

Developmental perspective on the evolution of sexual ornaments

Alexander V. Badyaev*

*Department of Ecology and Evolutionary Biology, University of Arizona,
Biosciences West, 1041 E. Lowell Street, Tucson, AZ 85721, USA*

ABSTRACT

Sexual ornaments are favoured to be both less integrated with other organismal traits for greater expression, and yet more integrated with organismal development and functions to better indicate the physiological quality of an organism. Two conceptual approaches in morphological evolution – the consideration of internal and external processes and the evolution of integration and modularity – are useful in resolving this apparent paradox, yet these approaches are mostly overlooked in studies of the development of sexual displays. Moreover, whereas recent studies have recognized the evolutionary continuum of the mechanisms by which sexual selection operates, the consequences for the evolution of development of sexual displays are not well understood. Here I suggest that the concept of morphological integration may provide a useful framework for understanding the development and evolution of sexual ornamentation.

Keywords: integration, modularity, sexual displays, sexual selection, signals.

INTRODUCTION

Paradox of an ideal sexual ornament: exaggerated yet honest

Developmental processes determine patterns of covariation among traits and thus influence direction and speed of evolution. Whereas it is widely recognized that an outcome of selection for the internal cohesiveness of an organism during development (i.e. internal selection) determines the range of phenotypes that will be subject to external selection (Schmalhausen, 1949; Whyte, 1965; Schlichting and Pigliucci, 1998), the relative importance of internal and external selection in determining evolutionary change is widely debated (Arthur, 2000, 2002; Chipman, 2001; Fusco, 2001).

The external environment might play a major role in the evolution of sexual ornaments because the selection pressures that affect their evolution are mostly due to the phenotypes of other individuals. For example, in sexual ornaments that function as signals, the sensory characteristics of the opposite sex exert selection pressures on the ornament design (Endler,

* e-mail: abadyaev@email.arizona.edu

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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; Dixson and Anderson, 2002), or that of pollinators (Creswell, 1998; Giurfa *et al.*, 1999), exerts selection pressures on the design of the sexual trait.

Whereas the ultimate target of external selection is the elaboration of sexual ornaments, the proximate target is the underlying relationship between the expression of the ornament and condition of the organism – that is, the developmental integration of the sexual ornament. For example, sexual traits are often expressed only late in ontogeny but require prolonged development, as in the case of song, where learning and production requires the precise development of song nuclei and neural pathways to produce song complexity, which is the target of sexual selection (Nowicki *et al.*, 1998).

The relative importance of internal and external processes is central to the current debate on the evolution of sexual ornamentation. Some authors argue that internal selection (i.e. a trait's developmental processes) determines which morphological traits are most suitable for elaboration by sexual selection. This is because the development of a trait determines its integration into functions of an organism and thus its condition-dependence. Therefore, some morphological traits may be developmentally predisposed for sexual selection because of their existing dependence on organismal condition (e.g. health) or high phenotypic variability (Endler, 1992; Schluter and Price, 1993). Others suggest that greater integration into organismal functions (greater condition-dependence) can be accomplished easily when sexual selection favours trait elaboration, and a prior developmental predisposition to condition-dependence is not required (Price *et al.*, 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) (Endler, 1983; Hill, 1996; Badyaev and Hill, 2000). Others disagree (Griffith and Sheldon, in press) and there are empirical examples supporting each point of view (e.g. Veiga and Puetra, 1996; Hill, 1999), 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 (e.g. Dale, 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 have suggested that external sexual selection for symmetry in bilateral sexual ornaments favours the evolution of developmental pathways that minimize developmental instability in sexual traits caused by their great exaggeration (Møller, 1992; Morris, 1998). Others argue that asymmetry is a by-product of selection on ornament size and not itself a target of sexual selection (e.g. Evans, 1993; Tomkins and Simmons, 1996).

Similarly, two prevalent explanations for the maintenance of additive genetic variance in sexual traits focus on the relative importance of internal and external mechanisms of an ornament's condition-dependence. Pomiankowski and Møller (1995) suggested that the continuous elaboration of a sexual ornament favours the accumulation of developmental modifiers that, by limiting developmental integration (interrelationships with other organismal processes during development), facilitate production of an ever larger ornament. In 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. Thus, both theories suggest that external selection acts on aspects of developmental integration, either limiting it – by the evolution of ornament-specific developmental modifiers (Pomiankowski and Møller, 1995) – or strengthening it – by multiplication of pathways involved in ornament development (Rowe and Houle, 1996).

The current debate over the primacy of external versus internal selection in the evolution of sexual ornamentation is illustrated in several unresolved paradoxes. For example, sexual traits, such as deer antlers, are under directional selection for greater expression, and this selection favours flexible allometric relationships (e.g. weaker integration) between sexual traits and the rest of the organism (Eberhard, 1985; Emlen and Nijhout, 2000). At the same time, sexual traits are thought to indicate the physiological condition and health of an individual, such that the expression of sexual traits represents a thorough summary of many organismal processes – that is, sexual traits should be involved and integrated into many organismal functions (Wedekind, 1992). This represents a paradox whereby 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, the development of sexual ornaments is expected to be well integrated in the ontogeny of an organism. To be an indicator of health, sexual ornaments need to be consistently costly to an organism (Zahavi, 1975), yet individuals that breed more than once should modify their investment of resources in the development of sexual ornamentation at each breeding bout (Kokko, 1998; Badyaev and Qvarnström, 2002). Facultative investment in sexual ornamentation should thus reduce the integration of sexual trait development with that of the rest of an organism, which will make sexual ornaments less reliable indicators of overall quality (Badyaev and Duckworth, 2003). This represents another paradox whereby greater expression of costly sexual traits favours developmental pathways that reduce the trait's condition-dependence.

The debate over the primacy of internal versus external selection can be resolved if one considers that the co-evolution of male strategies to reduce condition-dependence in sexual ornaments and of female strategies to restore that condition-dependence produces distinct temporal patterns of the developmental integration of sexual ornaments with organismal functions.

ORGANISMAL INTEGRATION OF SEXUAL ORNAMENTS

The reliability of exaggerated ornaments as indicators of individual condition is reinforced by the viability costs of the possession and maintenance of large ornaments and by the non-flexible costs of ornament production (Iwasa *et al.*, 1991). From an ontogenetic perspective, the greater expression of a sexual ornament in adults reflects an organism's ability to successfully accommodate the ornament's costly development. This can be accomplished by an increased and more efficient allocation of resources, so that a progressively smaller increase in condition is amplified into a progressively larger sexual ornament. Alternatively, ornament elaboration might be enabled by a decrease in the integration between sexual ornaments and the rest of an organism. Both of these processes reduce the developmental costs of sexual ornamentation for males and lead to the concurrent female strategies to restore these costs.

Male perspective: evolution of cost-reducing strategies in the development of sexual ornaments

Selection for greater exaggeration of costly sexual ornaments might favour the evolution of modular (i.e. ornament-specific) developmental pathways that are less dependent on organismal condition (greater modularity of an ornament's development), as well as the evolution of facultative and context-dependent expression of costly sexual ornaments (greater modularity in an 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 by a more efficient developmental pathway (Figs. 1a and 2a), or by the faster growth of a sexual ornament relative to an increase in condition (Figs. 1b and 2b). In both cases, selection for

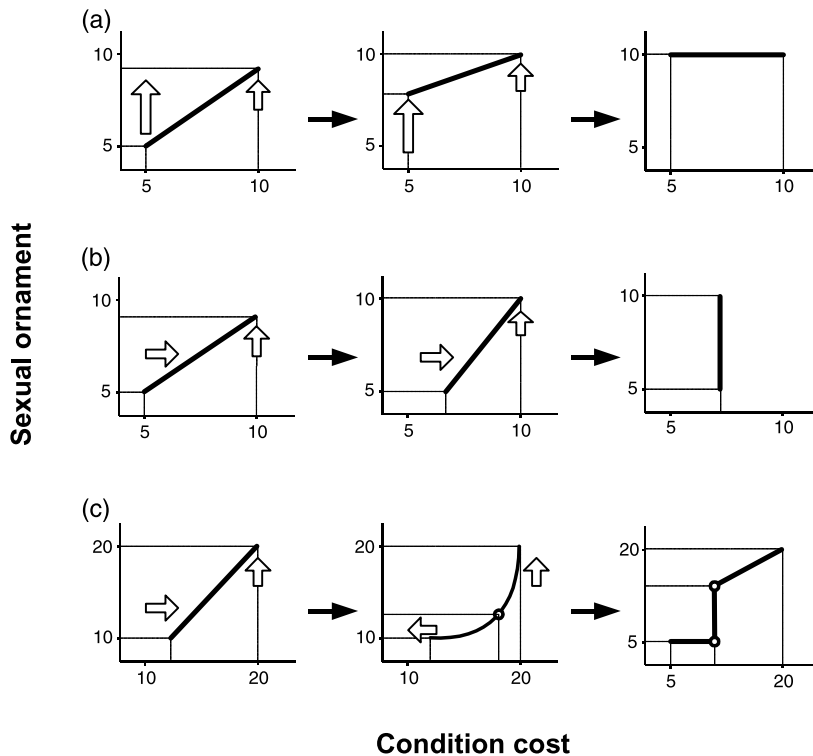


Fig. 1. Hypothetical scenarios of evolution of cost-reducing strategies in the expression of sexual ornament. (a) Selection (arrows) for cheaper expression of a more exaggerated ornament is greater on ornaments with smaller costs and favours an increase in the amount of precursor of the ornament (i.e. increase in the intercept), leading to the loss of the condition-dependent expression and to the maximum elaboration of the sexual ornament. (b) Selection for higher condition-dependence and greater exaggeration leads to an increase in the rate, and to a decrease in the duration, of growth of the sexual ornament, ultimately resulting in the loss of condition-dependence in ornament expression. (c) As in (b), but disproportionately greater costs of ornament expression at intermediate condition lead to selection against expressing the ornament at low condition and selection for greater expression of the ornament at high condition, favouring facultative trait expression regulated by a condition-dependent developmental switch.

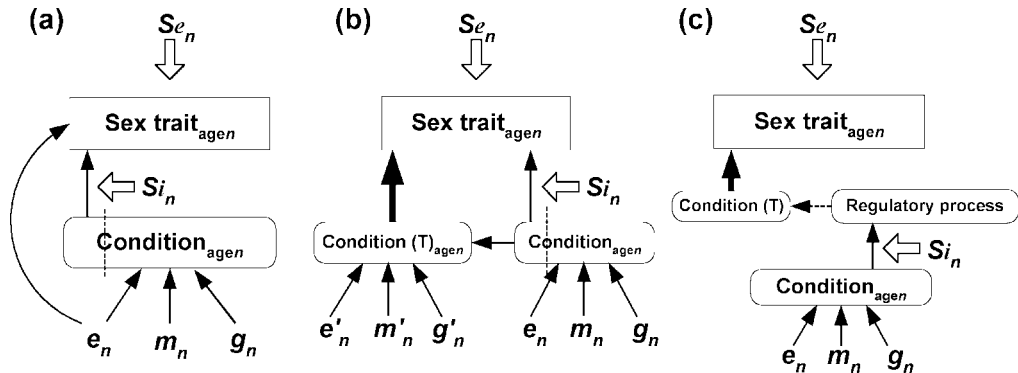


Fig. 2. Conceptual model of cost-reducing strategies in sexual ornament expression corresponding to Fig. 1. Organismal condition at age n depends on environmental (e_n), maternal (m_n) and direct genetic effects (g_n). The allocation of overall condition to the production of a sexual trait (indicated by vertical dotted line and an upward pointing arrow) is governed by internal developmental processes Si . The condition-dependent sexual trait is a subject of external selection (Se), which acts, indirectly, on the aspects of internal development of a sexual trait, i.e. on Si . (a) Increase in the amount of precursor of sexual ornament (Fig. 1a) is enabled by the evolution of a direct path from environment (e) to sexual trait expression. (b) Increase in the rate, and decrease in the duration, of sexual trait development (Fig. 1b) 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. 1c) is enabled by the evolution of a condition-sensitive regulatory switch activating the ornament-specific developmental pathway (T) without direct transfer of resources.

cost-reduction acts to modify the link between organismal condition and the production of the sexual ornament to enable greater expression of sexual ornamentation without a corresponding increase in cost.

For example, because animals cannot synthesize carotenoids, the presence of carotenoid-based pigmentation in integuments can indicate individual foraging ability and higher quality (Endler, 1983; Hill and Montgomerie, 1994; Hill *et al.*, 2002). 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, including evolving developmental pathways that deposit diet-derived pigments in sexual ornaments directly and with little processing (Fox *et al.*, 1969; Hill, 1994; Badyaev and Duckworth, 2003). For example, males can: (1) preferentially forage on carotenoid-rich foods or types of carotenoids that can be deposited directly and passively (i.e. without energetically expensive metabolism); (2) alter the expression of carotenoid ornaments by concentrating carotenoid deposition; (3) modify integument structures to increase the display of carotenoids already absorbed; (4) display carotenoids for a longer time after consumption (Brush and Seifried, 1968; Olson, 1970; Hudon, 1991; Kodric-Brown, 1998); or (5) produce a substitute red pigmentation that is visually indistinguishable from carotenoid-based pigments (Grether *et al.*, 1999) (Fig. 2a).

Selection for greater elaboration of sexual ornaments can favour their context-dependent expression and, accordingly, in many taxa the most elaborate sexual ornaments are expressed facultatively (Emlen and Nijhout, 2000). Facultative expression is enabled by

the evolution of temporal modularity in developmental pathways of an ornament (Figs. 1c and 2c), and there are several advantages to such expression. First, it enables greater capitalization on environmental condition in the production of sexual ornaments when such condition improves. 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 at their greatest.

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 the production of larger traits (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). Furthermore, temporal modularity in ornament production can enable the sex-limited expression of an ornament for which the developmental pathways are shared between the sexes. 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 (Lozano, 1994; Camplani *et al.*, 1999; Blount *et al.*, 2003).

Eventually, the interaction between an ornament-specific developmental pathway and other processes of an organism might occur without the transfer of resources and thus not represent a continuous trade-off (Fig. 2c). Instead, this interaction can be mediated by threshold-like regulatory mechanisms (e.g. hormones) in which development of an ornament is triggered by the release of resource-level sensitive hormones, but without the actual material transfer (Emlen and Nijhout, 2000; Moczek *et al.*, 2002; Radwan *et al.*, 2002).

Female perspective: evolution of cost-restoring strategies in the development of sexual ornaments

Female mate choice should favour the maintenance and strengthening of condition-dependence in male sexual ornaments (Fig. 3). Here I focus on three such strategies. First, female choice might favour the evolution of traits that amplify variation 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 developmental pathways of ornament elaboration. Finally, females might prefer complex sexual ornaments or ornaments that require prolonged growth, because these ornaments are less likely to be produced by modular and ornament-specific developmental pathways.

Within-ornament amplifiers of variation and condition-dependence in sexual ornamentation can increase the precision of a female's choice of males' ornaments (Fig. 3). For example, tail markings and pigment-free spots are more common in birds with longer tails (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

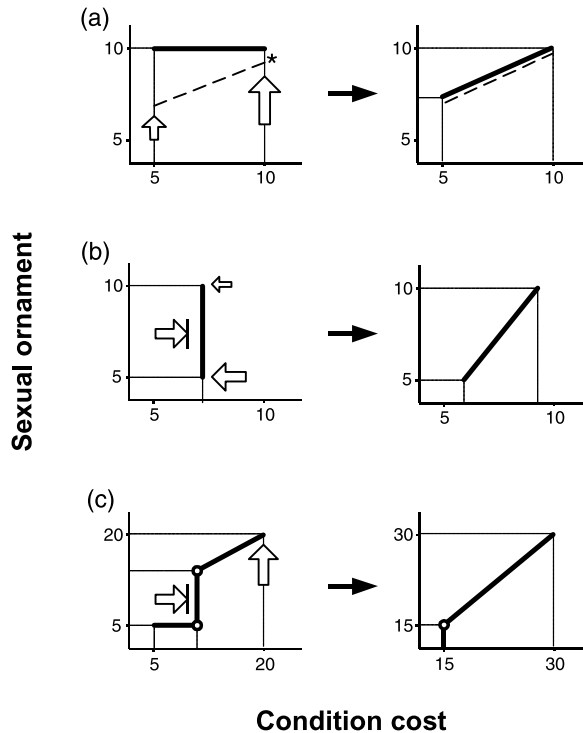


Fig. 3. Hypothetical scenarios of evolution of strategies to restore condition-dependence in sexual ornaments (corresponding to Fig. 1). (a) Female preference (vertical arrows) for the within-ornament features, such as morphological amplifiers or behavioural displays (shown by dashed line and an asterisk), the exaggeration of which is not related to the established pathways of ornament elaboration, but which are necessary for ornament expression (Fig. 1a). Female preference for more 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 (rightward pointing arrow), in combination with 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. 1b). (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. 1c).

prefer males with longer tails, but where individual variation in the condition-dependence of tail length itself might be reduced. 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 ornaments is amplified in males by dynamic display of this trait (Hill *et al.*, 1999).

Similarly, fluctuating asymmetry (random developmental deviations from perfect symmetry in bilateral structures) in sexual ornaments can amplify the condition-dependence of the development and production of exaggerated sexual ornaments. Female preference can favour greater integration of ornament development with organismal functions by targeting asymmetry itself (Fig. 3), especially in sexual traits for which bilateral

symmetry is of crucial functional importance (e.g. tail streamers in birds). For example, symmetry of floral sexual displays in plants often requires organism-wide (i.e. not trait-specific) integration (Conner and Sterling, 1996). Continuous female preference for an ornament that is both exaggerated and integrated into organismal functions should, at the advanced stages of ornament elaboration, produce a negative relationship between fluctuating asymmetry of an ornament and its elaboration (Møller and Pomiankowski, 1993). For example, in wild turkeys, *Meleagris gallopavo*, the relationship between the absolute asymmetry of tarsal spurs and spur length was negative only in older males that attained near maximum spur length and experienced strong sexual selection on spur length and asymmetry (Badyaev *et al.*, 1998).

Long-growing ornaments better reflect an individual's average life-long condition than ornaments that the development and expression of which are shorter and less integrated. For example, although the ability to produce complex songs in birds is not expressed until the adult stages, it is dependent on the precise development of brain structures and neural pathways necessary for song learning (Nowicki *et al.*, 2000). 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 in the adult stages. Thus, a female preference for more complex male songs might translate into a preference for individuals that are in better 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 reduced development of the wattle in the adult ages (Ohlsson *et al.*, 2002). An interesting example of displays that have a relatively short expression but prolonged development is the life-long advancement of males to the centre of leks in the black grouse, *Tetrao tetrix* (Kokko *et al.*, 1999). Proximity to the centre of the lek is costly to achieve and maintain, and males at the centre of leks are preferred by females.

EVOLUTIONARY CHANGES IN MODULARITY IN SEXUAL ORNAMENTS

Below I outline a hypothetical scenario of how a combination of concurrent male and female strategies can produce a sexual ornament that is both integrated into organismal functions and sufficiently flexible to allow for greater elaboration. In three main stages, a combination of (a) distinct patterns of selection on individual components of a sexual ornament, (b) developmental independence of these components, and (c) stabilizing selection on the entire sexual ornament, should favour the evolution of composite sexual ornaments whose components reliably reflect the condition of an entire organism across a wide array of environments.

Selection for greater exaggeration of sexual ornaments results in a weakening of the integration of the ornament with the rest of the organism

Female selection of a male's sexual ornament favours traits with greater detectability and high phenotypic variation (Schluter and Price, 1993). Once a trait is targeted by sexual selection, female preference for both cheaper and more efficient ways to discriminate among potential mates should favour larger expression and greater individual variation in the male's sexual ornament. Initially, selection for greater elaboration of sexual display favours

its greater condition-dependence, strengthening and expanding of the existing links between ornament and organismal condition (Rowe and Houle, 1996).

Selection for greater ornament exaggeration is selection against the developmental pathways that limit elaboration of sexual ornamentation (Møller and Pomiankowski, 1993; Pomiankowski and Møller, 1995). A good illustration of this are the disruptions of developmental integration of sexual ornaments that lead not only to greater variation in ornament size but also to an increase in developmental abnormalities associated with ornament production. This is seen in the initial increase in the exaggeration and fluctuating asymmetry of a sexual ornament during the transition from a monogamous to a polygynous mating system in birds (Cuervo and Møller, 1999), and as a consequence of directional selection on sexual ornamentation in several insect species (e.g. Hunt and Simmons, 1997).

Selection for stronger condition-dependence of a sexual ornament favours its greater developmental integration

Because of the reduction in the developmental integration that accompanies selection for greater exaggeration, the sexual ornament becomes progressively less informative about processes other than those exclusively involved in its production. Male cost-reducing strategies of ornament elaboration (Fig. 1) facilitate the formation of ornament-specific developmental pathways and further decrease ornament condition-dependence and, subsequently, a population phenotypic variation in ornament expression (Price *et al.*, 1993).

Females' counterbalancing of a decrease in condition-dependence of male ornaments favours greater expression of the ornament and its greater condition-dependence (Fig. 3), which is selection for strengthening the links between ornament expression and the rest of the organismal traits (i.e. greater developmental integration). At this stage, however, the developmental pathways of exaggerated sexual ornaments have acquired some independence from the organism's condition. 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. 3b). 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).

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 (Gerhardt, 1991; Wedekind, 1992; Moore, 1997). Selection by female choice is expected to be stronger on components of a sexual ornament that better indicate male performance under local environmental conditions. Furthermore, selection across variable environments will favour different aspects of ornament elaboration, eventually resulting in lower integration among ornament components and greater integration of components of an ornament with organismal processes that most directly affect their production (Wedekind, 1992, 1994; Badyaev *et al.*, 2001; Badyaev and Young, in press).

Table 1. Empirical patterns of morphological integration in sexual ornaments

Patterns of integration	Taxa	Specific patterns(proposed mechanisms)	References
Weak developmental integration	Hominoïd primates	Highly variable and sexually dimorphic growth of canine teeth (lack of constraints imposed by occlusion during growth)	Schwartz and Dean (2001)
	Lowland gorilla, <i>Gorilla gorilla</i> ; grizzly bear, <i>Ursus arctos</i>	Greater response to developmental stress in canines than in molariform dentition (weaker developmental integration of canines)	Manning and Chamberlain (1994), Badyaev (1998)
	Reindeer, <i>Rangifer tarandus</i> ; fallow deer, <i>Dama dama</i>	Greater change in developmental stability of antlers compared with other skeletal structures following environmental change (weaker developmental integration of antlers)	Fölstad <i>et al.</i> (1996), Putman <i>et al.</i> (2000)
	Dung beetle, <i>Onthophagus</i> ; stalk-eyed flies; earwigs, <i>Forticula</i> ; <i>Drosophila</i> flies	Faster evolution and greater diversification of sexual traits (highly variable and environmentally-dependent developmental integration between sexual traits and other body traits)	Emlen and Nijhout (2000), Baker and Wilkinson (2001)
	Passerine birds; Cardueline finches, <i>Carduelinae</i>	Faster evolution and greater within- and among-species diversification of carotenoid versus melanin sexual ornamentation (weaker developmental integration of carotenoid-based ornaments)	Gray (1996), Hill (1996), Badyaev and Hill (2000), Badyaev <i>et al.</i> (2002)
	House finch, <i>Carpodacus mexicanus</i>	Variable developmental integration among components of sexual ornamentation between populations and throughout a lifetime of birds in subsequent molts	Badyaev <i>et al.</i> (2001), Badyaev and Duckworth (2003)
	Peccaries, <i>Tyassiuidae</i>	Rapid elaboration and greater sexual dimorphism in several skull traits following weakening of their developmental integration with neighbouring structures (historical changes in developmental integration)	Wright (1993)
Greater functional integration	Sepsid flies, <i>Sepsidae</i> ; damselfly, <i>Calopterygidae</i>	Rapid exaggeration and diversification of abdominal lobes that stimulate females during copulation (greater functional integration of components of diverse developmental origins)	Eberhard (2001), Cordoba-Agular (2002)
		Rapid diversification of function in developmentally distinct genital components	

Primates	Rapid exaggeration and diversification of distal penile structures favoured by female choice (greater functional integration of genital components of diverse developmental origins)	Dixson and Anderson (2002)
Flowering plants (review)	Rapid and precise changes in floral structure in concordance with morphology of pollinators (selection for greater functional integration of flower components)	Conner and Sterling (1996), Giurfa <i>et al.</i> (1999)
Cockroach, <i>Nauphoeta cinerea</i>	Complexity of sex pheromone is maintained by selection for greater functional integration of components of distinct developmental origin	Moore (1997), Moore <i>et al.</i> (2001)
Oropendolas	Structural similarity in songs of 14 species maintained by the need of functional integration of song production	Price and Lanyon (2002)
House finch; common redpoll, <i>Carduelis flammea</i>	Close functional integration between developmentally independent ornament components illustrated by the opposite relationship between elaboration and integration in two species	(Badyaev and Young, in press)
Cichlid fish	Rapid change in coloration pattern enabled by greater functional integration of multiple components of distinct developmental origins	Seehausen <i>et al.</i> (1999)
Treefrogs, <i>Hylidae</i>	Close integration of static and dynamic components of song favoured by selection for species-specific patterns of vocalization	Gerhardt (1991), Gerhardt <i>et al.</i> (1996)
Hybrids of domestic birds	Evolutionary lability of ornaments corresponds to their genetic integration	Price (2003)
Weaker evolutionary and genetic integration with other traits		
Flycatchers, <i>Ficedula</i>	Reduced recombination rates among loci determining components of sexual plumage ornamentation (high genetic integration among ornament components and weak genetic integration with other organismal traits)	Saetre <i>et al.</i> (2002)
Water strider, <i>Aquarius remigis</i>	Weak genetic integration between copulatory structures and the rest of the organismal traits	Preziosi and Roff (1998)

EMPIRICAL PATTERNS IN SEXUAL ORNAMENTS

The expected outcome of the evolutionary processes outlined above is that sexual ornaments should have: (a) weaker developmental integration with the rest of the organism to enable greater exaggeration at lower cost; (b) greater functional integration and modularity to enable a faster and more precise response to changes in external selection; and (c) weaker genetic integration with the rest of the organismal traits and weaker evolutionary integration between components of an ornament to reflect a history of fluctuating directional selection for elaboration (Table 1). 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 with non-sexual traits.

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 (Table 1). For example, in many species of carnivores and primates, canine teeth play an important role in sexual displays and are often under directional selection for increased length (Manning and Chamberlain, 1994; Badyaev, 1998). A defining feature of canines is the lack of occlusion – a correspondence in tooth cusp patterns and position between the 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 occlusion during ontogeny is a powerful force behind extensive diversification of canines among mammals. Weaker integration of canines with the rest of the dentition leads to their highly variable growth patterns both between the sexes and among even closely related species, as well as to a higher response to environmental stress (Schwartz and Dean, 2001; see Table 1), a common pattern for sexual traits (reviewed in Møller and Swaddle, 1997; see Table 1).

The effect of developmental integration on variability and diversification in sexual ornaments is clearly illustrated by contrasting developmental properties of weakly integrated carotenoid and strongly integrated melanin ornaments of animals, especially of birds and fishes. In birds that possess both kinds of ornamentation, less integrated carotenoid ornaments have greater evolutionary lability and diversification, higher variation among environments both within and among species, and a greater response to stress both within and among species, compared with melanin-based ornaments (Gray, 1996; Hill, 1996; Badyaev and Hill, 2000; McGraw and Hill, 2000; Badyaev *et al.*, 2001; Badyaev and Young, in press; see Table 1).

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 (Table 1). For example, copulatory structures in many animal groups are composite sexual traits in which components of different developmental origins are under external selection that favours their greater functional integration (Table 1). Weak developmental integration with other organismal

traits and close functional integration of genital components enables these structures to achieve both rapid exaggeration and functional precision in their morphological evolution (Table 1).

In flowering plants that depend on pollinators, selection favours 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). Consequently, stabilizing selection on flower structure is often consistent with the patterns of functional integration favoured by pollinator morphology (Giurfa *et al.*, 1999). Stronger functional integration within the 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). Similarly, greater functional integration of developmentally independent components maintains the stability and composite nature of many acoustic and visual sexual displays (Table 1).

CONCLUSIONS

Two conceptual approaches to the study of morphological evolution – the 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 both the evolution of sexual ornamentation and the mechanisms of sexual selection. Moreover, because investment in sexual ornaments is a part of the reproductive strategy of the entire organism, the evolution of sexual displays needs to be considered in the context of the performance of the entire organism and the organism's interactions. Recent synthesis of the sexual selection theory explicitly recognizes the evolutionary continuum of the mechanisms by which sexual selection operates (e.g. Kokko *et al.*, 2002; Shuster and Wade, 2003). However, the consequences of the continuum in the mechanisms of sexual selection for the evolution of development of sexual displays and ornamentation are not well understood. The perspective outlined here, with its specific focus on the evolution of development and morphological integration, may provide a useful framework for understanding the evolution of sexual ornamentation.

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