

SUBADULT PLUMAGE IN THE HOUSE FINCH AND TESTS OF MODELS FOR THE EVOLUTION OF DELAYED PLUMAGE MATURATION

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ABSTRACT.—In many passerine species males do not attain definitive breeding plumage until after their first potential breeding season. Such delayed plumage maturation has been the subject of numerous studies, most of which have focused on the adaptive value of female-like plumage for young males in single populations. Thus, although studies of delayed plumage maturation have been presented as tests of evolutionary hypotheses, most have lacked an appropriate comparative perspective. Moreover, most studies of subadult plumage in passerines have been conducted without information on the general function of ornamental plumage in the species being studied. A study of delayed plumage maturation in the House Finch (*Carpodacus mexicanus*) provided an opportunity to overcome these problems. The function and proximate control of ornamental plumage coloration in House Finches have been studied extensively. In addition, House Finches occupy a wide range across North America with approximately 15 subspecies recognized, and populations vary in expression of delayed plumage maturation. In most populations, including the most familiar subspecies, *C. m. frontalis*, males acquire definitive basic plumage in their first prebasic molt. In at least three populations, *C. m. griscomi* of southern Mexico, *C. m. amplus* of Guadalupe Island, and Great Basin populations of *C. m. frontalis*, however, males do not acquire definitive plumage until the completion of their second prebasic molt, spending their first potential breeding season in a female-like plumage. Using a composite phylogeny and parsimony analysis, I show that delayed plumage maturation likely was lost in the ancestral House Finch population and was regained independently by the three taxa in which it is now observed. Thus, delayed plumage maturation in the House Finch is a derived trait. In addition, I show that the acquisition of delayed plumage maturation is associated with a reduction in the extent of ornamental plumage (i.e. a reduction in patch size). These observations support the idea that delayed plumage maturation in the House Finch is an adaptation to increased production costs of red ornamental display plumage in some populations. Received 28 November 1995, accepted 25 April 1996.

DELAYED PLUMAGE MATURATION describes a developmental pattern generally limited to males, whereby individuals do not acquire definitive breeding plumage until after their first potential breeding season (Rohwer et al. 1980, Rohwer and Butcher 1988). Studies of delayed plumage maturation most frequently concern Temperate Zone passerines that spend only one potential breeding season in a subadult plumage (Rohwer and Butcher 1988, Butcher and Rohwer 1989, Zack and Stutchbury 1992). Despite a substantial literature on delayed plumage maturation (see Zack and Stutchbury 1992), our understanding has advanced relatively little since interest in the topic was first ignited by Rohwer et al. (1980). I believe that the ma-

ajority of research on delayed plumage maturation in passerines suffers from two fundamental problems: (1) lack of a general understanding of the function of ornamental plumage coloration, and (2) lack of an appropriate comparative approach to testing hypotheses for the evolution of delayed plumage maturation.

The first of these problems clearly is a case of putting the cart before the horse. Ornamental plumage coloration, either bright structural coloration, bright carotenoid-based coloration, or highly contrasting melanin-based coloration, is universally assumed to function as a signal in avian communication (Butcher and Rohwer 1989). Signaling generally is believed to occur in the context of either intersexual or intrasexual interactions (Butcher and Rohwer 1989), but predator-prey interactions also have been considered (Götmark 1992, 1993). An assump-

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tion of the basic function of plumage coloration serves as the foundation for most hypotheses concerning delayed plumage maturation, and yet the function of ornamental plumage coloration has been studied in few species and rarely in combination with studies of delayed plumage maturation (see Butcher and Rohwer 1989, Savalli 1995). Thus, most studies of delayed plumage maturation are built on a foundation of untested assumptions.

The second major problem—drawing evolutionary inference from studies of present utility—is not limited to studies of delayed plumage maturation but has been a general shortcoming of studies in behavioral ecology (Felsenstein 1985, Brooks and McLennan 1991, Harvey and Pagel 1991). In the past few years, a number of new and powerful tools for testing hypotheses of trait evolution have been proposed (Brooks and McLennan 1991, Harvey and Pagel 1991, Maddison and Maddison 1993). A few studies of delayed plumage maturation tested for patterns among passerines with no attempt to correct for phylogeny (Studd and Robertson 1985, Lyon and Montgomerie 1986), primarily because these studies were completed before robust comparative methods had been developed. More recently, studies have used a comparative approach that controls for the effects of phylogeny (Björklund 1991, Chu 1994). The majority of studies that purport to test evolutionary hypotheses, however, are studies of the function (or lack thereof) of subadult plumage in single populations (see Thompson 1991, Enstrom 1992). From such single-species/population studies, evolutionary conclusions are drawn.

Lack of a rigorous and consistent definition of delayed plumage maturation also has led to confusion in the field. Biologists are in general agreement on the sorts of plumage development patterns among passerines that constitute delayed plumage maturation, but lists of species with and without delayed plumage maturation vary among authors (Rohwer et al. 1980, Studd and Robertson 1985, Lyon and Montgomerie 1986, Rohwer and Butcher 1988). Rohwer et al. (1980), who are cited almost universally as the basic reference on delayed plumage maturation, define it as males "achiev[ing] obvious plumage maturity 1 yr after their first potential breeding season" (Rohwer et al. 1980). Thompson (1991), in contrast, focused on the distinction between somatic maturity and plumage maturity and de-

fining delayed plumage maturation as "delayed acquisition of adult plumage by sexually mature birds" (Thompson 1991). The problem with these definitions is how one interprets "obvious plumage maturity" and "sexually mature." In many species with ornamental coloration of the breeding plumage, yearling males are, on average, less brightly or distinctly colored than adult males (e.g. Pine Siskin [*Spinus pinus*], Yunnick 1976; Eastern Bluebird [*Sialia sialis*], Pitts 1985; Canada Warbler [*Wilsonia canadensis*] and other parulid warblers, Rappole 1983). Nevertheless, authors are in agreement that these species do not show delayed plumage maturation. Similarly, exactly when a bird becomes "sexually mature" is ambiguous because yearling males of many passerines have smaller testes and produce less sperm than older males (Wright and Wright 1944, Selander and Hauser 1965, Payne 1969, Samson 1976, Foster 1987, Møller and Erritzøe 1988, Hill 1994c). Many of the species in which full testicular development is delayed beyond the first year are considered to show delayed plumage maturation, so "sexual maturity preceding plumage maturity" cannot be applied to these species.

The ambiguity that can arise with previous definitions of delayed plumage maturation is best illustrated with an example using North American *Carpodacus* finches. In attempts to classify North American *Carpodacus* as having or lacking delayed plumage maturation, the Purple Finch (*C. purpureus*) and Cassin's Finch (*C. cassinii*) are designated as having delayed plumage maturation, and the House Finch (*C. mexicanus*) of the familiar Pacific Coast population usually is designated as lacking delayed plumage maturation (Rohwer et al. 1980, Studd and Robertson 1985, Rohwer and Butcher 1988; but see Lyon and Montgomerie 1986). Authors make this distinction even though it is well known that yearling male House Finches, on average, have drabber ornamental plumage than do older males (Michener and Michener 1931, Gill and Lanyon 1965, Hill 1992). Clearly it is important to distinguish between age-related variation in plumage brightness (as is seen in the House Finch) and age-specific variation in plumage pattern (as in Cassin's Finch, Purple Finch, and, as I describe in this paper, some populations of House Finch; Fig. 1). Thus, I propose the following definition of delayed plumage maturation in males: The delayed acquisition of definitive nuptial plumage until after

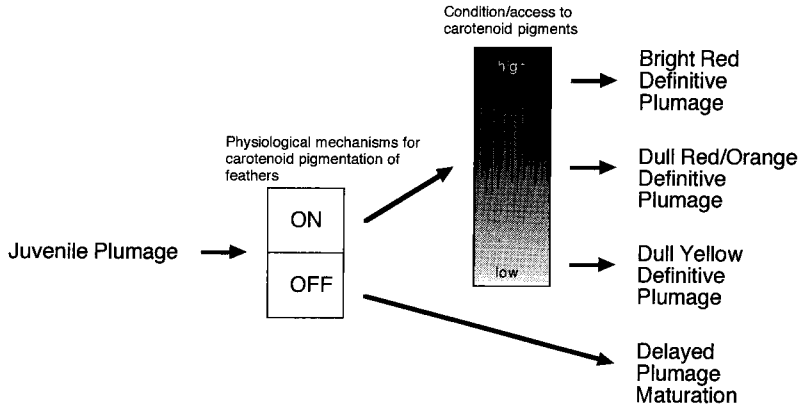


FIG. 1. Flow chart illustrating the sources of variation in expression of ornamental plumage coloration in male House Finches. Delayed plumage maturation results from the shutting down of the potential for pigment uptake by growing feathers, not from a lack of available pigment or a lack of appropriately timed molt.

the first potential breeding season such that the subadult plumage has a pattern distinct from that of males in definitive plumage but not necessarily from that of females. The importance of the distinction between the plumage pattern and the mean plumage brightness of yearling and older males will become more evident as I describe geographic variation in acquisition of definitive plumage in the House Finch. In using "first potential breeding season," I make no assumptions about the testicular development of males other than that enough sperm is produced to fertilize eggs.

In this paper, I use this definition of delayed plumage maturation to describe variation in expression of both delayed plumage maturation and extent of ornamental pigmentation in definitive plumage both within and among populations of the House Finch. More is known about the function, evolution, and proximate control of ornamental plumage coloration in the House Finch than in any other passerine species. Moreover, there are approximately 15 subspecies or populations of House Finches that vary in presence/absence of delayed plumage maturation as well as in the extent of ornamentation of definitive plumage, making the House Finch an ideal taxon for comparative study. (See Moore [1939] for a detailed description of the morphology and distribution of House Finch taxa in North America and Hill [1993b] for an explanation of the exclusion in this paper of some taxa described by Moore [1939]. Figure 2 shows the subspecies of House Finches and their approximate distributions based on Moore

[1939], with an updated distribution of *C. m. frontalis* [Hill 1993a].)

Functional hypotheses to explain the evolution of delayed plumage maturation are numerous, and many proposed hypotheses differ only in detail. Thompson (1991) recognized eight distinct models for the evolution of delayed plumage maturation that he divided into hypotheses of winter adaptation and summer (breeding) adaptation (see Zack and Stutchbury [1992] for additional information on the origin and development of these hypotheses). Three models of the function of delayed plumage maturation propose that subadult plumage is an adaptation to the winter (nonbreeding) environment. The "winter status signaling hypothesis" proposes that subadult plumage signals subordinate status, which aids yearling males in avoiding aggression from older, more experienced males in their first winter. The "winter female mimicry hypothesis" proposes that, if males allow females access to resources, yearling males can benefit by mimicking the appearance of adult females and deceptively acquiring resources from adult males. The "winter cryptic hypothesis," proposes that ornamental plumage coloration increases the vulnerability of males to predators, so yearling males benefit by having a less-well-ornamented plumage. Additionally, five hypotheses propose breeding-season functions for delayed plumage maturation. The "summer female mimicry" and "juvenile mimicry" hypotheses state that yearling males benefit from reduced aggression from adult males by mimicking females or juveniles,

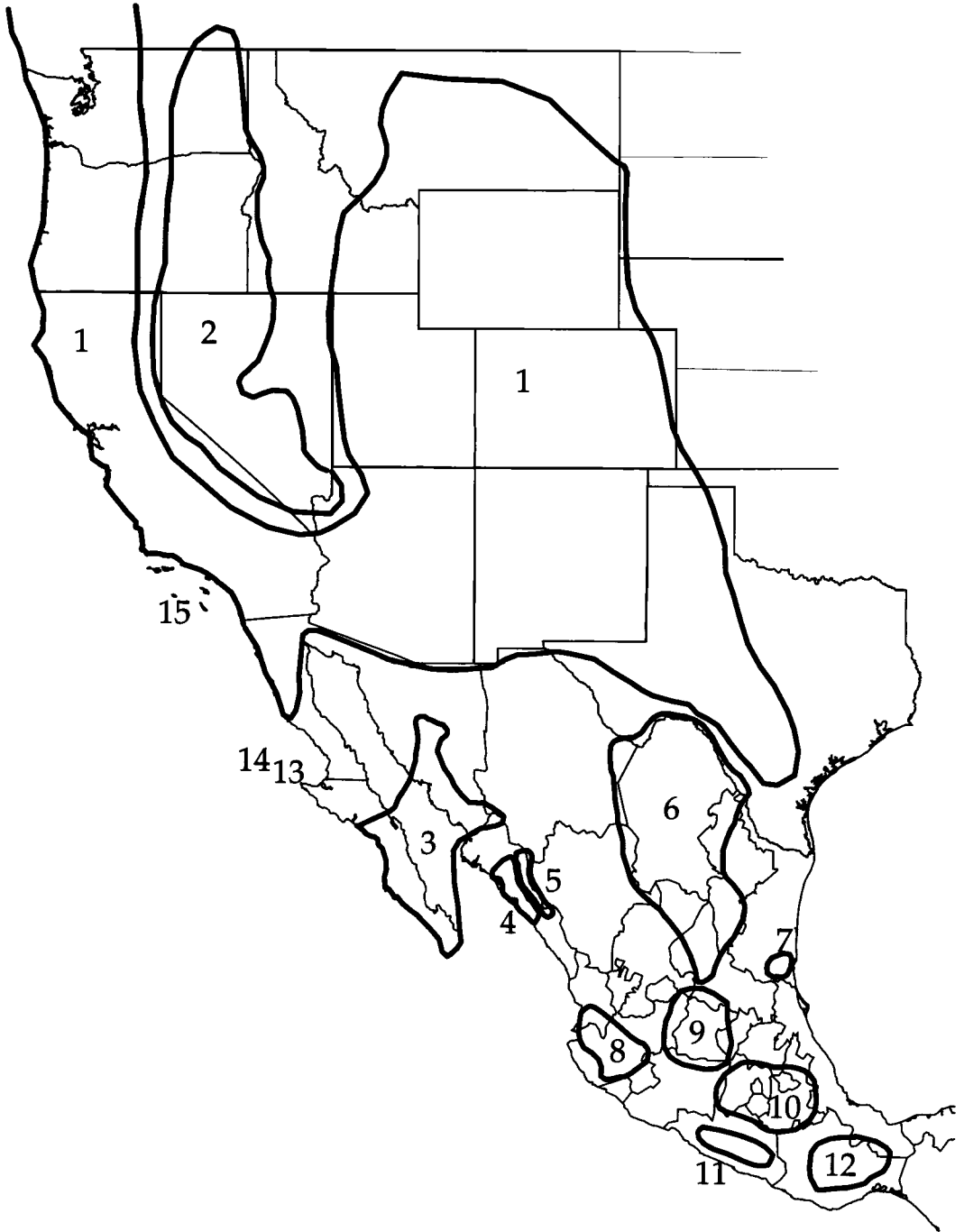


FIG. 2. Approximate geographic ranges of the subspecies of House Finches. Ranges are redrawn from Moore (1939) except for *frontalis*, which has undergone extensive range expansion in the U.S. since 1939. Range of the Great Basin population of *frontalis* is proposed to extend to British Columbia. Eastern U.S. and Hawaiian ranges of *frontalis* are not shown. Many of the gaps among the depicted ranges have populations of House Finches of unknown subspecies affiliation (see Moore 1939). 1, *frontalis*; 2, Great Basin *frontalis*; 3, *ruberrimus*; 4, *rhodopnus*; 5, *altitudinus*; 6, *potosinus*; 7, *nigrescens*; 8, *coccineus*; 9, *centralis*; 10, *mexicanus*; 11, *griscomi*; 12, *roseipectus*; 13, *mcgregori*; 14, *amplus*; 15, *clementis*.

TABLE 1. Number of male House Finches captured and examined at various locations.

Location	Subspecies	Date	Number
Ann Arbor, Michigan	<i>frontalis</i>	February to July 1988-90	548
Ann Arbor, Michigan	<i>frontalis</i>	December 1989	46
Long Island, New York	<i>frontalis</i>	December 1989	38
San Jose, California	<i>frontalis</i>	February 1990	118
San Jose, California	<i>frontalis</i>	August 1992	134
Honolulu, Hawaii ^a	<i>frontalis</i>	January 1989	7
Pohakuloa, Hawaii ^b	<i>frontalis</i>	January 1989	49
Kingston, Ontario	<i>frontalis</i>	August 1991	38
Auburn, Alabama	<i>frontalis</i>	July 1993 to August 1995	330
Guerrero, Mexico	<i>griscomi</i>	January 1990	48
Guerrero, Mexico	<i>griscomi</i>	September 1992	96

^a Island of Oahu.

^b Island of Hawaii.

respectively. The "summer cryptic hypothesis" differs from the winter cryptic hypothesis only in invoking breeding-season advantages such as reduced conspicuousness to rival males. To be distinct from the winter cryptic hypothesis, this hypothesis requires a prealternate (spring) molt that makes yearling males less conspicuous (Thompson 1991). The "molt constraint hypothesis" proposes that yearling males are unable to obtain definitive breeding plumage either because they lack the energy needed for feather replacement or because the molt sequence to which they are constrained (due to past history) precludes the acquisition of definitive plumage in their first year. Finally, the "summer status signaling hypothesis" proposes that yearling males benefit from reduced aggression from adult males by honestly signaling their subordinate status. This hypothesis requires that there be a male-biased sex ratio, that females choose mates based on male attributes (vs. defended resources), and that yearling males have few opportunities for successful reproduction in competition with adult males (Thompson 1991).

House Finches have only one annual molt, and they change appearance between seasons only through wear of buffy feather tips. Thus, it is difficult to distinguish among summer and winter costs and benefits in this species. Nevertheless, the breeding and nonbreeding biology of *C. m. frontalis* House Finches have been well studied, so the general applicability of various functional hypotheses to explain delayed plumage maturation can be examined. In this paper, I will first establish that delayed plumage maturation meets the basic requirements of an adaptation (sensu Coddington 1988, O'Hara

1988). I will then trace plumage characters on a phylogeny of House Finch populations and show that delayed plumage maturation is associated with a reduction in the extent of carotenoid pigmentation in definitive plumage. Lastly, I will assess the validity of hypotheses on the function of delayed plumage maturation in the House Finch by comparing predictions of models with observations of my own or from the literature.

METHODS

Plumage states of subspecies.—I captured and examined House Finches of the subspecies *C. m. frontalis* in a variety of locations and of the subspecies *C. m. griscomi* in Chilpancingo, Guerrero, Mexico (see Table 1 for specific collecting localities, dates, and number of males examined). I use "HY" (hatching year) to describe birds in the calendar year of their birth, "AHY" to describe birds in at least their second calendar year, "yearling" to describe birds in their first basic plumage, and "older" to refer to birds in their second or subsequent basic plumages.

When House Finches were captured in winter and spring (December to July), gender was determined primarily by plumage color and pattern (see Hill 1993a), although I determined gender by examination of gonads whenever possible. I also determined the gender of individuals in Ann Arbor, Michigan by behavior during breeding. For each bird examined, I recorded the hue, intensity, and tone of carotenoid-based plumage by comparison with plates in the *Methuen Handbook of Colour* (Kornerup and Wanscher [1983]; see Hill [1992, 1993b] for details of the plumage-scoring technique), and I recorded the extent of ventral carotenoid pigmentation (i.e. patch size) by estimating the percentage of ventral plumage with carotenoid pigmentation (see Hill 1992, 1993b). In late summer and autumn I aged birds as HY or AHY by

TABLE 2. Number of male study skins of nine House Finch subspecies examined by the author (P) or by museum staff (O) in various museums.* Observations of *C. m. frontalis* and *C. m. grisei* based on live birds (see Table 1).

Subspecies	UMMZ		BRMU		CAAD		FMNH		WVZ		MVZ	
	P	O	P	O	P	O	P	O	P	O	P	O
<i>clementis</i>	25	0	0	0	1	6	0	0	0	1	0	0
<i>mcgregori</i>	0	0	0	0	0	0	0	1	0	0	0	2
<i>amplus</i>	6	0	0	0	6	11	1	9	0	1	1	5
<i>potosinus</i>	15	0	0	0	0	0	0	6	0	3	1	5
<i>centralis</i>	0	0	0	0	0	0	0	7	0	0	0	1
<i>coccineus</i>	7	0	0	28	1	4	0	6	0	4	0	2
<i>ruberrimus</i>	13	0	0	0	0	0	2	31	0	3	0	27
<i>mexicanus</i>	3	0	0	26	0	0	0	2	0	2	0	2
<i>roseipectus</i>	2	0	0	2	0	0	0	0	0	9	0	0

* UMMZ, University of Michigan Museum of Zoology; BRMU, British Museum; CAAD, California Academy of Natural Sciences; FMNH, Field Museum of Natural History; WVZ, Western Foundation of Vertebrate Zoology; MVZ, Museum of Vertebrate Zoology, University of California Berkeley.

plumage (Hill 1993a) or by examining skulls for ossification. I could not age birds during winter and spring sampling.

During summer and autumn sampling, I recorded the extent of body molt and primary molt, the coloration of old (i.e. soon-to-be-molted) feathers, and the coloration of incoming feathers (see Hill et al. 1994a for details of scoring molt and the coloration of incoming feathers). In San Jose, California and Guerrero, Mexico in autumn of 1991, I collected 351 individuals for a diet study; gender of these individuals was determined by gonadal examination. Subsets of individuals captured in Ann Arbor, San Jose, the Big Island of Hawaii, and Guerrero were held in outdoor aviaries through at least one prebasic molt (see Hill 1992, 1993b). Each captive was scored for plumage brightness and patch size at the time of capture and after each molt in captivity.

Finally, I examined all specimens of House Finches in the University of Michigan Museum of Zoology, including at least two males from all subspecies of House Finches except *C. m. nigrescens*, *C. m. rhodoptus*, and *C. m. altitudinis*. In addition, I obtained from several museums specimens of male House Finches from Mexico that had been determined by museum staff to have basic plumage with limited carotenoid pigmentation. I also requested a tally of all specimens examined. From this information I compiled a summary of the number of specimens from each subspecies that were examined either by myself or by museum personnel (Table 2).

Comparative analysis.—No well-supported phylogeny exists for House Finch lineages in North America. However, in a previous study (Hill 1994b) I conducted a simple cladistic analysis based on morphological characteristics that indicated that the three southernmost subspecies form a clade, with *grisei* and *mexicanus* as each other's closest relative and *roseipectus* as a sister lineage to these two. This finding is consistent with Moore's (1939) suggestion that the three

southern subspecies of House Finch were isolated from other populations in the Pleistocene. Furthermore, Sharpe (1888:421 in Moore 1939) described the northern and central populations of the House Finch as specifically distinct (*Carpodacus frontalis*) from the southern Mexican populations of *C. mexicanus*. As a working hypothesis of the evolutionary relationships of House Finch populations, I add three additional groupings among House Finch lineages. First, I follow Power's (1979) proposal that House Finches of the subspecies *clementis* from the northern California Islands are derived from the mainland population of *C. m. frontalis*, and that the subspecies *mcgregori* and *amplus* from the southern California Islands are derived from the mainland population of *C. m. ruberrimus*. Second, I assume that the Great Basin population of *C. m. frontalis* is a sister lineage to the populations of *frontalis* that bound it on the west, south, and east. Because the birds in these populations are so similar that they warrant no taxonomic distinction (AOU 1957), treating them as sister taxa seems reasonable. Also, based on evidence from molecular studies (Martin and Johnson 1986), I considered the two North American outgroups, Cassin's Finch and Purple Finch, to be more closely related to each other than either is to the House Finch clade. As a second outgroup, I used Eurasian *Carpodacus* finches and characterized them as having delayed plumage maturation and a medium patch of red (Clement et al. 1993; Fig. 3).

To look at the likely sequence of evolutionary change relative to delayed plumage maturation and extent of ventral carotenoid pigmentation (hereafter "patch size") across the House Finch clade, I conducted a concentrated changes test (Maddison 1990) using the computer program MacClade (Maddison and Maddison 1993). The concentrated changes test cannot be used if the clade of interest is polytomous (Maddison and Maddison 1993), so I resolved the polytomies in the *C. mexicanus* clade either by removing taxa (*coccineus*, *potosinus*, *centralis*, *mcgregori*, and cle-

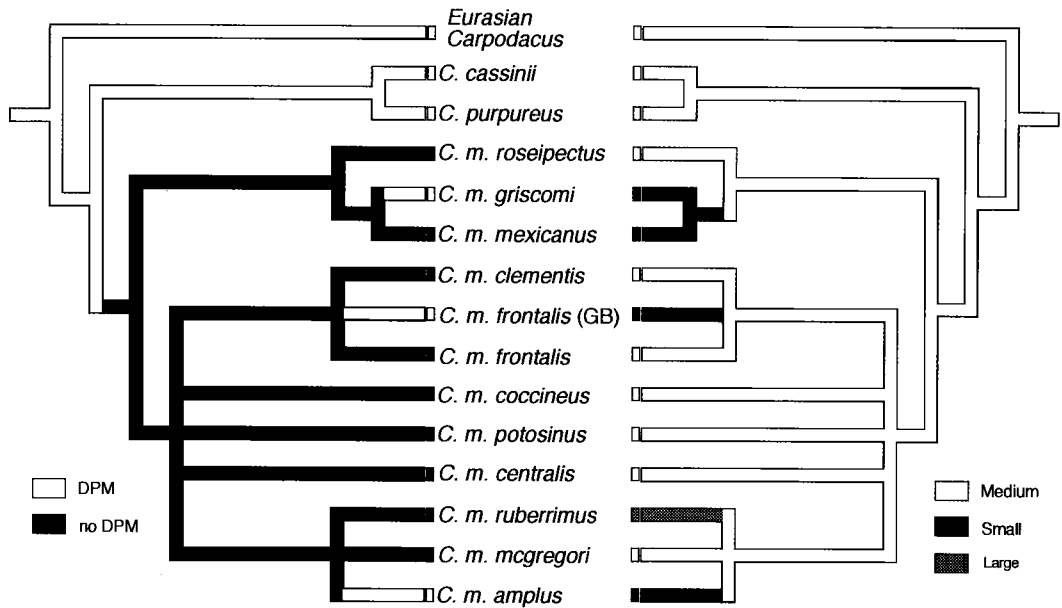


FIG. 3. A composite phylogeny of House Finch lineages based on a cladistic analysis (Hill 1994b) and biogeographical and morphological evidence summarized in Power (1979). *C. m. frontalis* (GB) is the Great Basin population. Evolution of the characters delayed plumage maturation (left side) and patch size (right side) was traced on the phylogeny, and the states of interior nodes were optimized according to Farris (1970).

mentis) or by testing various equally parsimonious trees.

RESULTS

PLUMAGE PIGMENTATION AND MOLT

General scheme for the species.—House Finches undergo one complete prebasic molt annually, except that some HYs retain a variable number of juvenal remiges (Michener and Michener 1940, Stangel 1985, Hill 1993a). The only change in appearance outside of the molting period is a slight brightening of plumage in definitive males that results from wear of buffy feather edges (Grinnell 1911). Thus, the appearance of House Finches does not vary dramatically across seasons.

House Finches are highly sexually dichromatic. Females are drab with a streaky brown-and-buff plumage pattern and, at most, a faint wash of pink on the rump, crown, and ventral plumage (Hill 1993c). In contrast, older males have extensive carotenoid-based (Brush and Power 1976) ornamental plumage on their head, underside, and rump that varies from pale yellow to bright red (Michener and Michener 1931;

Hill 1990, 1993b). In addition to differences in the extent and brightness of carotenoid-based plumage pigmentation, the sexes also differ in the pattern of melanin pigmentation. Females have dark-brown melanin pigmentation along the rachis of feathers on the rump, forecrown, and upper breast and throat that is lacking in males. Even in the rare instances in which females have brighter carotenoid pigmentation than drab older males (Hill 1993b, c), melanin pigmentation within the patches of carotenoid pigmentation distinguishes females from males. Thus, males and females typically vary in the relative brightness of carotenoid pigmentation, but they nearly always show absolute differences in the pattern of melanin pigmentation. A tradeoff between intense carotenoid pigmentation and melanin pigmentation is a general feature of contour feathers in the House Finch (and in other cardueline finches; Hill and Benkman 1995). Feathers that have the potential for intense carotenoid pigmentation lose the dark melanin pigmentation along the rachis. Thus, reduced melanin pigmentation and increased carotenoid pigmentation in the ventral plumage are two sides of the same coin. Presence of melanin pigmentation is a better index of a

feather's potential for ornamental display, however, because carotenoid pigmentation is dependent on diet (Hill 1992, 1993b).

Subspecies C. m. frontalis.—Delayed plumage maturation is virtually absent in the subspecies *frontalis* (Michener and Michener 1940, Hill 1993a). The only exceptions that I have encountered involved two males in first basic plumage. On 1 November 1988, I captured a bird in southeastern Michigan that I determined was an HY based on skull ossification. I sexed it as a female because of its plumage. It had a small and relatively drab patch of red on its rump; a pink wash over its throat, upper breast, and crown; and heavy melanin streaking on its rump, crown, throat, and upper breast. The bird was held in captivity and by chance was assigned to a diet supplemented with canthaxanthin (see Hill 1992, 1993b, c for details of diet). When it molted the next summer, it grew a bright red plumage. This second basic plumage was strikingly different from the first basic plumage not only in having much more intense and extensive red carotenoid pigmentation on the crown, rump and ventral feathers, but also in lacking the melanin pigmentation in areas pigmented by carotenoids (rump, crown, throat, and upper breast feathers). Thus, its plumage increased in brightness and changed from a pattern typical of females to that typical of males. In spring of 1990, this bird was placed in a cage with a female from Michigan and allowed to breed, producing three male offspring. The captive-born males were fed a diet supplemented with canthaxanthin during their first prebasic molt, and each grew a bright red plumage with no melanin streaking on the fore-crown, throat, or rump. The second exception occurred on 20 February 1990 on the University of Michigan campus when I color-banded and released a bird that had female-type plumage. The pattern and coloration of its carotenoid pigmentation were similar to that described for the male noted above. Over the next two months I observed this bird many times, and it always behaved like a male. It sang frequently and was treated like a male by both males and females in the area. As is typical of unpaired males, it vigorously courted unattended females whenever it had the opportunity, and it frequently intruded on pairs. Unfortunately, this bird did not pair in 1990 and did not return to the study site the next year. Although it could have been a female with aberrant behavior, I believe that

it was a male with female-like, first-basic plumage.

In Michigan I observed 270 breeding pairs of *frontalis* for four seasons and maintained 97 males and 84 females in captivity. I also sexed 133 males and 69 females by gonadal examination in California (Hill et al. 1994a). Thus, subadult plumage occurs in roughly 0.4% (i.e. 2/500) of *frontalis* males. Interestingly, Moore (1939) examined 350 study skins of male *frontalis* from the Pacific Coast region and found three female-plumaged males in basic plumage (0.9%). These calculations tally males in all age cohorts. Because males House Finches show subadult plumage only in their first basic plumage, these calculations and those that follow are not estimates of the proportion of yearling males with delayed plumage maturation and should be used only as an index of the relative frequency of delayed plumage maturation in various populations.

These observations emphasize the importance of distinguishing between age-related variation in plumage brightness and age-specific variation in plumage pattern (Fig. 1). As I argued in the introduction, the latter is delayed plumage maturation, and the former is not. Although *frontalis* males typically do not display delayed plumage maturation, within any population males vary in expression of carotenoid-based plumage coloration from dull yellow to bright red (Michener and Michener 1931; Gill and Lanyon 1965; Hill 1990, 1993b). The same range of variation in male coloration occurs in all age classes, but, on average, yearling males are drabber than older males (Hill 1992). This variation cannot be considered delayed plumage maturation because it is not an age-specific plumage pattern (Fig. 1). In contrast, the two males with female-like first basic plumage exhibited delayed plumage maturation because their plumage pattern was age-specific (see Fig. 1).

Subspecies C. m. griscomi.—The pattern of plumage development shown by >99% of *frontalis* males is not the pattern in all populations of House Finches. In *griscomi*, which occurs only in the mountains of Guerrero in southern Mexico (Moore 1939; Fig. 2), males show age-related variation in plumage brightness and age-specific variation in plumage pattern. Adult *griscomi* of both sexes are similar to those of *frontalis* in plumage color and pattern except that male *griscomi* have substantially smaller patches of

ventral carotenoid pigmentation than male *frontalis* (Moore 1939; Hill 1993b, 1994b). The first basic plumage of *griscomi* males, however, is distinctly different in pigment pattern from the definitive basic plumage. Unlike adult males, yearling males have heavy melanin streaking on their upper breast and throats, and most also have heavy streaking on their forecrowns. The brightest yearling males have bright red rumps completely lacking melanin streaking, patches of red plumage on the breast (but <20% of feathers pigmented in definitive plumage), and scattered red feathers on the forecrown and over and behind the eye. The hue of ornamental plumage in yearling males ranges from drab yellow to bright red, and the drabest individuals lack carotenoid coloration on their head and ventral surface but still have extensive rump coloration. Thus, the first basic plumage of male *griscomi* is distinct from female basic plumage or male definitive basic plumage.

One important observation is that the female-like plumage of the forecrown and upper breast and throat of male *griscomi* in first basic plumage is acquired during the first prebasic molt and does not result from retention of female-like juvenal feathers. I confirmed this by collecting 63 molting HY males in Guerrero during autumn 1992. Each bird was sexed by gonadal examination, and all of them were growing upper breast/throat or crown feathers that had little or no carotenoid pigmentation and heavy melanin streaking. That males grow a female-like basic plumage rather than retaining a female-like juvenal plumage bears directly on some models for the evolution of delayed plumage maturation, as will be discussed below.

In an experiment to determine the genetic basis for the difference in patch size between populations of *frontalis* and *griscomi*, I crossed a female *frontalis* from Michigan with a male *griscomi* (see Hill 1993b). The single male offspring of this cross was fed a diet supplemented with canthaxanthin and grew definitive basic plumage in its first prebasic molt. Thus, based on very limited data, it appears that either genes for female-like first basic plumage are recessive to genes for definitive first basic plumage, or that conditions in captivity preclude the expression of delayed plumage maturation.

Great Basin population of C. m. frontalis.— Moore (1939) recognized the Great Basin population of House Finches as a distinct subspecies, *C. m. solitudinis*, based on body size, the

extent of red on the underside and back, and ground color. The range of this "subspecies" extends from the southern Nevada and southeastern Idaho to southwestern Washington and south-central British Columbia (Fig. 2). Birds from the Great Basin are similar to Pacific Coast birds in size, shape, and extent of ventral red pigmentation, and the AOU (1957) reported insufficient differences between House Finches of the Pacific Coast and the Great Basin to warrant subspecies status for the interior birds. They lumped the two populations into one subspecies, *C. m. frontalis*. However, the AOU apparently did not consider differences in first basic plumage between the populations. Van Rossem (1936:52–53) reported that all male House Finches in his study population in the Ruby Mountains of Nevada (in the range of Moore's *solitudinis*) had female-like first basic plumage. In describing the occurrence of female-like first basic plumage among all populations of House Finches, Moore (1939) reported that "Sixty-four percent of aberrant individuals come from this region, ranging from Colorado to Arizona, Nevada and southeastern Oregon, in which regions only thirty-three per cent of our total number of specimens were collected." Surprisingly, there are no more recent or detailed accounts of delayed plumage maturation in House Finches in this region, although the need for observations from the Great Basin population of House Finches has been noted by Rohwer et al. (1980) and Thompson (1991). From the evidence at hand, I conclude that the House Finch population in at least the southern Great Basin (and probably the entire Great Basin) is distinct from Pacific Coast and Rocky Mountain populations in having male first basic plumage that is female-like.

The extent of ventral carotenoid pigmentation (patch size) of males in definitive plumage in this population apparently is reduced compared with other populations of *frontalis*. In describing the Great Basin population, Moore (1939) stated that males are "much less extensively red than *frontalis* or *smithi*" (the latter two populations referring to the northern and southern Rocky Mountain populations under Moore's taxonomy). Moore (1939) illustrated the patch size of Great Basin finches as being like that of *C. m. amplus* (see below), i.e. substantially smaller than coastal California birds. Thus, it appears that this is another small-patched population. Unfortunately, I have seen no speci-

mens from this region to confirm either delayed plumage maturation or reduced patch size.

Subspecies C. m. amplus.—Males from Guadalupe Island (*C. m. amplus*) display a female-like first basic plumage. Eight of the 40 (20%) study skins of males that I examined showed a female-like plumage. This is a significantly higher frequency of delayed plumage maturation than was recorded in either *frontalis* or *ruberrimus*, and I conclude that male *amplus* typically exhibit delayed plumage maturation. Interestingly, three of the males that I examined were completely female-like, either lacking carotenoid pigmentation or having a pale wash of color on their rump. These are the most female-like males in first basic plumage that I have seen in any population of House Finch. The museum labels on two of these males (California Academy of Natural Sciences nos. 38118 and 38119) indicated that the males were breeding when collected. To my knowledge, these are the only records of male House Finches breeding in subadult plumage.

Male *amplus* in definitive plumage also have small patches of ventral coloration. In earlier papers I had seen few skins of male *amplus* and classed them as having medium-sized patches (Hill 1993b, 1994b). However, *amplus* patch size (mean proportion of ventral plumage = $0.320 \pm \text{SD of } 0.02, n = 7$) is consistently smaller than that of male *frontalis* from Coastal California ($\bar{x} = 0.658 \pm 0.11, n = 548$) but not significantly different from that of male *griscomi* ($\bar{x} = 0.242 \pm 0.04, n = 41$; $F = 341.7, \text{df} = 2 \text{ and } 596, P = 0.001$; Sheffe test at $P < 0.05$ indicates that *frontalis* has a larger patch than both *amplus* and *griscomi*, which do not differ from one another). Thus, *amplus* should be classed as having small ventral patches of carotenoid pigmentation. Along with small patches of ventral carotenoid coloration, a relatively large proportion of male *amplus* has orange or yellow rather than red carotenoid pigmentation (Moore 1939; pers. obs.). These males appear female-like because of their drab ornamental coloration. Close inspection, however, reveals that, although the plumage of the crown and throat/upper breast that normally would contain red coloration is washed out, feathers within these patches lack heavy melanin pigmentation along the rachis. These drably plumaged males were not counted among those with delayed plumage maturation.

Other subspecies of House Finches.—To my knowledge, in all other populations of House

Finches males typically acquire definitive plumage during their first prebasic molt. Yearling males from the subspecies with the largest patches of ventral red coloration (i.e. *ruberrimus* from southern Baja peninsula and coastal Sonora) rarely show delayed plumage maturation. Moore (1939) found 7 female-like males in first basic plumage out of approximately 200 males examined (~3%). I found 1 of 76 male *ruberrimus* in collections to have female-like plumage (1.3%). It appears that, as in populations of *frontalis*, a small proportion of HY male *ruberrimus* have female-like plumage. However, the majority of males apparently reach definitive plumage in their first prebasic molt, and I do not classify this population as having delayed plumage maturation. The two populations of House Finches best represented in museum collections are *ruberrimus* and *frontalis* from the U.S. Pacific Coast. These also are the two subspecies in which a low incidence of female-like plumage among males has been detected. It may prove that delayed plumage maturation exists in low frequencies in all populations of House Finches.

COMPARATIVE ANALYSIS

Based on parsimony analysis, the common ancestor of House Finches and other *Carpodacus* had delayed plumage maturation, but the common ancestor of extant House Finch lineages underwent developmental acceleration (sensu Björklund 1991), gaining a definitive first basic plumage (Fig. 3). Delayed plumage maturation in male *griscomi*, *amplus*, and Great Basin *frontalis* is derived from an ancestral condition with a definitive first basic plumage (Fig. 3). Small patch size likely evolved on three separate occasions from a larger-patched ancestral state (Fig. 3). Regardless of what phylogeny was used (see Methods), the probability that observed patterns of correlated character evolution occurred by chance was low ($P = 0.03$ when taxa were removed; $P < 0.01$ for all equally parsimonious, fully resolved trees). In other words, across the House Finch clade, delayed plumage maturation and reduced patch size co-evolved.

ASSESSMENT OF FUNCTIONAL MODELS

The winter status signaling hypothesis proposes that subadult plumage reliably signals an individual's status. A basic assumption of this

hypothesis is contradicted by observations from several studies of *frontalis* males. Brightly colored males are not dominant to males with drabber plumage, and females are dominant to males (Brown and Brown 1988, Hill 1990, Belthoff and Gauthreaux 1991, Belthoff et al. 1994). Moreover, *frontalis* females are more aggressive toward drab males than toward bright males (Belthoff and Gowaty 1996). Under these conditions, subadult plumage would not signal low status, and there is a cost to being drab versus bright. Consequently, the winter status signaling hypothesis can be rejected as a likely explanation for delayed plumage maturation in the House Finch.

The winter female mimicry hypothesis originally was proposed to explain dominance interactions in House Finches (Brown and Brown 1988). If males allow females access to resources, yearling males can benefit by mimicking the appearance of adult females and deceptively acquiring resources from adult males. Because female House Finches regularly supplant males in contests over resources (Thompson 1960, Belthoff and Gauthreaux 1991, Belthoff et al. 1994), the basic premise of this hypothesis is sound. However, yearling males would potentially lose as well as gain by mimicking females, because females mate preferentially with the most brightly plumaged males available (Hill 1990, 1991, 1994b; see below). Thus, for the winter female mimicry hypothesis to operate, benefits from resource acquisition must outweigh the costs of lost mating opportunities. In *griscomi* (for which delayed plumage maturation has been best described and documented), yearling males are not completely female-like (they have bright rumps and variable color on their head and breast), and females rarely show carotenoid-based coloration (Hill 1993c). Thus, the validity of this hypothesis in explaining delayed plumage maturation ultimately depends on sexual recognition mechanisms.

The winter cryptic hypothesis proposes that ornamental plumage coloration increases the vulnerability of males to predators. One observation supports the basic premise of this model: Definitive basic body feathers with ornamental coloration have buffy tips that partly conceal ornamental coloration, making males less brightly colored (Grinnell 1911, Hill 1993b). The buffy tips are worn off by late winter in time for courtship and pairing (Grinnell 1911; Hill 1993a, b). Possible explanations for the buffy

feather tips are concealment of ornamental plumage from predators or from conspecifics. Because plumage brightness does not appear to function as a status signal in intrasexual interactions, and drabber male plumage elicits increased aggression from females, predation risk seems the most likely explanation for the buffy tips. If males can benefit from partially concealing colorful plumage during the winter, then they would benefit even more by lacking colorful plumage altogether. In contrast to the predictions of this model, I found that brightly plumaged males had higher overwinter mortality than drably plumaged males (Hill 1991). I interpreted this result as indicating a difference in the physiological condition of drably and brightly plumaged males, not a difference in the cost of bright feathers per se. Another problem with the cryptic hypothesis as a universal explanation for delayed plumage maturation is that one of the three subspecies of House Finches with delayed plumage maturation, *C. m. amplus*, is found on an island with few predators. Thus, support for the winter cryptic hypothesis as an explanation for delayed plumage maturation in House Finches is mixed.

Four of the five hypotheses that invoke adaptation in the summer (breeding) season can be excluded from further consideration because they contradict basic observations of the breeding biology of House Finches. The summer female mimicry and juvenile mimicry hypotheses state that yearling males benefit from reduced aggression from adult males by mimicking females or juveniles, respectively. The female mimicry hypothesis centers on the establishment of site dominance and territories, and because male House Finches do not defend territories (Hill 1993a), it is not applicable to this species. One possible role for female mimicry in a nonterritorial species such as the House Finch is that a female-like appearance might aid males in gaining extrapair copulations (Hill et al. 1994b). However, because females choose males based on plumage brightness (Hill 1990, 1991, 1994b), it is unlikely that a female-like plumage would be beneficial. The juvenile mimicry hypothesis also can be eliminated because birds in juvenal plumage are present for only a relatively brief period in late spring and summer, at which time there are no apparent reproductive advantages of mimicking a juvenile.

The summer cryptic hypothesis differs from the winter cryptic hypothesis only in invoking breeding-season advantages such as reduced conspicuousness to rival males. To be distinct from the winter cryptic hypothesis, this hypothesis requires a prealternate (spring) molt that makes yearling males less conspicuous (Thompson 1991). Yearling male House Finches in subadult plumage undergo only minimal change in brightness due to feather wear because they have little ornamental plumage to cover and uncover. Moreover, I have seen no evidence of a prealternate molt in male House Finches. From extensive aviary and field studies, I am confident that *griscomi* and populations of *frontalis* from Hawaii, Michigan, and coastal California have no prealternate molt. The prealternate molt suggested by Thompson (1991) for male *frontalis* in Arizona has not been confirmed and probably represents adventitious feather replacement (see Michener and Michener 1940). Thus, there is no support for the summer cryptic hypothesis in the House Finch.

The molt constraint hypothesis proposes that yearling males are unable to obtain definitive breeding plumage either because they lack the energy needed for feather replacement or because the molt sequence to which they are constrained due to past history precludes the acquisition of definitive plumage in their first year. Because yearling House Finches of all subspecies, including those with and without delayed plumage maturation, replace all body plumage in their first prebasic molt, yearling males are subject to no phylogenetic or "energy-to-grow-feathers" constraint. Because ornamental coloration in House Finches is a function of dietary carotenoids during molt (Brush and Power 1976; Hill 1992, 1993b, 1994a), young males in some populations might simply lack the carotenoid pigments needed to pigment ornamental feathers. Evidence suggests, however, that to display a female-like first basic plumage, males have altered their physiology so that carotenoid pigments are not taken up and deposited by follicles as they develop (Fig. 1). Such a change in follicle uptake must be the case for yearling male *griscomi* because they have relatively bright red or orange rumps and have carotenoid pigments circulating in their blood during growth of their first basic plumage (as indicated by reddish plasma during molt; Hill et al. 1994a). Moreover, all male House Finches have access to at least some carotenoid pigments (Inouye,

Hill, and Montgomerie unpubl. data). Birds that are most deficient in carotenoid intake still grow pale yellow feathers, not feathers devoid of pigments (Brush and Power 1976; Hill 1992, 1993b). In the first basic plumage of male *griscomi*, *amplus*, and Great Basin *frontalis*, the upper ventral and crown feathers are not just drab, they completely lack carotenoid pigmentation and have heavy melanin pigmentation along the shaft. Thus, yearling males in populations with delayed plumage maturation follow a developmental strategy that insures that they will have a poorly ornamented first breeding plumage regardless of their carotenoid intake or physiological condition (Fig. 1). Drab House Finch plumage resulting from low intake of carotenoids during molt and drab plumage resulting from a failure of feather follicles to take up carotenoids during molt are fundamentally different phenomena, which is why I make a distinction between an age-specific plumage pattern (delayed plumage maturation) and age-related variation in expression of ornamental coloration (not delayed plumage maturation; Fig. 1).

Only one summer hypothesis generally is consistent with observations of House Finch breeding biology. The summer status signaling hypothesis proposes that yearling males benefit from reduced aggression from adult males by honestly signaling their subordinate status. This hypothesis requires a male-biased sex ratio, females that choose mates based on male attributes versus defended resources, and that yearling males have few opportunities for successful reproduction in competition with adult males (Thompson 1991). House Finches meet all of these conditions. All populations of House Finches have a male-biased sex ratio (Hill et al. 1994b), with the most extreme ratio recorded in populations of *griscomi* (Hill et al. 1994b). Males defend no resources during breeding, and females choose mates based on expression of carotenoid ornamentation, which serves as an honest signal of male quality (Hill 1990; 1991; 1994b, d; Hill and Montgomerie 1994). However, there are no obvious benefits to yearling males of signaling subordinate status during breeding. Because adult males are not territorial, and foraging generally is uncontested away from nests and mates, yearling males need only avoid nests and mates to avoid aggression from adult males (Hill 1993a). However, if yearling males benefited by being near aggressive adult

males and their mates, either by gaining experience or by gaining access to unpaired females, then summer status signaling could work. The hypothesis needs to be tested by presenting males with adult- and subadult-plumaged intruders during the breeding season.

DISCUSSION

Evolutionary patterns and inference about adaptation.—Two hypotheses to explain delayed plumage maturation (Björklund 1991, Chu 1994) suggest that it is incorrect to view the phenomenon as a derived developmental pattern, and, consequently, that most functional and physiological constraints hypotheses are founded on a false assumption. In a comparative study of family and subfamily groupings within nine-primaried oscines, Björklund (1991) found evidence that delayed plumage maturation is the primitive condition and that, rather than species with delayed plumage maturation being developmentally retarded, species without delayed plumage maturation are developmentally accelerated. Moreover, Björklund suggested that delayed plumage maturation in males may be a consequence of selection for retention of drab plumage in females. In a more detailed comparative study, Chu (1994) used a cladistic analysis to show that delayed plumage maturation in Charadriiformes (gulls, terns, and shorebirds) is a result of changes in juvenal plumage superimposed on a primitive molt scheme. Thus, in at least some charadriiforms, subadult plumage simply is an incidental consequence of selection on juvenal plumage and retention of primitive molt patterns. In Chu's taxa, "delayed plumage maturation" has no adaptive explanation. While Chu's study was conducted on nonpasserines, he suggested that the hypothesis might also apply to some passerines.

By looking at changes in plumage maturation among lineages of *C. mexicanus* as well as related outgroups, it is clear that delayed plumage maturation in this species is neither an epiphenomenon as proposed by Chu (1994), a result of selection on female color, nor a retained primitive character (Björklund 1991). The common ancestor of North American *Carpodacus* finches had a female-like first basic plumage, which was lost in the common ancestor of modern subspecies of House Finches. Three House Finch lineages secondarily and independently evolved a female-like first basic plumage. In these lin-

eages delayed plumage maturation is a derived developmental pattern. Moreover, delayed plumage maturation was acquired with retention of the primitive molt sequence, no change in the plumage coloration of juveniles, and no change in female plumage coloration. The change in the first-year appearance of males in these populations results from loss of carotenoid pigmentation and gain of melanin pigmentation along the rachis of feathers on the crown and throat/upper breast (Fig. 1). The characters that changed in *C. m. griseus*, *C. m. amplus*, and Great Basin *C. m. frontalis* were not an incidental consequence of selection on other traits. Thus, we are left with a derived change in the ornamentation of first basic feathers in three lineages and a reasonable expectation that there is some functional basis for the change.

All the more interesting is the observation that in at least two House Finch subspecies (*frontalis* and *ruberrimus*), a small proportion of yearling males shows a female-like first basic plumage. This suggests that rather than delayed plumage maturation being lost entirely in the common ancestors of most extant House Finch populations, genes for a female-like first basic plumage were reduced to low frequency. This being the case, re-acquisition of delayed plumage maturation in a House Finch lineage would require only an increase in the frequency of the trait in the population, not evolutionary novelty. The existence of the trait at low frequencies means that phylogenetic constraints cannot explain the lack of delayed plumage maturation in some populations. Thus, when applied to the House Finch, hypotheses proposed to explain delayed plumage maturation are really addressing changes in gene frequencies in different lineages. Natural or sexual selection are the likely forces to effect such change.

Population comparisons.—Carotenoid-based plumage coloration is costly to produce (Hill 1996). It requires that birds have access to good nutritional resources during molt (Hill and Montgomerie 1994), which in turn requires that birds be healthy and energetic. Only a very few males in any population reach maximum ornament expression (Hill 1993b). Most males achieve average plumage brightness, and some end up in drab breeding plumage (Hill 1993b). In this competitive arena, yearling males generally fare poorly relative to older males, and even in populations in which yearling males have definitive plumage, they are relatively drab

in ornamental coloration (Hill 1992, 1993b). Thus, the evolutionary decision faced by yearling males is whether or not to have *potential* to attain fully pigmented plumage (Fig. 1). If they elect to grow a definitive first basic plumage, the extent to which maximum ornamentation is realized depends on the individual's foraging success and/or physiological condition during molt (Hill and Montgomerie 1994; Fig. 1). When males have delayed plumage maturation, they shut down the physiological mechanisms needed to put carotenoid pigments in feathers (Fig. 1), insuring that their plumage will be poorly ornamented. In a sense, yearling males that follow the latter strategy "redshirt" themselves for their first potential breeding season. (In U.S. college athletics, "redshirt" individuals forego competing in their freshman year; most do so to gain size, experience, and maturity while retaining eligibility to participate.) The question is, why?

Each of the three functional hypotheses for the evolution of delayed plumage maturation that are not contradicted by the biology of House Finches (i.e. the winter cryptic, winter female mimicry, and summer status signaling hypotheses) propose that yearling males are at a competitive disadvantage and that they forsake ornamental plumage to escape the costs of such ornamentation. The models differ in the details of the proposed costs and benefits of well-ornamented first basic plumage, but they are not mutually exclusive. We can summarize the three models into a general hypothesis for House Finches as follows. Yearling males are at a disadvantage in competition with older males over food resources, including carotenoid pigments. Even if they attempt to grow a definitive plumage in their first year, yearling males are likely to have a relatively drab ornamental coloration. With relatively drab plumage, yearling males can expect low reproductive success, because female House Finches use male coloration as a primary criterion in mate choice (Hill 1990, 1991, 1994b). Thus, the benefits of a definitive first basic plumage are likely to be low. Furthermore, there may be substantial costs of definitive first basic plumage. Compared with a streaky brown female plumage, ornamental plumage (even if it is relatively drab) may increase vulnerability to predators. Because plumage coloration is a reliable indicator of male quality, predators may actually target poorly ornamented males over females or well-ornamented

males because they are easier to catch. If so, then a female-like plumage would have obvious benefits. Moreover, a female-like plumage may reduce aggression from males and especially females (Belthoff and Gowaty 1996) in winter and from males in summer.

The really interesting question is why delayed plumage maturation is advantageous for yearling males in some populations but not others. The simple answer is that the evolution of delayed plumage maturation results from shifts in the costs and benefits of definitive first basic plumage. For a more meaningful answer we must deduce how and why costs and benefits of ornamental coloration are changing among populations. One very suggestive pattern is that three of the four populations of House Finches with reduced patches of ventral coloration have delayed plumage maturation. A concentrated changes test indicated that the co-occurrence of reduced patch size and delayed plumage maturation is unlikely to have occurred randomly.

Ornamental plumage coloration entails two very different sorts of costs. One is the cost of garnering, transporting, modifying, and depositing the pigments needed for a showy display (Hill 1996). This is the costs of production and is borne during molt. Other potential costs occur after the ornament has been created; these are the costs of maintaining or carrying the ornament around. The relationship between patch size and delayed plumage maturation probably relates to production costs.

Previously, I proposed that patch size in male House Finches evolved in response to changes in the availability of carotenoid pigments (i.e. to changes in the cost of production). When carotenoid pigments are scarce, males benefit by concentrating available resources, and patch size shrinks (Hill 1994b, d, 1995, 1996). An increase in the scarcity of carotenoid resources (which equates to increased cost of ornament production) would also increase the disparity between yearling and older males in plumage coloration. Thus, production costs may limit the benefits of producing a bright first basic plumage in some populations and shift the balance in favor of waiting until the second basic plumage. Preliminary analyses of the carotenoid content of food consumed by *frontalis* and *griscomi* indicate that male *griscomi* are more carotenoid-limited than male *frontalis* (Inouye, Hill, and Montgomerie unpubl. data). This supports the idea that the production costs of ornaments are

higher in populations with delayed plumage maturation.

In contrast to production costs, maintenance costs are borne after the trait has been produced. In terms of bird coloration, these costs are increased aggression from conspecifics and increased risk to predation. In general, yearling males will be at the greatest disadvantage and bear the highest maintenance cost for ornamental traits in situations where male-male competition is highest. To my knowledge, male House Finches in all populations are monogamous (Hill 1993a). However, there is a male-biased sex ratio in all populations (Hill et al. 1994b). The highest male bias recorded for House Finches was in a population of *griscomi* in which males have delayed plumage maturation. At present, the connection between delayed plumage maturation and sex ratio remains anecdotal, but the prediction could be more rigorously tested in future research.

CONCLUSIONS

I have shown that 3 of 15 lineages of House Finches have evolved delayed plumage maturation independently. Delayed plumage maturation in *griscomi*, *amplus*, and Great Basin *frontalis* is neither a retained primitive character nor the result of selection on another trait, such as timing of molt or female coloration. Thus, delayed plumage maturation in House Finches meets the minimum requirements for a trait that arose as an adaptation through natural or sexual selection. Because much is known about the function and proximate control of plumage coloration in both the breeding and nonbreeding seasons, I was able to assess the applicability of general models for the evolution of delayed plumage maturation in House Finches. Only three models are consistent with what is known about House Finch biology. These models propose that males compete poorly in their first year and that a drab first basic plumage helps them to avoid aggression from conspecifics, or reduces their risk of predation. The co-evolution of delayed plumage maturation and reduced expression of ventral coloration within the House Finch clade supports the idea that the evolution of delayed plumage maturation is tied to the production costs of ornament display. This study provides the best evidence to date that, at least in some species of passerines, delayed plumage maturation is a derived de-

velopmental condition, and that posing evolutionary questions about the origin of delayed plumage maturation is reasonable.

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