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ORIGINAL ARTICLE

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Elaborately ornamented males avoid costly parental care in the house finch (*Carpodacus mexicanus*): a proximate perspective

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Abstract Selection should favor flexibility in reproductive tactics when the combination of sexual traits and reproductive behaviors that achieve the highest fitness differs between males within a population. Understanding the functional significance of variation in male reproductive tactics can provide insight into their evolution. Male house finches (*Carpodacus mexicanus*) in a Montana population display continuous variation in parental tactics: males with more elaborated (redder) plumage color provide little or no parental care compared to less elaborated (dull) males. Here, we first determined whether elevation of prolactin (a pituitary hormone) was related to variation in male parental tactics and, second, we used the relationship between prolactin levels and parental behavior to investigate why redder males avoid a high investment in parental care. We found that prolactin elevation was closely associated with paternal care. In addition, males with redder plumage color had low prolactin levels, whereas dull males, which provision twice as frequently, had high levels of prolactin. We also found that male condition was unrelated to plumage color but negatively related to prolactin levels. These results suggest that the low provisioning of redder males was not due to physiological constraints, but instead reflected a tactic to avoid the costs associated with parental care. The condition benefits accrued by redder males may explain their higher post-breeding survival compared to dull males. Moreover, dull males were previously shown to have higher pairing success than redder males, suggesting that the relationship between male plumage color and parental care may reflect individually optimized parental tactics.

Keywords House finch · Life history · Prolactin · Reproductive tactic · Sexual ornament

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Introduction

Male sexual ornamentation and parental care are aspects of reproductive investment, and thus are subject to life history trade-offs (McLain 1991; Gustafsson et al. 1995; Höglund and Sheldon 1998). Increased investment in either of these traits comes at the expense of investment in other traits important to survival or reproduction (Stearns 1989). Moreover, trade-offs can also occur among these traits whereby an increased investment in sexual ornamentation can lead to decreased investment in parental care (Price et al. 1993; Kokko 1998). Consequently, male investment in sexual ornamentation and parental behavior depends not only on female preferences for more elaborate male sexual ornaments, but also on the future survival probability and current and future mating opportunities of males (Badyaev and Qvarnström 2002). In species where sexual ornaments indicate male parental ability, these life history trade-offs play an important role in shaping the relationship between sexual trait elaboration and parental care (Kokko 1998).

The optimal allocation of resources to sexual ornamentation and parental care varies between individuals because differences in age, experience and condition affect investment in reproduction (van Noordwijk and de Jong 1986; McNamara and Houston 1996; Kokko 1997). Moreover, an individual's reproductive decisions are affected by the age, experience and quality of their mates and competitors (Svensson and Sheldon 1998). Individual variation in life histories and a variable breeding environment should favor flexibility in male reproductive tactics allowing individuals to optimize their reproductive effort depending on their current state and the context of breeding (Houston and McNamara 1992; Gross 1996). Although variation in parental care signaled by a male's sexual trait is common in birds (Studd and Robertson 1985; Qvarnström 1997; Buchanan and Catchpole 2000; Sanz 2001), the functional significance of this relationship is often unknown. Understanding the costs and benefits of male investment in sexual traits and parental behavior can provide insight into why males pursue a particular reproductive tactic.

Hormones, which can mediate the expression of reproductive trade-offs (Sinervo and Svensson 1998; Ketterson and Nolan 1992) are important in the development of alternative reproductive tactics of males (Moore 1991; Nijhout and Wheeler 1982). For example, in dung beetles the presence of juvenile growth hormone during a sensitive stage of development determines whether males will grow into a horned or hornless morph (Emlen and Nijhout 1999) which in turn determines whether males will use fighting or sneaking behaviors to access females (Emlen 1997). Furthermore, in birds, testosterone elevation has well documented effects on male reproductive tactics (see Ketterson and Nolan 1994 for review). Testosterone elevation decreases male investment in parental behavior and stimulates the expression of mate attraction behavior (Silverin and Wingfield 1982; Ketterson et al. 1992; Stoehr and Hill 2000) and thus plays a prominent role in the expression of polygynous versus monogamous mating tactics of males (Wingfield and Farner 1993).

As metabolic signals that mediate the interaction between an organism's state and behavior, hormones are one step closer to the cues that stimulate the expression of a particular behavior. As such, measuring hormone levels may allow for an accurate assessment of motivational state, particularly because variation in behavior can only be partially sampled while hormone levels can be objectively quantified. For example, an individual that is highly motivated to care for offspring may spend time watching for nest predators and defending the nest, competing over high quality food resources for young, and may also bring food to offspring. Typically, only one or a few of these behaviors is measured as an estimate of parental care, although each of these behaviors contribute to an individual's overall investment in offspring care (Clutton-Brock 1991). Because each of these aspects of parental care is likely to be influenced by common physiological mechanisms, such as hormonal elevation (Buntin 1996), measuring variation in hormone levels may allow for a more comprehensive assessment of an individual's motivational state than sampling a single aspect of parental behavior.

Prolactin is a pituitary hormone that is closely associated with parental care in many species and has been shown to enhance the expression of parental behavior in several domestic species of birds (reviewed in Buntin 1996). Moreover, prolactin levels are closely associated with parental behavior in studies of free-living populations of birds (Goldsmith 1982; Silverin and Goldsmith 1990; Seiler et al. 1992; Vleck et al. 2000). These studies indicate that prolactin elevation stimulates the expression of parental behavior and therefore this hormone is a prime candidate for studying proximate influences on variation in male parental behavior. Here, we studied the relationship between prolactin and male parental care and used variation in this hormone as a proxy for male parental behavior to investigate the causes of variable parental tactics in male house finches (*Carpodacus mexicanus*).

In a population of house finches in Montana, male parental behavior varies in relation to the elaboration of sexual plumage ornamentation. The plumage color of male house finches varies continuously from dull yellow to bright red (Hill 2002). Redder (more elaborated) males in this population feed nestlings very little whereas dull (less elaborated) males feed nestlings nearly twice as often (Badyaev and Hill 2002). Similarly, redder males feed their incubating females significantly less than do dull males (Badyaev and Hill 2002). In the first part of the study, we describe the relationship between prolactin and male parental tactics. Specifically, we predicted that redder males would have lower prolactin levels than dull males in correspondence with the parental tactics expressed in this population.

In the second part of the study, we measured variation in male condition (see methods for details) to investigate the causes of variable investment in parental behavior by males. Previous study of this population showed that redder males had low pairing success compared to dull males because older females preferentially mated with males that provision more during both incubation and the nestling period (Badyaev and Hill 2002). In turn, redder males had low offspring recruitment compared to dull males (Badyaev and Hill 2002) and thus it is unclear why they avoid investing in parental care. Because male house finches are not polygynous and the rate of extra-pair paternity is extremely low (<5%; Badyaev et al. 2001), the benefits of avoiding parental care for redder males cannot be explained by increased fitness through extra-pair copulations. Instead, the tactic of redder males is more likely to be related to the energetic costs associated with parental care.

To investigate this possibility, we measured male condition during the parental care period to determine whether redder males might be less capable of high investment in parental care due to energetic constraints. If so, we expected redder males to be in relatively poor condition compared to dull males. Alternatively, redder males may be capable of provisioning young, but they may be less motivated to invest in provisioning than dull males. In this case, we predicted that male condition would be either unrelated to plumage color or redder males would be in better condition than dull males as has been shown in other populations of house finches (Hill 2002).

Finally, we looked at the consequences of high parental investment by analyzing the relationship between prolactin levels and male condition. If parental investment is costly, as has been shown in a number of species (Owens and Bennett 1994; Ots and Hörak 1996; Fargallo et al. 2001), we predicted that high prolactin levels (a proximate indicator of parental investment) should be associated with relatively poor male condition.

Methods

We studied a resident population of house finches inhabiting an isolated area of suitable habitat near Missoula, in northwestern Montana (USA). Since 1994, all finches on the study site were captured, measured and marked with a unique combination of one aluminum and three colored plastic rings. The data used in this study were collected in 2001. We determined all pairing and nesting affiliations of breeding adults (Badyaev and Martin 2000; Badyaev and Hill 2002), and assigned paternity with DNA fingerprinting analyses to ensure that male paternity was not a confounding factor in paternal investment decisions (see Badyaev et al. 2001 for details).

We assessed male condition by measuring hematocrit, the percentage of blood consisting of red blood cells. Hematocrit is characterized by large fluctuations on a relatively short time scale (Clemens 1990; Ots et al. 1998) and reflects short-term changes in condition (Brown 1996). Furthermore, in house finches, males showing signs of physiological stress have low hematocrit scores (Duckworth et al. 2001). Thus, hematocrit score is a suitable estimate of males' current condition status. To measure prolactin and hematocrit scores, we captured males in mist nets and traps at feeders between 0800 and 1100 hours throughout the breeding period and collected approximately 200 μL of blood from the brachial vein using micro-hematocrit capillary tubes. Immediately after sampling, we separated the plasma by spinning the blood in a portable microhematocrit centrifuge at 2,700 rpm. We measured the percent of red blood cells in each capillary tube using a hematocrit measurement card. Hematocrit percentages were arcsin-transformed before analyses. The separated plasma was stored at −80°C until radioimmunoassay (RIA) analysis.

Plasma prolactin levels were determined in duplicate samples using a postprecipitation, double-antibody RIA. This assay uses purified chicken prolactin as a standard and antisera against chicken prolactin derived from rabbits. 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 house finch plasma did not differ from the slope of the diluted chicken standard. This indicates that this heterologous RIA can be used to assess relative levels of house finch prolactin as has been shown in several other avian species (e.g., Schoech et al. 1996; Brown and Vleck 1998).

Upon capture, we photographed the carotenoid-based breast plumage patch of each male using a 4-megapixel digital camera mounted in a standard position. Males were kept in a standardized position by placing them on a neutral gray photoboard on the dorsal side with the anterior point of the beak held in place (see Badyaev et al. 2001 for details of the protocol and the repeatability of measurements). Pigment hue was the average of the hue assessment in three different areas (ca. 3×2 feathers) within a breast patch. We recorded pigment hue on a scale of 1 to 10 following the protocol for visual assessment outlined in Badyaev et al. (2001).

In house finches, only the female incubates, but males regularly bring food to incubating females (Hill 2002). Male provisioning of the female during incubation has been previously considered a form of parental behavior in the house finch (Hill 1991), thus we measured male provisioning rates of both the nestlings and the female to determine whether either of these behaviors is associated with male prolactin levels. We recorded the number of incubation provisioning trips of males during 90-min nest watches on the 5–8th day of incubation. We monitored nests with binoculars from a parked car 4–8 m from the nest. Food transfers both on and near the nest were recorded. We watched each nest during two to four 90-min periods between 0800 and 1100 hours. The number of nestling provisioning trips by a male was recorded during similar 90-min nest watches on day 5–8 post-hatch. In house finches, the number of nest visits by the 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), and male feeding rate is not affected by brood size (Stoehr et al. 2001).

We sampled a total of 51 males for prolactin levels. Males were divided into the following categories according to their stage of breeding at the time of capture: pre-breeding (males that were paired but had not yet initiated nesting), nest-building, incubation, and nestling stage (this stage includes males feeding either nestlings or recently fledged offspring). In our analysis of the relationship between prolactin and male provisioning rates of the female and nestlings we only included males that were captured and sampled within 24 h of conducting observations of their parental care. In our analyses of the relationships between prolactin, hematocrit, and plumage hue we did not have all of these measures on every male captured. Therefore, we used a subset of 'incubation' or 'nestling' males for some of the analyses. The relationship between prolactin levels and provisioning behavior was analyzed using a non-parametric test for association, Kendall's coefficient of rank correlation (Sokal and Rohlf 1981). All other relationships were analyzed using General Linear Models (SAS Institute, v. 8.0).

Results

Plasma prolactin levels of males increased as breeding progressed ($F_{3,47}$=78.43, P<0.0001; Fig. 1), being the lowest in individuals that were paired but not yet breeding and reaching the highest levels during nestling feeding. Post hoc analyses revealed significant differences in the level of prolactin in males sampled during each stage of breeding (pre-breeding compared to building: $F_{1,18}$=36.21, P<0.0001; building compared to incubation: $F_{1,14}$=23.21, P<0.001; incubation compared to nestling feeding: $F_{1,31}$=8.51, P<0.01). In the sample of males

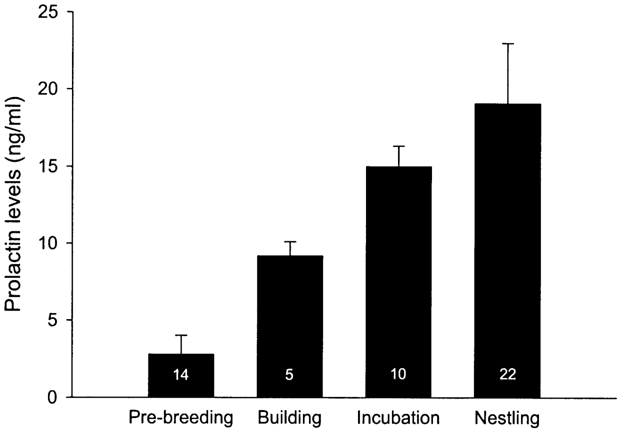

Fig. 1 Mean and SE of prolactin levels of male house finches (*Carpodacus mexicanus*) sampled during the breeding season. Pre-breeding refers to males that had paired but had not yet initiated breeding. Levels are highest during parental stages. Numbers on bars are sample sizes. See text for analysis of differences between stages

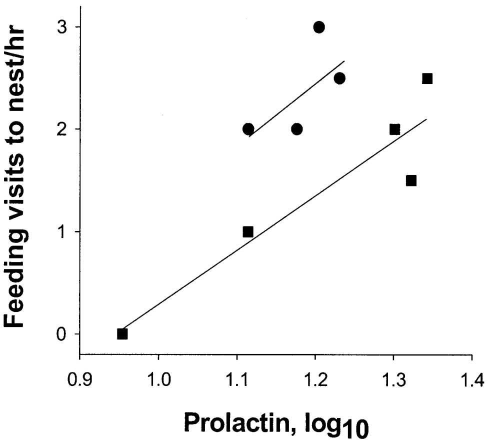

Fig. 2 Correlation between prolactin levels and male provisioning of female (circles, *n*=4) and nestlings (squares, *n*=5)

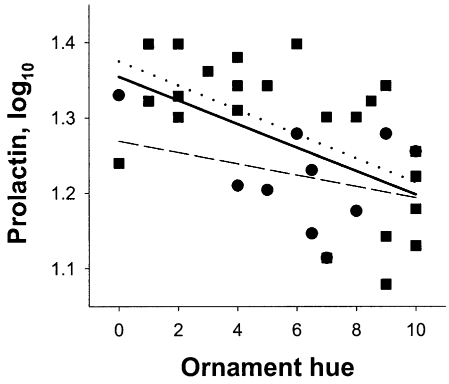

Fig. 3 Relationship between male prolactin levels and ornament elaboration (higher hue values indicate redder plumage color) during feeding of incubating females (circles, n=10, dashed line) and nestlings (squares, n=22, dotted line). Solid line indicates overall least-squares regression

where prolactin was measured within 24 h of the observation of parental care, males that had a higher level of prolactin provisioned their nestlings more frequently (Kendall's tau=0.80, P=0.05; n=5; Fig. 2). There was a non-significant positive relationship between male prolactin levels and the rate at which they provisioned their incubating female (Kendall's tau=0.54, P=0.27; n=4; Fig. 2).

Males with a more elaborated sexual ornaments had lower prolactin levels than less ornamented males during the parental care period ($F_{1,33}$=13.52, b_{ST}=–0.54, P<0.001, Fig. 33). The strength of this relationship differed between nestling and incubation stages: there was a significant relationship between male plumage color and prolactin during nestling feeding period ($F_{1,21}$=10.26, b_{ST}=-0.57, P=0.004), but not during the incubation period ($F_{1,9}$=1.02, b_{ST}=-0.38, P=0.35). There was no relationship between male hue and the age of the nestlings a male was attending ($F_{1,11}$=0.1, b_{ST}=0.04, P=0.93), ruling out sampling bias as an explanation for the relationship between prolactin levels and male plumage hue. None of the nests of males measured in this study had extra-pair young.

Prolactin levels were negatively related to hematocrit in males throughout the parental care period (overall: $F_{1,31}$=6.31, b_{ST}=–0.42, P=0.02; Fig. 4A), including when their mate was incubating ($F_{1,15}$=16.27, b_{ST}=–0.73, P=0.001) and in males feeding nestlings ($F_{1,17}$=4.26, b_{ST}=–0.45, P=0.06). There was a nonsignificant positive relationship between hematocrit and male plumage elaboration (overall: $F_{1,29}$=2.79, b_{ST}=0.29, P=0.11; incubation: $F_{1,9}$=0.15, b_{ST}=0.13, P=0.7; nestling feeding: $F_{1,19}$=2.62, b_{ST}=0.41, P=0.10; Fig. 4B). A multiple regression of the effects of prolactin and male hue on hematocrit was significant ($F_{2,26}$=4.37, b_{ST}=–0.44, P=0.02) and showed that male prolactin levels explained more of the variance in hematocrit (b_{ST}=–0.44, t=–2.52, P=0.01) than did male plumage elaboration (b_{ST}=0.23, t=1.93, P=0.10).

Discussion

The evolution of conditional reproductive tactics enables individuals to optimize their allocation of resources in relation to their current state (Gross 1996). This often leads to flexibility in the expression of behaviors that are important to reproduction (Komers 1997). Because hormones are thought to provide a link between individual state and the expression of behavior (Sinervo and Svensson 1998), measuring variation in hormone levels

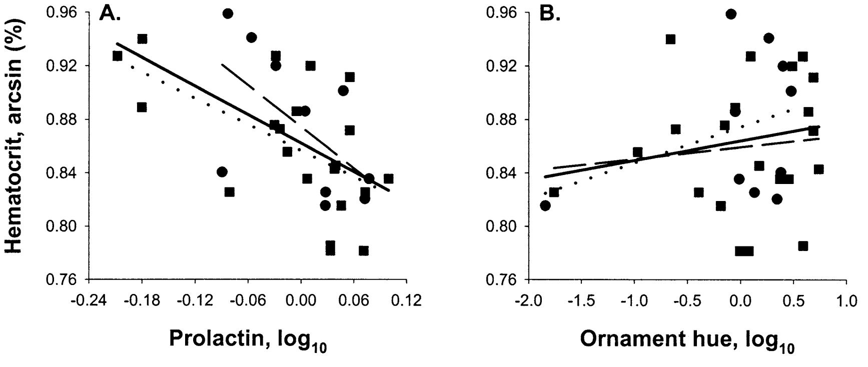

Fig. 4 Relationship between hematocrit and **A** prolactin levels and **B** ornament elaboration (higher hue values indicate redder plumage color) of males during feeding of incubating females (circles, n=10, dashed lines) and nestlings (squares, *n*=18, dotted lines). Solid lines indicate overall least-squares regression

allows for a means of quantifying an individual's motivational state.

In this study, we found that the reproductive tactics of individual males were reflected in their prolactin levels. First, as expected, prolactin levels were closely associated with male parental behavior: prolactin levels increased throughout the breeding cycle, reaching the maximum level during the nestling stage (Fig. 1) similar to patterns found in other altricial species (for review see Brown 1985; Buntin 1996). In addition, prolactin elevation was positively related to male provisioning of nestlings (Fig. 2). And finally, prolactin levels were strongly negatively related to male plumage color (Fig. 3). As predicted, redder males had low levels of prolactin while dull males had high prolactin levels.

Hormones are important in mediating the interaction between stimuli from the environment, the expression of behavior, and reproductive trade-offs (Ricklefs and Wikelski 2002), yet few studies have explored the links between the variable expression of behavior and individual variation in hormone elevation in natural populations. However, in birds, studies on testosterone and mating behaviors and studies on prolactin and parental behaviors are two notable exceptions (e.g., Brown and Vleck 1998; Schoech et al. 1996; Ridder et al. 2000; Vleck et al. 2000). For example, Silverin and Wingfield (1982) found that monogamous and polygynous male pied flycatchers (*Ficedula hypoleuca*) differed in testosterone profiles. In addition, Khan et al. (2001), found significant differences in prolactin elevation between helpers and breeders in red-cockaded woodpeckers (*Picoides borealis*). Similarly, in this study we found that prolactin levels varied in males pursuing different reproductive tactics. However, our results differ from the studies cited above, in that variation in the reproductive tactics of male house finches cannot be grouped into discreet categories. Both provisioning rates and plumage color vary continuously in close correspondence to one another (Badyaev and Hill 2002). Continuously varying reproductive strategies may be common in nature, yet most studies of reproductive tactics focus on discreet alternative phenotypes (Gross 1996; Nijhout 2003). It will be interesting to see whether there are differences in the underlying physiological mechanisms of continuous and discreet reproductive tactics. Many hormone-dependent traits develop only when hormone titers reach a certain threshold (Hews and Moore 1997). We found a positive relationship between the level of nestling provisioning by males and their prolactin levels. However, whether this reflects a dose-dependent relationship is not clear. Although the variation in the tactics of male house finches is continuous, other factors besides prolactin elevation may also affect male parental investment (Hews and Moore 1997). Comparisons of the underlying physiology and development of discrete versus continuously varying reproductive tactics will provide insight into how environmental variation is translated into phenotypic variation, an important link for understanding the evolution of adaptive plasticity in behavior (Nijhout 2003).

Our results raise the question of the causal nature of the relationship between prolactin elevation and parental behavior. Are the elevated prolactin levels of duller males a cause or consequence of their higher provisioning rates? Experimental studies have found that administration of prolactin stimulates parental behavior (Horseman and Buntin 1995; Li et al. 1995; Wang and Buntin 1999). However, stimuli from offspring and cues from parent-offspring interactions might also promote or sustain elevated levels of prolactin (Buntin 1979; Richard-Yris et al. 1998; Wang and Buntin 1999). Experimental manipulation of prolactin elevation will be necessary to determine whether it regulates the parental tactics of males in this population.

In male house finches, duller males benefit from a high investment in parental care because this leads to higher pairing success in future breeding attempts and higher recruitment of offspring compared to redder males (Badyaev and Hill 2002). Given the apparent benefits of investing in parental behavior, why do redder males avoid it? The low provisioning of nestlings by the most elaborated males in this population could be because (1) redder males over-invested in their sexual trait (Kokko 1998) and thus are in poorer condition than dull males making them less capable of provisioning their young, or (2) redder males are capable of provisioning young, but they are less motivated to invest in provisioning than dull males. We found no relationship between male plumage elaboration and male condition. This suggests that both poorly and elaborately ornamented males should be equally capable of investing in parental care.

Redder males might benefit from avoiding a high investment in parental care if this behavior is costly. Here, we showed that males with higher prolactin levels, and consequently higher parental investment, were in poor condition compared to males with low prolactin. The negative relationship between male hematocrit and prolactin levels supports the idea that parental care is costly for males. Similarly, a trade-off between caring for offspring and maintaining individual condition was found in chinstrap penguins (*Pygoscelis antarctica*) where high investment in nest maintenance behavior resulted in lowered hematocrit (Fargallo et al. 2001). Although our study does not provide experimental evidence that increased parental behavior decreases male condition, this is the simplest explanation for the relationship between hematocrit score and prolactin levels for two reasons. First, it is unlikely that poor condition would cause an increase in prolactin levels. In studies of domestic animals, poor nutritional condition often decreases prolactin levels (Rhind et al. 1980; Petitclerc et al. 1983; Miller et al. 1998). Second, using a multiple regression model we were able to determine the relative importance of the effects of plumage color and prolactin elevation on hematocrit. Accounting for any possible effects of male plumage color made the relationship between prolactin and hematocrit stronger, supporting the interpretation that prolactin elevation may, through its effects on parental investment, decrease male condition.

The immediate costs of investing in parental effort will affect males' investment in other life history traits. Redder males in this population have higher overwinter survival than dull males (Badyaev and Martin 2000), which may be a direct consequence of avoiding parental care during breeding. Thus, although in the short term redder males have lower offspring recruitment, the fitness consequences of avoiding parental investment may be offset by higher survival in the long term. Following changes in individual male's plumage color and parental behavior across multiple years will be an important next step in determining whether the short term avoidance of parental investment by redder males leads to enhanced fitness over their life.

While these results provide evidence for the functional significance of the relationship between plumage color and parental behavior, the cues that regulate male parental investment decisions in this population are still unknown. A male's reproductive tactic is set for the next breeding season during fall molt, when his sexual trait is developed. The carotenoid plumage coloration of male house finches is influenced by nutritional status, parasitic infection, and the availability of carotenoids in the environment (Hill 2002). However, the importance of these factors in determining the elaboration of carotenoid plumage coloration in birds can vary geographically (Hudon and Brush 1989) and also across an individual's life (Badyaev and Duckworth 2003). In this population, the expression of plumage coloration is only condition-dependent in males molting into adult plumage for the first time. In older males, plumage color is most affected by their pairing status in the previous year (Badyaev and Duckworth 2003). Because a male's plumage color can, in turn, affect a male's ability to attract a mate, the condition of males during their first molt may have important cascading effects on their lifetime reproductive strategy.

What cues during breeding cause redder males to provision less than dull males? One obvious answer is that males alter their parental behavior in response to the level of care that their female provides. Females often provision more when paired to an attractive male (Burley 1988; Möller and DeLope 1995). However, experimental evidence from this population indicates that males do not alter their provisioning effort when their females are removed (A.V. Badyaev, unpublished data). Thus, male parental behavior is not affected by the level of care that a female provides, at least not in the short term. However, the possibility that male parental care patterns are set early in the nesting period in response to female behavior warrants further exploration.

Alternatively, a male's reproductive tactic may depend on an external factor such as the demographic composition of the population. Female choice of elaborately ornamented males is age-dependent in this population (Badyaev and Hill 2002). Young females preferentially pair with more ornamented males while older, more experienced females pair with duller males. Thus, the ratio of young to old females within the population will have important consequences for the benefits a male can accrue by adopting a particular tactic. If males have the ability to assess the age of females in mixed-sex foraging flocks in the fall, the time during which they molt into their breeding plumage, it may affect their decisions about investing in plumage ornamentation. Further investigations of the proximate basis for variation in male reproductive behavior and plumage ornamentation in this population are necessary to understand which environmental cues most influence the expression of male tactics. In turn, studies of the physiological basis of variable reproductive tactics can help us understand how environmental variation is translated into phenotypic variation.

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