Functional Avian Endocrinology

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Evolution of plasticity in hormonally-integrated parental tactics: An example with the house finch

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Introduction

The evolution of behavioral plasticity, particularly the evolution of context-dependent (i.e., conditional) mating tactics, is one of the most controversial and least understood phenomena in evolutionary theory (18, 44, 50). On the one hand, a growing number of behavioral studies document the benefits of alternative mating tactics where individuals adjust their reproductive behaviors and morphologies to a particular breeding context which ultimately enables them to achieve high fitness even in the most rare of environmental circumstances (8, 23, 37, 47). For example, the costs and benefits of female choice of a particular male sexual trait, as well as male investment into a sexual trait, may depend on the circumstances in which mating occurs (8). It is often assumed explicitly that because such context-dependency is enabled by individual phenotypic plasticity, no genetic polymorphism for distinct mating behaviors and morphologies is needed (2, 24). On the other hand, population genetics theory shows that these assumptions would actually preclude the evolution of context-dependency, which requires inheritance of reliable context-recognition even for the most rare contexts, as well as strong and predictably frequent selection favoring the formation a particular mating strategy (25, 26, 44, 48). Thus, conditions required for the evolution of context-dependency in mating tactics are not likely to extend to fluctuating and infrequent contexts and to all individual morphologies (3, 44).

In theoretical studies, the resolution of this paradox depends on explicit consideration of the demographic dynamics of a population; the lack of such consideration in the past has prevented addressing the basic issue of the importance of population fluctuations as a source of selective pressures promoting genetic polymorphism and/or phenotypic plasticity (27, 28, 34, 36). For example, whereas theoretical modeling suggests that plastic parental strategies will evolve under ecological conditions that promote genetic differentiation and the maintenance of genetic polymorphism, no study of parental strategies so far has investigated the evolution of genetic polymorphism and/or phenotypic plasticity in a unified framework that incorporates ecological, behavioral, and demographic considerations. In empirical studies, resolution of this paradox requires understanding the mechanisms that "switch" phenotypes from one ontogenetic trajectory to the other (1, 21, 36, 49). Such switches are variably called "modifier genes for behavior expression", "developmental switchpoints", or "social status-dependent switchpoints" which betrays the uncertainty about their nature – some assume that these switches are genetically determined, some that they are induced by population dynamics, and some that they are created during ontogeny (13, 32, 35, 38, 46).

Especially puzzling and most revealing are cases when the same individuals employ distinct mating tactics across different breeding contexts. The distinct and demographically structured parental strategies of socially monogamous house finches (*Carpodacus mexicanus*) (5) provide an opportunity to investigate experimentally the developmental and behavioral components of conditional mating tactics. In this species males use distinct parental tactics depending on elaboration of their sexual ornamentation. The fitness consequences of each parental tactic depend on the demographic composition of the population, and across their lifespan, males' parental tactics closely correspond to annual changes in sexual ornamentation (4, 5). In this review, we first address the proximate hormonal mechanisms behind dichotomous parental strategies indicated by continuous sexual ornamentation. Second, we examine how these hormonal mechanisms integrate proximately the expression of sexual ornamentation and parental behaviors. Finally, we discuss how the sensitivity to behavioral and ecological cues for switching between alternative parental tactics can evolve.

Distinct parental tactics in relation to sexual ornamentation

House finch males molt into new sexual ornamentation once a year after the breeding season and based on the elaboration of plumage ornamentation males can be separated into two groups – from orange to purple ("red" hereafter) and from uncolored to bright yellow ("yellow" hereafter) (4). Red and yellow colors in these groups are produced by different carotenoid catabolisms and elaboration within each color category is distinct biochemically (6, 11, 29).

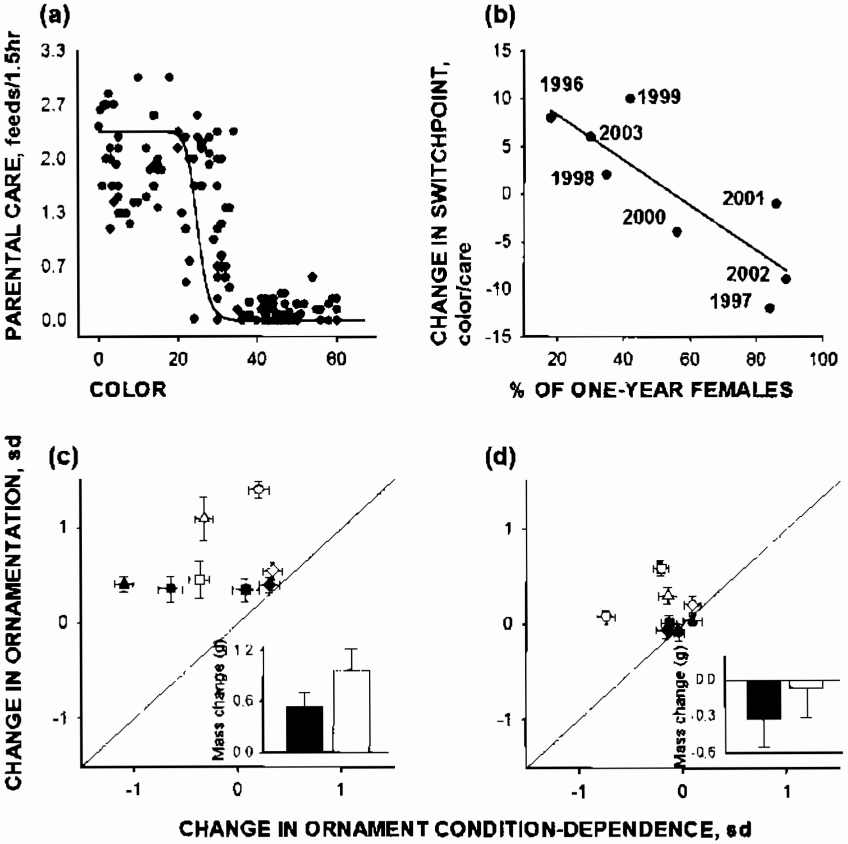

Fig. 1 (**a**) Red (color score >20) and yellow males have distinct parental tactics in Montana house finches, 1995-2003 (5), (**b**) Switchpoint between parental tactics (1st derivative of male color by male care shown in a) varies with the female age ratio in breeding population; (**c-d**) Summary of the changes in sexual ornamentation (in standard deviations) between subsequent molts and changes in ornament condition-dependence (in standard deviations) between subsequent molts in (**c**) after first breeding season (i.e., between postjuvenile and the first postbreding molts) and (**d**) after the second breeding season (i.e, between the first and the second postbreeding molts). Points above diagonal indicate that change in sexual ornamentation are greater than expected from the corresponding change in condition-dependence (hue: •; saturation: ■; area: ▲; hue asymmetry: ♦). Black symbols indicate change in males that were paired and white symbols indicate males that were single during breeding season preceding molt. Inserts show the change in body mass between molts in males that were paired (black) and single (white) between the molts (4).

A male sexual ornamentation is closely linked to his mating tactic (Fig. 1a). Red males pair earlier, but do not provision incubating females and nestlings, whereas yellow males pair later, but provide most of the food for female and nestlings (5). Consequently, for red males offspring recruitment is primarily affected by earlier nest initiation and number of mates, while in yellow males it is affected most by male provisioning of nestlings (5).

Males change both sexual ornamentation and mating tactics in both directions across their lifespan. Males can live up to 6 years undergoing repeated and reversible changes in ornamentation and mating tactics between subsequent molts (4). During the initial (postjuvenile) molt, the expression of ornamentation is dependent on condition; however the condition-dependence of ornamentation decreases sharply throughout a male's lifetime, and in older males, switching between plumage morphs is largely independent of condition during molt (Fig. 1cd, 4, 11). The fitness consequences of male mating tactics depend strongly on the ratio of "old" (i.e., older than a year) and "young" (i.e., second-year) females in the population (Fig. 1b, 5). Red males are strongly preferred by young females, whereas older females avoid red males and prefer yellow males. This pattern of preference is due to overinvestment into parental care by females that initially mate with red non-parental males (5). The experience-mediated female choice of male plumage morph results in close concordance between the ratio of males' morph and the demographic composition of a population (Fig. 1b).

Empirical evidence for hormonal integration of parental tactics: Natural patterns

Paternal care in the house finch is closely linked with the plasma level of prolactin – a pituitary hormone that is associated with paternal care in many passerines (12, 22, 30, 40, 41). Free-living parental (yellow) males had the highest prolactin levels during provisioning of incubating females, and especially nestlings and fledglings (Fig. 2a, 20). Among these parental males, the level of plasma prolactin was positively correlated with the intensity of provisioning (Fig. 2d, 20). Parental males with higher levels of prolactin had lower hematocrit counts during the provisioning period and postbreeding molt (Fig. 2c, 20), and suffered higher overwinter mortality compared to red (non-parental) males and yellow males that provisioned less (7, 20). During nestling provisioning period, yellow and red males have nonoverlapping hormonal profiles of plasma prolactin (Fig. 2ab): red (non-parental) males have much lower levels of prolactin compared to yellow (parental) males (20).

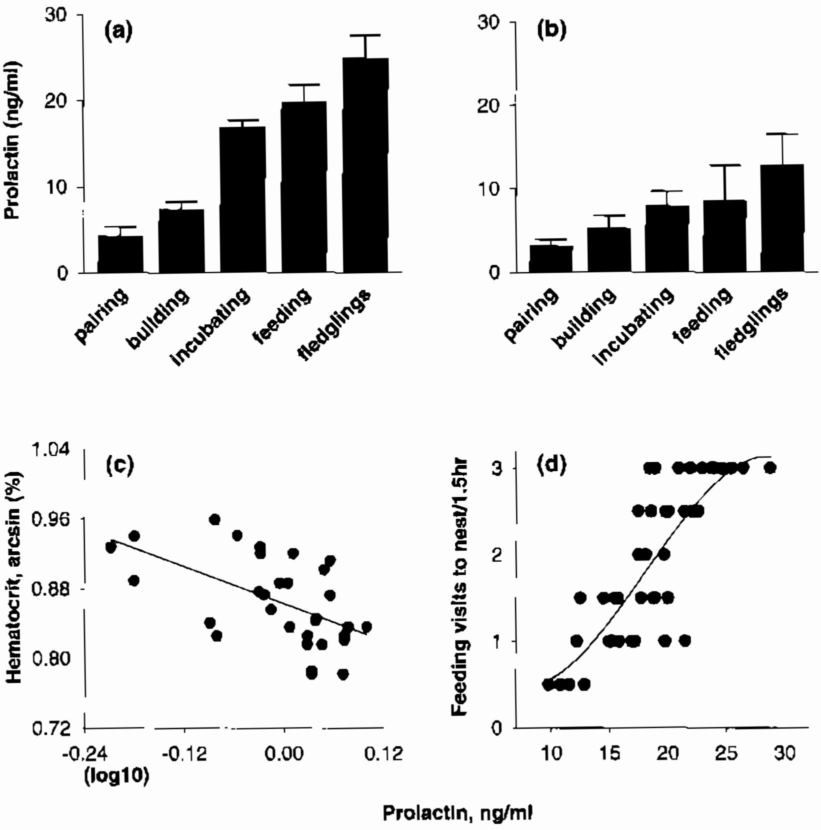

Fig. 2 **(a-b)** Plasma prolactin levels in relation to breeding cycle stage in **(a)** parental (yellow) males, and **(b)** non-parental (red) males (5, 20, including data from 2002-2003); **(c)** Plasma prolactin level (log10) in relation to hematocrit level (arsin) during nestling provisioning period (20); **(d)** Plasma prolactin levels in relation to nestling provisioning frequency immediately preceding prolactin sampling (20, including data from 2002-2003).

Experimental evidence for hormonal integration of parental tactics: Creating *reversed* mating tactics with hormonal implants

Long-term collection of hormonal profile data from breeding finches at our study populations (9, 20) enabled us to calibrate and test on a captive population delayed-release, 2mm-diameter, subcutaneous hormonal implants of vasoactive intestinal peptide (VIP hereafter; that stimulates the pituitary to increase a male's own secretion of prolactin), and hormonal implants of bromocryptine (that blocks the production of prolactin in some male vertebrates) (31, 33, 39, 40, 42).

To validate the performance of these implants in house finches, we captured nine males from the study population and measured their baseline prolactin levels (Fig. 3a). We transported the birds to an aviary facility and assigned them randomly to a treatment group. Each male was implanted subcutaneously with either one bromocryptine (released 0.24 mg/day for 21 days), one VIP (released 7 μg/day for 14 days), or one control pellet (vehicle only; Innovative Research of America, USA). All implants, including placebos, are designed to last only to the end of the release period. Males were kept in captivity on an *ad lib* seed diet, water, and vitamin supplements, and on natural photoperiod. Each male was sampled for prolactin on days 1, 3 and 5 after implantation with the exception of two males that we bled on days 1, 2, and 5 instead. All males were released at the site of capture on day 6. We subsequently recaptured and sampled for prolactin all of the VIP and placebo implanted males but did not recapture the bromocryptine implanted males, although these males were repeatedly re-sighted at the feeder stations.

Both VIP and bromocryptine implants, but not placebo implants, had a significant effect on the level of plasma prolactin in males by day 3 post-implantation (Fig. 3a). In males with baseline levels of prolactin, VIP strongly increased plasma prolactin to a level typically seen in intensively provisioning males (20) (Fig 3a). Bromocryptine implants sharply lowered the level of plasma prolactin beyond detectable levels.

Following this validation experiment, in 2001-2003, we implanted 24 red (non-parental) males with VIP implants and 37 yellow (parental) males with bromocryptine implants (Fig. 3b). For all males, we conducted a pre-implantation nestling provisioning watch on day 3-5 of the nestling stage. Males were subsequently captured, either at the nests (parental yellow males) or at the feeding stations (nonparental, red males) sampled for plasma prolactin (20) and implanted with VIP, bromocryptine, or placebo pellet as describe above. On day 7-9 of the nestling stage, we conducted a post-implantation observation of male provisioning behavior and obtained plasma prolactin samples from implanted males that were captured opportunistically during daily captures. Both pre- and post-implantation behavioral observations were conducted by the same technician who was unaware of the experimental objectives and also did not know which males were assigned to which group.

VIP implants of red (nonparental) males and bromocryptine implants of yellow (parental) males reversed males' parental behavior within a breeding season (Fig. 3c). VIP-implanted red males became parental and fed their nestlings, whereas bromocryptine-implanted yellow males stopped feeding their nestlings (Fig. 3c). There were no other changes in males' behavior either towards their females or other birds. Control males did not change their provisioning frequency (Fig. 3c). Placebo implants did not affect male behaviors in other studies of this species (45).

Taken together, these results show that (i) house finch males have two parental tactics invariantly indicated by two states of sexual ornamentation, (ii) males switch between the plumage morphs and parental tactics throughout their lifetime, (iii) male's switching of mating tactics between years is linked with the female age ratio in a population, and (iv) males with distinct paternal tactics have non-overlapping profiles of plasma prolactin that proximately integrates ornament elaboration and parental behavior.

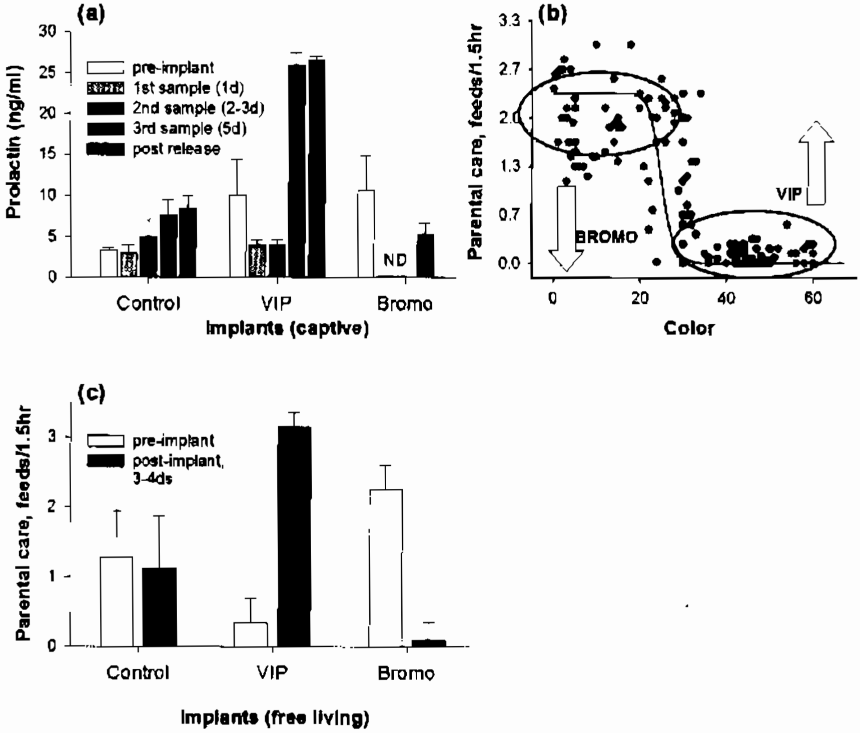

Fig. 3 **(a)** Plasma prolactin levels in control-, VIP, and bromocryptine (Bromo) implanted male house finches. ND indicates levels below detectable. Males were sampled for prolactin three times within five days post-implantation and within a week after release (post-release); **(b)** Experimental design to reverse parental behavior in relation to sexual ornamentation by subcutaneous implants of VIP to red (non-parental) males and bromocryptine to yellow (parental) males. **(c)** Pre- and post-implantation nestling provisioning frequency in Control males, red males implanted with VIP, and yellow males implanted with bromocryptine.

Evolution of hormone-mediated behavioral plasticity in parental tactics: Unresolved questions

Two questions remain unresolved. First, what are the cues for switching between elaboration morphs/parental tactics? Second, how does the ability of males to detect and implement these cues evolve? We propose three general alternative hypotheses for the evolution of hormonally-mediated plasticity in parental tactics in this system.

First, integration of sexual morph and parental tactic can be established simultaneously, under shared developmental cues, during the color acquisition in the fall ("*developmental integration*" of color and behavior). In this case, the cue could include demographic composition of the population or it can be a passive consequence of the overlap between parental care and molt. Male finches undergo postbreeding molt in fall flocks with the same birds as will be breeding at the study site the following year (10), so that the demographic composition of the population in the fall may serve as a cue for development of male's mating tactic. The female age ratio changes strongly among years (Fig. 1b). Thus, immediate developmental cues for changes in tactic can include age-specific food competition (including competition for carotenoid-rich food) or some form of cognitive assessment of general age-composition in the fall (19). Alternatively, simultaneous developmental integration of color and behavior can be due to shared hormonal signaling associated with production of prolactin (14, 15). For example, parental males have higher circulating prolactin late in the summer and this can, potentially, delay their molt onset and affect molt duration (16, 17). If shorter molt results in yellow ornamentation, then this could produce an association between parental behaviors, molt duration, and subsequent color (A. Dawson, pers. comm.).

Second, integration can be established sequentially with color being established in the autumn and the behavioral tactic, independently, during the following breeding season ("*behavioral integration*"). In this case, the cues can include speed of pairing. Color can be determined in the autumn molt (as a result of variation in the access to carotenoid-rich diet, duration of molt, health, or prior breeding season behaviors, whereas the parental behavior can be a consequence of a lag in female choice in the spring – later selected males might be more willing to provide care (43).

Finally, yearly variation in parental tactics can be due to annual population fluctuation of the age ratio of males with particular life history characteristics (e.g., non-parental red males might be younger than males of other tactic) and the parental tactic can be due to heritable association of color and behavior ("*genetic integration*") (1, 3).

Further experiments in this study system should examine, in particular, the effect of plasma prolactin on molt onset and duration (and resulting color morph), the effect of demographic composition of the population at the time of molt on the sex- and age-specific aggression and competition for carotenoid-rich foods as well as hormonal profiles. Further examination of endocrinological mechanisms behind both the integration of sexual ornamentation and parental care and ecological and behavioral cues for implementation of a particular parental tactic is a necessary next step to understand the evolution of behavioral plasticity.

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