spans increase mating success, the exaggerated eye stalks of males results in them having a much larger moment of inertia for their bodies than do females, meaning that males require larger torques to turn the body while flying, potentially severely hindering male flight performance (Ribak & Swallow, 2007). However, contrary to these predictions, males of the dimorphic species *Teleopsis dalmanni* performed as well, or better, than females during free-flying turning behavior (Ribak & Swallow, 2007) and males of the dimorphic species *T. whitei* had only slightly (though significantly) lower vertical velocities compared to the monomorphic *T. quinqueguttata* (Swallow et al., 2000). Studies on stalk-eyed fly flight performance to date suggest that males appear to compensate for their biomechanical disadvantages with increased thorax size (a proxy of flight musculature) and wing size (Swallow et al., 2000; Ribak & Swallow, 2007).

In a study of seven species of stalk-eyed flies (Husak et al., data not shown), there was strong evidence for compensation by males in dimorphic species (*T. dalmanni*, *T. whitei*, *T. thaii* and *Diasemopsis meigenii*). As in studies of birds with tail ornaments, for males of dimorphic stalk-eyed fly species there was a positive relationship between residual eye span and residual wing length (Figure 2A) and wing area. On the other hand, there was no compensation in the three monomorphic species studied (*T. quinqueguttata*, *T. quadriguttata* and *D. signata*; Figure 2B), where exaggerated eyestalks do not provide a mating advantage for males (Wilkinson et al., 1998; Panhuis & Wilkinson, 1999). Because dimorphism and monomorphism are both present in the two genera of stalk-eyed flies studied, and both states have evolved independently multiple times (Baker & Wilkinson, 2001), it is likely that compensation has also evolved independently multiple times. As in barn swallows (Møller et al., 1995a), the females of two species of dimorphic stalk-eyed flies (*T. whitei* and *T. thaii*) also showed a positive relationship between relative eye span and relative wing length (Figure 2A), but not wing area (Husak et al., data not shown). Since there is a genetic correlation between male and female eye span (Wilkinson, 1993) and females in dimorphic species also have long eye stalks compared to monomorphic species (Wilkinson & Dodson, 1997), it is likely that females of species with especially long eye stalks (e.g., *T. whitei* and *T. thaii*) must also compensate for the aerodynamic burden (Husak et al., data not shown). In other words,

(a)

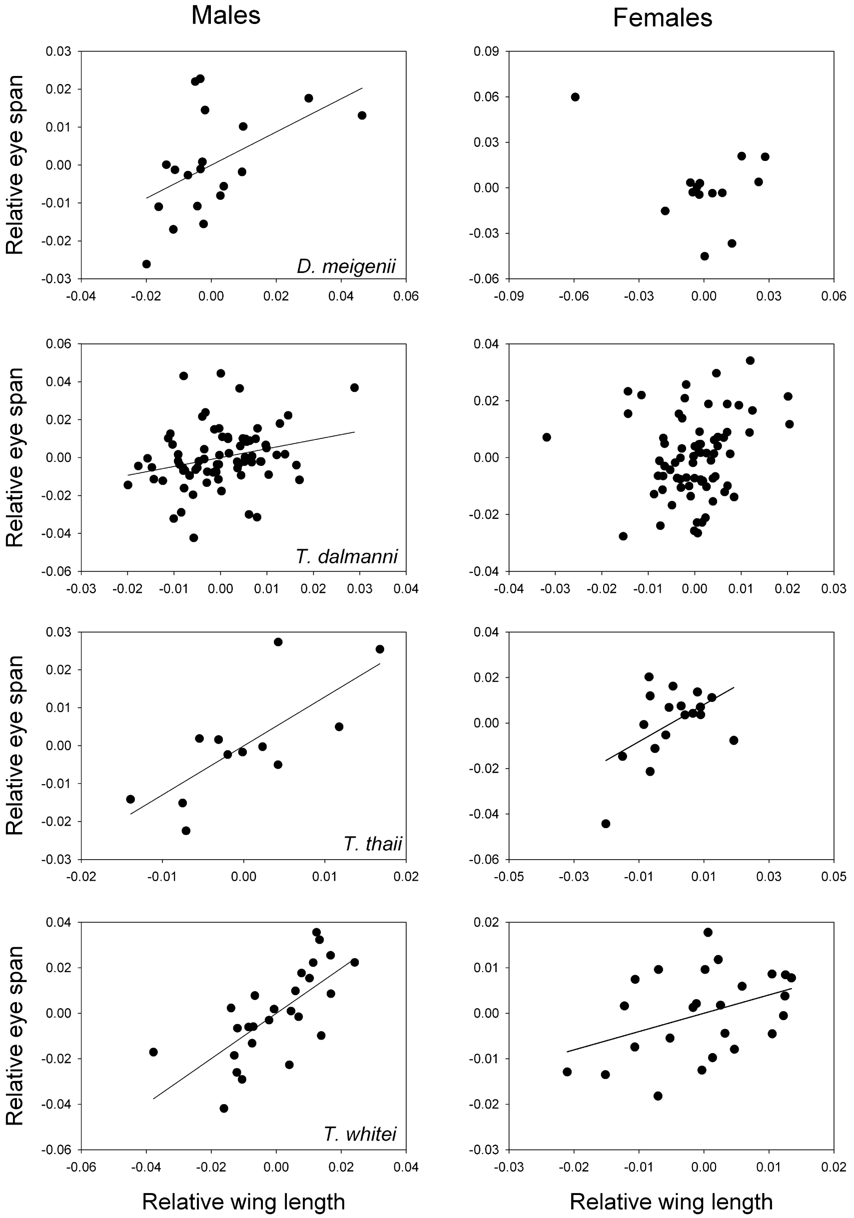
Males
Females
Relative eye span
Relative wing length
D. meigenii
T. dalmanni
T. thaii
T. whitei

Figure 2.

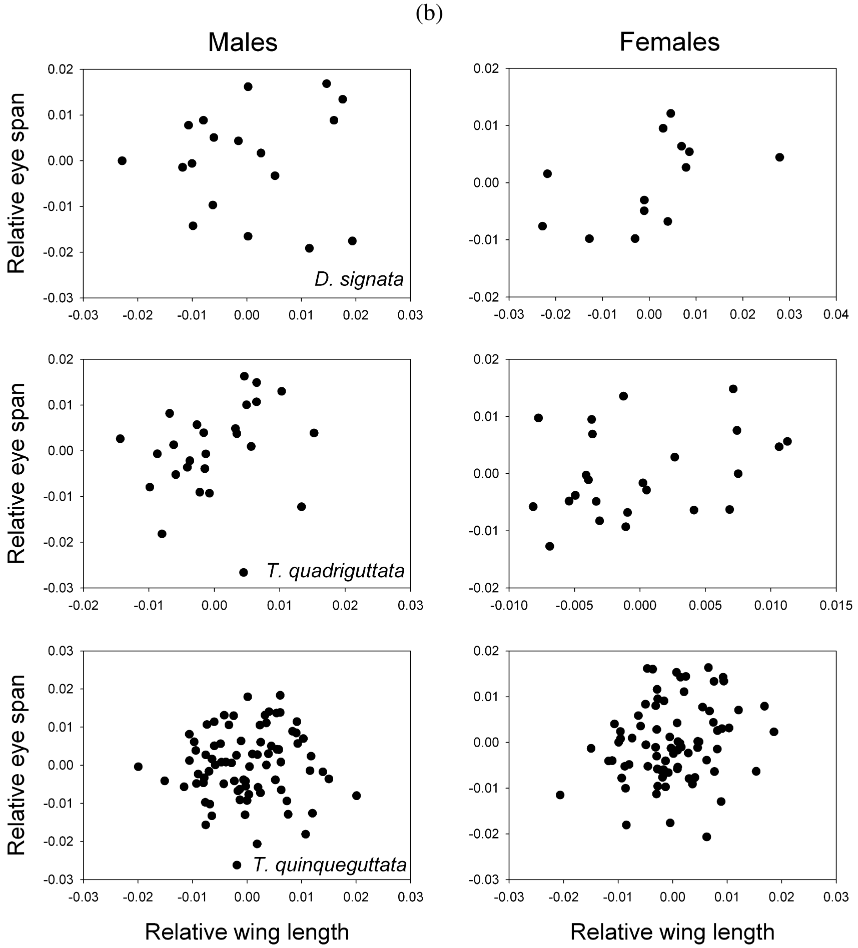

Figure 2. (Continued.) (a) Relationships between relative eyespan and relative wing length for males (left) and females (right) of four dimorphic species of stalk-eyed flies. Relative trait values were calculated from separate linear regressions on log-transformed variable regressed on body length. Lines in the figure represent least-squares linear regression lines (where relationships were significant) and are for illustrative purposes as in Figure 3. (b) Relationships between relative eyespan and relative wing length for males (left) and females (right) of three monomorphic species of stalk-eyed flies. None of the relationships were statistically significant (Husak et al., data not shown).

sexual selection on males may result in a correlated increase in female eye span and, therefore, in increased costs for females via genetic correlations (see below). These findings, taken together, are consistent with the hypothesis that natural selection favours traits in stalk-eyed flies that allow compensation for the detrimental locomotor effects of sexually selected ornaments: in this case, exaggerated eyestalks.

5. Inter-specific comparative examples of compensation

If ornaments result in evolutionarily significant performance and physiological trade-offs, then patterns of correlated evolution should be reflected in the lineage's phylogenetic history as it evolved and diversified. Thus, if performance decrements generated by ornaments are selectively important, compensatory morphological and behavioural changes should arise to mitigate performance trade-offs associated with them. This result is predicted because individuals that can reduce the negative impact of secondary sexual characters will be at a selective advantage. Genetic drift, while capable of producing interspecific variation, will not tend to produce patterns of correlated evolution. Inter-specific comparisons and correlations, thus, allow in depth investigation of the product of 'natural experiments' (Feder et al., 2000). Whereas intra-specific studies can allow tests of fitness costs of ornaments within a population, comparative studies in a phylogenetic framework can help to elucidate when compensatory mechanisms arose and whether they are evolutionarily associated with ornament morphology. Comparative analyses may also discern whether the same compensatory trait(s) evolves when ornament exaggeration evolves, or if other compensatory traits may be present.

Song flight, for example, is an energetically expensive sexual signal that is widespread among bird species, most likely requiring high endurance capacity (Hedenström & Møller, 1992). Although song flight is not an ornament, it may reduce flight performance, and one means of compensating is to have larger wings. Hedenström & Møller (1992) looked across 16 passerine bird species, 8 pairs of sister taxa where one had song flight and the other did not, to determine how dimorphism in morphology differed between the two groups. They found that species with song flight did not differ in body size from those without, but species with song flight had greater wing span and wing area, lower wing loading, and higher aspect ratio compared to species without song flight. These results suggest that manoeuvrability and flapping flight performance have likely undergone selection to reduce costs associated with song flight.

In sexually dimorphic widowbirds and bishops (genus *Euplectes*), the elongated tail ornament is used as a cue during female mate choice, and may be up to four times the body length of a male in some species (e.g., long-tailed widowbirds; Andersson & Andersson, 1994). As in other birds with tail ornaments, these exaggerated ornaments are predicted to reduce flight performance (Balmford et al., 1993). However, when looking across 13 species of *Euplectes*, sexual dimorphism in tail length was positively correlated with dimorphism in wing length (Andersson & Andersson, 1994), suggesting that males compensate for elaborate tail ornaments. This relationship was even stronger when only species with display flying were included, a situation where compensatory flight performance would likely experience stronger selective pressure. In a similar, but larger, comparative analysis, tail length dimorphism was correlated with wing length dimorphism across 57 bird species in 13 families (Balmford et al., 1994). However, since ornamented birds may be more likely to be migratory, and undergo selection for associated flight performance traits (Fitzpatrick, 1994), it would be interesting to see how considering migration effects would influence this study. Nevertheless, the broad taxonomic coverage and use of phylogenetically correct statistical methods in this latter study provide strong support for the hypothesis that tail ornamentation and wing dimorphism co-evolve to offset costs of ornamentation.

Among stalk-eyed flies (Diopsidae), the males of species that are dimorphic for eye span may have eye spans that far exceed their body length (Wilkinson & Dodson, 1997). However, the elongated peduncles on which the eyes and antennae are placed are not sex-limited, such that species with large male eye spans also have females with large eye spans compared to species monomorphic for eye span (Baker & Wilkinson, 2001; Husak et al., data not shown). Important for studying the evolution of ornaments, exaggerated male eyestalks have re-evolved multiple times in stalk-eyed flies, as has the loss of dimorphism (Wilkinson & Dodson, 1997; Baker & Wilkinson, 2001), providing an evolutionary scenario to test for correlated evolution of compensatory mechanisms for exaggerated ornaments. A comparative study of 10 stalk-eyed fly species that incorporated statistical methods to account for phylogeny in all analyses revealed several key findings supporting the hypothesis that wing size and shape have coevolved with eye span to compensate for the exaggerated ornament (Ribak et al., 2009). Among males, but not females, residual eye span (residuals derived from a regression on body mass) was correlated with residual wing length, indicating that when males of a species have relatively long eyestalks, they also have relatively long wings. Further, sexual dimorphism in eye span of stalk-eyed flies was found to be positively evolutionarily correlated with sexual dimorphism in wing length and wing area. Sexual dimorphism in eye span was also found to be negatively evolutionarily correlated with dimorphism in wing loading. Finally, sexual dimorphism in eye span was found to be positively evolutionarily correlated with dimorphism in the third moment of wing area, a biomechanical measure which describes how area is distributed along the length of the wing and is related to the aerodynamic moment generated by the wings (Weis-Fogh, 1973; Ribak et al., 2009). These results taken together suggest that changes in wing morphology over evolutionary time are at least partly due to compensation for the burden of exaggerated eyestalks.

5.1. Genetic correlations and compensatory traits

Because the exaggerated ornaments exhibited by males of sexually dimorphic species are thought to be costly, it is generally assumed that female ornament expression is closer to the optimum level set by natural selection (Lande, 1980) and, therefore, males are expected to experience higher costs and, ultimately, to experience reduced survival compared to females (e.g., Andersson, 1994; Husak et al., 2006; but see Jennions et al., 2001; Worthington & Swallow, 2010). However, this assumption too may be overly simplistic because, in many cases, homologous traits in males and females share a similar genetic architecture which, in turn, may constrain the independent evolution of the sexes. Indeed, cross-sex genetic correlations for ornaments are often positive and large (see Kraaijeveld et al., 2007 and Poissant et al., 2010 for reviews). Because of these often tight genetic correlations, sexual selection on male ornaments can result in correlated responses in females, pulling their phenotype beyond the 'optimum level' set by natural selection. For example, based on parent-offspring regression analyses, Møller (1993) found a strong positive genetic correlation between male and female tail length in barn swallows ($r_{\mathrm{MF}} = 0.54 \pm 0.16$). Accordingly, not only did males show a positive relationship between tail feather length and wing span, but so did females (Møller et al., 1995a; see also Roff et al., 2004). Similarly, Wilkinson (1993) found positive genetic covariance for both relative and absolute eye span ($r_{\mathrm{MF}} = 0.39 \pm 0.05$ and $r_{\mathrm{MF}} = 0.29 \pm 0.05$, respectively) in the stalk-eyed fly (*Teleopsis dalmanni*) based on correlated responses to bidirectional selection for male eye span. Baker & Wilkinson (2001) suggested that the genetic correlation structure between the sexes has likely influenced the evolution of sexual dimorphism and eye-span allometry in the family Diopsidae. To the extent that female ornaments evolve beyond the optimum set by natural selection, females too should experience the predicted detrimental effects of an enlarged ornament and, therefore, be expected to evolve compensatory traits just as do males. In support of this idea, a recent study of seven species of stalk-eyed flies (Husak et al., data not shown) found strong evidence for compensation not only by males in dimorphic species (*T. dalmanni*, *T. whitei*, *T. thaii* and *Diasemopsis meigenii*) but also by females in the two most extremely dimorphic species surveyed (*T. thaii* and *T. whitei*). In these two species residual wing length was correlated to residual eye span in both males and females, suggesting that, just as in males, there is some compensation among females of these species for large eyestalks via longer wings. However, in the two dimorphic species that were not as extreme with regard to eye span (*T. dalmanni* and *D. meigenii*), no evidence for compensation was found.

Given that females may also experience the detrimental effects of enlarged ornaments, perhaps the absence of sex differences in average performance or survival reported in previous studies (e.g., Anholt, 1997; Ribak & Swallow, 2007; reviewed in Kotiaho, 2001) should come as no surprise, especially if both sexes have evolved compensatory mechanisms. We would then anticipate that costs of bearing ornaments and/or the degree of compensation would be more starkly contrasted in species in which ornament expression is limited to one gender only. Fortunately, in many species, ornament expression is sex limited. For example, eye stalks have evolved independently in at least eight families of acalyptrate Dipteran families, and in seven of the eight families eye stalk-expression is limited to males only (Wilkinson & Dodson, 1997). Similarly, head projections of ‘antlered’ flies (Wilkinson & Dodson, 1997) and many species of dung beetles (Emlen et al., 2005) are expressed in males only. To our knowledge, no one has tested for sex related performance differences in species with sex-limited ornament expression. We note that there are cases where the evolution of male and female ornaments are due to selective advantages for both sexes (e.g., Kraaijeveld et al., 2007; Simmons & Emlen, 2008) and that sexual dimorphism can result from gains and losses of male and female ornaments (e.g., Wiens, 2001). In cases where female ornaments have a selective advantage, one would expect also to see correlated evolution of compensatory traits.

6. A model to test costs of ornaments

By simultaneously considering ornament size and the magnitude of compensatory traits, one can conduct more specific tests for the costs of exaggerated ornaments. Husak et al. (data not shown) proposed a model with such an approach (Figure 3A), where individuals in a population are considered in 'compensation space' relative to each other. When looking at relative ornament size plotted against the relative magnitude of some compensatory trait(s), the best-fit regression line (linear or curvilinear) represents the average compensatory ability in the population. Those above the line have ornaments larger than their compensatory ability on average, and are 'under-compensating' for their ornament, whereas those below the line have compensatory mechanisms greater than required for their relative ornament size, and are 'over-compensating'. An interesting empirical question is what determines the amount of variation around a population mean when examining relationships such as the general one in Figures 3 and 4. While this question is beyond the scope of this paper, the answer may be related to the

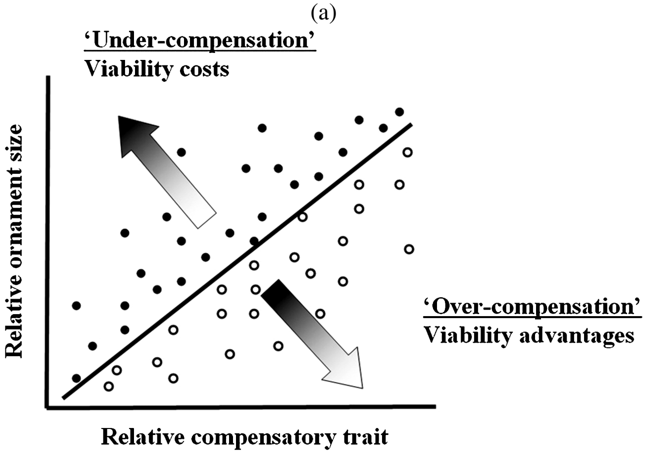

Figure 3.

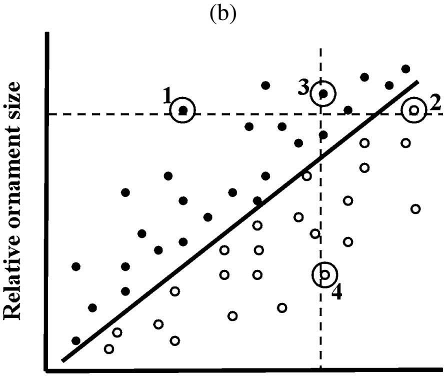

Figure 3. (Continued.) (a) Hypothetical illustration of compensation for exaggerated ornaments as proposed by Husak et al. (data not shown). Examining relationships between ornament size and compensatory traits can allow more specific hypothesis tests for costs of ornaments. Individuals above the regression line (filled, black circles; 'under-compensating') have ornaments that are larger than their predicted compensatory abilities and should have performance and/or survival (i.e., viability) costs. Individuals below the line (open circles; 'over-compensating') have greater compensatory traits than 'necessary' for their ornament size and should have performance and/or survival (i.e., viability) advantages. As the distance from the regression line increases above the line (i.e., as residuals increase positively), costs are predicted to increase. Conversely, as the distance increases below the line (i.e., residuals become more negative), viability advantages should increase. The line does not represent a theoretical or biomechanical optimum amount of compensation for varying ornament sizes, but instead the average relative compensatory ability within a sex in a population from which one can derive hypotheses about relative costs. (b) For example, the individuals represented by points 1 and 2 have similar relative eyespans, but individual 1, with its relatively lower compensatory ability ('under-compensating'), is predicted to have higher costs than 2 ('over-compensating'). Individuals 3 and 4 have similar compensatory traits, but 3 is predicted to have higher costs despite having a higher probability of mating success than 4 during any given attempt. On the other hand, 4 may live longer to accumulate matings and have similar net fitness as 3.

intensity and form of selection on the relevant traits, the degree of condition-dependence of the traits, canalisation of the traits, and/or the degree of fluctuation of selective pressures on the traits, among other possibilities. Regardless, the prediction is that, on average, the 'under-compensating' individuals should have viability costs, whereas the 'over-compensating' individuals should have viability advantages (Figure 3A). Further, the more positive the residual for an individual (i.e., the higher above the line), the higher the viability costs should be. It is important to note that the regression line in

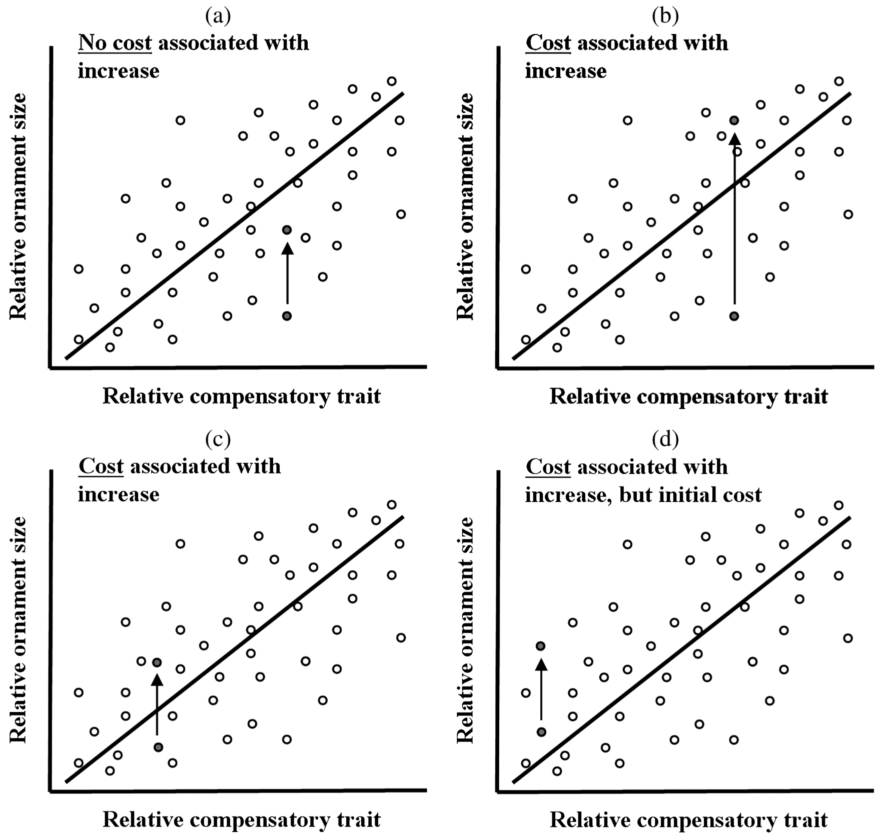

Figure 4. Hypothetical examples of how increasing the relative size of a signal may (a) not result in a cost to the individual (b, c) result in a survival cost to the individual, or (d) appear to result in a survival cost. See text for detailed explanation.

Figure 3A does not represent a biomechanical or physical 'optimum' compensatory ability that is calculated to provide the necessary amount of compensation to overcome the cost. Instead, the line represents average compensation for a sex within a population, which allows a way to compare relative compensatory abilities among individuals within a population to determine which should have higher costs. It is analogous to examining the fitness of individuals in 'morphological space' as has been done in numerous studies (Kingsolver et al., 2001; Blows, 2007). This is an appropriate approach for those hoping to measure actual fitness costs of ornaments. Figure 3B shows examples of how one might test for relative costs in a population. Individuals 1 and 3 are 'under-compensating' relative to others in the population and should have higher viability costs from their ornaments compared to the 'over-compensating' individuals 2 and 4. Examining individuals 1 and 2 reveals that two individuals may be nearly identical in relative ornament size, yet are predicted to have very different costs based on how they can compensate for their ornament.

The predictions for viability relative to ornament size are clear from the model show in Figure 3A, but the effects of compensatory traits on fecundity are less straightforward. In many cases, increasing relative ornament size will increase the probability of successfully mating with a potential mate (Andersson, 1994; Cotton et al., 2006). However, the multiplicative nature of fitness (Getty, 1998, 2006) may allow individuals with small relative ornaments, but 'over-compensating' traits, to have similar net fitness due to their predicted higher survival. For example, individuals 3 and 4 in Figure 3B have similar values for their compensatory trait, yet individual 3 has a much larger ornament. Individual 3 may have a higher probability of acquiring a potential mate at any given point in time, but its absence of adequate compensatory abilities for its relative ornament size may reduce its probability of survival or reduce longevity. On the other hand, individual 4 may have a lower probability of acquiring a potential mate at any given point in time, but its more than adequate compensatory abilities may increase its probability of survival or increase longevity such that it can accumulate matings and its lifetime reproductive success may be similar to individual 4. These predictions of course depend on the mating system and life history of the species.

One could also examine multiple compensatory traits in multivariate space, such as with a principal components analysis that includes multiple morphological, physiological, or performance traits. In such a multivariate analysis, the x-axis would be principal component scores or some other such composite variable. A multivariate approach could reveal important combinations of compensatory traits that form multiple 'solutions' to offset costs of exaggerated ornaments. Considering multiple, closely related species may be informative as to the range of potential compensatory traits used within a lineage. These issues raise the important question of how one identifies potentially important compensatory traits. The examples discussed above involve ornaments that are predicted to directly (biomechanically) reduce performance and, thus, survival, or indirectly reduce survival via increased conspicuousness. Future investigators should consider the ornament or signal of interest in relation to how it is predicted to be costly to the one bearing it. If one can hypothesize a potential performance (or survival) cost to test, then one can hypothesize what performance or physiological traits may act to reduce that cost. Obviously, speculating on which traits will be compensatory or not will depend on the species and ornament of interest. We caution against simply measuring all possible traits one can measure and looking for a relationship between relative ornament size and those traits. This may result in spurious 'just-so' stories about compensation. Instead, compensatory traits should be logically, and in many cases biomechanically, linked to potential costs of an ornament. Appropriate manipulation experiments can confirm or at least help to clarify the causal link between the ornament of interest and compensatory traits (e.g., Møller et al., 1995b,c).

7. Manipulating ornaments

Correlational studies examining how natural variation in ornament size is related to a proxy of fitness have been complimented by manipulation experiments, where ornaments are increased or decreased in size, and compared to controls. Manipulating the phenotype can be extremely useful for elucidating how one aspect of an organism affects fitness (e.g., Sinervo et al., 1992; Ketterson et al., 1996). For example, male barn swallows with elongated tails caught only smaller, suboptimal prey compared to males with shortened tails, which caught higher quality, large prey (Møller, 1989; Møller et al., 1995c), and experimental tail feather elongation of male scarlet-tufted malachite sunbirds resulted in decreased time spent flying and reduced efficiency at aerial insect capture (Evans & Thomas, 1992). However, such manipulation experiments have resulted in mixed results, with some revealing costs associated with increased ornament size and others not (reviewed in Kotiaho, 2001; Oufiero & Garland, 2007; see also references above). The ambiguous findings across studies are not surprising when one considers the effect that compensatory traits may have on the results of manipulation studies. Whereas the previous examples of barn swallows and scarlet-tufted malachite sunbirds suggest that elongation beyond the ability to compensate compromises aerial performance and may incur costs, this is not necessarily the predicted result of manipulation experiments. The results that one obtains in such a study will depend on whether compensatory traits have evolved and how the treatment groups are assigned with regard to individual compensatory abilities. Increasing relative ornament size should hypothetically increase probability of mating success at any given attempt, but the effect on performance and survival depends on initial compensatory ability. Not all individuals are necessarily expected to have decreased survival or performance with increased ornament size. We illustrate these points in Figure 4 in relation to the model presented in Figure 3.

One methodology is to randomly sample individuals, increase ornament length in one-third of them, decrease it in another one-third, and do a sham manipulation (i.e., a control) in the remaining third. We focus first on the comparison of individuals with increased ornaments to control individuals, as this is where costs are typically expected to be revealed (e.g., Møller, 1989; Saino et al., 1997). The responses to increased ornamentation will depend on the manipulated individuals' initial compensatory abilities (Figure 4), as well as the magnitude of increase in the ornament. If an individual is already over-compensating, increasing relative ornament size may not have any effect on performance or survival compared to individuals that are under-compensating (Figure 4A). Conversely, if that same individual has a much larger increase in the magnitude of ornament increase, then there may be a detectable cost (Figure 4B). Alternatively, an individual may have ornamentation increased by the same magnitude as the individual in Figure 4A, but it is sufficient to result in a viability cost (Figure 4C). Finally, if an individual is already under-compensating, increasing ornamentation would seemingly result in a cost, but that individual would have already been incurring costs relative to other individuals in the population (Figure 4D), making the manipulation an unnecessary endeavour and the results potentially difficult to interpret. If one takes a truly random sample from a population to increase ornamentation, approximately half will be under-compensating and half will be over-compensating, and the results of the experiment will depend on the magnitudes of under- and over-compensation, as well as the magnitude of ornamentation increase. It is easy to see why manipulation experiments may result in unpredictable or even contradictory results.

The same problems exist for control individuals. Some may be under-compensating prior to the experiment (e.g., individual 1 in Figure 3B), making them appear to have a cost due to a sham manipulation, or they may be initially over-compensating, resulting in the expected no-cost when compared to other individuals. Reducing relative ornament size should decrease the probability of mating success at any given attempt, but the viability effects on survival or performance will be affected in similar ways as increasing ornamentation, again depending on initial compensatory ability and the magnitude of the decrease. The point we are trying to make is that manipulation experiments should consider these issues carefully during experimental design. When manipulating individuals in a population, one needs to know where each is relative to others in terms of compensatory ability relative to ornament size. That is, producing an empirical figure as in Figure 3A will help decide which individuals to use and how much to increase or decrease ornamentation, as well as which individuals should be used as controls.

8. Conclusions

The classic scenario of natural selection constraining the evolution of exaggerated ornaments (Darwin, 1871; Andersson, 1994) is much more complex when considering the effects of compensatory traits (Oufiero & Garland, 2007; Husak et al., data not shown). There is consistent evidence among flying insects and birds studied to date that ornamentation is associated with corresponding changes to the flight apparatus to reduce the potential performance costs of ornament exaggeration. If the evolution of compensation reduces costs of ornaments, then sexual selection may allow further exaggeration of ornaments over evolutionary time (Møller, 1996). Constraints on ornamentation would then be determined by resource availability and/or the ability to evolve compensatory mechanisms. Since there are likely also constraints on the evolution of compensatory abilities (e.g., wings can only become so long or wide for a given body size range before they become detrimental to flight performance and survival), there are still limits to exaggeration. However, when the ‘limits’ of one compensatory trait are reached, other traits may be used to compensate. This sets the stage for a wide variety of phenotypes within a lineage that phylogenetically informed, comparative studies can explore. Such an approach can allow tests of ultimate explanations for variation in ornament exaggeration that is found within many lineages. For example, within stalk-eyed flies eye span may vary by an order of magnitude among species (Wilkinson & Dodson, 1997; Baker & Wilkinson, 2001), and the same is true for the length of the sword among males of swordtail fish species (Pyron, 1996; Oufiero & Garland, 1997). Comparative studies will allow a test of whether this inter-specific variation within a lineage or group of closely related species is due to variation in female preference, variation in environmental conditions (e.g., predation pressure), limits to the evolution of compensatory traits, differences in developmental integration and modularity, or some combination of these (Emlen, 2001; Tomkins et al., 2005). As a compliment, intra-specific studies of compensation can test whether individuals with large relative ornaments and correspondingly high compensatory abilities actually have the highest fitness in the population compared to those with smaller ornaments and lower compensatory abilities. Manipulation experiments that take into account the relative compensatory abilities of test subjects may shed additional light on signal costs and the evolution of reliability.

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