

# PHENOTYPIC INTEGRATION

Studying the Ecology and Evolution  
of Complex Phenotypes

---

*Massimo Pigliucci*  
*Katherine Preston*

**OXFORD**  
UNIVERSITY PRESS

2004

### 3

## Integration and Modularity in the Evolution of Sexual Ornaments

### *An Overlooked Perspective*

---

ALEXANDER V. BADYAEV

#### **Paradox of an Ideal Sexual Ornament: Exaggerated and Flexible Yet Honest**

The expression of sexual ornaments often reflects male health and overall physiological condition, and females mating with the most ornamented males are assumed to produce the best-adapted offspring and receive the most benefits from such males (Andersson 1994). However, there are a number of unresolved issues in the evolution of sexual traits that reflect males' condition.

On one hand, sexual traits, such as deer antlers, beetle horns, or elongated bird tails, are under strong directional selection for greater expression, and this selection favors reduced integration (e.g., favors modified allometric relationships) between sexual traits and the rest of the organism (Eberhard 1985; Emlen and Nijhout 2000). Indeed, most sexual traits are "stand-alone" structures (e.g., deer antlers are far less integrated and more variable than frontal bones of which they are a part). On the other hand, sexual traits are expected to indicate the physiological condition and health of an individual, such that the expression of sexual traits represents a complex summary of many organismal processes (Wedekind 1992; Johnstone 1995). However, to be such a summary, sexual traits should be highly integrated into many organismal functions. This represents a paradox where sexual traits are expected to be both less integrated for greater expression, and more integrated to better indicate physiological quality.

Similarly, to be a reliable reflection of organismal processes, sexual ornaments (or, more precisely, the pathways that lead to development of sexual ornaments) are expected to be well integrated in the ontogeny of an organism. To be an

indicator of health, these traits need to be costly to an organism (Zahavi 1975; Andersson 1982; Grafen 1990), yet there is an advantage to modify investment of resources into the development of sexual ornamentation depending on life history and context of breeding (Höglund and Sheldon 1998; Kokko 1998; Badyaev and Qvarnström 2002). Facultative investment into the production of sexual ornamentation should favor relative independence of developmental pathways of non-sexual traits and sexual ornaments, which will make the latter less reliable indicators of overall quality. This represents another paradox where costly indicators of individual condition can evolve only if it is possible for an organism to accomplish and “survive” their ontogeny. Yet developmental mechanisms enabling this survival will make sexual ornaments less integrated with organismal functions and thus less reliable indicators of them.

The concepts of morphological integration and modularity have provided valuable insights into the evolution of complex biological structures (Olson and Miller 1958; Schlichting and Pigliucci 1998; Wagner 2001). Whereas it is clear from the above discussion that these concepts are central to the ontogeny, function, and evolution of sexual ornamentation, they are mostly overlooked. Here I discuss how the concepts of integration and modularity can facilitate our understanding of unresolved issues in the evolution of sexual traits.

## **Designing Sexual Traits: Relative Importance of Internal and External Selection**

### **Why Sexual Traits?**

Sexual traits are unique in that the environment in which they function is mostly external to the organism, and the selection pressures that affect their evolution are mostly due to phenotypes of other individuals. For example, some sexual ornaments function as signals affecting the behavior of the opposite sex, in which case the sensory characteristics of the opposite sex exert selection pressure on the sexual ornament design and function (Guilford and Dawkins 1991; Endler 1992; Rowe 1999). Other sexual traits function to facilitate mate choice, copulation, or gamete transfer mechanistically, as in the case of animals' genitalia or plants' flower displays. In this case the morphology of the other sex (Eberhard 1985; Arnqvist and Rowe 2002; Dixson and Anderson 2002), or that of pollinators (Creswell 1998; Giurfa et al. 1999), exerts selection pressures on the design of the sexual trait (see Armbruster et al., Chapter 2, this volume).

Organismal traits are subject to two general kinds of selection pressures: internal and external. Internal selection is selection for the internal cohesiveness of an organism during development or function (Whyte 1965; Schlichting and Pigliucci 1998; Wagner and Schwenk 2000). Such selection typically is not sensitive to the external environment, but it is an outcome of the internal selection that determines which phenotype will experience external, or environmental, selection (Fusco 2001; Arthur 2002). Whereas the morphology of sexual ornaments might be affected mostly by external selection (e.g., by other individuals), as exemplified by low genetic correlations of sexual ornaments with other morpho-

logical structures (e.g., Preziosi and Roff 1998, see below), external selection for greater condition-dependence of sexual ornaments acts, indirectly, on the developmental aspects of the sexual ornament (Fig. 3.1). Thus, whereas the proximate target of external selection is the elaboration of sexual ornaments, the ultimate target is the underlying relationship between the expression of the ornament and condition of the organism, that is, the developmental integration of the ornament.

### Relative Importance of External and Internal Selections

While often not stated explicitly, the relative importance of internal and external processes is central to current debate on the evolution of sexual ornamentation. Some authors argue that it is the internal selection (i.e., a trait's developmental processes) that determines which morphological traits are most suitable for elaboration by sexual selection. This is because the development of a trait determines its integration into organismal functions and, thus, its condition-dependence.

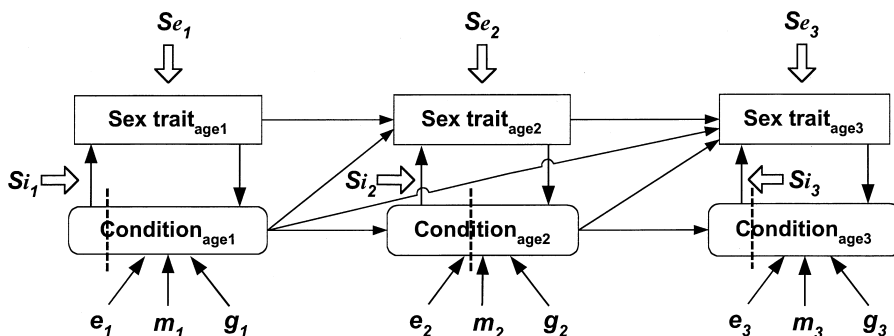


Figure 3.1 Conceptual model of the ontogeny of a sexual trait. At each age  $n$ , organismal condition depends on environmental ( $e_n$ ), maternal ( $m_n$ ), and direct genetic effects ( $g_n$ ). At each age, the allocation of overall condition to the production of a sexual trait (indicated by vertical dotted line and an arrow pointing up) is governed by internal developmental processes  $S_i$  (internal selection). At each age, the condition-dependent sexual trait (or its precursor) is a subject of external selection ( $S_e$ ). Age-specific  $S_e$  acts, indirectly, on the aspects of internal development of a sexual trait (or its precursor), i.e., on  $S_i$  as well as on the overall condition (arrow pointing down), because of the organism-wide costs of expression of the sexual trait. Depending on the similarity in the age-specific effects of  $e$ ,  $m$ , and  $g$ , organismal condition at each age can influence organismal condition at subsequent ages. Depending on the duration of development and its complexity, the sexual trait (or its precursor) at each age can affect sexual traits at subsequent ages. Thus, at each age, the sexual trait is affected by (1) direct effects of age-specific condition, (2) direct effects of the sexual trait (or its precursor) at preceding ages, (3) indirect effect of organismal condition at preceding ages on current condition and on allocation of condition to the sexual trait, and (4) indirect effect of the sexual trait (or its precursor) at preceding ages on preceding and current condition as well as on preceding and current allocations to sexual traits. At each age, limiting the number of these effects or decreasing their strength (i.e., by decreasing the overlap in the effects of  $e$ ,  $m$ , and  $g$  among ages) will decrease the condition-dependence of sexual ornamentation.

Therefore, some morphological traits may be developmentally predisposed to be targeted by sexual selection because of their existing dependence on condition or high phenotypic variability (Endler 1992; Schluter and Price 1993). Other authors suggest that greater integration into organismal functions can be accomplished easily when sexual selection favors greater trait elaboration, and a prior developmental predisposition to condition-dependence is not required (Grafen 1990; Price et al. 1993). Moreover, elaboration of sexual traits is often triggered by a sensory bias of the receiver and different traits are susceptible to this bias in different environments regardless of their initial developmental integration and condition-dependence (Endler 1992; Schluter and Price 1993).

For example, some researchers have argued that developmental properties make carotenoid-based coloration a more reliable indicator of individual condition in animals, and thus a more frequent target of sexual selection, than melanin- or non-pigment-based coloration (which have both fewer environmental components in their production and stronger developmental integration among these components (Gray 1996; Hill 1999; Badyaev and Hill 2000; McGraw and Hill 2000; Badyaev and Young 2003). Other researchers disagree strongly (Jawor and Breitwisch 2003) and there are many empirical examples supporting each point of view. There are sexually selected carotenoid indicators of condition (Kodric-Brown 1989; review in Hill 1999), melanin-based indicators of condition (Veiga and Puetra 1996; Griffith et al. 1999; Fitze and Richner 2002), non-pigment-based coloration indicators of condition (Keyser and Hill 2000), as well as examples of the lack of strong condition-dependence in and corresponding lack of sexual selection on each of these sources of ornament coloration (Seehausen et al. 1999; Dale 2000; McGraw and Hill 2000; Pryke et al. 2001).

On the other hand, developmental patterns in sexual ornaments can themselves be a product of external selection. For example, some authors suggest that external sexual selection for symmetry in bilateral sexual ornaments favors the evolution of developmental pathways that minimize developmental instability in sexual traits caused by their great exaggeration (Møller 1992a, 1992b; Thornhill 1992; Swaddle and Cuthill 1994a, 1994b; Badyaev et al. 1998; Møller and Thornhill 1998; Morris 1998). Other authors argue that asymmetry is a by-product of selection on ornament size and not itself a target of sexual selection (Evans 1993; Tomkins and Simmons 1996; Hunt and Simmons 1997; David et al. 1998; Cuervo and Møller 1999b; Breuker and Brakefield 2002).

Similarly, two prevalent explanations for the maintenance of genetic variance in sexual traits focus on the relative importance of internal and external processes for accomplishing an ornament's condition-dependence. Pomiankowski and Møller (1995) suggested that the continuous elaboration of a sexual ornament and increasing benefits of such elaboration (i.e., due to external selection) favor the accumulation of developmental modifiers that, by limiting developmental integration, facilitate production of an ever larger ornament. By contrast, Rowe and Houle (1996) suggested that selection for greater elaboration of a sexual ornament results in an increase in the number of condition-dependent (and not specific to an ornament) inputs into ever more expensive production of an ornament, thus increasing integration of the ornament with the rest of the organism. Because greater elaboration of sexual ornamentation requires both weaker devel-

opmental integration and stronger external selection, it seems that neither of these viewpoints can, by itself, fully account for the evolution of exaggerated and condition-dependent sexual ornaments. But, importantly, both theories suggest that external selection acts on aspects of developmental integration, either limiting it—by evolution of ornament-specific developmental modifiers (Pomiankowski and Møller 1995)—or strengthening it, by evolution of greater pleiotropy of ornament development (Rowe and Houle 1996; Kotiaho et al. 2001).

Here I suggest that both viewpoints are correct and that the argument over the primacy of internal development versus external selection can be resolved if one considers a likely sequence in the evolution of sexual ornaments. This is because the coevolution of male strategies to reduce condition-dependence in sexual ornaments and female strategies to restore the condition-dependence results in distinct temporal patterns of developmental integration of sexual ornaments into organismal functions (i.e., its condition-dependence).

## **Process of Organismal Integration in Sexual Ornaments**

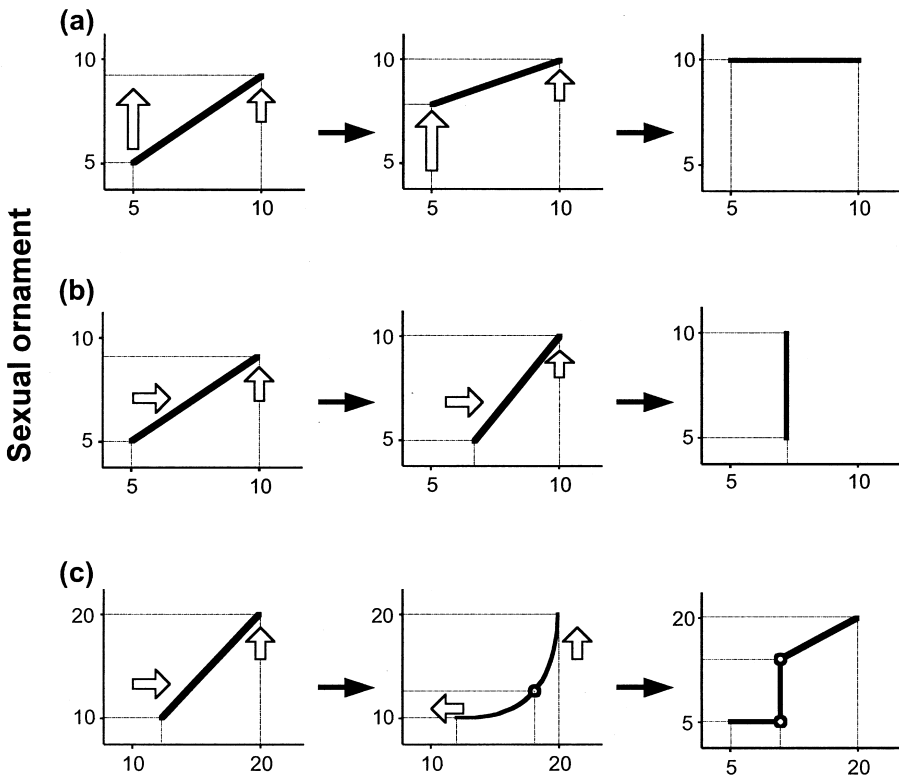
### **Directional Selection on Sexual Ornaments**

Sexual ornaments are expected to be under directional sexual selection favoring their further exaggeration (Andersson 1994). The reliability of exaggerated ornaments as indicators of individual condition is reinforced by viability costs of the expression of large ornaments (Zahavi 1975), by costs of ornament production (e.g., Arnqvist 1994), or by the processes that are proximately unrelated to either production or expression, but reflect general viability (Hamilton and Zuk 1982; Fölstad and Karter 1992, reviewed in Iwasa et al. 1991).

From an ontogenetic perspective, the greater expression of a sexual ornament in adults reflects an organism's ability to successfully accomplish the ornament's expensive development (Fig. 3.1). Two general processes produce ornament elaboration during development. First, ornament elaboration is accomplished by the increased and more efficient allocation of resources and condition so that a progressively smaller increase in condition is amplified into a progressively larger sexual ornament. Second, ornament elaboration is enabled by a decrease in the integration (i.e., by the evolution of flexible allometric relationships) between sexual ornaments and the rest of an organism. This might be accomplished by weakening the pathways that affect the ornament development. Both of these processes might ultimately reduce the developmental costs of sexual ornamentation for males and will lead to the evolution of female strategies to restore these costs.

### **Males: Evolution of Cost-Reducing Strategies in the Development of Sexual Ornaments**

Consistent directional selection for greater exaggeration of costly sexual ornaments favors the evolution of cost-reducing strategies in their development (Fig. 3.2). These strategies can be divided into two general groups. First, selection might favor the evolution of ornament-specific developmental pathways that are



**Condition cost**

Figure 3.2 Hypothetical scenarios of evolution of cost-reducing strategies in the expression of sexual ornament. (a) Selection (arrows) for cheaper expression of more exaggerated ornament is greater on the ornaments with smaller costs and favors an increase in the amount of precursor of the ornament (i.e., increase in the intercept) leading to the loss of the condition-dependent expression and to the maximum expression of sexual ornament. (b) Selection for higher condition-dependence and greater exaggeration leads to an increase in the rate and to a decrease in duration of growth of the sexual ornament ultimately resulting in the loss of condition-dependence in ornament expression. (c) Same as in (b), but disproportionately greater costs of ornament expression at intermediate condition lead to selection against expressing ornament at low condition and selection for greater expression of ornament at high condition, favoring facultative trait expression regulated by a condition-dependent developmental switch.

less dependent on organismal condition, that is, favor greater modularity of a sexual ornament’s *development*. Second, selection might favor the evolution of facultative and context-dependent expression of condition-dependent sexual ornaments, that is, favor greater modularity in a sexual ornament’s *expression*.

The initial elaboration of a condition-dependent ornament under directional selection can be accomplished by an increase in the amount of its developmental precursor or a more efficient developmental pathway (Figs. 3.2a and 3.3a), or by

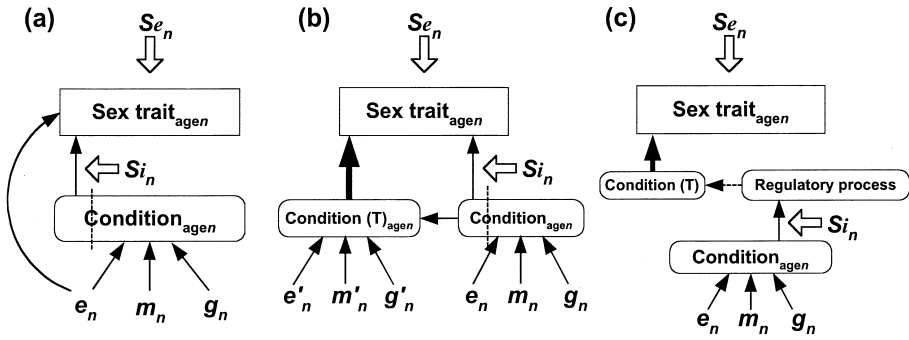


Figure 3.3 Conceptual model of cost-reducing strategies in sexual ornament expression corresponding to Fig. 3.2. (a) Increase in the amount of precursor of sexual ornament (Fig. 3.2a) is enabled by the evolution of a direct path from environment ( $e$ ) to sexual trait expression. (b) Increase in rate and decrease in duration of sexual trait development (Fig. 3.2b) is enabled by the evolution of an ornament-specific developmental pathway (T) in addition to the pathway from general condition to the ornament. (c) Facultative expression of exaggerated sexual ornament (Fig. 3.2c) is enabled by the evolution of a condition-sensitive regulatory switch activating the ornament-specific developmental pathway (T) without direct transfer of resources.

the faster growth of a sexual ornament relative to an increase in condition (Figs. 3.2b and 3.3b). In both cases, selection for cost reduction acts to modify the link between organismal condition and the production of sexual ornament in order to enable greater expression of sexual ornamentation without a corresponding change in cost.

For example, because animals cannot synthesize carotenoids, the presence of carotenoid-based pigmentation in integuments can indicate individual foraging ability (Endler 1983). Thus, females that prefer males with greater expression of carotenoid-based colors will select better-quality mates (Hill 1999). However, once female preference for carotenoid-based coloration is established, there are a number of ways for males to express greater carotenoid ornamentation at lower costs (Hill 1994; Badyaev and Duckworth 2003). For example, males can preferentially forage on carotenoid-rich foods or types of carotenoids that can be deposited directly (i.e., without energetically expensive metabolism) (Fig. 3.3a). Males can alter the expression of carotenoid ornaments by concentrating carotenoid deposition (e.g., limiting the ornamental patch size to increase the intensity of color: Hill 1993), by altering integument structures to increase the display of carotenoids already absorbed (Brush and Seifried 1968; Olson 1970), or by displaying carotenoids for a longer time after consumption (Kodric-Brown 1998). Some bird species, such as flamingoes (*Phoenicopterus* spp.), orioles (*Icterus* spp.), and scarlet ibises (*Endocimus ruber*), apparently have evolved highly specialized pathways for carotenoid metabolism (Figs. 3.2b and 3.3b) that enable them to efficiently extract and deposit carotenoids from food with minimal cost to the organism (e.g., Fox et al. 1969; Mulvihill et al. 1992; Fitze and Richner 2002).



However, female choice of an ornament does not seem to persist until complete loss of its condition-dependence (i.e., the last stages in Fig. 3.2a,b); that is, condition-dependent sexual traits rarely form multiple ornaments (Møller and Pomiankowski 1993b; Iwasa and Pomiankowski 1994; Prum 1997; Badyaev and Hill 2003; Badyaev et al. 2002). This suggests that females either switch to a more informative trait or modify their preference to restore the condition-dependence of the ornament.

Selection for greater elaboration of sexual ornaments can favor their environment- and context-dependent expression and, accordingly, in many taxa the most elaborate sexual ornaments are expressed facultatively (Figs. 3.2c and 3.3c) (Emlen and Nijhout 2000). Facultative expression might be enabled by the evolution of temporal modularity in developmental pathways of an ornament (Figs. 3.1 and 3.3c), and there are many advantages to such expression. First, it enables greater capitalization on environmental condition in production of sexual ornaments when such condition improves (i.e., by lessening the link between condition at age<sub>*n*-1</sub> and at age<sub>*n*</sub> in Fig. 3.1). A costly and exaggerated ornament might be expressed only when food is abundant, when predators are rare, or when the benefits from the trait display are the highest. Emlen and Nijhout (2000) showed that the evolution of threshold expression of sexual ornamentation is favored when the high costs of exaggerated ornaments provide increasingly lower reproductive benefits to individuals of intermediate quality and intermediate ornament elaboration (Zahavi 1975).

Evolution of temporal modularity in an ornament's developmental pathways also enables age-specific expression of sexual ornaments, which is beneficial when older individuals are able to channel more resources into production of larger traits (Hansen and Price 1995; Kokko 1997; Badyaev and Qvarnström 2002). For example, male zebra finches (*Taeniopygia guttata*) that were subjected to nutritional stress during growth were nevertheless able, when adults, to develop sexual ornamentation indistinguishable from that of control birds (Birkhead et al. 1999). Moreover, temporal modularity in ornament production can enable the sex-limited expression of an ornament for which the developmental pathways are shared between the sexes (Badyaev 2002). Thus, an exaggerated sexual ornament of a male may indicate the elaboration of a physiological process that is beneficial to both male and female offspring of this male (Kodric-Brown and Brown 1984). For example, the decoupling of carotenoid consumption, which is present in both sexes, from carotenoid deposition, which occurs only in the male's integument, might be accomplished by temporal modularity of ornament development. This enables the evolution of female preference for foraging characteristics that are important for both sexes because of immunological and other health benefits of carotenoid consumption.

Proximately, the facultative expression of sexual ornaments might be enabled by the decoupling of organismal condition from the ornament-specific developmental pathways (Figs. 3.2c and 3.3c; Badyaev and Duckworth 2003). Eventually, the interaction between an organism and an ornament-specific developmental pathway might occur without the transfer of resources and thus might not represent a continuous tradeoff (Fig. 3.3c). Instead, the interaction between an organism and ornament development can be mediated by threshold-like regulatory

mechanisms (e.g., hormones; see Emlen and Nijhout 2000 for examples in insects) in which development of an ornament is triggered by the release of resource-level sensitive hormones, but without the actual material transfer. Once this mechanism is in place, differences in costs and benefits of ornament expression between environments can lead to rapid evolution of threshold sensitive controls (such as the degree and timing of sensitivity to hormones) without corresponding changes in the rules of allocation of resources to sexual traits (Moczek and Nijhout 2002). In contrast, in species where thresholds are governed by condition, environmental induction of trait development modifies actual allocation of resources to a sexual trait and comes at the expense of overall organismal condition (Radwan et al. 2002). In addition, hormone-sensitive thresholds can enable sex-limited and age-limited expression of an indicator of a process that is shared between the sexes or across ages (see above, Badyaev 2002). However, the evolution of complete modularity in facultatively expressed sexual ornaments might be rare because sexual ornaments often require prolonged development and female choice will favor greater temporal integration of sexual ornamentation.

#### Females: Evolution of Cost-Restoring Strategies in the Development of Sexual Ornaments

Females' mate choice should favor maintenance of condition-dependence in male sexual ornaments (Fig. 3.4). First, female choice might favor the evolution of amplifiers of quality within sexual ornaments. Second, females might base their choice on within-ornament traits that are necessary for ornament maintenance and production, but not directly related to the established pathways of ornament elaboration. Finally, females might base their preference on complex sexual ornaments or ornaments that require prolonged development, because these ornaments better summarize individual condition and are less likely to be produced by developmental pathways that are independent of males' condition.

Within-ornament amplifiers of condition-dependence in sexual ornamentation can increase the precision of females' discrimination among males' ornaments (Fig. 3.4). For example, tail markings and pigment-free spots are more common in birds with longer tails (Hasson 1989; Fitzpatrick 1998). Such markings make tail feathers more susceptible to abrasion and to damage by parasites and thus can reveal individual quality in species in which females prefer males with longer tails, but where individual variation in the condition-dependence of tail length itself might be reduced (Fitzpatrick 1998, 1999). Amplifiers of condition may take the form of displays, such as in the dark-eyed juncos (*Junco hyemalis*) where the expression of condition-dependent melanin spots is reinforced by dynamic plumage displays of males (J. A. Hill et al. 1999). Similarly, in birdsongs, narrow-frequency bandwidth notes are strongly amplified by transmission through dense vegetation, and this environment-enhanced transmission increases the efficiency of male song in attracting a female (Slabbekoorn et al. 2002).

In the song of some birds, different elements are more difficult to produce than others. For example, the duration of pauses between the syllables and the time a male is able to maintain a maximum sound amplitude during rapid frequency modulations is limited by the costs of song production (e.g., Lambrechts 1996;

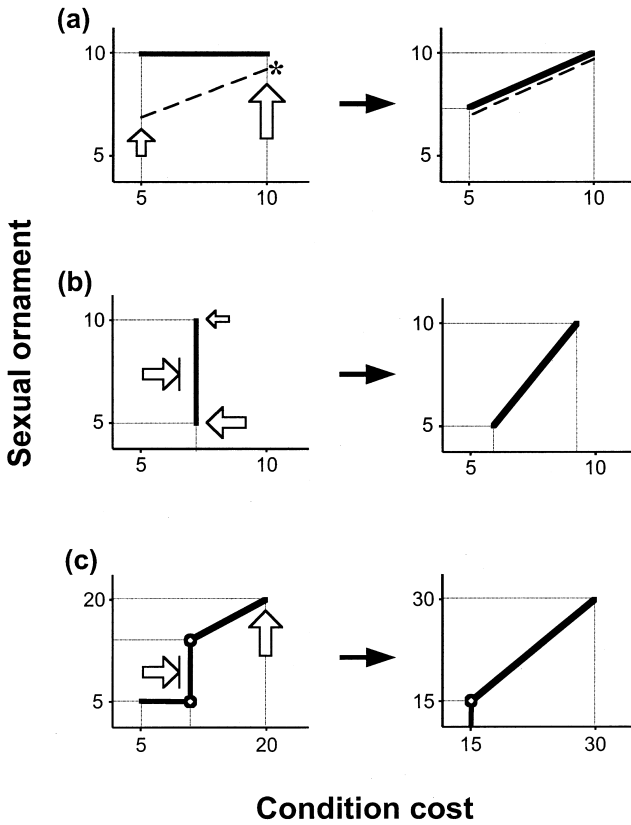


Figure 3.4 Hypothetical scenarios of evolution of strategies to restore condition-dependence in sexual ornaments (corresponding to Fig. 3.2). (a) Female preference (vertical arrows) for the within-ornament features, such as morphological amplifiers or behavioral displays—(shown by dashed line and an asterisk), exaggeration of which is not related to the established pathways of ornament elaboration, but that are necessary for ornament expression (Fig. 3.2a). Female preference for greater exaggerated ornaments of individuals in higher condition leads to a restoration of condition-dependence of an ornament. (b) Female preference for greater condition-dependence of an ornament (right-pointing arrow) in combination with a greater selection for a decrease in condition-dependence of smaller ornaments (due to their reduced benefits and higher costs; larger lower arrow), restores the condition-dependence of an ornament (Fig. 3.2b). (c) As in (b), but selection for greater condition-dependence of the threshold itself in combination with selection for greater exaggeration increases the slope between the ornament and the condition at the large values of ornamentation (Fig. 3.2c).

Podos 1997) and delivery (e.g., Richards and Wiley 1980; Badyaev and Leaf 1997). A recent study of dusky warblers (*Phylloscopus fuscatus*) showed that females have stronger preference for a male's ability to produce these particularly costly elements (e.g., maintenance of high sound amplitude) than for other song structures (Forstmeier et al. 2002; see also Vallet et al. 1998).

Similarly, fluctuating asymmetry (random developmental deviations from perfect symmetry in bilateral structures) in sexual ornaments can amplify the condition-dependence of development and production of exaggerated sexual ornaments. Female preference can favor greater integration of ornament development with organismal functions by targeting asymmetry itself (Fig. 3.4). For example, accomplishing symmetry of floral sexual displays in plants often requires organism-wide (i.e., not trait-specific) integration (Conner and Sterling 1996; Creswell 1998). Continuous female preference for an ornament that is both exaggerated and integrated into organismal functions may ultimately produce a negative relationship between fluctuating asymmetry of an ornament and ornament elaboration (Møller and Pomiankowski 1993a). However, this relationship is only expected at the advanced stages of ornament elaboration. For example, in wild turkeys (*Meleagris gallopavo*), the relationship between the asymmetry of right and left tarsal spurs and mean spur length was distinct between young and older males (Badyaev et al. 1998). The relationship was negative only in older males that attained near-maximum spur length and experienced strong sexual selection on spur length and asymmetry. The asymmetry was not related to spur size in young males that did not participate in mating and had shorter spurs.

Sexual ornaments are often expressed only late in ontogeny, but may require prolonged development. Long-growing and long-lasting ornaments thus better reflect an individual's average condition than ornaments the development and expression of which is shorter and less integrated. For example, although the ability to produce complex songs in birds is not expressed until adult stages, it is dependent on the precise development of brain structures and neural pathways necessary for song learning (Nowicki et al. 1998). An individual's ability to buffer nutritional stress during the development of song-related brain nuclei might be reflected in the ability to produce complex songs at adult stages. Thus, a female preference for more complex male songs might translate into a preference for individuals that are in higher condition and health over the life span (Nowicki et al. 2000). Similarly, the expression of a sexual ornament, a wattle, in adult ring-necked pheasants (*Phasianus colchicus*) reflected nutritional condition early in life. Males that were raised under nutritional stress showed lesser development of wattle at subsequent ages (Ohlsson et al. 2002). In wild turkeys, tarsal spurs that grow continuously throughout life were a better indicator of an individual long-term condition and viability than feather beards that grow mostly during older ages (Badyaev et al. 1998). An interesting example of displays that have a relatively short expression but prolonged development is the lifelong advancement to the center of leks in the black grouse (*Tetrao tetrix*) (Kokko et al. 1998, 1999). Proximity to center of the lek is costly to achieve and maintain, and males at the center of leks are preferred by females.

Female preference favors male ornaments that are closely linked to individual condition, but because male condition and the benefits that females receive are specific to the environment, different aspects of male condition are important to different females in different environments (Wedekind 1994; Qvarnström 2001; Badyaev and Qvarnström 2002). Moreover, a consistent female preference for higher elaboration of condition-dependent ornaments is accompanied by the evolution of male strategies to reduce the cost of such elaboration (Fig. 3.2). A

combination of female preference for different aspects of male condition and male strategies to weaken developmental integration in sexual ornamentation, should favor the evolution of composite sexual ornaments whose components are linked to different organismal processes and can reliably reflect condition across a wide range of environments. Here I outline one hypothetical scenario of how a combination of male and female strategies can produce a sexual ornament that is both integrated into organismal functions and sufficiently flexible to allow for greater elaboration. There are three main stages (Fig. 3.5).

### Stage 1: Selection for Greater Exaggeration of Sexual Ornaments

Initial female selection of a male's sexual ornament favors traits with greater detectability and high phenotypic variation (Guilford and Dawkins 1991; Endler 1992; Schluter and Price 1993). Thus, traits that have weaker developmental integration with other traits and traits with greater environmental components in their development or expression (such as displays dependent on ambient light or diet-dependent pigmentation) may be predisposed to be targeted and elaborated by sexual selection. Once a trait is targeted, female preference for both cheaper and more efficient ways to discriminate among potential mates and for displays with stronger condition-dependence should favor larger expression and greater individual variation in the male's sexual ornament (Fig. 3.5). Initially, selection for greater elaboration of sexual display favors its greater condition-dependence, strengthening and expanding the existing links between ornament and condition (Rowe and Houle 1996). Eventually, greater integration with organismal functions increases the phenotypic variance in the sexual ornament and thus limits the effectiveness of external selection to accomplish progressively stronger condition-dependence (Price et al. 1993; see below).

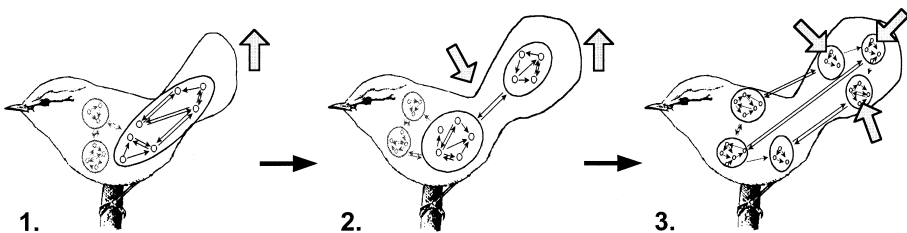


Figure 3.5 Conceptual illustration of the evolution of modularity in sexual ornaments. Small circles and thin arrows within drawings indicate individual physiological processes and their interactions. Large ellipses indicate modules of these processes. Large arrows illustrate external selection. Stage 1: Selection favors greater exaggeration of sexual traits, leading to decrease in their integration with organismal functions. Stage 2: Selection favors both further exaggeration of a sexual ornament (that is increasingly produced by ornament-specific pathways) and greater integration of ornament-specific pathways into organismal functions. Stage 3: Different components of the sexual ornament reflect different organismal processes and are selected in different environments producing a composite and dynamic sexual ornament. See text for discussion.

Selection for greater ornament exaggeration is selection against the developmental pathways that limit variation in sexual ornamentation (Møller and Pomiankowski 1993a; Pomiankowski and Møller 1995). Thus, the disruption of developmental integration of sexual ornaments leads not only to greater variation in ornament size but also to an increase in developmental abnormalities associated with ornament production. For example, the initial increase in the exaggeration of a sexual ornament during the transition from a monogamous to a polygynous mating system in birds was accompanied by an increase in both variation in ornament size and in fluctuating asymmetry of the ornaments (Cuervo and Møller 1999a, 2001). Similarly, in several insect species, directional selection on the size of a sexual ornament was accompanied by an increase in its fluctuating asymmetry, indicating disruption of developmental pathways of ornament production (Hunt and Simmons 1997; Civetta and Singh 1998; David et al. 1998; Breuker and Brakefield 2002). Importantly, at this stage, an increase in fluctuating asymmetry is ornament-specific, that is, developmental mistakes arise from a disruption of ornament production, not from the costs of ornament elaboration to the organism. For example, in birds ornamental feathers typically have higher phenotypic variation and greater fluctuating asymmetry than non-ornamental feathers (Alatalo et al. 1988; Møller and Hoglund 1991; Pomiankowski and Møller 1995; Cuervo and Møller 2001). Moreover, there is often no correlation between developmental instability of ornamental and non-ornamental feathers, suggesting that developmental mistakes are trait-specific and not due to organism-wide costs (Cuervo and Møller 1999b).

Overall, at this stage, selection for greater exaggeration of sexual ornamentation results in weakening the integration of the ornament with the rest of the organism (Fig. 3.5).

### Stage 2: Selection for Greater Condition-Dependence of Exaggerated Sexual Ornaments

As a by-product of weakening developmental integration that accompanies selection for greater exaggeration of a sexual ornament, the ornament becomes progressively less informative about processes other than those exclusively involved in its production (Fig. 3.5). Cost-reducing strategies of ornament elaboration facilitate the formation of ornament-specific developmental pathways and further decrease the dependence between ornament expression and organismal condition. An important consequence of weaker condition-dependence is a decrease in phenotypic variation in ornament expression within a population (Price et al. 1993; Rowe and Houle 1996; Fig. 3.5).

A set of female strategies to counterbalance a decrease in phenotypic variance and condition-dependence of male ornaments favors both greater expression of the ornament and its greater condition-dependence (Figs. 3.4 and 3.5). This is selection strengthening the link between ornament expression and the rest of the traits of an organism. At this stage, however, the developmental pathways of exaggerated sexual ornaments have acquired some independence from the organism's condition (Fig. 3.5). Thus, selection for their greater condition-dependence is likely to capitalize on the general costs that well-elaborated ornaments now

impose on the entire organism (i.e., organism-wide costs of trait elaboration; Fig. 3.4b).

For example, great elongation of tail feathers or greater asymmetry in tail feathers leads to an organism-wide compensation for both the size of sexual ornaments and their asymmetry (Evans 1993; Evans et al. 1994). Male barn swallows (*Hirunda rustica*) with greatly elongated but asymmetrical tail feathers undergo compensatory muscle development, providing an example of organism-wide compensation for a by-product of great elaboration in sexual ornaments (Møller and Swaddle 1997, p.181). Similarly, individual plants of higher physiological quality had greater developmental stability in flower structures and produced more symmetrical flowers (Møller 1996). In horned beetles, the diversification of sexually selected horns is facilitated by within-species costs that the most exaggerated expression of horns imposes on other traits of the developing organism (Emlen 2001).

Consequently, condition-dependence in the developmental pathways of a sexual ornament can be acquired or lost as a result of selection. For example, populations of the collared flycatcher (*Ficedula albicollis*) differ in condition-dependence of the forehead patch size—a sexually selected plumage ornament—despite the similarity in additive genetic variance and phenotypic variance of this sexual trait across populations (Qvarnström 1999; Hegyi et al. 2002).

Overall, at this stage, selection for stronger condition-dependence of a sexual ornament favors an increase in integration of the sexual ornament into organismal functions (Fig. 3.5). The condition-dependence favored at this stage is largely due to general viability costs imposed by an ornament and only to a small degree due to costs of specific ornament-producing pathways.

### Stage 3: Selection for Complex Sexual Ornaments: Greater Expression and Process-Dependence

As expression of a sexual ornament becomes progressively more integrated into organismal functions, some components of a sexual ornament may reflect specific organismal processes better than others (Wedekind 1992; Fig. 3.5). Selection by female choice is expected to be stronger on components of a sexual ornament that are more relevant locally, that is, better indicate male performance under local environmental conditions (Wedekind 1994; Zuk and Johnsen 1998; Badyaev et al. 2001; Calkins and Burley 2003). Also, the benefits of preference for some features of the male phenotype may differ between females; that is, benefits can be context- and individual-specific (Jang and Greenfield 2000; Qvarnström 2001; reviewed in Badyaev and Qvarnström 2002). Furthermore, selection across variable environments will favor different aspects of ornament elaboration (Brooks and Couldridge 1999; Day 2000), ultimately resulting in lower integration among ornament components and greater integration of components of an ornament with organismal processes that most strongly affect their production (Figs. 3.5 and 3.6).

Stability of composite and condition-dependent sexual ornaments might be maintained by multiple inputs of resources and energy (Johnstone 1995) and by more efficient recognition of a composite ornament by a female (Brooks and

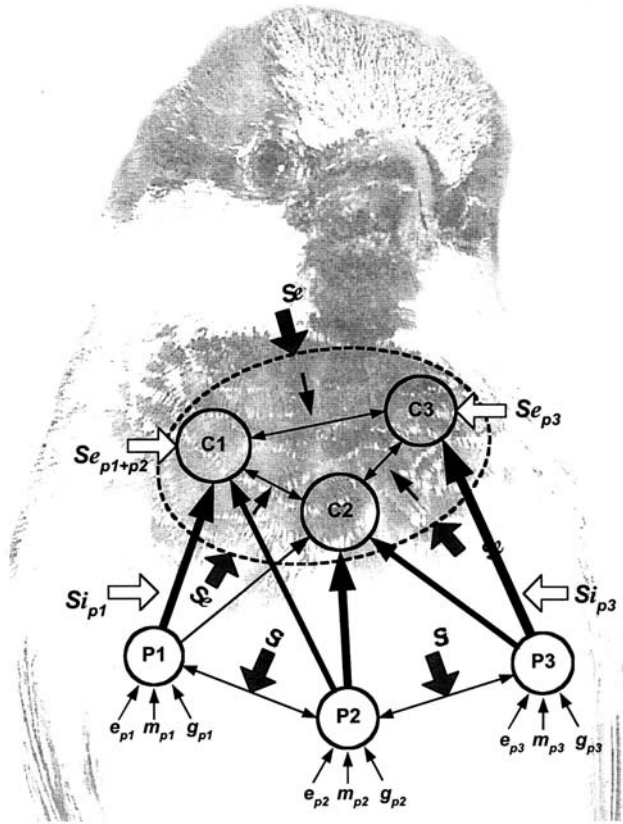


Figure 3.6 Conceptual illustration of the development and maintenance of a composite sexual ornament. Each of the components of the ornament (C1, C2, and C3; e.g., hue, area, and pattern) are mainly affected by one physiological process (P1, P2, and P3). Some organismal processes affect more than one ornamental component (e.g., P2 affects C1 and C2), and some ornamental components are affected by more than one organismal process (e.g., C1 is affected by P1 and P2). External selection acting on individual components of an ornament, proximately acts on the internal processes that produce them (e.g.,  $Se$  on C1 acts on P1 and P2 and on the allocation of P1 and P2 to the production of C1, i.e., on  $Si_{p1}$  and  $Si_{p2}$ ). External selection ( $Se$ ) acting on the entire ornament, proximately acts on the developmental and functional interactions (double-headed arrows) of ornamental components. Internal selection on the coordination of organismal performance ( $Si$ ) acts on the interactions among physiological processes. Composite sexual ornament is produced and maintained by a combination of developmental and functional integration of its components.

Couldridge 1999; Rowe 1999; Fig. 3.6). For example, carotenoid-based ornamentation of house finches requires a coordination of multiple processes associated with carotenoid consumption, digestion, transportation, and deposition (Fig. 3.7). Each of these processes has different costs in different environments: environmental variation in carotenoid-rich food affects consumption, gut parasite infestation affects digestion, and availability of oils in food affects deposition of lipid-soluble



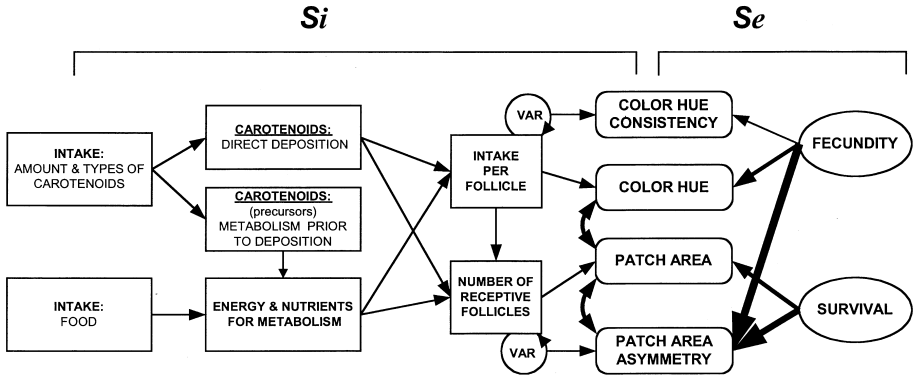


Figure 3.7 Internal (*Si*) and external (*Se*) selection on the components of the carotenoid-based sexual ornament in the house finch. Carotenoid pigments can be either ingested directly or metabolized from suitable carotenoid precursors. Direct use of dietary pigments moves carotenoids along the top of the figure and avoids most dependence of body condition, whereas use of carotenoids metabolized from dietary precursors leads to greater dependence on the energy and health state of the individual. Thus, condition-dependence of individual components of carotenoid ornamentation varies across environments. Thickness of arrows illustrates observed intensity of fecundity and survival selections on individual components of an ornament in the Montana population. Different episodes of external selection act on different components of ornament producing variable patterns of functional integration across environments. Double-headed arrows show observed patterns of developmental integration between ornamental components. Note that, for example, whereas hue and area are developmentally integrated, this integration is not maintained by external selection (modified from Badyaev et al. 2001).

carotenoids into plumage (Brush and Power 1976; Hill and Montgomerie 1994; Thompson et al. 1996). However, despite environmental variation in the degree of condition-dependence of each of these processes (Hill et al. 2002) and corresponding variation in female choice of different components in different environments, production of carotenoid-based sexual ornaments requires some degree of integration among these pathways, thus maintaining some developmental interdependence among the ornament components across environments (Badyaev et al. 2001; Fig. 3.7).

The composite nature of sexual ornaments can be maintained by the requirements of sexual display expression and function, that is, its functional integration (Fig. 3.6). Both ornament-specific and general pathways may be needed for sexual ornament expression and function and this can maintain its complex structure. For example, complex vocalizations of male treefrogs (Hylidae) consist of a combination of highly variable “dynamic” features, production of which is costly, and “static” features that are required to accomplish species-specific patterns of vocalizations or needed to produce “dynamic” features of a song (Gerhardt 1991; Murphy and Gerhardt 2000; see review in Wiley 2000). Greater exaggeration of antler size in cervids might favor the development of additional processes that maintain antler integration (such as within-antler branching patterns or coordi-

nation of antler weight on each side of the body). Similarly, greater developmental stability of complex feather ornaments in birds may be maintained by compensatory within-trait integration of growth (Aparicio and Bonal 2002).

Overall, a combination of (1) distinct patterns of selection on individual components of a condition-dependent sexual ornament, (2) partially independent development of these components, and (3) stabilizing selection on the whole sexual ornament, should favor the evolution of composite sexual ornaments whose components reliably reflect the condition of an entire organism across a wide array of environments (Figs. 3.5 and 3.6).

### Meeting the Expectations: Empirical Patterns in Sexual Ornaments

The expected outcome of the evolutionary processes outlined above is that sexual ornaments should have (1) weaker developmental integration with the rest of the organism to enable greater exaggeration at lower cost; (2) greater functional integration and modularity to enable faster and more precise response to changes in external selection; and (3) weaker genetic integration (coinheritance) with the rest of the organismal traits and weaker evolutionary integration between components of an ornament. Taken together, these patterns should produce sexual ornaments that are highly sensitive to environmental variation, variable within and between populations, and have high rates of evolutionary diversification compared to nonsexual traits. Here I review empirical support for these expectations.

#### Weaker Developmental Integration

Weaker developmental integration of sexual traits with the rest of an organism and the associated greater sensitivity to environmental variation is well documented. For example, in many species of carnivores and primates, canine teeth play an important role in sexual displays. These teeth are often under directional sexual selection for greater length, and sexual dimorphism in canines is common (Kay et al. 1988; Manning and Chamberlain 1993; Badyaev 1998). A defining feature of canines is the lack of occlusion—a correspondence in tooth cusp patterns and position between upper and lower jaw—which is present in other types of dentition in these species and is necessary for food processing. The lack of constraints imposed by the needs of occlusion during ontogeny is a powerful force behind canine development, evolution, and extensive diversification among mammals. Weaker integration of canines with the rest of the dentition leads to their highly variable growth rates and patterns both among closely related species and even between the sexes (Schwartz and Dean 2001). In grizzly bears (*Ursus arctos horribilis*) and in lowland gorillas (*Gorilla gorilla*), less developmentally integrated canines are under directional selection for increase in males and are sexually dimorphic, whereas more functionally and developmentally integrated premolar and molar teeth are under stabilizing selection and are not different between the sexes (Manning and Chamberlain 1993, 1994; Badyaev 1998). Following strong

environmental stress, size variation, developmental abnormalities, and fluctuating asymmetry strongly increased in weakly integrated canine dentition in both species, whereas the variation and developmental stability of well-integrated premolar and molar dentition was only weakly affected (Manning and Chamberlain 1993, 1994; Badyaev 1998). Similarly, in peccaries (Tyassuidae), the weakening of developmental integration of several skull traits with neighboring structures led to rapid elaboration and greater sexual dimorphism in these structures as well as to their greater diversification among species (Wright 1993; see also Badyaev and Foresman 2000).

Numerous studies have documented that weak developmental control of elaboration of sexual traits leads to their greater environmental sensitivity (reviewed in Møller and Swaddle 1997). For example, administering antihelminthic medicine to infected reindeer (*Rangifer tarandus*) had a greater effect on size and asymmetry of less developmentally integrated antlers compared to more integrated skeletal structures (Fölstad et al. 1996). Size and asymmetry of antlers in fallow deer (*Dama dama*) were more responsive to changes in environmental condition than more developmentally integrated skeletal traits (Putman et al. 2000). Similarly, stress had a stronger effect on size and asymmetry of weakly integrated and sexually selected traits in horned beetles (*Onthophagus taurus*) and stalk-eyed flies (*Cyrtodiopsis dalmanni*) compared to nonsexual traits (Hunt and Simmons 1997; David et al. 1998).

In many insect groups, highly variable allometric relationships between exaggerated sexual ornaments and other body traits are enabled by the close dependence of these allometric relationships on environmental variation (Emlen and Nijhout 2000). Consequently, lower developmental integration of exaggerated sexual ornaments with the organism may be responsible for their faster evolution and greater diversification in a number of insect groups (Simmons and Tomkins 1996; Emlen 2000; Baker and Wilkinson 2001; Moczek and Nijhout 2002).

The effect of weak developmental integration on variability and diversification in sexual ornaments is clearly illustrated by contrasting developmental properties of carotenoid-based and melanin-based ornaments of animals, especially of birds and fishes. Because more precursors of carotenoid-based pigmentation have to be acquired from the environment, carotenoid coloration is more dependent on environmental variation than melanin-based ornamental coloration (Endler 1983; Hill 1999; Badyaev and Hill 2000). Environments differ in amount and quality of carotenoid precursors (Grether et al. 1999; Hill et al. 2002), resulting in environmental variation in the amount of metabolism that the consumed carotenoids have to undergo before deposition (Fig. 3.7). Moreover, there are few constraints on carotenoid deposition: the presence of lipid-soluble carotenoids in integument is enabled by the presence of oil or fat there (Brush 1978). Because of the flexible pattern of deposition, carotenoid-based ornaments rarely form clearly delineated patterns of coloration, instead mostly producing patches of variable color with amorphous borders.

In contrast, melanin-based ornamentations have strong developmental and genetic integration of production and deposition. Melanins are synthesized during amino acid metabolism, specifically by a breakdown of tyrosine under the enzyme tyrosinase, and most of the precursors required for this synthesis have limited

environmental or diet-dependence (Fox 1976), although detailed studies are rare (e.g., Murphy and King 1987). Melanin deposition in integuments depends on the duration of melanocyte activity, on the interaction of the melanocyte with the epidermis, and, in some taxa, on concerted interactions among different melanocytes, and these processes are under precise developmental and genetic control (see reviews in Price and Pavelka 1996; Seehausen et al. 1999; Badyaev and Hill 2000; Jawor and Breitwisch 2003). Consequently, melanin-based pigmentation commonly forms complex coloration patterns such as regular spots, stripes, streaks, and clearly delineated caps and bars. Comparative studies suggest that a strong, and invariant with the degree of elaboration (Badyaev and Young 2003), developmental integration of melanin-based pigmentation has an important effect on historical patterns of its elaboration (Price and Pavelka 1996). The effect of differences in developmental integration of carotenoid and melanin ornaments on their variability and diversification is seen in cardueline finches—a group of birds that possess both kinds of ornamentation. In these birds, carotenoid ornaments have greater evolutionary lability and diversification (Gray 1996; Badyaev and Hill 2000), higher variation among environments both within and among species (Hill 1993; Badyaev et al. 2002), and greater response to stress both within and among species (Badyaev and Ghalambor 1998; McGraw and Hill 2000), compared to melanin-based ornaments.

This, however, does not mean that melanin-based ornaments are poor indicators of condition. Instead, their greater integration into multiple organismal functions make them, in a sense, better indicators of the organismal condition. It is exactly because of the multiple controls of their development that melanin-based sexual ornaments rarely achieve a level of variability and environmental sensitivity comparable to that of carotenoid-based ornamentation: stronger developmental integration of melanin coloration constraints its elaboration. Additional mechanisms, such as behavioral displays or development stability, often amplify the condition-dependence of melanin ornaments, and these amplifiers are often under selection for further elaboration (Møller et al. 1996; Fitzpatrick 1998; Hill et al. 1999).

### Greater Functional Integration

Weaker developmental integration of sexual ornaments with the rest of an organism, which enables their greater elaboration, is accompanied by their greater functional integration, which results in their greater and faster diversification.

Copulatory structures in many animal groups provide examples of composite sexual traits in which components of different developmental origins are under external selection that favors their greater functional integration (Eberhard et al. 1998; Arnqvist and Rowe 2002; Kopp and True 2002). For example, abdominal lobes in male sepsid flies (Sepsidae) are used to stimulate females during copulation (Eberhard 2001). Strong female preference for exaggeration of these traits in combination with a diverse developmental origin of their components and their close functional integration, results in both exaggeration and diversification of abdominal lobes in sepsid flies (Eberhard 2001; see also Kopp and True 2002 for similar results in *Drosophila*). Similarly, studies of primates revealed that external

genital anatomy, especially penile morphology, is extremely diverse and differs markedly among closely related species and subspecies (e.g., Anderson 2000). For example, distal structures, such as keratinized spines and plates on genitalia, play an important role in female choice in these species (Dixson 1987), and the complexity and evolutionary diversification of distal penile structures is greater in species with a higher intensity of sexual selection (Dixson and Anderson 2002). Overall, weak developmental integration with other organismal traits, a modular structure, and close functional integration of genital components favored by external selection, enables these structures to achieve both rapid exaggeration and precision in their morphological evolution (reviewed in Eberhard 1985; Dixson and Anderson 2002).

In flowering plants that depend on pollinators, selection favors the evolution of structures that enable both a greater attraction of pollinators (which requires greater exaggeration) and a better mechanistic fit between pollinators and flower structures (which requires greater functional integration between flower parts) (Berg 1960; see also Armbruster et al., Chapter 2, this volume). Consequently, stabilizing selection on flower structure is often consistent with the patterns of functional integration favored by pollinator morphology (Giurfa et al. 1999; see Eberhard et al. 1998 for a similar result in copulatory structures). Stronger functional integration within structures of flowers, but low integration between flowers and the rest of a plant, may enable faster and more precise change in flower morphology in order to track the morphology of pollinators (Berg 1960; Conner and Sterling 1996). When selection pressures imposed by pollinators are not consistent (e.g., due to their variable morphologies), selection may favor weaker functional integration among flower parts to enable greater variability (Armbruster et al. 1999).

In the cockroach *Nauphoeta cinerea*, males produce a sex pheromone that consists of many chemical components (Moore 1997). Whereas each of the individual components is under directional selection by different functions and has a different developmental origin (Moore and Moore 1999; Moore et al. 2001), the entire composition of the pheromone is under stabilizing selection (Moore 1997). Similarly, a remarkable structural similarity in complex courtship song among fourteen species of oropendolas despite distinct selection on its components might be accomplished by the need for functional integration of song production (Price and Lanyon 2002). Overall, functional integration of a sexual trait, despite its diverse developmental origins, maintains its stability and composite nature (Gerhardt 1991; Wedekind 1994; Moore 1997; Moore and Moore 1999; Seehausen et al. 1999; Murphy and Gerhardt 2000; Badyaev et al. 2001; Fig. 3.7).

### Weaker Evolutionary and Genetic Integration

Weaker developmental integration of condition-dependent components of sexual ornaments may account for their weak genetic and evolutionary integration. Price (2002) found that the patterns of co-inheritance of sexual displays in avian hybrids show a historical hierarchy of evolutionary lability that roughly corresponds to the genetic and developmental integration in sexual displays.

Ornaments that were affected by fewer genetic factors or developmental pathways (such as color variants) showed higher evolutionary lability (see also Price 1996; Badyaev and Hill 2003; Price and Bontrager 2001). Traits with more integrated development (such as feather structures) showed intermediate lability and diversification, whereas the most complex, long-developing, and pleiotropic sexual displays (such as flight displays) showed the strongest evolutionary integration and stability and persisted throughout multiple hybridization events. Seehausen et al. (1999) analyzed evolution of color patterns in relation to their developmental and functional properties in more than 700 cichlid species. They found that a distinct developmental origin and weak developmental integration of components of sexual coloration resulted in their high evolutionary lability. Interestingly, conserved patterns of coloration were maintained across species by the similarity in selection for greater functional integration of color components (e.g., selection for better environmental matching of color patterns) and not by developmental integration. In cardueline finches, the components of sexual ornamentation that showed the highest within-species variability, also varied the most among species along an ecological gradient (Badyaev 1997). In male oropendolas, complex structural features of courtship song were retained across multiple speciation events, whereas song components that were less integrated with the rest of the song and were more susceptible to environmental variation showed the highest evolutionary lability (Price and Lanyon 2002; see also Slabbekoorn and Smith 2002). Similarly, Wiens (2000) found that complex behavioral displays were more constant, whereas display morphology, such as coloration, varied extensively among species of lizards (see Irwin 1996 for review).

Several studies documented weaker genetic integration of sexual traits with the rest of the organism—a pattern consistent with their greater functional integration despite distinct developmental origins. Saetre et al. (2002) documented reduced recombination rates among loci determining components of sexual plumage ornamentation (plumage color, collar area, and forehead patch height) in two species of *Ficedula* flycatchers compared to nonsexually selected plumage traits. Sex linkage, high genetic integration of the sexual ornament's multiple components, and weak genetic integration with other organismal traits contributed to reduced within-species polymorphism and high segregation between flycatcher species (Saetre et al. 2002; see also Ranz et al. 2003 and review in Reinhold 1998). Similarly, Preziosi and Roff (1998) found weak genetic integration between copulatory structures of the water strider (*Aquarius remigis*) and the rest of the organismal traits. These patterns are in close correspondence with the rapid evolution of these traits across taxa (Arnqvist and Rowe 2002).

### **Ultimate Integration of Sexual Ornaments: “Mating Phenotype”**

Investment into sexual ornaments and investment in mate choice are parts of reproductive allocation of an entire organism and thus are subject to both life-history tradeoffs and the effects of the environment in which breeding occurs. Context- and environment-dependence in the expression of sexual ornaments

(which is enabled by their developmental modularity), and in the preference for these ornaments, favor the evolution of reproductive strategies that maximize an organism's reproductive success under variable conditions of breeding (Gross 1996; Höglund and Sheldon 1998; Badyaev and Qvarnström 2002).

Facultative expression of sexual ornamentation (Fig. 3.2) facilitates the evolution of alternative condition-dependent reproductive tactics (Gross 1996; Emlen and Nijhout 2000), and the decision to adopt a particular suite of reproductive behaviors might be phenotypically indicated by the elaboration of a sexual trait. For example in the horned beetle, males employ different reproductive tactics depending on the size of their horns. Large males use their larger horns in direct competition with other males over access to females, whereas small males avoid direct competition with other males by sneaking into female nesting tunnels—a behavioral tactic facilitated by their smaller horns (Emlen 1997). In the mite *Sancassania berlesei*, expression of a most beneficial morph of sexual ornament for a given colony density is accomplished by sensitivity of sexual trait development to a pheromone whose concentration depends on colony density (Radwan et al. 2002).

In the house finch, males with different elaboration of condition-dependent sexual ornamentation adopt a distinct set of parental behaviors (Badyaev and Hill 2002; Duckworth et al. 2003). What is indicated by the elaboration of sexual ornamentation differs between finch populations, but in each one, females base their choice of male parental behaviors on the elaboration of the male's sexual ornamentation. Thus, female choice favors hormonally mediated “functional integration” of male sexual behaviors and male sexual ornamentation. Similarly, composite sexual ornaments can enable more efficient assortative mating (Wedekind 1992; Tregenza and Wedell 2000), thus influencing further elaboration of sexual ornaments. Therefore, to fully understand the evolution of sexual displays, we need to study the entire mating phenotype which includes the functional integration of morphology and behavior for both sexes.

In conclusion, two major, conceptually inspired, approaches to the study of morphological evolution—relative importance of internal and external processes and the evolution of morphological integration—are mostly overlooked in studies of sexual ornamentation. Yet these concepts are central to understanding the evolution of sexual ornamentation and the mechanisms of sexual selection. Moreover, because investment into sexual ornaments is a part of the reproductive strategy of the entire organism, the evolution of sexual displays should be considered in the context of the performance of the entire organism and organism's interactions. Recent synthesis of the sexual selection theory explicitly recognizes the evolutionary continuum of the mechanisms by which sexual selection operates and, on a population level, firmly places sexual selection in the framework of life-history evolution (Gross 1996; Höglund and Sheldon 1998; Badyaev and Qvarnström 2002; Kokko et al. 2002). However, the consequences of the continuum in the mechanisms of sexual selection for the evolution of sexual displays and ornamentation are not well understood. The perspective outlined here, with specific focus on the evolution of development and morphological integration, may provide a useful framework for understanding the evolution of sexual ornamentation.

*Acknowledgments* I thank R. Duckworth, M. Pigliucci, K. Preston, E. Snell-Rood, and R. Young for discussion and comments, and the National Science Foundation (DEB-0075388, DEB-0077804, and IBN-0218313) for funding this work.

### *Literature Cited*

- Alatalo, R. V., J. Hoglund, and A. Lundberg. 1988. Patterns of variation in tail ornament size in birds. *Biological Journal of the Linnean Society* 34:363–374.
- Anderson, M. J. 2000. Penile morphology and classification of bushbabies (subfamily Galagoninae). *International Journal of Primatology* 21:815–830.
- Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society* 17:375–393.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Aparicio, J. M., and R. Bonal. 2002. Why do some traits show higher fluctuating asymmetry than others? A test of hypotheses with tail feathers of birds. *Heredity* 89:139–144.
- Armbruster, W. S., V. S. Di Stilio, J. D. Tuxill, T. S. Flores, and J. L. V. Runk. 1999. Covariance and decoupling of floral and vegetative traits in nine Neotropical plants: a re-evaluation of Berg's correlation-pleiades concepts. *American Journal of Botany* 86:39–55.
- Arnqvist, G. 1994. The cost of male secondary sexual traits: developmental constraints during ontogeny in a sexually dimorphic water strider. *American Naturalist* 144:119–132.
- Arnqvist, G., and L. Rowe. 2002. Antagonistic coevolution between the sexes in a group of insects. *Nature* 415:787–789.
- Arthur, W. 2002. The emerging conceptual framework of evolutionary developmental biology. *Nature* 415:757–764.
- Badyaev, A. V. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behavioral Ecology* 8:675–690.
- Badyaev, A. V. 1998. Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears. *Behavioral Ecology* 9:339–344.
- Badyaev, A. V. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution* 17:369–378.
- Badyaev, A. V., and R. A. Duckworth. 2003. Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird. *Journal of Evolutionary Biology* 16:1065–1076.
- Badyaev, A. V., and K. R. Foresman. 2000. Extreme environmental change and evolution: stress-induced morphological variation is strongly concordant with patterns of evolutionary divergence in shrew mandibles. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267:371–377.
- Badyaev, A. V., and C. K. Ghalambor. 1998. Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches. *Oikos* 82:319–324.
- Badyaev, A. V., and G. E. Hill. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society* 69:153–172.
- Badyaev, A. V., and G. E. Hill. 2002. Parental care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. *Behavioral Ecology* 13:591–597.
- Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to history and current selection. *Annual Reviews of Ecology and Systematics* 34:27–49.
- Badyaev, A. V., and E. S. Leaf. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk* 114:40–46.



- Badyaev, A. V., and A. Qvarnström. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *Auk* 119:301–310.
- Badyaev, A. V., and R. L. Young. 2003. Complexity and integration in sexual ornamentation: an example with carotenoid and melanin plumage pigmentation. *Evolution and Development*. In press.
- Badyaev, A. V., W. J. Etges, J. D. Faust, and T. E. Martin. 1998. Fitness correlates of spur length and spur asymmetry in male wild turkeys. *Journal of Animal Ecology* 67:845–852.
- Badyaev, A. V., G. E. Hill, P. O. Dunn, and J. C. Glen. 2001. “Plumage color” as a composite trait: developmental and functional integration of sexual ornamentation. *American Naturalist* 158:221–235.
- Badyaev, A. V., G. E. Hill, and B. V. Weckworth. 2002. Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. *Evolution* 56:412–419.
- Baker, R. H., and G. S. Wilkinson. 2001. Phylogenetic analysis of sexual dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae). *Evolution* 55:1373–1385.
- Berg, R. L. 1960. The ecological significance of correlation pleiades. *Evolution* 14:171–180.
- Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266:385–390.
- Breuker, C. J., and P. M. Brakefield. 2002. Female choice depends on size but not symmetry of dorsal eyespots in the butterfly *Bicyclus anynana*. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269:1233–1239.
- Brooks, R., and V. Couldridge. 1999. Multiple sexual ornaments coevolve with multiple mating preferences. *American Naturalist* 154:37–45.
- Brush, A. H. 1978. Avian pigmentation. Pp. 141–161 in A. H. Brush, ed. *Chemical Zoology*. Academic Press, New York.
- Brush, A. H., and D. M. Power. 1976. House finch pigmentation: carotenoid metabolism and the effect of diet. *Auk* 93:725–739.
- Brush, A. H., and H. Seifried. 1968. Pigmentation and feather structure in genetic variants of the Gouldian finch, *Poephila gouldiae*. *Auk* 85:416–430.
- Calkins, J. D., and N. Burley. 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Animal Behaviour* 65:69–81.
- Civetta, A., and R. S. Singh. 1998. Sex and speciation: genetic architecture and evolutionary potential of sexual vs nonsexual traits in the sibling species of the *Drosophila melanogaster* complex. *Evolution* 52:1080–1092.
- Conner, J. K., and A. Sterling. 1996. Selection for independence of floral and vegetative traits: evidence from correlation patterns in five species. *Canadian Journal of Botany* 74:642–644.
- Creswell, J. E. 1998. Stabilizing selection and the structural variability of flowers within species. *Journal of Botany* 81:463–473.
- Cuervo, J. J., and A. P. Møller. 1999a. Ecology and evolution of extravagant feather ornaments. *Journal of Evolutionary Biology* 12:986–998.
- Cuervo, J. J., and A. P. Møller. 1999b. Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system. *Biological Journal of the Linnean Society* 68:505–529.
- Cuervo, J. J., and A. P. Møller. 2001. Components of phenotypic variation in avian ornamental and non-ornamental feathers. *Evolutionary Ecology* 15:53–72.
- Dale, J. 2000. Ornamental plumage does not signal male quality in red-billed queleas. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267:2143–2149.
- David, P., A. Hingle, D. Greig, A. Rutherford, A. Pomiankowski, and K. Fowler. 1998. Male sexual ornament size but not asymmetry reflects condition in stalk-eyed flies. *Proceedings of Royal Society of London Series B: Biological Sciences* 265:2211–2216.
- Day, T. 2000. Sexual selection and the evolution of costly female preferences: spatial effects. *Evolution* 54:715–730.

- Dixson, A., and M. Anderson. 2002. Sexual selection and the comparative anatomy of reproduction in monkeys, apes, and human beings. *Annual Review of Sex Research* 12:121–144.
- Dixson, A. F. 1987. Observations on the evolution of genitalia and copulatory behaviour in male primates. *Journal of Zoology* 213:423–443.
- Duckworth, R. A., A. V. Badyaev, and A. F. Parlow. 2003. Males with more elaborated sexual ornamentation avoid costly parental care in a passerine bird. *Behavioral Ecology and Sociobiology*. In press.
- Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA.
- Eberhard, W. G. 2001. Multiple origins of a major novelty: moveable abdominal lobes in male sepsid flies (Diptera: Sepidae), and the question of developmental constraints. *Evolution and Development* 3:206–222.
- Eberhard, W. G., B. A. Huber, R. L. Rodriguez, R. D. Briceno, I. Salas, and V. Rodriguez. 1998. One size fits all? Relationship between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* 52:415–431.
- Emlen, D. J. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology* 41:335–341.
- Emlen, D. J. 2000. Integrating development with evolution: a case study with beetle horns. *BioScience* 50:403–418.
- Emlen, D. J. 2001. Costs and the diversification of exaggerated animal structures. *Science* 291:1534–1536.
- Emlen, D. J., and H. F. Nijhout. 2000. The development and evolution of exaggerated morphologies in insects. *Annual Reviews in Entomology* 45:661–708.
- Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes* 9:173–190.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139:S125–S153.
- Evans, M. R. 1993. Fluctuating asymmetry and long tails: the mechanical effects of asymmetry may act to enforce honest advertisement. *Proceedings of the Royal Society of London Series B: Biological Sciences* 253:205–209.
- Evans, M. R., T. L. F. Martins, and M. P. Haley. 1994. The asymmetrical cost of tail elongation in red-billed streamertails. *Proceedings of the Royal Society of London Series B: Biological Sciences* 256:97–103.
- Fitze, P. S., and H. Richner. 2002. Differential effect of a parasite on ornamental structures based on melanins and carotenoids. *Proceedings of Royal Society of London Series B: Biological Sciences* 13:401–407.
- Fitzpatrick, S. 1998. Birds' tails as signaling devices: markings, shape, length, and feather quality. *American Naturalist* 151:157–173.
- Fitzpatrick, S. 1999. Tail length in birds in relation to tail shape, general flight ecology and sexual selection. *Journal of Evolutionary Biology* 12:49–60.
- Fölstad, I., and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603–622.
- Fölstad, I., P. Arneberg, and A. J. Karter. 1996. Parasites and antler asymmetry. *Oecologia* 105:556–558.
- Forstmeier, W., B. Kempenaers, A. Meyer, and B. Leisler. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269:1479–1485.
- Fox, D. L. 1976. *Avian Biochromes and Structural Colors*. University of California Press, Berkeley.
- Fox, D. L., V. E. Smith, and A. A. Wolfson. 1969. Carotenoid selectivity in blood and feathers of lesser (Africa) Chilean and Greater (European) flamingos. *Comparative Biochemical Physiology* 23:225–232.
- Fusco, G. 2001. How many processes are responsible for phenotypic evolution? *Evolution and Development* 3:279–286.

- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour* 42:615–635.
- Giurfa, M., A. Dafni, and P. R. Neal. 1999. Floral symmetry and its role in plant-pollinator systems. *International Journal of Plant Sciences* 160:S41–S50.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Gray, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *American Naturalist* 148:453–480.
- Grether, G. F., J. Hudon, and D. F. Millie. 1999. Carotenoid limitation of sexual coloration along an environmental gradient in guppies. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266:1317–1322.
- Griffith, S. C., I. P. F. Owens, and T. Burke. 1999. Environmental determination of a sexually selected trait. *Nature* 400:358–360.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11:92–98.
- Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42:1–14.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- Hansen, T. F., and D. K. Price. 1995. Good genes and old age: do old mates provide superior genes? *Journal of Evolutionary Biology* 8:759–778.
- Hasson, O. 1989. Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proceedings of the Royal Society of London Series B: Biological Sciences* 235:383–406.
- Hegyi, G., J. Torok, and L. Toth. 2002. Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. *Journal of Evolutionary Biology* 15:710–719.
- Hill, G. E. 1993. Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). *Biological Journal of the Linnean Society* 49:63–89.
- Hill, G. E. 1994. Trait elaboration via adaptive mate choice: sexual conflict in the evolution of signals of male quality. *Ethology, Ecology, and Evolution* 6:351–370.
- Hill, G. E. 1999. Mate choice, male quality, and carotenoid-based plumage coloration: a review. *Proceedings of the XXII International Ornithological Congress, Durban*, 1654–1668.
- Hill, G. E., and R. Montgomerie. 1994. Plumage colour signals nutritional condition in the house finch. *Proceedings of the Royal Society of London Series B: Biological Sciences* 258:47–52.
- Hill, J. A., D. A. Enstrom, E. D. Ketterson, V. J. Nolan, and C. Ziegenfus. 1999. Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behavioral Ecology* 10:91–96.
- Hill, G. E., C. Y. Inouye, and R. Montgomerie. 2002. Dietary carotenoids predict plumage coloration in wild house finches. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269:1119–1124.
- Höglund, J., and B. C. Sheldon. 1998. The cost of reproduction and sexual selection. *Oikos* 83:478–483.
- Hunt, J., and L. W. Simmons. 1997. Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behavioral Ecology and Sociobiology* 41:109–114.
- Irwin, R. E. 1996. The phylogenetic content of avian courtship display and song evolution. Pp. 234–252 in E. P. Martins, ed. *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, New York.
- Iwasa, Y., and A. Pomiankowski. 1994. The evolution of mate preferences for multiple sexual ornaments. *Evolution* 48:853–867.
- Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences. II. The handicap principle. *Evolution* 45:1431–1442.

- Jang, Y., and M. D. Greenfield. 2000. Quantitative genetics of female choice in an ultrasonic pyramid moth, *Achroia grisella*: variation and evolvability or preference along multiple dimensions of the male advertisement signals. *Heredity* 84:73–80.
- Jawor, J. M., and R. Breitwisch. 2003. Melanin ornaments, honesty, and sexual selection. *Auk* 120:249–265.
- Johnstone, R. A. 1995. Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology* 177:87–94.
- Kay, R. F., J. M. Playcan, K. E. Glander, and P. C. Wright. 1988. Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology* 77:385–397.
- Keyser, A. J., and G. E. Hill. 2000. Structurally based plumage coloration is an honest signal of quality in male Blue Grosbeaks. *Behavioral Ecology* 11:202–209.
- Kodric-Brown, A. 1989. Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. *American Naturalist* 124:309–323.
- Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. *American Zoologist* 38:70–81.
- Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist* 124:309–323.
- Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41:99–107.
- Kokko, H. 1998. Should advertising parental care be honest? *Proceedings of the Royal Society of London Series B: Biological Sciences* 265:1871–1878.
- Kokko, H., J. Lindstrom, R. V. Alatalo, and P. T. Rintamaki. 1998. Queuing for territory position in the lekking black grouse (*Tetrao tetrix*). *Behavioral Ecology* 9:376–383.
- Kokko, H., P. T. Rintamaki, R. V. Alatalo, J. Höglund, E. Karvonen, and A. Lundberg. 1999. Female choice selects for lifetime lekking performance in black grouse males. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266:2109–2115.
- Kokko, H., R. Brooks, J. M. McNamara, and A. I. Houston. 2002. The sexual selection continuum. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269:1331–1340.
- Kopp, A., and J. R. True. 2002. Evolution of male sexual characters in the Oriental *Drosophila melanogaster* species group. *Evolution and Development* 4:278–291.
- Kotiaho, J. S., L. W. Simmons, and J. L. Tomkins. 2001. Towards a resolution of the lek paradox. *Nature* 410:684–686.
- Lambrechts, M. M. 1996. Organization of birdsong and constraints on performance. Pp. 305–321 in D. E. Kroodsma and E. H. Miller, eds. *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, Ithaca, NY.
- Manning, J. T., and A. T. Chamberlain. 1993. Fluctuating asymmetry, sexual selection and canine teeth in primates. *Proceedings of the Royal Society of London Series B: Biological Sciences* 251:83–87.
- Manning, J. T., and A. T. Chamberlain. 1994. Fluctuating asymmetry in gorilla canines: a sensitive indicator of environmental stress. *Proceedings of the Royal Society of London Series B: Biological Sciences* 255:189–193.
- McGraw, K. J., and G. E. Hill. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267:1525–1531.
- Moczek, A. P., and H. F. Nijhout. 2002. Developmental mechanisms of threshold evolution in a polyphenic beetle. *Evolution and Development* 44:252–264.
- Møller, A. P. 1992a. Female swallows show preference for symmetrical male sexual ornaments. *Nature* 357:238–240.
- Møller, A. P. 1992b. Patterns of fluctuating asymmetry in weapons: evidence for reliable signaling of quality in beetle horns and bird spurs. *Proceedings of the Royal Society of London Series B: Biological Sciences* 248:199–206.

- Møller, A. P. 1996. Developmental stability of flowers, embryo abortion, and developmental selection in plants. *Proceedings of the Royal Society of London Series B: Biological Sciences* 196:53–56.
- Møller, A. P., and J. Hoglund. 1991. Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proceedings of the Royal Society of London Series B: Biological Sciences* 245:1–5.
- Møller, A. P., and A. Pomiankowski. 1993a. Fluctuating asymmetry and sexual selection. *Genetica* 89:267–279.
- Møller, A. P., and A. Pomiankowski. 1993b. Why have birds got multiple ornaments? *Behavioral Ecology and Sociobiology* 32:167–176.
- Møller, A. P., and J. P. Swaddle. 1997. *Asymmetry, Developmental Stability, and Evolution*. Oxford University Press, Oxford.
- Møller, A. P., and R. Thornhill. 1998. Bilateral symmetry and sexual selection: a meta-analysis. *American Naturalist* 151:174–192.
- Møller, A. P., R. T. Kimball, and J. Erritzoe. 1996. Sexual ornamentation, condition, and immune defense in the house sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology* 39:317–322.
- Moore, A. J. 1997. The evolution of social signals: morphological, functional, and genetic integration of the sex pheromone in *Nauphoeta cinerea*. *Evolution* 51:1920–1928.
- Moore, A. J., and P. J. Moore. 1999. Balancing sexual selection through opposing mate choice and male competition. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266:711–716.
- Moore, A. J., P. A. Gowaty, W. G. Wallin, and P. J. Moore. 2001. Sexual conflict and the evolution of female mate choice and male social dominance. *Proceedings of the Royal Society of London Series B: Biological Sciences* 268:517–523.
- Morris, M. R. 1998. Female preference of trait asymmetry in addition to trait size in swordtail fish. *Proceedings of the Royal Society of London Series B: Biological Sciences* 265:907–911.
- Mulvihill, R. S., K. C. Parkes, R. C. Leberman, and D. S. Wood. 1992. Evidence supporting a dietary basis of orange-tipped rectrices in the cedar waxwing. *Journal of Field Ornithology* 63:212–216.
- Murphy, C. G., and H. C. Gerhardt. 2000. Mating preference functions of individual female barking treefrogs, *Hyla gratiosa*, for two properties of male advertisement calls. *Evolution* 54:660–669.
- Murphy, M. E., and J. R. King. 1987. Dietary discrimination by molting white-crowed sparrows given diets differing only in sulfur amino acid concentration. *Physiological Zoology* 60:279–289.
- Nowicki, S., S. Peters, and J. Podos. 1998. Song learning, early nutrition and sexual selection in songbirds. *American Zoologist* 38:179–190.
- Nowicki, S., D. Hasselquist, S. Bensch, and S. Peters. 2000. Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267:2419–2424.
- Ohlsson, T., H. G. Smith, L. Raberg, and D. Hasselquist. 2002. Pheasant sexual ornaments reflect nutritional conditions during early growth. *Proceedings of the Royal Society of London Series B: Biological Sciences* 269:21–27.
- Olson, E. C., and R. L. Miller. 1958. *Morphological Integration*. University of Chicago Press, Chicago.
- Olson, S. L. 1970. Specializations of some carotenoid-bearing feathers. *Condor* 72:424–430.
- Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–551.
- Pomiankowski, A., and A. P. Møller. 1995. A resolution of the lek paradox. *Proceedings of the Royal Society of London Series B: Biological Sciences* 260:21–29.

- Preziosi, R. F., and D. A. Roff. 1998. Evidence of genetic isolation between sexually monomorphic and sexually dimorphic traits in the water strider *Aquarius remigis*. *Heredity* 81:92–99.
- Price, J. J., and S. M. Lanyon. 2002. Reconstructing the evolution of complex bird song in the oropendolas. *Evolution* 56:1517–1529.
- Price, T. 1996. An association of habitat with color dimorphism in finches. *Auk* 113:256–257.
- Price, T., and A. Bontrager. 2001. Evolutionary genetics: the evolution of plumage patterns. *Current Biology* 11:R405–408.
- Price, T., and M. Pavelka. 1996. Evolution of a colour pattern: history, development, and selection. *Journal of Evolutionary Biology* 9:451–470.
- Price, T., D. Schluter, and N. E. Heckman. 1993. Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society* 48:187–211.
- Price, T. D. 2002. Domesticated birds as a model for the genetics of speciation. *Genetica* 116:311–327.
- Prum, R. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). *American Naturalist* 149:668–692.
- Pryke, S. R., S. Andersson, and M. J. Lawes. 2001. Sexual selection on multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463.
- Putman, R. J., M. S. Sullivan, and J. Langbein. 2000. Fluctuating asymmetry in antlers of fallow deer (*Dama dama*): the relative roles of environmental stress and sexual selection. *Biological Journal of the Linnean Society* 70:27–36.
- 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.
- Qvarnström, A. 2001. Context-dependent genetic benefits from mate choice. *Trends in Ecology and Evolution* 16:5–7.
- Radwan, J., J. Unrug, and J. L. Tomkins. 2002. Status-dependence and morphological trade-offs in the expression of a sexually selected character in the mite, *Sancassania berlessei*. *Journal of Evolutionary Biology* 15:744–752.
- Ranz, J. M., C. I. Castillo-Davis, C. D. Meiklejohn, and D. L. Hartl. 2003. Sex-dependent gene expression and evolution of the *Drosophila* transcriptome. *Science* 300:1742–1745.
- Reinhold, K. 1998. Sex linkage among genes controlling sexually selected traits. *Behavioral Ecology and Sociobiology* 44:1–7.
- Richards, D. G., and R. H. Wiley. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist* 115:381–399.
- Rowe, C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* 58:921–931.
- Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition-dependent traits. *Proceedings of the Royal Society of London Series B: Biological Sciences* 263:1415–1421.
- Saetre, G.-P., T. Borge, K. Lindroos, J. Haavie, B. C. Sheldon, C. Primmer, and A.-C. Syvanen. 2002. Sex chromosome evolution and speciation in *Ficedula* flycatchers. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270:53–59.
- Schlichting, C. D., and M. Pigliucci. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland, MA.
- Schluter, D., and T. Price. 1993. Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London Series B: Biological Sciences* 253:117–122.
- Schwartz, G. T., and C. Dean. 2001. Ontogeny of canine dimorphism in extant hominoids. *American Journal of Physical Anthropology* 115:269–283.

- Seehausen, O., P. J. Mayhew, and J. J. M. Van Alphen. 1999. Evolution of colour patterns in East African cichlid fish. *Journal of Evolutionary Biology* 12:514–534.
- Simmons, L. W., and J. L. Tomkins. 1996. Sexual selection and the allometry of earwig forceps. *Evolutionary Ecology* 10:97–104.
- Slabbekoorn, H., and T. B. Smith. 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 357:493–503.
- Slabbekoorn, H., J. Ellers, and T. B. Smith. 2002. Birdsong and sound transmission: the benefits of reverberations. *Condor* 104:564–573.
- Swaddle, J. P., and I. C. Cuthill. 1994a. Female zebra finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society of London Series B: Biological Sciences* 258:267–271.
- Swaddle, J. P., and I. C. Cuthill. 1994b. Preference for symmetric males by female zebra finches. *Nature* 367:165–166.
- Thompson, C. W., N. Hillgarth, M. Leu, and H. E. McClure. 1996. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *American Naturalist* 149:270–294.
- Thornhill, R. 1992. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behavioral Ecology* 3:277–283.
- Tomkins, J. L., and L. W. Simmons. 1996. Dimorphisms and fluctuating asymmetry in the forceps of male earwigs. *Journal of Evolutionary Biology* 9:753–770.
- Tregenza, T., and N. Wedell. 2000. Genetic compatibility, mate choice and patterns of parentage. *Molecular Ecology* 9:1013–1027.
- Vallet, E., I. R. Beme, and M. Kreutzer. 1998. Two-note syllables in canary songs elicit high levels of sexual displays. *Animal Behaviour* 55:291–297.
- Veiga, J. P., and M. Puetra. 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London Series B: Biological Sciences* 263:229–234.
- Wagner, G. P. 2001. *The Character Concept in Evolutionary Biology*. Academic Press, San Diego.
- Wagner, G. P., and K. Schwenk. 2000. Evolutionary stable configurations: functional integration and the evolution of phenotypic stability. *Evolutionary Biology* 31:155–217.
- Wedekind, C. 1992. Detailed information about parasites revealed by sexual ornamentation. *Proceedings of the Royal Society of London Series B: Biological Sciences* 247:169–174.
- Wedekind, C. 1994. Mate choice and maternal selection for specific parasite resistance before, during and after fertilization. *Proceedings of the Royal Society of London Series B: Biological Sciences* 346:303–311.
- Whyte, L. L. 1965. *Internal Factors in Evolution*. George Braziller, New York.
- Wiens, J. J. 2000. Decoupled evolution of display morphology and display behavior in phrynosomatid lizards. *Biological Journal of the Linnean Society* 70:597–612.
- Wiley, R. H. 2000. A new sense of complexities of bird songs. *Auk* 117:861–868.
- Wright, D. B. 1993. Evolution of sexually dimorphic characters in peccaries (Mammalia, Tyassuidae). *Paleobiology* 19:52–70.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. *Journal of Theoretical Biology* 53:205–214.
- Zuk, M., and T. S. Johnsen. 1998. Seasonal changes in the relationship between ornamentation and immune response in red jungle fowl. *Proceedings of the Royal Society of London Series B: Biological Sciences* 265:1631–1635.