Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird

A. V. BADYAEV* & R. A. DUCKWORTH†

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA
†Biology Department, Duke University, Durham, NC, USA

Abstract

Male investment into sexual ornamentation is a reproductive decision that depends on the context of breeding and life history state. In turn, selection for state- and context-specific expression of sexual ornamentation should favour the evolution of developmental pathways that enable the flexible allocation of resources into sexual ornamentation. We studied lifelong variation in the expression and condition-dependence of a sexual ornament in relation to age and the context of breeding in male house finches (*Carpodacus mexicanus*) – a species that develops a new sexual ornament once a year after breeding. Throughout males' lifetime, the elaboration of ornamentation and the allocation of resources to the development of sexual ornamentation depended strongly on pairing status in the preceding breeding season – males that were single invested more resources into sexual ornamentation and changed ornamentation more than males that were paired. During the initial (post-juvenile) moult, the expression of ornamentation was closely dependent on individual condition, however the condition-dependence of ornamentation sharply decreased throughout a male's lifetime and in older males expression of sexual ornamentation was largely independent of condition during moult. Selection for early breeding favoured greater ornamentation in males that were single in the preceding seasons and the strength of this selection increased with age. On the contrary, the strength of selection on sexual ornamentation decreased with age in males that were paired in the preceding breeding season. Our results reveal strong context-dependency in investment into sexual ornamentation as well as a high flexibility in the development of sexual ornamentation throughout a male's life.

Introduction

Female mate choice often favours sexual ornaments and displays that reliably indicate a male's physiological condition (Andersson, 1994). Consistent female preference for greater elaboration of sexual ornamentation in males is thought to increase the cost of ornament production and thus reinforce the reliability of an ornament as an indicator of individual condition (Zahavi, 1975; Grafen, 1990). For this reinforcement to be

Correspondence: Alex V. Badyaev, Ecology and Evolutionary Biology, BSW, PO Box 210088, 1041 E. Lowell, University of Arizona, Tucson, AZ 85721-0088, USA.
Tel: 520 626 8830; fax: 520 621 9190;
e-mail: abadyaev@email.arizona.edu

effective, the allocation of resources to the developing sexual ornament should be fixed (de Jong, 1993; Roff *et al.*, 2002), so that progressively more elaborated ornamentation exerts a progressively greater cost of production. Yet, theory and empirical observations suggest that the allocation of organismal condition to sexual ornamentation should be flexible because it is closely associated with a male's life history state and with the ecological and social context of breeding (McLain, 1991; Price *et al.*, 1993; Gustafsson *et al.*, 1995; Svensson & Sheldon, 1998; Widemo & Saether, 1999; Badyaev & Qvarnström, 2002).

Whereas several studies have addressed age-dependent and life-history state dependent variation in the resource allocation to sexual ornamentation (e.g. Kokko, 1997;

Proulx *et al.*, 2002), it is largely overlooked that selection favouring flexibility in the investment into sexual ornamentation might favour the evolution of ornament-specific developmental pathways that lessen the condition-dependence of sexual traits and eventually decouple organismal condition and the expression of sexual ornamentation (Emlen & Nijhout, 2000; Badyaev, 2003). Moreover, the modifications of the link between organismal condition and sexual ornamentation have different consequences for males and females.

From a male perspective, selection by females for more elaborated sexual ornamentation should be countered by the evolution of developmental pathways that reduce the cost of ornament production (Hill, 1994; Emlen & Nijhout, 2000; Badyaev, 2003). Cheaper ornament elaboration may be accomplished by more efficient allocation of resources to sexual ornamentation, by displays that amplify the sexual ornament, and by a decoupling of resource allocation to sexual traits from other organismal functions – i.e. by evolution of ornament-specific developmental pathways (Fig. 1). These processes will

Fig. 1 Conceptual illustration of the change in sexual ornamentation between subsequent moults as a result of changes in both allocation of condition to sexual ornamentation (i.e. pool of resources) and developmental costs of ornamentation (i.e. amount of resources required for ornament elaboration). Solid line indicates initial condition-dependence, dotted line indicates condition-dependence of sexual ornament in a subsequent moult. Arrow in the upper left corner shows whether the ornamentation is expected to increase (⇑), decrease (⇓), or remains the same (=) between subsequent moults. Increase in sexual ornamentation is expected from either greater allocation of condition, lower developmental costs, or both. The latter two cases are documented in this study and are indicated above by an asterisk. Decrease in sexual ornamentation is expected from either greater developmental costs, lower allocation of condition, or both.

ultimately reduce the developmental cost of sexual ornamentation for males. From a female perspective, these strategies should be countered by preferences for more complex or longer-developing and more elaborated sexual ornaments thereby strengthening the condition-dependence of male ornamentation (reviewed in Badyaev, 2003). Importantly, a combination of female preferences for greater condition-dependence of elaborated sexual ornaments and male strategies to modify the development of sexual traits to reduce their costs, will favour the evolution of developmental pathways that enable flexible and context-dependent allocation of resources into sexual ornamentation.

Species that change their sexual ornamentation after each reproductive bout during a lifetime provide an opportunity to examine life-history and context-dependent variation in the allocation of resources into sexual ornamentation. Both an organism's pool of resources (condition) and the allocation of these resources to sexual ornamentation can change between successive acquisitions of ornamentation (i.e. moults) (Fig. 1). A change in allocation to sexual ornamentation between successive moults can lead to a change in sexual ornamentation even when individual condition remains constant (Fig. 1). Similarly, a change in individual condition between successive moults can result in a change in sexual ornamentation even when allocation rules remain constant (Fig. 1). Moreover, selection for more efficient or cheaper expression of sexual ornamentation can produce greater sexual ornamentation even when individual condition remains constant if it favours a decrease in the developmental costs of sexual traits (Fig. 1). This can be accomplished by the evolution of ornament-specific and modular developmental pathways that bypass most of the organismal functions and thus reduce the condition-dependence resulting from the allocation of organismal resources.

Indeed, numerous studies have documented rapid evolution of allometric relationships and developmental links between sexual ornamentation and other organismal traits (Eberhard, 1985; Schlichting & Pigliucci, 1998; Emlen & Nijhout, 2000; Baker & Wilkinnson, 2001; Emlen, 2001; Dixson & Anderson, 2002). For example, in the case of environmentally-derived sexual ornamentation (e.g. carotenoid-based colouration – the focus of this study) selection may favour the evolution of developmental pathways that deposit diet-derived pigments into sexual ornaments directly and with little processing (Hill, 1994; Badyaev, 2003). Such developmental pathways can evolve to enable greater expression of passively ingested carotenoids (e.g. Brush & Seifried, 1968; Hudon, 1991) and ultimately produce geographical variation in sexual ornamentation across species as a result of increased carotenoid content in a diet (e.g. Hudon & Brush, 1989; Witmer, 1996).

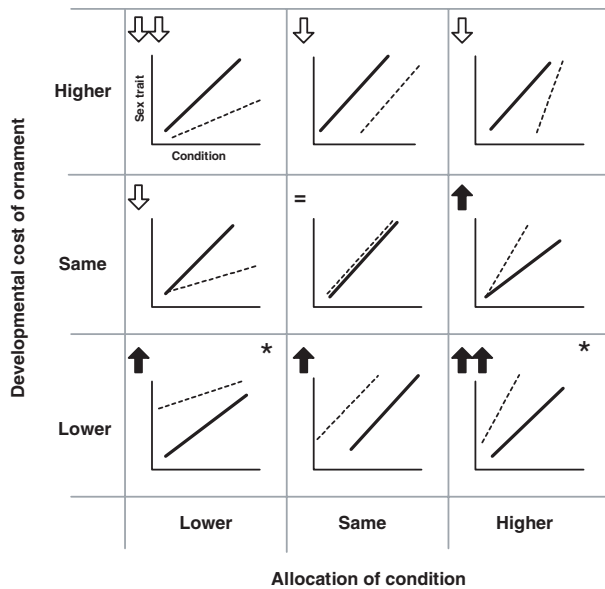In this study, we examined lifelong variation in the expression and condition-dependence of male sexual

ornamentation in a free-living population of house finches (*Carpodacus mexicanus*) in Montana. Male house finches have carotenoid-derived plumage ornamentation that is characterized by several developmentally distinct components – plumage hue, saturation, patch area, and hue consistency (Badyaev *et al.*, 2001a; Hill, 2003). These ornamental components have significant, but flexible environment- and condition-dependence and, correspondingly, are subject to variable female preference and selection (Hill *et al.*, 1999; Badyaev *et al.*, 2001a). House finches acquire sexual ornamentation initially during post-juvenile moult in the first year of life (at about 100–150 days of age) and thereafter, following each breeding season, moult into new ornamental plumage (Fig. 2). This pattern provides us with the opportunity to examine variation in the allocation of resources to sexual ornamentation in relation to male age and the context of the previous breeding attempt, as well as the consequences for future breeding attempts.

Here, we first examine changes in the condition-dependence of sexual ornamentation between the first (initial) and subsequent yearly acquisitions of sexual ornamentation. Secondly, we show that both the expression of sexual ornamentation and the condition-dependence of sexual ornamentation covary strongly with male's pairing success in the breeding season preceding the moult. Third, we partition sexual selection intensity into selection on sexual ornamentation itself and selection on condition during moult and examine changes in the relative intensity of these selection pressures in relation to male age and pairing success.

Materials and methods

Field methods

We studied a resident population of the house finches near Missoula, Montana (for details of the study site and field protocol see Badyaev & Martin, 2000). The study site was a cluster of buildings and ornamental bushes set in open grassland. Finches nested in two-meter-high identical ornamental bushes provided at the study site. Each year, from 1995 to 2002, all resident male finches were captured, measured and marked with a unique combination of one numbered and three coloured plastic rings. At any time during the breeding season, the resident population consisted of about 20 breeding pairs, their nestlings, and about 60–70 adult finches that were either between nesting attempts or unpaired. All resident finches remained in the vicinity of the study area throughout the breeding season.

Non-locally hatched juvenile males first arrive at the study site following large-scale movements of the late-summer dispersal, when 80–150 days of age (Badyaev *et al.*, 2001b). Those juvenile males that remain at the study site during their post-juvenile moult typically remain at the site during subsequent years. In addition,
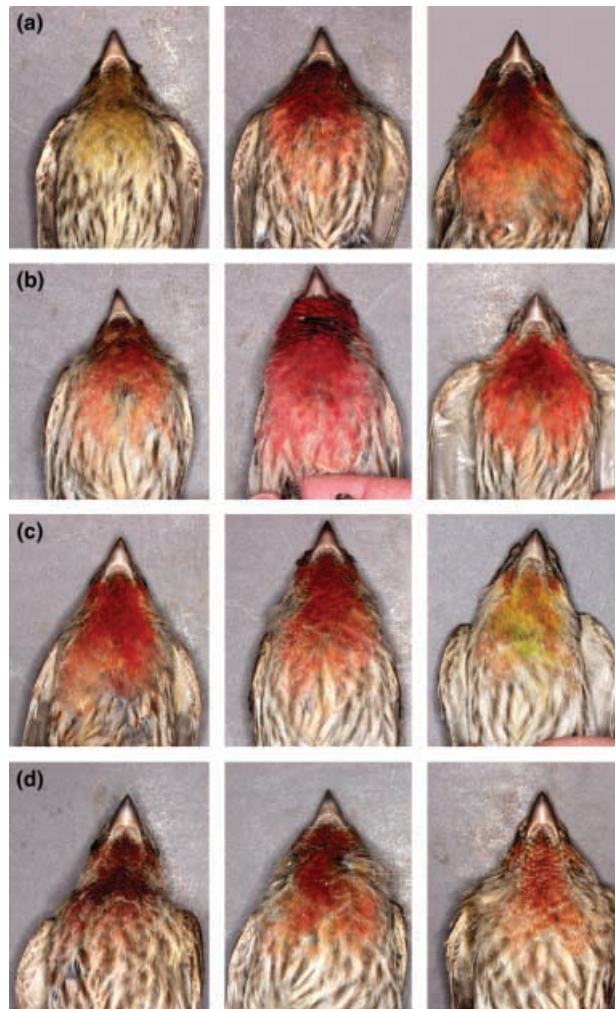

Fig. 2 Examples of changes in sexual ornament expression between the initial (post-juvenile) acquisition (left), after the second moult (first post-breeding; middle), and after the third moult of life (right) in male Montana house finches. In the male in (a) sexual ornamentation increases after subsequent moults, in the male in (b) the highest expression is after the second moult, in the male in (c) sexual ornamentation decreases after subsequent moults, and in the male in (d) expression of sexual ornamentation is approximately similar between subsequent moults.

about five to six locally hatched males per year remained at the site to breed in the subsequent years. Non-locally hatched juvenile males were captured within the first week of their arrival at the study site and banded initially with a single aluminum band that was later augmented with three colour bands in those males that remained at the study site and initiated post-juvenile moult (Badyaev *et al.*, 2001b).

Strong fidelity of adult house finches to the location of previous breeding and the isolation of our study site allowed us to assign males' ages and to follow individual male's moult patterns for up to 7 years (see Badyaev &

Martin, 2000). For this study, we used males that hatched and underwent their first moult during 1995–2001. Selection on early pairing and nest initiation of these males was measured during the 1996–2002 breeding seasons. Males were considered single if they remained without a mate for the entire breeding season. Paired males raised either one or more broods and both were included in our analyses. Nesting censuses were conducted daily and all nests were found as they were being constructed. We used nest initiation date as a proxy for the pair formation because in this population, earlier nesting by previously single males is a result of faster pairing (Badyaev & Hill, 2002). Because extra-pair paternity is exceedingly low in this population and is not associated with the traits under study (Badyaev *et al.*, 2001a), we did not include extra-pair paternity in our estimates of selection on male sexual ornamentation. Resident males were captured, measured, and photographed (see below) repeatedly from mid-February to late September. For this study, we only used measures of male body mass taken during post-breeding moult or within 2 weeks of the moult. Similarly, we used images of males obtained after the post-breeding moult.

Measurement of sexual ornamentation

Resident males that completed the post-breeding moult were captured and their carotenoid-based breast plumage patch was photographed using a 35 mm camera (in 1995–97) or 4-megapixel digital camera (1998–2002) outfitted with a ring flash and mounted in a standard position (Badyaev *et al.*, 2001a). Males were kept in a standardized position by placing them on the dorsal side with the anterior point of the beak held in place (see Badyaev *et al.*, 2001a for details of the protocol; Fig. 2). In all years, the photograph was taken with a constant distance and light settings against a neutral gray (Kodak) background with scale markings. All photo images taken in 1995–98 were transferred to digital image files and standardized against the identical neutral gray background and to a standard scale size using Adobe Photoshop 7.1 (Adobe Systems, Inc. San Jose, CA, USA). The analysis of an error associated with bird position in the photostand is reported in Badyaev *et al.* (2001a).

For the ventral plumage ornamentation of each male we recorded (1) plumage hue – a measure of continuous pigment elaboration that varies from dull yellow to deep purple, (2) hue saturation – a measure of colour intensity, (3) patch area – the number of ornamental feathers with carotenoid pigmentation and (4) hue asymmetry – a measure of consistency in plumage hue among the feathers within the ornamented patch. All measurements were carried out by RAD using SigmaScan Pro 5.0 image analysis software (SPSS, inc., Chicago, IL). 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 measurement 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 using the hue function of SigmaScan. This technique allowed us to sample every part of the breast patch and therefore obtain an accurate representation of the overall hue and saturation of the breast patch. The SigmaScan software measures hue based on a smooth continuum of visible colour with the following benchmarks: $0° =$ red, $40° =$ yellow, $90° =$ green, $170° =$ blue, $210° =$ purple, $255° =$ red. The reddest (most ornamented) males had scores between 250 and 255 and to standardize the colour scores to a linear scale, we subtracted $256°$ from scores in this range and inverted the scale. Thus, in our dataset males with the highest scores of hue were the most ornamented. The saturation ranges from 0 (gray) to 100% (full colour). Hue consistency (hue asymmetry hereafter) across the patch was recorded on a scale of 1–10, as a percent of feathers different in hue group (unpigmented, yellow, orange and red) 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%. High resolution and magnification of the original digital images allowed us to assess pigment asymmetry for each feather of the breast ornamentation (Badyaev *et al.*, 2001a).

All components of male colouration were measured twice, several weeks apart, and prior to the tabulation of the male age and pairing data. Furthermore, an observer bias is avoided by automated features of hue, saturation, and area measurements in SigmaScan software that fills out the data sheet automatically when the observer works with an image. Measurements of ornament patch area, hue, saturation, and hue asymmetry across the patch were highly repeatable and the variance associated with measurement error was sufficiently small (Table 1).

Male condition and condition-dependence of sexual ornamentation

We used male body mass during moult and the residuals of body mass on tarsus size as a measure of male physiological condition. The results were identical for the body mass and residual analyses, thus only the results for body mass are shown. In this population, body mass is an appropriate measure of physiological condition for three reasons. First, a concurrent study found close correlation between body mass and haematocrit – a reliable measure of male immediate physiological condition (Duckworth *et al.*, in press). Secondly, body mass closely covaried with parental expenditure and provisioning rates (Badyaev & Hill, 2002). Thirdly, body mass is closely

Table 1 Measurement error and repeatability for breast patch hue, saturation, area (in pixels^2/100), and hue asymmetry in male house finches. Individual variation is nested within year of life and the measurement error within an individual.

Trait	Source of variation	d.f.	Mean square	F
Patch area		364†	3080.548	18.85***
	Individual	137	6034.839	36.93***
	Side	1	442.471	2.44
	Individual*Side	63	797.513	4.88***
	Measurement‡	63	190.489	1.17
	Repeatability	0.96 ± 0.003***		
Hue asymmetry		180§	30.782	4.28***
	Individual	94	24.673	3.34***
	Measurement‡	57	7.219	0.98
	Repeatability	0.98 ± 0.002***		
Pigment hue		10969¶	2318.063	52.54***
	Individual	132	3901.303	88.42***
	Measurement††	66	6.546	0.15
	Repeatability	0.99 ± 0.001***		
Saturation		10969¶	6501.251	99.14***
	Individual	132	5826.394	88.85***
	Measurement††	65	372.228	4.68*
	Repeatability	0.94 ± 0.002***		

*$P < 0.1$; **$P < 0.05$; ***$P < 0.001$; †total d.f., two sides are measured per individual; ‡includes repositioning and re-measuring; §one value per individual measurement; ¶total d.f. including multiple (80–100) measures along the grid within each measurement session; ††includes multiple measures within a session, repositioning, and measurement error between the sessions.

associated with overwinter and post-breeding survival (Badyaev & Martin, 2000; Badyaev *et al.*, 2001b). Male house finches do not store carotenoids used for ornament production for more than 2 weeks (Hill, 2003), thus measuring body mass during moult is a good approximation of the condition-dependence of carotenoid consumption, deposition and metabolism.

We used standardized regression coefficients (in standard deviations) of a regression of body mass during moult on the expression of sexual ornament following moult as a measure of the condition-dependence of sexual ornamentation. The change in condition-dependence of sexual ornamentation between the subsequent moults was the difference between the standardized regression coefficients (in standard deviations) calculated for each moult. The standard error for the difference between regression coefficients was obtained by resampling with replacement of each of the individual males (i.e. a pair of measurements) comprising the regression in both moults. Because repeated measures of individual males were used for these calculations, the differences between standardized regression coefficients reflect differences in correlation of body mass during moult and sexual ornamentation without the confounding effects of population composition during different years. Repeated measures of male ornamentation between years revealed that *both* an increase and decrease in sexual ornamentation were common (see below) and that *both* directions of change were present in later age classes. Thus, our estimates of condition-dependence and ornamentation change between years were not biased by resampling error.

Variances associated with remeasuring ($n = 2$ sets) and the along-grid measurements (80–100 repeats for hue and saturation measures) were calculated with a mixed model nested ANOVA and are shown in Table 1. Repeated measures were nested within a measuring set and the set was nested within an individual and the year of life. The repeatability (R) was $R = \sigma^2_W/(\sigma^2_W + \sigma^2_E)$ where σ^2_W is the variance among n individuals and σ^2_E is the variance among k measures within n individuals. Standard error of R was $SE(R) = [2(1 - R^2)(1 + (k - 1)R^2)/(k(k - 1)(n - 1))]^{1/2}$. The F-value was a ratio of MS_W and MS_E (Becker, 1984). The relative strength of selection for earlier nesting was estimated with partial selection differentials from a multiple regression of nesting date (Julian) on components of male's sexual ornamentation and male's body mass during moult within each age class and pairing status group.

Results

During the first (post-juvenile) moult, expression of sexual ornamentation was closely dependent on body mass for all ornamental components (Fig. 3). Males that were heavier during their first moult produced ornaments that were larger ($b_{ST} = 0.55$, $n = 46$, $t = 4.34$, $P < 0.001$) more exaggerated in hue ($b_{ST} = 0.48$, $n = 47$, $t = 3.77$, $P = 0.004$), more saturated in colour ($b_{ST} = 0.31$, $n = 47$, $t = 2.31$, $P = 0.02$), and with more consistent colour distribution ($b_{ST} = -0.34$, $n = 42$, $t = -2.50$, $P = 0.01$; Fig. 3).

Following their first post-breeding moult (i.e. after the first breeding season) males changed the elaboration of
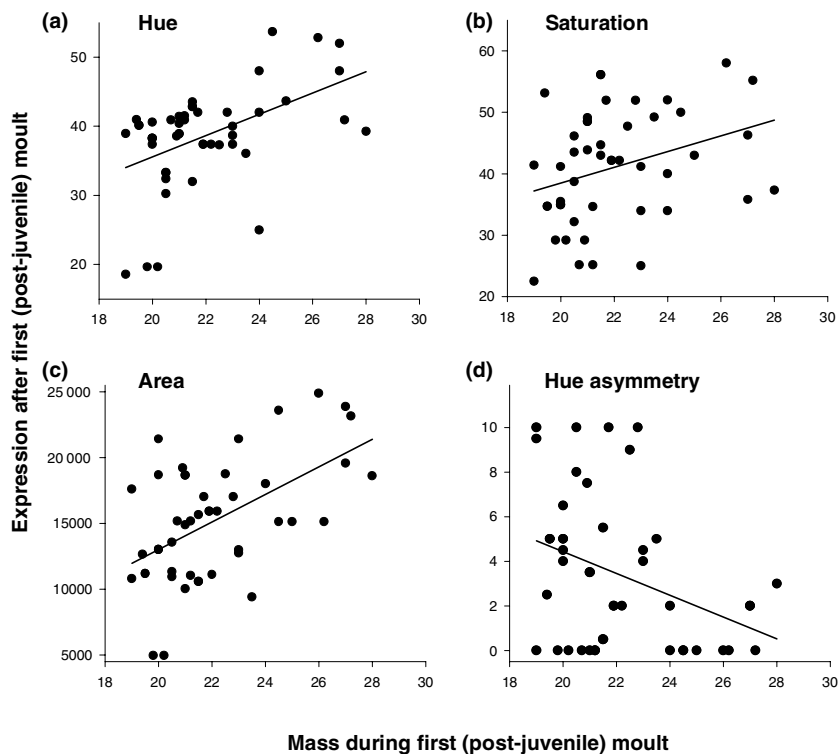
Fig. 3 Simple regression plots illustrating the condition-dependence of the initial (i.e. after the post-juvenile moult) sexual ornamentation in male house finches from the Montana population.

all components of their sexual ornament, with the exception of hue asymmetry, compared with the sexual ornament produced after the first moult of life (Fig. 4). However, males that were single in their first breeding season increased the hue and the area of their ornament more than males that were paired (hue: $F = 5.01$, $P = 0.02$; area: $F = 3.10$; $P = 0.05$; Fig. 4). Similarly, in the subsequent year, males that were single during their second breeding season increased the elaboration of their sexual ornamentation (Fig. 5), whereas the males that were paired during their second breeding season increased only patch area and decreased both the hue and the hue asymmetry of their ornament following the post-breeding moult (Fig. 5; paired vs. single: hue: $F = 2.98$, $P = 0.06$; saturation: $F = 31.58$, $P < 0.001$; area $F = 11.81$, $P = 0.003$; hue asymmetry: $F = 11.72$, $P = 0.003$).

Despite an increase in the expression of sexual ornamentation, its condition dependence (i.e. correlation with body mass during moult) either decreased or remained unchanged between the initial and the first post-breeding moult, and between first post-breeding moult and the second post-breeding moult (Figs 4 and 5). However, the allocation of condition to sexual ornamentation depended on a male's pairing status in the season preceding moult and on male's age (Table 2, e.g. Fig. 4: paired vs. single – hue: $F = 8.56$, $P = 0.02$; saturation: $F = 3.00$, $P = 0.06$; area: $F = 2.31$, $P = 0.08$, hue asymmetry: $F = 7.65$, $P = 0.03$; Fig. 5: paired vs. single – hue:

$F = 12.06$, $P = 0.002$; saturation: $F = 0.03$, $P = 0.96$; area: $F = 0.31$, $P = 0.88$, hue asymmetry: $F = 1.65$, $P = 0.13$). Allocation of condition during moult to the expression of ornament's hue, saturation and area depended on male pairing success in the season preceding the moult (Table 2, significant Status by Mass interaction). Similarly, the allocation of condition during moult to the expression of ornament's hue, area, and hue asymmetry varied with male age (Table 2, significant Mass by Year of life). Only production of the patch area was consistently condition-dependent, however it also varied with pairing success and the age of a male (Figs 4 and 5, Table 2).

Change in the expression of the sexual ornament between subsequent post-breeding moults was not associated with the change in condition during moult (Table 2). Instead the condition-allocation to all components of sexual ornamentation varied with the pairing success of males during the preceding breeding season (Table 2). The contribution of pairing success in the preceding breeding season to a change in the expression of the sexual traits varied with the age of males (Table 2, significant status by year interaction).

Throughout their lifetime, males that were single during the breeding season were heavier during post-breeding moult compared with males that were paired (paired vs. single – first breeding season: 0.52 ± 0.17 (SE) vs. 0.97 ± 0.25, $F = 3.54$; $P = 0.05$; second breeding season: -0.32 ± 0.23 vs. -0.06 ± 0.25, $F = 2.14$; $P = 0.08$).
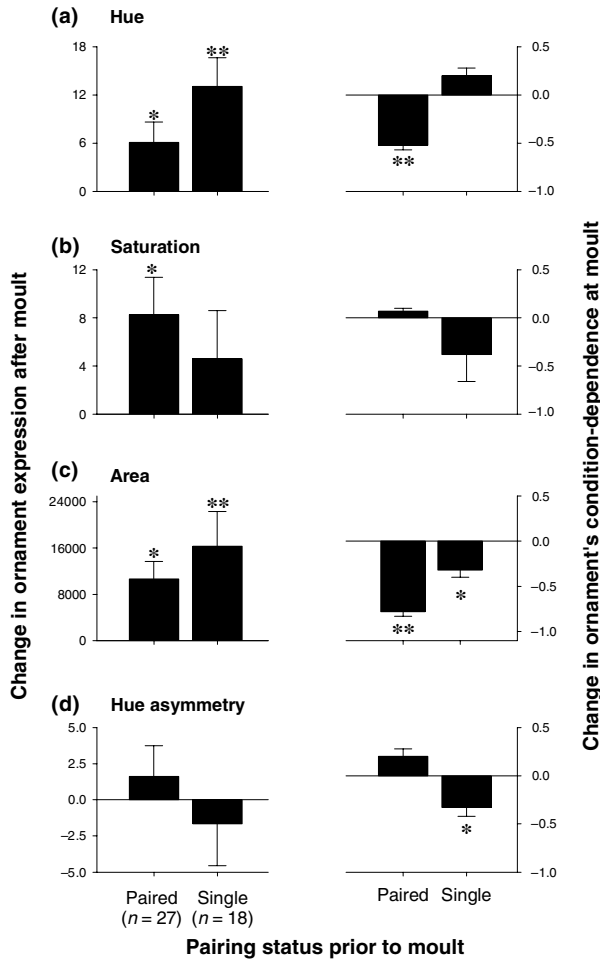
Fig. 4 Left panel: change in the expression of sexual ornament between the initial (post-juvenile) and the first post-breeding (i.e. following the first breeding season) moults in males that were paired or single during breeding season preceding the moult. Right panel: change in the condition-dependence (differences between standard regression coefficients, in standard deviations) between the initial (post-juvenile) and the first post-breeding moults in males that were paired or single during breeding season preceding the moult. Asterisks indicate significant difference from zero: *$P < 0.05$, **$P < 0.01$. See Table 2 and the text for the tests of differences between the pairing status groups.

Fig. 5 Left panel: change in the expression of sexual ornament between the first post-breeding and the second post-breeding (i.e. after the second breeding season) moults in males that were paired or single during breeding season preceding the moult. Right panel: change in the condition-dependence (differences between standard regression coefficients, in standard deviations) between the first post-breeding and the second post-breeding moults in males that were paired or single during breeding season preceding the moult. Asterisks indicate significant difference from zero: *$P < 0.05$, **$P < 0.01$. See Table 2 and the text for the tests of differences between the pairing status groups.

However, the higher condition of single males during post-breeding moult did not directly translate into their greater sexual ornamentation because of the overall decrease in the allocation of condition to the sexual ornament between subsequent moults (Figs 4 and 5; Table 2).

We evaluated the relative strength of selection for earlier pair formation and earlier nest initiation on body mass during previous moult and on the sexual ornament itself. During the first breeding season, selection for earlier nesting favoured both greater body condition and
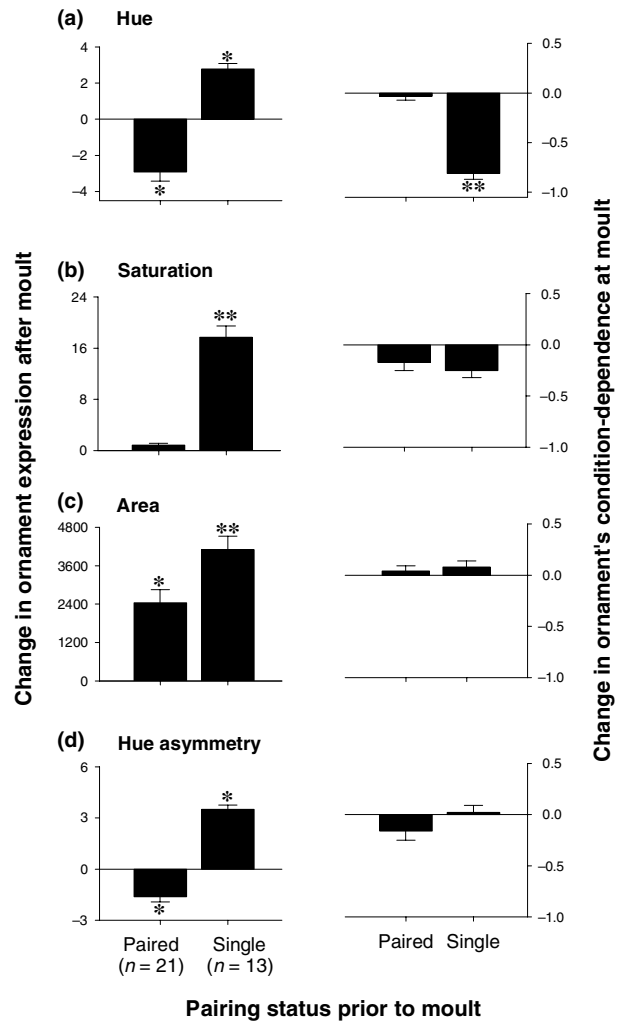
greater ornament saturation and area (Fig. 6). In the subsequent breeding seasons, targets of selection for earlier breeding were different between males that were paired in the previous season and the males that were single (Fig. 6). In males that were paired during the previous season (and thus often retained the previous mate), selection for earlier nest initiation acted mostly on body mass and not on sexual ornamentation (Fig. 6). In males that were single in the previous season (and thus

Table 2 Sexual trait expression following post-breeding moult and change in sexual trait expression between the subsequent moults in relation to pairing status in the season preceding moult (status), body mass during moult (mass), year of life (year), and the interactions among these factors.

Trait	Source of variation												
	Status		Mass		Year		Status × mass		Status × year		Mass × year		Mass × status × year	
Expression after moult	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Hue	2.16	0.14	3.99	0.04	2.06	0.15	8.52	**0.001**	5.54	0.02	8.83	**0.001**	6.53	**0.012**
Saturation	6.85	**0.009**	1.04	0.30	3.03	0.04	8.09	**0.004**	4.00	0.019	2.38	0.07	4.62	**0.011**
Area	3.57	0.06	6.54	**0.012**	5.24	**0.007**	15.52	**0.001**	0.22	0.63	5.05	**0.008**	0.47	0.49
Hue asymmetry	1.52	0.22	0.45	0.50	1.93	0.16	3.58	0.06	5.78	**0.004**	7.48	**0.003**	2.10	0.15

Change in expression between moults	Status		Change in mass		Year		Status × mass		Status × year		Mass × year		Mass × status × year	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Hue	3.80	0.06	0.79	0.95	0.98	0.39	16.20	**0.001**	12.15	**0.001**	2.93	0.07	1.84	0.19
Saturation	1.57	0.22	4.67	0.04	2.78	0.09	8.42	**0.01**	12.00	**0.003**	4.03	0.03	4.76	0.04
Area	0.14	0.88	0.44	0.53	2.52	0.11	4.50	**0.01**	2.93	0.09	1.55	0.22	2.07	0.16
Hue asymmetry	4.83	0.03	0.57	0.46	3.04	0.06	5.87	**0.006**	6.11	**0.02**	0.23	0.63	1.74	0.20

Note: boldface P-values indicate significance after the within-model Bonferonni adjustment ($n = 7$, initial $\alpha = 0.1$).

needed to attract a mate) the selection on ornament components was consistently strong, whereas the selection on body mass was weak (Fig. 6). These results are concordant with the greater increase of sexual ornamentation between subsequent moults in males that were single compared with males that were paired prior to moult (Figs 4 and 5).

Discussion

To be a reliable indicator of health and organismal condition, sexual ornaments have to be costly to an organism (Zahavi, 1975; Andersson, 1982). These costs can be maintained by patterns of resource allocation into the development of sexual ornamentation (Williams, 1966; Iwasa et al., 1991). However, because male investment into sexual ornamentation is part of organismal reproductive investment, this investment is subject to life history trade-offs as well as to the ecological and social contexts in which breeding occurs (Partridge & Endler, 1987; Gustafsson et al., 1995; Höglund & Sheldon, 1998; Svensson & Sheldon, 1998). Similarly, female choice of male's sexual ornamentation might depend on her investment into mate choice, experience and quality, as well as the environmental and social context of breeding (Jennions & Petrie, 1997; Qvarnström, 2001; Kokko et al., 2002). In addition, because the direct benefits that a female acquires through preference for sexual ornamentation are often specific to a particular environment of breeding, different aspects of male condition and sexual ornamentation are important to different females in different environments (Wedekind, 1992; Badyaev & Qvarnström, 2002). Thus, investment into sexual ornamentation, i.e. its condition-dependence, should vary strongly with the demographic composition of a population (because of both experience- and age-related variation in investment and choice) and the environment of breeding (Gross, 1996; Kokko, 1998; Proulx et al., 2002). Consequently, variation in the social and ecological environments of breeding may explain the often documented differences in condition-dependence of sexual ornamentation and female preference for sexual ornamentation between populations (reviewed in Badyaev & Qvarnström, 2002; Hegyi et al., 2002) and between ages within the same population (this study, Candolin, 2000a,b; Engqvist & Sauer, 2002; Török et al., 2003).

Our study of lifelong variation in the expression and condition-dependence of sexual ornamentation in Montana house finches produced three main results. First, we found that both the expression of sexual ornamentation and its condition-dependence were context- dependent (i.e. varied with male's pairing success in the previous breeding season) and age-dependent. Secondly, the condition-dependence of sexual ornamentation declined with age and, in older males, even substantial change in sexual ornamentation was independent of condition during moult. Thirdly, selection on sexual ornamentation and selection on condition itself differed between males of different pairing status. In males that were single in the previous season and thus needed to attract a mate, selection for early nesting favoured greater exaggeration of sexual ornamentation, whereas in males that were paired in the previous season, selection favoured males in better condition during moult and did not act on ornamentation. Moreover, condition-dependency and
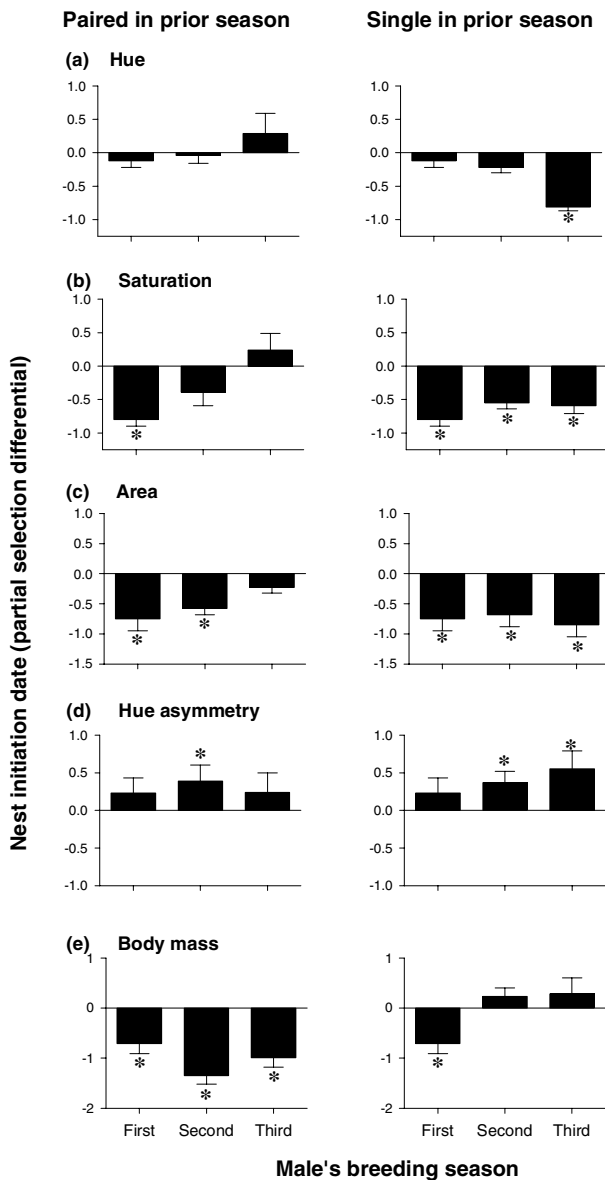
Paired in prior season

Single in prior season

(a) Hue

(b) Saturation

(c) Area

(d) Hue asymmetry

(e) Body mass

First Second Third

First Second Third

Male's breeding season

Nest initiation date (partial selection differential)

Fig. 6 Relative strength of selection (in standard deviations) for earlier nest initiation date that acts on (a) ornament hue, (b) ornament saturation, (c) patch area, (d) hue asymmetry and (e) body mass during moult in males that were paired (left) and single (right) during breeding season preceding the moult. Asterisks indicate significant difference from zero of individual selection differentials: *$P < 0.05$, **$P < 0.01$.

expression differed among components of the sexual ornament corroborating previous findings of the ornament's low developmental integration and distinct selection pressures on its components (Badyaev *et al.*, 2001a; Badyaev & Young, in press). Taken together, these results reveal a strong context-dependency of sexual ornamentation as well as a high flexibility in the developmental pathways that produce sexual ornamentation.

These results raise several questions. First, why does the pairing status and age of males affect the subsequent modification of sexual ornamentation? Secondly, how are some males able to express progressively greater sexual ornamentation at lower costs during subsequent moults? Thirdly, why does the intensity of sexual selection on ornamentation vs. condition during moult differ between males of different pairing status? More generally, selection for facultative and flexible investment into the production of sexual ornamentation should favour the independence of ornament-specific developmental pathways from the rest of organismal functions. This independence will make sexual ornaments less reliable indicators of organismal quality. Thus, it is unclear how the condition-dependence of sexual ornamentation (i.e. during initial post-juvenile moult) is maintained.

Male's pairing success in the season preceding the moult strongly correlated with the change in the expression of sexual ornamentation between the first (post-juvenile) and the second (first post-breeding) moults, and especially between the second and the third moults. These results are consistent with the patterns of selection on single and paired males – pairing success of males that were single, and thus needed to attract a mate, was mostly because of elaboration of their sexual ornamentation. In this population, females that breed for the first time, select mates primarily based on their sexual ornaments and prefer males with more elaborated ornamentation (Badyaev & Hill, 2002). Because most mates of previously single males, especially of older males, are young females (ibid.), the directional selection on male ornamentation is mostly because of preferences by these females.

On the other hand, females that breed for more than 1 year appear to base their mating decisions primarily on male provisioning ability (Badyaev & Hill, 2002) – thus preference by these females is unlikely to result in significant directional selection on plumage ornamentation. Because male provisioning abilities correlate with male overall condition (Duckworth *et al.*, in press), the preference by older females for greater parental investment can produce selection on male condition that we documented here. An interesting extension of this finding is that the importance of elaborating sexual ornaments for pairing success and thus the investment into a sexual ornament should vary with the demographic composition of the population (Kokko, 1998).

Greater investment into sexual ornamentation by males that were single can be a result of their higher overall condition at the time of moult compared with males that were paired. Parental investment, especially nestling provisioning, is costly to males – males that provision more are in lower physiological condition during the nesting season and have lower post-breeding survival (Duckworth *et al.*, in press). If the allocation of organismal resources to sexual ornamentation remains

the same between subsequent moults, the relatively higher condition can result in greater sexual ornamentation. However, the condition-dependence of sexual ornamentation had decreased or remained the same between subsequent moults in males that were single. Thus, it is unlikely that the greater condition of single males directly translated into their greater sexual ornamentation. These results differ from those predicted by recent theoretical treatments of age-related variation in the condition-dependence of sexual ornamentation (Kokko, 1997; Proulx et al., 2002), where reliable signalling of male condition by sexual ornaments is expected to increase with age because the decline in residual reproductive value is different between males of high and low quality. It would be interesting to consider, in models of age-dependent advertisement, the changes in the developmental costs of the ornament (e.g. specific developmental pathways that reduce the costs of ornament production with age).

Consistent directional selection for greater elaboration of sexual ornaments increases the cost of their production favouring the evolution of cost-reducing pathways (Hill, 1994; Emlen & Nijhout, 2000; Emlen, 2001). For example, selection may favour more efficient development of a sexual ornament such that a progressively smaller increase in condition is amplified into a larger sexual ornament. In addition, the reduction of the developmental costs of a sexual trait can be accomplished by evolving ornament-specific developmental pathways that bypass most of the organismal functions (de Jong, 1993, 1999; Badyaev, 2003). In both cases, selection for lower condition-dependence acts to modify the link between sexual ornament production and other organismal functions.

These processes are well illustrated by studies of carotenoid-based sexual ornamentation – the subject of this study. Once female preference for diet-dependent carotenoid ornamentation is established, further selection for greater elaboration of carotenoid-based male ornamentation can favour a number of cost-reducing strategies by males (Hill, 1994). For example, males can preferentially forage on carotenoid-rich foods, deposit diet-derived carotenoids directly into the integument without energetically expensive metabolism, alter the expression of carotenoid ornaments by concentrating carotenoid deposition, or modify integument structures to increase the display of carotenoids already absorbed (Brush & Seifried, 1968; Olson, 1970; Hudon & Brush, 1989; Hudon, 1991; Kodric-Brown, 1998).

The most pronounced and widespread change in the expression of sexual ornamentation found in this study is between the initial and the subsequent (the first post-breeding) moult. It is noteworthy that the initial moult is the only moult of male house finches during which non-pigmented feathers are replaced with pigmented ones. The subsequent moults (including the first post-breeding) involve changes from old pigmented feathers to new ones. The size of the ornamented patch is determined by the number of feather follicles activated to uptake carotenoids, whereas colour hue is determined by the amount and the types of carotenoids taken up by the follicle during feather growth (Badyaev et al., 2001a; Hill, 2003). Thus, if the initial ornament development (i.e. during post-juvenile moult) includes establishment of pathways of follicle activation and carotenoid delivery to the ornamented patch, these pathways may then be re-used and elaborated with lower costs to the organism during subsequent moults. This suggestion is corroborated by a close dependence of the initial moult, but not the subsequent moult on individual condition and by experiments showing that the area of sexual ornament is less sensitive to environment during moult than other ornamental features in older finches (Hill, 2003). Alternatively, older males may be able to produce more elaborated ornaments because they are more efficient in finding a carotenoid-rich diet, or in the consumption, processing and deposition of carotenoids (see above). Similarly, Veiga & Puerta (1996) found that in older male house sparrows (Passer domesticus), nutritional condition during moult had a smaller effect on sexual ornamentation compared with younger males. Other avian studies that documented a greater increase in sexual ornamentation between the first two moults of life [e.g. Michigan house finches (Hill, 1992), collared flycatchers Ficedula albicollis (Hegyi et al., 2002; Török et al., 2003)], attributed these changes to the greater condition of older males. However, our results suggest that changes in trait expression over the life of an individual are not necessarily produced by changes in organismal condition, but instead can be because of changes in the condition-dependence of the ornament itself. One possibility unexplored in this study is that in older males, the cost of sexual ornamentation is largely imposed by its maintenance (Iwasa et al., 1991) (e.g. predation risk, parasite exposure, social interaction with other males) and not its production (Hooper et al., 1999; Török et al., 2003). For example, paired and single males may differ in the frequency and intensity of male–male conflicts or paired males may be more susceptible to parasites and predators as a result of their parental provisioning.

In conclusion, individual optimization of reproductive effort might favour the evolution of context- and state-dependent expression of sexual ornamentation and, correspondingly, the evolution of context- and state-dependent female choice. We have shown that male investment into sexual ornamentation varies across a lifetime depending on the context of breeding and life history stage. Female preference for male sexual ornamentation and thus the evolution of sexual ornamentation should vary with the demographic composition of the population and the social and ecological contexts of breeding. Such context-dependence favours variable allocation of resources into sexual ornamentation that is enabled by flexible pathways of ornament development.

Acknowledgments

References

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. *Biol. J. Linnean Soc.* **17**: 375–393.

Andersson, M. 1994. *Sexual Selection.* Princeton University Press, Princeton.

Badyaev, A.V. 2003. Integration and modularity in the evolution of sexual ornaments: An overlooked perspective. In: *The Evolutionary Biology of Complex Phenotypes* (M. Pigliucci & K. Preston eds), pp. 50–79. Oxford University Press, Oxford.

Badyaev, A.V. & Hill, G.E. 2002. Parental care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. *Behav. Ecol.* **13**: 591–597.

Badyaev, A.V. & Martin, T.E. 2000. Sexual dimorphism in relation to current selection in the house finch. *Evolution* **54**: 987–997.

Badyaev, A.V. & Qvarnström, A. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *Auk* **119**: 301–310.

Badyaev, A.V. & Young, R.L. Complexity and integration in sexual ornamentation: an example with carotenoid and melanin plumage pigmentation. *Evolution and Development* in press.

Badyaev, A.V., Hill, G.E., Dunn, P.O. & Glen, J.C. 2001a. Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. *Am. Nat.* **158**: 221–235.

Badyaev, A.V., Whittingham, L.A. & Hill, G.E. 2001b. The evolution of sexual size dimorphism in the house finch. III. Developmental basis. *Evolution* **55**: 176–189.

Baker, R.H. & Wilkinnson, G.S. 2001. Phylogenetic analysis of sexual dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae). *Evolution* **55**: 1373–1385.

Becker, W.A. 1984. Repeatability. In: Manual of Quantitative Genetics, pp. 37–41. Academic Enterprises, Pullmas, WA.

Brush, A.H. & Seifried, H. 1968. Pigmentation and feather structure in genetic variants of the Gouldian finch, *Poephila gouldiae. Auk* **85**: 416–430.

Candolin, U. 2000a. Changes in expression and honesty of sexual signaling over the reproductive lifetime of sticklebacks. *Proc. R. Soc. B Biol. Sci.* **267**: 2425–2430.

Candolin, U. 2000b. Increased signaling effort when survival prospects decrease: male-male competition ensures honesty. *Anim. Behav.* **60**: 417–422.

Dixson, A. & Anderson, M. 2002. Sexual selection and the comparative anatomy of reproduction in monkeys, apes, and human beings. *Annu. Rev. Sex Res.* **12**: 121–144.

Duckworth, R.A., Badyaev, A.V. & Parlow, A.F. Elaborately ornamented males avoid costly parental care in the house finch (Carpodacus mexicanus): a proximate perspective. *Behav. Ecol. Sociobiol.* in press.

Eberhard, W.G. 1985. *Sexual Selection and Animal Genitalia.* Harvard University Press, Cambridge, Mass.

Emlen, D.J. 2001. Costs and the diversification of exaggerated animal structures. *Science* **291**: 1534–1536.

Emlen, D.J. & Nijhout, H.F. 2000. The development and evolution of exaggerated morphologies in insects. *Annu. Rev. Entomol.* **45**: 661–708.

Engqvist, L. & Sauer, K.P. 2002. A life-history perspective on strategic mating effort in male scorpionflies. *Behav. Ecol.* **13**: 632–636.

Grafen, A. 1990. Biological signals as handicaps. *J. Theor. Biol.* **144**: 517–546.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**: 92–98.

Gustafsson, L., Qvarnström, A. & Sheldon, B.C. 1995. Trade-offs between life history traits and a secondary sexual character in male collared flycatcher. *Nature* **375**: 311–313.

Hegyi, G., Torok, J. & Toth, L. 2002. Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. *J. Evol. Biol.* **15**: 710–719.

Hill, G.E. 1992. The proximate basis of variation in carotenoid pigmentation in male house finches. *Auk* **109**: 1–12.

Hill, G.E. 1994. Trait elaboration via adaptive mate choice: sexual conflict in the evolution of signals of male quality. *Ethol. Ecol. Evol.* **6**: 351–370.

Hill, G.E. 2003. *A Red Bird in a Brown Bag: The Function and Evolution of Colorful Plumage in the House Finch,* Oxford Ornithology Series.

Hill, G.E., Nolan, P.M. & Stroehr, A.M. 1999. Pairing success relative to male plumage brightness and pigment symmetry in the house finch: temporal and geographic constancy. *Behav. Ecol.* **10**: 48–53.

Höglund, J. & Sheldon, B.C. 1998. The cost of reproduction and sexual selection. *Oikos* **83**: 478–483.

Hooper, R.W., Tsubaki, Y. & Siva-Jothy, M.T. 1999. Expression of a costly, plastic sexual trait is correlated with age and condition in a damselfly with two male morphs. *Physiol. Entomol.* **24**: 364–369.

Hudon, J. 1991. Unusual carotenoid use by western tanager (*Piranga ludoviviana*) and its evolutionary implications. *Can. J. Zool.* **69**: 2311–2320.

Hudon, J. & Brush, A.H. 1989. Probably dietary basis of a color variant of the cedar waxwing. *J. Field Ornithol.* **60**: 361–368.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences II. The handicap principle. *Evolution* **45**: 1431–1442.

Jennions, M.D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**: 283–327.

de Jong, G. 1993. Covariances between traits deriving from successive allocations of a resource. *Funct. Ecol.* **7**: 75–83.

de Jong, G. 1999. Unpredictable selection in a structured population leads to local genetic differentiation in evolved reaction norms. *J. Evol. Biol.* **12**: 839–851.

Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. *Am. Zoologist* **38**: 70–81.

Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behav. Ecol. Sociobiol.* **41**: 99–107.

Kokko, H. 1998. Should advertising parental care be honest? *Proc. R. Soc. B Biol. Sci.* **265**: 1871–1878.

Kokko, H., Brooks, R., McNamara, J.M. & Houston, A.I. 2002. The sexual selection continuum. *Proc. R. Soci. B Biol. Sci.* **269**: 1331–1340.

McLain, D.K. 1991. The r-K continuum and the relative effectiveness of sexual selection. *Oikos* **60**: 263–265.

Olson, S.L. 1970. Specializations of some carotenoid-bearing feathers. *Condor* **72**: 424–430.

Partridge, L. & Endler, J.A. 1987. Life history constraints on sexual selection. In: *Sexual Selection: Testing the Alternatives* (J.W. Bradbury & M. Andersson, eds) pp. 265–277. Wiley & Sons, Dahlem.

Price, T., Schluter, D. & Heckman, N.E. 1993. Sexual selection when the female directly benefits. *Biol. J. Linnean Soc.* **48**: 187–211.

Proulx, S.P., Day, T. & Rowe, L. 2002. Older males signal more reliably. *Proc. R. Soc. B Biol. Sci.* **269**: 2291–2299.

Qvarnström, A. 2001. Context-dependent genetic benefits from mate choice. *Trends Ecol. Evol.* **16**: 5–7.

Roff, D.A., Mostowy, S. & Fairbairn, D. 2002. The evolution of trade-offs: testing predictions on response to selection and environmental variation. *Evolution* **56**: 84–95.

Schlichting, C.D. & Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*, Sinauer Associates, Sunderland, MA.

Svensson, E. & Sheldon, B.C. 1998. The social context of life history evolution. *Oikos* **83**: 466–477.

Török, J., Hegyi, G. & Garamszegi, L.Z. 2003. Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers. *Behav. Ecol.* **14**: 382–388.

Veiga, J.P. & Puetra, M. 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus. Proc. R. Soc. B Biol. Sci.* **263**: 229–234.

Wedekind, C. 1992. Detailed information about parasites revealed by sexual ornamentation. *Proc. R. Soc. B Biol. Sci.* **247**: 169–174.

Widemo, F. & Saether, S.A. 1999. Beauty in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol. Evol.* **14**: 26–31.

Williams, G.C. 1966. *Adaptation and Natural Selection: a Critique of Some Current Evoluionary Thought*. Princeton University Press, Princeton.

Witmer, M. 1996. Consequences of an alien shrub on the plumage coloration and ecology of cedar waxwings. *Auk* **113**: 735–743.

Zahavi, A. 1975. Mate selection – a selection for a handicap. *J. Theor. Biol.* **53**: 205–214.