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SYNTHESIS

Evolvability and Robustness in Color Displays: Bridging the Gap between Theory and Data

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Abstract Evolution of diet-derived sexual ornaments—some of the most spectacular and diverse traits in the living world—highlights the gap between modern evolutionary theory and empirical data on the origin and inheritance of complex environment-dependent traits. Specifically, current theory offers little insight into how strong environmental contingency of diet-dependent color biosynthesis and environmental variability in precursor supply can be reconciled with extensive evolutionary elaboration, diversification, and convergence of diet-dependent displays among animal taxa. Moreover, biosynthetic pathways of diet-derived displays combine seemingly irreconcilable robustness, lability, and modularity to facilitate elaboration under variable environmental conditions. Here I show that an ontogenetic decrease in the predictability of an association between organismal and environmental components of color biosynthesis and the corresponding evolutionary transition from short-term epigenetic inheritance of peripheral biosynthetic components to genetic inheritance of the most reliable upstream components link the causes of developmental variation with the causes of inheritance in diet-derived displays. Using carotenoid-based colors as an empirical model, I outline general principles of a testable evolutionary framework of diversification and functional robustness of diet-derived displays, and suggest that such a framework provides insight into the foundational question of evolutionary biology—how to connect causes of within-generation developmental variation with causes of among-generation and among-taxa variation and thus with causes of evolution?

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Introduction

Deterministic Forces in Development: A Need for a New Evolutionary Framework

The diversity of animal colors and color patterns—from extravagant elaboration of sexual displays to precise environment-matching of camouflage colors, to striking convergence in complex color patterns between distinct taxa—have long been an illustration of the power of evolution. Yet, this diversity also highlights a number of inconsistencies in modern evolutionary theory. On the one hand, the patterns of evolutionary diversification and convergence in animal colors are attributed to modifications of an inherited genetic toolkit of developmental pathways (Carroll, Grenier, & Weatherbee, 2001; Davidson, 2006; Wilkins, 2001) or, more rarely, to the evolution of a direct genotype–phenotype correspondence (Hoekstra, 2006; Majerus & Mundy, 2003). On the other hand, the bright colors of many animals, in particular those derived from carotenoids, must be obtained from the environment each generation (Britton, 1998; Brush, 1990) which means organisms must deal with highly variable and often unpredictable precursor supplies across environments and generations. Current theory offers little insight into how such environmental contingency in diet-dependent color biosynthesis can be reconciled with evolutionary elaboration, complexity, and convergence of diet-derived displays, the patterns typically attributed to genetic inheritance. The fundamental question here is the central question of evolutionary biology—how to reconcile the *causes* of within-generation developmental variation with the *causes* of among-generation and among-taxa variation and thus the causes of evolution (Lewontin, 1983). I show here that carotenoid-based colors discussed in this essay are not a special case, but rather a particularly convenient illustration of not only the gap between the concepts of modern evolutionary theory and vast amounts of unexplained empirical patterns of diet-derived display evolution, but also of the ways this gap can be bridged.

How do environmentally-dependent displays evolve elaboration and repeated convergence over evolutionary time? A typical answer to this question invokes regulatory mechanisms that modulate pre-existing developmental pathways, accommodate a variety of environmental inputs, and produce species-specific features (Stern, 2000; Davidson, 2006). While the recent focus on developmental evolution of regulatory mechanisms illuminates some of the most spectacular diversifications (reviewed in Carroll, 2005) it does not answer the question of the *origin* of developmental pathways that are being modulated or the ways in which these pathways are inherited; i.e., how are the regulators themselves regulated and how does precise activation of complex inherited pathways evolve?

Evolution of environmentally-dependent color displays illustrates that it is not helpful to assign a greater causal role to some developmental factors (such as inherited genetic developmental mechanisms) over others if all are required to produce a normal phenotype (Lewontin, 1974). In the case of carotenoid-based colors, a simple switch in diet due to introduction of an exotic plant species (Baker & Baker, 1990; Hudon & Brush, 1989), climate change (Linville & Breitwisch, 1997), consumption of an artificial carotenoid compound (McGraw & Hardy, 2006), or experimental exclusion of carotenoids from the diet (Brockmann & Völker, 1934; Stradi, Pini, & Celentano, 2001) can all drastically alter the phenotype, often of an entire population (e.g., Witmer, 1996). Could the ease with which the phenotype is altered by carotenoid precursors be attributed to the features of a genetically inherited biosynthetic and developmental machinery? In other words, could inherited machinery be expected to have pre-planned ‘‘solutions’’ for all possible environmental contingencies in carotenoid availability and, most importantly, discriminate among these adaptive and maladaptive, rare and common scenarios in building the phenotype? If yes, then how can such contingency evolve? If not, then its causal contribution to generating diversity in diet-dependent displays is likely to be limited.

Conventional evolutionary theory hypothesizes that the developmental processes that produce phenotypes are independent from the selection subsequently sorting these phenotypes (Huxley, 1942; Mayr, 1963). However, diet-derived carotenoids not only produce animal colors, but also influence color perception and color preferences through their presence in the retina. Moreover, the ubiquitous presence of sexual imprinting and cultural inheritance in animals not only affects the patterns of selection on color (e.g., in mate choice), but also, through learned foraging preferences for species- and sex-specific color precursors, affects the acquisition of substances needed for both color production and perception (reviewed in Badyaev, 2005a). This confounds production and selection, but, more importantly, emphasizes that diet-dependent animal colors develop and evolve precisely *because* they are open to environmental modifications.

Thus, diet-derived color displays challenge us to examine the relationship between acquired/inherited, environmental/genetic, and selection/production features of the phenotype making them a particularly good model to understand one of the most fundamental questions in the evolution of complex traits—what is the cause of their evolutionary diversification and convergence? Can we, in other words, construct a testable evolutionary theory that will speak the same language as the empirical patterns described above, that will enable us to reconcile environmental contingency of carotenoid biosynthesis with evolutionary diversity in elaborated and complex carotenoid-derived displays?

To be useful, such a theory would need to address a number of fundamental evolutionary questions, many of which can be answered using carotenoid-based colors as an example. Does organismal diversification occur via modification of existing developmental pathways or through the evolution of novel pathways? Why and how do novel forms appear? How can the environmental dependency of trait development be reconciled with the evolutionary persistence, elaboration, and diversification of such traits? Shouldn’t environmental lability preclude the evolution of robust developmental pathways? How and why do some developmental pathways persist unexpressed for millions of generations? Why do similar forms appear repeatedly? Can *differences* in form among taxa be used to infer the *origin* of form within taxa (e.g., do evolved developmental pathways bear the marks of past organism–environment interactions)? Do existing forms limit the introduction of new elements? What accounts for a punctuated pattern of evolution in diversifications, and how to reconcile this with frequently assumed incremental changes in underlying development?

To answer these questions for the evolution of environment-dependent displays, we need a conceptual framework that traces color diversification from its developmental origin to the evolution of its genetic inheritance. Below I discuss the main themes of such a framework, focusing on the relationship among the units of developmental variation, the units of selection, and the units of inheritance in color displays, especially in carotenoid-based displays of birds.

Developmental Diversification in Color Displays

Reconciling Robustness and Environmental Sensitivity: General Principles of Carotenoid Biosynthesis

Despite being one of the most diverse natural products, with more than 700 described compounds, carotenoids are synthesized by only a limited number of highly conserved modifications of upstream pathways followed by a downstream network of enzyme and metabolite interactions (Britton, 1998) that produce, at a network's periphery, an array of carotenoid products. However, animals cannot produce carotenoids de novo and instead obtain carotenoids, at variable stages of biosynthesis, with the diet. Thus, the biosynthetic pathways with which animals process environmentally-derived carotenoid compounds for their displays should reflect several demands. First, these pathways should allow uptake of highly derived carotenoid compounds as well as their less derived precursors. Second, they should enable metabolism of a wide array of distinct precursors. Third, they should be able to metabolize a precursor to a highly derived form to produce an elaborate display (Fig. 1). There are several defining features of carotenoid biochemical networks that facilitate evolution of these features.

First, carotenoid enzymes are remarkably interchangeable both among metabolic levels within an organism and across distant species (Reeves, 2003; Schmidt-Dannert, Umeno, & Arnold, 2000; Schwab, 2003). Thus, when modification of an upstream mechanism produces a novel carotenoid or when a highly derived carotenoid is consumed with food (thus skipping the upstream metabolic steps), downstream enzymes are nevertheless able to recognize the common motifs and configurations of these compounds and either metabolize them further or pass them along (Lee & Schmidt-Dannert, 2002; Mijts, Lee, & Schmidt-Dannert, 2004, Fig. 1). Such recognition is facilitated by a conserved pattern of carotenoid modifications that frequently involves elongation with preserved end motifs, such that downstream enzymes need to recognize only a particular end group, rather than an entire molecular structure (Britton, 1998). Such recognition might provide the mechanism for a defining feature of animal carotenoid coloration—its remarkable openness to input of novel, often highly derived carotenoid compounds from the environment (Fig. 1, Hudon & Brush, 1989; Witmer, 1996). The ability to express such novel carotenoid compounds is beneficial when such compounds enable greater and less costly ornamentation (Fig. 1). However, because no metabolic machinery is added to the recipient developmental pathway, the ability to express such novel and often rare compounds likely depends on the interchangeability of carotenoid enzymes in existing developmental pathways.

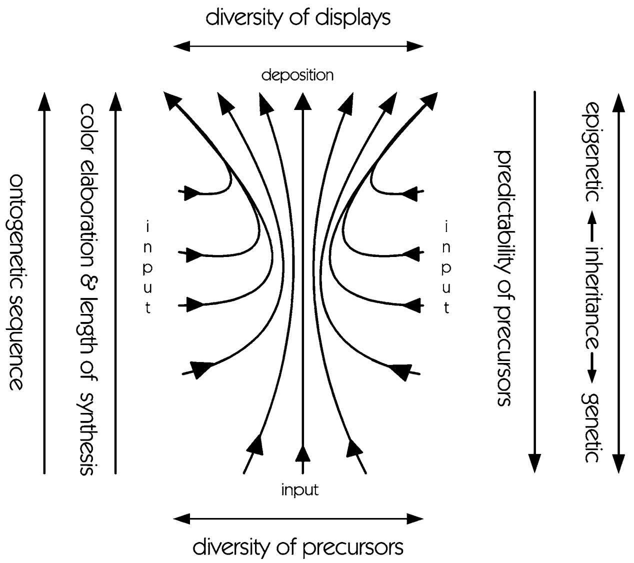

Fig. 1 Conceptual illustration of the ontogenetic relationship between elaboration of color display and length of corresponding carotenoid synthesis, predictability of precursor availability, and specificity of carotenoid enzymes. Biosynthesis can accommodate precursors of different derivations and at different ontogenetic stages (shown by input arrows). Relative importance of genetic and epigenetic inheritance of biosynthesis varies with ontogenetic changes in predictability of organism–precursor associations

Second, extensive branching and interconnectivity of enzyme and metabolite pathways, typical for carotenoid networks, result in a remarkable robustness of carotenoid biosynthesis, such that a single precursor can be converted to multiple final compounds, and several pathways can produce the same final pigment from different precursors (Fraser, Shimada, & Misawa, 1998; Mijts et al., 2004, Fig. 1). Such robustness and redundancy might enable evolutionary persistence of carotenoid production networks and account for the retention of unused and unexpressed pathways of such networks in the absence of a suitable environmental precursor (Badyaev, 2005a; Firn & Jones, 1996; Vitkup, Kharchenko, & Wagner, 2006), ultimately facilitating convergence in environment-based colors among distinct taxa. Moreover, the network complexity and enzyme interchangeability can facilitate evolvability of carotenoid pathways by enabling accumulation, without expression, of mutations or minor modifications of upstream mechanisms (Alberch, 1991; Aharoni et al., 2005; Vitkup et al., 2006; Wagner, 2005). Evolutionary retention of such unexpressed pathways or mutations by network complexity is often revealed with experiments using novel dietary pigments (Hill & Benkman, 1995), hormonal manipulations (Kimball & Ligon, 1999), and genetic crosses or hybrids (Panov, 1989). Such robustness, however, not only can hinder the ornament elaboration that is often favored by sexual selection (Badyaev, 2004a, b; Badyaev & Young, 2004), but can also limit its inheritance (see below).

Third, upstream carotenoid enzymes seem to have a greater specificity to precursors compared with downstream enzymes (Mijts et al., 2004; Umeno, Tobias, & Arnold, 2005); experimental manipulation of upstream enzyme specificity leads to the production of a wide variety of novel carotenoid compounds in the lab (Tobias & Arnold, 2006)—a feature of crucial importance for the diversification, appearance and elaboration of novel carotenoid-based ornaments (Fig. 1, see below). Finally, robustness and functionality of carotenoid pathways is ensured by dose-dependent regulatory ‘‘switches’’ that have a direct, modular effect on production of individual compounds and determine transport of rate-limiting enzymes and precursors (Lee & Schmidt-Dannert, 2002; Mijts et al., 2004). The crucial feature of such distributed and modular regulatory activity at the periphery of carotenoid biosynthesis is that it makes the entire biochemical network less susceptible to the loss of function and yet open to innovation and diversifications of color patterns.

Reconciling Robustness and Environmental Sensitivity: The Level of Organism

A central feature of carotenoid-based coloration in birds is that its diversification is proximately linked to organism-wide consumption, transport, and metabolism of carotenoids (Fig. 2). Once absorbed in the intestine, dietary carotenoids are incorporated in lipoproteins that transport them to the sites of storage or metabolism and, for carotenoids allocated to color ornamentation, to the sites of deposition—the feather follicles (reviewed in McGraw, 2006; Parker, 1996). Species (and sexes in sexually dimorphic species) vary in the amounts, ways, and kinds of carotenoids they absorb and transport, and in whether they deposit dietary carotenoids unchanged or metabolized (Brush, 1978; Fox, Smith, & Wolfson, 1969; Negro, Tella, Hiraldo, Bortolotti, & Prieto, 2001; Stradi, 1998). Species also vary in the location of metabolism of feather-bound carotenoids, from central metabolism sites (such as the liver) and subsequent organism-wide circulation of transformed carotenoids in some species, to feather-follicle specific metabolism and deposition in other species (Kritzler, 1943; McGraw, 2004, 2006; Parker, 1996). The deposition of carotenoids in the feather follicle similarly varies from passive lipid diffusion (Lucas & Stettenheim, 1972) where patterns of coloration are determined largely by variation in feather growth (Badyaev & Landeen, 2007), to the formation of variable bonds with feather keratin that results in production of distinct colors (Bleiweiss, 2004; Blanco, Frias, Garrido-Fernandez, & Hornero-Mendez, 2005; Desselberger, 1930). Overall, however, the necessity of organism-wide transportation of carotenoids (Tella et al., 2004) may be a limiting factor in the evolution of carotenoid-based displays, favoring evolution of distributed, tissue specific, and context-specific regulatory controls. At the same time, such a link to shared organism-wide functions should facilitate inheritance and evolutionary persistence of carotenoid pathways despite their sex- age- and season-specific expression.

Regulatory modifications at the periphery of carotenoid pathways, such as selective uptake of only some of the circulating carotenoids or truncation of carotenoid uptake at the deposition site, seem to account for the majority of sex-, age-, and season-specific carotenoid-based plumages in species that otherwise show no differences between sexes, ages, and seasons in carotenoid consumption, transportation or metabolism (Fig. 2b, Brush, 1978; Goodwin, 1952; Inouye, Hill, Stradi, & Montgomerie, 2001; McGraw, 2004; Stradi, Rossi, & Bellardi, 1996). In most natural pigmentation systems, such peripheral truncation or diversion of products from deposition seems to be regulated epigenetically and often varies with age, sexual maturity, dominance status, and season and can be modified by hormonal treatment (reviewed in Badyaev, 2005a). For example, house finch (*Carpodacus mexicanus*) nestlings and juveniles often directly channel dietary carotenoids to plumage, a phenomenon that disappears as birds mature and develop elaborate age- and sex-specific carotenoid ornamentation (e.g., shift from Fig. 2a to b; pers. obs.). In other cases, especially in fancy poultry breeding, the feather follicle regulation of pigment deposition can evolve toward increased genetic control (Somes, 2003). Overall, such control of deposition at the network periphery ensures the robustness of the entire carotenoid transportation and deposition network much the same way as distributed regulatory modules enable robustness of carotenoid biosynthetic pathways.

Greater modularity of carotenoid pathways can be accomplished by decoupling of metabolism (Fig. 2c), transport (Fig. 2d), absorption from food (Fig 2e), or intake (Fig. 2f) of carotenoids used in ornamentation and carotenoids used in other organismal functions. Modularity in metabolism of ornamental carotenoids in birds typically involves feather follicle-specific processing of carotenoids (Brush, 1967; Fox et al., 1969; McGraw, 2004; Schlinger, Fivizzani, &Callard, 1989), whereas modularity in transportation might be accomplished by using distinct classes of lipoproteins for transportation of ornamental vs. other carotenoids (McGraw & Parker, 2006; Trams, 1969), a process that can also enable selective absorption of ornamental carotenoids in the intestine (Fox et al., 1969; Parker, 1996; Tyczkowski & Hamilton, 1986). Birds can also select specific ornamental carotenoids during foraging

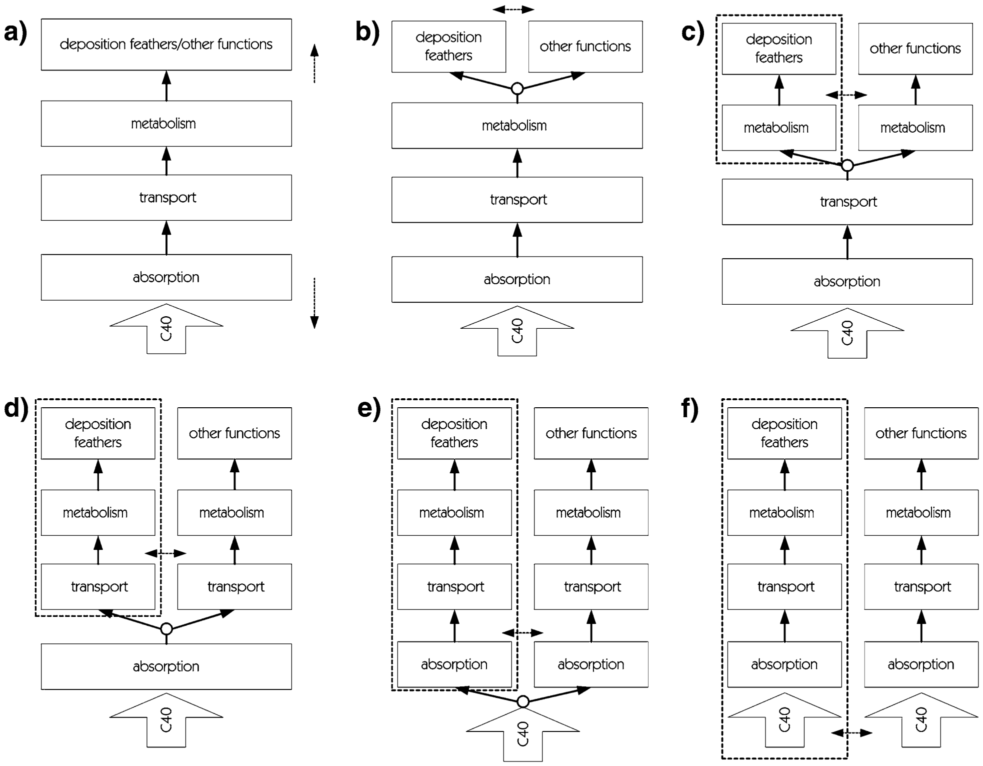

Fig. 2 Conceptual illustration of organism-wide processing and partitioning of consumed carotenoids (arrow with C40) for ornamentation vs. other functions. (**a**) Default state—no separation in intake, intestinal absorption, plasma transport, metabolism, or deposition of carotenoids between ornaments and other functions. Progressive partitioning and modularity at (**b**) deposition stage, (**c**) deposition and metabolism stages, (**d**) deposition, metabolism, and transport stages, (**e**) deposition, metabolism, transport, and absorption stages, and (**f**) all stages. Dashed contour outlines the boundaries of ornament-specific developmental module. Circle with two arrows indicate location of a developmental switchpoint for carotenoid allocation to ornament vs. other functions. Double headed arrow shows the phenotypic expression of a trade-off between expression of carotenoid ornamentation and other organismal functions

and thus decouple their consumption from that of other carotenoids (Fig. 2f, Hill, 2003). Finally, carotenoid storage and inheritance (Fig. 2e, f) limits the effects of environmental variability on carotenoid ornamentation; species vary widely in their ability to store diet-derived carotenoids from several years (Kritzler, 1943) to a few days (Test, 1969), and parental transference of carotenoids with egg yolk, food, or esophageal secretion not only provides initial pigments for the plumage coloration in some species, but can also facilitate carotenoid metabolism (see below).

Evolution of condition-dependence of carotenoid displays. The extent to which the expression of carotenoid-based plumage reflects organismal condition (e.g., fitness and performance in a particular environment) depends, proximately, on the location of regulatory switches on a carotenoid network (double-headed arrows in Fig. 2 indicate location of the main tradeoff under each scenario). Regulatory switches in Fig. 2 harbor condition-dependence to a degree that depends on their developmental linkage to the organism-wide carotenoid absorption, transportation, and deposition (Badyaev, 2004a). Consistent with such linkage is the observation that selection favoring extreme elaboration of carotenoid-based ornamentation in poultry often exposes extensive pleiotropic effects of carotenoid production on general growth and metabolism (Bitgood & Somes, 2003; Minvielle, Gourichon, & Moussu, 2005), and the documentation of temporally variable developmental trade-offs between carotenoid-based displays and other organismal functions (Badyaev & Duckworth, 2003; Badyaev & Vleck, 2007).

With this background in mind, how can we reconcile the diversity of biochemical, anatomical and physiological pathways by which animals convert environmentally available carotenoid precursors into their colorful displays with evolutionary persistence and elaboration of such displays? Central to this question is the understanding of fitness consequences of such variation, i.e., selection on ornament development.

Selection of Color Display Development

Selection on carotenoid pathways has favored only a small subset (described above) of all chemically accessible or structurally possible pathways; experimental relaxation of selection results in explosive diversification of both carotenoid products and their synthetic pathways (Arnold, Wintrode, Miaazaki, & Gershenson, 2001; Umeno et al., 2005). Why have so few pathways been exploited in the evolution of animal displays? Selection on carotenoid-based displays is expected to favor several seemingly contradictory features (Badyaev, 2004a): carotenoid displays are favored to combine robustness (to persist under diverse conditions) with environmental lability (to accommodate environmental variability in precursors) and combine extreme modularity (to enable greater elaboration) with greater organism-wide integration (to indicate organismal health and performance). With these general features of carotenoid pathways in mind, we can now revisit common patterns and targets of selection on color displays (Fig. 3a).

Selection for within-individual diversification of color displays should favor an increase in specificity of basal precursor uptake and greater branching and lesser connectivity of specific downstream enzymes, such that a single precursor can be converted into a wide variety of color displays (Fig. 3b). Selection for diversification can favor increased mutational or environmental lability of basal enzymes and greater specificity of downstream pathways which would similarly enable conversion of a novel precursor into a variety of novel colors. Such a pattern might be favored, as an initial step of ornament evolution, by sensory drive mechanisms of sexual selection or by selection for flexible, reversible, and life-history stage-dependent color polymorphisms.

Selection for stability and robustness of color displays would favor lesser specificity of basal enzymes and increased interconnectivity and interchangeability of downstream enzymes, so that diverse carotenoid precursors and metabolites can be accommodated and channeled through the network (Fig. 3c). Under this scenario, environmental variability in the amounts and kinds of precursors would not jeopardize the expression of carotenoid-based colors, a pattern evident in some domesticated species that were selected to maintain carotenoid-based coloration on a variety of diets (Craig & Foote, 2001; Somes, 2003; see also Hadfield & Owens, 2006). Precision of expressed colors (Fig. 3c) despite interchangeability of pathways can be accomplished by discarding unwanted final products during feather-specific carotenoid uptake or by depositing a mixture of different carotenoid types produced by distinct biosynthetic pathways. The latter would account not only for the continuous pattern of evolutionary change in carotenoid-based colors (e.g., Omland & Hofmann, 2005), despite discontinuous actions of enzymes underlying their biosynthesis, but also for the repeated convergence in color patterns in many lineages.

Robustness and redundancy of carotenoid pathways can enable pathway duplication and functional release, thus facilitating the evolution of modularity (Wagner & Altenberg, 1996; Young, Haselkorn, & Badyaev, 2007). *Selection for modularity*—greater integration among a set of elements involved in production of a color display (Fig. 3e) and weaker integration with other organismal structures should favor pathway duplication, as well as elimination or shortening of metabolic steps to accomplish greater linearity and additivity between elements of color production (Badyaev, 2005a). Such selection is commonly associated with greater elaboration of carotenoid displays; for example, modular transport of feather-bound carotenoids (Trams, 1969) is associated with extreme carotenoid coloration of the Scarlet Ibis (*Eudocimus rubber*). Further, robustness of carotenoid pathways is enhanced by their association with developmental mechanisms of feather growth (reviewed in Badyaev & Landeen, 2007); because feather growth is commonly assumed to be under stabilizing selection, such association can enable sustainable elaboration of carotenoid components favored by

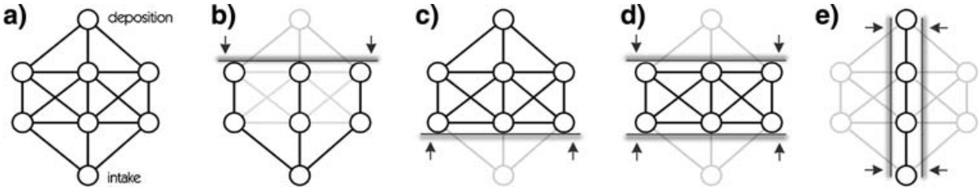

Fig. 3 Conceptual illustration of modifications of carotenoid biosynthesis network. Circles indicate enzyme nodes, connecting lines show transportation pathways of metabolites, and arrows with gray lines indicate direction and pattern of selection. Ontogeny proceeds from intake (bottom) to deposition (top). (**a**) Default state, (**b**) selection for within-individual diversification of color displays favors lesser connectivity of biosynthetic pathways, greater specificity in intake, and divergence at deposition pathways, (**c**) selection on redundancy of color displays favors lesser specificity of intake and greater interchangeability and connectivity of biosynthetic pathways, (**d**) selection on condition-dependency of color displays favors lesser specificity in intake and deposition pathways and greater integration among biosynthetic pathways and other organismal functions, and (**e**) selection on modularity in color displays favors specificity in intake, biosynthetic and deposition pathways, and linearity and exclusivity of the connections among them. Configuration shown in black in (**b**–**e**) is favored by selection

directional selection on carotenoid displays (Baatz & Wagner, 1997; Griswold, 2006).

Selection for condition-dependency in sexual ornamentation acts against modularity in color acquisition and development (Fig. 3d). Such selection would favor greater interconnection among elements and pathways of color production and lesser specificity of biosynthetic steps at either deposition or uptake stages, enabling, in the context of female choice under sexual selection, a comparison of the ability of individuals to develop color displays in different environmental contexts (Badyaev & Qvarnström, 2002; Badyaev, 2004b, 2005a).

Conflicting demands of robustness and elaboration in the development of carotenoid displays generate a number of testable evolutionary predictions. First, longer, more complex, and more robust developmental and biochemical pathways (Figs. 1, 2a, and 3d) should limit diversification of ornaments within a clade, but should facilitate convergence in displays by limiting assessable pathways of their development. Second, common dependence on organism-wide consumption and transport of carotenoids should result in a ubiquity of condition-dependent regulatory switches at the biosynthetic network periphery, indeed a common empirical finding. Third, greater modularity in developmental and biochemical pathways needed for elaboration of sexual ornaments should, in turn, make these pathways particularly vulnerable to disappearance under fluctuating environmental conditions or sex-linked inheritance. This predicts an empirical association between greater elaboration and greater diversification in color ornaments. Such association, in combination with selection for initial diversification of color displays (Fig. 3b) would produce an explosive diversification of carotenoid displays punctuated by periods of building up robustness and thus stasis and convergence in display expression (Badyaev, 2004a; Badyaev & Hill, 2003).

Reconciling Environmental Contingency and Inheritance in Color Phenotypes

What governs the development and diversification of biosynthetic pathways constructed each generation to accommodate environmental contingency of carotenoid-based displays? As the above discussion suggests, environmental contingency of carotenoid displays *determines* the evolutionary lability of their developmental causes. Yet, it is unclear *how* environmental sensitivity can evolve to enable developmental pathways to ‘‘predict’’ the precursor supply and to benefit from historical ‘‘experience’’ with such precursor, a situation similar to the evolution of stress-resistance strategies (e.g., Gluckman, Hanson, & Beedle, 2007; Young & Badyaev, 2007). The central issue here is the connection between the causes of developmental variation of carotenoid displays and the causes of inheritance of this variation, and there are three main principles behind such a connection.

First, reliability and predictability of the association of internal and external elements of carotenoid biosynthesis decreases through a displays’ ontogeny. Second, multiple inheritance systems are involved in development of colors and there might be an evolutionary transference from epigenetic to genetic inheritance systems. Third, robustness and environmental lability of complex networks might enable phenotypic and genetic accommodation of novel carotenoid elements; genetic accommodation of such novel environment-derived elements could be, in fact, the most common pathway for the evolutionary diversification of diet-derived displays.

Among the most ubiquitous patterns in carotenoid biosynthesis is an ontogenetic decrease in enzyme specificity, predictability of environmental components of biosynthetic pathways, and the similarity among individuals in developmental processes, which facilitates greater genetic heritability of the earliest and the most basal ontogenetic processes (Fig. 1). On the other end of the spectrum is epigenetic inheritance of the least reliable and most diverse peripheral processes and precursors in carotenoid metabolism (Fig. 1). For example, egg yolk carotenoids derived from maternal diet or transferred to offspring with food or esophageal secretion not only provides a source for coloration of offspring plumage in some species (Fitze, Tschirren, & Richner, 2003; Slagsvold & Lifjeld, 1985) but, more importantly, can provide the earliest, most reliable and locally appropriate, or the rarest sources of precursors needed for developmental formation of carotenoid biosynthetic pathways. Experimental prevention of carotenoid precursor transfer to offspring through yolk makes offspring unable to develop normal coloration later in life even on a normal diet (Blount, Metcalfe, Birkhead, &Surai, 2003; Karadas, Pappas, Surai, & Speake, 2005; Koutsos, Clifford, Calvert, & Klasing, 2003; Surai & Speake, 1998; Surai et al., 1998). Just as ubiquitous as yellow carotenoid-derived color of egg yolk in birds are behavioral inheritance and imprinting (Cate & Bateson, 1988; Cushing, 1941), including of species-specific food sources of carotenoid precursors. Such short-term inheritance enables rapid spread of a novel carotenoid source in a population, producing temporal and spatial similarity among individuals in developmental accommodation of the novel source, and thus significantly facilitating evolution (Jablonka, 2001; Oyama, 2000). Genetic inheritance of the most predictable upstream components and epigenetic inheritance of short-term modifications or peripheral components may reflect successive accumulation of the most recurrent, and thus now most basal, environment–organism developmental configurations over millions of generations. It is precisely this successive accumulation that builds in contingency and redundancy in carotenoid developmental pathways that can be used instantaneously when the present and past environmental conditions match (Caropale, 1999; Chetverikov, 1926; Gilbert, 2001, 2005; Wagner, 2003; Young & Badyaev, 2007).

This view emphasizes genetic inheritance as the most reliable mechanism for evolutionary retention of the most recurrent organism–environment interactions. Within each generation, however, coloration 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 acquisition, metabolism, transportation, and deposition (Badyaev, 2005a). To the extent these ‘‘developmentally entangled’’ (sensu Rice, 2001) complexes of traits have independent effects on fitness, they are influenced by natural selection and the predictability of such selection favors stable configurations among these elements (Wagner & Schwenk, 2000). In turn, the complexity of biosynthetic pathways not only facilitates retention of novel elements, but also determines the similarity in pathways in which novel change is expressed among individuals (e.g., Badyaev & Foresman, 2004), facilitating a uniform response to novel selection pressures (West-Eberhard, 2003). The higher fitness of individuals possessing the novel element might ultimately lead to genetic assimilation of the novel precursor or metabolite in the new environment (Badyaev, 2005a; Gilbert, 2001; Nanjundiah, 2003; Pigliucci, Murren, & Schlichting, 2006; Schmalhausen, 1949; West-Eberhard, 2005). Specifically for evolution of carotenoid displays in birds, there is a close association between complex developmental circuitry of feather diversification (Prum, 2005; Yu, Wu, Widelitz, & Chuong, 2002; Yu et al. 2004; Yue, Jiang, Widelitz, & Chuong, 2005) and carotenoid deposition (Lucas & Stettenheim, 1972; Olson, 1970; Troy & Brush, 1983). Such entanglement with feather growth might facilitate genetic assimilation of a novel carotenoid compound, resulting in frequently documented modification of feather structure following deposition of a novel carotenoid pigment (Hudon 1991; reviewed in Badyaev & Landeen, 2007). It seems likely, therefore, that genetic assimilation and genetic accommodation might not only serve as a bridge between ubiquitous environmental induction of novel carotenoid elements and genetic inheritance of carotenoid coloration, but also be the most common pathway for the evolutionary diversification of diet-dependent colors.

Because animal color patterns combine components of distinct developmental origins into co-inherited and complex configurations, the study of animal coloration was central to the foundational work of quantitative genetics and the modern evolutionary theory. In this essay, I suggest that it is similarly uniquely suited, not only to resolve currently unanswered questions of diversification in organismal forms, but perhaps to usher in a novel evolutionary synthesis that integrates explicitly trait origination, maintenance, and evolution.

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