

Context-dependent development of sexual ornamentation: implications for a trade-off between current and future breeding efforts

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Abstract

Allocation of resources into the development of sexual displays is determined by a trade-off between the competing demands of current reproduction and self-maintenance. When reproduction overlaps with acquisition of sexual ornamentation, such as in birds with a yearly post-breeding moult, such a trade-off can be expressed in elaboration of sexual traits used in subsequent matings. In turn, selection for elaboration of sexual ornaments should favour resolution of this trade-off through a modification of the ornaments' development, resulting in variable and life history-dependent development of sexual displays. Here we examined a novel hypothesis that the trade-off between current reproduction and development of sexual ornamentation in the house finch (*Carpodacus mexicanus*) can be mediated by the shared effects of prolactin – a pituitary hormone that regulates both parental care and moult in this species. We compared developmental variation in sexual ornamentation between breeding, nonbreeding, and juvenile males and examined the relative contribution of residual levels of prolactin and individual condition during moult to the acquisition of sexual ornamentation. Males that invested heavily in parental care entered post-breeding moult in lower condition and later in the season, but their higher plasma prolactin was associated with shorter and more intense moult ultimately resulting in equal or greater elaboration of sexual ornamentation compared with nonparental males. Elaboration of sexual ornamentation of nonparental males that entered moult in greater condition, but with lower prolactin, was produced by longer and earlier moult and by lesser overlap in moult between sexual ornaments. Ornamentation of juvenile males that acquire sexual ornamentation for the first time was closely associated with physiological condition during moult. We discuss the implications of such context-dependent ontogenies of sexual ornamentation and resulting differences in condition-dependence of sexual traits across life history stages on the evolution of female preference for elaborated sexual displays.

Introduction

Female preference for elaborated sexual displays leads to greater costs of display's development and maintenance, and thus ensures that displays reflect males' genetic and phenotypic quality (Andersson, 1994). When investment

into development of and preference for sexual ornamentation varies with life history state or ecological and social context of breeding (Fitzpatrick *et al.*, 1995; Höglund & Sheldon, 1998; Svensson & Sheldon, 1998, Badyaev & Qvarnström, 2002, Hunt *et al.*, 2005), selection should favour evolution of flexible and context-dependent ontogenies of sexual ornamentation (Emlen & Nijhout, 2000; Badyaev, 2004, 2005). Because similar sexual ornaments can be produced by a variety of developmental mechanisms (e.g. Lindström *et al.*, 2005; Tomkins *et al.*, 2005), knowledge of the details of development of

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sexual ornamentation across breeding contexts and life history states is necessary for understanding their evolution.

In birds, the trade-off between allocation to sexual plumage and other organismal functions, such as survival, maintenance, or breeding occurs during moult (Svensson & Hedenstrom, 1999). Consequently, overlap between reproduction and moult often reduces parental effort and reproductive success (Morton & Morton, 1990; Svensson & Nilsson, 1997; Hemborg & Merila, 1998; Hemborg, 1999), and can lessen elaboration of sexual ornamentation for the subsequent breeding season (Dawson *et al.*, 2000; Griffith, 2000; Dawson, 2004). Yet, the period of moult also represents an arena for the resolution of these trade-offs through the evolution of moult schedules that minimize overlap with breeding, temporal separation of moult of nonsexual and sexual ornamentation, as well as changes in moult duration and intensity (Jenni & Winkler, 1994; Svensson & Hedenstrom, 1999; Hemborg *et al.*, 2001).

Interestingly, two seemingly antagonistic processes in birds – greater investment into parental care and moult of new sexual ornaments are affected by the same hormone – pituitary prolactin (Schwabl *et al.*, 1988; Dawson & Sharp, 1998; Vleck *et al.*, 2000; Ziegler, 2000; Khan *et al.*, 2001; Kuenzel, 2003; Dawson, 2006); experimental blocking of prolactin prevents moult (Dawson & Sharp, 1998) and stops male parental care (Badyaev & Duckworth, 2005). Thus, resolution of the trade-off between current reproduction and development of future plumage ornamentation should involve not only individual variation in allocation and acquisition of resources, but also modification of the regulating effects of prolactin. However such effects are rarely studied (but see Zera & Harshman, 2001; Ricklefs & Wikelski, 2002; Harshman & Zera, 2006).

Here, we examined life history- and age-dependent developmental variation in sexual ornamentation in male house finches (*Carpodacus mexicanus*) in a native population in Arizona. Males acquire sexual ornamentation when 90–120 days old and thereafter moult into new ornamental plumage every year, during summer or at the end of the breeding season. Male finches vary widely in the amount of energetically expensive parental care they provide and this variation is regulated by prolactin (Duckworth *et al.*, 2003; Badyaev & Duckworth, 2005). Thus, comparison of development of sexual ornamentation between males that differ in parental investment enables direct examination of the effects of residual condition (expected to be *high* in nonparental males and *low* in parental males) and residual prolactin (expected to be *low* in nonparental males and *high* in parental males) on the acquisition of future sexual ornamentation.

Here we test a novel hypothesis that the trade-off between current reproduction and development of sexual ornamentation can be partially modulated by

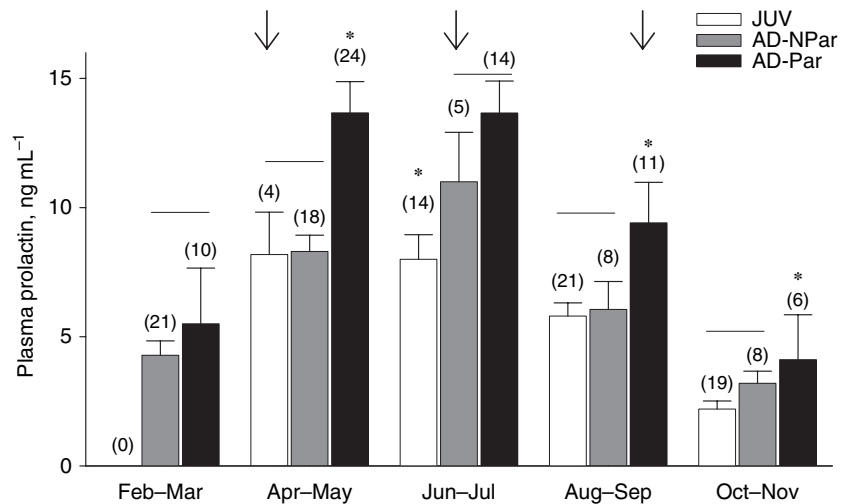
shared effects of residual parental prolactin on ornament elaboration. We propose that, in males providing extensive parental care, the residual effects of high prolactin levels on carotenoid transport (Barron *et al.*, 1999; Gossage *et al.*, 2000) and feather growth may reduce the cost of moult of sexual ornamentation; such cooption can ultimately lead to the evolution of developmental co-regulation of parental care and elaboration of sexual ornamentation. In this study, we first use path analysis to show that male age and life history classes differ in the development of sexual ornamentation. Secondly, we suggest that the shared effects of prolactin on parental care and moult might enable males that invest heavily into current reproduction to nevertheless develop elaborated ornamentation for the subsequent breeding season, supporting empirical documentation of extensive diversity in direction and strength of trade-offs between current and future reproductive effort in birds (reviewed in Badyaev & Qvarnström, 2002). Thirdly, we corroborate previous findings of distinct condition-dependence of male sexual ornamentation across ages and life history states in this species and discuss the consequences of such developmental variation for both the trade-off between current and future reproductive investment and the evolution of female choice of sexual ornamentation.

Materials and methods

Study population and data collection

We studied house finches in a resident population in south-western Arizona since 2002. Birds were trapped year around, three to four times a week, at eight permanent feeding stations and marked with a unique combination of one aluminium and three coloured plastic rings. We determined sex of juvenile males prior to moult with PCR primers that anneal to conserved exonic regions and amplify across an intron in both CHD1-W and CHD1-Z genes. The study population of individually marked birds is closely monitored through detailed daily behavioural observations and censuses and recaptures at regular intervals (protocol in Badyaev *et al.*, 2006). All nesting and most pairing affiliations are known for resident birds, nests are followed from the onset of building, and the extent of male parental care is assessed through filming of nests during incubation and nestling period. Only the female incubates, but males regularly bring food to incubating and brooding females and nestlings, and only males provision the brood of fledglings for up to 2 weeks after they leave the nest. For this study, a male was considered 'nonparental' when it was a resident at the study site from the beginning of the breeding season (i.e. regularly resighted and recaptured from 1 February), but did not have a nest that progressed past building. Nonparental status of males was further confirmed by documenting their low level of circulating

Fig. 1 Plasma prolactin (mean \pm SEM) in relation to time of the season, age and parental status of male house finches. JUV, juvenile males undergoing their first moult into sexual plumage; AD-NPar, adult males that did not provide parental care during the breeding period prior to moult and AD-Par, adult males that provided parental care in the season prior to moult. Line connects means that are not significantly different within a time interval, asterisks indicate significant difference at 0.05 level, arrows show (left to right) the first documentation of sexual ornament moult in juveniles, adult nonbreeding and adult breeding males correspondingly. Number in parentheses is sample size for each group and time interval.



prolactin during the breeding season (Fig. 1, see below), and by the absence of conspicuous parental care of fledglings. Nonparental males can sire offspring in other nests (Lindstedt *et al.*, 2007), but do not provide parental care. We analysed both male body mass and the residuals of body mass on tarsus size (all males combined; $F_{1,109} = 11.85$, $P < 0.001$, $R^2 = 0.18$; linear regression: mass = $6.25 (\pm 3.77 \text{ SD}) + 0.63 (\pm 0.18) \text{ tarsus}$, $t = 3.44$, $P < 0.001$) as a measure of male physiological condition during moult. The residual measure is more appropriate for the study of relative allocation to the development of sexual ornamentation among male groups (Badyaev & Duckworth, 2003), and because the results were similar for both measures, we used only residuals for body mass during moult hereafter. Relative individual condition was assessed twice, in adult males during March (the onset of breeding season), and during moult, and in juvenile males at 40–50 days of age (when allometric relationship between body mass and tarsus is identical to that of adult males Badyaev & Martin, 2000), and during moult. We used date of fledging – the beginning of male-only parental care of fledglings – to measure proximity of current reproduction to the onset of moult of sexual ornamentation. Because males' caring for fledglings late in the season is associated with either repeated breeding attempts or with longer male care, we used the start of brood paternal care as a measure of breeding effort in path analyses (see below).

Moult and ornamentation measurements

During post-breeding moult, resident males were captured with stationary traps and mistnets between 06:00 and 09:00 hours at feeding stations, sampled for plasma within 20 min of capture, and measured. We photographed crown, rump and breast ornamented plumage patches of moulting males with a 5-megapixel digital camera outfitted with a ring flash and mounted in a standard position (for details of protocol see Badyaev &

Duckworth 2003). For post-breeding plumage ornamentation of each male, we measured with SIGMASCAN Pro 5.0 (SPSS, inc.): (1) plumage hue – pigment elaboration from dull yellow to deep purple, (2) colour intensity that ranges from 0 (grey) to 100% (full colour), (3) patch area – total area of the ornamental feathers with pigmentation on each breast side and on rump and (4) hue asymmetry – a measure of consistency in plumage hue between feathers of each ornamented area. A straight line was drawn on the frontal image of each bird from the base of the bill to the lowest pigmented feather on the breast to delineate left and right sides. All pigmented feathers on a male's breast were traced on the left and right sides and patch area was calculated in SIGMASCAN. Side measures were added together to obtain the total patch area, or subtracted, unsigned to obtain area asymmetry. To measure colour hue and intensity, a 10×10 pixel grid was overlaid on each ornament patch and one pixel was sampled in each square of the grid. Hue asymmetry across the patch was recorded as a number of feathers coloured differently (among categories 'unpigmented', 'yellow spectrum', 'orange spectrum' and 'red spectrum') between the left and right side divided by the total number of pigmented feathers. All components of male colouration were measured twice and the measurements were highly repeatable (Badyaev & Duckworth 2003).

Upon capture, occurrence of moult – presence of at least one growing feather within an ornament – was recorded for each of the three ornament areas: crown, breast and rump. For the path analyses (see below) we used a subset of 109 males from the 2005 breeding season with known breeding status, age, at least four recaptures during moult, post-moult ornamentation measures, as well as prolactin and condition measures during moult. *Onset of moult* for each ornament was a midpoint between the date of capture when the ornament was not moulting and the subsequent recapture showing evidence of moult, *the end of moult* for each ornament was a midpoint

between the date of the last occurrence of moult within an ornament and the subsequent capture showing completion of moult. Regular recapture intervals assure the compatibility of these relative estimates of moult parameters between groups of males in this study. The absolute values of onset, end, and duration of moult were estimated with 4–5 days precision. Per cent of overlap in moult among the ornaments – *moult intensity* – was the duration (in days) of moult overlap of all three ornaments divided by the total duration of moult for each individual.

Hormonal sampling and assays

Upon capture we collected *c.* 100 μL of blood from the brachial vein, and immediately separated the plasma by spinning the blood in a microhaematocrit centrifuge at 2700 rpm. Plasma was stored at -80°C until radioimmunoassay analysis. Plasma prolactin levels were assayed by radioimmunoassay using purified chicken prolactin (reference preparation AFP-10328B) as a standard and a rabbit antiserum (AFP-151040789) raised against prolactin (after Badyaev *et al.*, 2005). We radiolabelled chicken prolactin (AFP-4444B) with I^{125} using chloramine-T. Samples were run in duplicate with 18 μL of plasma except for about 5% of samples for which we did not have enough plasma to run a duplicate. The intra-assay coefficient of variation was 11.9% and the least detectable concentration for this volume was 1 ng mL^{-1} . Dilutions of a plasma pool from house finches demonstrated a high cross-reactivity with the antisera, and the slope of the logit-transformed curve for finch plasma did not differ from the slope of the diluted chicken standard (Duckworth *et al.*, 2003).

Statistical analyses

To test differences in moult parameters among groups of males, we used nonparametric two-tailed Kruskal–Wallis tests, difference in prolactin levels was assessed with a general linear model. Hue and area parameters of the same individual were intercorrelated among ornaments and thus we constructed two linear principal components, where Hue (principal component 1) = $0.60\text{ Breast hue} + 0.52\text{ Crown hue} + 0.60\text{ Rump hue}$ (eigenvalue $\lambda = 2.36$, explaining 78.2% variance), and Area (principal component 1) = $0.70\text{ Breast area} + 0.70\text{ Rump area}$ ($\lambda = 1.03$, 52.8% of variance). We used path analyses coefficients of *a priori* hypothesized path model to quantify the relative strength of prolactin and condition at moult, as well as the effect of moult schedule and intensity on the elaboration of fully grown sexual ornaments. Path coefficients and Akaike's Information Criterion (AIC) were estimated using the PROC CALIS of SAS software (SAS Institute Inc.), significance of each path coefficient was tested with multiple regression analyses. Overall fit of the models were likelihood ratio

tests for the concordance between the elements in the covariance matrix obtained from the data and the matrix predicted by the path coefficients. Nonsignificant χ^2 values indicate a lack of difference between predicted and observed values and thus a good fit of data by the model.

Results

Plasma prolactin levels varied seasonally, reaching the highest levels in mid-summer and declining thereafter. However, the seasonal profiles were distinct among male groups ($F_{9,183} = 11.94$, $P < 0.001$; Time period, $F_{4,183} = 16.82$, $P < 0.01$, Male group: $F_{2,183} = 3.69$, $P = 0.04$): parental males had higher prolactin than nonparental and juvenile males from April to May and from August to November (Fig. 1; all groups compared, April–May: Kruskal–Wallis $\chi^2 = 6.83$, $P = 0.05$; June–July: $\chi^2 = 6.59$, $P = 0.06$; August–September: $\chi^2 = 8.29$, $P = 0.04$ and October–November: $\chi^2 = 7.53$, $P = 0.05$).

Parental males had greater overlap in moult of sexual ornaments (Kruskal–Wallis $\chi^2_2 = 17.31$, $P < 0.001$; Fig. 2a), started moult later in the season ($\chi^2_2 = 11.29$, $P = 0.003$; Fig. 2b) and completed moult faster ($\chi^2_2 = 9.38$, $P = 0.05$; Fig. 2b). Greater temporal overlap between male care of fledglings and moult of sexual ornaments was associated with higher prolactin and lower condition during moult (Figs 2a,c and 3); parental males entered moult with higher circulating prolactin levels, but in lower condition compared with nonparental and juvenile males ($\chi^2_2 = 8.94$, $P = 0.01$ and $\chi^2_2 = 9.12$, $P = 0.01$; Fig. 2c). Relative condition at the onset of breeding season or for 50–60 days old juvenile males (see *Methods*) did not differ between breeding and nonbreeding males ($\chi^2 = 0.47$, $P = 0.9$), and tended to be lower in juvenile males ($\chi^2 = 6.34$, $P = 0.06$; Fig. 2c). Development of sexual ornamentation differed strongly among male groups. In parental males, greater post-moult ornamentation area and hue were closely associated with greater prolactin during moult and, indirectly associated with the positive effects of prolactin on moult overlap among sexual ornaments and earlier moult onset (Figs 4, 5 and S1). Hue and area asymmetry in ornaments increased with moult duration and was correlated negatively (hue asymmetry) and positively (area asymmetry) with overlap in moult among sexual ornaments (Figs S2 and S3).

Males differed in the extent to which prolactin and condition during moult contributed to the elaboration of sexual ornamentation (Fig. 5). In parental males, variation in prolactin accounted for more than 75% of variation in ornament hue, area, hue asymmetry, and area asymmetry of post-moult sexual ornamentation, whereas in nonparental adult males, prolactin was less important compared with the effects of condition on the elaboration of post-moult sexual ornamentation (Fig. 5). In juvenile males, condition during moult had a stronger

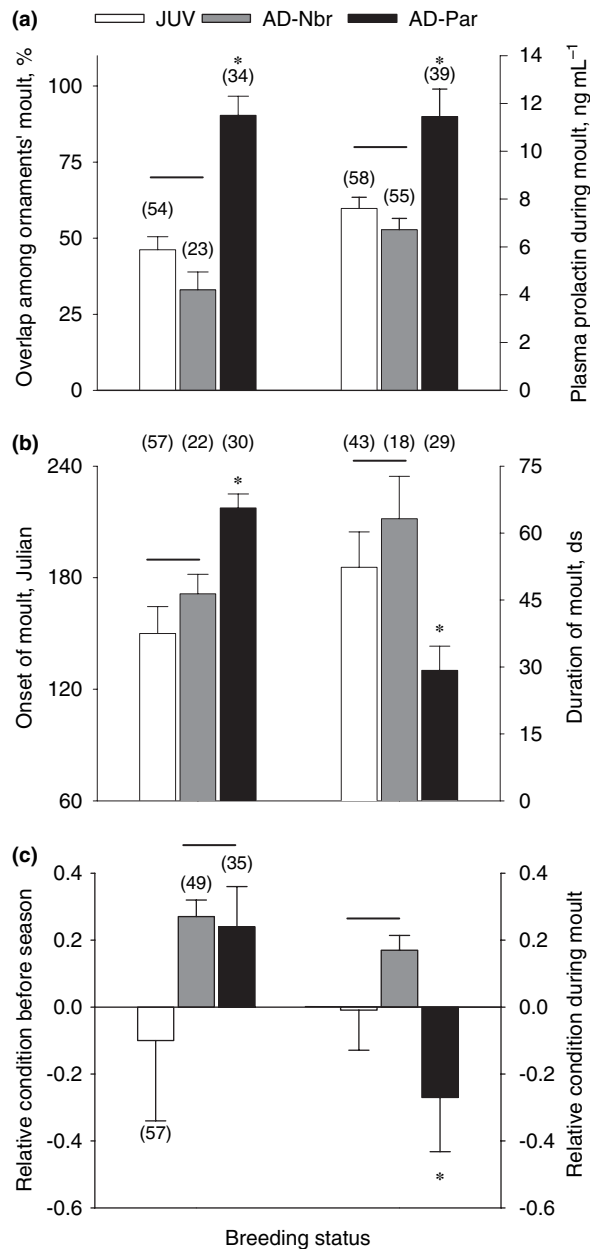


Fig. 2 Differences among male groups in (a) overlap among ornaments during moult (left) and prolactin level during moult (right), (b) development of sexual ornamentation and (c) relative condition at the onset of breeding season (adult males) or 50–60 days old (juvenile males) (left) and, for the same group of males, during moult (right). See Fig. 1 for abbreviations.

effect on both elaboration of ornament hue and hue asymmetry compared with other males (Fig. 5). Parental males developed more elaborated post-moult sexual ornamentation in hue (breast: $\chi^2_2 = 6.82$, $P = 0.04$, rump: $\chi^2_2 = 8.47$, $P = 0.01$, crown: $\chi^2_2 = 5.97$, $P = 0.05$; Fig. 6a), and had lower hue asymmetry in breast orna-

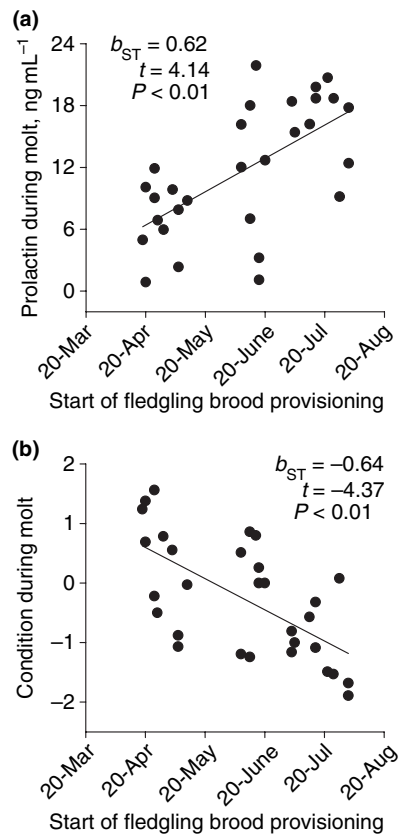


Fig. 3 Partial linear regression plots illustrating the relationship between proximity of male care of fledglings to the onset of moult and (a) prolactin during moult, and (b) condition during moult. Parental males only.

ment ($\chi^2_2 = 7.97$, $P = 0.02$; Fig. 6d). Other components of post-moult sexual ornamentation did not differ among the male groups (Fig. 6).

Discussion

Allocation of resources to elaboration of sexual ornaments is subject to a trade-off between the competing demands of reproduction and survival (Partridge & Endler, 1987; Höglund & Sheldon, 1998; Badyaev & Qvarnström, 2002). When the resolution of this trade-off varies among individuals and environments, an organism's ability to acquire resources for development of sexual displays can be indicated by the displays' condition-dependence (Pomiankowski & Møller, 1995; Rowe & Houle, 1996; Cotton *et al.*, 2004; Hunt *et al.*, 2004a,b). Proximately, the evolution of condition-dependence is linked to the variability of sexual ornament's development across breeding contexts and life history states (Badyaev, 2004, 2007), however such variability is rarely examined.

We found that development of sexual ornamentation varied with males' reproductive status and age. Males

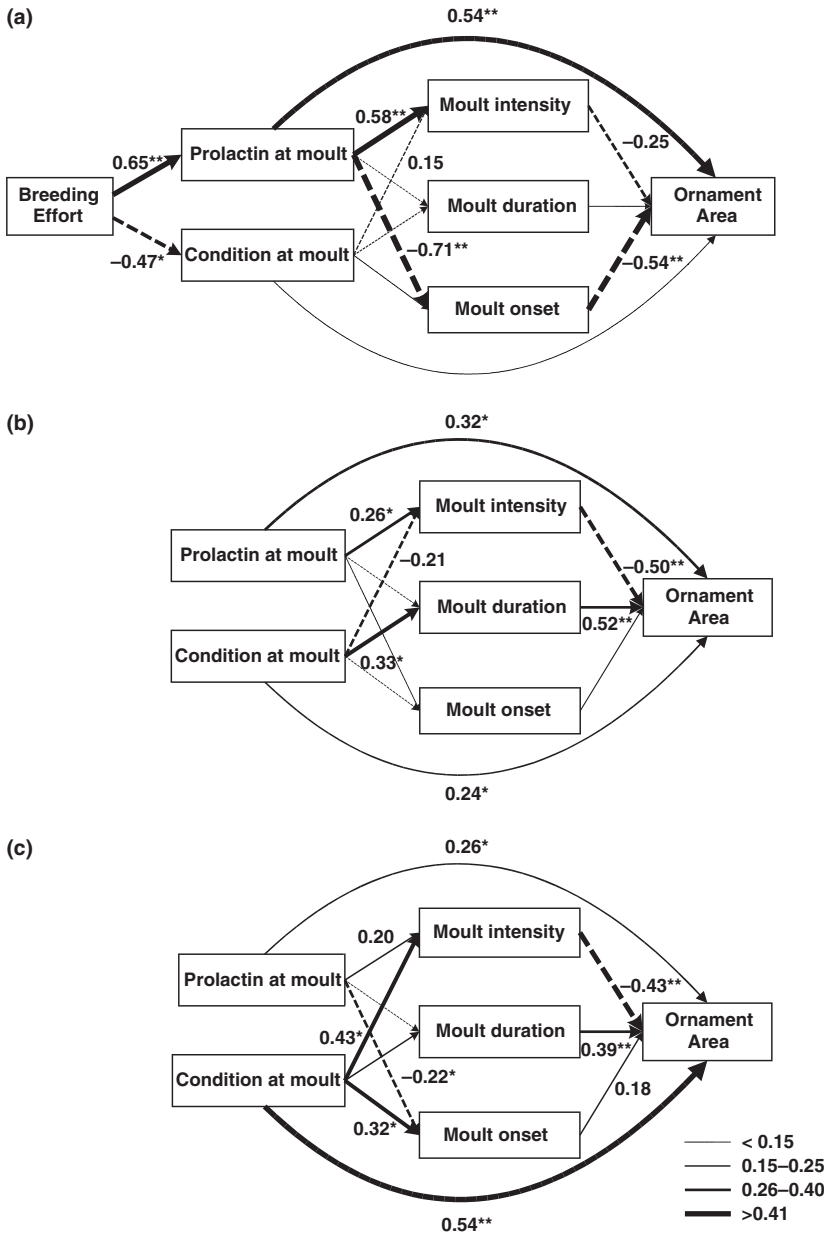


Fig. 4 Path diagrams illustrating the relationship between male sexual ornamentation (area), prolactin, and condition during moult, and development of ornamentation in (a) adult parental males (model's $\chi^2_6 = 7.12$, $P = 0.4$, $AIC = -7.7$), (b) adult non-parental males ($\chi^2_5 = 0.97$, $P = 0.9$, $AIC = -5.6$) and (c) juvenile males ($\chi^2_5 = 1.02$, $P = 0.9$, $AIC = -7.2$). Single-headed arrows show that change in the variable at the base of the arrow will cause a change in the one at the arrow's head. Positive effects are indicated by solid lines and negative effects by dashed lines. Thickness of arrows indicates the magnitude (in SD), and asterisks show statistical significance of the effect. Only coefficients > 0.15 are shown. Breeding effort is the proximity of male's fledgling care to the onset of moult (from Fig. 3). See Online Figs 1–3 for path diagrams of development of ornament hue, hue consistency, and ornament asymmetry. Significance at * $P < 0.05$ and ** $P < 0.01$.

that invested more into parental care and entered post-breeding moult in lower physiological condition compared with nonbreeding males were nevertheless able to develop the same elaboration of sexual traits as males that did not provide parental care. This might have been enabled by distinct developmental pathways of ornamentation between parental and nonparental males (Figs 4, 5 and S1–S3), the former capitalizing on the shared effects of elevated prolactin – a hormone involved in regulation of both paternal care and moult in this species. We found that in all male groups prolactin had strong and direct effects on elaboration of sexual orna-

mentation, corroborating previous studies of prolactin effects in this species (Duckworth *et al.*, 2003; Badyaev & Duckworth, 2005). These findings raise four main questions. First, what are the proximate mechanisms behind the direct effects of prolactin on ornament elaboration? Secondly, how can co-regulation of parental care and moult by prolactin originate and evolve? Thirdly, what are the consequences of such co-regulation for both the trade-off between current reproduction and development of future sexual ornamentation and the evolution of condition-dependent sexual ornamentation? Finally, what are the implications of this mechan-

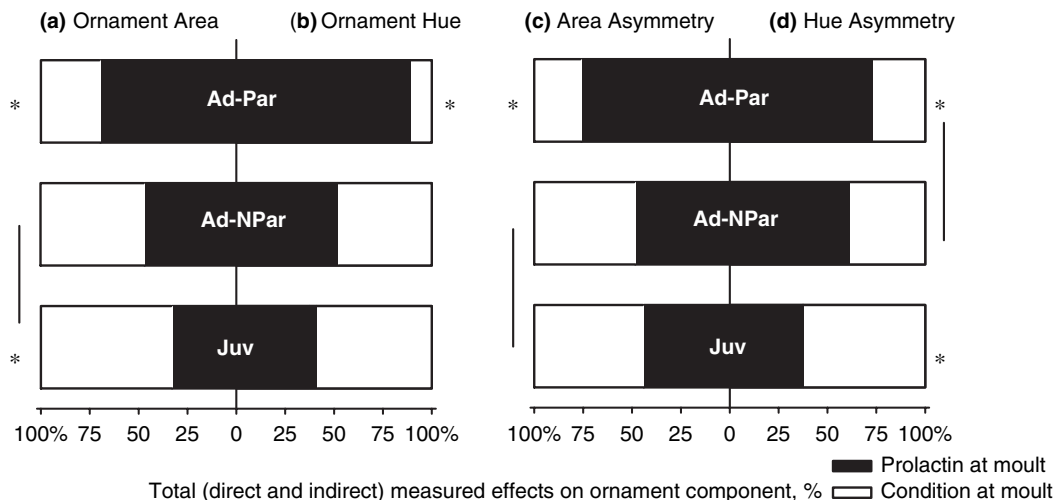


Fig. 5 Contribution of the total measured effects (direct and indirect) to the expression of sexual ornamentation in male house finches in (a) ornament area (only parental male group differs $Z = 3.39, P < 0.05$), (b) ornament hue (all groups differ, $Z > 5.41, P < 0.01$), (c) ornament area asymmetry (only parental male group differs, $Z = 3.51, P < 0.05$) and (d) hue asymmetry (only juvenile male group differs, $Z = 3.21, P < 0.05$). Shown are percentages of the total variance accounted by the effects measured in path models in Figs 4 and S1–S3. Line connects proportions that are not significantly different among groups, an asterisk indicates that proportions of prolactin and condition effects are different within a group (binomial test at $p = q = 0.5$).

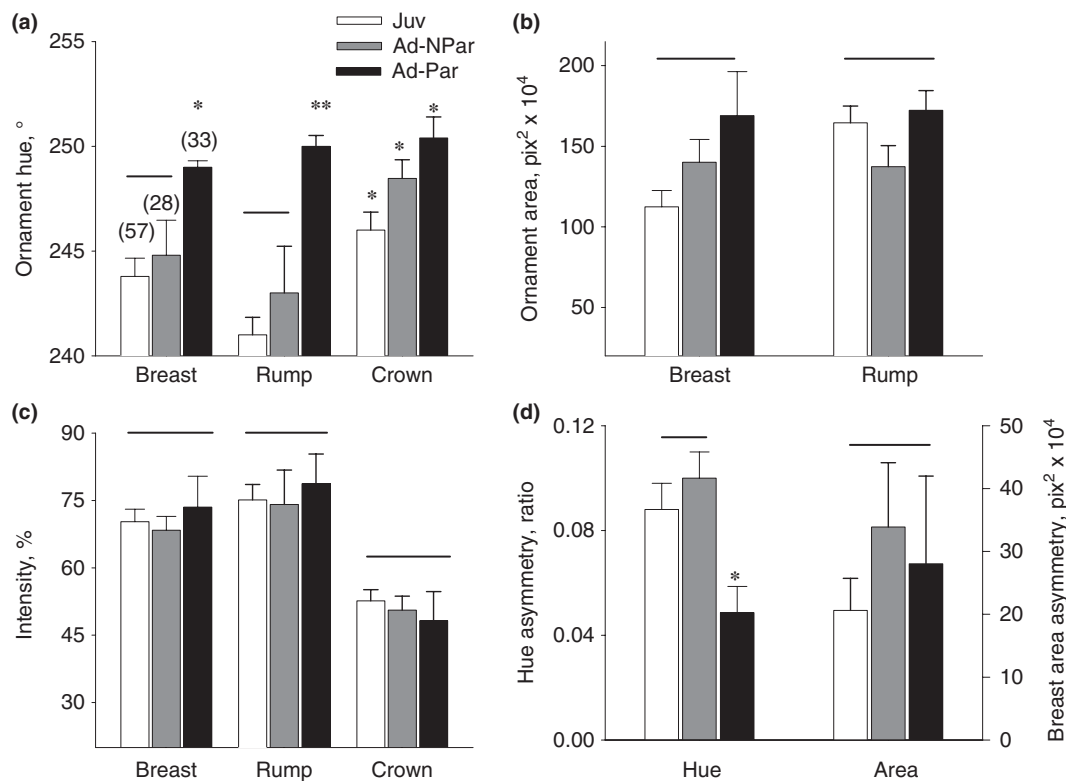


Fig. 6 Post-moult sexual ornamentation in relation to male's preceding parental status and age for (a) hue of breast, rump and crown ornaments, (b) area of breast and rump ornaments, (c) colour intensity in breast, rump and crown ornaments, and (d) hue asymmetry and breast area side asymmetry. See Fig. 1 for details.

ism for the origin of behavioural polymorphism (e.g. association of a mating tactic and sexual display) often documented in birds?

Whereas many studies have documented a separate effect of prolactin on either moult or parental care (Schwabl *et al.*, 1988; Dawson & Sharp, 1998; Vleck *et al.*, 2000; Ziegler, 2000; Khan *et al.*, 2001; Duckworth *et al.*, 2003; Kuenzel, 2003; Badyaev & Duckworth, 2005; Dawson, 2006), the shared effect of prolactin on both parental care and moult of sexual traits have not been examined before. However, several authors documented an association between male parental care and moult. For example, in male pied flycatchers (*Ficedula hypoleuca*), the onset of moult was closely linked to the beginning of male care of fledglings (and thus to the highest levels of circulating prolactin; Silverin, 1980) even when fledgling date was experimentally manipulated (Hemborg, 1998, 1999). We suggest that the proximate mechanisms behind direct effects of prolactin on ornament development (Fig. 4) are prolactin's facilitation of lipoprotein-mediated carotenoid transport (Barron *et al.*, 1999; Gossage *et al.*, 2000), and keratin metabolism (Rose *et al.*, 1995); this idea is corroborated by two previous findings of an association between carotenoid-based sexual ornamentation, ornamental feather growth and circulating prolactin in wild birds (Duckworth *et al.*, 2003; Pr eault *et al.*, 2005; Badyaev & Landeen, 2007). Moreover, shorter and more intense moult under the direct effect of prolactin resulted in greater consistency of colour deposition and greater coordination of activated feather follicles across an ornament (i.e. lesser asymmetry; Figs S3 and S4), thus further implicating the shared effects of prolactin on post-breeding moult in parental males. Interestingly, greater ornament elaboration was associated with later onset of moult in early moulting juveniles, but earlier onset of moult in later moulting adults (Figs 1, 4a vs. c and S1), suggesting the presence of an optimal ornament moult period, probably linked to environmental availability of dietary carotenoid precursors.

A shared hormonal link for regulation of parental care and moult might have evolved through a common dependency of breeding and prolactin production on photoperiod (Chakraborty, 1995; Dawson, 1997, 2006; Dawson & Sharp, 1998; Sharp *et al.*, 1998; Maney *et al.*, 1999), such that breeding necessarily delays moult onset past the time when photoperiod-induced prolactin levels (initiating moult) would be the highest (Fig. 1). Parental males' subsequent compensation for a later moult with a greater residual level of circulating prolactin and greater residual sensitivity to prolactin (e.g. higher density of prolactin receptors in integument tissues, Lopez *et al.*, 1995; Rose *et al.*, 1995) can lead to the evolution of hormonal co-regulation of moult and parental care. Alternatively, the shared effects of prolactin on carotenoid transport and paternal care might be a consequence of selection on carotenoid-based indicators of paternal care (Rothschild, 1975; Hoelzer, 1989).

In iteroparous animals that develop a new sexual display for each bout of mating, the relative importance of allocation and acquisition of resources for the development of sexual ornaments depends on the strength of female choice of each of these components across a lifetime (e.g. Hunt *et al.*, 2005; Miller & Brooks, 2005; Chenoweth *et al.*, 2006). Thus, multiple alternative ways of acquiring resources for the development of a sexual ornament, as documented in this study, would reduce the potential for formation of a genetic correlation between ornament expression and organismal condition and, thus, the utility of sexual ornaments as indicators of genetic quality (e.g. Badyaev, 2004). In accordance with these predictions, we found no evidence for ornament-mediated selection for genetic quality and no difference in lifetime fitness of variable expression of ornament elaboration in this species (Badyaev & Hill, 2002; Oh & Badyaev, 2006). Instead, extensive variation in elaboration of sexual ornamentation and its condition-dependence in relation to social and ecological context of breeding, generated selection on direct phenotypic benefits indicated by ornamentation, such as past and future parental care and parasite resistance (e.g. Hill, 1991).

The results of this study provide insight into proximate mechanism behind the previously documented change in condition-dependence of sexual ornamentation in relation to male age and breeding status in a Montana population of this species. In that population, the decrease in condition-dependence of sexual ornamentation was accompanied by both a decrease in phenotypic variance in ornamentation in older age classes and weaker female selection on the condition-dependent component of sexual ornamentation (Badyaev & Duckworth, 2003; Badyaev & Young, 2004). In juvenile male house finches, the first moult might involve establishment of pathways that activate delivery of carotenoid pigment to ornamental feather follicles, and follicles' uptake and metabolism of carotenoid precursors. If such establishment of developmental pathways is costly, then it might account for greater condition-dependence of the first moult compared with subsequent moults of sexual ornamentation (e.g. Fig. 4, Badyaev, 2007). If the mechanism of prolactin co-regulation of parental care and moult operates in that population, then it can not only provide a proximate link between males' breeding status and condition-dependence of subsequent sexual ornamentation, but also illustrates that the same elaboration of sexual ornamentation can be produced by a variety of developmental pathways (e.g. Figs 4 vs. 6, see also Badyaev, 2007). Noteworthy in this context is that a majority of studies documenting significant condition-dependence in sexual ornamentation in birds are conducted in 1-year-old individuals.

Furthermore, the shared effects of prolactin on paternal care and moult might account for the association of

sexual phenotype and reproductive strategy (e.g. Maney *et al.*, 2005), such as observed in a Montana population of house finches, where males with yellow and red ornamentation differ in parental strategies and frequently change the strategies within their lifetime (Badyaev & Duckworth, 2005). More generally, the developmental association between paternal care and acquisition of subsequent sexual ornamentation underscores the importance of context-dependent ontogenetic variation in sexual ornaments for the evolution of mate choice of these ornaments.

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Supplementary material

The following supplementary material is available for this article:

Figure S1 Path diagrams illustrating the relationship between male sexual ornamentation (hue), prolactin, and condition during moult, and development of ornamentation in relation to male's reproductive status.

Figure S2 Path diagrams illustrating the relationship between area asymmetry of male sexual ornamentation, prolactin, and condition during moult, and development of ornamentation in relation to male's reproductive status.

Figure S3 Path diagrams illustrating the relationship between hue asymmetry (consistency) of male sexual

ornamentation, prolactin, and condition during moult, and development of ornament development in relation to male's reproductive status.

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