

## THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE HOUSE FINCH. II. POPULATION DIVERGENCE IN RELATION TO LOCAL SELECTION

ALEXANDER V. BADYAEV,<sup>1,2</sup> GEOFFREY E. HILL,<sup>2</sup> ANDREW M. STOEHR,<sup>2,3</sup> PAUL M. NOLAN,<sup>2</sup> AND  
KEVIN J. MCGRAW<sup>2,4</sup>

<sup>1</sup>*Division of Biological Sciences, The University of Montana, Missoula, Montana 59812-1002*

*E-mail: abadyaev@selway.umt.edu*

<sup>2</sup>*Department of Biological Sciences, Auburn University, Auburn, Alabama 36849*

**Abstract.**—Recent colonization of ecologically distinct areas in North America by the house finch (*Carpodacus mexicanus*) was accompanied by strong population divergence in sexual size dimorphism. Here we examined whether this divergence was produced by population differences in local selection pressures acting on each sex. In a long-term study of recently established populations in Alabama, Michigan, and Montana, we examined three selection episodes for each sex: selection for pairing success, overwinter survival, and within-season fecundity. Populations varied in intensity of these selection episodes, the contribution of each episode to the net selection, and in the targets of selection. Direction and intensity of selection strongly differed between sexes, and different selection episodes often favored opposite changes in morphological traits. In each population, current net selection for sexual dimorphism was highly concordant with observed sexual dimorphism—in each population, selection for dimorphism was the strongest on the most dimorphic traits. Strong directional selection on sexually dimorphic traits, and similar intensities of selection in both sexes, suggest that in each of the recently established populations, both males and females are far from their local fitness optimum, and that sexual dimorphism has arisen from adaptive responses in both sexes. Population differences in patterns of selection on dimorphism, combined with both low levels of ontogenetic integration in heritable sexually dimorphic traits and sexual dimorphism in growth patterns, may account for the close correspondence between dimorphism in selection and observed dimorphism in morphology across house finch populations.

**Key words.**—Fecundity, house finch, overwinter survival, pairing success, phenotypic selection, population divergence, sexual size dimorphism.

Received December 20, 1999. Accepted May 18, 2000.

Patterns of population variation play an important role in evolutionary diversification, and many insights into evolutionary processes have come from studies of within-species variation. Traditionally, the mechanisms behind population divergence have been examined by taking either direct or indirect approaches. The indirect approach involves the comparison of phenotypic and genetic variance-covariance structures to infer the roles of drift and selection in population divergence (Lofsvold 1988; Turelli 1988; Cheverud 1989; Baker 1992; Björklund 1994; Schluter 1996; Merilä and Björklund 1999; Arnold and Phillips 1999; Roff and Mousseau 1999; reviewed in Roff 2000). Specifically, temporal and spatial constancy or proportionality of covariance structure among populations is expected under evolution by genetic drift (Lande 1980a; Lofsvold 1988; Roff 2000), but distinct covariance patterns should result from divergent directional selection (Lande 1985; Riska 1985; Kohn and Atchley 1988; Zeng 1988; Shaw et al. 1995). Under the assumption of homogeneous genetic variance-covariance matrices it is possible to use observed morphological differences among populations to reconstruct the historical patterns of selection responsible for divergence (e.g., Price and Grant 1985; Grant and Grant 1995; Cheverud 1996; Roff and Fairbairn 1999). In contrast, the direct approach to the study of population divergence involves the comparison of current phenotypic selection to observed morphology in several populations (e.g., Schluter and Grant 1984; Grant and Grant 1989; Endler

1995). In this approach, differences in local selection pressures found among populations are then related to observed morphological divergence (e.g., Grant and Grant 1989, 1995; Merilä et al. 1994).

These two approaches to the study of morphological divergence also have been used in studies of sexual dimorphism. Sexual dimorphism can evolve when there are differences in sex-specific selection pressures, sex-biased phenotypic and genetic variation, or genetic correlation between sexes (Darwin 1871; Ralls 1976; Lande 1980b; Slatkin 1984; Arak 1988; Shine 1989; Moore 1990; reviewed in Andersson 1994). Thus, to reveal mechanisms behind variation in dimorphism, researchers have used comparative studies to examine morphology in species and populations where sexes were expected to differ in any of these factors (e.g., Cheverud et al. 1985; Rising 1987; Webster 1992; Promislow et al. 1994; Martin and Badyaev 1996; Andersen 1997; Badyaev 1997a,b; Lindenfors and Tullberg 1998; Masterson and Hartwig 1998; reviewed in Badyaev and Hill 1999). In another approach, researchers compared phenotypic selection on the sexes and variation in sexual dimorphism in different populations (e.g., Johnston and Fleischer 1981; Price 1984a,b; Weatherhead et al. 1987; Fairbairn and Preziosi 1996; Powell and King 1997; Wikelski and Trillmich 1997). The strongest inference about the mechanisms behind population divergence is provided by studies that employ both comparative and direct approaches to the study of sexual dimorphism (e.g., Price 1984a,b; Björklund and Lindén 1993; Preziosi and Fairbairn 1996; Ferguson and Fairbairn 2000).

Sexual dimorphism is generally interpreted as being the outcome of sexual selection. Within populations, however,

<sup>3</sup> Present address: Department of Biology, University of California, Riverside, California 92521.

<sup>4</sup> Present address: Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853.

stronger selection for sexual dimorphism is not always associated with greater dimorphism. For instance, sexual selection favoring dimorphism can be opposed by natural selection on the same traits (e.g., Howard 1981; Price 1984a,b; Weatherhead et al. 1987; Katsikaros and Shine 1997; Powell and King 1997; Badyaev and Martin 2000a), by selection on closely correlated traits in the opposite sex (Lande 1980b; Reeve and Fairbairn 1996), or by selection during different life stages of the organism (e.g., Schluter and Smith 1986; Merilä et al. 1997; reviewed in Schluter et al. 1991). Thus, long-term studies of phenotypic selection on each sex over several episodes of selection and on several traits are especially valuable for examining mechanisms behind variation in sexual dimorphism.

We studied the evolution of sexual size dimorphism in a small passerine bird—the house finch (*Carpodacus mexicanus*). House finches are native to western North America from southern Oregon and southern Wyoming south to Oaxaca, Mexico (Hill 1993a). Over the last few decades, house finches have greatly expanded their range, spreading north from the central Rockies into Montana, and spreading across eastern North America from a small introduced population in New York (Badyaev and Hill 2000). Newly established house finch populations now occupy regions that are climatically and ecologically distinct (Hill 1993a).

Previous studies of these recently established populations revealed rapid and extensive among-population divergence in sexual size dimorphism (Hill 1993a; Badyaev and Martin 2000a; Badyaev and Hill 2000). Within-population genetic and phenotypic covariance structure had limited effect on the direction and rate of population divergence, and the evolution of covariance structure was very different for the two sexes (Badyaev and Hill 2000). These results suggest that diversifying local selection pressures are the likely mechanism behind the population divergence (Lande 1985; Riska 1985). However, differences in the selection pressures for sexual dimorphism in the various populations and the effects of such selection on expression of dimorphism have never been directly established. Here, we use data from three geographically separated, individually marked, and resident house finch populations over four years and through several episodes of selection, to examine whether among-population differences in current net selection on each sex is associated with among-population variation in sexual size dimorphism.

This paper consists of three parts. First, for each population, we describe patterns of sex-specific selection in relation to success at obtaining a mate (pairing selection), within-season fecundity (fecundity selection), and overwinter survival (survival selection). Second, we examine the concordance between current net selection for sexual dimorphism (i.e., differences in net selection pressures between males and females) and observed sexual dimorphism in each population. Finally, we discuss mechanisms that may enable populations to diverge in sexual dimorphism in response to differing local selection that populations experience.

## METHODS

### *Data Collection*

This study was carried out in three recently established resident house finch populations—in Ann Arbor, southeast-

ern Michigan (hereafter Michigan, in 1988–1991); in Auburn, east-central Alabama (Alabama, 1993–1997); and in Missoula, northwestern Montana (Montana, 1995–1999). Michigan and Alabama populations were 10–15 years old and the Montana population was 25–30 years old at the time they were studied (Badyaev and Hill 2000). For detailed description of the study sites and field techniques in Michigan population see Hill (1993b); in Alabama population, Hill et al. (1999); in Montana population, Badyaev and Martin (2000a,b). Here we summarize the most essential details of data collection and selection measurements. A total of 6382 resident finches were trapped during January–March and August–October, measured and marked with a unique combination of one aluminum and three colored plastic rings. All captured individuals were aged as hatching-year birds and after-hatching-year birds (hereafter adults) according to Hill (1993a), and only adult resident birds were used in this study. Every year, all resident birds were individually marked in the Montana study site (Badyaev and Martin 2000a), and about 90% were marked in both the Michigan and Alabama study sites (Hill et al. 1999).

House finches form strong pair associations, and pairing status of individuals is easily determined from the beginning of the breeding season (e.g., Hill et al. 1999; Badyaev and Martin 2000a). 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. Only birds that were present at the study sites from the beginning of the breeding season were used in the analyses of pairing selection. In populations used in this study, extra-pair fertilizations do not exceed 6–7% (Hill et al. 1994; A.V. Badyaev and P.O. Dunn, unpubl. obs). Either loss of within-pair paternity or gain of extra-pair paternity was not associated with any morphological traits under this study (ibid.), and thus do not bias our estimates of pairing success and fecundity.

Strong fidelity of adult house finches to the location of previous breeding (Hill 1991, 1993a; Hill et al. 1999; Badyaev and Martin 2000a) 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. The reliability of this method was confirmed in a long-term study of the house finch population in Montana, where most of individuals that died during winter were found within the study site (for details, see Badyaev and Martin 2000a).

Most 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 within-season fecundity in the house finch, and pairs that nest earliest produce more broods and have larger clutch sizes than pairs that nest later (e.g., Hill et al. 1994). Thus, we used a product of the standardized first-egg Julian date and the first clutch size as a measure of fecundity. We assigned a breeding bird a “high fecundity” status if its fecundity was higher than the median for the population in a given breeding season. “Low fecundity” status was assigned if the within-season fecundity measure was lower than the median. We used categorical classification of fecundity to facilitate

comparison between selection episodes and the levels of sexual dimorphism in finches (see below). To avoid pseudoreplication, for all selection analyses we used data for only one year of residence at the study site per bird. Thus, our selection estimates (below) are not confounded by age-related changes in pairing success or fecundity.

We measured: bill length from anterior end of nostril to the tip of upper mandible; tarsus length (left and right); wing (right, flattened); tail; and body mass. To estimate measurement error, all morphological measures were repeated twice (i.e., four times for the bilateral traits) in the Montana sample. In all populations the average of all available repeated measures was used for further analyses. Because the measurements of fully grown adult finches were taken during approximately two month episodes in the prebreeding season, the effects of seasonal variation were minimized. Within-capture session measurement error estimated from a one-way ANOVA accounted for about 7–10% of variation in most morphological traits, and for 18% of variation in body mass in the Montana population (Badyaev and Martin 2000a). All linear data were ln-transformed, body mass was cube-root transformed, and all data were zero-mean standardized before the analyses.

#### *Description of Dimorphism and Selection*

To evaluate the concordance between current selection and observed sexual dimorphism, we needed a method that allows similar scaling and direct comparisons of these values. To this end, we used two techniques. First, to facilitate comparisons with other studies, for each trait we report standardized differences between sexes and conventional directional selection differentials. Because sexes did not differ in phenotypic variance across studied populations (Badyaev and Hill 2000), standardized sexual dimorphism for each trait was calculated as a difference between male and female values divided by a square root of the pooled variance. The standardized selection differentials were calculated for each trait as a difference in standardized values between “before” selection (i.e., trait value for all birds before either breeding season or winter) and “after” selection (i.e., trait values of either paired, high fecundity, or surviving birds), divided by a square root of the before-selection variance (e.g., Endler 1986). Both sexual dimorphism and selection differentials were in the units of standard deviation.

However, for structural and intercorrelated traits such as those examined in this study (e.g., tarsus, wing, and tail) the first method confounds differences in overall size of individuals with differences in size-independent variation in each trait (i.e., “shape”); it is biologically more appropriate to describe trait variation in size and shape factors (Wright 1923; Crespi and Bookstein 1989). Thus, we also used path analysis to examine both sexual dimorphism and selection on morphology (e.g., Björklund and Linden 1993). Tests for homogeneity of trait covariances showed no significant differences between male and female matrices (e.g.,  $\chi^2 = 23.31$ ,  $df = 28$ ,  $P = 0.72$ ; Badyaev and Martin 2000a). Therefore, pooled matrices were used in further analyses. We extracted the first eigenvector of the pooled covariance matrix; this vector was referred to as general size in subsequent analyses.

Sexual dimorphism in shape factors was the difference in least-squared means of each trait calculated from ANCOVA of sex and each trait with general size and year as covariates (Björklund and Linden 1993, Badyaev and Martin 2000a). We arbitrarily assigned positive signs to traits for which males were the larger sex or for which selection favored larger values in males (see below) and negative signs for traits for which females were the larger sex or for which selection favored larger values in females.

Similarly, we calculated directional selection differentials as the differences in adjusted means between groups (i.e., paired vs. single males) from ANCOVA with selection group, year, and each trait (Crespi and Bookstein 1989). Calculations were made separately for each sex. As above, general size and year were used as covariates for estimating selection differentials on shape factors. Means were compared with two-tailed *t*-tests. For ease of the interpretation, we also present raw morphological data for selection in all populations. Net selection on each sex was a sum of signed directional selection differentials for pairing, fecundity, and survival selection. In addition, for each selection episode we calculated a differential of selection for sexual dimorphism as a difference between selection on males and females. For example, pairing selection differential of (−0.25) on female wing length and pairing selection differential of (+0.50) on male wing length would result in pairing selection of (+0.75) for dimorphism in wing length. Thus, net selection for sexual dimorphism was the sum of signed selection differentials for both sexes for each selection episode.

The use of the same model to describe both sexual dimorphism and current selection enabled us to directly estimate the concordance between current morphology and selection. For example, if current selection favors increased sexual dimorphism, the difference in selection differentials between males (larger sex) and females (smaller sex) should be positive; whereas, if current selection favored decreased dimorphism, the difference in selection differentials between the larger and smaller sex should be negative (Crespi and Bookstein 1989; Björklund and Lindén 1993; Badyaev and Martin 2000a). In addition, if current selection favors 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.

## RESULTS

### *Population Differences in Sexual Dimorphism and Phenotypic Selection*

Populations strongly differed in sexual dimorphism and the direction of dimorphism was often reversed among populations (Fig. 1; Population: all  $F_s > 23.0$ ,  $P < 0.001$ ), but there were some general patterns. In all populations, males were significantly larger than females (Tables 1–4); the Alabama population had the highest and the Montana population had the lowest sexual dimorphism in size. When dimorphism in general size was accounted for, males in all populations had disproportionately longer wings and were

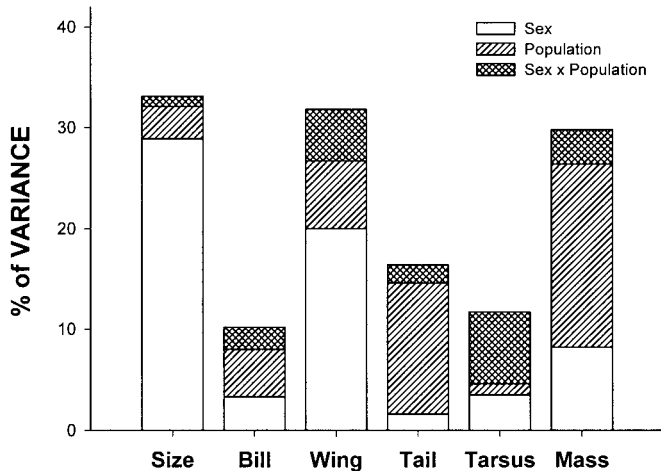


FIG. 1. Percent of total variance (calculated from variance components) partitioned among Sex, Population, and the Sex × Population interaction for overall size factor and shape factors for each trait for three recently established populations of the house finch (see Methods for details).

disproportionately lighter compared to females (Table 4). However, the degree of dimorphism in these traits varied among populations. For example, the sexes were the most different in the relative body mass in Michigan, and they were the most similar in relative body mass in Montana. The sexes were most different in relative bill length in Alabama, and they were least different in Montana. Moreover, sexual dimorphism in relative tail and tarsus length was often reversed among populations (Fig. 1; sex × population interaction for tail:  $F = 10.58, P < 0.0001$ ; and tarsus:  $F = 16.22, P < 0.0001$ ). Males had disproportionately longer tails for their size than females in the Michigan population, but shorter tails in the Montana and, especially, the Alabama populations (Table 4). Similarly, males had disproportionately longer tarsi than females in Alabama and Michigan, but shorter tarsi in Montana (Table 4). Overall, aside from general size and body mass dimorphism, Alabama finches were the most di-

morphic in bill and wing length, Michigan finches were the most dimorphic in tail length, and Montana finches were the most dimorphic in wing length (Table 4).

In all populations and in both sexes, selection favored change in morphology with respect to all three episodes of selection that we measured: pairing success, overwinter survival, and within-breeding season fecundity (Tables 1–4). In Michigan, fecundity selection exerted the strongest effects on morphology (Tables 1, 4, 5). In males, fecundity selection favored greater size, longer wings and tails, shorter bill and tarsus, and smaller body mass (Tables 4, 5). In females, fecundity selection primarily favored changes in morphology in the opposite direction: decrease in general size, tail and tarsus length, but increase in bill length and body mass (Tables 1, 4, 5). In males, paired individuals were larger and had disproportionately longer wings and tails compared to unpaired individuals (Tables 1, 4, 5), but the effects of pairing selection were small (Table 4, see below). Survival selection favored smaller size and shorter tarsi in both sexes, as well as longer bills and tails in males, but not females (Table 4). Net selection for dimorphism (Tables 4, 5) favored significant dimorphism in general size and relative tail length (males larger), as well as an increase in body mass dimorphism (females larger; Tables 4, 5).

In Alabama, survival selection favored the greatest changes in morphology (Tables 2, 4, 5). Survival selection favored decrease in general size in both sexes, as well as longer bills, tails, tarsi, and greater mass in males and the opposite changes in females (Tables 4, 5). Fecundity selection favored greater size, longer wings, shorter bill and tail, and greater mass in males, but the opposite changes in females (Tables 4, 5). Paired males were larger and had longer tails compared to single males (Tables 2, 4, 5). Net selection for dimorphism favored significant increase in size dimorphism and body mass dimorphism (males larger), as well as relative bill and wing lengths (females larger; Tables 4, 5).

In Montana, pairing and fecundity selections exerted the most pressure on morphology (Tables 4, 5). Paired males were larger and had longer wings than single males, while

TABLE 1. Morphology, (mean [SD]) of Michigan house finches with respect to pairing success, fecundity, and overwinter survival in 1988–1991.

Trait	Pairing		Fecundity		Survival	
	Paired	Single	High	Low	Survived	Nonsurvived
<b>Males</b>						
<i>n</i>	206	397	40	39	136	211
Bill length	<b>8.70</b> <sup>1</sup> (0.35)	<b>8.65</b> (0.36)	8.73 (0.39)	8.77 (0.35)	8.64 (0.36)	8.62 (0.36)
Wing length	<b>80.44</b> (1.97)	<b>80.13</b> (1.92)	<b>81.30</b> (1.99)	<b>80.14</b> (1.99)	78.00 (1.98)	78.20 (2.05)
Tail length	<b>59.90</b> (2.23)	<b>59.36</b> (2.13)	<b>60.70</b> (2.51)	<b>59.32</b> (2.19)	59.41 (2.02)	59.45 (2.26)
Tarsus length	17.13 (0.60)	17.14 (0.66)	17.05 (0.73)	17.12 (0.75)	<b>16.97</b> (0.71)	<b>17.17</b> (0.69)
Body mass	21.55 (1.27)	21.42 (1.19)	21.71 (1.10)	21.75 (1.23)	21.52 (1.27)	21.52 (1.20)
<b>Females</b>						
<i>n</i>	402	0	35	31	81	107
Bill length	8.68 (0.34)	—	8.65 (0.38)	8.62 (0.30)	8.63 (0.36)	8.67 (0.36)
Wing length	77.87 (1.89)	—	78.71 (1.41)	78.48 (1.75)	76.69 (1.93)	76.60 (2.21)
Tail length	57.76 (2.58)	—	58.01 (1.92)	59.07 (2.01)	57.66 (2.27)	58.14 (3.39)
Tarsus length	17.19 (0.61)	—	17.02 (0.60)	17.17 (0.57)	16.99 (0.65)	17.12 (0.63)
Body mass	22.12 (1.46)	—	22.92 (1.33)	22.53 (1.75)	22.53 (1.61)	22.25 (1.40)

<sup>1</sup> Mean trait values shown in bold indicate significant difference between groups (e.g., paired vs single) after within-selection group adjustments for multiple comparisons.

TABLE 2. Morphology, (mean [SD]) of Alabama house finches with respect to pairing success, fecundity, and overwinter survival in 1993–1997.

Trait	Pairing		Fecundity		Survival	
	Paired	Single	High	Low	Survived	Nonsurvived
<b>Males</b>						
<i>n</i>	96	157	45	46	78	94
Bill length	8.93 (0.34)	8.72 (0.39)	8.70 (0.36)	8.81 (0.28)	8.93 (0.70)	8.94 (0.51)
Wing length	<b>80.18</b> <sup>1</sup> (2.13)	<b>79.64</b> (1.81)	<b>81.54</b> (1.39)	<b>79.55</b> (2.24)	78.63 (1.80)	79.96 (2.23)
Tail length	<b>60.72</b> (2.16)	<b>59.36</b> (2.39)	<b>60.92</b> (1.61)	<b>59.43</b> (2.67)	59.15 (3.35)	58.74 (2.88)
Tarsus length	17.19 (0.68)	16.95 (0.72)	<b>17.05</b> (0.80)	<b>16.06</b> (0.54)	17.63 (1.20)	17.58 (0.85)
Body mass	20.69 (1.77)	20.17 (1.29)	20.82 (1.28)	20.29 (1.22)	20.61 (1.14)	20.29 (1.50)
<b>Females</b>						
<i>n</i>	128	0	31	39	45	46
Bill length	8.78 (0.37)	—	8.91 (0.29)	8.67 (0.33)	8.99 (0.31)	9.31 (0.65)
Wing length	77.13 (2.02)	—	77.02 (1.89)	77.90 (1.69)	78.32 (1.77)	77.92 (1.68)
Tail length	57.49 (2.68)	—	59.00 (2.93)	58.00 (2.55)	58.31 (1.87)	59.21 (2.13)
Tarsus length	16.80 (0.65)	—	16.94 (0.71)	16.46 (0.76)	17.07 (0.72)	17.38 (1.55)
Body mass	20.22 (1.36)	—	20.65 (1.38)	20.94 (1.53)	19.73 (1.53)	20.35 (1.39)

<sup>1</sup> Same as in Table 1.

the differences were reversed for females (Tables 3–5). Similarly, fecundity selection favored larger size, longer wings, and greater mass in males, but the opposite changes in females. Survival selection favored smaller size in males and larger size in females, but favored mostly similar changes between sexes for the remaining traits (Tables 4, 5). Net selection favored greater dimorphism in general size, relative wing length, and body mass (males larger; Tables 4, 5).

Overall, populations varied in both patterns of sexual dimorphism and current selection pressures; populations strongly differed in the targets of and the intensity of episodes of selection on morphological traits.

#### Current Selection in Relation to Sexual Dimorphism

In all populations, net selection for dimorphism was highly concordant with observed sexual dimorphism; the most dimorphic traits were the subject of the most intense current selection (Table 4). For example, in Michigan, pairing and

fecundity selections favored increase in dimorphism in tail length, and tail length was the most dimorphic “shape” trait in that population (Table 4, Fig. 2). Similarly, in Montana net selection for dimorphism was the strongest for wing length, and wing length was the most dimorphic “shape” trait in that population. In Alabama, net selection favored sexual dimorphism in general size, wing and tail, and these were the most dimorphic traits in that population (Tables 4, 5; Fig. 2).

The concordance between net selection for dimorphism and observed dimorphism was highest in the Michigan population (Kendall’s coefficient of correlation:  $r = 0.94$ ,  $P < 0.001$ ), followed by the Montana ( $r = 0.63$ ,  $P = 0.003$ ) and Alabama ( $r = 0.40$ ,  $P = 0.06$ ; Fig. 2) populations. In all populations, pairing and fecundity selections were similar and, with the exception of the Michigan population, favored changes opposite of those favored by survival selection (Tables 4, 5; Fig. 2).

TABLE 3. Morphology, (mean [SD]) of Montana house finches with respect to pairing success, fecundity, and overwinter survival in 1995–1999.

Trait	Pairing		Fecundity		Survival	
	Paired	Single	High	Low	Survived	Nonsurvived
<b>Males</b>						
<i>n</i>	117	101	81	81	108	63
Bill length	8.52 (0.77)	8.15 (1.03)	8.80 (0.30)	7.99 (0.89)	8.28 (0.92)	8.42 (0.82)
Wing length	<b>80.35</b> <sup>1</sup> (1.56)	<b>78.74</b> (1.70)	<b>81.04</b> (1.30)	<b>79.12</b> (1.56)	79.69 (1.65)	80.02 (1.54)
Tail length	59.62 (4.03)	58.50 (2.44)	60.92 (2.08)	57.58 (5.33)	59.59 (3.11)	58.70 (4.25)
Tarsus length	17.14 (0.91)	17.41 (0.81)	17.03 (0.88)	17.57 (1.00)	17.32 (0.95)	17.12 (0.77)
Body mass	<b>21.34</b> (1.35)	<b>22.32</b> (1.76)	<b>22.43</b> (1.07)	<b>21.10</b> (1.65)	21.91 (1.68)	21.54 (1.45)
<b>Females</b>						
<i>n</i>	118	71	81	78	59	61
Bill length	8.22 (0.77)	8.60 (0.82)	8.56 (0.51)	8.09 (0.80)	<b>8.58</b> (0.75)	<b>7.89</b> (0.87)
Wing length	<b>76.00</b> (1.70)	<b>77.98</b> (1.69)	<b>76.01</b> (1.98)	<b>77.95</b> (1.54)	<b>78.29</b> (1.76)	<b>76.15</b> (2.17)
Tail length	56.03 (3.42)	57.98 (2.56)	57.86 (2.34)	56.21 (3.68)	57.78 (3.26)	56.30 (3.79)
Tarsus length	17.00 (0.87)	17.28 (0.70)	16.82 (1.03)	16.98 (0.94)	17.84 (0.83)	17.01 (0.85)
Body mass	22.39 (1.59)	22.23 (1.54)	22.27 (1.27)	22.08 (1.61)	22.00 (1.05)	22.71 (1.92)

<sup>1</sup> Same as in Table 1.

TABLE 4. Sexual size dimorphism (SSD1) and directional selection for pairing success, breeding season fecundity, and overwinter survival in the house finches, when overall size and shape are extracted for each trait (path analyses methods). Values are differences between sexes<sup>1</sup> and between groups<sup>2</sup> (e.g., paired vs. single) in the size and shape factors. All values were multiplied by 10<sup>2</sup>.

Trait	SSD1	Pairing		Fecundity		Survival		Net selection for sexual dimorphism <sup>3</sup>
		M	F	M	F	M	F	
Alabama								
SZ <sup>4</sup>	<b>123.73</b>	<b>50.68</b>	0	13.71	-29.02	-27.05	<b>-89.72</b>	<b>156.08</b>
BL	<b>-1.47</b>	-0.19	0	<b>-1.01</b>	<b>1.63</b>	1.06	-0.38	<b>-1.39</b>
WL	<b>1.45</b>	0.10	0	0.43	<b>-0.60</b>	<b>-0.53</b>	<b>1.35</b>	<b>-0.75</b>
TL	<b>-0.62</b>	0.82	0	-1.02	<b>1.69</b>	0.15	-1.29	-0.45
TR	<b>0.85</b>	-0.64	0	0.13	1.05	0.62	-0.10	-0.84
BM	<b>-3.03</b>	-0.78	0	2.15	<b>-3.29</b>	0.65	-1.33	6.67
Michigan								
SZ	<b>97.12</b>	<b>38.06</b>	0	<b>57.93</b>	-7.95	-11.29	-8.22	<b>101.41</b>
BL	<b>-1.19</b>	0.20	0	-0.82	0.48	0.40	-0.28	-0.42
WL	<b>1.17</b>	0.12	0	<b>0.57</b>	0.26	-0.11	0.18	0.14
TL	<b>1.40</b>	0.21	0	<b>0.97</b>	<b>-1.41</b>	0.19	-0.51	<b>3.02</b>
TR	<b>0.92</b>	-0.42	0	-0.81	-0.59	<b>-0.86</b>	-0.36	-1.14
BM	<b>-4.73</b>	0.10	0	-1.37	1.71	0.19	1.12	<b>-3.91</b>
Montana								
SZ	<b>89.44</b>	<b>73.27</b>	-17.34	43.53	-37.18	-26.58	34.99	<b>109.75</b>
BL	<b>-0.25</b>	-0.92	-1.54	-0.63	-0.12	-0.96	0.36	-1.21
WL	<b>1.22</b>	<b>0.95</b>	<b>-1.18</b>	0.63	-0.72	0.16	0.50	<b>3.14</b>
TL	-0.18	-0.14	-0.36	-1.69	-1.75	0.91	0.86	0.33
TR	<b>-0.86</b>	-0.35	-0.37	0.05	-0.34	0.25	1.07	-0.41
BM	<b>-1.66</b>	-0.01	<b>3.22</b>	1.42	-0.99	-1.07	<b>-2.82</b>	<b>0.93</b>

<sup>1</sup> Dimorphism in size is the difference between sexes in the first eigenvector values of the pooled covariance matrices for all 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 and year as covariates. Bold values indicate significance after the table-wide Bonferroni adjustments.

<sup>2</sup> Directional selection differentials, for each sex, are the differences in adjusted means between groups (i.e., paired vs. single males) from ANCOVA with selection group, year, and each trait, with general size and year as covariates (for shape factors).

<sup>3</sup> Net selection for SSD is the sum of signed selection differentials for both sexes for each selection episode.

<sup>4</sup> SZ, general size; BL, bill length; WL, wing length; TL, tail length; TR, tarsus length; BM, body mass.

The direction of selection on sexually dimorphic traits was generally reversed between males and females (Tables 4, 5). However, the intensity of selection did not differ between sexes. For example, selection differentials for fecundity and survival selections (Table 5) were similar between males and

females across all populations (pairwise  $t = 1.36$ ,  $P = 0.18$ ), within each population (i.e., Michigan,  $t = 0.91$ ,  $P = 0.38$ ; Alabama,  $t = 1.51$ ,  $P = 0.18$ ; Montana,  $t = 0.21$ ,  $P = 0.83$ ), and for each selection episode (fecundity,  $t = 1.49$ ,  $P = 0.14$ ; survival  $t = 0.007$ ,  $P = 0.99$ , Table 5). In Michigan and

TABLE 5. Standardized sexual size dimorphism (SSD2) and selection differentials for three episodes of selection in the house finches for each trait (univariate analyses). Bold indicates significant difference from zero. All values are in standard deviations. Trait abbreviations as in Table 4.

Trait	SSD2	Pairing		Fecundity		Survival		Net selection for sexual dimorphism
		M	F	M	F	M	F	
Alabama								
BL	<b>+0.26</b>	+0.07	0	<b>-0.11</b>	<b>+0.27</b>	-0.01	<b>-0.34</b>	0.02
WL	<b>+1.11</b>	+0.26	0	+0.14	<b>-0.22</b>	-0.12	-0.15	<b>0.65</b>
TL	<b>+0.67</b>	<b>+0.45</b>	0	<b>-0.13</b>	<b>+0.31</b>	+0.06	-0.27	<b>0.34</b>
TR	<b>+0.62</b>	+0.00	0	<b>-0.09</b>	+0.16	+0.03	-0.47	<b>0.25</b>
BM	<b>+0.20</b>	+0.06	0	<b>+0.07</b>	<b>-0.12</b>	-0.13	-0.27	<b>0.39</b>
Michigan								
BL	+0.20	+0.10	0	-0.09	+0.04	+0.03	-0.06	0.06
WL	<b>+0.70</b>	<b>+0.42</b>	0	<b>+0.50</b>	-0.07	-0.08	-0.03	<b>0.94</b>
TL	<b>+1.07</b>	<b>+0.37</b>	0	<b>+0.35</b>	<b>-0.20</b>	-0.00	-0.11	<b>1.33</b>
TR	-0.03	+0.01	0	-0.05	<b>-0.11</b>	-0.21	-0.12	-0.02
BM	<b>-0.52</b>	+0.11	0	-0.01	+0.15	-0.00	+0.13	<b>-0.18</b>
Montana								
BL	<b>+0.23</b>	+0.05	-0.18	-0.07	-0.24	-0.09	-0.02	<b>0.33</b>
WL	<b>+0.92</b>	<b>+0.75</b>	<b>-0.69</b>	<b>+0.34</b>	<b>-0.33</b>	-0.04	<b>+0.46</b>	<b>1.61</b>
TL	<b>+0.36</b>	+0.05	-0.25	-0.07	-0.18	+0.03	+0.07	<b>0.37</b>
TR	<b>-0.21</b>	-0.09	-0.11	-0.05	<b>-0.24</b>	-0.00	+0.19	0.02
BM	-0.12	-0.02	<b>+0.14</b>	+0.14	-0.24	-0.08	<b>-0.10</b>	<b>0.24</b>

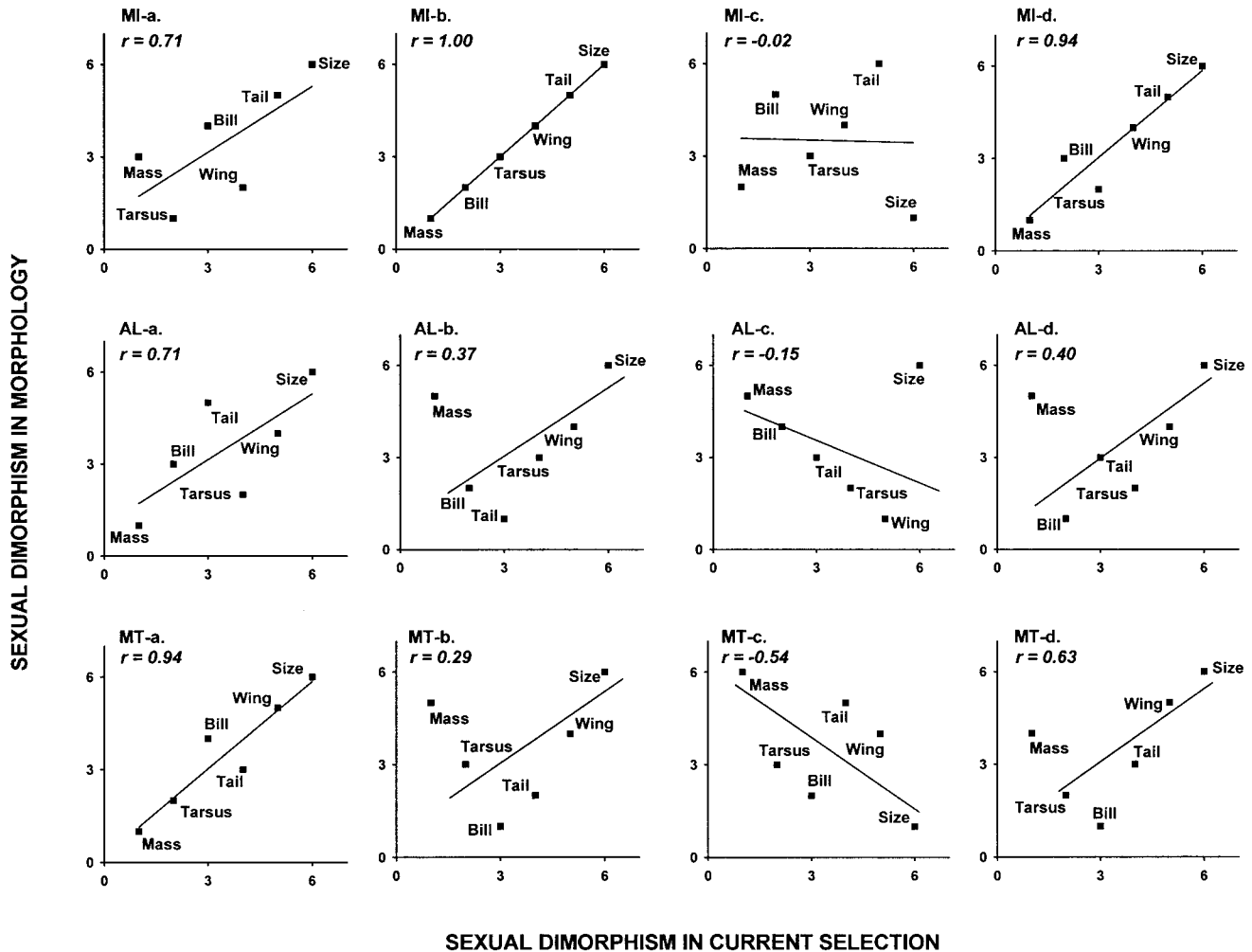


FIG. 2. Plots illustrating the relationship between sexual dimorphism in current selection pressures and the observed sexual dimorphism in morphology for three populations of the house finch (MI, Michigan; AL, Alabama; and MT, Montana). Sexual dimorphism in morphology is the rank of sex differences in measurements. Sexual dimorphism in selection pressures is the rank of sex differences in selection pressures for each selection episode—selection for (a) pairing success, (b) high breeding season fecundity, (c) overwinter survival, and for (d) net selection for sexual dimorphism—the sum of signed selection differentials for both sexes for each selection episode.

Alabama populations, all females were paired (i.e., there was no pairing selection on females based on morphology). However, in the Montana population, where pairing selection on females is significant (Table 3), pairing selection pressures were similar for males and females (Table 4). Thus, in all populations, both sexes appear to be equally far from their fitness optima; net selection for dimorphism results from selection pressures that are similar in magnitudes but of opposite direction for the two sexes.

#### DISCUSSION

Theory predicts that variation in sexual dimorphism will be the result of the combined effects of differences in sex-specific selection pressures, sex-biased phenotypic and genetic variation, and genetic correlation between sexes (Lande 1980b). Thus, divergence in sexual dimorphism among taxa can be accounted for by differences in phenotypic and genetic variation in sex-specific morphology and selection pressures (e.g., Leutenegger and Cheverud 1982; Cheverud et al. 1985;

Rising 1987; Webster 1992; Andersen 1997; Katsikaros and Shine 1997; Lindenfors and Tullberg 1998; reviewed in Badyaev and Hill 1999). Here we documented that recently established house finch populations differed in patterns of sex-specific selection, including the targets and intensity of selection, and they varied in the relative contribution of different selection episodes to net selection on morphological traits. We also showed that in each population, the patterns of observed sexual dimorphism and current net selection for dimorphism are highly concordant; net selection for dimorphism is strongest on the most dimorphic trait (Fig. 2).

To understand the potential mechanisms behind these patterns, we need to address several questions. First, does net selection for dimorphism primarily result from selection on males, females, or both sexes? Second, what are the ecological differences among populations or other factors behind population variation in relative importance of selection episodes (e.g., survival versus fecundity selections). Finally, what are the phenotypic and genetic mechanisms enabling

house finches to achieve close concordance between dimorphism in selection and dimorphism in morphology in each population?

In each house finch population, variation in sexually dimorphic traits in both sexes had strong fitness consequences (Tables 1–5), and the direction of morphological changes favored by net selection was often opposite for males and females (Tables 4, 5; see also Ralls 1976; Price 1984a; Weatherhead et al. 1987; Arak 1988; Moore 1990; Martin and Badyaev 1996; Wikelski and Trillmich 1997). For example, in Alabama, fecundity selection favored shorter bills in males but longer bills in females (Tables 2, 4); in Michigan, fecundity selection favored longer tails in males but shorter tail in females (Tables 1, 4). However, selection intensity was not significantly different between the sexes, suggesting that, in each population, sexual dimorphism arises from differences in selection pressures between both males and females, and is maintained by adaptive responses in both sexes.

The recent origins and the peripheral locations of the studied populations, as well as potential gene flow from the central parts of the house finch range (Vazquez-Phillips 1992) may prevent males and females from achieving optimal morphology for the local ecological conditions (e.g., García and Kirkpatrick 1997; Holt and Gomulkiewicz 1997). This may account for strong directional selection on morphology in both sexes found in this study (e.g., selection differentials close to one standard deviation, Table 5). Alternatively, strong net selection on both sexes can result from local selection pressures that fluctuate temporally (e.g., Benkman and Miller 1996; Reznick et al. 1997; Badyaev and Martin 2000a). Regardless of the mechanism, close and consistent concordance between current selection and observed dimorphism across ecologically distinct locations (Fig. 2) indicates that variation in sexual dimorphism is adaptive in these populations.

Despite pronounced variation among populations in selection (Tables 4, 5), some patterns were common to all populations. For example, in all populations, selection for higher fecundity in females favored smaller females (Table 4). Similarly, in all populations, structurally larger males had a higher probability of obtaining a mate, and males with longer wings had higher within-season fecundity (Table 4). It has been suggested previously that higher fecundity of smaller female altricial birds arises from a physiological advantage to small body size; smaller females reach the energetic requirements for self-maintenance faster, convert a greater proportion of consumed resources into reproduction, and therefore breed earlier (e.g., Downhower 1976; Murphy 1986). In turn, across many bird species (e.g., Perrins 1979), including the house finch (Hill et al. 1994; McGraw et al. 2000; Badyaev and Martin 2000a), early breeding is commonly associated with greater within-season fecundity.

The general concordance between the changes favored by pairing selection and the changes favored by fecundity selection on males (Fig. 2a,b) suggests that females (a selective agent for pairing selection on males) may discriminate among males based on morphological traits that enhance fecundity. Because male house finches do not defend breeding territories or participate in nest building (Hill 1993a), these phenotypic benefits are most likely related to male provisioning of fe-

males during incubation and brooding (Hill 1991). Indeed, structurally larger males provisioned nestlings and females more often than smaller males (A. Badyaev, unpubl. obs.). At the same time, in all populations, structurally larger males suffered lower overwinter survival than smaller males (Table 4). Similarly, in the Montana population, strong pairing and fecundity selection for smaller size in females may be partially offset by survival requirements; survival selection in Montana favored larger females (Tables 3, 6; see also Price 1984b; Price and Grant 1984; Wikelski and Trillmich 1997).

The populations differed in the contribution that different episodes of selection made to overall net selection (e.g., Fig. 2). For example, in the Michigan population, observed sexual dimorphism was most concordant with patterns favored by selection for higher fecundity, while patterns of dimorphism in survival selection pressures did not correlate with observed dimorphism (Fig. 2). On the contrary, in the Montana population, changes in dimorphism favored by survival selection closely negatively correlated with observed dimorphism (Fig. 2). Given substantial differences in ecological conditions among populations, it is not surprising that the relative importance of selection episodes differed. Within-population experimental studies are needed to identify the exact ecological, behavioral, and physiological factors behind differences in selection pressures.

The important question is how does the concordance between dimorphism and selection arise in the house finch populations? Of special interest is an apparent conflict between rapid phenotypic changes in sexual dimorphism (Fig. 1; Badyaev and Hill 2000) and the lack of sex-biased phenotypic and genetic variance in morphology of adult house finches (A. Badyaev, L. Whittingham, and G. Hill, unpubl. data). In the house finch, as in other avian studies (Price 1984a; Price 1996), between-sex genetic correlations for morphological traits are close to one. Therefore, short-term evolutionary change in sexual dimorphism should be strongly constrained (e.g., Price 1996; Merilä et al. 1998), and the slow evolution of dimorphism should result in the lack of fit between current ecological conditions and the expression of dimorphism (e.g., Rogers and Mukherjee 1992). These predictions are contrary to both the extensive and rapid divergence in sexual dimorphism (Hill 1993a; Badyaev and Hill 2000) and the close concordance between current selection and current appearance that we observed among house finch populations in this study (see also Badyaev and Martin 2000a).

Sexual dimorphism in ontogenetic patterns (Masterson and Leutenegger 1992; Richtsmeier et al. 1993; Leigh and Shea 1996) could provide a solution to this puzzle. While evolution of sexual dimorphism in adults may be constrained by genetic correlations between sexes (Lande 1980b), selection acting on developmental time or other aspects of growth trajectories can strongly affect sexual dimorphism, even in the presence of high between-sex genetic correlations (e.g., Reeve and Fairbairn 1996; Badyaev et al. 2001). In Montana house finches, sexes strongly differed in growth rates, growth duration, and selection pressures during ontogeny (Badyaev et al. 2001). Thus, population differences in either growth patterns or selection during growth could produce substantially different levels of sexual dimorphism over short periods of



time (e.g., James 1983; Larsson and Forslund 1991; Cooch et al. 1996).

In summary, our study of population variation in phenotypic selection for sexual dimorphism has produced three principal results. First, populations differed in intensity of selection episodes, the contribution of each episode to the net selection, and in the targets of selection. Significant net selection for sexual dimorphism in each population resulted from differences in direction of selection on the sexes, suggesting that in each of the recently-established populations, sexual dimorphism arises from adaptive responses in males and females. Second, in each population, current net selection for sexual dimorphism was highly concordant with observed sexual dimorphism; in each population, selection for dimorphism was the strongest on the most dimorphic traits. Finally, population differences in patterns of selection on dimorphism, combined with both low levels of ontogenetic integration in heritable sexually dimorphic traits and sexual dimorphism in growth patterns may account for the close correspondence between dimorphism in selection and observed dimorphism in morphology across house finch populations.

#### ACKNOWLEDGMENTS

We are grateful to K. Bright, D. Emlen C. Ghalambor, P. Martin, J. McKay, W. Parson, and J. Stamps for discussion and advice. We thank two anonymous reviewers and H. L. Gibbs for very helpful suggestions, most of which are incorporated here. K. Faughnan, T. Fondell, C. Ghalambor, B. Heidinger, and A. Rapone helped in the field. In Montana this work was made possible by support of R. McCue and the personnel of the Vigilante MiniStorage who kindly allowed us to work on their property. GEH was supported by grants from the American Museum of Natural History, a Hinsdale-Walker Grant from the University of Michigan, the College of Science and Mathematics at Auburn University, and by National Science Foundation grant IBN-9722171. During writing, AVB was supported by a postdoctoral fellowship from the College of Science and Mathematics at Auburn University and by National Science Foundation grant DEB-0075388. Banding for this study were conducted under the U.S. Fish and Wildlife Service permits 21661 (GEH) and 21635 (AVB).

#### LITERATURE CITED

- Andersen, N. M. 1997. A phylogenetic analysis of the evolution of sexual dimorphism and mating system in water striders (Hemiptera: Gerridae). *Biol. J. Linn. Soc.* 61:345–368.
- Andersson M. 1994. *Sexual selection*. Princeton Univ. Press, Princeton, NJ.
- Arak, A. 1988. Sexual dimorphism in body size: a model and a test. *Evolution* 42:820–825.
- Arnold, S. J., and P. C. Phillips. 1999. Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53:1516–1527.
- Badyaev, A. V. 1997a. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behav. Ecol.* 8:675–690.
- . 1997b. Covariation between sexually selected and life history traits: an example with Cardueline finches. *Oikos* 80:128–138.
- Badyaev, A. V., and T. E. Martin. 2000a. Sexual dimorphism in relation to current selection in the house finch. *Evolution* 54:987–997.
- . 2000b. Individual variation in growth trajectories: Phenotypic and genetic correlations in ontogeny of the house finch (*Carpodacus mexicanus*). *J. Evol. Biol.* 13:290–302.
- Badyaev, A. V., and G. E. Hill. 1999. Variation in avian sexual dimorphism in relation to phylogeny and ecology: a review. Pp. 1687–1705 in N. Adams and R. Slotow, eds. *Proc. 22 Int. Ornithol. Congr. University of Natal, Durban, South Africa*.
- . 2000. The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. *Evolution* 54:1784–1794.
- Badyaev, A. V., L. A. Whittingham, & G. E. Hill. 2001. The evolution of sexual dimorphism in the house finch: III. Developmental basis. *Evolution*. *In press*.
- Baker, A. J. 1992. Genetic and morphometric divergence in ancestral European and descendent New Zealand populations of chaffinches (*Fringilla coelebs*). *Evolution* 46:1784–1800.
- Benkman, C. W. and R. E. Miller. 1996. Morphological evolution in response to fluctuating selection. *Evolution* 50:2499–2504.
- Björklund, M. 1994. Processes generating macroevolutionary patterns of morphological variation in birds: a simulation study. *J. Evol. Biol.* 7:727–742.
- Björklund, M., and M. Linden. 1993. Sexual size dimorphism in the great tit (*Parus major*) in relation to history and current selection. *J. Evol. Biol.* 6:397–415.
- Cheverud, J. M. 1989. A comparative analysis of morphological variation pattern in the papionins. *Evolution* 43:1737–1747.
- . 1996. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*S. fuscicollis*) tamarins. *J. Evol. Biol.* 9:5–42.
- Cheverud, J. M., M. M. Dow, and W. Leutenegger. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39:1335–1351.
- Cooch, E. G., D. B. Lank, and F. Cooke. 1996. Intra-seasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser show goose. *J. Anim. Ecol.* 65:439–450.
- Crespi, B. J., and F. L. Bookstein. 1989. A path-analytical model for the measurements of selection on morphology. *Evolution* 43:18–28.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. John Murray, London.
- Downhower, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263:558–563.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton Univ. Press, Princeton, NJ.
- . 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.* 10:22–29.
- Fairbairn, D. J., and R. F. Preziosi. 1996. Sexual selection and the evolution of sexual size dimorphism in the water strider, *Aquarius remigis*. *Evolution* 50:1549–1559.
- Ferguson, I. M., and D. J. Fairbairn. 2000. Sex-specific selection and sexual dimorphism in the waterstrider *Aquarius remigis*. *J. Evol. Biol.* 13:160–170.
- García, G., and M. Kirkpatrick. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51:21–28.
- Grant, B. R. and P. R. Grant. 1989. *Evolutionary Dynamics of a Natural Population*. Univ. of Chicago Press, Chicago, IL.
- Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339.
- . 1993a. House Finch. *In* A. Poole, P. Stettenheim, and F. Gill, eds. *The birds of North America*. No 46. The Academy of Natural Sciences, Philadelphia, PA.
- . 1993b. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution* 47:1515–1525.
- . 1993c. Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). *Biol. J. Linn. Soc.* 49:63–86.

- Hill, G. E., R. Montgomerie, C. Roeder, and P. T. Boag. 1994. Sexual selection and cuckoldry in a monogamous songbird: implications for theories of sexual selection. *Behav. Ecol. Sociobiol.* 35:193–199.
- Hill, G. E., P. M. Nolan, and A. Stroehr. 1999. Pairing success relative to male plumage brightness and pigment symmetry in the house finch: temporal and geographic constancy. *Behav. Ecol.* 10:48–53.
- Holt, R. D., and R. Gomulkiewicz. 1997. How does immigration influence local adaptation? A reexamination of a familiar paradigm. *Am. Nat.* 149:563–572.
- Howard, R. D. 1981. Sexual dimorphism in bullfrogs. *Ecology* 62:303–310.
- James, F. C. 1983. Environmental component of morphological differentiation in birds. *Science* 221:184–186.
- Johnston, R. F., and R. C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. *Auk* 98:504–511.
- Katsikaros, K., and R. Shine. 1997. Sexual dimorphism in the tusked frog, *Adelotus brevis*: the roles of natural and sexual selection. *Biol. J. Linn. Soc.* 60:39–51.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *Am. Nat.* 150:1–23.
- Kohn, L. A. P., and W. R. Atchley. 1988. How similar are genetic correlation structures? Data from mice and rats. *Evolution* 42:467–481.
- Lande, R. 1980a. The genetic correlation between characters maintained by pleiotropic mutations. *Genetics* 94:203–215.
- . 1980b. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* 34:292–305.
- . 1985. The dynamics of peak shifts and the patterns of morphological evolution. *Paleobiology* 12:343–354.
- Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. *J. Evol. Biol.* 4:619–636.
- Leigh, S. R. and B. T. Shea. 1996. Ontogeny of body size variation in African apes. *Am. J. Phys. Anthropol.* 99:43–65.
- Leutenegger, W., and J. Cheverud. 1982. Correlates of sexual dimorphism in primates: ecological and size variables. *Int. J. Primat.* 3:387–402.
- Lindfors, P., and B. S. Tullberg. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biol. J. Linn. Soc.* 64:413–447.
- Lofsvold, D. 1988. Quantitative genetics of morphological differentiation in *Peromyscus*. II. Analysis of selection and drift. *Evolution* 42:54–67.
- Martin, T. E. and A. V. Badyaev. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution* 50:2454–2460.
- Masterson, T. J. and W. C. Hartwig. 1998. Degrees of sexual dimorphism in *Cebus* and other New World monkeys. *Am. J. Phys. Anthropol.* 107:243–256.
- Masterson, T. J. and W. Leutenegger. 1992. Ontogenetic patterns of sexual dimorphism in the cranium of Bornean orang-utans (*Pongo p. pygmaeus*). *J. Hum. Evol.* 23:3–26.
- Merilä, J., and M. Björklund. 1999. Population divergence and morphological integration in the greenfinch (*Carduelis chloris*)—evolution against the trajectory of least resistance? *J. Evol. Biol.* 12:103–112.
- Merilä, J. M. Björklund and L. Gustafsson. 1994. Evolution of morphological differences with moderate genetic correlations among traits as exemplified by two flycatcher species (*Ficedula*, *Muscicapidae*). *Biol. J. Linn. Soc.* 52:19–30.
- Merilä, J., B. C. Sheldon, and H. Ellegren. 1997. Antagonistic natural selection revealed by molecular sex identification of nestling collared flycatchers. *Mol. Ecol.* 6:1167–1175.
- . 1998. Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis*. *Evolution* 52:870–876.
- McGraw, K. J., A. M. Stoehr, P. M. Nolan, and G. E. Hill. 2000. Sexual selection for male plumage ornamentation in the house finch: the role of asynchronous breeding by females. *J. Avian Biol.*: *In press*.
- Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual and intersexual selection. *Evolution* 44:315–331.
- Murphy, M. T. 1986. Body size, and condition, timing of breeding, and aspects of egg production in Easter kingbirds. *Auk* 103:465–475.
- Perrins, C. M. 1979. *British tits*. Collins, London.
- Powell, R. A., and C. M. King. 1997. Variation in body size, sexual dimorphism and age-specific survival in stoats, *Mustela erminea* (Mammalia: Carnivora), with fluctuating food supplies. *Biol. J. Linn. Soc.* 62:165–194.
- Preziosi, R. F., and D. J. Fairbairn. 1996. Sexual size dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: body size, components of body size and male mating success. *J. Evol. Biol.* 9:317–336.
- Price, D. K. 1996. Sexual selection, selection load and quantitative genetics of zebra finch bill colour. *Proc. R. Soc. Lond. B* 263:217–221.
- Price, T. D. 1984a. The evolution of sexual dimorphism in Darwin's finches. *Am. Nat.* 123:500–518.
- . 1984b. Sexual selection in body size, territory, and plumage variables in a population of Darwin's finches. *Evolution* 38:327–341.
- Price, T. D., and P. R. Grant. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38:483–494.
- . 1985. The evolution of ontogeny in Darwin's finches: a quantitative genetic approach. *Am. Nat.* 125:169–188.
- Promislow, D. E. L., R. D. Montgomerie, and T. E. Martin. 1994. Sexual selection and survival in North American waterfowl. *Evolution* 48:2045–2050.
- Ralls, K. 1976. Mammals in which females are larger than males. *Q. Rev. Biol.* 51:245–276.
- Reeve, J. P., and D. J. Fairbairn. 1996. Sexual size dimorphism as a correlated response to selection on body size: an empirical test of the quantitative genetic model. *Evolution* 50:1927–1938.
- Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.
- Richtsmeier, J. T., J. M. Cheverud, S. E. Danahey, B. D. Corner, and S. Lele. 1993. Sexual dimorphism of ontogeny in the crab-eating macaque (*Macaca fascicularis*). *J. Hum. Evol.* 25:1–30.
- Rising, J. D. 1987. Geographical variation of sexual dimorphism in size of savannah sparrows (*Passerculus sandwichensis*): a test of hypotheses. *Evolution* 41:514–524.
- Riska, B. 1985. Group size and geographical variation of morphometric correlation. *Evolution* 39:792–803.
- Roff, D. 2000. The evolution of the G matrix: selection or drift? *Heredity* 84:135–142.
- Roff, D., and D. J. Fairbairn. 1999. Predicting correlated responses in natural populations; changes in JHE activity in the Bermuda population of the sand cricket, *Gryllus firmus*. *Heredity* 38:440–450.
- Roff, D. A., and T. A. Mousseau. 1999. Does natural selection alter genetic architecture? An evaluation of quantitative genetic variation among populations of *Allonemobius socius* and *A. fasciatus*. *J. Evol. Biol.* 12:361–369.
- Rogers, A. R., and A. Mukherjee. 1992. Quantitative genetics of sexual dimorphism in human body size. *Evolution* 46:226–234.
- Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.
- Schluter, D. and P. R. Grant. 1984. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution* 38:856–869.
- Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and life history trade-offs. *Proc. R. Soc. Lond. B* 246:11–17.
- Schluter, D., and J. N. M. Smith. 1986. Natural selection on beak and body size in the song sparrow. *Evolution* 40:221–231.
- Shaw, F. H., R. G. Shaw, G. S. Wilkinson, and M. Turelli. 1995. Changes in genetic variances and covariances: G whiz! *Evolution* 49:1260–1267.

- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* 64:419–461.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. *Evolution* 42:1342–1348.
- Vazquez-Phillips, M. A. 1992. Population differentiation of the house finch (*Carpodacus mexicanus*) in North America and the Hawaiian islands. M.S. Thesis. The University of Toronto, Toronto, Ontario.
- Weatherhead, P. J., H. Greenwood, and R. G. Clark. 1987. Natural and sexual selection on body size in red-winged blackbirds. *Evolution* 41:1401–1403.
- Webster, M. S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). *Evolution* 46:1621–1641.
- Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* 51:922–936.
- Wright, S. 1923. The theory of path coefficients. *Genetics* 8:239–255.
- Zeng, Z. B. 1988. Long-term correlated response, interpopulation covariation and interspecific allometry. *Evolution* 42:363–374.

Corresponding Editor: H. Lisle Gibbs