

Complexity and integration in sexual ornamentation: an example with carotenoid and melanin plumage pigmentation

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Abstract

Sexual ornaments often consist of several components produced by distinct developmental processes. The complexity of sexual ornaments might be favoured by mate choice of individual components in different environments which ultimately results in weak interrelationships (integration) among the developmental processes that produce these components. At the same time, sexual selection for greater exaggeration of individual components favours their stronger co-dependence on organismal resources. This should ultimately produce stronger condition-mediated integration among ornaments' components in individuals with the most exaggerated ornamentation. Here we distinguish between these two sources of integration by examining the relationship between integration and elaboration of sexual ornamentation in three bird species: two with carotenoid-based sexual ornamentation (the house finch, *Carpodacus mexicanus* and common redpoll, *Carduelis flammea*) and a species with melanin-based sexual ornamentation (house sparrow, *Passer domesticus*). We found that integration of components varied with elaboration of carotenoid-based ornamentation but not of melanin ornamentation. In the house finches, integration was the highest in individuals with small ornaments and decreased with ornament elaboration whereas the pattern was the opposite in common redpolls. These results suggest that in these species integration and complexity of carotenoid-based ornamental components are due to shared condition-dependence of distinct developmental pathways, whereas integration and complexity of the melanin ornamentation is due to organismal integration of developmental pathways and is largely condition- and environment-invariant. Thus, functionally, ornamentation of the house sparrows can be considered a single trait, whereas complexity of the house finch and redpoll ornamentation varies with ornament elaboration and individual condition.

Introduction

Female choice of mates is often based on sexual ornamentation that reveals male physiological condition and health (Kodric-Brown & Brown, 1984; Andersson, 1986). Such preference favours traits that are well integrated into multiple organismal processes and thus summarize reliably male's overall condition (Zahavi, 1975; Grafen, 1990). Yet, because benefits that females

receive from mating are often specific to the ecological and social environment in which breeding occurs, different aspects of male condition might be important in different environments (Tregenza & Wedell, 2000; Qvarnström, 2001; Badyaev & Qvarnström, 2002; Wedekind, 2002). Moreover, the production of composite sexual ornamentation is affected by organismal processes with varying degrees of condition-dependence (Wedekind, 1992; Pomiankowski & Møller, 1995; Møller, 1996). A combination of female preference for different aspects of male condition and variable condition-dependence of developmental pathways that produce male sexual ornaments often result in the evolution of composite sexual displays (Gerhardt, 1991; Wedekind,

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1992; Moore, 1997; Calkins & Burley, 2003; Badyaev, 2004).

A better understanding of the evolution of sexual ornaments and preference for these traits requires a conceptual perspective that explicitly incorporates developmental and functional interrelationships (integration) between components of ornamentation, yet current studies of sexual selection largely ignore developmental concepts. The developmental perspective states that selection on sexual ornamentation is the selection on aspects of its ontogeny (Emlen & Nijhout, 2000; West-Eberhard, 2003); the ultimate target of selection for greater condition-dependence and exaggeration of sexual ornamentation is then the allocation of resources and energy between developmental pathways that construct the sexual ornament and those that produce the rest of the organism (Badyaev, 2004).

A close correlation between components of a sexual ornament can be produced either by shared developmental pathways (developmental integration) or by the involvement in the same function (functional integration). Distinguishing between these sources of integration is crucial for understanding the evolution of sexual ornamentation under sexual selection. For example, close developmental integration among components of a composite sexual trait might be maintained by within-organism selection favouring developmental cohesiveness of a composite trait (Whyte, 1965; Schlichting & Pigliucci, 1998; Wagner & Schwenk, 2000; Badyaev, 2004). The intensity and pattern of such selection might be invariant across a range of external environments (Nijhout & Emlen, 1998; Wagner & Schwenk, 2000; Fusco, 2001). Consequently, sexual selection that favours greater developmental integration of a sexual ornament might ultimately act on organismal properties that enable maintenance of organismal homeostasis across a wide range of environments. On the contrary, close functional integration of a complex sexual display might be due to selection exerted by other individuals (e.g. opposite sex, signal receivers, predators) or the external environment (Guilford & Dawkins, 1991; Endler, 1992; Moore, 1997; Calkins & Burley, 2003). The intensity of such selection varies strongly with social and ecological environments in which breeding occurs and, thus, sexual selection for closer functional integration ultimately acts on individual condition (i.e. individual performance in a given environment) (de Jong, 1993; Price *et al.*, 1993; Pomiankowski & Møller, 1995; Rowe & Houle, 1996; Dale *et al.*, 2001).

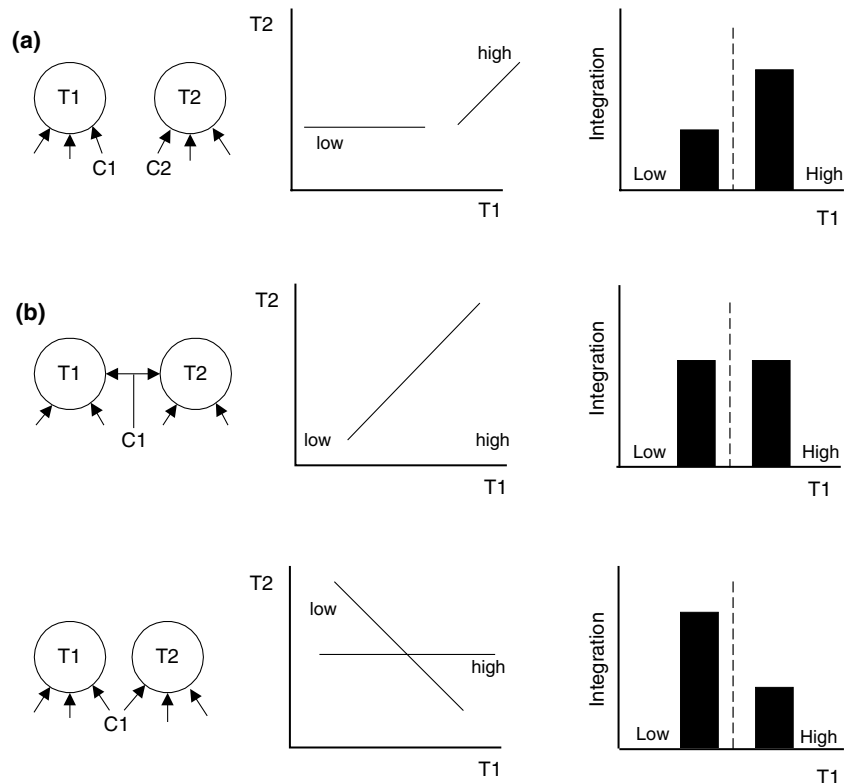
Contrasting integration of ornaments' components across levels of ornament elaboration allows for the ability to distinguish between several scenarios of integration in sexual ornamentation (see below), with the ultimate goal to understand what, in composite sexual ornaments, constitutes a 'trait' – the unit that is, functionally, a target of current selection (Nijhout, 1994; Wagner, 2001). Different levels of developmental integration and co-dependence on organismal condition

result in distinct relationships between ornament integration and elaboration (Fig. 1; de Jong, 1993; Nijhout & Emlen, 1998; Emlen & Nijhout, 2000; Stevens *et al.*, 2000; Dale *et al.*, 2001). First, if components of sexual ornamentation do not share either a common resource pool or developmental precursors (Fig. 1a), the relationship between them is expected to remain constant across levels of elaboration. However, on a population level, the integration between these developmentally-independent components will be higher in individuals with a greater exaggeration of sexual ornamentation because these individuals will have maximum expression of these components because of their higher condition (Fig. 1a). Second, if components divide resources by constant allocation rules, the relationship between integration of components and ornament elaboration is expected to remain constant (Fig. 1b, above). Finally, if components of sexual ornament trade-off common resources during development (Fig. 1b, below), their integration will depend on the pool of shared resources. Integration of ornament's components is expected to be stronger in individuals in low condition, and weaker in individuals in higher condition (Fig. 1b, below).

Contrasting roles of developmental integration vs. shared condition-dependence are well illustrated by comparing carotenoid and melanin-based ornamentation. In birds, carotenoid-based plumage ornamentation depends on the ingestion of carotenoid precursors, and components of carotenoid-based ornamentation are expected to be closely related to individual condition and individual ability to extract carotenoids from the environment (Endler, 1983; Hill, 1999; Badyaev & Hill, 2000). In contrast, the production of melanin-based ornamentation depends more on individual physiological processes and less on the environment (Fox, 1976; Murphy & King, 1987; McGraw & Hill, 2000). Thus, the integration of components of carotenoid ornamentation should be mediated by common condition-dependence because of the distinct effect of environment on individual ornamental components (Cheverud, 1996; Dale *et al.*, 2001). Such integration is expected to vary across environments and between individuals in different physiological condition (Fig. 1; Badyaev *et al.*, 2001). In contrast, integration between components of melanin-based ornamentation is likely to be due to close and invariant interrelationships between developmental processes (Fig. 1; Dale *et al.*, 2001) and, thus, is not expected to vary across environments or levels of elaboration.

Here we examine patterns of integration between components of sexual ornamentation in three species of passerine birds (Fig. 2) – the house finch *Carpodacus mexicanus*, common redpoll *Carduelis flammea*, and the house sparrow *Passer domesticus*. In all three species, ornamental coloration plays an important role in sexual displays and is a subject of sexual selection (Møller, 1990; Hill, 1991; Knox & Lowther, 2000). We specifically considered four distinct components of breast plumage

Fig. 1 Conceptual illustration of shared developmental pathways of two components of a sexual ornament (T1 and T2) versus shared condition-dependence on integration of sexual ornamentation. (a) Left: developmentally independent T1 and T2 have separate inputs of organismal condition (C1 and C2). Centre: the slope of the relationship between T1 and T2 is zero, except in high quality individuals; Right: integration among ornament components will be stronger in individuals with greater elaboration of ornamentation and of higher quality; (b). Above: left: developmentally independent T1 and T2 have common and invariant input of organismal resources C1; centre: the relationship between T1 and T2 is consistently positive; right: integration among components of ornamentation will not vary with ornament elaboration. (b) Below: left: developmentally independent T1 and T2 trade-off common input of organismal resources C1; Centre: the relationship between T1 and T2 depends on individual quality; it is negative in low quality individuals and zero in high quality individuals. Right: integration of ornamentation will be weaker in individuals in higher physiological condition (with greater elaboration of sexual ornamentation).



ornamentation (after Hill, 1992, 1994; Badyaev *et al.*, 2001): (1) pigment elaboration (hue) – a function of both the quantity of pigments deposited in growing feather and of pigment metabolism (Stradi *et al.*, 1997; Jawor & Breitwisch, 2003), (2) ornament area – a function of number of feather follicles that are receptive to pigment uptake during moult, (3) hue consistency – a variation among follicles in the type and amount of deposited pigment and (4) area symmetry – bilateral consistency of follicle activation – a function of additional, organism-wide, processes during moult (Badyaev *et al.*, 2001).

We first show that despite distinct biochemical origin of carotenoid and melanin ornamentation (Brush & Power, 1976; Troy & Brush, 1983; Stradi *et al.*, 1997), variation in their components is similar among three species. Secondly, we document that inter-correlations between ornament components vary with ornament elaboration. Thirdly, we examine the contribution of individual variation to integration of sexual ornaments in the three species. We show that integration among components of carotenoid-based ornamentation is likely due to a shared co-dependence of developmentally distinct pathways on individual condition, whereas integration in melanin-based ornamentation is mostly because of shared developmental pathways (i.e. developmental integration) and is condition-invariant. We discuss the implications of these findings to the evolution of sexual ornamentation.

Materials and methods

The study site was a cluster of ornamental shrubs and small trees set in an open grassland near Missoula, Montana (for details of the study site and field protocol see Badyaev & Martin, 2000). Seventy-nine resident male house sparrows, 95 resident male house finches, and 76 wintering male common redpolls were captured during February–March, 2002 and 2003, at permanent feeding stations using mist-nets. In redpolls, only individuals with pronounced breast ornamentation [i.e. older than a year of age (Knox, 1988)] were used in these analyses. Because of the continuous monitoring of the resident house finch and house sparrow populations at the study site since 1994, the age of most individuals was known. For this study, we used male house finches that were 1 year old (second-year males) at the time of capture and male house sparrows that were either 1 or 2 years old (second- or third-year males). The short capture period allowed us to minimize the effects of sampling and feather wear as well as standardized the time since the post-breeding (early autumn) moult in all three species.

Ornamental breast patch (Fig. 2) of all males was photographed using a 4-megapixel digital camera outfitted with a ring flash and mounted in a standard position (see Badyaev *et al.*, 2001 for details of the protocol). Males were placed in a standardized position on the dorsal side with the anterior point of the beak held in place. The

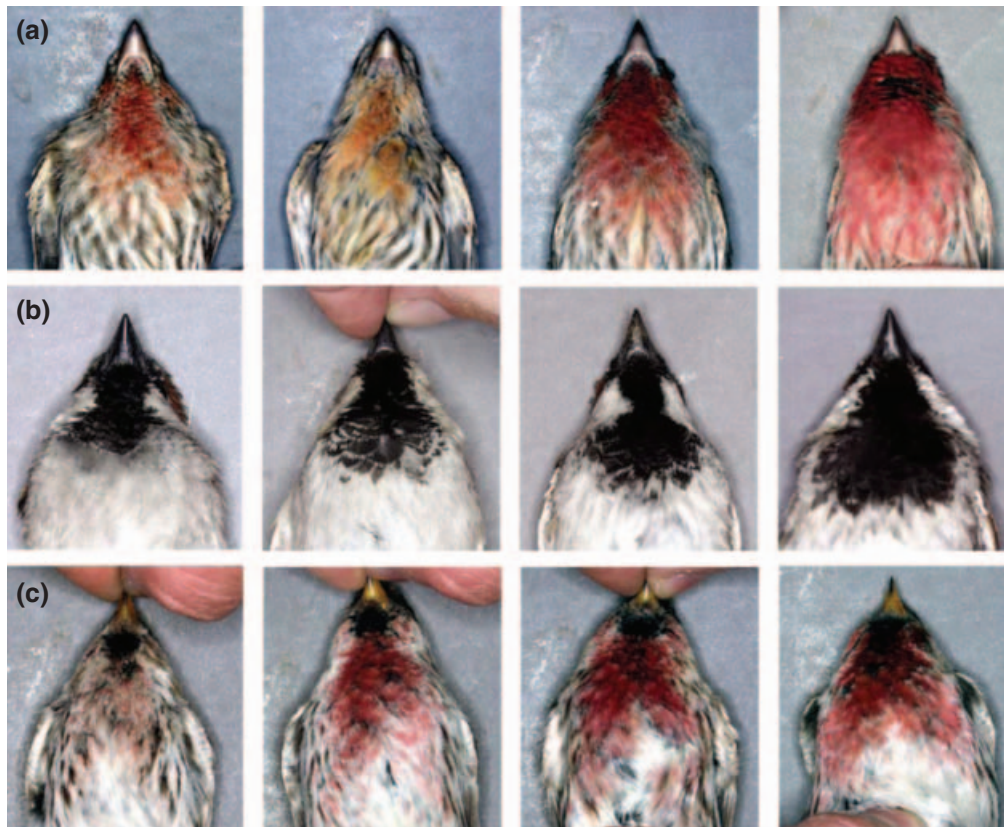


Fig. 2 Examples of levels of elaboration of sexual ornaments (increasing from left to right) in (a) carotenoid-based coloration of house finches, (b) melanin-based coloration of house sparrows, and (c) carotenoid-based coloration of common redpolls.

photography was done with constant distance and light settings against a neutral gray background with scale markings and colour standards; outside light was blocked (see Badyaev *et al.*, 2001; and Badyaev & Duckworth, 2003 for analyses of the effect of bird position in the photostand on repeatability of measured traits).

For the ventral plumage region of each male we recorded (1) plumage hue – a measure of continuous pigment elaboration (from yellow to purple and from gray to black) within the range of male coloration at tenths of percentiles from 1 to 10, (2) patch area – the area of all ornamental feathers with ornamental pigmentation, (3) patch area asymmetry – a measure of bilateral symmetry in the number of ornamented feathers between left and right side and 4) hue consistency – a measure of consistency in plumage hue across the ornamented patch (Badyaev *et al.*, 2001). Patch area and asymmetry were measured with SigmaScan Pro 5.0 image analysis software (SPSS, Inc.). To measure patch area, a straight line was drawn on the image from the base of the bill to the lowest pigmented feather on the breast. All pigmented feathers on a male's breast were traced using colour thresholds first on the left side and then on the right side, and patch area was calculated using the trace measure-

ment and area function in SigmaScan. Left and right sides were added together to obtain the total patch area. To measure colour hue and colour saturation, a 10×10 pixel grid was overlaid on each image and one pixel was sampled in each square of the grid that covered the breast patch. This technique allowed us to sample every part of the ornamental patch and, therefore, obtain an accurate representation of the overall hue (see Badyaev & Duckworth, 2003 for details). Hue consistency across the patch was recorded on a scale of 1–10, as a per cent of feathers different in hue group between the left and right side – at tenths of percentiles: 0–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100%. All components of male coloration were measured twice and several days apart. Variances associated with remeasuring ($n = 2$ sets) were calculated with a mixed model nested ANOVA and are shown in Fig. 6.

Within each species sample, birds were classified based on the area of the ornamental patch into three categories with equal number of birds in each one: 'small ornament' (lower 33%), 'medium ornament' (middle 33%) and 'large ornament' (upper 33%). Area and area asymmetry measures were natural log-transformed and hue and hue consistency were arcsin-transformed before the analyses.

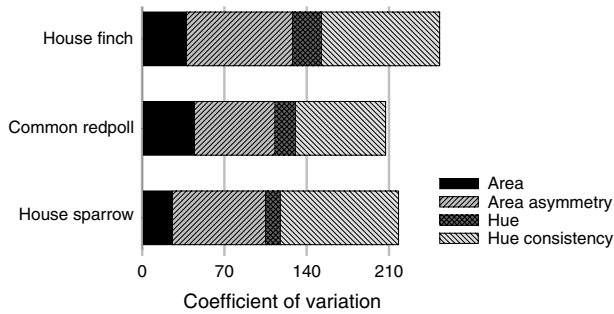


Fig. 3 Variation (coefficient of variation) of four ornamental components in the house finch, common redpolls, and the house sparrow.

Index of integration among components of sexual ornamentation (hereafter integration) was calculated as the first eigenvalue of the correlation matrix of the normal-

ized data. Differences between integration levels within each species were assessed with multiple range *t*-test.

Results

Components of sexual ornaments had similar variability among the three species (Fig. 3). The species with the most variable area of ornamentation was the common redpoll (CV = 36.6%), followed by the house finch (29.0%) and the house sparrow (26.6%). Hue was the most variable in the house finch (18.9%), followed by redpoll (16.3%) and the house sparrow (13.8%). Area asymmetry and hue consistency were more variable in the house finch (109.5 and 90.3% correspondingly) and the house sparrow (106.2 and 79.2%) compared with redpoll (76.3 and 68.8%; Fig. 3).

Integration among ornamental components differed among levels of ornament expression and species (Fig. 4). In the carotenoid-based ornament of the house finch,

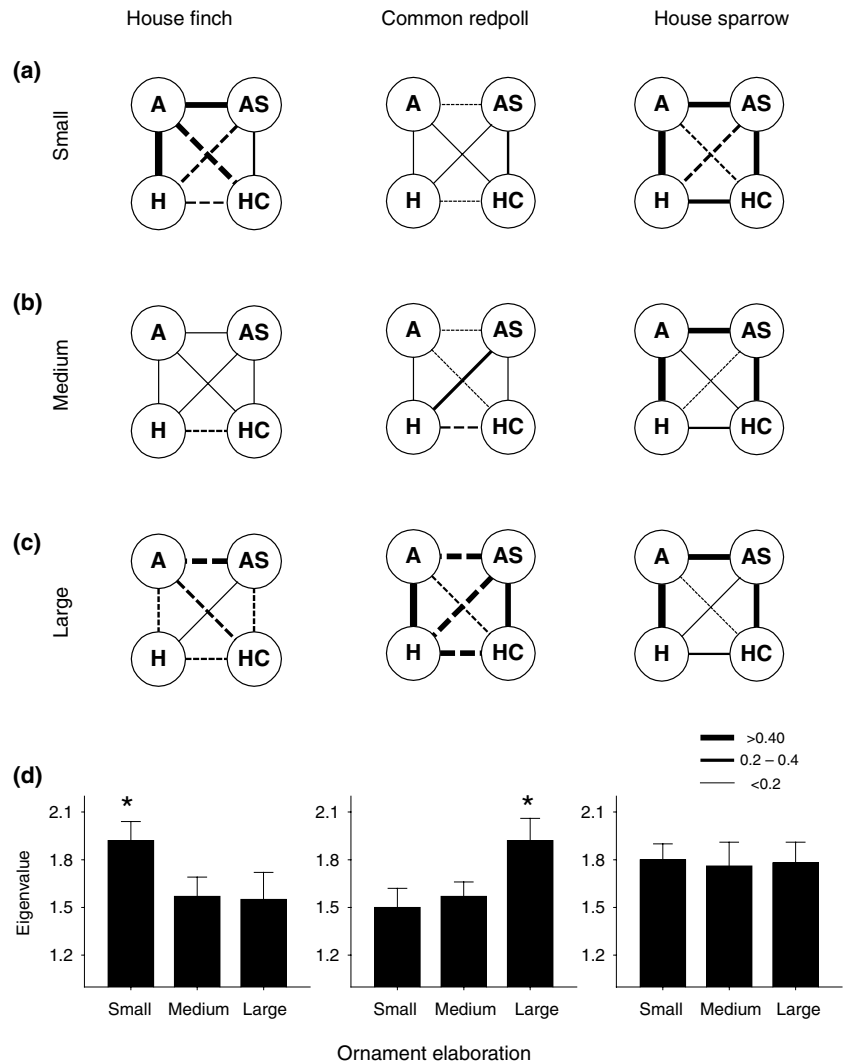


Fig. 4 (a–c) Partial correlations among ornamental components (A, area; H, hue; AS, area asymmetry; HC, hue consistency) in (a) small ornaments, (b) medium ornaments and (c) large ornaments. (d) Index of integration (first eigenvalue of correlation matrix; mean and bootstrapped SE) among ornamental components in the house finch (left), common redpoll (centre), and the house sparrow (right). Integration is the strongest in males with small ornamentation in the house finches ($t = -6.51, P < 0.01$), in males with most elaborated ornaments in the common redpoll ($t = 5.88, P < 0.01$) and not different among levels of elaboration in the house sparrow ($t = 0.11, P = 0.87$). Asterisk indicates statistical significance at $\alpha < 0.05$. Thick lines indicate standardized regression coefficients that were significant at $\alpha < 0.05$ (thickness is proportional to strength), thin lines indicate nonsignificant regressions, dashed lines indicate negative regressions.

integration was the highest in the least ornamented males (Fig. 4d). In males with a small sexual ornament, partial correlations were particularly high between hue and area and between area and hue consistency (Fig. 4a). In this group, greater elaboration of area and hue components was associated with greater asymmetry and lesser hue consistency (Figs 4a and 5). In males with a large sexual ornament, the relationship between area and area asymmetry was strongly negative (Figs 4c and 5b) – males with a maximum elaboration of an ornament had the most symmetrical ornamentation (Fig. 5). In males with intermediate sexual ornament, ornamental components were not correlated (Figs 4b and 5).

In common redpolls, carotenoid-based ornamental components were largely independent of each other in males with small and intermediate sexual ornaments (Figs 4a, b and 5). In males with large ornamentation, the integration and partial correlations among components were high (Figs 4c, d and 5a). Similarly to the house finch, in males with large sexual ornaments, the relationships between area and area asymmetry was strongly negative (Fig. 5b); males with a maximum exaggeration of sexual ornamentation had the most symmetrical ornamentation (Figs 4c and 5).

In melanin-based ornamentation of the house sparrow, integration was high and did not differ between levels of ornament elaboration (Fig. 4d). Males with greater elaboration of sexual ornamentation had the least symmetrical ornaments (Figs 4c and 5b), and partial correlations between hue and area of ornament were particularly high in males with small sexual ornamentation (Figs 4a and 5a).

Contribution of among-individual variation to ornament integration differed between species and levels of ornament elaboration (Fig. 6; $F_{\text{species} \times \text{level}} = 2.19$, d.f. = 4, $P = 0.04$; overall $F = 38.43$, d.f. = 220, $P < 0.001$). In the house finch, the contribution of individual variation to ornament integration was the greatest in males with small sexual ornament, and the lowest in males with large sexual ornament (Fig. 6a; $F_{\text{level}} = 42.73$, d.f. = 2, $P < 0.001$; $F_{\text{individual}} = 2.87$, $P = 0.0004$; $F_{\text{level} \times \text{individual}} = 2.46$, d.f. = 11, $P = 0.02$; overall $F = 9.20$, d.f. = 49, $P < 0.001$). On the contrary, in common redpolls, the contribution of individual variation to ornament integration was the highest in males with the most exaggerated ornaments, and the lowest in males with small and medium ornaments (Fig. 6b; $F_{\text{level}} = 26.5$, d.f. = 2, $P < 0.001$; $F_{\text{individual}} = 9.90$,

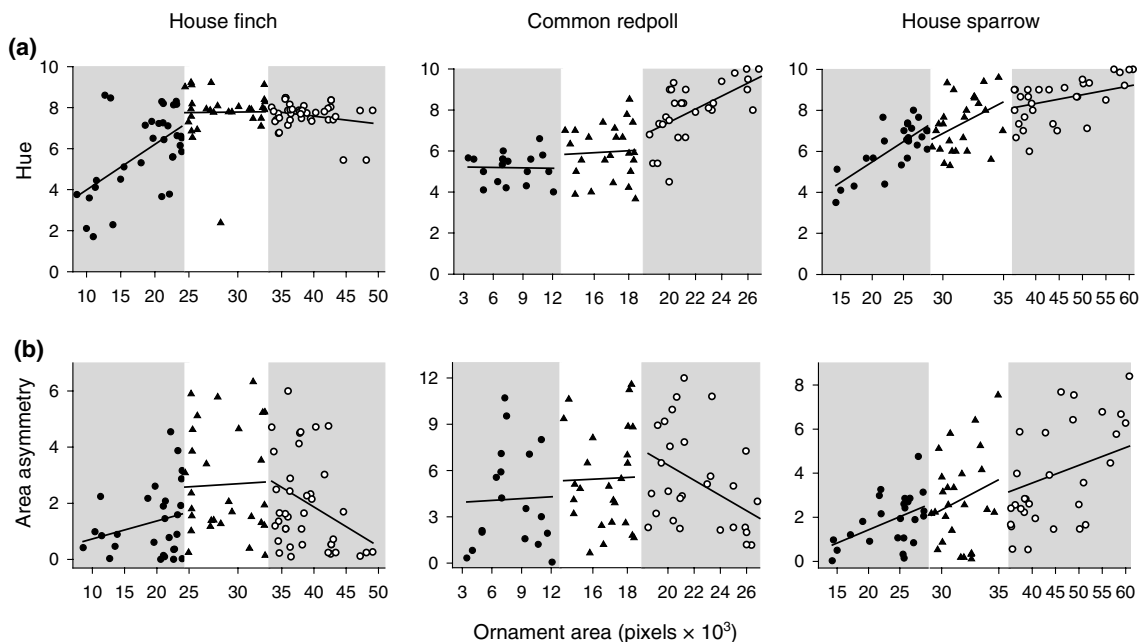


Fig. 5 Simple regression plots illustrating the relationship between ornamental area and (a) hue of ornamentation in the house finch [left; small ornamental area: $b_{ST} = 0.57$, $t = 3.78$, $P < 0.001$; medium ornamental area: $b_{ST} = 0.01$, $t = 0.10$, $P = 0.91$; large ornamental area: $b_{ST} = -0.23$, $t = 1.54$, $P = 0.13$], common redpoll (centre; small: $b_{ST} = -0.03$, $t = 0.11$, $P = 0.90$; medium: $b_{ST} = 0.05$, $t = 0.24$, $P = 0.81$; large: $b_{ST} = 0.64$, $t = 4.29$, $P < 0.001$), and the house sparrow (right; small: $b_{ST} = 0.77$, $t = 5.65$, $P < 0.001$; medium: $b_{ST} = 0.41$, $t = 2.03$, $P = 0.05$; large: $b_{ST} = 0.44$, $t = 2.70$, $P = 0.02$), (b) area asymmetry in the house finch (left; small: $b_{ST} = 0.26$, $t = 1.29$, $P = 0.20$; medium: $b_{ST} = 0.04$, $t = 0.22$, $P = 0.87$; large: $b_{ST} = -0.33$, $t = -2.00$, $P = 0.05$), common redpoll (centre; small: $b_{ST} = 0.03$, $t = 0.12$, $P = 0.87$; medium: $b_{ST} = 0.02$, $t = 0.12$, $P = 0.91$; large: $b_{ST} = -0.44$, $t = -2.45$, $P = 0.02$), and the house sparrow (right; small: $b_{ST} = 0.48$, $t = 2.61$, $P = 0.01$; medium: $b_{ST} = 0.20$, $t = 1.07$, $P = 0.31$; large: $b_{ST} = 0.41$, $t = 2.29$, $P = 0.03$). Alternatively shaded areas represent levels of ornament elaboration (small, medium, large; from left to right).

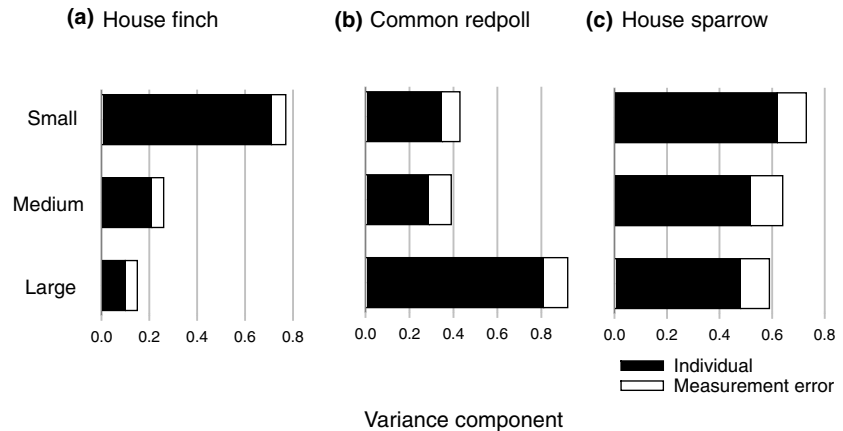


Fig. 6 Contribution of among-individual variation (i.e. individual identity) and measurement error to variation in integration index of sexual ornamentation across levels of ornament elaboration in (a) the house finch, (b) common redpoll, and (c) the house sparrow.

$P < 0.001$; $F_{\text{level} \times \text{individual}} = 2.16$, $P = 0.03$; overall $F = 32.4$, d.f. = 64, $P < 0.001$). In house sparrows, the contribution of individual variation to ornament elaboration was high but did not differ between levels of ornamentation (Fig. 6c; $F_{\text{level}} = 0.80$, d.f. = 2, $P = 0.45$; $F_{\text{individual}} = 7.95$, $P < 0.001$; $F_{\text{level} \times \text{individual}} = 0.08$, $P = 0.96$; overall $F = 12.84$, d.f. = 70, $P < 0.001$).

Discussion

Sexual ornaments often consist of multiple components of distinct developmental origin (Wedekind, 1992; Emlen & Nijhout, 2000). Variable and flexible relationships among components during development (i.e. weak developmental integration because of shared developmental precursors or developmental pathways) might enable rapid elaboration and diversification of composite sexual traits (Badyaev, 2004). For example, the rapid evolution and diversification of complex pheromones and acoustic signals (Gerhardt, 1991; Moore, 1997; Murphy & Gerhardt, 2000), composite components of genital morphology (Eberhard, 1985; Cordoba-Aguilar, 2002; Dixon & Anderson, 2002), floral displays (Conner & Sterling, 1996; Armbruster *et al.*, 1999), sexually selected weapons such as canine teeth and antlers (Manning & Chamberlain, 1993; Wright, 1993; Schwartz & Dean, 2001) and carotenoid-based sexual ornamentation (Badyaev & Hill, 2000) is thought to be facilitated by weak developmental integration among display components in combination with strong sexual selection for precise function of an entire sexual display.

Studies of complexity and integration between components of sexual displays have provided important insights into the evolution of mechanisms that produce complex sexual traits (reviewed in Badyaev, 2004). For example, in the cockroach *Nauphoeta cinerea*, males produce a sex pheromone that consists of many chemical components (Moore, 1997). Whereas each of the individual components is under directional selection by different functions (e.g. Moore & Moore, 1999), the

entire composition of the pheromone is maintained by internal stabilizing selection (*ibid.*). Similarly, in the house finch, the composite nature of carotenoid-based plumage ornamentation might be maintained by variable natural selection on its components (Badyaev *et al.*, 2001). Weak developmental integration among components of sexual ornaments in this species is further revealed by flexible allocation of organismal resources into components of sexual ornamentation between successive moults of the same individual (Badyaev & Duckworth, 2003).

The contrast between the patterns produced by shared developmental pathways and those produced by co-dependence of distinct developmental pathways on organismal condition is evident in comparison of selection on carotenoid- vs. melanin-based sexual ornamentation – the focus of this study. Because more precursors of carotenoid-based pigmentation have to be acquired from the diet, carotenoid coloration is highly dependent on the external environment (Endler, 1983). The functional expression of carotenoid-based ornamentation requires coordination of developmentally distinct processes of carotenoid consumption, digestion, transportation and deposition (Badyaev *et al.*, 2001; Hill, 2003). Each of these processes has different costs in different environments and might be subject to different intensity of sexual selection (Seutin, 1994; Badyaev *et al.*, 2001).

By contrast, melanin-based sexual ornamentation has strong developmental integration of production and deposition. Melanins are synthesized during amino-acid metabolism, and most of the precursors required for this synthesis are produced by within-organismal processes (Fox, 1976; Jawor & Breitwisch, 2003). Melanin deposition in integuments depends on the activity of melanocytes, the interaction of the melanocyte with the epidermis, and, in some taxa, concerted interactions among different melanocytes, and these developmental processes are strongly integrated (references in Price & Pavelka, 1996; Seehausen *et al.*, 1999; Badyaev & Hill, 2000). Because of the extensive integration of melanin

developmental pathways in multiple organismal functions, melanin ornaments should be good indicators of the organismal homeostasis but lesser indicators of local adaptation or performance in local environment compared with carotenoid ornaments (Badyaev, 2004). Strong internal integration of production of melanin-based ornaments may limit their variability and sensitivity to external environment compared with that of carotenoids (Gray, 1996; Badyaev *et al.*, 2002; Badyaev & Hill, 2003). However, stronger genetic determination of melanin ornaments makes them excellent signals of individual identity; the majority of cases of plumage polymorphism in birds are genetically determined and environment-invariant melanin based morphs (reviewed in Lank, 2002; Galeotti *et al.*, 2003).

Our study of the origin of complexity in sexual ornamentation produced three main results. First, we found that integration among components of sexual ornamentation varied with elaboration of carotenoid-based plumage in redpolls and house finches, but did not vary with elaboration of melanin-based ornamentation in house sparrows. Second, the correlation between integration and elaboration was positive in redpolls and negative in house finches. In both species, only individuals with the most elaborated ornaments accomplished the most symmetrical and consistent in colour ornamentation suggesting that these individuals were in better overall condition. Finally, we documented that contribution of among-individual variation to integration of an ornament was the highest in the least ornamented house finch males and in the most ornamented redpoll males, but was not different across levels of ornament elaboration in the house sparrow.

Taken together, these results suggest that integration in composite carotenoid-based ornamentation of house finches and redpolls is produced by shared condition-dependence of distinct developmental pathways. On the contrary, integration of the composite melanin-based ornamentation of the house sparrows might be due to shared developmental pathways with limited effects of shared condition- or environment-dependence. These results raise several questions. First, why are the patterns of integration different between the two species with carotenoid-based ornamentation? Secondly, why is integration invariant across levels of ornament elaboration in melanin ornamentation of the house sparrow? Thirdly, what are the consequences of the documented patterns of integration to sexual selection on ornamentation?

Sexual selection studies commonly treat sexual ornamentation as single traits despite wide recognition of distinct developmental processes that produce ornament components. This is often justified by the observation of close correlations between ornament components in a fully developed ornament. For example, individuals with the largest area of sexual ornamentation might also have the most colour-saturated ornamentation. However,

such integration of the most elaborated ornaments can be due to individuals in better condition being able to produce a maximum expression of several developmentally distinct components. Integration because of shared condition-dependence might conceal the composite nature of sexual ornamentation.

Results of this study suggest that close integration of ornamental components in carotenoid-based ornamentation is a result of a shared condition-dependence of components rather than their shared developmental pathways (Fig. 4, see also Seutin *et al.*, 1992). These results, in combination with field documentation of distinct selection on different components of carotenoid ornamentation, and the experiments revealing distinct developmental pathways of carotenoid ornament production (Hill, 2000; Badyaev *et al.*, 2001; Badyaev & Duckworth, 2003) suggest that each of the components of carotenoid-based ornamentation constitutes an individual 'trait' and integration among these components in the full expression of the ornament is accomplished by shared condition-dependence. Dale *et al.* (2001) suggested that common condition-dependence produces close integration among components of sexual ornamentation. The results of our study extend these ideas by suggesting that integration of sexual ornamentation depends on ornament elaboration in traits that reveal individual performance in a particular environment, but not in traits with lesser condition-dependence.

On the contrary, in melanin-based ornamentation of the house sparrow, integration among components was strong and not different between levels of ornament elaboration. Studies of environmental dependency of melanin-ornamentation of house sparrow differ in conclusions (e.g. Veiga & Puetra, 1996; Gonzalez *et al.*, 1999; Griffith *et al.*, 1999), however, most have suggested that the expression of components of melanin-based ornamentation is difficult to decouple by manipulating diet and other aspects of the external environment (e.g. Evans *et al.*, 2000). The contribution of individual variation to the integration of components was uniformly high between levels of elaboration of melanin ornamentation (Fig. 6). Moreover, individuals with the largest expression of sexual ornamentation had the highest asymmetry in ornament distribution (Fig. 5b). Taken together, these results point to a limited role of the external environment in the expression of ornamentation of house sparrows in this population. Close and invariant (in relation to ornament elaboration) integration of components of melanin ornamentation suggests that the entire ornament of the house sparrow is a single 'trait', such that selection acting on one of the components will have strong effects on other components because of the integrated developmental pathways. These results are consistent with pronounced effect of strong developmental integration of melanin ornamentation on historical patterns of their diversification (Price & Pavelka, 1996).

Why is the relationship between integration and elaboration of a composite sexual ornament opposite in the house finches and the redpolls? The lack of integration among ornamental components in male house finches with the most elaborated ornaments (Fig. 4c,d) may be due to ornament-specific developmental pathways that accomplish lesser condition dependence of the sexual ornamentation. For example, only during the first moult of life do house finches develop pathways of carotenoids deposition in the unpigmented feathers. Replenishing of carotenoid pigment and other necessary components (e.g. oils) in growing feather follicle in subsequent moults might utilize already established developmental pathways, as these moults involve changes from pigmented to pigmented feathers. Alternatively, more ornamented males might be able to find better quality carotenoid precursors thus lessening the condition-dependence of carotenoid metabolism (Badyaev *et al.*, 2001; Badyaev & Duckworth, 2003). Thus, the greater integration of less elaborated ornamentation in house finches may be a consequence of a resource allocation trade-off between ornamental components. On the contrary, in the common redpoll, the most elaborated ornaments had the strongest integration (Fig. 4d). This result is expected if developmental pathways of ornamental components are relatively independent but individuals at higher physiological condition are able to produce the maximum expression of ornamental components which, secondarily, results in their greater integration (Fig. 1a, Dale *et al.*, 2001). In redpolls, males that were able to produce the most elaborated sexual ornament also had the most symmetrical ornamentation indicating that these males might be in better physiological condition (Fig. 5b).

If integration of components is produced by shared developmental pathways, then the contribution of among-individual variability (e.g. individual differences in condition) to integration is expected to be similar across the levels of ornament elaboration. Alternatively, if integration among components is accomplished by a co-dependence of distinct developmental pathways on organismal condition, the contribution of individual variability to ornament integration is expected to vary across levels of ornament elaboration. As predicted, in melanin-based ornamentation of the house sparrow, individual variability contributed similarly to integration at all levels of ornament elaboration (Fig. 6c). In contrast, in carotenoid ornamentation of redpolls and house finches, contribution of individual variability (Fig. 6a,b) mirrored the changes in integration across levels of exaggeration of sexual ornamentation – a pattern consistent with condition-dependence of integration among components.

This study shows that the developmental complexity of sexual ornamentation can be concealed by shared condition-dependency of its components. Thus, in sexual

ornaments with high propensity for environment- and condition-dependency (such as in diet-dependent carotenoid ornamentation), the complexity of sexual ornamentation and, consequently, the targets of sexual selection might depend on ornament elaboration and should be taken into consideration by researchers. Uncovering developmental and functional interrelationships among the components of sexual ornamentation is an important step to a better understanding of the evolution of these traits.

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