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# Evolution of sexual dimorphism in birds: Ecological patterns current selection and ontogenetic variation

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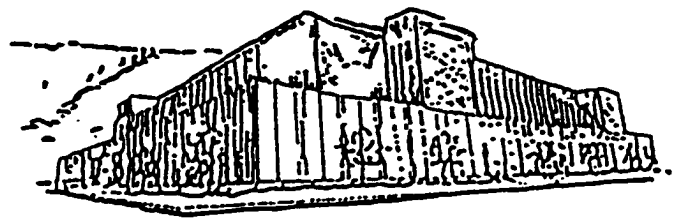

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# EVOLUTION OF SEXUAL DIMORPHISM IN BIRDS:

# ECOLOGICAL PATTERNS, CURRENT SELECTION, AND ONTOGENETIC VARIATION

by

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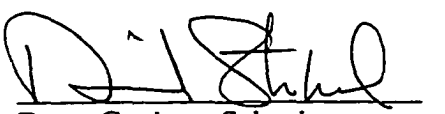

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## ABSTRACT

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Evolution of sexual dimorphism in birds: ecological patterns, current selection, and ontogenetic variation (118 pages).

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Theory suggests that variation in sexual dimorphism can be attributed to the combined effects of differences in sex-specific selection pressures, sex-biased phenotypic and genetic variation, and genetic correlation between sexes. Because each of these factors is a result not only of current, but also of ancestral condition, phylogeny must play a central role in attempts to understand the evolution of sexual dimorphism. I discuss how with an historical approach to the study of sexual dichromatism, it is possible to 1) test between the roles of selection and drift, 2) distinguish between evolutionary constraints and evolutionary forces such as sexual selection, and 3) test specific models of trait evolution. At the population level, evolution of sexual dimorphism is best understood by detailed examination of current selection pressures, ontogenetic patterns, and phenotypic and genetic variation in sexually dimorphic traits. I conducted such a study in a recently established natural population of the house finch (*Carpodacus mexicanus*). I found strong current selection on sexually dimorphic traits, and significant heritabilities of these traits. Current selection on pairing status, overwinter survival, and within-season fecundity acted on similar traits and with similar intensity between males and females, but often in opposite directions, thus favoring sexual dimorphism. To evaluate whether changes in sexual dimorphism are possible in our study population in response to this selection, I examined phenotypic and genetic aspects of ontogenetic variation. I found significant heritable variation in sexually dimorphic traits during ontogeny and low covariation in these traits among and within ages. Both results suggest that developmental patterns are unlikely to exert strong constraints on the evolutionary change in morphology of the house finch. Strong selection on heritable sexually dimorphic traits and low levels of ontogenetic morphological integration in these traits may have accounted for close congruence between current selection and sexual dimorphism in our population, and ultimately contributed to the profound population-level divergence in sexual dimorphism in this species.

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Finally, I thank my family for all their love and encouragement throughout my multi-year and multi-continent journey to rather vaguely defined destinations of an academic career.

It is nice to be done...

# GENERAL INTRODUCTION

Theory suggests that variation in sexual dimorphism can be attributed to the combined effects of differences in sex-specific selection pressures, sex-biased phenotypic and genetic variation, and genetic correlation between sexes. Because each of these factors is a result not only of current, but also of ancestral condition, phylogeny must play a central role in attempts to understand the evolution of sexual dimorphism. In Chapter I, I discuss how with an historical approach to the study of sexual dichromatism, one can test between the roles of selection and drift in changes of sexual dichromatism. Where selection appear to have played a role in the evolution of sexual dichromatism, a phylogenetic perspective may allow to distinguish between evolutionary constraints and forces such as sexual selection. And finally, if sexual selection is invoked, historical data, such as mapping phylogenetic trajectories can help test specific models of trait evolution.

At the population level, evolution of sexual dimorphism is best understood by detailed examination of current selection pressures, ontogenetic patterns, and phenotypic and genetic variation in sexually dimorphic traits. For example, sexual dimorphism is thought to have evolved in response to selection pressures that differ between males and females. Thus, if current selection is important in the evolution and maintenance of sexual dimorphism, the observed sexual dimorphism should be at least partially congruent with patterns of current selection. However, this congruence, or more generally, the population' potential to respond to selection pressure is largely determined by the amount of heritable ontogenetic variation among individuals. Therefore, understanding of growth trajectories and their variation in a population are important for predicting evolutionary change.

In Chapters II and III, I examine current selection pressures, variation in sexual dimorphism, and ontogenetic patterns in a recently established natural population of the house

finch (*Carpodacus mexicanus*). I specifically address the following questions: (1) Is variation in sexually dimorphic traits selectively neutral?, (2) Do sexes differ in intensity of current selection on morphology?, (3) Does ontogeny of sexually dimorphic traits constrain their response to selection?, and (4) Are patterns of sexual dimorphism concordant with current selection pressures? I show in Chapter II that variation in sexually dimorphic traits in both sexes of the house finch had strong fitness consequences. I found that current selection operated with similar intensity on both sexes, but selection often acted in the opposite directions on the same traits of males versus females. I suggest that strong selection of heritable sexually dimorphic traits (Chapter II) in combination with low levels of ontogenetic morphological integration in these traits (Chapter III) may have accounted for close congruence between current selection and sexual dimorphism found in the Montana population of the house finch.

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# CHAPTER I

## VARIATION IN AVIAN SEXUAL DICHROMATISM IN RELATION TO PHYLOGENY AND ECOLOGY: A REVIEW

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Extensive interspecific diversity in sexual dichromatism is assumed to follow from variation in intensity of sexual selection. In turn, the intensity of selection is strongly affected by ecological conditions. Indeed, numerous studies have found general concordance between direction of current sexual selection, ecological pressures, and degree of observed dichromatism. However, because current expression of sexual dichromatism is a result of not only of current selection, but also of ancestral condition, phylogeny must play a central role in attempts to understand the evolution of sexual dichromatism. With an historical approach to the study of sexual dichromatism, one can test between the roles of selection and drift in changes of sexual dichromatism. Where selection appears to have played a role in the evolution of sexual dichromatism, a phylogenetic perspective may allow to distinguish between evolutionary constraints and forces such as sexual selection. And finally, if sexual selection is invoked as an explanation, historical data, such as mapping phylogenetic trajectories can help test specific models of trait evolution.

# INTRODUCTION

Sexual dichromatism is thought to have evolved in response to selection pressures that differ between males and females. In turn, variation in sexual selection pressures may be influenced by ecological conditions. Variation in predation, parasitism, or the distribution and abundance of resources can shift the balance between the benefits of ornamental plumage and the cost of maintaining such traits; such environmental conditions can act on male and female plumage with varying degrees of independence. Ecological factors may also affect the expression of condition-dependent traits in different environments. Thus, diversity of ecological conditions often leads to extensive intra- and interspecific variability in sexual dichromatism.

While correlation between sexual dichromatism and ecological factors has been thoroughly documented (Anderson 1994), major questions remain. First, it is unclear why some groups of bird species show extensive variation in sexual dichromatism while other groups, often apparently subjects to similar variation in ecological conditions, are remarkably conservative in their sexual ornamentation and degree of dichromatism. Second, given high genetic correlation between sexes that is often found in morphological traits (e.g., Lande 1980), we need more information on how fast sexual dichromatism can evolve following an ecological change and whether taxa or trait groups differ in their ability to evolve dichromatism. Third, it is unclear to what degree ancestral dimorphic traits (such as pigment type and pigmentation distribution) and ontogenetic sequences of plumage traits may "set the stage" or bias the evolution of derived dimorphic traits, and whether such constraints differ between species groups. Finally, the role of sexual selection versus other

selective forces, and the roles of various mechanisms of sexual selection in the production of sexual dichromatism are highly debated issues. To address these questions, comparative analyses of sexual dichromatism in relation to ecological pressures should be accompanied by reconstruction of possible phylogenetic pathways of change leading to dichromatism. In this review, I will illustrate this approach by first briefly reviewing a series of studies that documented ecological correlates of variation in sexual dichromatism while statistically accounting for phylogeny. I then will show how reconstruction of evolutionary transformations in sexual traits may allow tests of the importance of processes and mechanisms behind the evolution of sexual dichromatism.

## 1. ECOLOGICAL PATTERNS OF SEXUAL DICHROMATISM: EXAMPLES OF PHYLOGENETIC STUDIES

### 1.1. Sexual dichromatism in relation to latitudinal distribution and migratory tendencies.

Strong association between sexual dichromatism, latitude of breeding, and migratory tendencies is one of the most frequently documented ecological patterns of sexual dichromatism. Higher latitude, migratory, and geographically widespread bird species are more sexually dimorphic than lower latitude, resident species, or species with limited geographic distribution (e.g., Mayr 1942; Grant 1965; Hamilton 1961; Bailey 1978; Scott & Clutton-Brock 1989; Fitzpatrick 1994; Peterson 1996; Omland 1997; Price 1998).

The examples in this section focus on three major explanations for these patterns - (1) geographical variation in patterns of sexual and natural selection pressures, (i.e.,

duration of mate sampling period and the importance of species recognition), (2) operation of non-selective factors, such as genetic drift, in resident, small, and isolated populations, that may be more common at lower latitudes, and (3) a combination of (1) and (2). For example, if intensity of sexual selection is influenced by the amount of genetic variation in populations, then reduced genetic diversity in small populations could reduce intensity of sexual selection and thus sexual ornamentation. These examples illustrate two points. First, knowledge of ancestral state of sexual dichromatism, sex-biased transitions in plumage brightness, and relative frequency of sexual dichromatism transformations across lineages allow us to derive unique testable explanations for latitudinal pattens of sexual dichromatism, and thus to distinguish among competing hypotheses (i.e., selective and non-selective evolutionary factors). Second, intraspecific studies that examine variation in sexual dichromatism in relation to population size (i.e., mainland versus island populations of a species), migratory tendencies (i.e., recently established urban resident populations of a migratory species) may be most informative for understanding of mechanisms behind the interspecific pattern.

Hamilton (1961) documented that in Parulidae and Icteridae, species at lower latitudes were less sexually dimorphic than their relatives at higher latitudes, a pattern that he largely attributed to a decrease in female brightness at higher latitudes. Noting that low-latitude species are more sedentary and maintain longer pair bonds than high-latitude species, Hamilton suggested that duller colouration of females may reduce intra-sexual aggression at the time of pair formation and increased sexual dichromatism could facilitate accurate species and mate recognition. Both of these processes may contribute to the rapid

reestablishment of territories and pair bonds favoured by short northern breeding season (Hamilton 1961). Bailey (1978) investigated latitudinal variation in colouration across 787 passerine species in North and Central America and also found that sexual dichromatism is more pronounced in high-latitude species, but that in dichromatic species female are brighter at higher latitudes. The particular factors behind this pattern remain to be examined. Several studies corroborated Hamilton's (1961) idea that greater dichromatism may be associated with a reduced mate-sampling period. Resident species and species that mate while in winter flocks may have more opportunities and a longer time to evaluate and compare potential mates based on actual performance. On the contrary, migratory species or species with high frequency of extra-pair fertilizations may have to base their mating decisions mostly on morphological traits such as bright plumage, often in the absence of direct comparison among males. These differences in traits used in mate selection decisions, and differences in the information content of condition-dependent traits in a given environment (Slagsvold & Lifjeld 1997) may account for greater sexual dichromatism in migratory species, found even when variation in geographical factors is statistically controlled (Fitzpatrick 1994; Badyaev 1997a).

Alternatively, latitudinal variation in sexual dichromatism could be explained by geographical variation in patterns of natural selection, such as latitudinal differences in the types and kinds of predation (i.e., by latitudinal variation in nest and adult predation, Martin 1995, see 1.3). If latitudinal patterns are mostly produced by changes in female brightness (i.e., females become duller at higher latitudes) we can predict positive correlation between risk of mortality and latitude. Alternatively, background-matching as a

predation-avoidance strategy may favour brighter colours for both sexes at lower latitudes (i.e., in the tropics Bailey 1978). Crucial to understanding the role of natural selection in shaping latitudinal gradient in sexual dichromatism is the phylogenetic information on whether latitudinal transitions in plumage brightness are sex-biased.

Dichromatic taxa tend to have wider geographic distributions than monomorphic taxa (e.g., Price 1998). However, interaction between species' dispersal and competitive abilities, and degree of sexual dichromatism is unclear. Species subject to strong sexual selection may be less ecologically plastic and have high extinction rates (McLain 1993; McLain *et al.* 1995; Sorci *et al.* 1998). Theory suggests that energy allocated towards sexual ornamentation may be unavailable for other traits associated with an organism's ability to track environmental changes, and strong local selection that favours location-specific partitioning of resources may limit species dispersal ability and, thus occupied range (Kirkpatrick & Barton 1997). However, sexually-dimorphic species tend to have wider geographical distributions (Price 1998), and may have greater physiological tolerances compared to monomorphic species (Badyaev & Ghalambor 1998).

Sexual dichromatism may be associated with the ability to tolerate environmental fluctuations when secondary sexual traits under current selection indicate adaptive abilities of an individual, such as an ability to tolerate energetic demands of long migrations and ability to select good quality wintering habitats (Fitzpatrick 1994). Fitzpatrick (1994) suggested that this mechanism is responsible for an association between migratory tendency and sexual dichromatism. She suggested that if sexual dichromatism indicates migratory abilities, then on a macroevolutionary level, a shift from migratory to resident status (such

as in island populations) should be followed by a transition between sexual dichromatism and monomorphism because of the loss of genetic variation in migratory genes and their limited usefulness in indicating phenotypic quality (Fitzpatrick 1994). She suggested that short mate-selection period of migratory species and strong selection for mate and species recognition may favour sexual dichromatism (see also Hamilton 1961). Under this hypotheses, gain in sexual dichromatism following the transition from resident to migratory status is as likely as loss of sexual dichromatism in resident population (Fitzpatrick 1994).

Crucial to the understanding of relative importance of selective and non-selective factors in latitudinal variation in sexual dichromatism is knowledge of the ancestral state of sexual dimorphism in a taxa. For example, sexual dichromatism in Anatidae is most common in species that have wide geographic distribution, breed at higher latitudes, and occur on mainland, while monochromatism prevails among non-migratory, southern species that have restricted, isolated ranges, and often occupy oceanic islands (Scott & Clutton-Brock 1989; Omland 1997 and references therein). Using phylogenetic reconstruction of sexual dichromatism, Omland (1997) showed that sexual dichromatism is an ancestral stage in dabbling ducks. Widespread and migratory species, when settling on islands and becoming isolated, may form monochromatic populations because of genetic drift and inbreeding common in small populations (Peterson 1996; Omland 1997; Burke *et al.* 1998). Both the genetic drift and selective explanation hypotheses predict equal gain and loss in sexual dichromatism state following shifts in migratory tendencies (Fitzpatrick 1994). However, given the complex and integrated nature of sex-limited traits (e.g., complex colour patterns), genetic drift alone would likely lead to biases in the direction of sexual dichromatism loss (e.g., Omland 1997).

Variation in sexual dichromatism may be influenced by interaction of selective and non-selective processes. For example, genetic drift and inbreeding in small island populations lead to low levels of genetic variation. In turn, reduced genetic variation in sexual traits and decreased among-individual variance may lower intensity of sexual selection and reduce sexual ornamentation (Burke *et al.* 1998; Petrie & Kempenaers 1998).

The roles of selective and non-selective processes in the rapid evolution of morphology in peripheral and isolated population is a debated issue (e.g., Mayr 1963, Garcia-Ramos and Kirkpatrick 1997). One approach suggests that gene flow into peripheral populations from the central part of the geographical range may prevent the local populations from evolving to the local optimum and thus facilitate strong directional selection. Providing significant heritability of traits, such selection can cause rapid morphological changes under conditions of reduced gene flow (e.g., Garcia-Ramos and Kirkpatrick 1997). Another approach argues that random genetic drift in isolated populations is enough to produce morphological changes (Mayr 1963). While random genetic drift may be not be a sufficiently strong force to produce large morphological changes (Lande 1980), it may be enough to account for the loss of complex, integrated, and sex-limited traits, such as plumage coloration (see above). Thus, the knowledge of phylogenetic relationship among populations in addition to the sequence of change in dichromatism states is crutial to the understanding of the relative importance of selective and non-selective processes in evolution of sexual dichromatism.

**1.2. Sexual dichromatism in relation to ecological factors affecting mating systems and parental care.**

Variation in sexual selection arising from variance in male reproductive success and parental investment can exert strong selection on sexual dimorphism (Payne 1984; Kirkpatrick & Ryan 1991; Williams 1992; Anderson 1994; Owens & Bennett 1997). For example, interspecific variation in the extent to which each sex contributes to parental care may influence sexual dimorphism because of the possible effects of parental investment on sexual selection (Trivers 1972). Thus, variation in ecological determinants of parental investment should cause variation in sexual dimorphism (Anderson 1994). Strong selection on male plumage ornamentation resulting from high variance in male reproductive success should push male morphology farther from a what is optimal under natural selection. If females obtain less benefit from plumage ornamentation then the result is increased sexual dichromatism. Across mating systems, variance in male reproductive success is expected to be higher in polygynous than in monogamous species and thus we predict greater sexual dichromatism in polygynous mating systems.

However, while close association between mating systems and ecological conditions is well established in birds (e.g., Owens & Bennett 1997 and references therein), direct association between mating systems and sexual dichromatism is rarely found. The examples in this section address this apparent paradox and illustrate three important points. First, the expected association between mating system and sexual dichromatism is often documented only when mating systems are clearly defined and sexual dichromatism is partitioned into components such as carotenoid-, melanin, or structurally based dichromatism (Payne 1984;

Scott & Clutton- Brock 1989; Møller & Birkhead 1994; Owens & Bennett 1994, 1995, 1997, 1998; Møller & Cuervo 1998). Second, phylogenetic information on sex-biased transitions in plumage brightness is very useful in drawing our attention to what exactly needs to be explained - change in male colouration, change in female colouration, or both. Recognition of the need to know which sex is changing appearance facilitated generation of testable hypotheses of association between mating systems, plumage brightness, and sexual dichromatism (Scott & Clutton-Brock 1989; Jones & Hunter 1993; Irwin 1994; Badyaev 1997a; Owens & Bennett 1997 1998; Burns 1998). Furthermore, a hierarchical approach to phylogenetic studies of life histories and mating system allows studies of temporal concordance between changes in plumage versus changes in mating systems (Owens & Bennett 1995, 1997). Finally, knowledge of transition sequences in mating system and ornamentation in both sexes were instrumental in advancing our understanding sexual dichromatism variation in lekking species.

In one of the first studies of association between mating system and sexual dichromatism, Crook (1964) showed that the monogamous weavers (Ploceidae) were monomorphic, while polygynous species were dichromatic. He attributed the pattern to the distribution of food and nesting habitat (Crook 1964). However, most recent studies have found that the association between mating system and dichromatism is not straightforward. Indeed, most passerines are sexually dimorphic regardless of their social mating system; polygynous European passerines are not more often sexually dimorphic in plumage than monogamous species (Møller 1986). Despite their polygynous mating system, many species of hummingbirds (Trochilidae) are monomorphic with female colouration showing the most variation (Bleiweiss 1992).

In one of the few studies that documented association between mating systems and sexual dichromatism, Scott and Clutton-Brock (1989) examined variation in plumage in 146 species of Anatidae. They carefully defined mating systems based on frequency of pairing, duration of pair bond, and partitioning of parental care, and found that sexual dichromatism was greater in species with frequent pair formations and distinct parental roles. Variation in male plumage brightness was most strongly correlated with frequency of pairing, paternal care, and nest dispersion (i.e., potentially with mating opportunities), while female brightness varied the most with nest placement and nesting habitat features (i.e., with predation risk) (Scott & Clutton-Brock 1989). These results corroborated Kear's (1970) findings that in the majority of monochromatic species of waterfowl both sexes shared parental duties, while in most dimorphic species females raised the young alone. Similarly, in passerines, males of monochromatic species were more likely to participate in nest building (Soler *et al.* 1998), and share incubation with females than males of dichromatic species (Verner & Willson 1969). Extensive paternal care is associated with both reduced mating opportunities for males, and greater predation risk. To distinguish between roles of mortality and mating opportunities in the association between sexual dichromatism and mating systems, it is necessary to know whether variation is due to male or female colouration changes. Owens and Bennett (1994) documented that adult mortality closely covaried with parental care, but not with sexual dichromatism across 37 Palearctic bird species (but see below). Their results suggested that the often-documented association between sexual dichromatism and parental care may be caused not by mortality due to parental care, but by variation in mating opportunities among species with different amount

of paternal care. Among socially monogamous passerines, variation in male plumage brightness was associated with differences in the frequency of extra-pair paternity; species with greater levels of extra-pair paternity had brighter males and greater sexual dichromatism (Møller & Birkhead 1994).

Owens & Hartley (1998) partitioned overall sexual dimorphism into components across 73 bird species and found that different types of dimorphism are affected by different selection pressures. Sexual dimorphism in size was strongly associated with variation in social mating system and parental roles (see also Björklund 1990, 1991; Webster 1992), while sexual dichromatism in plumage was most closely associated with levels of extra-pair paternity (see also Møller & Birkhead 1994), and more weakly with sex differences in parental care (e.g., Verner & Willson 1969, see below). Given distinct patterns of covariation among different types of dimorphism, it is interesting to examine evolutionary lability of various types of dimorphism. For example, frequency of extra-pair paternity often varies widely among different populations of the same species (Petrie & Kempenaers 1998). This variation may be more easily reflected in the evolutionary labile types of traits, such as carotenoid- based colours (Hill 1996a; Gray 1996; Hill & Brawner 1998; Badyaev & Hill, 1999; see 2.1). On the contrary, body size and dimorphism in ornamentation may be more phylogenetically constrained and morphologically integrated, and therefore vary only with most fundamental distinctions among mating systems.

In a series of comparative studies Owens and Bennett (1995, 1997, 1998) showed that patterns of diversification in mating systems and life history strategies are strongly historically nested. They argued that phylogenetically distant taxa may have converged on

similar mating systems despite different evolutionary histories. Thus, phylogeny and current selection may differentially contribute to variation in mating system across species. Ancient evolutionary events, such as ancestral changes in partitioning of parental care, nesting, and feeding habits may bias the predicted response of the lineage to current ecological conditions (Owens & Bennett 1997). This historical bias of taxa in adapting only a certain range of mating patterns, could also limit variation in sexual dichromatism, and more importantly, account for lack of contemporary association between sexual dichromatism and mating systems. Experimental manipulation of current selection pressures would induce predictably different changes in a mating system of certain taxa (such as propensity to desert mates if local mate availability is increased), depending of evolutionary history of the taxa (Owens & Bennett 1997).

Ecological determinants of paternal care are expected to cause variation in sexual dimorphism (Anderson 1994). Male parental investment differs with variation in ecological factors such as climate or resource (e.g., foraging or nesting sites) distribution. For example, colder nest microclimate and spatial separation of nesting and feeding resources (as found at high elevations) was commonly associated with greater male care (Badyaev 1997a; Badyaev & Martin, unpubl. manuscript). Thus, in monogamous species, the intensity of sexual selection should covary with ecological factors associated with the elevation of a species' breeding. This association was documented across 126 extant species of Cardueline finches; species occupying lower elevations were more sexually dimorphic in plumage than species at higher elevations, and the altitudinal variation was largely due to increased brightness of male plumage at lower elevations (Badyaev 1997a). Given that

altitudinal variation in sexual dichromatism was mostly contributed by changes in male plumage, further hypotheses and tests of potential cost of greater paternal care at high elevations, greater costs of bright male plumage production (i.e., diet and molt) and maintenance (i.e. variation in predation) were advanced (Badyaev 1997 ab; Badyaev & Martin, unpubl. manuscript).

Irwin (1994) examined variation in sexual dichromatism across Icterinae and reported that sexual dichromatism covaried with mating system and that polygynous species were more sexually dichromatic. Irwin found that association between sexual dichromatism and mating system was due largely to changes in female plumage; female colouration was more evolutionary labile than male colouration. Irwin suggested that variation in sexual dichromatism in Icterinae results from social selection on females rather than sexual selection on males. Selection on female by males to display brighter plumage should be greater in monogamous systems (Moreau 1960; Irwin 1994). This selection and more intensive female-female interactions may account for association between female plumage brightness, sexual dichromatism, and the mating system (Johnson 1988; Trail 1990; Bleiweiss 1992; Hill 1993a; Irwin 1994). These studies emphasized the importance of distinguishing between monomorphism when both sexes are bright and monomorphism where both sexes are dull. "Dull" monomorphism could arise from monogamous mating systems where mates have the extended opportunity to evaluate each other's relative quality based on performance and direct comparisons (e.g., mating while in winter flocks), and where selection pressures are similar between sexes. Examples could include monomorphism of non-migratory species and high-elevation species (Fitzpatrick 1994;

Badyaev 1997a). "Bright" monomorphism could result from similar selection pressures acting on the sexes and should be prevalent in monogamous mating systems with short mate-sampling periods (Jones & Hunter 1993; Irwin 1994).

Sexual dichromatism should be strongly associated with lek breeding, because variance in male reproductive success and hence sexual selection is assumed to be a very strong force in this mating system (Darwin 1871; Payne 1984; Kirkpatrick 1987). However a series of studies documented that lekking species are not more likely to be sexually dimorphic in plumage (e.g., Payne 1984; Höglund 1989). Studies of association between lekking and sexual dichromatism illustrate two points. First, it is important to know the sequence of transitions, i.e. whether shift to or from lekking behaviour precedes the change in sexual dichromatism. For example, if it is suggested that sexual dichromatism has evolved as a result of transition to lekking, it needs to be shown that shift to lekking resulted in sex-biased selection on plumage colouration. Second, examination of current selection in both sexes is needed to generate hypotheses about predicted patterns of colour variation in relation to lekking. Third, phylogenetic information about ancestral state of sexual dichromatism and plumage brightness in both sexes is most useful. For example, transition between monomorphic dull to monomorphic bright states is expected under strong correlated response of female characteristics to selection on males prior to evolution of sex-limited variation (Lande 1980). Increased risk of predation on leks may explain changes to monomorphic dull from sexually dimorphic or monomorphic bright as a result of transition to lekking (Bleiweiss 1997). Bleiweiss (1997) examined covariation of sexual dichromatism and plumage brightness with occurrence of lekking behaviour across 415 bird

species. Analysis of evolutionary transitions of plumage brightness in both sexes allowed him to conclude that in addition to sexual selection, predation risks and foraging behaviours associated with lekking are likely to constrain plumage variation among lekking species (Bleiweiss 1997).

### 1.3. Sexual dichromatism in relation to ecological factors affecting mortality and parasitism.

One explanation for sexual dichromatism is that it evolved through differential signaling of sexes to predators and selection for less conspicuous females (Wallace 1889; Baker & Parker 1979; Butcher & Rohwer 1989; Götmark 1992, 1993; Götmark *et al.* 1997; reviewed in Götmark 1998). The hypotheses of association between mortality and sexual dichromatism have been tested in two ways. First, researchers examined across-taxa variation in sex differences in mortality looking for evidence for sexual ornamentation cost. These studies tested the costs of sexual selection without the confounding effects of intraspecific variation in individual quality. However, most of the studies in this group have focused on variation in adult mortality, while dimorphism-induced variation in juvenile mortality is largely unexamined (e.g., Owens & Bennett 1994). Second, researchers have attempted to isolate factors or behaviours that affect mortality associated with sexual dichromatism. These studies looked for correlations between predation and display and mate-selection behaviours, participation in parental care (i.e., incubation, nestling provisioning), and plumage brightness and dichromatism. The inference from these studies is greatly strengthened by examining changes in sexual dichromatism as a consequence of

changes in nesting or displaying habits, or by applying a hierarchical approach to changes in sexual dichromatism, life history strategies, and mating systems.

Sexual dichromatism in birds is generally thought to arise from sexual selection favouring conspicuous colouration in males, although natural selection (e.g., predation) is thought to ultimately limit conspicuousness (Darwin 1871; Fisher 1930; Hingston 1933; Kirkpatrick *et al.* 1990; Promislow *et al.* 1992, 1994; Götmark *et al.* 1997). Alternatively, bright colouration may be favoured by predation because it advertises that a prey is unprofitable and degree of sexual dichromatism may be a direct function of the difference between the sexes in their profitability to a predator (Cott 1946; Baker & Parker 1979; Butcher & Rohwer 1989; Götmark 1992, 1993, 1994, 1998). Promislow *et al.* (1992, 1994) have examined variation in sex-specific mortality schedules as consequences of the costs of sexual ornamentation in passerines and waterfowl. They suggested that female mortality may constrain the upper limit of sexual dichromatism in species by limiting the maximum mortality rate of males. In turn the brightness of males could be further constrained by additional mortality associated with bright plumage and more intensive sexual competition (Promislow *et al.* 1992, 1994; Promislow 1996). Similarly, Götmark *et al.* (1997) showed that predation on adult chaffinches (*Fringilla coelebs*) exerts greater pressure on female colouration than on male colouration, and could ultimately lead to variation in sexual dichromatism. In cardueline finches, variation in sexual dichromatism and plumage brightness in both sexes closely corresponded to variation in life history traits; sexual dichromatism was negatively correlated with fecundity because the association between plumage brightness and fecundity was different for males and females. Male plumage brightness was negatively correlated with clutch size and numbers of broods, but female brightness was positively correlated with clutch size across finches (Badyaev 1997b).

Examining variation in sex-specific costs of plumage brightness along an altitudinal gradient, Badyaev (1997b) found that the association between sexual ornamentation and fecundity was more similar between sexes in high-elevation species than in low-elevation species. Associations among plumage brightness and life history traits changed more with altitude for males than females, which is consistent with higher altitudinal variation in male plumage brightness in finches (Badyaev 1997a). Monomorphism of high elevation species may be caused by more similar selection pressures caused by equal sharing of parental care between sexes at higher altitudes. Badyaev & Martin (unpubl. manuscript) suggested that elevational variation in sexual dichromatism (Badyaev 1997a) is due to both higher adult mortality at lower elevations and reduced juvenile mortality at higher elevations (Badyaev 1997bc). While low elevations favour increased and more elaborated sexual ornamentation, development of such traits commonly results in reduced juvenile survival (Owens & Bennett 1994). Thus, prevalence of monomorphism across high elevation species could contribute to higher juvenile survival (Badyaev 1997c).

While a number of studies clearly established the relationship between sexual dichromatism and mortality, two problems persist: (1) the specific factors (e.g., variation in mating and parental behaviours) behind this relationship remain to be examined, and (2) studies that would allow directional hypotheses of causality are needed. Below I will review some factors that may mediate an association between sexual dichromatism and mortality.

If nest predation constrains brightness (i.e., Wallace 1889; Baker & Parker 1979; Shutler & Weatherhead 1990; Johnson 1991), female brightness should vary with nest predation, particularly in species where only the female incubates eggs and broods young. In contrast, male brightness may not vary as strongly with nest predation because of the reduced time males spend at the nest. Sexual dichromatism has been argued to vary inversely with nest predation (Scott &

Clutton-Brock 1989; Shutler & Weatherhead 1990; Johnson 1991), although the association was never directly examined. By separately examining male and female plumage across Parulidae and Carduelinae, Martin & Badyaev (1996) found that female plumage brightness varied among nest heights. They found that female plumage brightness was negatively correlated with nest predation and the pattern of males and females was distinctly different. These results suggested that nest predation may place greater constraints on female than male plumage brightness, at least in taxa where only females incubate eggs and brood young. Martin & Badyaev (1996) found that female plumage patterns vary at least partly independently of male patterns, emphasizing the need to consider both female and male plumage variation in tests of plumage dimorphism. In warblers and finches, sexual dichromatism differed between ground- and off-ground-nesting species, but the relationship between plumage dimorphism and nest predation was positive rather than negative (Shutler & Weatherhead 1990; Johnson 1991). Moreover, differences in sexual dichromatism between ground- and off-ground-nesting birds result only partially from decreased male brightness (Shutler & Weatherhead 1990; Johnson 1991) and is contributed mostly by the increase in female brightness in ground-nesting birds related to their reduced risk of nest predation as compared to shrub-nesters (Martin & Badyaev 1996). Effects of nest predation on sexual dichromatism are most evident when one separately examines sexual dichromatism in different body parts. For example, dichromatism of rump but not breast strongly covaried with nest placement across Carduelinae (Badyaev 1997a). Variation in parasite prevalence across nesting and foraging strata could also contribute to vertical stratification of sexual dichromatism and plumage brightness (Hamilton & Zuk 1982; Garvin & Remzen 1997)

The importance of current variation in nesting biology to variation in sexual

dichromatism was challenged by the view that mortality variation is almost entirely due to ancient evolutionary events, and that current variation in nesting and feeding habits is largely irrelevant to current avian life history strategies (Owens & Bennett 1995). If ancient and hierarchically-nested evolutionary diversifications (e.g., changes in nest placement) were associated with changes in sexual dichromatism, we should see concordant and similarly historically-nested patterns of divergence in sexual dichromatism. However, other studies suggested that large-scale diversification in life histories are produced by more recent ecological changes (e.g, Martin & Clobert 1996). These examples illustrate that to properly test the association between nesting and foraging habits and sexual dichromatism one must examine historical transitions in sexual dichromatism and plumage brightness in relation to changes in nesting strata or parental behaviour (e.g., Owens & Bennett 1994, 1997).

**1.4. Sexual dichromatism in relation to sensory characteristics, physical features of habitat, and diet**

Ecological change associated with exploitation of new habitats is often accompanied by changes in mate recognition traits. These novel traits may evolve as a result of either preexisting sensory biases within lineages or characteristics of new environments that make certain traits more easily perceived (Schluter & Price 1993; Price 1998; Endler and Westcott 1998). Physical characteristics, such as abrasiveness, UV radiation, and thermoregulation requirements could ultimately constrain sexual dichromatism by favouring certain pigmentation and patterns of colouration (Burtt 1989). The examples in this section emphasize three points. First, comparative studies need to show that colour patterns are indeed preceded by habitat shifts (e.g., Marchetti

1993). Second, it needs to be shown that divergence into different habitats promotes divergence in sexually selected traits (Schluter & Price 1993; Barraclough *et al.* 1995; Badyaev and Leaf 1997, Price 1998; Møller & Cuervo 1998). Finally, interactions among habitat characteristics, display behaviour, and plumage colouration have to be examined on a macroevolutionary scale (Endler & Théry 1996; Irwin 1996).

Physical features of habitats may favour certain plumage pigmentation and thereby constrain distribution of other types of pigments or structural colours. For example, birds living in more abrasive environments have more melanin in their plumage (Burtt 1989) and the body surfaces that are more vulnerable to wear and abrasion have a higher proportion of melanin pigmentation (Fitzpatrick 1998). In turn, the presence of melanin may affect distribution of structural colours (reviewed in Prum 1998) and carotenoid-based pigmentation (references in Savalli 1995). High concentration of pigments may protect birds from UV radiation; higher sexual dichromatism in tanagers breeding at higher elevations (Brush 1970) may be attributed to this factor. Marchetti (1993) has shown that colour, colour patterns, and sexual dichromatism across species can be related adaptively to the light environment, where bright species occupy dark habitats. Götmark and Hohlfält (1995) found that male and female pied flycatchers (*Ficedula hypoleuca*) are about equally difficult to detect and therefore male plumage may be an example of disruptive crypsis.

Price (1996) examined variation in sexual dichromatism across finch species, and found that drier and more open habitats had a lower proportion of dichromatic species than did closed and moist habitats. Similarly, cardueline finches dwelling in closed habitats were more sexually dimorphic in plumage than related species in open habitats (Badyaev 1997a). However, plumage dichromatism in finches is associated with solitary nesting and most open habitat species are semi-colonial (Badyaev 1997a). Thus, habitat influences may be confounded by effects of nest

dispersion. Price (1996) suggested that finches in the closed habitats may breed at higher densities and thus have increased potential for extra-pair paternity (Møller & Birkhead 1993, but see Westneat & Sherman 1997). The association between habitat type and sexual dichromatism documented by Price (1996) could be confounded by differences in latitudinal distribution of finches, migratory tendencies, and differences in predation and parasitism risk (see 1.3).

Endler & Théry (1996) and Endler and Westcott (1998) reported extremely high degree of ambient light specificity in display behaviours in several tropical species. However, it is unclear whether such behaviours follow existing colouration patterns to maximize its function, or the colouration patterns evolve as a result of the light environment or display behaviours (Endler & Théry 1996). Phylogenetic analysis of transition sequence among light environments, behaviour, and plumage colouration patterns will further our understanding of the roles behaviour, ecology, and phylogenetic constraints play in the evolution of colouration patterns and sexual dichromatism.

Differences among habitats and geographical locations in food composition may influence sexual dichromatism (Abbot *et al.* 1977), especially in the diet-dependent components of sexual dichromatism (Hill 1993b, 1994b). For example, geographical variation in intensity of red colouration among populations of House Finches (*Carpodacus mexicanus*) was influenced by local access to carotenoids (Hill 1993b). However, female House Finches from all locations preferentially paired with brighter males (Hill 1994b; see 2.4 below).

## 2. EVOLUTION OF SEXUAL DICHROMATISM: EXAMPLES OF PHYLOGENETIC STUDIES.

### 2.1 Historical variation in complexity and components of sexual dichromatism.

Utilization of phylogenetic methods together with a consideration of the source of plumage colouration (melanin, carotenoid, or structural) as well as developmental constraints and pathways

allow testing of the signal content of plumage colours and a better understanding of the roles that developmental and phylogenetic constraints play in evolution of sexual dichromatism. The examples in this section illustrate three points. First, different components of sexual dichromatism (i.e., carotenoid or melanin-based pigmentation, and structural colouration) have different evolutionary lability and distinct signal functions in behavioural interactions. Consequently, sexual dichromatism in these different types of colouration shows distinct patterns of covariation with selection pressures. Second, phylogenetic information is essential for an understanding of the sequence of transitions in complex sexual traits (i.e., colour patterns and colour combinations) and hence constraints on plumage colour patterns. Finally, traits may differ in the amount of sex-limited genetic variance or the information they provide in a given environment (Møller & Pomiankowski 1993; Marchetti 1998). These differences may cause biased evolution of sexual dichromatism in such traits. Phylogenetic methods allow us to understand the direction and magnitude of change in these traits by reconstructing their ancestral states.

In a series of comparative studies Hill (Hill 1994a, 1996a; Badyaev & Hill 1999) suggested that because carotenoid-based plumage colouration is more dependent on condition and less constrained developmentally than is melanin-based colouration, variation in sexual dichromatism should be driven more by changes in carotenoid-based colouration between males and females than by changes in melanin-based colouration. Badyaev and Hill (1999) examined this hypothesis and found that across all cardueline species (1) carotenoid-derived colouration has changed more frequently than melanin-based colouration; (2) in both sexes increase in carotenoid-based colouration, but not in melanin-based colouration, was strongly associated with increase in sexual dichromatism, and (3) sexual dichromatism in carotenoid-based colouration contributed more to overall dichromatism than sexual dichromatism in melanin-based plumage. These results corroborated previous findings that in finches, the degree of sexual dichromatism of

carotenoid-based plumage colouration increased with plumage redness, but not with amount of black pigmentation (Hill 1996a).

These findings supported the results of Gray's (1996) analyses of male plumage variation across all North American passerines. Gray found that the amount of carotenoid pigmentation in male plumage was positively associated with overall dichromatism, while the amount of melanin and structural colouration in male plumage was not related to overall dichromatism. Analyzing patterns of variation across different clades of passerines, Gray (1996) noted that carotenoids appear to be used as ornamental signals by granivorous and insectivorous taxa (for which they are present in the diet but not overly abundant), but not used by frugivorous (for which they are overly abundant in the diet) or carnivorous taxa (for which they are rare in the diet). Consequently, Owens & Hartley (1998) found that carotenoid-, melanin- and structurally-derived sexual dichromatism do not show similar patterns of covariation with social mating systems, parental roles, and ecological conditions.

Phylogenetic methods were instrumental in revealing the roles of developmental constraints in the expression of colours, and especially of colour patterns. The similarity of colouration patterns and pigment distribution across a wide range of avian species implies common developmental mechanisms and constraints. In their comprehensive study of the evolution of colours and colour patterns in *Phylloscopus* warblers, Price & Pavelka (1996) showed that component elements of melanin-distribution patterns were repeatedly gained and lost during evolution. Price & Pavelka (1996) suggested that once evolved in some distant ancestor, the pattern of colouration may persist in a lineage (even when not expressed in the current phenotype), and can quickly reappear after loss given favourable selection pressures. Moreover, further selection may bias evolution of other components of the phenotype in the context of the patterns already present (i.e., overlay of different pigments, display postures emphasizing colouration pattern, etc.)

(Price & Pavelka 1996). Thus, identification of evolutionary sequences of colouration patterns is essential to the study of sexual dichromatism (Price & Pavelka 1996).

Schluter & Price (1993) noted that selection for sexual dimorphism will favour traits with a greater amount of sex-limited genetic variance, greater relevance to current condition, or easier detection. Therefore, under certain conditions, these traits (such as songs, various displays) will be more likely to invade a sexually dichromatic population, and thus bias evolution and establishment of other sexually dimorphic traits. For example, predation may limit variation in sexual dichromatism in Parulinae warblers, and song complexity may replace plumage characteristics as the target of sexual selection (Shutler & Weatherhead 1990). Similarly, Bailey (1978) suggested that structural colours are favoured by selection in the tropics because structural colours are easily changed by behavioural displays depending on variable light conditions in closed and dark tropical habitats (see also Endler & Théry 1996 and references therein).

Phylogenetic analyses of sexual dichromatism variation allow the identification of taxa groups that (1) retained sexual dichromatism after the termination of selective forces that caused then, and (2) show no variation in sexual dichromatism despite changes in selective pressures assumed to cause variation in sexual dichromatism (e.g., Sheldon & Whittingham 1997). Such biases in sexual dichromatism variation could be a result of phylogenetic constraints (McKitrick 1993; Miles & Dunham 1993). Potential causes of such biases in evolution of sexually dimorphic traits could include: reduced additive genetic variance and limited phenotypic variation, close genetic covariance among components of sexual dichromatism, phenotypic plasticity that could reduce selection pressures on sexual dichromatism (such as behavioural modification of displays), stabilizing selection in which a trait is maintained by selection against alternative phenotypes, and pleiotropy (see reviews in Miles & Dunham 1993; Edwards & Naeem 1989; McKitrick 1993; Leroi *et al.* 1994). Sheldon and Whittingham (1997) noted that phylogenetic methods may be used

to distinguish sexual dichromatism variation due to current stabilizing selection (i.e. selection based on current ecological conditions) from phylogenetic conservatism caused by other evolutionary forces (Miles & Dunham 1993; Leroi *et al.* 1994).

**2.2. Phylogenetic inferences about origin of sexual dichromatism.**

Sexual dichromatism arises from sex-limited expression of genes or from selection acting on traits with sex-limited or sex-biased genetic variation (Lande 1980). However, once sex-limitation is established, variation in sexual dichromatism can be affected by both non-selective and selective factors (Anderson 1994). The examples in this section illustrate that phylogenetic methods can be used to distinguish among variation in sexual dichromatism produced by various evolutionary processes (e.g., Sheldon & Whittingham 1997)

Sexual dichromatism can evolve if there is sex-limited genetic variation or if sex-limited expression of some genes is favoured by sex-biased selection pressures. The sources of sex-linked variation could range from mutations on sex-chromosomes (Hutt 1949) to sex-limited expression of genes (Lande 1980). Several studies suggested that expression of sex-limited gene effects (such as colour or specific pattern) may be dependent on sex-specific hormonal balance (references in Owens & Short 1995). In their review, Owens & Short (1995) provided evidence that expression of secondary sexual colours in males is controlled by the absence of estrogen rather than the presence of testosterone. Thus, if sexual dichromatism is determined by sex-limited expression that is pleiotropically mediated (i.e., through hormonal balance), we can predict (1) easier and faster loss than gain of male secondary sexual colours, and (2) more frequent phylogenetic transition from dichromatism to monochromatism than from monochromatism to dichromatism (e.g., Price & Birch 1996; Omland 1997; see 2.3). If sexual dichromatism results from mutations on sex chromosomes that are magnified by selection favouring dichromatism, no directional biases

between loss and gain of sexual dichromatism are expected.

Once sex-limitation is established, genetic drift, selection, and genetic interactions could influence the evolution of sexual dichromatism. On a macroevolutionary scale, genetic drift is not expected to produce consistent convergences of sexual dichromatism with other factors (e.g., ecological conditions) across lineages (Leroi *et al.*, 1994; Sheldon & Whittingham 1997). On the contrary, if sexual dichromatism evolved in response to selection, change in sexual dichromatism should follow a certain sequence, e.g., transitions in environments or behaviours should be followed by transitions in traits. Pleiotropic interactions should produce multiple and simultaneous effects on sexually-dimorphic traits (Sheldon & Whittingham 1997 and references therein; see 2.3).

**2.3. Phylogenetic reconstructions of plumage dichromatism.**

*2.3.1. Phylogenetic reconstruction of sexual dichromatism transformations* —. The evolution of sexual dichromatism requires sufficient additive genetic variance for a response to selection. Initial response to change in selection pressures may be limited because of high genetic correlation between the sexes (Lande 1980). One way to explore whether the amount of additive genetic variance biases evolution of sexual dichromatism is to examine the relative frequency of changes between monomorphism and dimorphism, as well as the variance in rates of evolution of male and female plumage traits (e.g., Price & Birch 1996). The examples discussed in this section suggest that the evolution of sexual dichromatism is largely unconstrained by the lack of genetic variance and that evolutionary losses of sexual dichromatism are more likely that gains. It is suggested that genetic drift and inbreeding in small parapatric populations, combined with biases towards loss of sex-limited and complex characters have probably caused repeated loss of sexual dichromatism in birds (Peterson 1996; Omland 1997; Price 1998).

Price and Birch (1996) estimated the frequency of evolutionary transitions in dichromatism

across 5,298 passerines and found that (1) sexual dichromatism evolved independently and numerous times, indicating that the evolution of sexual dichromatism was largely unconstrained by an absence of genetic variance, and (2) transitions from sexual dichromatism to monomorphism were more likely than transition from monomorphism to sexual dichromatism. Omland (1997) reached similar conclusions in his study of Anatidae. He showed that (1) sexual dichromatism is an ancestral trait, and (2) evolution of sexual dichromatism was biased towards loss of dichromatism. Similarly, Burns (1998) found that tanagers (Thraupidae) descended from an ancestor that was dichromatic with colourful males and dull females. These findings are corroborated by Peterson (1996) study in which he examined geographical variation in sexual dichromatism in 158 species of birds representing 43 families and concluded that sexual monomorphism with bright males and dull females is a likely ancestral stage in birds.

*2.3.2. Phylogenetic reconstructions of transformations in male and female plumage –.* Several phylogenetic studies addressed whether transition of dichromatism states are due to male or female evolution. Examining the relative frequency of bright and dull monomorphism, and sexual dichromatism, Peterson (1996) concluded that the evolution of female plumage contributed to the evolution of sexual dichromatism as often as did evolution of male plumage. Changes in male and female plumage contributed equally to variation in sexual dichromatism, and males were five times more likely to lose bright plumage than to gain it, while in females the trend was the opposite (Peterson 1996). The fact that loss of sexual dichromatism occurs in both directions (to "dull" and to "bright" monomorphism) makes it less likely that selection can explain the majority of cases, leading Peterson (1996) to propose genetic drift as a potential evolutionary force behind variation in sexual dichromatism (see also Björklund 1990, 1991). Björklund (1991) documented that in two lineages of blackbirds, sexual dichromatism resulted from a loss of female brightness rather than a

gain in male brightness. Similarly, Irwin (1994) found that changes in female plumage were more frequent than changes in male plumage, and that females were brighter in monogamous than in polygynous mating systems in Icterinae. These results corroborated Moreau (1960) observation that an association between plumage brightness and mating systems is mostly due to variation in female plumage. Using phylogenetic reconstructions, Burns (1998) found that in tanagers, transitions in sexual dichromatism where only males or only females changed were more common than transitions where both sexes changed. Female plumage brightness changed at least twice more often than male plumage (Burns 1998).

**2.4. Sexual dichromatism in relation to mechanism of sexual selection.**

Phylogenetic analyses provide a powerful way of testing predictions of different sexual selection mechanisms. The examples in this section illustrate two points. First, hypotheses of sexual selection mechanisms can be tested by experimental examination of the congruence between current male phenotype and current female preferences, as well as by examining the general concordance between phenotypic appearance and current ecological conditions. Second, different selection models make distinct predictions of diversification patterns, hierarchical complexity, and convergence among lineages, thus allowing strong inferences about sexual selection mechanisms.

Hill (1994b) proposed that in the absence of changes in female preferences or viability costs, the sensory exploitation and the runaway models (reviewed in Anderson 1994) cannot account for reduction in sexually selected trait. Specifically, in the runaway model of sexual selection male appearance closely covaries with female preference, while under indicator models, females display preferences for extreme development of traits, while males are constrained (i.e., by physiological and energetics costs) in the ability to develop more elaborated ornaments (Hill 1994a, 1996a). Examining these predictions in geographic variation in male appearance and female

preference across subspecies of the House Finch, Hill (1994a) concluded that the models of "non-adaptive" (e.g., runaway) mate choice can be rejected. In the study of the delayed attainment of ornamental breeding plumage by young males (i.e. delayed plumage maturation), Hill (1996b) documented that selection acting on physiological trade-offs (size and colour of the patch in the House Finch) could cause concordant evolution of the expression of the ornamental trait in adults and the developmental speed at which the trait is acquired.

Recent studies of bowerbirds (Ptilonorhynchidae) by Kusmierski *et al.* (1997) and manakins (Pipridae) by Prum (1994, 1997) showed that patterns of trait distribution and differential evolutionary lability of traits could be used to uncover mechanism of selection operating within a lineage. In the runaway model, drift along equilibria lines between male trait and female preference produces periods of rapid evolution resulting in large-scale diversifications and elaboration of male secondary sexual traits (Lande 1980, Kirkpatrick 1987). Thus, the runaway model predicts (1) rapid differentiation in secondary sexual traits and evolution of multiple secondary sexual traits among lineages with little convergence between lineages, and (2) historically-nested distribution of traits that are shared among lineages within a clade (Prum 1997). The quality-indicator models of sexual selection predict different historical patterns. Because quality indicators are costly, selection on such traits would ultimately result in reduced genetic variance in these traits (reviewed in Anderson 1994). Thus, evolution of multiple indicator traits is strongly constrained because evolution of a new indicator would favour elimination of previous ones (Hill 1994a, 1996a; Iwasa & Pomiankowski 1994). Consequently, indicator models predict sequential evolution of increasingly informative and increasingly constrained sets of traits within lineages (Hill 1994a, 1996a; Prum 1997). The "chase-away" process of sexual selection (Holland & Rice 1998) also predicts sequential evolution of more exaggerated traits, but that evolution should be accompanied by selection for retention of existing traits. Sensory bias models predict

frequent convergence in traits across lineages that share wide and similar preexisting biases (Anderson 1994; Hill 1994a; Irwin 1996). The sensory drive hypothesis predicts strong convergence of preferences and traits across lineages with similar ecological conditions (Hill 1994a; Prum 1997). Similarly, if sexual traits evolve to minimize costs associated with mate sampling and selection, strong convergences in sexual traits among lineages that share similar ecological condition are expected (Schluter & Price 1993; Prum 1997; Price 1998). Finally, direct selection for species recognition should favour uniqueness of displays, and selects against shared traits among lineages, thus resulting in decreased trait diversity and reduced hierarchical structure within a lineage (Hamilton 1961; Grant 1965; Grant & Grant 1997; Prum 1997; Price 1998).

Kusmierski *et al.* (1997) found that in bowerbirds, sexually dimorphic plumage characters were extremely labile and, aside from few constraints on fundamental levels of display and plumage patterns, sexual dichromatism appeared to be largely unconstrained. This pattern of plumage variation was most consistent with the predictions of runaway models of sexual selection. Prum (1997) tested predictions of various models of sexual selection on display traits in manakins. He found that (1) diversity of manakin traits was explosive, indicating that evolution of these traits is largely unconstrained. Patterns of diversity and hierarchical structure of these displays within lineages was most consistent with the predictions of runaway and sensory bias mechanisms (Prum 1997, see also Irwin 1996) and also may be consistent with phylogenetic predictions of the "chase-away" model of sexual selection (Holland & Rice 1998).

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## CHAPTER II

# SEXUAL DIMORPHISM IN RELATION TO CURRENT SELECTION IN THE HOUSE FINCH

RRH: Dimorphism and selection in the house finch

*Abstract.* — Sexual dimorphism is thought to have evolved in response to selection pressures that differ between males and females. If current selection is important in the evolution and maintenance of sexual dimorphism, the observed sexual dimorphism should be at least partially congruent with patterns of current selection. Our aim in this study was to determine the role of current net selection in shaping and maintaining contemporary sexual dimorphism in the house finch (*Carpodacus mexicanus*). We found strong selection on sexually dimorphic traits, significant heritabilities of these traits, and a close congruence between current selection and patterns of sexual dimorphism in the house finch in Montana population. Strong directional selection on sexually dimorphic traits, and similar intensities of selection in each sex, suggested that sexual dimorphism arises from adaptive responses in males and females, with both sexes being far from their local fitness optimum. We suggest that continuous immigration from central areas of house finch geographical range may prevent our peripheral study population from reaching its ecological optima, thereby facilitating strong selection on morphological traits. Strong selection of heritable sexually dimorphic traits in combination with low levels of ontogenetic morphological integration in these traits may have accounted for close congruence between current selection and sexual dimorphism, and ultimately contributed to the unusually high colonization abilities of the house finch compared to other cardueline finches.

*Key words.*— Sexual dimorphism; pairing success; overwinter survival; fecundity; house finch; peripheral population, local adaptation.

The relative importance of selection in evolution and maintenance of sexual dimorphism is a much debated issue. On one hand, sexual dimorphism is regarded as an outcome of sex-specific patterns of current sexual and natural selection (e.g., Darwin 1871, Ralls 1976, Lande 1980, Slatkin 1984, Arak 1988, Shine 1989). Indeed, concordance between current environmental conditions and degree of dimorphism is well documented (e.g., Earhart and Johnson 1970, Johnston and Fleischer 1981, Carothens 1982, Payne 1984, Moore 1990, Webster 1992, Promislow et al. 1994, Martin and Badyaev 1996, Mitani et al. 1996, Badyaev 1997ab, Poulin 1997, Wikelski and Trillmich 1997, Badyaev and Ghalambor 1998). The importance of current selection in explaining observed patterns of sexual dimorphism is further supported by the considerable heritable genetic variation in many sexually dimorphic traits (e.g., Cowley et al. 1986, Cowley and Atchley 1988, Reeve and Fairbairn 1996) and by the examples of rapid phenotypic changes in dimorphism under artificial selection (e.g., Wilkinson 1993). On the other hand, studies of sexual dimorphism suggest that allometric and developmental patterns (Alberch 1982, Leutenegger and Cheverud 1982, Wagner 1988), differences in such patterns among phylogenetic lineages (i.e., phylogenetic constrains; Cheverud et al. 1985, Kappeler 1996), and the patterns of genetic correlations of a species (e.g., Cheverud 1984, Lande 1985, Lofsvold 1988, Rogers and Mukherjee 1992), strongly bias or limit the ability of an organism to respond to changing selection pressures.

While most studies of sexual dimorphism have focused on population-level explanations, especially the deterministic (selective) processes, the relative importance of various selective forces in shaping current variation in sexual dimorphism is not well

understood (reviewed in Badyaev 1999). For example, sexual dimorphism is generally interpreted to be a result of sexual selection. However, close concordance between contemporary sexual selection and current degree of sexual dimorphism is not necessarily expected. First, sexual dimorphism in a species may be ancestral to ecological divergence or speciation (e.g., Björklund 1991a, Schluter and Price 1993, T. D. Price 1998) and thus variation in sexual dimorphism in response to changes in selection may be reduced by patterns set over evolutionary time. Second, sexual selection favoring dimorphism may be opposed by natural selection on the same traits (e.g., Howard 1981, T.D.Price 1984ab, Weatherhead et al 1987, Fairbairn and Preziosi 1996, Wikelski and Trillmich 1997), selection on closely correlated traits in the opposite sex (Lande 1980, Reeve and Fairbairn 1996), or selection during the life history (reviewed in Schluter et al. 1991). Alternatively, no relationship is expected when sexually dimorphic traits lack appropriate genetic variability, are genetically correlated (e.g., by linkage, epistasis, or pleiotropy), or when phenotypic plasticity (such as behavioral modification of displays) reduces selection pressures on sexually dimorphic traits (Badyaev 1999). Moreover, the concordance between current selection and current dimorphism does not necessarily imply the adaptiveness of sexual dimorphism, bacause sexual dimorphism may arise independently of adaptations within each sex if there is sex-biased variance in traits (e.g., Johnston and Fleischer 1981, Cheverud et al. 1985, Reeve and Fairbairn 1996). Finally, once a population is adapted to a particular environment, selection may be detectable only on unusual phenotypes, and a large amount of phenotypic variation in sexual dimorphism may be selectively neutral (e.g., Lande 1976). Thus, study of an association between current sexual dimorphism and current net selection on morphology in natural populations is especially needed to examine the relative importance of evolutionary forces and constraints in the evolution of sexual dimorphism (e.g., Björklund and

Lindén 1993, Preziosi and Fairbairn 1996).

Strong selection, immigration, and dispersal are often typical of peripheral or recently established populations (Holt and Gomulkiewicz 1997, Kirkpatrick and Barton 1997), and these processes can greatly modify allele frequencies and ultimately influence genetic and phenotypic correlations among traits (e.g., Shaw et al. 1985). Consequently, examination of morphological variation in such species and populations allows greater inference about evolutionary forces and constraints that affect sexual dimorphism (e.g., Endler 1986, Rising 1987, Wikelski and Trillmich 1997). A recently-established (15-18 years ago) population of house finches (*Carpodacus mexicanus*) in NW Montana provided a unique opportunity to examine the relationship between dimorphism and current selection. First, given the peripheral location of the NW Montana population and continuous immigration of juveniles from ecologically distinct California and Oregon locations (Badyaev, unpubl. data), we predicted strong directional selection on morphology in this local population (e.g., García and Kirkpatrick 1997). Second, while it is known that house finches are sexually dimorphic and the extent of dimorphism varies among populations (Hill 1993ab, Badyaev, unpubl. data), it is unclear whether such variation is due to selection differences among populations (e.g., Vazquez-Phillips 1992).

Our aim was to determine the role of current selection in shaping and maintaining contemporary sexual dimorphism in the house finch in Montana. We studied large, individually-marked, resident population over four years and several selection episodes to examine the fitness consequences of variation in sexual dimorphism. While considerable attention has been paid to sexual dichromatism in this species (reviewed in Hill et al. 1998), variation in size dimorphism was not studied. Thus, we primarily focused on variation in sexual size dimorphism. This paper has three parts. We first described current sexual dimorphism in the house finch in size and shape factors based on a path analysis model. Second, we used the same path analysis model to calculate

selection differentials for pairing (paired versus non-paired birds), survival (survived versus did not survive), and fecundity (above- versus below-average fecundity). Finally, we examined concordance between the direction and magnitude of current selection and observed sexual dimorphism. We used the same multivariate model to describe both sexual dimorphism and current selection in order to estimate concordance between current morphology and selection. For example, if current selection favored increased sexual dimorphism, the difference in selection differentials between males (larger sex) and females (smaller sex) should be positive; whereas, if current selection favored decreases in dimorphism, the difference in selection differentials between the larger and smaller sex should be negative (Crespi and Bookstein 1989, Björklund and Lindén 1993). In addition, if current selection favored greater dimorphism, then for each trait we should find a positive correlation between the magnitude of difference in selection differentials between sexes and magnitude of sexual dimorphism. A negative or no correlation is expected when current selection favors monomorphism (Björklund and Lindén 1993) or selection is not acting on sexually dimorphic traits.

## METHODS

### *Data Collection*

This study was carried out on a resident house finch population at an isolated area, 3 km w of Missoula, Montana. The study site was located in an open field, and contained several hundred of 1-3 m high ornamental bushes used by finches for nesting, and several large coniferous trees used by finches for roosting. In 1995-98, all resident finches were trapped during January-March and August-October, and measured and marked with a unique combination of one aluminum and three colored plastic rings. All individuals were aged as HY (hatching year) and AHY (after hatching year) according to Hill (1993a). Finches foraged within the area, and on

shortgrass prairie and agricultural fields surrounding the area. At any time during the breeding season, the resident population consisted of about 20 breeding pairs, their nestlings, and about 60-70 adult finches that were either between nesting attempts or unpaired. A bird was considered a resident if it roosted on the area for 14 consecutive days. All resident finches were present in the vicinity of the area throughout the breeding season and despite extensive searches, we documented no breeding by resident marked finches outside of our study site. The closest suitable breeding habitat and the closest nest of an unmarked house finch pair was about 4 km from our study site.

House finches form a strong pair association (Hill 1993a), and paired individuals are easily determined from the beginning of the breeding season (e.g., Hill et al. 1998, Badyaev, pers. obs). A bird was considered not paired when it was a resident at the study site from the beginning of the breeding season but was never seen with a mate. The open landscape of the study site made it easy to observe pairing status of birds. Several birds that appeared at the study site late in the season and became residents were not included in the pairing selection analyses. High-levels of extra-pair paternity could bias estimates of pairing success (Webster et al. 1995). However, extensive studies of extra-pair paternity in the house finch failed to detect any significant levels of extra-pair fertilizations (Hill et al. 1994). Similarly, while copulations between social mates were frequently observed, we never observed copulations with extra-pair birds in our population. Thus, we assume extra-pair fertilizations to be rare.

House finches show strong nest site fidelity and typically return to renest at the same location (i.e., the same juniper bush) year after year (Hill 1991, 1993a, Hill et al. 1998, Badyaev pers. obs). Strong fidelity of adult house finches to the location of previous breeding, and an isolated location of our study site allowed us to assign overwinter survival status to the resident birds. A bird was considered to have "survived" when it was a breeding adult in the previous summer and was seen the following year after March. A breeding adult that did not appear in the

study site the following year was assigned "did not survive" status. Despite capturing more that 1,400 house finches in fall and early-winter flocks around the study site and in Missoula, we never encountered an individual previously assigned "did not survive" status. No resident individuals appeared at the study site after missing a breeding season. Moreover, most of the overwinter mortalities of resident birds occurred within the study site. Dead birds were collected by one of us (AVB) and other personnel near roosting trees following snow storms or unusually cold overnight temperatures. Birds that died as a result of collisions with glass, vehicles, and fences were not included in the survival analyses.

Field observations were conducted daily from 0430 to 0800 and 1400-1600 during March and April and 0430 to 1300 and 1600-2000 during May - August. All but 6 nests were found at the stage of early nest building, and first-egg date was reliably determined for all breeding pairs. Nest initiation date is the most important predictor of overall reproductive success in the house finch (e.g., Hill et al. 1994, 1998, Badyaev unpubl. data). Pairs that nest earliest also produce more broods and have larger clutch sizes than pairs that nest later (Hill 1993a). We used a linear combination of the first-egg date (eigenvector = -0.79) and the first clutch size (eigenvector = 0.79) as a measure of fecundity. This measure was most consistently and highly correlated with the number of broods per season, renesting intervals, and clutch sizes than any other variable we have considered (see also Hill et al., 1994). We assigned a breeding bird a "high fecundity" status if its fecundity was higher than the average in the population that year. "Low fecundity" status was assigned if the fecundity measure was lower than the average. To avoid pseudoreplication, for all selection analyses we used birds only during their first year of residence at the storage site, or the first year of survival.

The following measures were taken: bill length from the angle of the skull to the tip of the upper mandible; bill width at the anterior end of nostrils; bill depth in a vertical plane at the

anterior end of the nostrils over both mandibles; tarsus length (mean of left and right); tail length measured from the cloacal notch to tip of the longest rectrices; wing (mean of left and right, flattened), body mass (in grams to an accuracy of 0.1 g), plumage coloration (males only, see below). All traits were measured with digital calipers to an accuracy of 0.05 mm. All morphological measures were repeated two times and the average of repeated measures was used for further analyses. Measurements of adults were taken during either pre- or post-breeding season short capture sessions, thus minimizing the effects of seasonal variation. At the time of the fall captures, HY birds were fully-grown – for measured morphological traits no growth occurs after 70-80 days of age (Badyaev and Martin, ms). All morphological data were ln-transformed and zero-mean standardized before the analyses. All measurements were conducted by AVB.

In order to estimate measurement error for each trait we calculated repeatabilities for all traits from variance components of ANOVA. Resident birds were recaptured several times during year, so all available repeated measures for all individuals and traits within each capture season (7-14 days) were included. Within-capture session measurement error accounted for about 7-10% of variation in most morphological traits, and for 26% of variation in body mass.

In males, carotenoid-based coloration of crown, lores, breast, and rump was evaluated for brightness, extent, and hue. All characters were evaluated on 0-to-10 scale and hue was estimated on the yellow-to-red scale (0-10). The first principal component of brightness, extent, and hue measures was calculated for each body part separately. Plumage score was then the sum of these eigenvectors for all body parts.

### *Description of Dimorphism, Selection, and Genetic Variation*

When morphological traits are positively correlated (as they are in the house finch) they cannot be regarded as separate characters. It is more biologically appropriate to examine variation

in unobserved size and shape factors (Wright 1923, Crespi and Bookstein 1989). Thus, we used path analysis to examine sexual dimorphism and selection on morphology (Bookstein 1989, Crespi and Bookstein 1989, Björklund and Linden 1993). Size and shape factors were calculated separately for bill (bill length, bill depth, bill width) and body (tarsus length, wing length, body mass) measurements. Dimorphism was calculated separately for each age (AHY and HY). We first assessed homogeneity of covariance matrices between males and females for bill and body characters. Tests for homogeneity of covariances showed no significant differences between male and female matrices for each group of traits (e.g., AHY birds: $\chi^2 = 23.31$, $df = 28$, $P = 0.72$; HY birds: $\chi^2 = 33.54$, $df = 28$, $P = 0.22$). Thus, pooled matrices were used in further analyses. We then extracted first eigenvectors of the pooled covariance matrices. These vectors were general size (bill size and body size) in further analyses. Sexual dimorphism in shape factors for bill and body was the difference in least-squared means of each trait calculated from ANCOVA of sex and each trait with general size (bill size or body size) and year as covariates (Rohlf and Bookstein 1987, Björklund and Linden 1993).

Similarly, selection differentials were the differences in adjusted means (directional selection $a$) between groups (i.e., paired and not paired) from ANCOVA with selection group, year, and each trait (Crespi and Bookstein 1989). Calculations were made separately for each sex. As before, general size and year were used as covariates for estimating selection differentials on shape factors. Stabilizing selection ($C$) was estimated by comparing variances in each trait between groups. Selection on plumage coloration was calculated separately from other morphological traits. Means were compared with two-tailed $t$ - tests, and variances with an $F$ - test. For ease of the interpretation, we also present raw morphological data for selection during 1995-97.

The parent-offspring regression for a trait is the ratio of covariance between offspring and parents to the variance of the parents, and therefore could be used to estimate heritability of a trait

(Falconer and Mackay 1997). We estimated a single parent (female and male parent) and mid-parent vs. offspring regressions for ages 33 days after hatching. Correlations were calculated for all nestlings, i.e., parent values were re-used for every nestling in the brood (after Price and Grant 1985). To account for assortative mating between parents, we calculated partial correlations between a trait in a parent and an offspring while holding the trait value of the other parent constant. Unequal phenotypic variance of parents could bias a singe-parent versus offspring estimates of heritability (Falconer and Mackay 1996). However the male and female phenotypic variances for the measured traits were equal (Table 1).

## RESULTS

### *Sexual Dimorphism in the House Finch*

In AHY birds ($n$ = 379), the first principal component of the pooled within-age covariance matrix accounted for 47% of the total variance in bill characters (correlations with eigenvector = 0.55-0.65) and 45% of the total variance in body characters (correlations = 0.57-0.58). In HY birds ($n$ = 336), the first principal component accounted for 46% of the total variance in bill characters (correlations = 0.59-0.65) and 39% of the total variance in body characters (correlations = 0.54-0.56). In both age classes first eigenvectors were highly concordant with isometric vectors (vector correlations = 0.979-0.988, $\alpha$ = 8.9 -11.7°). Thus, first eigenvectors of all four matrices represented general size vectors.

In addition to sexual dichromatism in plumage coloration, male house finches were larger than females in bill, wing, and tail length (Table 1). In HY, birds males were also heavier than females (Table 1). When we used path analysis model to partition sexual dimorphism into variation in size and shape factors, we found that both HY and AHY males had larger body sizes and disproportionally longer wings than females (Table 4). HY males had larger bills, but shorter tarsi

than females of the same age. In AHY birds, females were disproportionally heavier for their size, had narrower bills, and longer tarsi than males of the same age (Table 4).

### *Current Selection in the House Finch*

*Pairing selection* —. A total of 154 AHY males and 122 AHY females were used in the analysis of pairing selection. Paired males tended to have longer bills and longer wings (Table 2), but did not differ from single males in plumage score ($P = 0.41$; Table 2). In females, paired females had significantly shallower and narrower bills, and shorter wings than unpaired females (Table 2). Path analysis models of pairing selection during 1995-97 (Table 3) indicated that pairing selection favored males that had disproportionally longer wings, larger bill size, and larger body size. Also, bill length variance differed between paired and unpaired males indicating disruptive selection (Table 3). In females, pairing selection acted on the same traits as in males, but in the opposite direction: pairing selection favored a decrease in bill and body sizes, and disproportionally shorter wings (Table 3). Also, paired and unpaired females significantly differed in variance in bill shape characters (Table 3).

*Survival selection* —. A total of 107 AHY males and 72 AHY females were used in the survival selection analysis. Males that survived had narrower and deeper bills, and more variable bill width compared to males that died during the winter (Table 2). Males that survived and did not survive were similar in plumage score ($P = 0.27$; Table 2). Females that survived had longer tarsi and wings, and less variable bill depth compared to females that died (Table 2). A path analysis of survival selection over 1995-97 indicated that, in males, selection favored smaller body size, disproportionally deeper but narrower bills, disproportionally shorter wings, and less variable bill length (Table 3). In females, selection mostly affected variance of the traits. We documented disruptive selection for overall bill size, and stabilizing selection for bill depth. Survival selection in

females also favored larger body size, larger bill size, deeper bills and longer tarsi (Table 3).

*Fecundity selection* —. A total of 102 AHY males and 99 AHY females were used in fecundity analyses. In both sexes, univariate analyses indicated differences between low- versus high- fecundity individuals. High-fecundity males had longer wings, shorter tarsi, shallower and narrower bills, and higher plumage score than low-fecundity males (Table 2). High-fecundity females had longer and shallower bills, and shorter wings than low-fecundity females (Table 2). Multivariate analyses of fecundity selection over 1995-97 revealed strong selection in both sexes. In males, selection for higher fecundity favored smaller bill size, larger body size, disproportionally longer and shallower bills, disproportionally longer wings, shorter tarsi, and heavier body mass (Table 3). In females, fecundity selection favored decrease in both bill and body sizes, decrease in bill depth and in relative wing length, but increase in body mass and tarsus length (Table 3).

## *Comparisons of Selection Episodes*

Multivariate analysis revealed that selection often operated on the same traits in males and females, but in opposite directions (Table 3). The intensity of selection (absolute values of selection differentials) was similar between sexes (Table 3). However, directional survival selection on relative bill depth and width, and wing length was stronger in males than in females (corresponding differences: $\Delta = 0.009$, $t = 14.00$, $P = 0.005$; $\Delta = 0.01$, $t = 34.00$, $P = 0.009$, and $\Delta = 0.002$, $t = 4.00$, $P = 0.05$), while survival selection on bill size was stronger in females than in males ($\Delta = -0.17$, $t = -8.83$, $P = 0.01$). Similarly, directional fecundity selection on relative bill depth and tarsus length was stronger in males than in females (corresponding differences $\Delta = 0.007$, $t = 4.14$, $P = 0.02$; $\Delta = 0.009$, $t = 4.04$, $P = 0.02$), but the pattern was the opposite for bill width ($\Delta = -0.016$, $t = -5.49$, $P = 0.01$).

*Current Selection in Relation to Sexual Dimorphism in the House Finch*

Pairing selection strongly favored sexual dimorphism in every year (Spearman $r$ = 0.23-0.85, Table 4), and overall current pairing selection was highly concordant with current dimorphism (AHY birds: Spearman $r = 0.70$, $P < 0.01$; HY birds: Spearman $r = 0.78$, $P < 0.001$; Table 4). On the contrary, survival selection strongly favored reduced dimorphism (Spearman $r$ = -0.57 - (-0.05), overall survival selection on AHY birds Spearman $r = -0.51$, $P = 0.003$, on HY birds: Spearman $r = -0.60$, $P < 0.001$). When pooled over the years of study, fecundity selection pressures tended to favor increased sexual dimorphism in AHY birds (Spearman $r$ = -0.28 - 0.53; overall fecundity selection on AHY birds: Spearman $r = 0.42$, $P = 0.04$; HY birds, Spearman $r$ = 0.30, $P$ =0.17; Table 4). The current net selection (combined standardized differentials of pairing, survival, and fecundity selections over 1995-97) was highly concordant with current sexual dimorphism in both age classes (AHY birds: Spearman $r = 0.78$, $P = 0.012$, HY birds: Spearman $r$ = 0.88, $P = 0.001$; Table 4).

Correlations between mid-parents and nestlings at age 33 were mostly significant for all traits, but body mass and bill depth (Table 5). Heritability estimates for bill traits continued to increase at later ages because of the late onset of growth of these traits, and strong compensatory growth during late ontogeny (Badyaev 1998, Badyaev and Martin, ms). Similarly, pronounced differences between male- and female-parent correlations were observed only for bill depth. Heritability estimates at age 33 varied from 0.20 to 0.62 for bill traits, and from 0.20 to 0.41 for body traits (Table 5).

## DISCUSSION

We found strong current selection on sexually dimorphic traits of the house finch. Both directional and stabilizing selection were documented. While individual selection components often

exerted opposite pressures on sexually dimorphic traits, the overall selection pressures were concordant with observed magnitude of sexual dimorphism (Table 4). Because sexually dimorphic traits of the house finch have significant heritabilities (Table 5, Badyaev and Martin, ms), the finding of strong current selection on these traits points to significant potential for evolutionary change. These findings raise several questions. First, do sexes differ in intensity of current selection that acts on their morphology, or does sexual dimorphism result from selection on one sex? Second, do measured selection components (i.e., pairing success, overwinter survival, or breeding season fecundity) differ in their effects on variation in sexual dimorphism? Third, given significant heritability of sexually dimorphic traits in the house finch, and strong current selection documented in this study, why is sexual dimorphism rather moderate in this species? Finally, what is the potential for evolutionary change in sexual dimorphism in the house finch?

The potential for the evolution of sexual dimorphism is partially determined by differences in selection intensity between sexes (e.g., Lande 1980, Arak 1988, Ydenberg and Forbes 1991). Many studies have implicated such intersexual differences in selection as a causal basis for the evolution of sexual dimorphism (e.g., Ralls 1976, T.D. Price 1984a, Weatherhead et al.1987, Arak 1988, Moore 1990, Martin and Badyaev 1996, Wikelski and Trillmich 1997). Similarly, we found that variation in sexually dimorphic traits in both sexes of the house finch had strong fitness consequences (Tables 2 & 3). Current selection operated with similar intensity on both sexes, but selection often acted in opposite direction on the same traits of males versus females. Therefore, we conclude that sexual dimorphism in this species is maintained by adaptive responses in each sex independently, and arises from directional differences in the selection pressures on both sexes.

Strong directional selection on house finch morphology in our population suggested that both sexes are far from their optimal morphology for the local ecological conditions. Alternatively, strong directional selection could result from fluctuating environmental pressures (e.g., differences

between years or seasons, Table 4; Benkman and Miller 1996, Reznick et al., 1997). For example, pairing and fecundity selection favored smaller size in females, but larger size in males (Tables 2 & 3). Selection for smaller size in females is frequently documented (e.g., Perrins 1979, Murphy 1986, see also Langston et al.1990). Such selection could potentially arise from a physiological advantage to small body size because smaller females may reach the energetic requirements for self-maintenance faster and therefore breed earlier, and convert a greater proportion of consumed resources into reproduction (e.g., Downhower 1976). Early breeding is commonly associated with greater fecundity (e.g., Perrins 1979, Murphy 1986). Similarly, in our population smaller females initiated nests earlier and laid larger clutches compared to larger females (Tables 2 & 3). In constrast, pairing and fecundity selection favored larger structural size in house finch males (Tables 2&3). Larger size may be favored becasue larger males provided more food to their mates and nestlings than smaller males (Badyaev, unpubl. data); in the house finch, sufficient provisioning of incubating females by males is essential to reproductive success (e.g., Hill 1991, Hill 1993a).

In both sexes, changes in morphological traits that increased fecundity and pairing success also reduced overwinter survival (Tables 2 & 3). For example, survival selection favored larger body size in females, while pairing success and high fecundity favored smaller female body size. Similarly, pairing success and high fecundity favored larger body size in males, while overwinter survival favored smaller male body size (Table 3). Similar trade-offs were observed in other systems. For example, in a population of Darwin's finches (*Geospiza fortis*), females with smaller bills had higher fecundity, but lower survival than individuals with larger bills (T.D. Price 1984b). Similarly, in marine iguanas (*Amblyrhynchus cristatus*) larger males had higher mating success, but lower survival than smaller males (Wikelski and Trillmich 1997). Such opposing selection pressures may also operate across life stages (reviewed in Schluter et al. 1991). For

example, immature female song sparrows (*Melospiza melodia*) with long bills survived their first winter better than short-billed individuals, but the latter had higher reproductive success (Schluter and Smith 1986). In the Darwin's finch, small birds of both sexes survived poorly as adults, but better as juveniles (T.D. Price 1984b, Price and Grant 1984). Similarly, in our study survival selection effects had greater negative correlations with sexual dimorphism in HY birds than with dimorphism of AHY birds (Table 4). This indicated that survival selection during the first winter of life may limit morphological differences between males and females favored by sexual selection on adults (Table 4; Badyaev, unplubl. ms).

Strong concordance between current selection on sexually dimorphic traits and observed level of sexual dimorphism in the house finch (Table 4) is surprising in the light of studies of morphological variation in other Cardueline finches. Björklund (1991b; 1994; Bjorklund and Merilä 1993) found low level of variation in morphological traits in carduelines, and suggested that the among-species variance could be most easily explained by long-term stabilizing selection (Björklund 1991b; see also van den Elzen et al. 1987). Moreover, in three species of cardueline finches, including the close relative of the house finch - the scarlet rosefinch (*Carpodacus erythrinus*), nestling growth trajectories showed high positive among-age and among-trait covariation, thus significantly limiting potential for morphological change under selection (Björklund 1993, 1994; see also Riska 1985). Consequently, most morphological differentiation among finch species was related to structural size (van den Elzen and Nemeschkal 1987, Björklund and Merilä 1993) and plumage patterns (Clement et al., 1993, Badyaev 1997a).

The close concordance between current selection and morphology of our house finches in the face of the conservatism of morphological variation in other Cardueline finches could be due to several reasons. First, in recently established marginal populations, such as in our study population, continuous gene flow from the central areas of the house finch geographical range

(e.g., Vazquez-Phillips 1992) may prevent the local population from reaching their ecological optima and thus facilitate strong directional selection on heritable traits (García-Ramos and Kirkpatrick 1997, Holt and Gomulkiewicz 1997). Unusually high dispersal rates of house finches and colonization of diverse ecological conditions (Vazquez-Phillips 1992, Veit and Lewis 1996) may further contribute to high potential for evolutionary change in this species. Consequently, house finch populations strongly diverge in sexual dimorphism (Badyaev and Hill, unpubl. ms). Second, the analysis of phenotypic variation in house finch growth revealed that, to the contrary of the other carduelines (e.g., Badyaev 1993, 1994; Björklund 1993), house finch ontogeny is the least constrained (Badyaev 1998, Badyaev and Martin, ms). Weak among-age and among-trait ontogenetic covariations and significant heritabilities imply significant potential for the evolutionary change, especially under strong short-term selection that is likely to accompany colonization (e.g., Zeng 1988). Low levels of integration during development and strong current selection on heritable traits may contribute to the highest colonization ability and the widest gradient of ecological conditions occupied by this species compared to other cardueline finches (e.g., Appendix 1 in Badyaev 1997a).

The response of both males and females to selection is composed of the direct response of each sex to selection on itself and the indirect response to selection on the other sex (Lande 1980, Cheverud et al. 1985). However, if sexes differ in the amount of genetic variance for the trait, sexual dimorphism can evolve even under similar selection pressures and high genetic correlation between sexes (Cheverud et al. 1985). We found no evidence for sex-biased variation in morphological traits under this study (see Methods, Table 1). Moreover, preliminary heritability estimates for morphological traits of juvenile males and females (method of Lande and Price 1989) suggested that genetic correlation between sexes is close to unity (Badyaev, unpubl. data), similar to that found in other avian studies (T.D. Price 1984a, D.K. Price 1996, Merilä et al. 1998). Thus,

it is likely that the evolutionary change is strongly constrained by high levels of genetic correlation between sexes (e.g., D.K. Price 1996, Merilä et al. 1998). While current selection for greater sexual dimorpshim in adults may be constrained by genetic correlations between sexes, selection acting on genes that control develpmental time or other aspects of growth trajetories may strongly influence sexual dimorphism even in the presense of high between-sex genetic correlations (Cheverud et al., 1983, Reeve and Fairbairn 1996). In the house finch, growth curves for males and females were not parallel during late ontogeny, and growth of sexes was terminated at different time (i.e., 33-50 days for females, and 75-117 days for males, Badyaev and Martin ms). Thus, sex differences in growth parameters may infuence the potential for evolutionary change in sexual dimorphism in the house finch (see also Cooch, et al. 1996).

Traits with a greater amount of sex-limited additive genetic variance, a lower degree of integration, and greater relevance to fitness under current conditions should be favored by selection for sexual dimorphism (Moller and Pomiankowski 1993, Schluter and Price 1993, Badyaev 1999). Among-trait variation in sex-limited additive genetic variance and the information the traits provide in different environments, may account for one of the most surprising results of this study - the lack of strong selection for elaborate carotenoid-based coloration in males (Table 2). Long-term study of several house finch populations in the eastern U.S. showed consistent and strong selection for brighter carotenoid-based coloration in male house finches (e.g., Hill 1991, 1993a). In a series of work, Hill (reviewed in Hill et al., 1998) documented strong pairing, fecundity, and survival selection for brighter carotenoid-based coloration in the house finch. Strong selection in eastern populations of house finches persisted even as the available variation in carotenoid plumage declined (Hill et al. 1998, Hill, pers comm.). In the contrast, we observed much more extensive variability in carotenoid coloration of males in our study population (Table 1), but we detected only weak fecundity selection on this trait. Morphological traits such as body size and bill traits

may provide more accurate information on individual quality and parental abilities than do plumage characteristics in conditions of newly established population. Alternatively, extensive variation in carotenoid-based plumage in our population may be maintained by male-male interactions (but see Belthoff et al., 1994; Badyaev and Rapone, ms), gene flow from other populations, and pleiotropic relations with other traits. Weak directional fecundity selection for brighter plumage in our population (Table 2) in combination with high availability of carotenoid-rich foods in suburban areas (e.g., Linville and Breitwish, 1997) may be sufficient to maintain this trait in our population.

In sum, we found strong fitness consequences of variation in sexual dimorphism in the house finch. Directional selection on sexually dimorphic morphological traits, and similar intensities of selection on each sex, suggested that sexual dimorphism in the house finch may arise from adaptive responses in both sexes. We suggest that continuous gene flow from the central areas of the house finch geographical range may prevent the local population from reaching their local fitness optima, thereby facilitating strong directional selection on morphological traits. This selection in combination with low levels of ontogenetic integration in heritable sexually dimorphic traits may account for the close correspondence between current selection and current sexual dimorphism in the house finch.

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Table 1. Descriptive statistics of morphological traits measured in the known-sex house finches in 1995-1998. Sample sizes - males: HY ($n$ = 184), AHY ($n$ = 194); females: HY ($n$ = 152), AHY ($n$ = 185).

| | | Males | Females | $P^1$ |
|---|---|---|---|---|
| Trait (in *mm*) | Age | Mean (SD) | Mean (SD) | |
| Bill Length | HY | 10.33 (0.38) | 10.23 (0.43) | 0.042 |
| | AHY | 10.33 (0.56) | 10.21(0.48) | 0.051 |
| Bill Depth | HY | 7.67 (0.38) | 7.62 (0.32) | 0.209 |
| | AHY | 7.91 (0.38) | 7.85(0.40) | 0.210 |
| Bill Width | HY | 7.16 (0.32) | 7.10 (0.28) | 0.095 |
| | AHY | 7.12 (0.33) | 7.18 (0.44) | 0.192 |
| Wing Length | HY | 79.11 (1.84) | 77.30 (2.22) | **0.000** |
| | AHY | 79.48 (1.79) | 77.39(2.07) | **0.000** |
| Tail Length | HY | 62.89 (2.60) | 63.00 (2.68) | 0.395 |
| | AHY | 63.52 (3.54) | 61.48(2.97) | 0.000 |
| Tarsus Length | HY | 20.60 (0.47) | 20.46 (0.55) | 0.035 |
| | AHY | 20.67 (0.82) | 20.53(0.72) | 0.098 |
| Body Mass, *g* | HY | 21.75 (1.24) | 21.25 (1.18) | **0.003** |
| | AHY | 21.72 (1.54) | 21.86(1.54) | 0.253 |
| Plumage score | AHY | 20.06 (6.08) | | |

[1] one-tailed test for difference in means between sexes; $P$-values in bold indicate significance after within-age group adjustment for multiple comparisons (Bonferroni $\alpha$ = 0.007).

Table 2. Morphology [(mean (SD)] of house finches with respect to pairing success, overwinter survival, and breeding season fecundity.

| Trait | | Pairing | | Survival | | Fecundity | |
|---|---|---|---|---|---|---|---|
| | | Paired | Single | Survived | Non-survived | High | Low |
| *Males* | *n* | 76 | 78 | 70 | 37 | 51 | 51 |
| | Bill Length | 10.76 (0.36) | 10.24 (0.48) | 10.22 (0.62) | 10.36 (0.76) | 10.39 (0.62) | 10.36 (0.47) |
| | Beak Depth | 8.06 (0.37) | 7.96 (0.34) | **8.19** (0.42) | 7.94 ( 0.40) | **7.90 (0.39)** | 8.18 (0.21) |
| | Beak Width | 7.12 **(0.41)** | 7.15 (0.23) | **7.05 (0.31)** | 7.30 (0.07) | **7.06 (0.49)** | 7.19 (0.24) |
| | Wing Length | **79.97** (1.54) | 78.24 (1.88) | 79.59 (1.70) | 79.85 (1.88) | **80.47** (1.35) | 79.38 (1.67) |
| | Tail Length | 62.95 **(4.12)** | 63.68 (2.49) | 63.21 **(3.35)** | 62.25 (5.07) | 62.94 (3.40) | 63.18 (5.19) |
| | Tarsus Length | 20.62 (0.90) | 20.75 (0.79) | 20.43 (1.00) | 20.60 (0.78) | **20.35** (1.02) | 20.96 (0.82) |
| | Body Mass | 21.58 (1.37) | 22.04 (1.60) | 20.80 (1.53) | 21.80 (1.42) | 21.78 (1.45) | 21.31 (1.51) |
| | Plumage | 21.47 (4.58) | 21.16 (5.74) | 21.71 (5.44) | 20.55 (5.42) | **22.95** (3.37) | 20.15 (5.05) |
| *Females* | *n* | 74 | 48 | 35 | 37 | 51 | 48 |
| | Bill Length | 10.12 **(0.36)** | 10.28 **(0.60)** | 10.28 (0.48) | 10.28 (0.37) | 10.13 (0.42) | 10.29 (0.28) |
| | Beak Depth | **8.01 (0.32)** | 8.24 **(0.11)** | 8.10 **(0.32)** | 8.12 (0.66) | **7.95** (0.28) | 8.10 (0.34) |
| | Beak Width | **7.10 (0.34)** | 7.56 (0.85) | 7.24 (0.29) | 7.09 (0.45) | 7.07 (0.27) | 7.07 (0.48) |
| | Wing Length | **76.84** (1.64) | 78.54 (1.81) | **78.58** (1.40) | 76.95 (1.21) | **76.03** (1.73) | 78.72 (1.59) |
| | Tail Length | 60.70 (3.64) | 62.00 (2.80) | 61.34 (3.35) | 60.18 (4.06) | 60.21 (2.57) | 60.86 (4.04) |
| | Tarsus Length | 20.47 (0.85) | 20.67 (0.83) | **21.20** (0.79) | 20.30 (0.50) | 20.50 (0.95) | 20.45 (0.84) |
| | Body Mass | 22.26 (1.61) | 22.31 (1.39) | 21.86 (1.18) | 22.26 (1.76) | 22.19 **(0.75)** | 22.30 (1.95) |

Mean trait values shown in bold indicate significant difference between groups (e.g., paired vs single) after within selection group adjustments for multiple comparisons. Bold values in parentheses indicate significant differences in variances between groups.

Table 3. Directional ($a$) and stabilizing ($C$) selection on pairing success, overwinter survival, and breeding season fecundity in the house finches

| Trait | Pairing | | | | Survival | | | | Fecundity | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Males | | Females | | Males | | Females | | Males | | Females | |
| | $a$[1] | $C$[2] | $a$ | $C$ | $a$ | $C$ | $a$ | $C$ | $a$ | $C$ | $a$ | $C$ |
| Bill Size[3] | **61.0** | 50.7 | **-119.4** | -79.1 | 4.4 | 75.8 | 23.4 | **-171.1** | **-63.0** | 108.2 | **-37.7** | -72.6 |
| Body Size | 55.0 | 97.2 | **-85.1** | 72.6 | **-10.0** | **-204.8** | **42.3** | -83.2 | **43.1** | **-141.8** | **-17.0** | **-29.4** |
| *Shape Factors*[4] | | | | | | | | | | | | |
| Bill Length | 0.3 | **-0.2** | 1.6 | **-0.2** | -0.2 | **0.3** | **-1.6** | 0.1 | **2.0** | -0.0 | -0.7 | 0.1 |
| B. Depth | 0.2 | 0.0 | 1.1 | **-0.1** | **1.5** | 0.0 | **0.5** | **0.04** | **-1.2** | 0.0 | **-0.5** | 0.0 |
| B. Width | -0.4 | 0.0 | -2.4 | **-0.3** | **-1.7** | 0.0 | 0.6 | 0.1 | -0.1 | 0.1 | 1.1 | -0.1 |
| Wing | **1.2** | 0.0 | **-1.0** | 0.0 | **-0.7** | 0.0 | -0.1 | 0.0 | **1.4** | 0.0 | **-0.6** | 0.0 |
| Tail | -1.2 | 0.1 | 0.7 | 0.0 | 0.9 | -0.1 | 0.0 | 0.0 | -1.1 | -0.1 | -0.5 | **-0.2** |
| Tarsus | -0.3 | 0.0 | 0.4 | 0.0 | -0.2 | 0.0 | **0.9** | 0.0 | **-1.2** | -0.0 | 0.4 | 0.0 |
| Mass | -1.4 | 0.1 | 1.2 | 0.0 | -0.2 | -0.1 | -2.5 | -0.1 | 1.1 | -0.2 | 0.4 | -0.4 |

[1] directional selection differentials are the differences in adjusted means between groups (i.e., paired and not paired) from ANCOVA with selection group, year, and each trait; general size and year are used as covariates for estimating selection differentials on shape factors.

[2] stabilizing selection differentials are the differences of variances in each trait between selection groups

[3] first eigenvectors of the pooled covariance matrices for bill and body traits

[4] shape factors for bill and body are least-squared means of each trait calculated from ANCOVA of sex and each trait with general size and year as covariates. All values are multiplied by $10^2$. Bold values indicate significance after within-selection group Bonferonni adjustments

Table 4. Current sexual dimorphism[1] in relation to current selection for sexual dimorphism[2] in the house finch. $\Delta a_r$ - sex differences in selection for pairing success, $\Delta a_F$ - selection for breeding season fecundity, and $\Delta a_s$ - selection for overwinter survival. All differentials are multiplied by $10^2$.

| Trait | Sexual dimorphism[1] | | $\Delta a_r$ | | | | $\Delta a_F$ | | | | $\Delta a_s$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AHY | HY | 1995 | 1996 | 1997 | All | 1995 | 1996 | 1997 | All | 1996 | 1997 | All |
| Bill Size | 10.3 | **38.3** | 180.7 | 55.2 | 284.7 | 125.5 | -7.6 | -144.0 | 12.6 | -25.3 | -13.2 | -19.0 | -19.0 |
| Body Size | **95.4** | **81.9** | 126.0 | 86.5 | 71.2 | 90.6 | 140.6 | -67.0 | 35.7 | 60.1 | 155.6 | -128.7 | 32.3 |
| *Bill Shape Factors* | | | | | | | | | | | | | |
| B. Length | 0.7 | 0.0 | -8.1 | 2.6 | -10.1 | -1.3 | 2.9 | 8.1 | -3.4 | 2.7 | 1.4 | 1.4 | 1.4 |
| B. Depth | 0.3 | -0.3 | -3.0 | -0.9 | -3.5 | -0.9 | -0.8 | -2.0 | 1.5 | -0.8 | 0.8 | 1.0 | 1.0 |
| B. Width | -0.9 | 0.3 | 7.5 | -0.9 | 9.6 | 2.0 | -2.1 | -3.9 | 1.1 | -1.2 | -1.8 | -2.3 | -2.3 |
| *Body shape factors* | | | | | | | | | | | | | |
| Wing | **1.1** | **0.9** | 3.7 | 1.3 | 1.4 | 2.2 | 0.7 | 2.7 | 0.1 | 2.0 | -2.0 | 0.2 | -0.8 |
| Tail | 0.2 | -1.1 | -8.6 | 2.8 | -2.8 | -1.9 | 1.1 | -3.3 | 3.8 | -0.6 | 2.2 | 1.3 | 0.9 |
| Tarsus | -0.9 | -0.5 | -0.3 | -1.3 | -0.6 | -0.7 | -1.3 | -1.2 | -2.0 | -1.6 | -0.6 | -2.5 | -1.1 |
| Mass | -2.7 | -0.2 | 3.0 | -8.1 | 1.6 | -2.6 | -1.2 | -1.0 | -1.9 | 0.7 | 1.3 | 4.4 | 2.3 |
| Spearman *r* correlation with sexual dimorphism[3] | | AHY | 0.38 | **0.85** | 0.23 | **0.70** | 0.41 | -0.28 | **0.53** | 0.42 | -0.05 | **-0.55** | **-0.51** |
| | | HY | **0.85** | 0.53 | **0.70** | **0.78** | 0.03 | -0.35 | 0.40 | 0.30 | -0.23 | -0.57 | **-0.60** |

[1] dimorphism in size is the differences between males and females in the first eigenvectors values of the pooled covariance matrices for bill and body traits; dimorphism in shape factors is the difference in adjusted means of each trait calculated from ANCOVA of sex and each trait with general size (bill size or body size) and year as covariates

[2] difference between selection differential for male trait and selection differential for female trait

[3] Spearman *r* in bold indicates significance after within- year Bonferroni adjustment ($\alpha < 0.017$).

Table 5. Heritabitility estimates for morphological traits in the house finch. *r* - squared partial coefficient of correlation between a trait in 33 days old offsping (50 nestlings from 26 families) and adult parents.

| Trait | Mother | | Father | | Mid-parent | |
|---|---|---|---|---|---|---|
| | *r* | *P* | *r* | *P* | *r* | *P* |
| Bill Length | 0.31 | 0.05 | 0.25 | 0.12 | 0.60 | 0.00 |
| Bill Depth | 0.22 | 0.08 | 0.04 | 0.49 | 0.20 | 0.10 |
| Bill Width | 0.21 | 0.09 | 0.69 | 0.00 | 0.62 | 0.00 |
| Wing | 0.45 | 0.02 | 0.36 | 0.04 | 0.41 | 0.02 |
| Tarsus | 0.28 | 0.05 | 0.18 | 0.17 | 0.21 | 0.05 |
| Body Mass | 0.19 | 0.75 | 0.18 | 0.83 | 0.20 | 0.29 |

## CHAPTER III

# PATTERNS OF ONTOGENETIC VARIATION IN A POPULATION UNDER STRONG SELECTION: AN EXAMPLE WITH THE HOUSE FINCH

RRH: Patterns of ontogenetic variation

*Abstract.* — Evolutionary change in morphology requires phenotypic and genetic variation in ontogenies. Therefore, understanding growth trajectories and their variation in a population is important for predicting evolutionary change. We examined patterns of growth in a natural population of the house finch (*Carpodacus mexicanus*) which is currently under strong natural selection. Our aim was to examine whether phenotypic and genetic patterns of variation during ontogeny are likely to constrain morphological change favored by selection acting on adults. We found highly variable patterns of allometric relationships during ontogeny, and documented that most individual variation in growth trajectories was associated with independent variation among ages. These results imply that phenotypic ontogenetic trajectories are not strongly constrained, providing that selection acts during most independent age periods. We found that frequent compensatory growth largely cancels out the initial differences among nestlings, potentially enabling house finches to raise offspring under diverse and unpredictable environmental conditions. Moderate levels of heritable variation in morphological traits, and low covariation among ages imply strong potential for evolutionary change in morphology under selection. We conclude that developmental patterns are unlikely to exert strong constraints on the evolutionary change in morphology in the house finch - this result is consistent with the profound population-level divergence in morphological patterns in this species.

*Key words:* developmental constraints; growth trajectories; heritability; house finch; phenotypic variation

Morphological differences among adults in a population arise through individual differences in developmental processes (Gould 1977, Alberch 1982). The cause of these differences in growth is often an interaction between genetic and phenotypic factors (e.g., Cowley and Atchley 1992). A fundamental tenet of evolutionary biology is that the amount of phenotypic variation in growth sets a limit to the amount of selection that can occur at any given moment, while the amount of genetic variation in the ontogenetic parameters sets the limit of evolutionary change. Because the potential of a population to respond to selection is limited by the extent to which ontogenetic variation is heritable (e.g., Atchley 1987, Cowley and Atchley 1992), knowledge of phenotypic and genetic aspects of ontogenetic variation is essential for understanding the potential for evolutionary change in a population.

Developmental systems are often under strong stabilizing selection to maintain homeostasis (e.g., Cheverud et al. 1983). Patterns of developmental and functional integration produced by this stabilizing selection strongly influence direction in which a population evolves, and may often oppose selection pressures acting on adults (Cheverud 1984, Lande 1985, Wagner 1988, Cowley and Atchley 1992, Björklund 1996a). Alternatively, strong and consistent directional selection for faster growth (i.e., during the nestling period in birds, Ricklefs 1968) could deplete genetic variance for growth patterns, constraining potential for evolutionary change in morphology. In either case, understanding variation and covariation of ontogenetic trajectories on addition to the patterns of current selection acting on morphology of adults is essential for predicting the potential and magnitude of evolutionary change in a population (e.g., Price and Grant 1985, Kirkpatrick

and Lofsvold 1989, 1992, Grant and Grant 1995, Björklund 1996a, Larsson et al. 1998).

Patterns of developmental variation and covariation often change during ontogeny (Atchley 1987, Zelditch and Carmichael 1989, Cowley and Atchley 1992, Cane 1993), and several studies found significant additive genetic variance for traits during growth (Kinney 1969, Atchley and Rutledge 1980, Cheverud and Buikstra 1981, Gebhart-Henrich and Marks 1993, reviewed in Noordwijk and Marks 1998). The presence of heritable variation, and the observation that patterns of growth are often optimized with the local environmental conditions (Cooch et al. 1991, reviewed in Gebhardt-Henrich and Richner 1998), as well as the results of successful artificial selection on growth chronology and rate (e.g., Kinney 1969, Atchley et al. 1997), suggest that growth patterns themselves can evolve (Kirkpatrick and Lofsvold 1992, Atchley et al. 1997). At the same time, empirical evidence from many species points to conservatism of developmental systems that often manifests itself in similarities between patterns of trait covariation within a particular ontogenetic stage (i.e., static allometry), and trait covariation across all ontogenetic stages (i.e., ontogenetic allometry) (e.g. Creighton and Strauss 1986, Wayne 1986 and references therein, Voss et al. 1990, Björklund 1994, 1996b; Emlen 1996, Fiorello and German 1997). Such conservatism in ontogenies despite presence of heritable variation at each growth stage may be explained by close covariation among developmental stages (e.g., Hazel et al. 1943, Eisen 1976, Cheverud et al. 1983, Kirkpatrick and Lofsvold 1989). Several studies suggested that close genetic and phenotypic correlations and autocorrelations throughout ontogeny could severely reduce independent variation of traits at different ages, limit the number of dimentions in growth trajectories, and thus present a powerful constraint on the

evolution of growth trajectories (McCarthy and Bakker 1979, Kirkpatrick and Lofsvold 1992; Björklund 1993, 1997; Klingenberg 1996). Other studies pointed out that changes in age-specific patterns of integration, ontogenetic variation in genetic variance, and phenotypic plasticity of growth trajectories could influence the time at which selection can act (e.g., Leamy and Cheverud 1984, Cheverud and Leamy 1985, Zelditch and Carmichael 1989, Cowley and Atchley 1992, Cane 1993, Atchley et al., 1997). Thus, some stages of development may be more sensitive to selection pressure than others (e.g., Gebhardt-Henrich and Marks 1993, Cheplick 1995), providing opportunity for evolutionary modification of even well-integrated ontogenetic trajectories.

Empirical studies of covariation patterns among traits at consecutive ages can indicate the potential for evolutionary change in ontogenies, i.e., "evolutionarily possible" changes (*sensu* Kirkpatrick and Lofsvold 1992). In addition, studies of populations under intense current selection on adults could provide insight into the extent to which the developmental architecture of a species limits the morphological change favored by selection on adults, i.e., "selectively favored" changes (*sensu* Kirkpatrick and Lofsvold 1992).

Here we examine the patterns of phenotypic and genetic variation in growth of the house finch (*Carpodacus mexicanus*). The recently-established natural population of house finches in NW Montana is under strong directional selection on adult morphological traits (Chapter II). In this study we examine "evolutionarily possible" changes by addressing four questions. First, do growth trajectories vary among individuals within a population? Second, do phenotypic constraints on growth limit morphological change in adults in our

population? Third, does ontogeny of morphological traits have heritable variation, and does heritability vary throughout ontogeny? Finally, what are the potential ecological and evolutionary consequences of ontogenetic patterns found in our study population?

## METHODS

### *Data collection*

This study was carried out on the resident house finch population at an isolated storage area of 675 x 200 m, 3 km west of Missoula, Montana. The study site was located in an open field, and contained several hundred of 1-3 m high ornamental bushes used by finches for nesting, and several large coniferous trees used by finches for roosting. In 1995-98 all resident finches were captured during January-March and August-October trapping sessions, measured and marked with a unique combination of one aluminum and three colored plastic rings. All individuals were aged to HY (hatching year) and AHY (after hatching year) category according to Hill (1993a). Finches foraged within the study site, and on shortgrass prairie and agricultural fields surrounding the study site. At any time during the breeding season, the resident population consisted of about 20 breeding pairs, their nestlings, and about 60-70 adult finches that were either between nesting attempts or unpaired. See Chapter II for additional description of field techniques.

Field observations were conducted daily from 0430 to 0800 and 1400-1600 during March and April and 0430 to 1300 and 1600-2000 during May - August 1995-1998. Growth parameters, heritability estimates (see below), and duration of nestling period did not differ among the three years of study, and the data were pooled. All, but 6 nests were found during early nest building allowing first-egg date and hatching to be reliably determined for all breeding pairs. Nestlings were individually marked on the day of hatching. Nestlings were measured on day 2, 4, 6, 8, 10,

12, 14, and 16. Premature fledging of nestlings of age 10 and older was successfully prevented by covering nests with dark cloth for 30 min before and after the measurements. After fledging, age categories were categorized as follows: 25-40 days after hatching - age 33, 45-55 days - age 50, 60 - 70 days - age 65, 71-75 days - age 73, 80-85 days - age 83, and 87-144 days - age 117. Sample sizes were as follows: age 2 - 35 nestlings (12 families), age 4 - 33 (12), age 6 - 33 (12), age 8 - 69 (18), age 10 - 80 (24), age 12 - 106 (26), age 14 - 68 (18), age 16 - 72 (20), age 33 - 50 (26), age 50 - 22 (12) males and 20 (11) females, age 65 - 13 (12) males and 12 (10) females, age 73 - 16 males and 12 females, age 83 - 12 males and 14 females; age 117 - 24 males and 15 females, and known-age sample of after-second-year (adult) birds used for this study - 38 males and 36 females.

The following measures were taken: bill length measured from angle of the skull to the tip of upper mandible; bill width at the anterior end of nostrils; bill depth in a vertical plane at the anterior end of nostrils over both mandibles; tarsus length (mean of left and right); wing (mean of left and right, flattened), and body mass (in grams to an accuracy of 0.05 g). All traits were measured with digital calipers to an accuracy of 0.05mm. All morphological measures were repeated two times and the average of repeated measures was used for further analyses. All measurements were conducted by AVB.

In order to assess measurement error for each trait in adult birds we estimated repeatabilities for all traits from intra-class variance components of ANOVA. Resident birds were recaptured several times during capture sessions (intensive capture efforts for 7-14 consecutive days), and all available repeated measures for all individuals and traits within each capture season were included. Within-capture session measurement error accounted for about 7-10% of variation in most morphological traits, and for 26% of variation in body mass. In nestlings, measurement error was estimated from ANOVA to separate within- and among-individual variance (all individuals were measured twice, see above). Error variance did not exceed 12% of the total

variance and was the largest for bill width and depth (6-12%) and smallest for body mass, wing and tarsus (3-4%, see Badyaev and Martin, ms. for more details). All morphological data were ln-transformed and zero-mean standardized before the analyses.

*Methodology of allometric comparisons*

Variability in size and shape among adults can be attributed to variability in the parameters of individual ontogenetic vectors (Gould 1977). Corresponding to the different sources of this variation is the distinction between static and ontogenetic allometry. Static allometry illustrates patterns of variation and covariation of traits among individuals within a particular ontogenetic stage (Gould 1977). Ontogenetic allometry illustrates trait covariation among all ontogenetic stages within a species or population (ibid.).

Because bivariate growth curves can be transformed into straight lines (e.g., Alberch et al. 1979), variability in ontogenetic vectors can be described by a slope, intercept and length of bivariate regressions (e.g., Shea 1985). The slope is referred to as the ontogenetic allometry coefficient and represents the ratio of relative growth for the two traits involved (Cock 1966, Table 1). However, slopes and intercepts are often estimated from regressions using animals at one age (the slope of this regression is referred to as the static allometry coefficient), instead of over the entire individual ontogeny. More generally, the static allometry coefficient represents relative growth when it is equal to the average ontogenetic allometry coefficient. Thus, to better estimate static and ontogenetic allometric coefficients, we need to use a method that allows simultaneous evaluation of variation in several groups (i.e., ages).

We used the common component analysis (CPCA, Flury 1988). The model underlying CPCA assumes that all group covariance matrices share the same eigenvectors, termed common principal components (CPC's), but that the eigenvalues associated with these CPCs are not

necessarily equal in different groups (Klingenberg and Zimmermann 1992, Klingenberg 1996, Klingenberg et al.1996). A single group (i.e., age-specific) CPC's which are estimated as the eigenvectors of the age-specific covariance matrices are considered to differ only by a sampling error (Flury 1988). On the contrary, the eigenvalues associated with CPCs are estimated separately. Thus, our CPC model assumes that allometric patterns are common to all ages, but the ages may differ in the amount of variation associated with this patterns (see below).

*Common principal components and estimates of growth trajectories*

Longitudinal growth studies with multiple measurements produce correlations both within and across stages. Because the patterns of variation and covariation in morphological traits are clearly similar among different ontogenetic stages (Cock 1966, Gould 1977, Table 1), the CPC's model assuming that the different ages share the same principal components may be especially appropriate (Klingenberg and Zimmermann 1992, Klingenberg 1996, Klingenberg et al.1996). In addition, the CPC model for longitudinal growth studies assumes that different components are uncorrelated not only within, but also across ages (Flury 1988, Klingenberg et al.1996). Because the CPCs are uncorrelated both within and across ages, the diagonal elements of each block of the CPC scores (see Klingenberg et al.1996 for graphic representations) can be used to study covariation among CPC scores among ages. Thus, unlike the original measurements, in which separate analyses of covariation among ages for each age ignore the correlations among traits, each CPC can be analyzed without any loss of information (reviewed in Klingenberg et al. 1996). Thus, similarly to conventional principal component analysis, the CPC model can be useful tool for reduction of dimensionality of the data (Flury 1988; Klingenberg and Zimmermann 1992). We evaluated the CPC model for age periods with Flury's (1988) decomposition of chi-square tests conducted with algorithms provided by P. Phillips ( http://wbar.uta.edu/software/ cpc.html) and

programs in SAS/IML (SAS Institute 1989) by C.P. Klingenberg (http://life. bio.sunysb. edu/morph/dcpc.exe).

To investigate patterns of variation and covariation among ages, we calculated principal component coefficients from a covariance matrix of CP1 scores for each age. To maintain adequate sample sizes, only ages 2 - 33 days were used in these analyses. High covariation among ages would produce a highly- integrated ontogeny where variation in one age would affect all subsequent groups. This ontogenetic pattern would produce monotonically increasing or decreasing PC1 loadings for each age (Klingenberg 1996; see also Kirkpatrick and Lofsvold 1989). Highly variable and distinct PC1 loadings among ages, and especially loadings of the opposite signs indicate negative covariation among some ages. Such ontogenetic patterns are considered "relatively unconstrained" and could be produced by compensatory growth of traits at different ages (Cheverud et al. 1983, Riska et al 1984, Klingenberg 1996).

*Description of allometric patterns, growth trajectories, and genetic parameters*

The standardized loading of a trait on the first principal component is the bivariate allometry coefficient of that trait with size. The isometric vector has the standardized loadings $(1/p)^{1/2}$ where $p$ is a number of traits. With nine traits, $(1/p)^{1/2}$ was 0.408, so that the ratio of each trait's loading with 0.408 is the bivariate allometry coefficient of that trait with overall body size. Thus, all loadings greater than 0.408 indicated positive allometry with size, while all loadings less that 0.408 indicated negative allometry with overall size (e.g., Shea 1985). Calculated for each age separately, these allometric relationships represent static allometric coefficients (Table 1). Because of significant deviations of age-specific vectors from isometry, we also estimated bivariate coefficients of traits in relation to each other (Shea 1985).

Additional information about differences in allometric patterns among ages can be obtained by comparison of the direction of the major axes of scatter data ellipsoids among several

ages. A most straightforward measure of differences between two groups (i.e., each age versus isometry) is the angle between principal components for these groups. For the principal components of two groups, the angle between them is the arc cosine of the inner product (vector "correlations") of the two vector elements.

To estimate variability in ontogenetic vectors over the entire growth sequence, we performed MANOVA of individuals and ages. Then, ontogenetic allometry coefficients (see above) can be estimated from the first principal component (PC1) of the among-age matrix of the sum of squares and cross-products (SSCP matrix) (after Klingenberg 1996). In this case, PC1 of the matrix is a vector of ontogenetic allometry. Standard errors were estimated from 30 random resamplings with replacement of the entire individual ontogenetic sequences. In most of the literature, ontogenetic allometry coefficients are estimated as PC1 of the conventional principal component analysis on data pooled over all individuals and all ages (Cock 1966, Gould 1977, Shea 1985, Björklund 1993 and references therein). However, the use of the SSCP matrix allows us to take full advantage of the longitudinal data in this study.

Morphological integration is the degree of interdependency among morphological parts that in combination produce an organized and integrated whole (Olson and Miller 1958). Specifically it is often assumed that the degree of functional and developmental interdependence among morphological traits is directly related to the degree of morphological integration among them (ibid.). Here, we estimate the degree of integration by an index $I$, where $I = [\sum(\Gamma i - 1)^2 / (n^2 - n)]^{1/2}$ such that $\Gamma i$ are the eigenvalues, and $n$ is the total number of characters in the correlation matrix (Olson and Miller 1958).

The parent-offspring regression for a trait is the ratio of covariance between offspring and parents to the variance of the parents, and therefore could be used to estimate the heritability of a trait (Falconer and Mackay 1997). We estimated single parent (female and male parent) and mid-

parent regressions for ages 2 - 50. Correlations were calculated for all nestlings, i.e., parent values were re-used for every nestling in the brood (after Price and Grant 1985). Maternal effects were estimated by subtracting the regression of offspring on father from that of offspring on mother (Lande and Price 1989). To account for assortative mating between parents, we calculated partial regression coefficients between a trait in a parent and an offspring while holding the trait value of the other parent constant. Unequal phenotypic variance of parents could bias a singe-parent versus offspring estimates of heritability (Falconer and Mackay 1996). However, the male and female phenotypic variances for the measured traits were equal (Chapter II).

## RESULTS

### *Description of growth and nestling static allometry*

Traits differed in an onset and intensity of growth (Fig. 1). In females, tarsus length reached adult size (measured as an adult female size) at 13 days (age 13 hereafter), wing reached adult size at age 33, bill length and width at age 50, and bill depth and body mass around age 73 (Fig. 1). In males, sexually dimorphic traits grew longer; sexual dimorphism in bill length and width reached their adult level at age 73, wing and body mass at age 73-83 (Fig. 1). For bill traits, the fastest growth occurred from ages 2 to 6 and then from fledging (age 16) to age 33 (Fig. 1). In body traits, most growth was from age 4 to 6 and then after fledging for body mass and wing length (Fig. 1).

The differences among traits in growth patterns were evident in static allometric relationships (Tables 1 and 2, Fig. 2). At age 2 most traits had a negative allometric relationship (i.e., relationship less than one) to tarsus length and bill depth (e.g., wing/tarsus = 0.393/0.446 = 0.881; bill length/bill depth = 0.393/0.431 = 0.912). Growth pattern from age 4 to age 12 was dominated by negative allometries of traits in relation to body size, in particular wing and body mass. These patterns changed drastically after fledging (age 16) when most traits had negative allometries in relation to bill traits, especially bill depth (Table 2). In addition to these general patterns, at age 4, an increase in bill length and depth were larger relative to other traits. At age 12, relative increase in tarsi was the most prominent in relation to other traits. Growth patterns changed at age 14 when all traits had negative allometries to bill length and depth. At fledging, relative growth gains were greater for wing, tarsus, and bill length, although the differences in slopes were small (Table 1).

Overall, bill traits often had negative allometry to size (i.e., loading less than the isometric loading = 0.40$\hat{8}$) before the fledging, and positive allometry to size after fledging (Tables 1 and 2).

Body traits had the opposite pattern, with exception of age 2, wing and body mass had positive allometry in relation to size before fledging and negative allometry to size after the fledgling (Tables 1 and 2). The first eigenvector showed considerable departures from isometry throughout the ontogeny. Angle between the first eigenvector and the isometric vector ranged from 2.5° at age 2 to 37° at age 8 (Table 3). The most significant deviations from isometry (e.g., 53.8° at age 73) occurred after fledging; these deviations were most likely associated with accelerated growth of sexually dimorphic traits in males (Fig. 1).

The level of morphological integration was highest (57-79%) at ages 2-6, then decreased to 40-50% during ages 10-33, and approached adult level of 27-28% by age 73 (Fig. 3, Tables 1 and 2). Analysis of static allometry showed that CPC1 was approximately an isometric size vector ($r_v$ with isometric vector = 0.9978, $\alpha$ = 3.8°) with positive and similar loadings to all traits (Table 4). Loading patterns of the remaining CPC's indicated independent ontogenetic variation among morphological traits. For example, CPC2 emphasized variation in bill length in contrast to other bill and body traits, while CPC3 did the same for bill length and wing. CPC4 contrasted bill width with bill depth development, and wing growth with other body traits, while CPC5 almost exclusively represented variation in body mass independently of other body traits. CPC6 contrasted tarsus growth with growth of other traits. Because the matrices with well-spaced eigenvalues are the most influential in common component analysis (Flury 1988), the overall static allometry patterns were mostly affected by ages 2-6, 12, and 16 (Table 4, Fig. 2, see below).

*Ontogenetic allometry, individual variation in growth, and growth trajectories*

Analyses of ontogenetic allometry revealed variable patterns of development, especially for body traits (wing, tarsus, and body mass). The first eigenvalue of the SSCP among-age matrix accounted for only 61.5% of the total variance, and the first two eigenvalues accounted for 78.2 %

of the total variance. Static and ontogenetic allometries were quite distinct (Fig. 2), probably reflecting the contrast between early- and late-maturing traits (i.e., body- versus bill traits, see below, Tables 1 and 2, Fig. 1).

Phenotypic correlations across age groups (not shown) were generally low and sometimes near zero or slightly negative. Age-specific covariance matrices were mostly distinct, even between consecutive ages (e.g., matrices for ages 6 and 8, ages 8 and 10, and ages 16 and 33 shared no common principal components (CPCs), $\chi^2 = 61.5$, df = 5, $P < 0.001$, AIC = 42.0; $\chi^2 = 24.5$, df = 5, $P < 0.001$, AIC= 56.5, and $\chi^2 = 20.4$, df = 5, $P = 0.001$, AIC = 42.0 correspondingly). The most similar ages were ages10 and 12, where matrices shared three of four CPCs: $\chi^2 = 18.7$, df = 12, $P = 0.05$, AIC = 36.7); and ages 12 and 14, where matrices shared two CPCs: $\chi^2 = 23.1$, df = 9, $P = 0.006$, AIC = 47.1). Similar patterns emerged from comparison of age-specific eigenvalues from common component analysis (Table 4). For example, in ages 2-6 the second largest eigenvalue was associated with CPC2, while in ages 8-10 with CPC4, in age 12 with CPC3, and in age 14 with CPC6 (Table 4).

Low phenotypic covariation across ages was evident in the patterns of age-specific variability, where the largest eigenvalue of the PCA on CPC1 scores accounted for only 44% of the total variation, and the first three eigenvalues accounted for 90% of the total variation (Fig. 4). None of the PCs accounted for most of the variation during all ages. Instead, PC1 primarily explained variability during early ages in contrast to ages 4, 14 and 33, PC2 accounted for variability in ages 4, and 8-33 in contrast to ages 2 and 6, and PC3 mostly explained variation during the first 4 days of the nestling period (Fig. 4). Thus, given that no single component accounted for variability in all ages simultaneously (Fig. 4), we found no evidence of strong phenotypic constraints on growth. While a large portion of variation in growth was still associated with one growth trajectory (PC1, Fig. 4), there were at least three directions for which considerable

phenotypic variation is present. The negative covariance observed between consecutive stages points to compensatory growth, especially between ages 2 and 4, and 16 and 33. Such compensatory growth is likely to balance the differences that were present among nestlings in the earlier ages (Fig. 5) and closely corresponds to the periods of maximum growth gains (Fig. 1). A decrease in total phenotypic variance of standardized traits with age (Fig. 5) and a decrease in sample variances for principal components (expressed as eigenvalues, Table 1 and 2) strongly suggests that compensatory growth is widespread during development in the house finch. Variances were the highest in ages 2-6 and gradually decreased with age (Fig. 5).

### *Genetic variation in growth*

Patterns of heritability were similar among traits. At early stages, correlations of nestling traits with female parent traits were generally high and significant, especially for body traits (wing, tarsus, and body mass; Fig. 6). During the same period, correlations with the male parent were often lower and non-significant. This difference between male and female correlations suggests maternal effects on nestling traits during early age (up to age 6, Fig. 6). The correlations between a single parent and nestlings increased with age, and several estimates reach significance by age 16 (Fig. 6). Similarly, correlations between mid-parent and nestlings increased with age and were significant for all traits by age 50 with the exception of body mass. Heritability estimates at age 50 were high and varied from 0.35 to 0.51 for bill traits, and from 0.32 to 0.55 for body traits.

## DISCUSSION

Evolutionary change in morphology requires phenotypic and genetic variation in ontogenies. Thus, understanding growth trajectories and their variation in a population is important to predict evolutionary change. Several problems need to be investigated. First,

examination of an association between morphological patterns of adults and morphological patterns prevailing during growth can reveal how closely static allometry correlate with ontogenetic allometry. Similarities between these allometries would imply that adult morphological patterns could be reliably predicted from morphological patterns during developments (e.g., Voss et al. 1990, Klingenberg and Zimmermann 1992, Björklund 1996b). Second, analyses of phenotypic covariation among traits at different ages can indicate potential for evolutionary change in ontogenies (Cheverud 1984, Lande 1985, Cowley and Atchley 1992). Specifically, close covariation among ages implies that selection on a trait at one age would result in changes in this trait for consecutive stages (e.g., Riska et al., 1984, Kirkpatrick and Lofsvold 1989). In addition, if close covariation among ages is accompanied by close integration among traits at each stage, the overall short-term change in morphology will be limited to a few directions only, irrespective of directions favored by current selection (Cheverud et al., 1983, Wagner 1988, Kirkpatrick and Lofsvold 1989). Third, the amount of heritable variation in ontogenies could limit the potential for evolutionary change (e.g., Atchley 1987). Moreover, the ontogenetic variation in heritability strongly influences outcome of selection (Atchley et al. 1990). Here we consider these problems in turn.

We found a large amount of phenotypic variation among ontogenetic trajectories in the natural population of the house finch. Static allometric relationships (i.e., bivariate slopes of PC1 loadings for each age, Tabes 1 and 2) varied during development mostly due to differences in the onset of growth and growth rates between bill and body traits (Fig. 1). Relative growth in body traits (i.e., tarsus, wing, and body mass) started earlier and continued at higher rates compared to later-maturing bill traits (bill length, width and depth) (Tables 1 and 2). Heterochrony in body and bill traits is widespread in Cardueline and Emberizidae finches (Grant 1981, Boag 1984, Björklund 1994), and may be related to the resources preferentially allocated to the traits with immediate

functional importance at a certain age (e.g., O'Connor 1977, reviewed in Starck 1998). For example, fast growth in body mass may be a priority for thermoregulation reasons (Cane 1993), while rapid growth of tarsi may be adaptive for intra-brood competition (Cane 1993, Teather and Weatherhead 1994 and references therein, Monk 1998), or for early leaving of the nest in areas with high nest predation (e.g., Ricklefs 1969, Björklund 1994, Martin 1995, 1996).

Principal component analysis of CPC scores for each age provides an estimate of phenotypic variation in ontogenies among individuals (Klingenberg et al. 1996). If most of the total variation is limited to the first principal component (i.e., approximation of size at each age), this would imply a phenotypic constraint on changes in any other direction (Klingenberg 1996; see also Kirkpatrick and Lofsvold 1992, Björklund 1993, 1996a, 1997). We found that the first eigenfunction illustrated variation in only certain ages, and accounted for only a moderate amount of the total ontogenetic variation (Fig. 4). Large amounts of variation accounted for by the first three eigenvalues implies significant potential for evolutionary change in these three directions. Our results suggest that as long as selection favors morphological change in directions described by these three eigenvalues (Tables 1 and 4, Fig. 4), phenotypic constraints during ontogeny are unlikely to strongly limit evolutionary change.

These results differ from those of several recent studies that documented lack of genetic and phenotypic variation for ontogenetic change other than change in overall size (e.g., Cheverud et al 1983, Leamy and Cheverud 1984, Kirkpatrick and Lofsvold 1992 and references therein, Klingenberg 1996). For example, Björklund (1993) used the infinite-dimensions method (Kirkpatrick and Lofsvold 1989) to analyze the phenotypic variation in ontogeny of three Cardueline finches, including a close relative of the house finch - common rosefinch (*C. erythrinus*). He found significant phenotypic ontogenetic variation in

only one growth trajectory - the "size" trajectory that accounted for the largest amount of variation in all ages simultaneously (see also Björklund 1997). Klingenberg (1996) suggested that similarities in covariance patterns among diverse taxonomic groups point to the universal pattern of autocorrelation among consecutive growth stages in the absence of compensatory growth. Klingenberg's (1996) re-analysis of available data-sets on growth indicated that phenotypic constraints on growth may not be as stringent when analyses account for autocorrelation among ages. Our analyses revealed that the amount of ontogenetic phenotypic variation is not closely constrained and production of a morphological change within limits outlined by the three dimensions (eigenvalues) may be possible. These results may provide an explanation for the patterns of multivariate morphological divergence among house finch populations (Badyaev and Hill, ms). The house finch populations in Alabama, California, Michigan, Mexico, and Montana were significantly different not only in overall size, but also in morphological covariance patterns (Badyaev and Hill, ms).

We found that while the first eigenvalue accounted for only a moderate amount of the total variation, the first two eigenvalues summarized a considerable amount of the variation (Fig. 4). This pattern was likely produced by alternation of positive and negative covariations between consecutive ages. Absence of strong autocorrelation among ages, and negative covariations between ages suggests widespread occurrence of compensatory growth in ontogeny of the house finch in our population. Patterns of compensatory growth (Riska et al. 1984) are evident in the ontogenetic variance patterns (Fig. 5): phenotypic variance is high during early ages and then reduced (compensated for) as individual growth trajectories converge to a "target" morphology (*sensu* Tanner 1963) at the end of growth (Fig. 5). Widespread compensatory growth and variation in trait integration throughout ontogeny of the house finch may account for changes in allometric

relationships described above (see also Smith and Wettermark 1995). Theory suggests that patterns of adult allometry and integration should be most congruent with allometries present during periods of maximum growth and maximum integration (e.g., when allometries relationships are most close to isometric) (Cock 1969, Cheverud 1982, Cane 1993). Thus, allometry of adult house finches should most closely resemble growth patterns found in ages 2-6 (Tables 1-3, Fig. 1). Indeed, allometry of fully grown house finches closely resembles that of hatchlings (Tables 1-3). However, compensatory growth at the intermediate stages greatly reduces the amount of individual variation present early in development (Table 1, Fig. 5). Levels of integration decreased after age 6 (Fig. 3), thus potentially enabling selection to act on variation in individual traits. Fluctuating integration and patterns of compensatory growth may provide additional opportunity for selection during ontogeny (e.g., Zelditch and Carmichael 1989).

Compensatory or "targeted" growth may be adaptive if it enables individuals to achieve the same adult size under diverse environment conditions (Riska et al. 1984, Cooch et al. 1991, 1996; Smith and Wettermark 1995, Larsson et al. 1998). For example, accelerated compensatory growth is often associated with intensive feeding after periods of malnutrition. The house finches in the recently-established population in NW Montana often hatch nestlings under extreme environmental conditions. First nests are initiated in late February-March when repeated snow storms and prolonged sub-zero temperatures severely limit food provisioning by parents (Badyaev, unpubl. data). Under such unpredictable and harsh conditions, flexible intra-brood growth rates should be highly beneficial. Later in the nestling period, during more favorable conditions, initial differences in size are often compensated by periods of accelerated growth (Fig. 5). Similarly, in early nesting pairs females often start incubating with the first egg, which leads to pronounced hatching asynchrony in our study population (Badyaev, pers. obs). In turn, hatching asynchrony leads to strong initial differences in size within a brood. Incubation from the first egg and pronounced

differences in hatchling sizes are common in cardueline finches that breed at high elevations (Badyaev 1990, 1997ab). In three species of high-elevation finches, high covariation among ages maintained the initial differences in nestling sizes throughout the entire nestling period, and the initial size differences were evident at the time of fledging (Badyaev 1990, 1993, 1994). On the contrary, in the house finch, low covariation among ages and strong compensatory growth during periods of maximum growth gains largely cancel out differences among nestlings present at the early stages (Figs. 5 and 6).

In addition to variation in environmental conditions and hatching asynchrony, differences in size at hatching could be due to maternal effects, such as egg size (e.g., Schifferli 1973). Differences between father vs. offspring and mother vs.offspring regressions point to strong maternal effects on hatching size (e.g., wing, tarsus, and body mass, Fig. 6). Maternal effects on offspring size largely disappeared by age 6 (Fig. 6). This corroborates conclusions from other studies that lasting maternal effects on adult morphology are rare, and most initial differences due to maternal effects disappear during the nestling period (e.g., Merila 1996, reviewed in Price 1998). However, some studies documented lasting effects of differences in egg-size and hatching size (e.g., in *Parus major* Schifferli 1973; *Branta leucopsis* Larsson et al., 1998). Lasting maternal effects in these examples may be due to weak compensatory growth under unfavorable environmental conditions (e.g., Larsson et al 1998; reviewed in Price 1998, Noordwijk and Marks 1998).

Heritability of trait variation increased with age (Fig. 6), partially because of decreased environmentally-induced phenotypic variation in most traits (Fig. 5). All traits, but body mass (a trait with the lowest repeatability in adults, Badyaev and Martin, ms), had high and significant heritabilities by age 50 (Fig. 6). Because the amount of evolutionary change is determined by the amount of genetic variation present at each selection event, high heritabilities suggest that

evolutionary response to selection is likely to be fast. Strong response to selection is further favored by low covariation among ages and traits, thus providing both opportunities for morphological change in many directions and opportunities for selection to act on individual traits.

This study suggests that the large amount of variation in individual ontogenetic trajectories, and moderate heritabilities of morphological traits may have accounted for close congruence between current net selection and morphological variation in adult house finches in our study population (Badyaev and Martin, ms). Evolutionary response to selection could also manifest itself in a strong adaptive divergence in morphological patterns among house finch populations (Badyaev and Hill, unpubl. ms). In addition, widespread occurrence of compensatory growth in the house finch ontogeny may have allowed development under a wide variety of environmental conditions, and ultimately contributed to the unusually high colonization abilities of this species.

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Table 1. Multivariate allometry and integration of morphological traits during early growth stages of the house finch. Shown are the first eigenvectors of age-specific matrices, and the proportion of total variance (%) accounted for by the first eigenvalue from the variance-covariance matrix of ln-transformed values.

| Trait | Age 2 | Age 4 | Age 6 | Age 8 | Age 10 | Age 12 | Age 14 | Age 16 |
|---|---|---|---|---|---|---|---|---|
| Bill Length | 0.393 | 0.530 | 0.322 | 0.453 | -0.007 | 0.260 | 0.515 | 0.410 |
| Bill Depth | 0.431 | 0.531 | 0.404 | -0.095 | 0.181 | 0.186 | 0.493 | 0.299 |
| Bill Width | 0.388 | 0.128 | 0.407 | 0.160 | 0.291 | 0.238 | 0.436 | 0.216 |
| Wing | 0.393 | 0.559 | 0.442 | 0.626 | 0.625 | 0.536 | 0.422 | 0.570 |
| Tarsus | 0.446 | 0.340 | 0.427 | 0.253 | 0.416 | 0.530 | -0.128 | 0.472 |
| Body Mass | 0.395 | -0.116 | 0.435 | 0.552 | 0.565 | 0.522 | 0.327 | 0.385 |
| % var | 82.17 | 57.76 | 82.46 | 56.88 | 42.85 | 51.69 | 47.70 | 43.76 |

Table 2. Multivariate allometry and integration of morphological traits during late growth stages of the house finch. Shown are the first eigenvectors and the proportion of total variance (%) accounted for by the first eigenvalue from the variance-covariance matrix of ln-transformed values. [1]Effects of sex are removed in ANCOVA for ages 50 and older.

| Trait | Age 33 | Age 50[1] | Age 65 | Age 73 | Age 83 | Age 117 | Adults |
|---|---|---|---|---|---|---|---|
| Bill Length | 0.514 | -0.325 | 0.186 | 0.579 | 0.469 | 0.563 | 0.448 |
| Bill Depth | 0.462 | 0.062 | -0.237 | 0.278 | 0.588 | 0.242 | 0.367 |
| Bill Width | 0.441 | 0.411 | 0.683 | 0.646 | 0.459 | 0.311 | 0.458 |
| Wing | 0.219 | 0.492 | 0.421 | -0.340 | -0.185 | 0.128 | 0.316 |
| Tarsus | -0.111 | 0.523 | 0.499 | 0.061 | 0.051 | 0.570 | 0.252 |
| Body Mass | 0.517 | 0.455 | 0.128 | 0.225 | 0.432 | 0.431 | 0.540 |
| % var | 52.52 | 47.62 | 34.70 | 32.50 | 39.97 | 35.20 | 40.10 |

Table 3. Ontogenetic vector correlations ($r_v$) and vector angles ($\alpha$) in the house finch. Shown are correlations and angles between age-specific vector and an isometric vector.

| Age | $r_v$ | $\alpha$ |
|---|---|---|
| Age2 | 0.999 | 2.5° |
| Age4 | 0.927 | 22.2° |
| Age6 | 0.995 | 5.7° |
| Age8 | 0.796 | 37.3° |
| Age10 | 0.845 | 32.3° |
| Age12 | 0.928 | 21.9 |
| Age14 | 0.843 | 32.5° |
| Age16 | 0.960 | 16.3° |
| Age33 | 0.834 | 33.5° |
| Age50 | 0.660 | 48.7° |
| Age65 | 0.686 | 46.7° |
| Age73 | 0.592 | 53.8° |
| Age83 | 0.741 | 42.2° |
| Age117 | 0.917 | 23.5° |
| Adults | 0.972 | 13.6° |

Table 4. Common principal-component eigenvectors and associated eigenvalues for the growth stages of the house finch. Eigenvalues are shown for each age.

| Trait | CPC1 | CPC2 | CPC3 | CPC4 | CPC5 | CPC6 |
|---|---|---|---|---|---|---|
| *Eigenvectors* | | | | | | |
| B. Length | 0.379 | 0.779 | 0.345 | -0.131 | -0.028 | -0.337 |
| B. Depth | 0.416 | -0.308 | -0.381 | -0.670 | -0.047 | -0.370 |
| B Width | 0.362 | 0.186 | -0.687 | 0.576 | 0.142 | -0.100 |
| Wing | 0.424 | -0.400 | 0.352 | 0.394 | -0.586 | -0.194 |
| Tarsus | 0.434 | 0.138 | -0.070 | -0.198 | -0.232 | 0.833 |
| Body Mass | 0.430 | -0.291 | 0.367 | 0.090 | 0.761 | 0.089 |
| *Eigenvalues* | | | | | | |
| $\lambda_{Age\ 2}$ | 4.916 | 0.560 | 0.337 | 0.033 | 0.153 | 0.000 |
| $\lambda_{Age\ 4}$ | 4.801 | 0.436 | 0.103 | 0.065 | 0.013 | 0.013 |
| $\lambda_{Age\ 6}$ | 4.921 | 0.466 | 0.186 | 0.175 | 0.018 | 0.233 |
| $\lambda_{Age\ 8}$ | 1.473 | 0.448 | 0.799 | 0.969 | 0.273 | 0.210 |
| $\lambda_{Age\ 10}$ | 2.05 | 1.012 | 0.643 | 1.189 | 0.186 | 0.565 |
| $\lambda_{Age12}$ | 3.185 | 0.638 | 0.860 | 0.614 | 0.146 | 0.629 |
| $\lambda_{Age14}$ | 1.871 | 0.181 | 0.630 | 0.482 | 0.641 | 1.005 |
| $\lambda_{Age\ 16}$ | 2.486 | 0.654 | 0.551 | 0.992 | 0.551 | 0.765 |
| $\lambda_{Age33}$ | 2.481 | 0.606 | 0.407 | 0.205 | 1.108 | 1.553 |

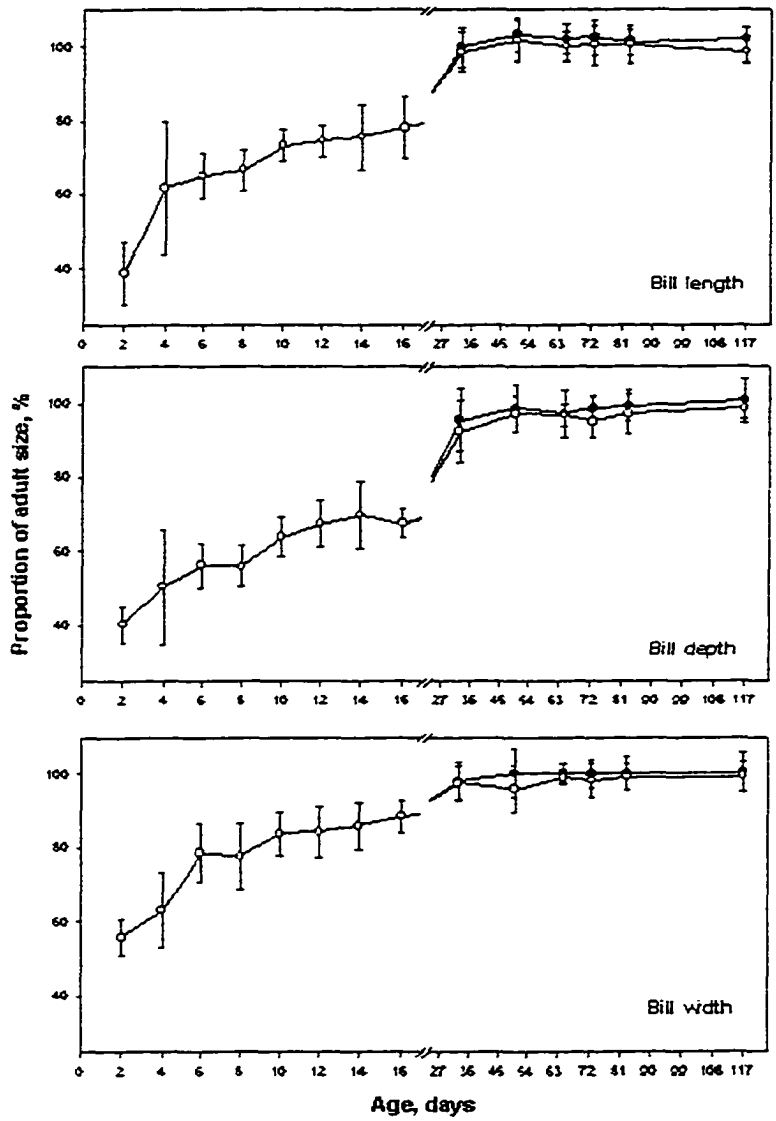



Figure 1 (A). Growth curves (mean and SE) illustrating the relationship between age (days) and the proportion of adult size (size of adult female) for bill traits in the house finch.

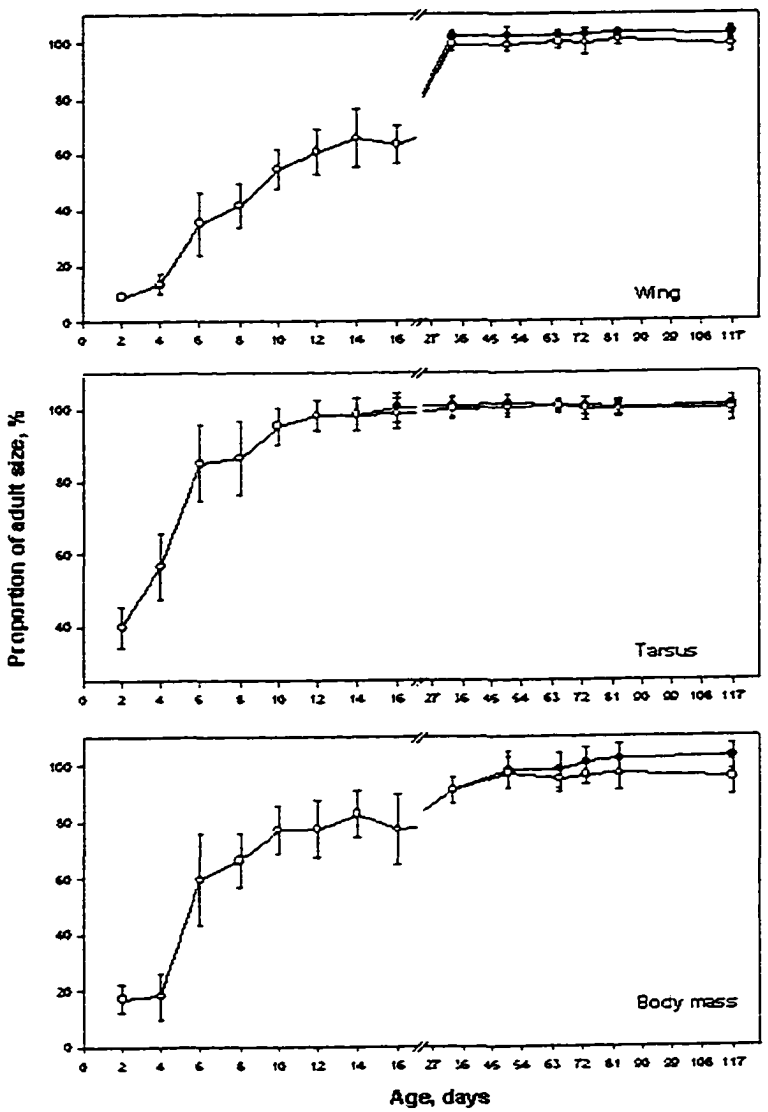



Figure 1 (B). Growth curves (mean and SE) illustrating the relationship between age (days) and the proportion of adult size (size of adult female) for body traits in the house finch.

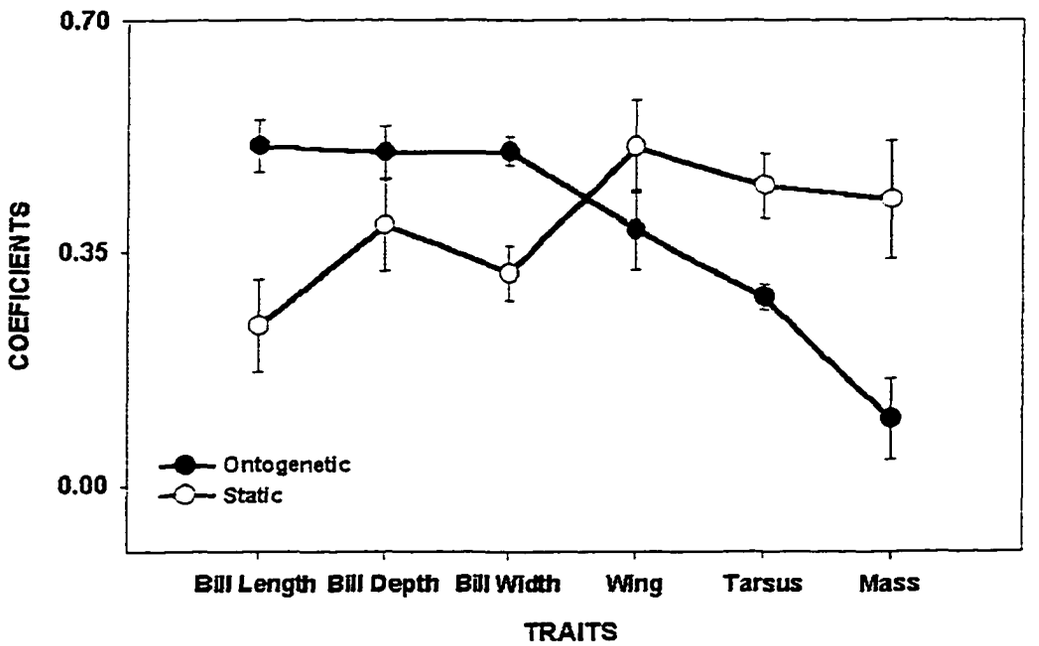



Figure 2. Static and ontogenetic allometry of the house finch growth. Static allometry is presented as the first common component (CPC1) of covariance matrices for each age; ontogenetic allometry is presented as the first principal component (PC1) of the among-age matrix of sums of squares and cross-products. Error bars are the bootstrapped SE of the estimates.

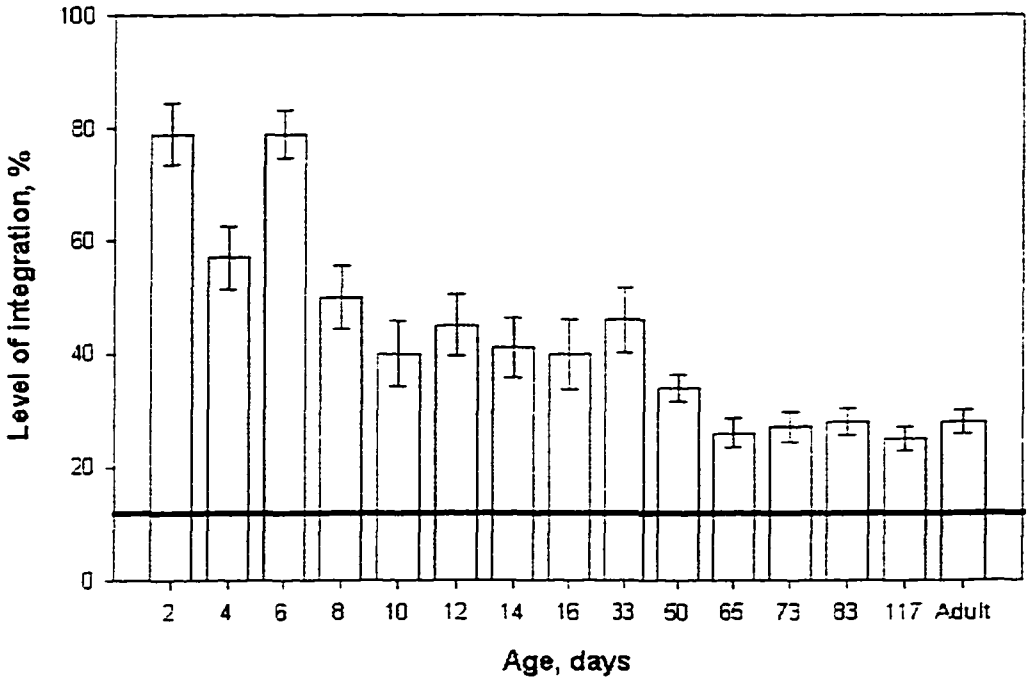



Figure 3. Level of morphological integration (degree of inter-dependence among morphological traits) in relation to age in the house finches. Horizontal line represents a random value of integration (Wagner 1984).

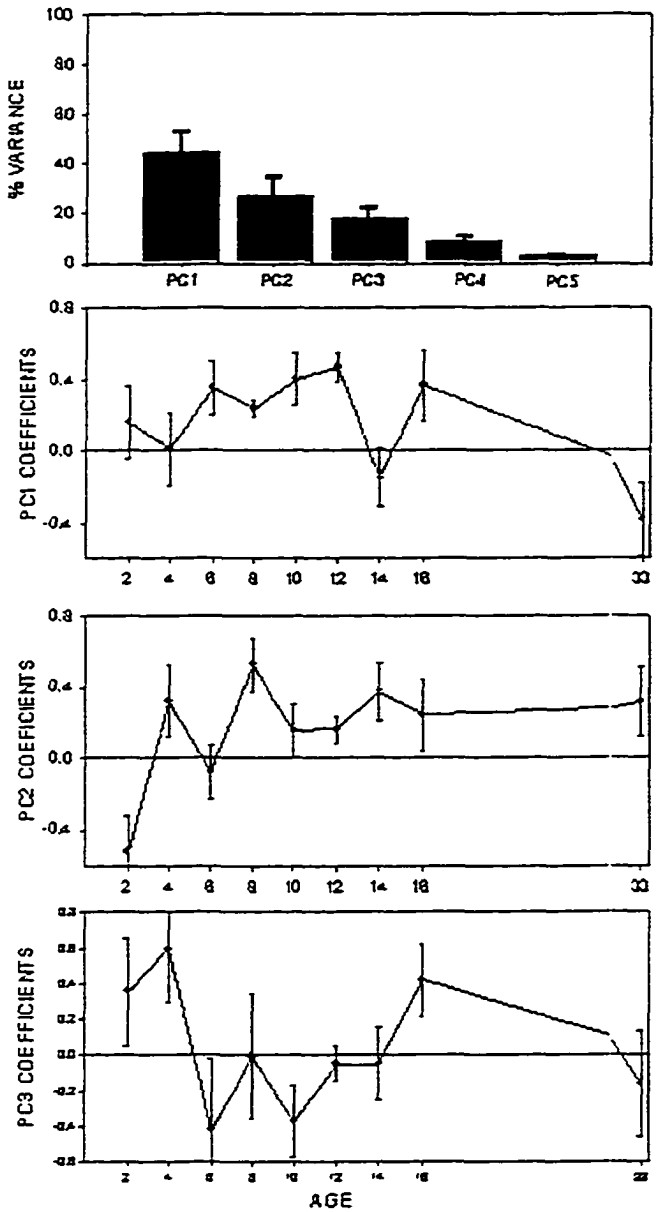



Figure 4. Patterns of individual variation and covariation in growth trajectories among different ages of the house finches. (A) Percentage of total variance explained by principal-component (PC) eigenvalues of covariance matrix of individual scores of the first common component (CPC) in all ages. Coefficients of the (B) PC1, (C) PC2, and (D) PC3 for each age group. Error bars are the bootstrapped SE of the estimates.

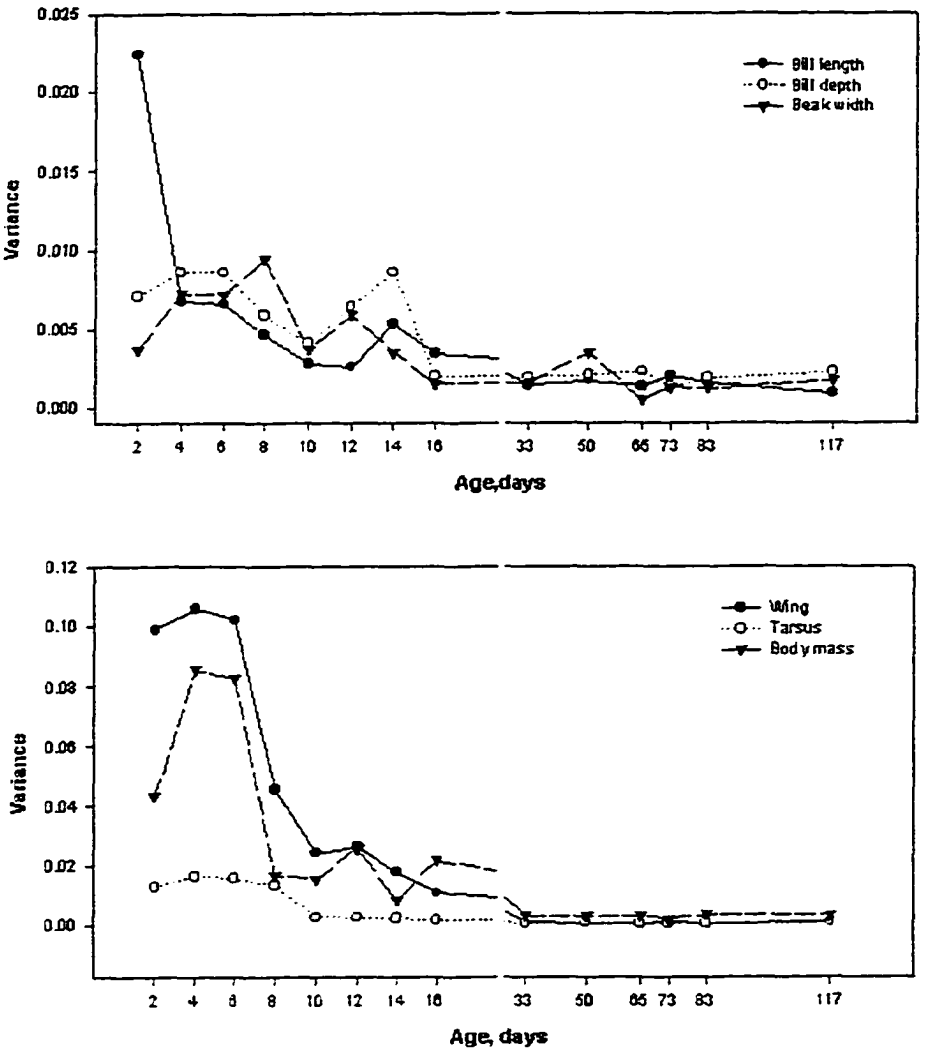



Figure 5. Total phenotypic variance in relation to age for bill traits (above), and body traits (below).

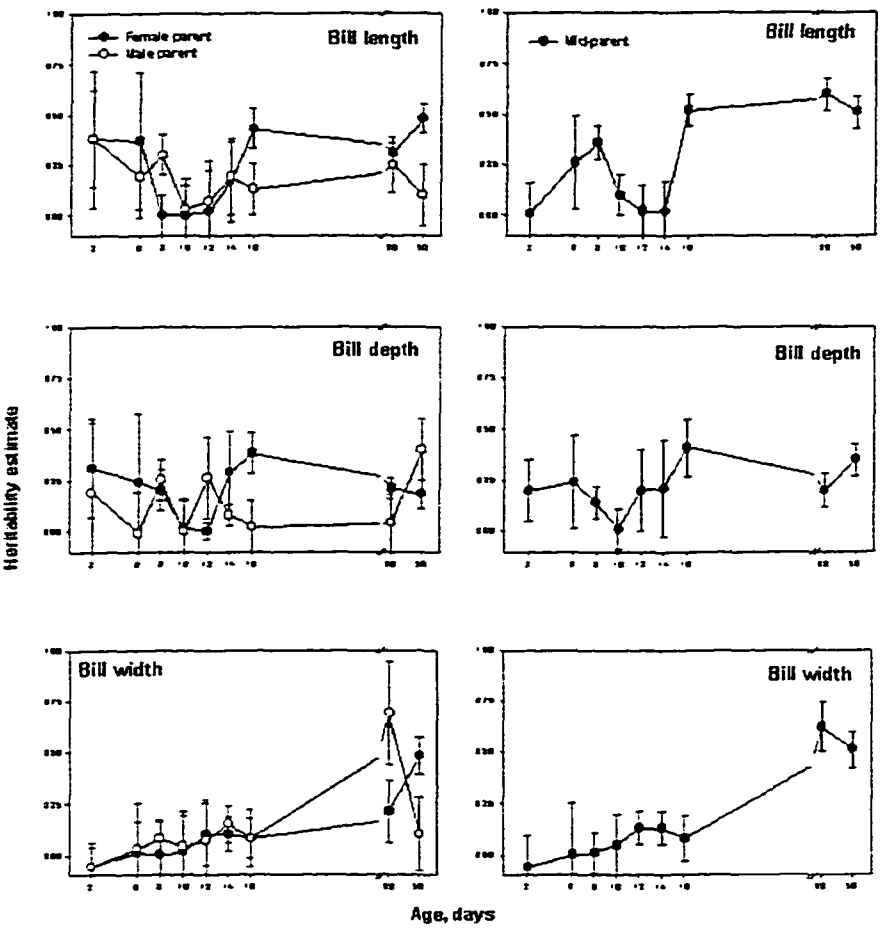



Figure 6A. Ontogenetic changes in partial correlations for bill traits between parents and offspring (controlling for the effect of one parent at the time), and correlations between mid-parent values and offspring.

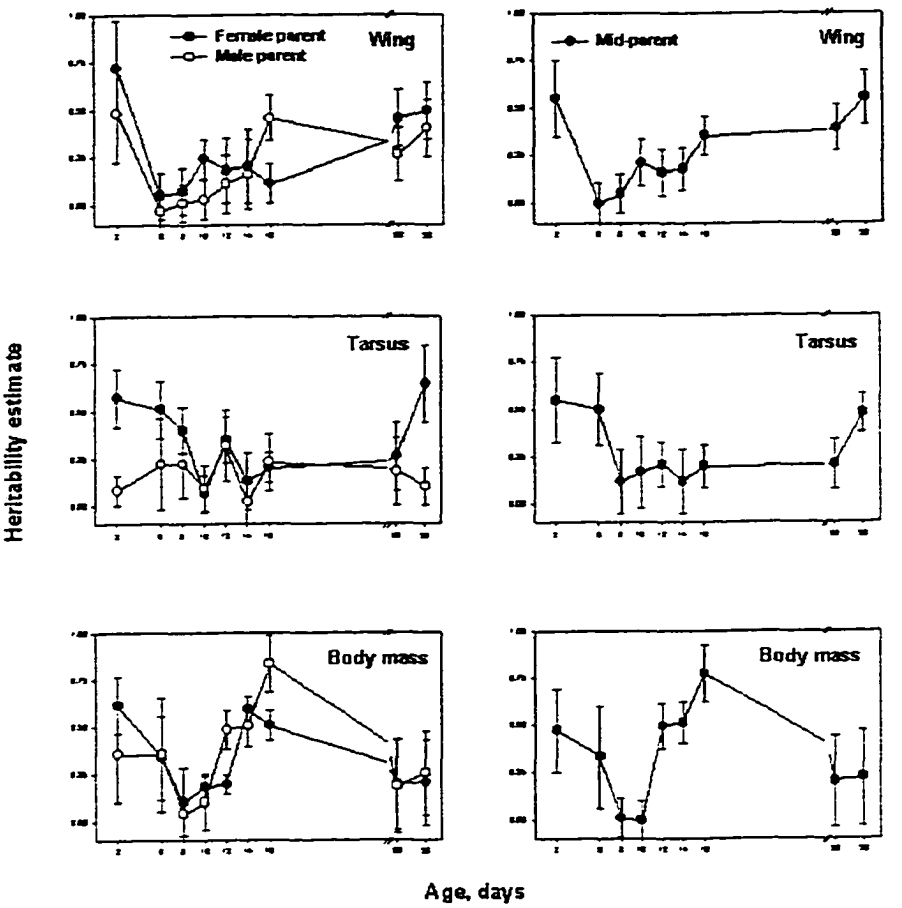
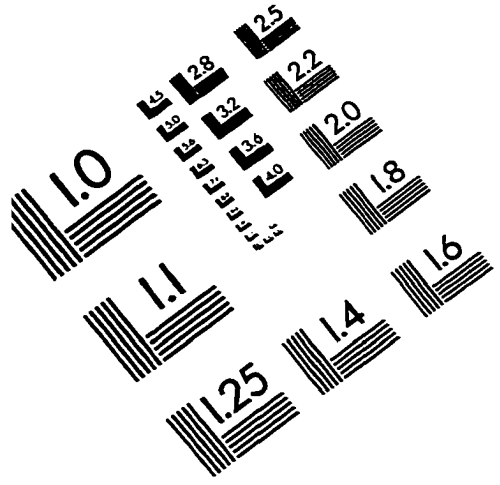
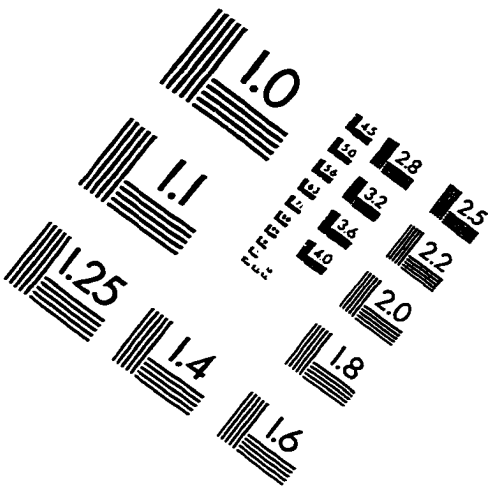
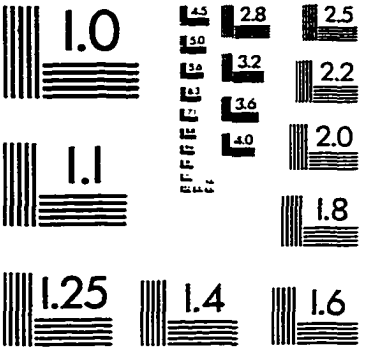


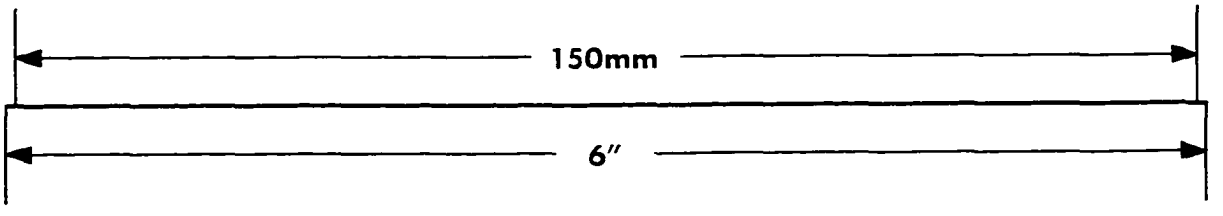

Figure 6B. Ontogenetic changes in partial correlations for body traits between parents and offspring (controlling for the effect of one parent at the time), and correlations between mid-parent values and offspring.

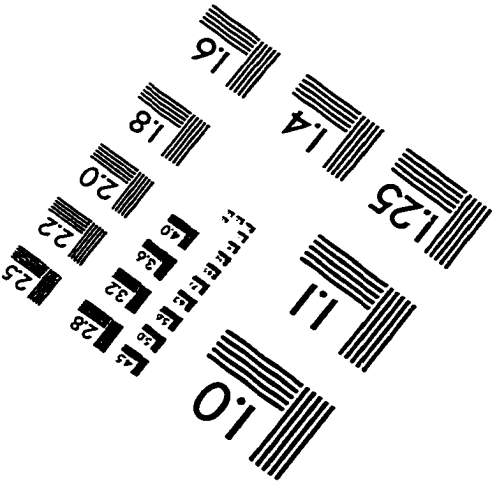
# IMAGE EVALUATION
# TEST TARGET (QA-3)

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