

Colorful Phenotypes of Colorless Genotypes: Toward a New Evolutionary Synthesis of Color Displays

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Evolution of Development in Color Displays: A Need for a New Conceptual Framework

Few animal taxa rival birds in richness and diversity of color displays, and few traits have stimulated more studies of natural and sexual selection than animal coloration. Although we have some understanding of why and when such diversity is favored, we know exceptionally little about how this diversity is generated and how it evolves.

This is especially unfortunate, given that studies of color variation were central to the foundational work in quantitative genetics and evolutionary theory. Working with distinct color variants of flowers, Gregor Mendel discovered discrete and heritable segregation of color between individuals, leading him to conclude that the phenotypic differences are caused by the sorting of heritable and environmentally invariant internal factors. Observing differences among species and domestic breeds in plumage color, Charles Darwin suggested that the differences among individuals and species are caused by their fit to the external environment or to the tastes of animal breeders. A synthesis of these two great insights posited that internal factors cause variation, whereas independent external factors sort, delete, or retain these variants (Lewontin

1983). Thus, at the base of the current theory of evolution is the foundational assumption of population genetics, stating that evolutionary change is an outcome of spontaneous and random generation of genetic variation and subsequent retention and sorting of this variation by natural selection and genetic drift (Futuyma 1998). Yet this view skips a crucial step in organic evolution—production of the phenotype—and so decouples the causes of within-generation variation from the causes of among-generation variation and thus of evolution (Schmalhausen 1949; Whyte 1965; Lewontin 1983; West-Eberhard 1989; Schlichting and Pigliucci 1998; Oyama 2000; Griffiths and Gray 2001). The result is that population genetics theory, which assumes that phenotypes are direct and heritable representations of genotypes (Falconer and MacKay 1996; Graur and Li 2000), does not provide a sufficient framework for understanding the origin and evolution of phenotypes, including the formation and diversification of color displays.

At the same time, studies of animal coloration are uniquely positioned to resolve these conceptual difficulties and to contribute to the novel evolutionary synthesis that explicitly integrates the origination, variability, and evolutionary maintenance of traits. For example, current evolutionary theory assumes that developmental processes that produce a phenotype are not dependent on the selection acting on that phenotype (and thus are not “visible” to this selection). Yet many avian studies document sexual selection for greater condition- and health-dependency of color ornaments (Chapter 4), explicitly suggesting that selection can act on the underlying development of displays (Badyaev 2004a; Badyaev and Young 2004). Moreover, the assumption that phenotypic differences are generated in a predictable manner by *internal* organismal factors is violated in several types of animal pigmentation that require consumption and subsequent developmental incorporation of pigments obtained from the external environment (Brush and Power 1976; Endler 1983; Hill 1992; Knüttel and Fiedler 2001). Similarly, the environment external to the organism is invariably incorporated into avian color displays that require environmental matching (e.g., bowerbirds displaying their plumage colors against their externally collected nest objects (Plate 20, Volume 1) or manakins exposing a particular color pattern under a certain ambient light (Plate 3, Volume 1)). The crucial importance of cultural inheritance and sexual imprinting (whereby phenotypes of one generation determine patterns and direction of sexual selection in the next; Cate and Bateson 1988; Grant and Grant 1996; Irwin and Price 1999; reviewed in Odling-Smee et al. 2003), sensory bias processes in mate choice (Sargent et al. 1998; Kamo et al. 2002; Rodd et al.

2002), and the importance of prior experience in both development of and selection on sexual traits (e.g., Badyaev and Qvarnström 2002; Sockman et al. 2002; Badyaev and Duckworth 2005) further violate the notion of the independence of selection and development of the phenotype.

More generally, the failure to incorporate a developmental perspective in studies of the diversification of animal displays has left us largely unprepared to explain a great number of fascinating empirical results. For example, despite an amazing diversity of avian color patterns, there is also an equally remarkable convergence of complex pigmentation patterns among phylogenetically distinct species (Price and Pavelka 1996; Omland and Lanyon 2000; Plate 32). Apparently, once formed, these patterns can be preserved without being expressed for millions of generations, suggesting that their highly modular (i.e., context-independent) genetic and developmental organization allow these patterns to appear intact in distinct lineages. Similarly, complex sex-specific color patterns can lay dormant in the opposite sex and appear under hormonal treatment or when selection against such expression ceases (Winterbottom 1929; Kimball and Ligon 1999; Lank et al. 1999; Badyaev 2002; reviewed in Badyaev and Hill 2003). What enables such complexity to be preserved when not expressed? And how is it created in the first place? Moreover, in all pigment classes of avian coloration, there are two distinct expressions of within-species variation (Chapter 2): continuous variation and dichotomous variation, in which individuals have distinct morphs of coloration (including those related to age and sex). Are these patterns a continuum produced by the same mechanisms?

Why does color polymorphism in some species result from developmental pathways that, invariably from the external environment or the organism's state, deliver the effects of a single point mutation to the expression of color in the entire phenotype (Ritland et al. 2001; Theron et al. 2001; Nachman et al. 2003; Mundy et al. 2004; Rosenblum et al. 2004), whereas in other species, the same color phenotype is accomplished by a multitude of variable and reversible epigenetic effects of temperature (Iljin and Iljin 1930), hormonal state (West and Packer 2002), and nutrition (Brush and Power 1976; Stradi et al. 2001)? Of the many mutations in hundreds of loci that affect diverse pigmentation within species (Barsh 2001; Bennett and Lamoreux 2003), why do only a handful account for nearly all cases of polymorphism within species, populations, and even animal classes (Newton et al. 2000; Ling et al. 2003; Mundy et al. 2004)? For example, the effect of a point substitution in the melanocortin-1 receptor (MC1R) gene on the production of white/black and

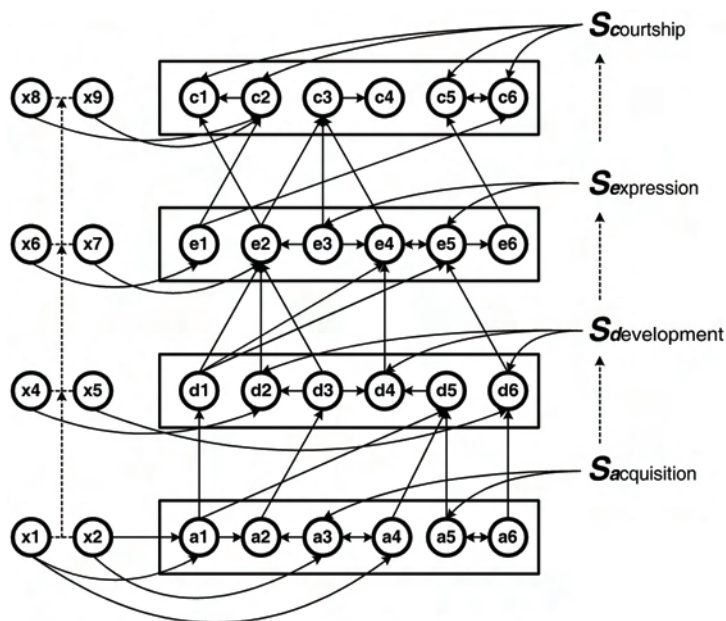


Figure 8.1. Conceptual illustration of within-phenotype color production and expression at four production stages (rectangular frames) and among individual elements (circles). Color production within a generation is a result of bottom-top interactions of elements at the stage of initial acquisition or genetic encoding (signified by a1, etc.), at the stage of development (d1, etc.), at the stage of phenotypic expression (e1, etc.), and the stage of courtship or other signaling displays that involve phenotypic expression of both color and behavior (c1, etc.). At each stage, production includes incorporation of elements external to the organism (x1, etc.), and expression of all elements within a phenotype (although not transitional pathways among them, shown by straight arrows) is subject to external selection (S). The expression of elements at each production stage consists of a combination of organismal elements at that and lower production stages, including incorporated external elements. For example, expression element e2 consists of incorporation (developmental entanglement) of external element x1 by acquisition element a1 and development elements d1 and a2, as well as d3 effects on d2, and d2 itself. External selection at each stage acts on some elements and their combinations. For example, expression of d2, d4, and d6 has fitness consequences during the stage of development. Both selection patterns and the elements of external environments (x elements) are not independent among production stages (dashed lines and arrows). Interactions among organismal elements within and between levels can be both linear and nonlinear; thus the cumulative effects of elements on one another are not additive.

black/yellow phenotypes is modular enough to persist in grafts transplanted between different animal classes (Ling et al. 2003), yet color polymorphism in congeners and even conspecifics is often produced by distinct and variable mechanisms (Barsh 1996; Hoekstra and Nachman 2003; MacDougall-Shackleton et al. 2003). Similarly, why do some bird species possess developmental processes that enable them to maintain carotenoid-based coloration in captivity despite drastic changes in diet, whereas other, often closely related species lose their coloration after the first molt (Dormidontov 1930; Stradi et al. 1997, 2001)?

Central, but implicit, in these questions is the notion that the processes and elements involved in color acquisition, encoding, development, and expression vary in their modularity—the ability to form and maintain a stable and largely independent network that retains its integration in different contexts and over evolutionary time scales (Wagner 2001; Schlosser and Wagner 2004; Callebaut and Raskin-Gutman 2005). In this chapter, I suggest that explicit consideration of the origin and inheritance of modularity and of the directionality and linearity of interactions between elements at different levels of color development (Figure 8.1) not only answers these questions, but also provides important insight into the evolution of diversity in avian color displays.

Evidence for Modularity in Encoding, Development, and Expression of Plumage Coloration

The variability and diversification of avian color displays are best understood by considering plumage ontogeny and evolution as a series of hierarchically arranged and recurrent developmental and functional modules, from feather-germ precursors to coordination of pigment distribution among follicles to complex courtship displays (Jiang et al. 1999; Chuong et al. 2000; Price 2002; Prum and Dyck 2003; Badyaev 2004b; Figure 8.1; Plate 24). Classic experiments that surgically transplanted feather follicles among body parts and individuals (Lillie and Wang 1941; Willier 1941) established the feather follicle as a module capable of normal feather morph production and pigment metabolism and uptake in a variety of contexts. For example, follicles transplanted from the embryonic wing bud of the striped mutant chicken (*Gallus gallus*) produced the striped phenotype in an unstriped host (Danfort and Foster 1929; Willier 1941; Nickerson 1944). Recent studies extended these findings by documenting remarkably conserved signaling modules at the level of the follicle and repeated co-option of early signaling pathways in distinct

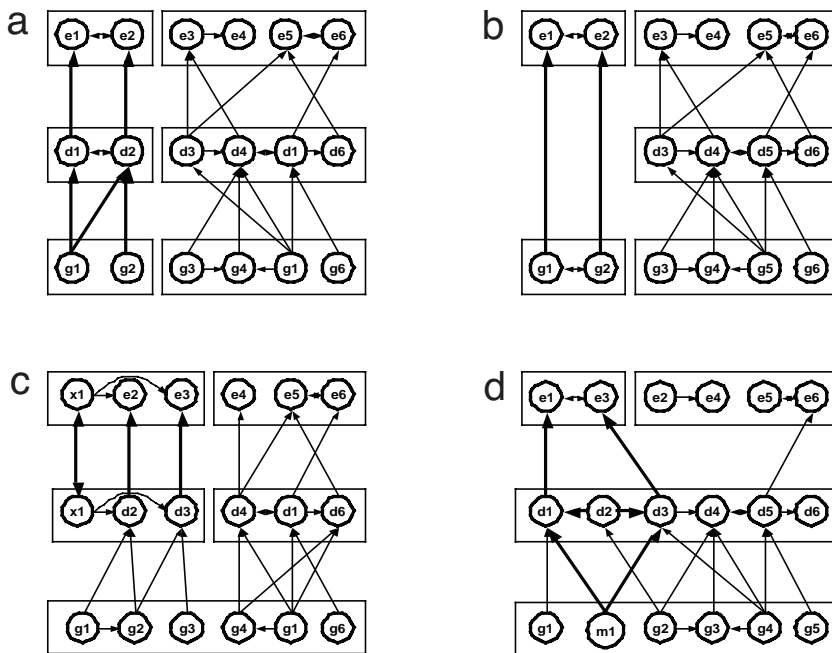


Figure 8.2. Conceptual illustration of modularity in color production across elements at three general production levels: encoding (signified by g1, etc.), development (d1, etc.), and expression (e1, etc.). (a) Modularity across all stages is produced by duplication of a pathway from g1 to d1, by strengthening pathways between d1 and d2 and e1 and e2 within stages, and by constructing pathways d1 → e1 and d2 → e2 (e.g., decoupling digestion of carotenoids from general metabolism and depositing them in integument). (b) Modularity between the encoding and expression stages is accomplished by a deletion of an intermediate stage and strengthening the pathways among elements within stages (e.g., direct/passive deposition of environmentally derived pigment into plumage, MC1R mutation of high developmental penetrance). (c) Modularity in the stages of development and expression is produced by incorporation of a shared environmental element (x1) that influences d2 and d3 at the developmental stage and e2 and e3 at the expression stage, thus producing direct paths d2 → e2 and d3 → e3 (e.g., incorporations of an environmentally derived substance such as oil that influences development of both pigment and feather structure and thus their coexpression). (d) Modularity in expression is produced by the effect of a modifier (m1) at encoding stage on expression of both d1 and d3, thus causing co-expression of e1 and e3 (e.g., influence of a modifier on early developmental effects of testosterone influencing both later expression of behavior and concurrent metabolism of melanin).

developmental contexts (Harris et al. 2002), as well as significant molecular linkage of genes encoding developmental aspects of plumage coloration (Bitgood and Somes 2003).

At first, such modularity in the encoding of early developmental pathways may not seem surprising—modularity in gene sequences (e.g., intron structure) is typical of eukaryotes and is thought to result from enhancer-independent transcription and from the versatility and complexity of developmental systems (Parthy 1999, 2003; Mattick and Gagen 2001). Yet phenotype-genotype modularity in coloration might be a highly derived outcome of selection. I suggest here that the MC1R genetic and developmental module of color production in the examples mentioned above or the effects of chromosome inversion on color morphs in some birds (Houtman and Falls 1994; Krüger et al. 2001) is an end-point of selection for the most predictable and efficient (i.e., context-independent) expression of a particular color (see below; Figure 8.2).

In any source of coloration, including carotenoid- and melanin-derived pigmentation, development of color expression can be either context-dependent (e.g., condition-dependent) or context insensitive (i.e., modular). The controversy over greater “condition dependence” of some pigments over others, especially in the behavioral ecology literature, stems from the assignment of the function (e.g., condition dependence) to a particular form (e.g., pigment in the food) prior to selection that produces (and defines) that function during development. Thus, as long as the function (here, condition dependence) is seen as pre-existing and uncoupled from a sexual ornament’s development, it does little to uncover the evolution of either condition dependence or a sexual ornament. It is not surprising, therefore, that some species with carotenoid-based ornamentation produce stable plumage color on virtually any diet, whereas the coloration of others is highly sensitive to pre-molt consumption of carotenoids. Similarly, in some species, melanin-based ornamentation is produced by environment-, context-, and sometimes taxa-invariant modular developmental processes, whereas in others, it depends on the local environment and individual health (reviewed in Badyaev 2004b). In either pigmentation type, a complete modularity in production of color (i.e., a linear representation between phenotype and genotype) is probably rare in natural systems. Genetically heritable color morphs, however, are common, especially in domestic breeds, where they can persist even in hybrids by forming intermediate patterns of color distribution and feather structures (e.g., Price 2002).

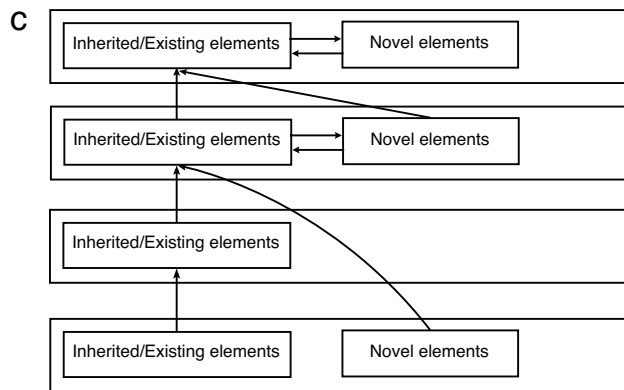
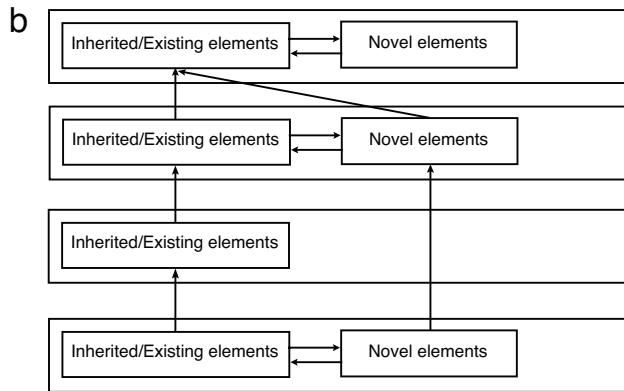
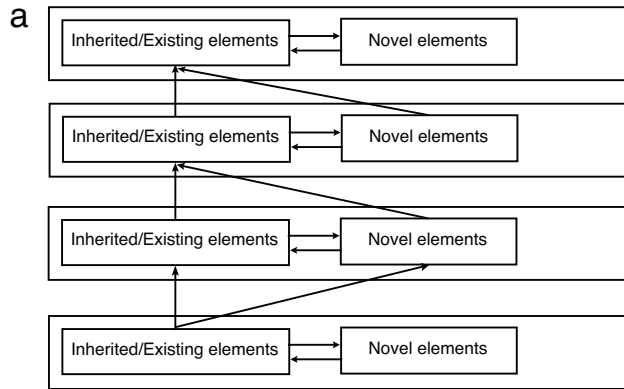
Extensive pleiotropic effects of color production on general growth and metabolism in poultry demonstrate that color production is often accomplished by recruitment of developmental pathways shared with other organismal functions (Somes 1980; Minvielle et al. 1999; Merat 2003; see also Badyaev 2005a). Because of such integration, the production of color display has to be decoupled from other organismal functions (Badyaev 2004a; Figure 8.2) to enable predictable and heritable expression of a color morph. Consequently, in most systems, modularity is confined to the late developmental stages; for example, sex- and age-specific pigmentation are accomplished at the level of the follicle and involve predictable epigenetic interactions (Punnett and Pease 1930; Somes 1971; George et al. 1981; Abdellatif 2001) rather than genetic mechanisms (Somes 2003). Late-stage regulation of melanin pattern expression may enable the historical persistence of developmental modules. Price and Pavelka (1996) hypothesized that, when the developmental module of a melanin-based pattern is formed, its phenotypic expression and retention are mediated by a switch-like sensitivity of regulatory receptors at late developmental stages. Thus, complex melanin-based coloration patterns, once formed, can appear in distant lineages without the need to construct complex developmental pathways anew, accounting for the striking similarity in complex melanin pigmentation patterns among unrelated species (Price and Pavelka 1996).

In a series of recent studies, Prum and co-workers (Prum and Williamson 2001, 2002; Prum and Dyck 2003) showed that within-feather pigmentation is produced by coordination of several basic modules of feather growth and pigment uptake (see also Jiang et al. 1999; Smyth 2003), so that almost the entire observed diversity of within-feather coloration patterns can be produced by a modification of only a few regulatory interactions between feather growth and pigment-uptake modules. Whereas phenotypic expression of each of these modules is context-independent, the regulatory interactions between them are mostly caused by diverse epigenetic and condition-dependent interactions, such as resource partitioning (Worley et al. 2003; Badyaev and Young 2004). Because such interactions are often diverse, novel, context-dependent, and non-additive, it is difficult for selection to accomplish their modification (Wagner and Mezey 2004). For example, artificial selection of poultry morphs with a goal of repeatable co-expression of a particular combination of pigmentation and feather patterns requires careful and lengthy breeding protocols that focus specifically on elimination of context-dependent and epistatic interactions among feather growth and pigment-uptake modules (Bartels 2003;

Smyth 2003). Similarly, in natural systems, sexual selection on maximum elaboration of color ornamentation acts, indirectly, on integration of developmentally distinct modules of plumage production by enhancing condition dependence in the relationships among modules (Badyaev et al. 2001; Badyaev and Young 2004). Finally, color patterns can result from hierarchical and temporal displacement and juxtaposition of several color-producing modules (e.g., carotenoid and melanin interactions at the level of follicle; Dickman et al. 1988; Maderspacher and Nusslein-Volhard 2003), although this mechanism is poorly studied in birds (Burt 1986; Badyaev and Hill 2003).

From the classical melanocyte transplant experiments to modern studies of sexual selection, the development and expression of melanin-based pigmentation in birds is often described as more modular in production and deposition than other sources of pigmentation, such as carotenoid-derived colors. Indeed, internally produced melanins can be incorporated into keratin in a highly structured fashion and often form complex patterns of plumage coloration (Jawor and Breitwisch 2003; Chapter 6, Volume 1; Plate 24). Moreover, transplants of melanocytes between embryos in poultry show that melanin synthesis and uptake is highly modular and host independent (e.g., Brumbaugh 1967). In the same breeds of poultry, however, the accumulation and distribution of melanin in follicles and feather tracts and the uptake of melanin into feathers are often regulated by complex signaling of hormones (e.g., estrogen, thyroid hormone, testosterone; George et al. 1981), as well as the effects of nutrition and temperature (Hutt 1949). Thus, in these cases, the development of melanin-based colors is modular, whereas its final expression varies across physiological and environmental contexts. For cases of non-modular development of melanin-based pigmentation see Badyaev (2004b).

Whereas in the majority of cases, melanin-based coloration is produced by flexible and diverse interactions of genetic and developmental mechanisms (Barsh 1996, 2001), there are several examples of nearly complete modularity across levels of genetic encoding, development, and phenotypic expression of melanin-based coloration. Because the population genetics' assumption of a linear and accurate representation of genotype in phenotype is satisfied in these exceptional cases, evolutionary theory can provide adequate explanations not just for the maintenance of the resulting morphs at the population level, but also for their evolutionary dynamics (Price and Bontrager 2001; Hoekstra and Price 2004). But such "textbook examples" are often the only examples; most gene and environment products involved in color development interact in complex and nonlinear ways, and the linear phenotype-genotype



representation is, most likely, a highly derived product of external selection (von Dassow and Munro 1999; West-Eberhard 2003).

In many taxa, allelic variation in the MC1R receptor gene acts as an on-off switch determining the deposition of melanin in the follicle, and several point mutations in this locus have been associated with cases of naturally and artificially selected color polymorphism. In wild birds, point mutations in MC1R lead to development of distinct plumage coloration in Lesser Snow Geese (*Anser caerulescens*), Parasitic Jaegers (*Stercorarius parasiticus*), and Bananaquits (*Coereba flaveola*; Theron et al. 2001; Mundy et al. 2004; Plate 28, Volume 1; Plate 26), where the phenotypic effects of such mutations are under strong sexual and natural selection. Generally, a mutation can be expressed at the level of phenotype (and thus become visible to selection) only if the phenotype can produce it (Arthur 2004; Figure 8.3). This, in turn, depends on a mutation's utilization of existing developmental routes—witness the major pleiotropic effects of many color mutations (Merat 2003; Somes 2003; Keeling et al. 2004)—as well as its ability to generate novel developmental pathways (Figure 8.3). In most cases, selection for the fixation of phenotypic expression of a mutation is very slow, not only because of the exceptional rarity of such mutations, but also (and mostly) because the developmental pathways by which such mutation is expressed differ among individuals, making selection ineffective. Thus, the key to the persistence of the MC1R mechanism across species might be a combination of its high mutability *and* a remarkable absence of pleiotropic effects (i.e., modularity in development and expression;

Figure 8.3. Conceptual illustration of within-generation interactions between novel and “inherited/existing” (here meaning either inherited by an organism or constructed at prior stages) components of color production at acquisition/encoding, development, expression, and display stages. (a) Default state. Appearance of a novel element at a lower level (e.g., genetic mutation, inclusion of novel environmental component) can be expressed and transferred to the upper level only if it can be accommodated by existing developmental pathways. Because of the complexity of developmental cascades, different phenotypes will transmit and express the effects of a novel element or mutation differently and by different developmental pathways, lowering the likelihood of its exposure to selection and evolutionary retention. (b) A major mutation of high developmental penetrance or a novel external element can construct novel color production directly, which will maximize both the chances of expression of a novel element and similarity of its expression among phenotypes. (c) Appearance of a novel element at the base level can influence existing pathways at the later stages that can express it with relatively small distortion and high similarity among phenotypes.

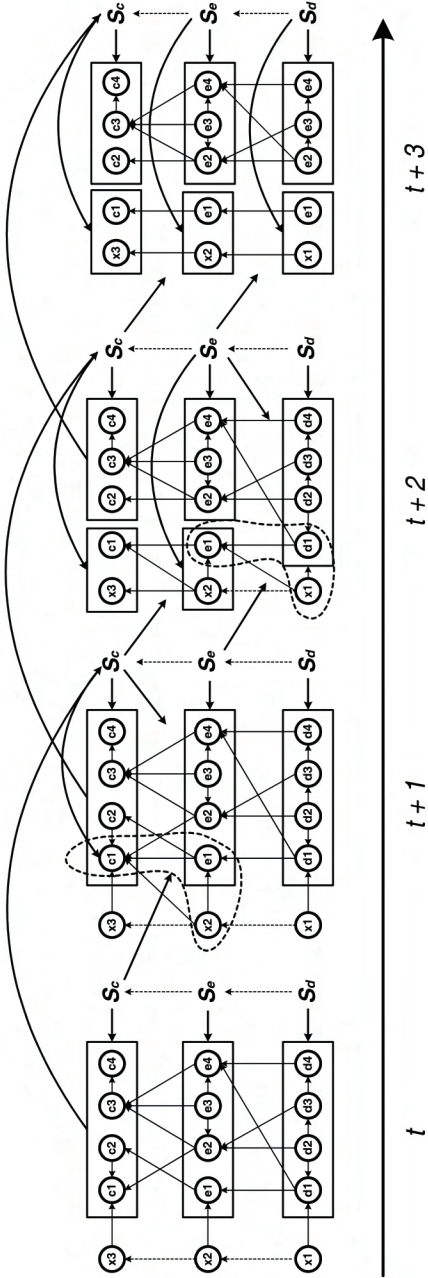


Figure 8.4. Conceptual illustration of the evolution of modularity within and across three production levels—development (signified by d1, etc.), expression (e1, etc.), and courtship (c1, etc.)—along four consecutive generations (t to $t + 3$). Within each generation, all production stages can incorporate elements of the environment (x1, etc.) and are subject of external selection on courtship (S_c), on color expression (S_e), and on color development (S_d). At generation t , the phenotype is a nonmodular, patterned structure with developmental incorporation of x1 (e.g., pigment precursor) at the stage of development, x2 (e.g., social interaction affecting hormone levels, precursor of feather structure) at the stage of expression, and x3 (e.g., ambient light, background color for display) at the stage of courtship. $S_c(t)$ acts indirectly on the most efficient incorporation of environmental elements into production of color. Because phenotypic expression of the courtship stage at generation t could influence S_c at generation $t+1$ (e.g., via sexual imprinting, the sensory drive process, or cultural inheritance), $S_c(t)$ will have an indirect effect on the most efficient incorporation of x2 and e1 into production of c1 (e.g., formation of a module that combines the effect of the external environmental cue for breeding with selection of the most favorable lighting in which to display). Therefore, c1($t + 1$) will have independent fitness consequences and $S_c(t + 1)$ can act on the efficiency of producing c1, whereas $S_c(t + 1)$ will have an indirect effect on the efficiency and reliability of incorporating x1($t + 2$) into d1($t + 2$) because of correlation between x1 and x2, which is now a part of the expression module and because of the dependence of S_e , S_e , and S_c within each generation; dashed arrows. At generation $t + 3$, x1, x2, and x3 are reliably incorporated at corresponding levels; the context independency of the resulting modules is assured by direct interactions between levels, their functional independence (being subject to S_e), and limited interactions with the elements outside modules at each level.

Ling et al. 2003; Mundy et al. 2004). Interestingly, the MC1R-produced modular polymorphisms only involve cases in which (1) melanin is distributed across most of the plumage area of a bird in an all-or-nothing pattern, (2) deposition of melanin is not coordinated with complex and variable interactions with feather structure, and (3) there is no age-dependency in color expression. In all other cases—for example, when melanin-based coloration involves parts of plumage involved in different functions (e.g., when plumage areas form the distinct functional modules for prey flushing and sexual displays in *Phylloscopus* warblers; Marchetti and Price 1997)—selection favors diverse genetic and developmental mechanisms of melanin deposition (Hoekstra and Nachman 2003; MacDougall-Shackleton et al. 2003; Doucet et al. 2004).

Carotenoid-based pigmentation differs from other types of pigmentation in that most of its components have to be obtained from the environment (e.g., consumed during foraging, delivered by parents during feeding, supplied with the yolk of eggs; Slagsvold and Lifjeld 1985; Hill 1992; Surai 1998; Fitze et al. 2003). Thus, all else being equal, early incorporation of externally-derived carotenoid components into an ornament's developmental pathways should lead to diverse ways by which individuals and species proceed with development of carotenoid-based colors, thereby resulting in greater individual- and condition-dependency of such ornamentation (Badyaev and Hill 2000; Badyaev et al. 2002; Chapter 12, Volume 1; Chapter 4; Figures 8.3 and 8.4). In theory, environmental variation in the availability and type of carotenoid precursors, as well as the diversity and complexity of developmental cascades of carotenoid metabolism, should prevent easy formation of modularity in carotenoid acquisition and development (but not in the expression; see below). Yet evidence suggests that, in the absence of selection causing and maintaining condition dependence in development, and under selection favoring the most efficient acquisition of color displays, evolutionary modularity evolves readily even in carotenoid-based ornamentation (Badyaev and Snell-Rood 2003; Badyaev 2004b).

In some species, direct and thus condition-independent phenotypic expression of acquired carotenoids results from the inability of developmental systems to recognize them. Such is the case of novel pigments from fruits of introduced ornamental shrubs appearing in the diet and coloration of Cedar Waxwings (*Bombycilla cedrorum*; Plate 30, Volume 2; Mulvihill et al. 1992; Witmer 1996) or from synthetic pigments provided to birds in captivity (e.g., Hill and Benkman 1995). In other species, such direct and context-invariant

transmission is accomplished by evolved modular pathways of carotenoid development, storage, or expression, as is the case with carotenoid plumage of flamingos, tanagers, and bullfinches (Brush 1990; Stradi et al. 1997, 2001). The difference between species in the environment- and context-dependency of their carotenoid-based plumage is well illustrated in captivity, where closely related birds with diverse types of carotenoid plumage are often kept on the same diet. Some species (e.g., Common Rosefinch [*Carpodacus erythrinus*], Pine Grosbeak [*Pinicola enucleator*; Plate 25, Volume 1]) are sensitive to the loss of the usual carotenoid precursors in their diet and change their color after a single molt. Other species (e.g., Common Redpolls [*Carduelis flammea*], Common Bullfinch [*Pyrrhula pyrrhula*]) are remarkably versatile in extracting or converting carotenoids and maintain species-specific carotenoid coloration for several molts (pers. obs.). Also crucial to this maintenance is the ability to store externally derived carotenoids, which gives individuals greater independence from the external environment and thus facilitates the formation of modularity in the acquisition and development of carotenoid coloration.

Similarly, expression and courtship displays associated with plumage coloration often involve the close integration of distinct organismal functions (e.g., color production, motor functions) and external environment (e.g., background matching). At first consideration, one might suppose that evolutionary modules in color expression and behavior would be rare. However, two factors might favor the evolution of integration of color expression, behavioral displays, and components of the external environment. First, behavioral displays involve only late stages of color production and require fewer interdependent stages (Figures 8.2 and 8.3). Second, the higher fitness of optimum color displays often requires their co-occurrence with some aspects of behavior (e.g., Badyaev and Duckworth 2005), such as displaying a particular color under particular ambient light or in a certain pattern against a particular background (Gilliard 1956; Endler and Théry 1996; Uy and Endler 2004). When such selection on co-expression is strong and recurrent, it can result in evolutionary coupling (see below) of behavior, color expression, and plumage patterns. This process is evident in the transference of plumage display postures among different contexts within and among species (Andrew 1960), in the cases of genetic inheritance of patterns of color displays (Price 2002), in the remarkable evolutionary retention of behavioral syndromes associated with feathers despite the loss of feathers (Vestergaard et al. 1999), and in modification of feather microstructure for deposition of different carotenoid types in sister taxa (Hudon 1991). Finally, distinct external selection on components of color or plumage

type can facilitate modularity in expression. Examples include cases in which feather tracks differ in the formation of fault bars in relation to strength of external selection on their functional significance (Burt 1986; Fitzpatrick 1998; Aparicio et al. 2003; Jovani and Blas 2004), and when integration among developmentally distinct components of carotenoid-based coloration of House Finches (*Carpodacus mexicanus*; Plate 14) varies adaptively among populations, degrees of elaboration, and subsequent molts (Hill 1996; Badyaev et al. 2001; Badyaev and Duckworth 2003; Badyaev and Young 2004).

Selection on Modularity in Encoding, Development, and Expression of Color Displays

Changes in the modularity in development require complementary effects of modifying integration both inside and outside of module components (Figure 8.2). For example, modularity in color production might be accomplished by duplication of elements or pathways (Figure 8.2a), by selection for linearity between elements at different developmental stages (Figure 8.2b), by eliminating or shortening developmental steps (Figure 8.2c), or by selection on intermediate modifiers that strengthen the relationship between elements of the module (Figure 8.2d; Badyaev 2004a).

There are six general scenarios for selection on the modularity of color production. First, modularity across production stages is favored when selection acts on color expression only and when this selection is recurrent, stabilizing, and consistent across environments (e.g., selection maintaining taxa-specific color patterns or distinct, genetically-based color morphs within a species). Second, when selection acts on color expression only (e.g., predation; Plate 4), but such selection fluctuates among ecological or social environments, two patterns of modularity evolve: (1) selection can favor the evolution of a context-sensitive threshold that regulates expression of color produced by alternative developmental modules (Badyaev and Qvarnström 2002), or (2) selection can favor the evolution of complex sexual traits that consist of developmentally independent modules (Wedekind 1992; Moore 1997; Badyaev et al. 2001). Selection might favor modularity in expression when the same color pattern has functions in different contexts with distinct fitness consequences (Badyaev and Hill 2003), for example, when color pattern is used in both flush-pursuit foraging and sexual displays.

Third, when selection is on color expression only, but is directional, it can act on the efficiency of color acquisition and development and will favor

modularity in both. For example, signaling functions of sexual displays are ensured by the costs of color expression and production (Andersson 1994). Selection for reduction of such costs will favor evolution of modularity in these stages (Badyaev 2004a). The combination of selection for reduction in color signal costs (e.g., within males) and opposing selection to restore condition dependency of color signals (e.g., by females) should result in the evolution of facultative and context-dependent expression of color displays or in evolution of complex displays consisting of several distinct modules (Hill 1994; Badyaev 2004a). For example, selection against modularity in sexual ornamentation can capitalize on developmental integration of feather growth and within-feather pigmentation (Prum and Williamson 2002) by favoring the evolution of new color expression that indicates condition-dependent growth of feathers, such as selection for pigment markings to reinforce condition-dependence of elongated ornamented feathers (Fitzpatrick 1998).

Fourth, when selection on color expression also acts directly on color acquisition and development, as does selection for condition dependency in sexual ornamentation, such selection will act against modularity in color acquisition and development, yet it might favor modularity at the expression stage. For example, consistent directional selection on the expression of carotenoid-based coloration in the absence of selection maintaining condition dependence in its production results in genetically inherited efficiency in extracting and storing carotenoids from carotenoid-poor environments (e.g., in modularity in carotenoid acquisition and development; Ryan et al. 1994; Craig and Foote 2001). However, in species in which external selection maintains condition- and environment-dependence in carotenoid expression, such expression is closely dependent on the local availability of carotenoids in the environment (i.e., strong context-dependency; Grether 2000; Hill et al. 2002).

Fifth, the importance of cultural inheritance, sexual imprinting, context-dependency, and prior experience in determining the direction and patterns of future selection on sexual traits (Odling-Smee et al. 2003) favor modularity in the expression of sexual ornamentation, because such modularity enhances functional versatility. For example, the evolution of complex visual displays in bowerbirds is favored by context- and age-dependency of selection on the expression of such displays (Coleman et al. 2004).

Finally, in the absence of consistent selection either on expression or on development (i.e., when the preferred color expression is not known from generation to generation), epigenetic developmental cascades (i.e., gravitation towards a particular state without a predetermined path; Sachs 1988) might be

favored over modularity because such development provides the cheapest way of developing color patterns and displays. This possibility has not been studied in birds, but many selectively neutral changes in coloration (as in some island birds) that are often attributed to “genetic drift” (Peterson 1996; Badyaev and Hill 2003; Johnson 2003) might be due to this mechanism.

Evolution of Modularity in Color Displays: Constructing Ways with Inherited Means

Selection on modularity in color displays is common and often favors co-expression of traits with distinct developmental histories and origins, for example, a combination of particular plumage colors, colorful items of environmental origin, and particular display behaviors. How can reliable and heritable associations among these traits evolve when, in isolation, each of these components would have no function?

Most theoretical studies assume that phenotypic modularity evolves as a direct consequence of modularity at the level of genotypes—gene duplication or novel mutation facilitate the formation of novel developmental pathways and thus enable phenotypic modularity (Wagner et al. 1997; Wagner and Mezey 2000; Ohta 2003; Force et al. 2004). This is difficult to accomplish because the downstream development is usually novel and diverse among individuals, and its (often epigenetic) patterns are unpredictable from the level of the genotypic module (Wagner and Mezey 2004; Wagner et al. 2005). (Interestingly, strong directional selection on expression of a trait might facilitate proliferation of novel developmental pathways to produce the trait and thus lead to its lower heritability. Whereas this phenomenon is usually explained by the exhaustion of genetic variance and fixation of preferred trait appearance, it can also be due to increased variability of production). Moreover, even when one assumes a direct and linear relationship between phenotype and genotype, modularity is still highly unstable under fluctuating directional selection on the phenotype (Wagner and Mezey 2000). Clearly, developmental complexity plays a crucial role in maintaining the stability of phenotypic modules once they evolve. Yet developmental complexity and variability is considered to be the main obstacle to the evolution of modularity in the first place.

This difficulty can be resolved if it is realized that all sources of organismal variation (Figure 8.1) are ultimately expressed by the same developmental pathways (Cheverud 1982) and have the potential to have the same effect on fitness (i.e., selection is insensitive to whether phenotypic variation is induced

environmentally, epigenetically, or genetically; Meiklejohn and Hartl 2002; Siegal and Bergman 2002). Some developmental pathways evolve under external selection for the most accurate or efficient expression, but others are related to cohesiveness, control, and regenerative functions of the developmental systems themselves (Schmalhausen 1949; Whyte 1965; Schlichting and Pigliucci 1998; Arthur 2004). These are subject to the environment-invariant and the final-expression-invariant internal selection, and it is complexity and canalization of these previously established (“pre-existing” *sensu* West-Eberhard 2003) pathways that produce stability and directionality in development (Sachs 1988; Jablonka et al. 1992; Waxman and Peck 1998). For example, Badyaev and Foresman (2000, 2004; Badyaev et al. 2005) found a nearly complete congruence of phenotypic and genetic variation in complex morphological characters, driven by selection-independent developmental patterns. Similarly, Ancel and Fontana (2000) showed that certain phenotypic patterns of RNA folding are particularly stable and less costly to produce, leading secondarily to genetic canalization of most adapted phenotypes.

The same principle applies to the evolution of modularity in color displays (Figure 8.4). Within each generation, a color pattern of an individual is constructed by an array of interacting elements, some inherited (genetically, behaviorally, ecologically, or parentally), some not, operating at the levels of color encoding, acquisition, development, and expression (Figure 8.1). To the extent they have independent effects on fitness, these components and their functional associations at each developmental stage are influenced by external selection (Figure 8.4). Persistency and consistency of such selection favors stable configuration among elements (Figure 8.4). In turn, the extent to which such functional modularity can be accomplished, when favored, depends on the similarity and predictability of developmental processes among phenotypes in a population (Arthur 2002; West-Eberhard 2003). Selection favoring modularity within or among levels is the selection for linear, more additive relationships between components across developmental levels (Rice 2001; Figure 8.2). In turn, the complexity of developmental processes, through canalizing effects of previously formed structures, can lead to the appearance of a novel developmental pathway in many individuals simultaneously, which greatly facilitates its evolutionary persistence (Jablonka et al. 1992; Badyaev and Foresman 2004; Badyaev 2005a,b). This can eventually lead to its genetic assimilation either when the fitness of individuals possessing the pathway is higher or when the costs of phenotype production with the incorporated component are lower (Masel 2004; Palmer 2004; Rice 2004b; Badyaev 2005a).

Interestingly, such “top-down” processes in the evolution of sexual displays are often, although implicitly, invoked in the studies of the sensory drive process. A sensory bias of the receiver initiates the selection for elaboration of sexual ornament of a signaler, with condition dependence in the development of such ornaments evolving secondarily under continuing selection for ornament elaboration (Schluter and Price 1993; Rowe and Houle 1996; Garcia and Ramirez 2005).

Production of color involves the developmental incorporation of components of the external environment (e.g., pigments or display conditions). Such developmental “entanglement” (sensu Rice 2004a) between elements at different levels can generate novel developmental arrangements and can bias evolutionary change (Fusco 2001; Salazar-Ciudad et al. 2001; Rice 2004a; Badyaev 2005b). When external selection acts on the co-occurrence of distinct developmental elements or when it acts on the efficiency of incorporating environmental components, it can have an effect on these developmental processes (Masel 2004; Rice 2004b; Figures 8.2 and 8.4). The developmental entanglement of inherited and noninherited components of color production (e.g., integration of a consumption of a certain carotenoid and the feather structure required for its expression, integration of color pattern and display behavior) can lead to their genetic canalization and coinheritance (i.e., evolutionary modularity; Fuller and Travis 2004; Palmer 2004; Rice 2004a). In some interesting cases, inclusion of the external environment influences both the development of the phenotype and selection on the phenotype simultaneously (Ryan et al. 1994; Sockman et al. 2002, 2004; Badyaev 2005a). For example, developmental incorporation of environmentally derived carotenoids into both integument coloration and the visual sensory system is important for development of both red plumage and visual preferences for such plumage (Bowmaker et al. 1993).

Once formed, the inheritance of complex color patterns that produce locally favored sexual signals depends on the transmission of an array of developmental resources necessary for reliable acquisition, development, and expression of its components across generations. Thus, crucial to the understanding of the evolution of sexual displays is the notion of plurality of inheritance systems, when the wide array of developmental resources and conditions transferred between generations enables similarity in developmental processes and phenotypes (Oyama 2000; Jablonka 2001). Moreover, behavioral inheritance and parental imprinting set the stage for the direction of selection in the next generation (Lewontin 1983; Wolf et al. 1998; Odling-Smee et al. 2003; Wolf

2003). For example, offspring preferences for sexual displays are often largely determined by parentally imprinted or learned local dialects and local, often artificial, appearances (Cate and Bateson 1988; Irwin and Price 1999; Sockman et al. 2002; Madden et al. 2004). Similarly, learned preference for certain foods can be crucial to acquisition of species-specific precursors of pigments, whereas learned preference for habitat features of display arenas can facilitate reproductive success (e.g., Cushing 1944). Moreover, sexually imprinted and genetically encoded traits can co-evolve and jointly determine predisposition to species-specific color displays and courtship patterns (Lachlan and Slater 1999; Rice 2004b). The interaction between behaviorally and genetically inherited preferences plays an important role in the evolution of genetic predisposition to displays that indicate local function versus displays that indicate species-specificity (Lachlan and Feldman 2003). Such interaction can explain the contrasting results of studies showing open-ended (Ryan et al. 2003) versus species-specific (Hill and McGraw 2004) preferences for the elaboration of condition-dependent sexual displays.

A Final Note

As I am writing this page, a bright magenta male Pyrrhuloxia (*Cardinalis sinuatus*; Plate 25) from my study population leads his three fledglings from one Prickly Pear Cactus (*Opuntia*) to another, feeding them pieces of red fruits outside my window. His fledglings acquired their red ornamentation while in the nest, with parents providing all the carotenoid precursors for their current plumage, some of which will be retained for their first breeding. As the fledglings follow the male, begging and waiting for food, they try to open the fruits on their own, learning both the appropriate sources of carotenoid precursors and the ways to find and acquire them—that is, learning both the problems and the solutions to the problems that existed in prior generations. The fledglings' imprinting on their parents' plumage phenotype not only results in species-specific affiliations—the fledglings do not mix with a large brood of Northern Cardinal (*C. cardinalis*; Plate 25) fledglings feeding with their parents on the pollen of the saguaro flowers nearby—but also sets the stage for their future preferences for sexual displays. It is hard to disagree that, in this case, developmental resources, behaviors, and preferences that are transferred across overlapping generations are at least as important to the production of offspring color display and shaping selection on this display as are the offspring's inherited genes. It is also clear from their current plumage color that

the young *Pyrrhuloxias* vary in how their developmental systems are utilizing these acquired and inherited resources to construct their phenotypes. To understand the evolution of color displays and to guide our empirical studies, we need a new conceptual framework that integrates explicitly the production of the phenotype within a generation with its change between generations.

Summary

The conventional interpretation of the modern evolutionary synthesis states explicitly that internal organismal factors (e.g., genes) that cause variation operate independently of external factors (e.g., selection) that delete or retain these variants. It has long been noted that such thinking skips a crucial step in organic evolution—the actual production of phenotype—and, as such, separates the causes of within-generation variation from the causes of among-generation variation. Very much alive is the general notion that Darwinian evolution requires a strict separation and independence of pre-existing (inherited) form and created (acquired) form. The result is that fascinating scientific advances in our understanding of developmental processes and molecular mechanisms co-exist currently with embarrassingly vague notions about the origin of these forms, the nature of deterministic forces in development, and, most importantly, the origin of genes. I suggest that studies of animal coloration are uniquely suited for a novel evolutionary synthesis that integrates the origination, maintenance and evolution of traits. I review the literature on avian coloration and build a conceptual framework that traces an evolutionary sequence from environmental induction of developmental plasticity, through phenotypic and genetic accommodation facilitated by developmental complexity and extended inheritance, to the evolution of genes and genetic inheritance as guarantors of the most recurrent and consistent organism-environment interactions. The ultimate reward of such a framework in relation to animal coloration, if successful, would be the answer to the foundational question of organic evolution—how to reconcile persistent within-species continuity in the development of displays with an origin of striking diversity in displays among species.

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