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Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch

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When individuals in a population differ in physiological condition and residual reproductive value, selection should favor phenotypic plasticity in reproductive investment such that individuals are able to adopt the reproductive tactic that results in the highest fitness under given conditions. Here we examined reproductive tactics in relation to the elaboration of condition-dependent sexual ornamentation (carotenoid breast coloration) in a Montana population of the house finches (*Carpodacus mexicanus*). Males used distinct reproductive tactics depending on elaboration of their sexual ornamentation. Males with red pigmentation (maximum ornament elaboration) paired with females that nested earlier, but these males did little provisioning of incubating females and nestlings. In contrast, males with yellow coloration paired with females that nested later, but these males fed female and nestlings more. Consequently, for red males offspring recruitment was primarily affected by earlier nest initiation, whereas in yellow males it was affected most by male provisioning. In males with intermediate plumage coloration, all measured components, nest initiation, provisioning of incubating female, and nestling feeding, strongly contributed to offspring recruitment. The fitness consequences of alternative reproductive tactics of males were influenced by breeding experience and fidelity of their mates. Among first-time breeders, red males achieved the highest fecundity because of the advantage gained through early nesting and pairing with more experienced females and because of compensation by their mates for low male provisioning of nestlings. Among experienced breeders, males with intermediate plumage coloration achieved the highest fecundity because of the combined benefits of relatively early pairing and high parental care. High variation in sexual ornamentation in a Montana population of house finches may favor distinct associations of sexual displays with a particular set of reproductive behaviors. *Key words: Carpodacus mexicanus,* conditional strategies, house finches, parental care, reproductive investment, secondary sexual traits. *[Behav Ecol 13:591–597 (2002)]*

Expression of secondary sexual traits is often closely linked to the overall physical condition and health of an individual and is under strong selection by female preference (e.g., Andersson, 1986; Price et al., 1993). Female preference for males in high overall condition, as advertised by development of condition-dependent sexual traits, evolves because of direct and indirect effects of male condition on female fitness (Andersson, 1994). Theory suggests that phenotypic effects of male condition that directly affect female survival and fecundity, such as help with raising offspring, generate much stronger selection on female preference than do indirect effects (Kirkpatrick, 1985; Kirkpartick and Barton, 1997). Consequently, males should invest in advertising such direct benefits, and females should be particularly responsive to male displays that accurately predict the resource investment of males (Westneat and Sargent, 1996).

Despite the apparent importance to females of direct phenotypic benefits associated with ornament display and the many empirical studies documenting that resource benefits are often associated with condition-dependent ornaments (reviewed in Andersson, 1994), the processes behind the evolution of female preference for condition-dependent sexual traits that indicate paternal care are not well understood. The central challenge is to understand the trade-offs between overall physiological condition, expression of condition-dependent sexual trait, and investment in parental care (e.g., Badyaev and Qvarnström, 2002; Höglund and Sheldon, 1998; Kokko, 1998; Price et al., 1993; Sheldon, 2000; Trivers, 1972; Williams, 1966). Such trade-offs can operate both within and across reproductive attempts. Within a current reproductive attempt, trade-offs may occur between investment in a condition-dependent sexual trait and investment in condition-dependent paternal activity (e.g., Hoelzer, 1989; Johnstone, 1995; Kokko, 1998; Qvarnström, 1997). For example, although condition-dependent ornaments must be costly to be honest, selection should not favor costs of ornament production or maintenance that would compromise parental care (e.g., Fitzpatrick et al., 1995; Martin and Badyaev, 1996; Owens and Bennett, 1994).

Across reproductive attempts, relative investment in condition-dependent traits and parental care should vary among individuals of different age and reproductive history (i.e., individuals of different residual reproductive value; e.g., Burley, 1986; Kokko, 1997; Smith, 1995; Williams, 1966). Younger individuals with greater future breeding prospects or individuals paired with lower quality mates may invest less parental care in the current reproductive attempt than is indicated by their condition-dependent trait. For example, if males with greater development of sexual traits attract better quality females, then, under certain conditions, such males may be expected

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Figure 1
Male house finches vary in expression of carotenoid-based plumage ornamentation. Shown are examples of breast-patch hue categories: yellow (left), intermediate (middle), and red (right).

to reduce parental care because of greater investment by their mates (Burley, 1986; Gowaty, 1996; Sheldon, 2000; Weatherhead and Robertson, 1979). Such confounding effects of female quality and effort on male investment strategies are especially strong in monogamous species where parental investment of sexes are similar and mutual mate choice is strong (e.g., Johnstone et al., 1996). Furthermore, individual condition may change since the formation of condition-dependent sexual trait (such as in distinct timing of molting in the fall and breeding in the spring in some birds). For example, in individuals experiencing environmentally induced decline in overall condition in the period between trait formation and trait use, the expression of a trait may no longer indicate parental care that the individual can afford to provide (e.g., Kokko, 1998; Qvarnström, 1999). Finally, on the individual level, fitness benefits of investment in condition-dependent sexual trait in relation to overall condition depend on population variation in expression of the sexual trait (Candolin, 2000; Gross, 1996; Kokko, 1998).

Ultimately, such individual variation in allocation in sexual traits and parental care should favor multiple solutions favoring a combination of particular suites of reproductive behaviors (Badyaev and Qvarnström, 2002; Gross, 1996). By adopting varying reproductive tactics, males and females can maximize current fitness in relation to variation in individual condition in a particular environment (e.g., Eadie and Fryxell, 1992; Kodric-Brown, 1986; Radwan, 1993). On the population level, variation in reproductive tactics should result in condition-mediated association between expression of the sexual trait (which indicates an individual's average condition) and benefits that the individual can provide (which is influenced by allocation into current reproductive effort in relation to condition), thus enabling evolution of female preference for a trait.

Adoption of a conditional reproductive strategy requires an individual's ability to choose a reproductive tactic based on the relative position of this individual in relation to others in a population (Gross, 1996; Kokko, 1998). The elaboration of an environmentally based sexual trait that is directly linked to individual condition is especially suitable for the evaluation of such position. In male house finches (*Carpodacus mexicanus*), elaboration of carotenoid ornamentation of breast plumage (Figure 1) is directly influenced by individual physiological condition, health status, and parasite exposure at the time of molt (Brawner et al., 2000; Hill, 2000). At the same time, acquisition of carotenoid pigments is determined by environmental variation leading to a wide fluctuation in the range of elaboration of carotenoid-based ornamentation and its association with overall condition among populations and across years (Badyaev et al., 2001a). Thus, fitness consequences of variation in carotenoid ornamentation strongly differ among house finch populations (cf. Badyaev and Martin, 2000; Hill, 2002).

We studied a large population of house finches in northwestern Montana to investigate whether males with different elaboration of a condition-dependent sexual trait used different reproductive tactics. First, we established that measured components of male reproductive investment had strong consequences for offspring recruitment. Second, we examined whether males with different elaboration of condition-dependent sexual traits used distinct reproductive tactics, and whether these tactics varied in fitness consequences. Third, we examined complementary interaction between male and female reproductive behaviors to address the role of female experience in the formation of female preferences for a male sexual trait.

METHODS

We studied a resident population of the house finches inhabiting an isolated area of suitable habitat near Missoula, in northwestern Montana, USA (for details of the study site and field protocol, see Badyaev and Martin, 2000). The study site was a cluster of buildings and 46 identical ornamental shrubs planted in a single line set in an open grassland. Finches used these 2-m-high ornamental shrubs for nesting and several large coniferous trees at the edge of the complex for roosting. Each year, from 1995 to 2000, all finches were captured during January–March, measured, and marked with a unique combination of one aluminum and three colored plastic rings. All pairing and nesting affiliations of breeding adults were determined (Badyaev and Martin, 2000), and social paternity was confirmed by DNA fingerprinting analyses (Badyaev et al., 2001a).

Upon capture, we photographed carotenoid-based breast plumage patch of each male using a 35-mm camera mounted in a standard position. Individuals were kept in a standardized position, on the dorsal side with the anterior point of beak held in place by a wire loop (Badyaev et al., 2001a). Resulting images were transferred to digital image files. To assess the effect of bird position in the photostand on repeatability of measured traits (repositioning error), we repositioned each male (i.e., taken from a photo setup, put back again, and rephotographed) three times. Each resulting image of the

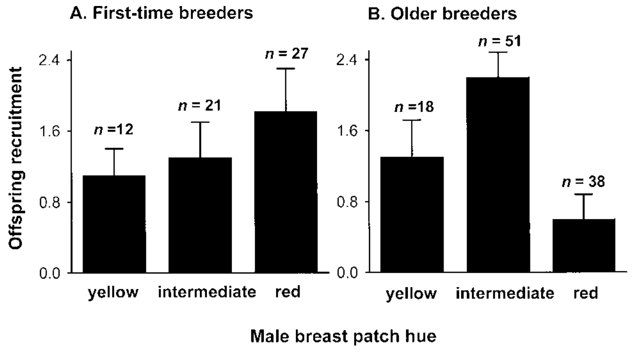

Figure 2
Relationship between male sexual ornamentation and within-season offspring recruitment in (A) first-time breeder males and (B) older males.

breast patch was further remeasured two times (measurement error) under 6× magnification in SigmaScan software (Jandel Scientific). Pigment hue was the average of the hue assessment in three different areas (ca. 3×2 feathers) within a breast patch. Following the protocol for visual assessment of hue outlined in Hill (1992), we recorded pigment hue on a scale of 1–10: 1–3 yellow, 4–7 intermediate (orange), and 8–10 red. Details of measurement error (df = 2490, mean squares [MS] = 0.03) and repeatabilities ($r = .99 \pm .001$, $p < .001$) for all 498 males in our study population (including all males under this study) are given in Badyaev et al. (2001a).

In 1996–2000, age and breeding experience (i.e., "first breeder," individuals breeding for the first time, and "older breeders," individuals breeding for second or more times) was known for most birds, as most the first-year breeders in the study site were marked as hatching-year birds in the preceding fall. In addition, strong fidelity of adult house finches to the location of previous breeding and the isolation of our study site allowed us to evaluate breeding experience and mate fidelity for all resident males and females (Badyaev and Martin, 2000). To avoid pseudoreplication, we used data for only one year of breeding per bird.

After leaving the nest at age 16 days, young finches remain within the study site until they are 100–120 days old (see Badyaev et al., 2001b, for details). As a part of an ongoing study of ontogeny of sexual dimorphism, young birds were recaptured once per 5–6 days until 100 days of age. Thus, for each breeding pair, we were able to obtain the number of offspring that survived to the age of 40 days (hereafter "offspring recruitment").

In house finches only the female incubates, but males regularly bring food to incubating females. We recorded the number of trips by males to provision incubating females during 90-min nest watches on days 7–8 of incubation. We monitored nests with binoculars or spotting scopes, from a parked car at the distance of 4–8 m. Food transfers both on and near the nest were recorded. In 1995–1999, each nest was watched during three 90-min periods (morning, midday, and afternoon), and the average number of trips was used for the analyses. In 2000, one 90-min period (between 0800 and 1100 h) was used. The number of nestling provisioning trips by male was recorded during similar 90-min nest watches on day 7 after hatching. In the house finches, the number of nest visits by a male is a reliable indicator of the amount of transferred food (i.e., an approximately equal amount of food is brought during each visit; Nolan et al., 2001).

We used path analysis to quantify the strength of direct and indirect effects of male ornamentation and parental care on offspring recruitment while accounting for correlations among components of parental care. We used multiple regressions to examine the direction of relationships between components of paternal care and offspring recruitment and to estimate standardized regression coefficients (b_{ST}, in standard deviations) and corresponding statistics associated with these effects.

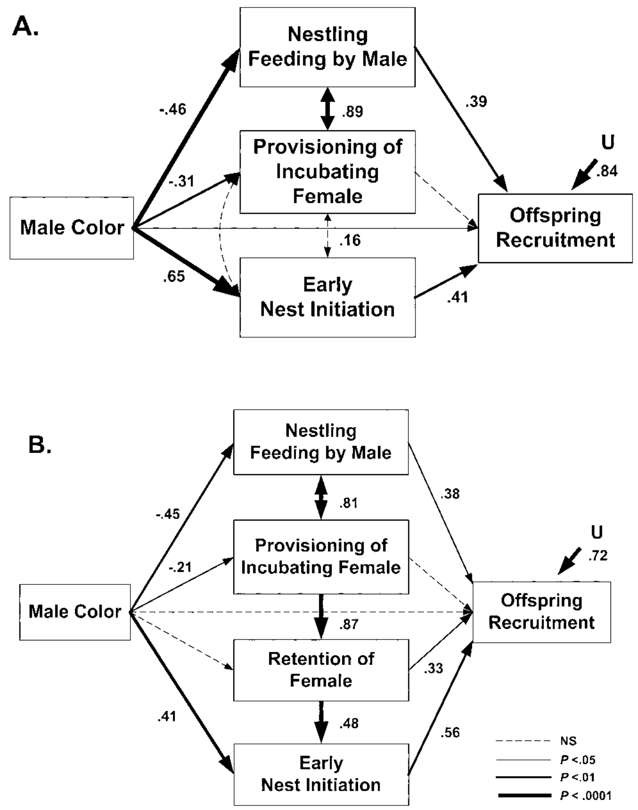

Figure 3
Path diagram illustrating the relationship among male sexual ornamentation (male color), parental care, retention of female (number of breeding attempts with the same female), and nest initiation date and within-season offspring recruitment for (A) first-time breeder males and (B) older males. Double-headed arrows indicate covariation between two variables. Single-headed arrows show that change in the variable at the base of the arrow will cause a change in the variable at the arrow's head. The single-headed arrows with "U" indicate effects of factors unmeasured in this study. Thickness of the arrows show the significance of the effect. Numbers next to lines indicate the strength of the path coefficients (in standard deviations).

RESULTS

Among first-breeders, red males had the highest offspring recruitment, followed by intermediate and yellow males (within-group difference: $F_{2,60} = 4.61$, $p = .03$; only red vs. yellow were significantly different in post-hoc comparisons; Figure 2A). Among older breeders, red males had the lowest, intermediate males had the highest, and yellow males had the intermediate level of offspring recruitment (within-group difference: $F_{2,107} = 10.6$, $p < .001$; all categories were different; Figure 2B).

Males with more elaborate ornamentation fed nestlings (young: $b_{ST} = -0.46$, old: -0.45) and incubating females ($b_{ST} = -0.31$ and -0.21) less than males with less elaborated ornamentation (Figure 3). Males with more elaborate ornamentation paired with females that initiated nests earlier ($b_{ST} = 0.65$ and 0.41; Figure 3). Greater offspring recruitment was

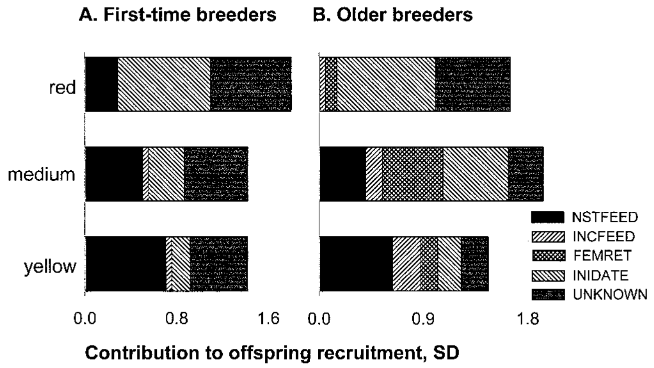

Figure 4
Contribution of parental care components (direct and indirect effects combined, in standard deviations, SD) to offspring recruitment of males with different ornamental elaboration for (A) first-time breeder males and (B) older males. Shown are the effects of nestling feeding by male (NSTFEED), provisioning of incubating female (INCFEED), retention of female (number of breeding attempts with the same female, FEMRET), nest initiation date (INIDATE), and the effects unmeasured in this study (UNKNOWN).

strongly positively associated with greater nestling provisioning (b_{ST} = 0.39 and 0.38), and, equally strongly, with early nest initiation (0.41 and 0.56).

In older breeders, number of breeding attempts with the same female ("retention of female"; Figure 3B) positively correlated with offspring recruitment (b_{ST} = 0.33) and strongly influenced nest initiation date (b_{ST} = 0.48); pairs that stayed together longer nested earlier. In turn, retention of female correlated with intensity of incubation feeding (b_{ST} = 0.87). Consequently, incubation feeding had significant indirect effects on offspring recruitment (i.e., through greater female retention: 0.87 × 0.33 = 0.29 and through earlier nest initiation: 0.87 × 0.48 × 0.56 = 0.23).

To evaluate contribution of different components of paternal care to offspring recruitment in relation to elaboration of sexual traits, we fitted path analysis models separately for yellow, intermediate, and red males. We summed all effects (direct and indirect) of each component for first breeders and older males separately (Figure 4). In first breeders, offspring recruitment of yellow males was mostly a result of greater nestling feeding (50% of total effects; Figure 4A). In intermediate males, both nestling feeding (36%) and early nest initiation (22%) contributed strongly to offspring recruitment (Figure 4A). In red males, offspring recruitment was mostly influenced by earlier nest initiation (45%) and, to a much lesser degree, by nestling provisioning (16%; Figure 4A). Males with different trait elaboration used distinct combinations of parental care components ($\chi^2 = 44.7$, df = 6, $p = .01$). Contribution of unknown (Figure 4; i.e., unmeasured) effects on offspring recruitment did not differ among three male categories (35%, 39%, and 39%). Overall, yellow and red males had the opposite tactics in relation to nestling feeding and nest initiation (Figure 4A). In older males, offspring recruitment of yellow males was mostly due to effects of nestling feeding (44%) and incubation feeding (16%; Figure 4B). In intermediate males, effects of nestling feeding (21%), female retention (27%), and nest initiation date (29%) were equally strong, while in red males, offspring recruitment was mostly affected by early nest initiation (52%; Figure 4B). Similarly to young males, contributions of different components of parental care differed strongly among males of different ornamental groups ($\chi^2 = 110.3$; df = 8; $p = .001$). In addition, the contribution of factors not measured in this study was greater in red males compared to other males (39% vs. 16% in both yellow and intermediate males). The sum of the effects was the highest for intermediate males due to strong effects of most components of parental care (Figure 4B).

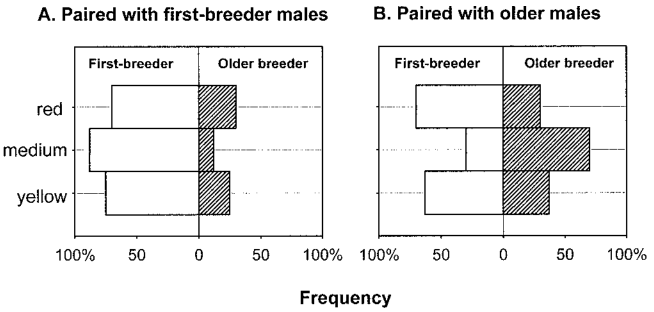

Figure 5
Association between female breeding experience and male ornamental elaborations for females paired with (A) first-breeder males and (B) older males.

During their first breeding season, most males were paired with first-breeder females (Figure 5A). Young red males were more likely to pair with older female than intermediate or yellow males ($\chi^2 = 9.96$; df = 2; $p = .007$; Figure 5A). Among older breeders, most yellow and red males were paired with first-breeder females, whereas intermediate males were paired mostly with older females ($\chi^2 = 36.8$; df = 2; $p = .001$; Figure 5B).

DISCUSSION

When individuals differ in physiological condition and residual reproductive value, selection should favor phenotypic plasticity in reproductive investment such that individuals adopt the reproductive tactic that allows them to achieve the highest fitness under given conditions (reviewed in Badyaev and Qvarnström, 2002; Gross, 1996; Kokko, 1998). The decision to adopt a particular suite of behaviors may depend on individual status relative to population variation in condition and can be phenotypically indicated by elaboration of a condition-dependent trait (Andersson, 1994).

Here we documented that male house finches adopt a conditional reproductive strategy indicated in part by elaboration of their sexual ornamentation. Males with less elaborate sexual traits (yellow color) and males with more elaborate sexual traits (red color) used distinct reproductive tactics: Red males paired early, but provisioned their nestlings less, whereas yellow males paired later, but provisioned their nestlings more. Investment in early nestling or offspring/mate provisioning resulted in approximately equal fecundity return, as measured by offspring recruitment (Figure 3), so in the absence of compensation by their mates, yellow and red males should have had similar fecundity. However, among first-year males, red males had higher fecundity than yellow males (Figure 2). This was due to higher paternal investment by females paired to red males. In a companion study, we removed for 24 h females paired to red and yellow males and examined male provisioning of nestlings during female absence. While provisioned only by a male, nestlings of red males grew less than 10% of normal rate, whereas nestlings of yellow males grew 60% of normal rate (Badyaev, in preparation). Thus, high investment in sexual ornamentation appears to enhance the reproductive success of young males by enabling them to attract females that nest early (e.g., Hill et al., 1994), that are more fecund, or that provision nestlings more because of the male's attractiveness (e.g., Burley, 1988; de Lope and Møller, 1993; Sandvik et al., 2000; Weatherhead and Robertson, 1979).

Reproductive tactics remained the same among older males: Red males paired early but provisioned young little, whereas yellow males paired late and provisioned young more. Among older males, however, the payoffs relative to male ornamentation were different. Older males with intermediate development of ornamental plumage were able to achieve the highest fecundity; the combined contribution of relatively early nesting and relatively high provisioning led to higher offspring recruitment for intermediate males than did the single-tactic strategies of either yellow or red males. In addition, the large contribution of unmeasured effects to fecundity of red males (Figure 4B) may indicate increased investment of the mates of red males to offspring recruitment (Badyaev, in preparation).

The observation in this study that the most highly ornamented males did not necessarily have the greatest fecundity (Figure 1B) suggests that it is an oversimplification to assume that elaboration of condition-dependent sexual traits should always be positively associated with greater reproductive success (e.g., Andersson, 1994). Instead, this association is best understood by examining relative allocation of resources between condition-dependent sexual traits and condition-dependent parental care. For example, if males overinvest (in relation to male average condition) in the development of a condition-dependent ornament, then ornament development may come at the expense of parental care and result in lower than average annual fecundity for the most ornamented males (e.g., Candolin, 2000; Pärt et al., 1992). Alternatively, males with more elaborate traits can invest less in parental care by manipulating investment of their mates and may compensate for reduced offspring output in a given season by increasing their probability of survival and hence their lifetime reproductive success (Burley, 1988; de Lope and Møller, 1993; Gowaty, 1996; Sheldon, 2000; Trivers, 1972). Indeed, in this study population, red males lived longer and were more likely to survive winters than males with intermediate or yellow coloration (Badyaev and Martin, 2000), whereas first-breeder females mated to red males were less likely to survive subsequent winters than females mated to yellow and intermediate males (Badyaev, in preparation).

Our observations from a Montana population of house finches differ substantially from observations of house finch populations in the eastern U.S. In two eastern populations, male plumage redness is positively associated with both early nesting date (Hill et al., 1999) and male provisioning of mates and nestlings (Hill, 2002). So, unlike in the Montana population, there appears to be only a single strategy for ornament display and parental care in these eastern populations. How do we reconcile these differences?

The key characteristic of a conditional strategy is that the decision of an individual to adopt a particular tactic depends on some aspect of individual status or condition relative to other individuals in a population (Gross, 1996). Such condition-dependent switchpoints (i.e., points of appropriate allocation to the alternative tactics for fitness maximization) should be sensitive to ecological and demographic events influencing fitness consequences of individual tactics (Dunn and Robertson, 1992; Eadie and Fryxell, 1992; Kokko, 1997, 1998; Radwan, 1993). We suggest that the evolution of such switchpoints may be influenced by the distribution of the expression of condition-dependent sexual traits within a population and by patterns of female learning and experience (see below), and that therein lies the key difference between the eastern and Montana populations of house finches. The mean plumage redness of male house finches is much higher and the range of color displays is much narrower in eastern populations than in Montana (Badyaev et al., 2001a; Hill, 2002). Less variation among males in plumage coloration may favor the adoption of a single reproductive strategy (i.e., when gain in male individual condition is evenly partitioned between a condition-dependent sexual trait and parental care it advertises; Kokko, 1998). Variation among populations and species of birds in the adoption of alternative reproductive strategies may account for frequently documented differences in association between male sexual ornamentation and male parental care (e.g., positive association: Hill, 1991; Linville et al., 1998; Wiehn, 1997; negative association: Burley, 1988; de Lope and Møller, 1993; Qvarnström, 1997; Studd and Robertson, 1985; no association: Lozano and Lemon, 1996; Sundberg and Larson, 1994; Wright and Cuthill, 1992; Yasukawa et al., 1987).

More generally, the direction of association between a condition-dependent sexual trait and paternal care depends on the relative importance of direct and indirect benefits in female mate choice (e.g., Fitzpatrick et al., 1995; Kokko, 1998; Price et al., 1993; Wolf et al., 1997). In turn, the relative importance of direct and indirect benefits to a female can change with female physiological condition and experience (e.g., Gowaty, 1996; Pärt et al., 1992) and with the frequency of alternative reproductive tactics in a population (Eadie and Fryxell, 1992; Radwan, 1993). For example, if a condition-dependent trait consistently indicates low parental care but high individual condition and if condition is heritable, then females in good condition may prefer more ornamented males because the indirect benefits they would obtain would exceed the costs of reduced parental care, for which they would be able to compensate (Kokko, 1998).

The importance of adaptive female choice in mediating the relationships between male trait elaboration and male fitness (Figure 2) is evident in the mating patterns of experienced and inexperienced females relative to male ornamentation (Figure 5; see Alonzo and Warner, 2000; Forsgren, 1997; Reyer et al., 1999). If males with the greatest trait elaboration provide the least parental care, and if male parental care is important to reproductive success, then experienced females should avoid pairing with redder males. Indeed, we observed that younger females paired with red males at a higher frequency than did older females (Figure 5). Initial preference for redder males in young females may be related to strong preference for redder ornamentation in several other populations of the house finches (Hill et al., 1999). Moreover, because of colonial nesting of house finches in our study population and their strong fidelity to breeding sites, females can directly observe parental care of males and thus select males on the basis of previous familiarity (Wagner, 1992). Direct selection of paternal care by females may lessen the association between sexual trait and fitness in older males (Figure 2B).

Our findings raise several questions. First, it is unclear what proximate mechanisms influence changes in conditional switchpoints and corresponding patterns of allocation to alternative strategies. In a companion study of this population, we found that high paternal care was closely associated with elevated levels of prolactin, a pituitary hormone that controls male parental behavior. We found that prolactin production is condition dependent and that higher physiological condition of red males during breeding was due to less investment in parental care as evidenced by their lower prolactin production (unpublished data). In addition, an increased level of testosterone, which is physiologically costly to maintain (Duckworth et al., 2001), decreased male parental care in the house finch (Stoehr and Hill, 2000). Thus, common condition dependence of prolactin and testosterone production and maintenance may provide a proximate link behind evolution of alternative mating tactics. The question of proximate control is especially interesting given strong population differences in allocation to alternative tactics. Second, the relative importance of direct and indirect genetic benefits of condition-dependent traits, especially those advertizing parental care, is not known. Such knowledge is crucial to an understanding of the evolution of reproductive tactics. Finally, individual variation in female mate choice as a result of learning and experience needs further study. Overall, an appreciation of individual variation in reproductive behaviors is an important step in establishing the selective pressures and mechanisms underlying the operation of sexual selection.

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