

Maternal Inheritance and Rapid Evolution of Sexual Size Dimorphism: Passive Effects or Active Strategies?

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ABSTRACT: Adaptive evolution is often strongly influenced by maternal inheritance that transfers the parental strategies across generations. The consequences of maternal effects for the offspring generation depend on the between-generation similarity in environments and on the evolved sensitivity of the offspring's ontogeny to maternal effects. When these factors differ between sons and daughters, maternal effects can influence the evolution of sexual dimorphism. The establishment of house finch populations across western Montana during the last 30 years was accompanied by rapid evolutionary change in sexual size dimorphism. Here I show that traits that changed the most across generations were most influenced by maternal effects in males but not females. Maternal effects differentially affected sons' and daughters' survival; greater maternal effects were commonly associated with higher survival of sons, especially when maternal and offspring environments were similar. Stronger maternal effects extended preselection phenotypic variance in morphological traits of males, thereby producing some locally adaptive phenotypes and lessening juvenile mortality. Thus, the observed sex-specific maternal effects and their contribution to the evolution of sexual size dimorphism are likely a passive consequence of the distinct sensitivity of sons and daughters to maternal adaptations to breeding in ecologically distinct parts of the house finch's expanding range.

Keywords: maternal effects, sexual size dimorphism, growth, survival selection.

In species that experience significant but short-term fluctuations in environment, maternal effects are often the most important of all developmental resources inherited by offspring. In invasive species, these effects enable across-generation transfer of adaptations to novel environments and, ultimately, facilitate evolutionary persistence of adap-

tive strategies (Baldwin 1896; West-Eberhard 1989; Jablonka et al. 1995; Lachmann and Jablonka 1996; Badyaev 2005). However, maternal effects expressed in the offspring phenotype are an outcome of both maternal and offspring strategies, and thus, depending on similarity of selection pressures acting on maternal and offspring generations and on the extent of overlap between these generations, maternal effects can either constrain or facilitate offspring adaptations (Kirkpatrick and Lande 1989; Cheverud and Moore 1994; Rossiter 1998; Wolf et al. 1998; Wolf and Wade 2001; Wilson et al. 2005). When selection pressures differ between males and females either within or between generations, or when sensitivity to maternal effects differs between the sexes, maternal effects can be strongly sex-specific and play an important role in the evolution of sexual dimorphism (Stamps and Krishnan 1997; Badyaev 2002; Badyaev et al. 2003a).

The evolution of sex-biased maternal strategies leading to sexual size dimorphism of offspring is poorly understood. Empirical studies often document highly flexible sex-specific maternal strategies that strongly enhance offspring adaptations in particular, often rare, environmental or behavioral contexts. For example, mothers can allocate variable amounts of nutrients and hormones to sons and daughters in relation to season, quality of their mates, or within-nest competition (Dijkstra et al. 1990; Dzus et al. 1996; Blanco et al. 2002; Anderson et al. 2003; Saino et al. 2003; Rosivall et al. 2004). In contrast, there is a frequent finding of inflexible maternal strategies that place strong constraint on sex-specific growth and sexual size dimorphism and are persistent enough to lead to the evolution of offspring strategies to overcome these constraints (Clark and Galef 1995; Lucas et al. 1996; Smith and Leigh 1998; Guégan et al. 2000; Uller 2003). For example, equal maternal provisioning of sons and daughters in strongly sexually dimorphic species is a powerful selection force on the growth of the larger sex (Ono and Boness 1996; Holden and Mace 1999). To better understand the evolutionary importance of maternal effects, we need to know how selection on males and females varies between maternal and offspring generations as well

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as whether maternal effects are passive consequences of maternal adaptations or active maternal manipulations of offspring phenotype (Rossiter 1998; Reece et al. 2002; West and Sheldon 2002; Morjan 2003). Here I examine the possibility that passive sex-biased maternal effects on early offspring growth in combination with sex-specific selection on offspring can lead to rapid evolution of sexual dimorphism in offspring morphology in the absence of active sex-specific maternal strategies.

A particularly suitable study system to examine this question is one that combines differential growth requirements of the sexes (as found in sexually dimorphic species) with differences in environments between generations (as found in invasive species). The establishment of the house finch (*Carpodacus mexicanus*) populations across western Montana during the last 30 years was accompanied by the rapid evolution of sexual size dimorphism (Badyaev and Hill 2000; Badyaev et al. 2001*b*). The persistence of newly established populations was strongly facilitated by sex-biased maternal effects on the ovulation sequence and incubation of eggs in a clutch (Badyaev et al. 2002*a*, 2003*a*). Within the offspring generation, these maternal effects were mostly caused by a greater sensitivity of male oocytes, embryos, and nestlings to conditions during growth (Badyaev et al. 2001*a*; Young and Badyaev 2004) and to age-specific variation in maternal strategies (Badyaev et al. 2003*a*, 2003*b*). Here I examine the consequences of maternal effects for the evolution of sexual size dimorphism across 10 generations of Montana house finches. First, I show that the amount of evolutionary change varies among individual traits and between the sexes. Second, I show that the most rapidly evolving traits have the greatest maternal and environmental effects. Third, I document sex-biased maternal effects on juvenile survival and examine the similarity between maternal and offspring environments in relation to the strength of maternal effects.

Materials and Methods

Study Population and Data Collection

The house finch study population is located near Missoula, in northwestern Montana. The first records of house finches in this location dated to the mid-1950s, but the first documented breeding occurred in the early 1970s (Badyaev and Hill 2000). Since 1995, all resident adults were marked with a unique combination of four rings, and all nests included in this study were found during building (detailed description of the study site and protocols in Badyaev and Martin 2000*b*). All resident finches remained in the vicinity of the study area throughout the breeding season and were recaptured reliably at regular

intervals, and seven morphological traits were measured (bill length, depth, and width; tarsus length; wing length; tail length; and body mass). Strong fidelity of adult house finches to the location of previous breeding and the isolation of the study site allowed us to assign birds' ages and to follow individual birds from hatching to up to 7 years of age (Badyaev and Martin 2000*b*; Badyaev and Duckworth 2003). About 15% of offspring measured in each year after 1995 were progeny of offspring hatched in the previous year (Sæther et al. 2004). The rest were progeny of juvenile finches that hatched in Missoula and settled at the study site during the late summer dispersal, when they were about 150–170 days of age (Badyaev et al. 2001*a*; Badyaev and Duckworth 2003). Data for house finches hatched in Missoula during the 1970s were from birds measured at the time of collection and subsequently held at the University of Montana's P. L. Wright Zoological Museum. To measure nestling hatching order and morphology, egg laying and hatching were monitored closely, eggs were numbered sequentially on the day of laying, and nestlings were marked within 2–3 h of hatching. Individual marking was renewed every second day until nestlings could be banded at 7–8 days of age (protocols in Badyaev et al. 2003*a*).

A blood sample was collected from each 7–8-day-old nestling, and the sex of nestlings was determined molecularly by amplification of an intron of the CHD1 genes on the sex chromosomes (Griffiths et al. 1998). Social paternity was known for all nests, and true paternity for pedigree determination was confirmed by genotyping all adults and offspring with 16 highly polymorphic species-specific microsatellite loci (K. Oh and A. V. Badyaev, unpublished manuscript). Paternity for a putative father was excluded if two or more loci did not match. Fewer than 5% of offspring each year were from extrapair matings (K. Oh and A. V. Badyaev, unpublished manuscript).

Between-Generation Change in Morphological Traits

Between-generation change in morphological traits was the difference between fully grown locally hatched offspring in year t and fully grown locally hatched offspring of the first-year parents in year $t + 1$. From the survival estimates, the true generation time in Montana house finches is 2.02 years; however, for simplicity and to emphasize that different generations were measured every year, the between-year change will be called the between-generation change hereafter. All birds in the population and in selection samples were individually marked, and selection episodes were defined as follows. Juvenile survival selection episode (Badyaev et al. 2001*a*): individuals that survived from 40–45 days of age (fully grown) to 70–80 days of age (no significant juvenile dispersal takes

place before that age). Winter survival (postjuvenile) selection episode (Badyaev et al. 2000; Badyaev and Martin 2000b): individuals that survived from postjuvenile molt (~110–120 days of age; September–October) to their first breeding season (February–March). “Maternal generation” selection was winter survival selection on females only, before their first breeding season. The univariate selection differentials, in the units of standard deviation, were calculated for each trait as a difference in untransformed trait means between “before” each selection episode and “after” each selection episode, divided by a square root of the before-selection variance. No transformations were used because plots of raw values had unimodal and normal distributions (except for body mass, measured in grams, that was scaled to 1/3 power when compared with traits with linear units). I also calculated selection differentials using ln-transformed (for linear traits) values to decouple trait means and variances. Selection differentials were calculated and tested for statistical significance within and among years with PROC GLM (SAS 9.0; SAS Institute 1989). Thus, for each bird breeding at the study site during the first year of life, the estimated selection episodes were juvenile survival and/or winter survival (maternal generation selection in the case of females).

When morphological traits are highly correlated, it is appropriate to describe their variation within generation or their change between generations in terms of size and shape factors. To examine the relationship of between-generation change and maternal contribution to morphological traits, I calculated change in size and shape factors separately for bill (length, depth, and width) and body (tarsus length, wing length, tail length, and body mass) measurements. Male and female correlation matrices of the between-generation change (table 1 in the online edition of the *American Naturalist*) were distinct, and thus, separate principal components were constructed for each sex. I extracted the first eigenvectors of the sex-specific matrix for bill and body traits. These vectors were the change in bill size and the change in body size (table 1). Shape factors for bill and body traits for each sex were the residuals from ANCOVA of each original trait with general size (bill size or body size) as a covariate (table 1; Badyaev and Martin 2000b). Similarly, to account for nonindependence of individual morphological traits within each generation, I extracted the first eigenvectors from the sex-specific matrix of trait measurements, separately for bill and body traits. These vectors were bill and body size within each generation, and the shape traits in individual traits were the residuals from ANCOVA with general size as a covariate. I then calculated the contribution of maternal effects to residual shape factors for each generation separately. Because cor-

relational structure differed between the sexes and among years, size and shape factors were used for assessment of maternal effects only (fig. 1).

Estimation of Maternal Effects

In 1995–2004, pedigree relations were known for a total of 892 birds in the genealogy with 153 different dams and 167 different sires. I used an animal model with restricted maximum likelihood estimation of variance components of fully grown traits in the “before selection” group of juveniles (Hendersson 1988; Lynch and Walsh 1998). All variance components were estimated for each sex with REML-VCE-5 software (Kovac and Groeneveld 2003) as follows. First, I used general linear model (PROC GLM) to identify fixed effects to include in the variance estimation analysis. Based on the outcome of PROC GLM, I considered the following terms in my first variance components’ model: nest identity (i.e., location in the row of 74 bushes where finches nest; random effect), year (here used as replicate from 1995 to 2004, fixed effect), hatching order (1–5, fixed effect), nest initiation date (Julian, fixed effect), and age in days (post-hatching, for repeated measures of the same individual postgrowth; fixed effect). In the second model, the nest identity term was replaced by two terms: maternal identity and paternal identity. Both were entered as random effects to separate maternal environmental and condition effects from additive genetic effects. I considered the sum of the effects of parental identities as “the maternal effect” contribution to a given trait. The percent of variance caused by individual effects was calculated from the total phenotypic variance, and the negative maximum likelihood estimations of variance were converted to 0. I used both first-breeder and older females for estimation of maternal effects. Only females breeding for the first time were included in other calculations. Cross-fostered nestlings and nests where eggs were cross-fostered were excluded from this analysis.

In addition, I estimated the relative strength of general maternal effects on variation in each trait of offspring from the regression coefficients of maternal trait versus mid-parent trait in a multiple regression on male and female offspring traits (Price and Grant 1985; Lande and Price 1989; Koerhuis and Thompson 1997). Maternal effects evaluated by this method necessarily include common environmental effects on offspring growth. Thus, the hatching order and nest initiation date terms were included as covariates in these regression models.

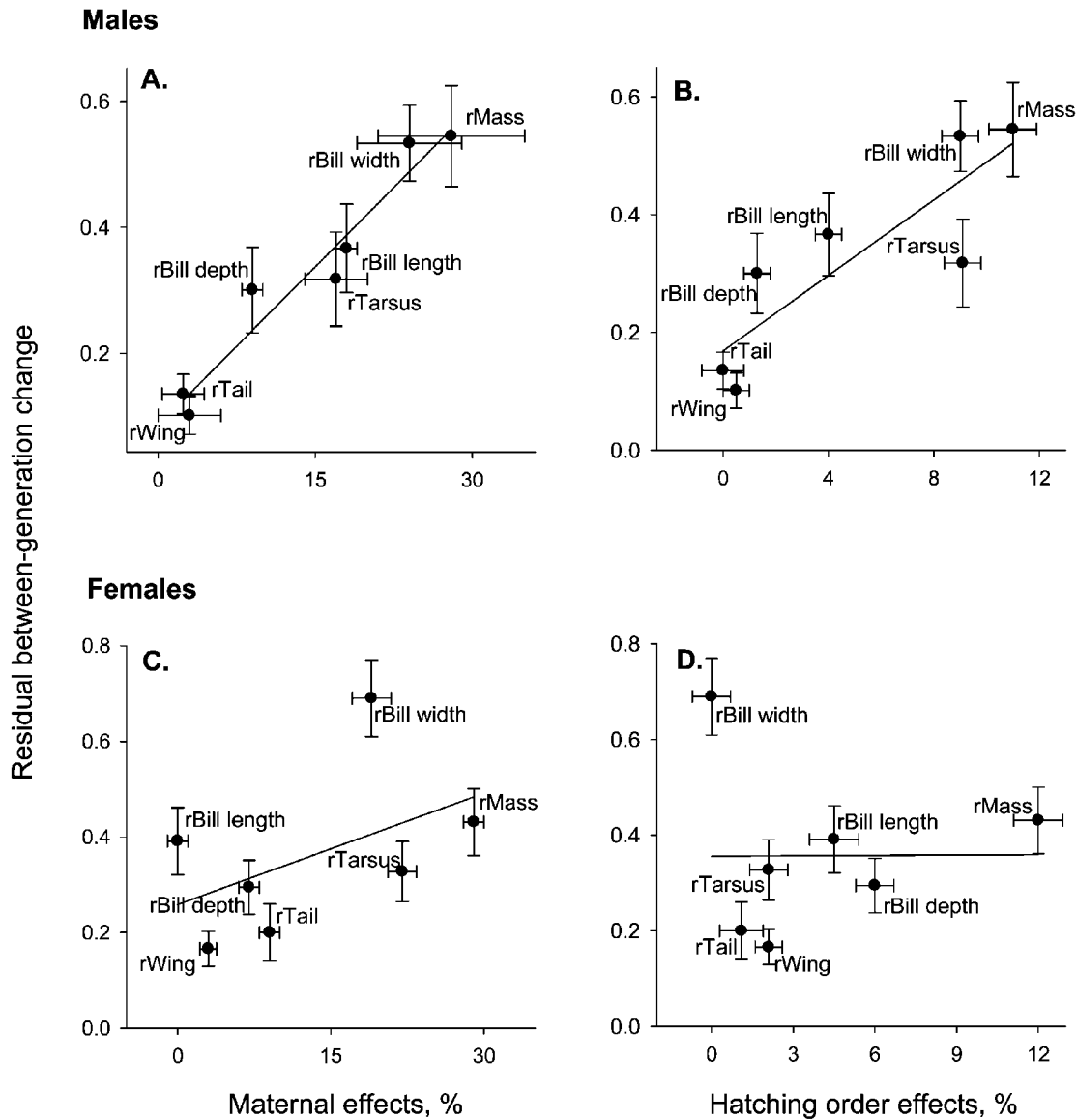


Figure 1: Between-generation change in residual shape traits (mean \pm 1 SE) in relation to relative contribution of maternal effects and hatching order effects (%) to the phenotypic within-generation variance in residual shape traits of males (A, B) and females (C, D). See table 1 in the online edition of the *American Naturalist* for details.

Results

Between-Generation Change in Morphology of Males and Females

Across 10 generations, bill length and width and tail length declined in both sexes, whereas tarsus length increased in males and decreased in females (figs. 2, 3). In males, the average between-generation change per year was the highest for bill width, body mass, and tarsus, and the lowest was for wing and tail length (figs. 2, 3). In females, the

greatest between-generation change was in bill traits, followed by tarsus length, body mass, and wing and tail lengths (figs. 2, 3). When the between-generation change of individual traits was decomposed into the change in size and shape components (table 1), the average between-generation change was the greatest in bill size (males: 1.58 ± 0.33 [SE]; females: 1.52 ± 0.41) and body size (males: 0.99 ± 0.34 ; females: 1.01 ± 0.18). In the residual shape traits, the average between-generation change in both sexes was the highest in body mass, bill width and

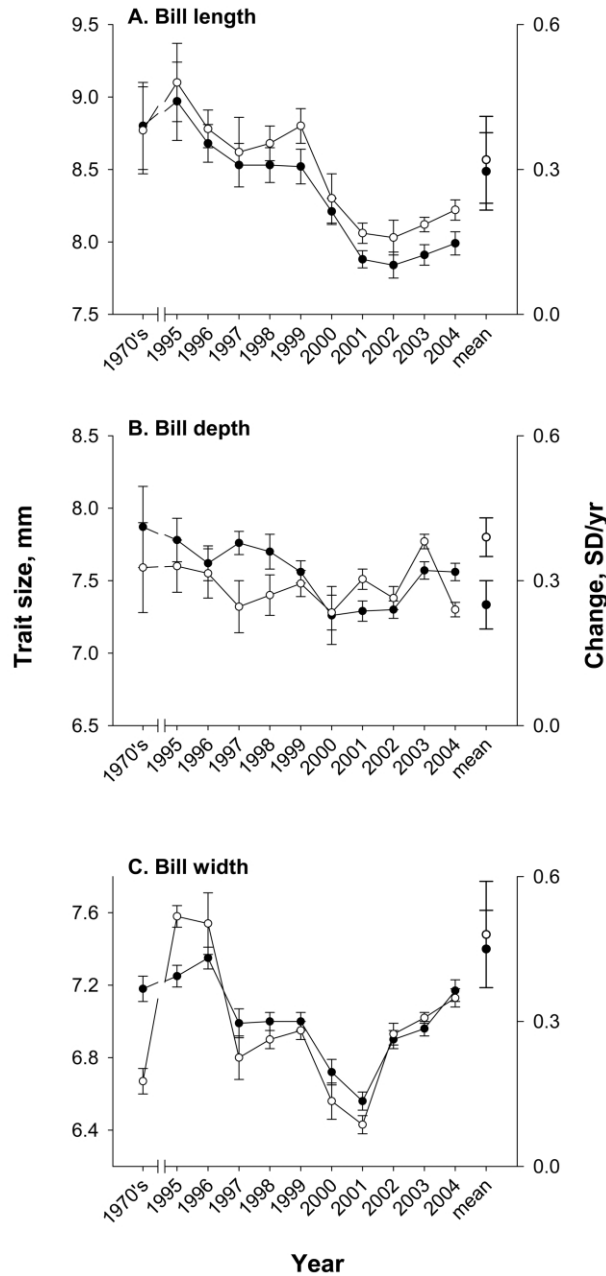


Figure 2: Morphological changes across consecutive generations of Montana house finches. Shown are means (± 1 SE) of traits measured in a preselection population of fully grown local juveniles hatched in a given year, except in the 1970s museum sample (see “Materials and Methods”). Sample sizes: the 1970s, 14 males, 18 females; 1995, 23, 24; 1996, 53, 42; 1997, 46, 52; 1998, 19, 22; 1999, 53, 44; 2000, 48, 26; 2001, 49, 55; 2002, 57, 66; 2003, 61, 67; and 2004, 48, 36. Right axis shows absolute values of the mean change between generations (in standard deviations: SD/year ± 1 SE of the mean) in males (solid circles) and females (open circles).

length, and tarsus, and the lowest was in bill depth and wing and tail length (table 1; fig. 1).

Maternal and Hatching Order Effects and Evolution of Sexual Size Dimorphism

Variance associated with maternal effects and hatching order effects varied among morphological traits (fig. 1). In fully grown sons, traits with greater maternal effects and traits that were most influenced by the hatching order showed the largest between-generation change (maternal effects: least squared $b = 0.55 \pm 0.06$, $t = 8.89$, $P < .001$; fig. 1A; hatching order effects: $b = 0.23 \pm 0.06$, $t = 3.73$, $P = .01$; fig. 1B). In daughters, neither maternal effects nor the effects of hatching order varied with the between-generation change (maternal effects: $b = 0.29 \pm 0.24$, $t = 1.21$, $P = .27$; fig. 1C; hatching order effects: $b = 0.01 \pm 0.12$, $t = 0.01$, $P = .98$; fig. 1D).

Maternal Effects in Relation to Selection on Offspring Generation

Maternal effects on offspring growth had distinct consequences for the mortality of sons versus daughters during their first summer (fig. 4). Greater maternal effects were associated with weaker selection on all measured morphological traits of sons (table 2), with the exception of bill depth, where intermediate maternal effects were most adaptive for offspring, and tail length, where selection did not vary with maternal effects (fig. 4). In daughters, greater maternal effects were associated with weaker selection only in bill depth and tail length but with stronger selection on tarsus length, whereas the mortality of daughters attributable to variation in other traits was unrelated to maternal effects (table 2; fig. 4). The sex difference in the slope of the relationship between maternal effects and selection on offspring generation reached statistical significance for bill width ($F = 6.03$, $df = 1, 19$, $P = .02$) and tarsus length ($F = 7.91$, $df = 1, 19$, $P = .001$; fig. 4).

Maternal Effects and Similarity of Selection Between Maternal and Offspring Generations

In sons, greater maternal effects were associated with weaker selection on offspring compared with selection on maternal generation in all measured traits but wing and tail length (table 2; fig. 5). On the contrary, maternal effects on the growth of daughters were not associated with differences in selection pressures between maternal and offspring generations, with the exception of selection on bill length that was stronger in daughter generation when maternal effects were greater (table 2; fig. 5). The sex differ-

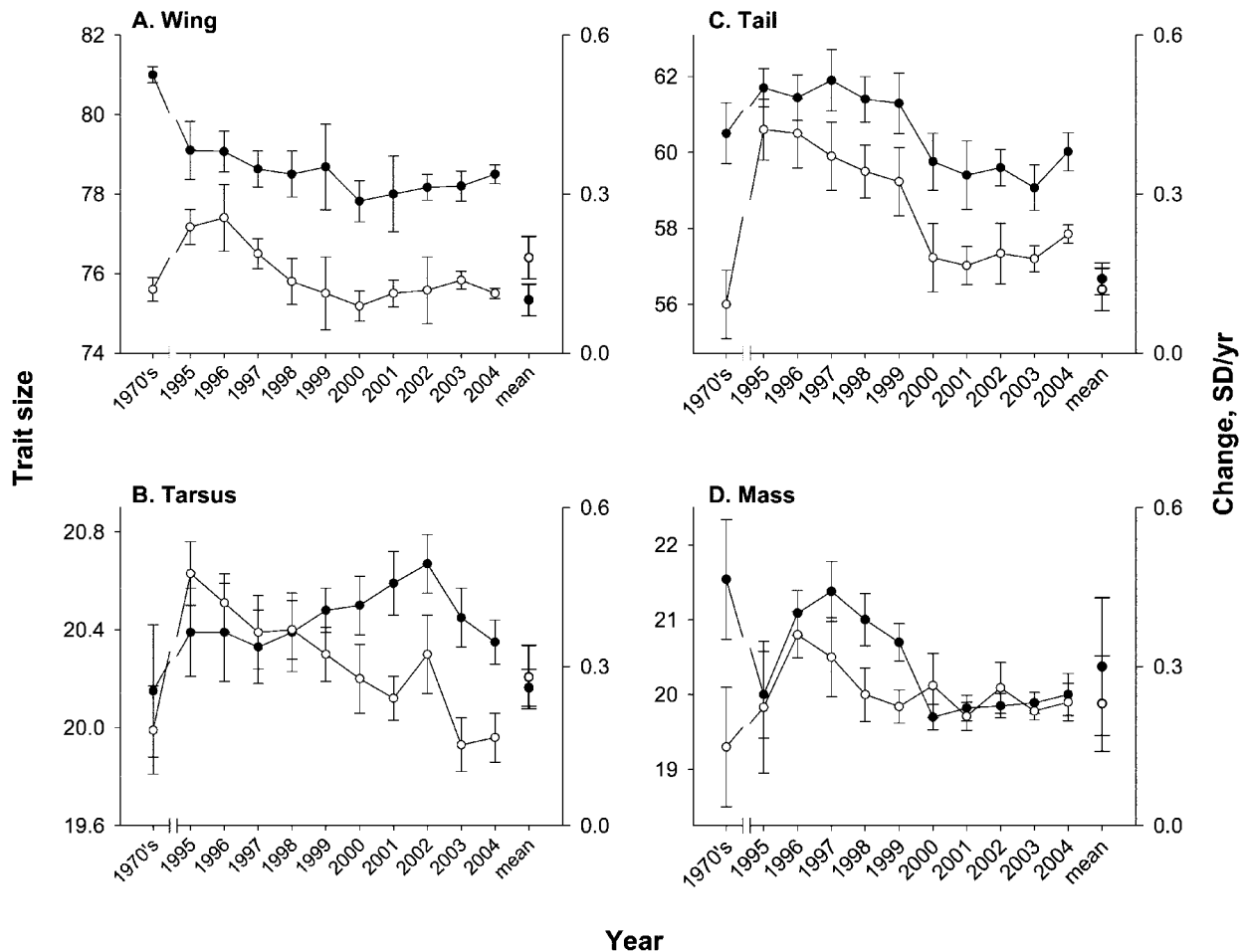


Figure 3: Morphological changes across consecutive generations of Montana house finches in (A) wing length, (B) tarsus length, (C) tail length, and (D) body mass. Right axis shows the mean between-generation change (in SD/year) in males (solid circles) and females (open circles). See figure 2 for details.

ence in the slope of the relationship between maternal effects and similarity of selection pressures between generations reached statistical significance for bill length ($F = 23.03$, $df = 1, 15$, $P < .001$), bill depth ($F = 5.00$, $df = 1, 15$, $P = .04$), and tail length ($F = 4.89$, $df = 1, 15$, $P = .04$; fig. 5).

Maternal Effects and Preselection Phenotypic Variance

In sons, greater maternal effects were associated with higher preselection phenotypic variance in bill length and width and wing and tarsus lengths but not in bill depth, tail length, or body mass (table 2; fig. 6).

In daughters, greater maternal effects were associated with higher preselection variance only in bill depth and tail length and were associated with lesser preselection var-

iance in tarsus length (table 2; fig. 6). The relationships between maternal effects and preselection variance were significantly different between the sexes for bill length ($F = 4.18$, $df = 1, 17$, $P = .05$), bill depth ($F = 4.51$, $P = 0.05$), bill width ($F = 4.03$, $df = 1, 15$, $P = .05$), and tarsus ($F = 7.58$, $df = 1, 15$, $P = .01$). Standardized selection differentials calculated on ln-transformed data, which decoupled the mean and variance of each trait, did not vary with maternal effects on the same traits (all t 's < 1.38 , P 's $> .12$); weaker selection was a result of increased preselection phenotypic variance of traits.

Discussion

Inheritance of parental adaptations and the environment of early growth not only affects development of offspring

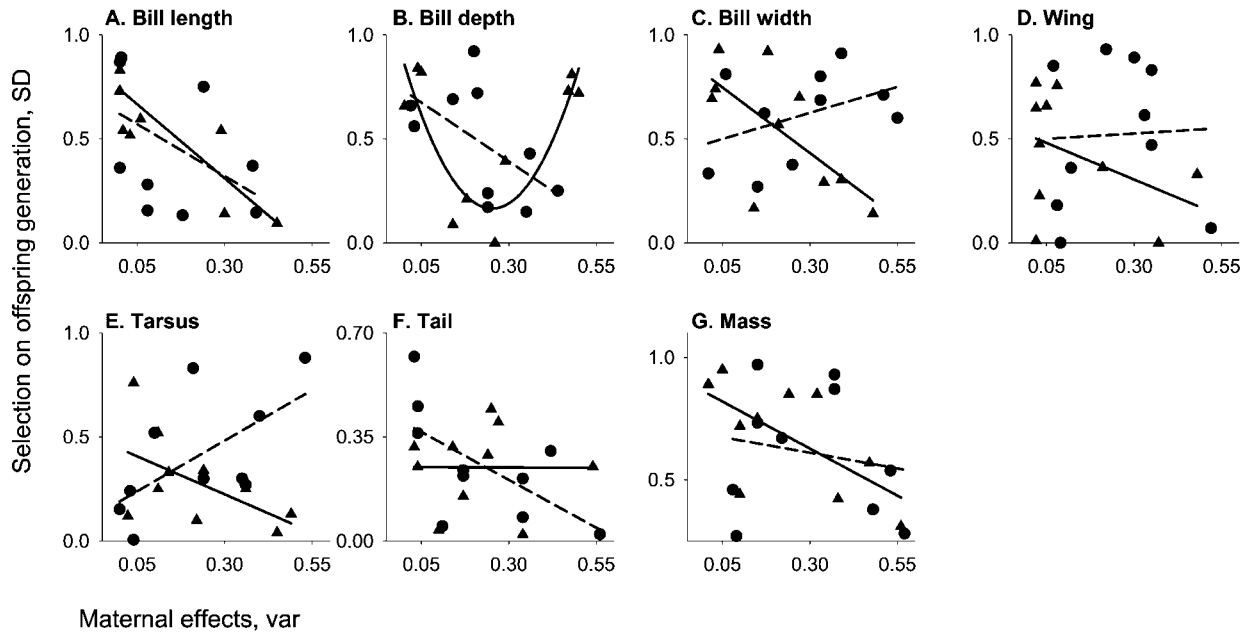


Figure 4: Linear differentials of juvenile survival selection in relation to contribution of maternal effects (variance; $\times 10^2$) in (A) bill length, (B) bill depth, (C) bill width, (D) wing length, (E) tarsus length, (F) tail length, and (G) body mass. Each point represents a generation; lines are least squares regressions with the exception of B (table 2). Triangles and solid line indicate males; circles and dashed line indicate females.

but also can set the stage for a lifelong response to selection pressures in the offspring generation (Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Rossiter 1996; Mousseau and Fox 1998; Meaney 2001). Maternal effects are commonly documented and extensively studied, but two aspects of their evolution have received less attention. First, adaptive consequences of maternal effects on offspring are often sex specific. How can such

sex specificity evolve, and is such sex bias a maternal or offspring adaptation? This is especially puzzling when the sex specificity of adaptive maternal effects is reversed between breeding attempts (Dijkstra et al. 1990; Blanco et al. 2002; Saino et al. 2003). Second, species that colonize new environments commonly experience novel selection pressures that differ between generations, thus making parental adaptations relevant to the parental gen-

Table 2: Maternal effects on morphological traits in relation to selection on offspring, similarity of selection between maternal and offspring generations, and phenotypic variance in offspring generation

Maternal effects	Selection on offspring				Similarity of selection between generations				Preselection phenotypic variance			
	Males		Females		Males		Females		Males		Females	
	b_{ST}	t	b_{ST}	t	b_{ST}	t	b_{ST}	t	b_{ST}	t	b_{ST}	t
Bill length	-.85	-4.58**	-.47	-1.50	-.70	-2.48**	.93	6.23**	.59	1.89*	-.21	-.58
Bill depth	-.67	-2.59**	-.57	-1.99*	-.78	-3.06**	.13	.32	.34	.95	.69	2.49**
Bill width	.73 ^a	2.38**	.41	1.29	-.60	-1.95*	-.02	-.06	.61	2.08**	-.25	-.69
Wing length	-.58	-1.80*	.04	.12	-.05	-.12	.06	.15	.67	2.37**	.41	1.20
Tarsus length	-.56	-1.87*	.61	2.19*	-.38	-2.03*	-.15	-.39	.57	1.81*	-.71	-2.66**
Tail length	.00	-.01	-.63	-2.30**	.51	1.47	-.56	-1.60	.13	.34	.63	2.15*
Body mass	-.64	-2.37**	-.18	-.52	-.37	-2.09**	-.08	-.22	.43	1.27	.13	.34

Note: The table shows standardized regression coefficients b_{ST} and associated statistics.

^a b^2 .

* $P < .01$.

** $P < .05$.

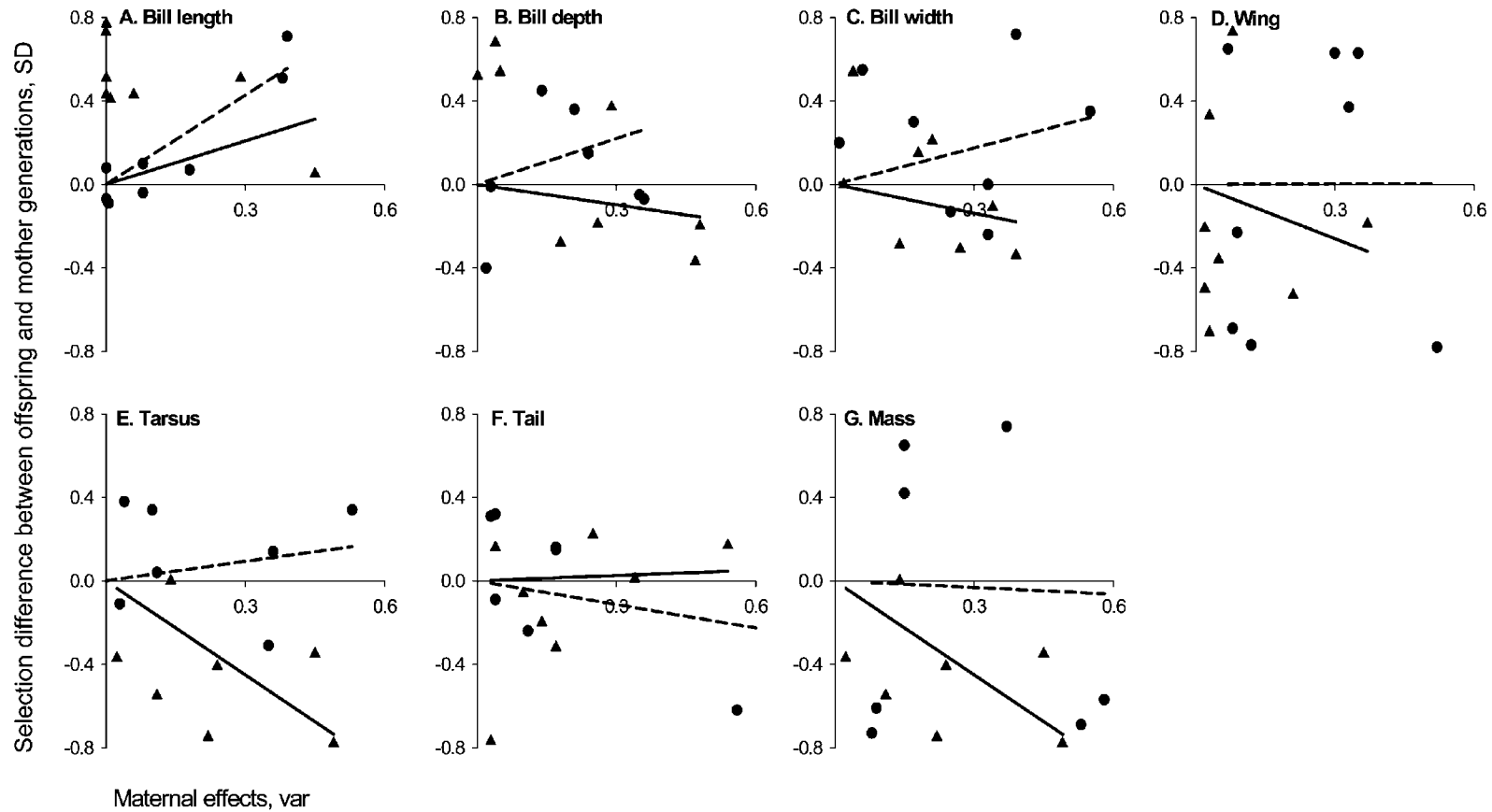


Figure 5: Similarity in strength of survival selection on the same traits in offspring (t year) and maternal ($t - 1$ year) generations (offspring minus maternal) in relation to maternal effects (variance; $\times 10^2$). Ordinate values below 0 indicate lesser mortality in offspring compared with maternal generations, whereas values above 0 indicate greater mortality in offspring compared with maternal generations. Each point represents a generation; lines are regressions through the origin for illustration only, regressions with intercept are shown in table 2. Triangles and solid line indicate males; circles and dashed line indicate females.

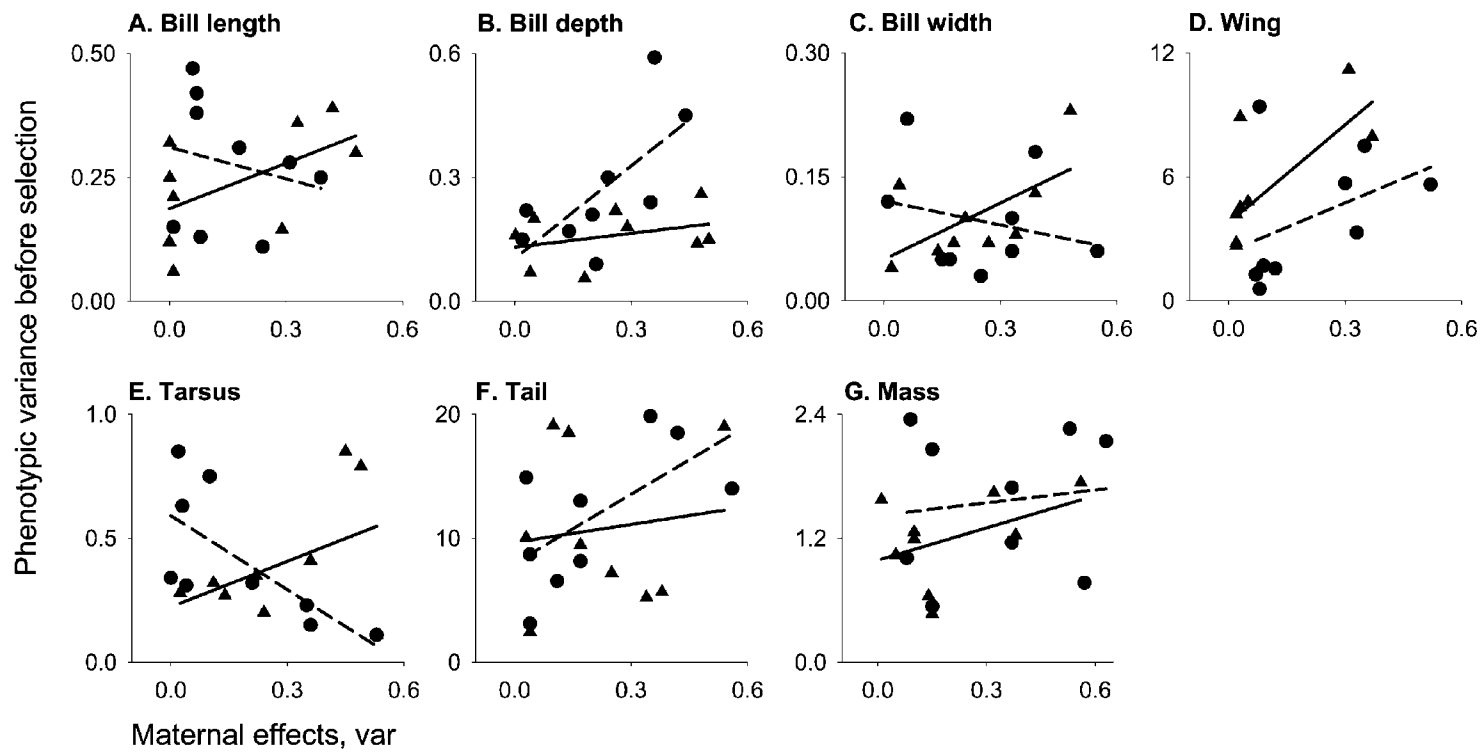


Figure 6: Phenotypic variance in preselection samples of fully grown juveniles in relation to contribution of maternal effects (variance; $\times 10^2$). Each point represents a generation; lines are least squares regression. Triangles and solid line indicate males; circles and dashed line indicate females.

eration only (Fear and Price 1998; Rossiter 1998). When the environment of growth is not predictable from the parental environment, offspring would benefit from greater flexibility in their development to accommodate novel environmental variation (Meaney 2001; Ancel Meyers and Bull 2002; Badyaev 2005). Under these circumstances, how do we reconcile directional environment-induced adaptations favored within each generation with general variance-increasing maternal effects that should be favored between generations? To resolve these questions, it is important to understand how the similarity between maternal and offspring environments influences the strength and patterns of maternal effects, as well as to establish whether maternal effects arose specifically because they convey adaptive advantage to offspring or as a by-product of a maternal strategy in which the adaptive value for the offspring emerged secondarily.

This study of rapid phenotypic evolution of sexual dimorphism in relation to maternal effects produced five principal results. First, I documented large and sex-specific maternal effects on within- and among-generation variation in morphological traits. Second, I found that the most rapidly evolving morphological traits had the highest contribution of maternal effects in males but not in females. Third, greater maternal effects were associated with lower mortality in sons but not daughters. Fourth, adaptive maternal effects on sons were greater when selection on the maternal generation was stronger. Finally, adaptive maternal effects on offspring morphology appear to result from increased preselection phenotypic variance in some morphological traits; greater maternal effects on male's morphology might be caused by greater sensitivity of males' growth to environmental conditions. Overall, these results suggest that in house finches, the observed strong maternal effects on offspring's sexual dimorphism morphology are likely a passive consequence of the distinct sensitivity of sons and daughters to adaptations of the maternal generation.

I found strong maternal effects on variation in growth in several morphological traits. In traits that grew to their asymptotic size during the nestling period (i.e., traits in which most growth occurs before fledging)—tarsus length, bill width, and body mass—up to 50% of variation was accounted for by maternal effects. On the contrary, variation in later-growing traits, such as wing and tail length and bill depth, was less influenced by maternal effects. Similarly, the duration of early growth, which is determined by the order in which nestlings hatched, accounted for up to 10% of variation in some morphological traits of fully grown juveniles. These findings corroborate the results of other studies of wild populations of vertebrates with extensive parental care that found that in some cases, more than half of phenotypic variation in

condition- and mass-related traits and more than 10% of variation in performance traits (such as parasite resistance, general health, and endurance) are often caused by maternal inheritance (Schluter and Gustafsson 1993; Milner et al. 2000; Coltman et al. 2001; Kruuk et al. 2001; Merilä et al. 2001; McAdam et al. 2002; Wilson et al. 2005).

When such strong maternal effects differ between the sexes, they can bias evolution of sexual size dimorphism in several ways (Rutledge et al. 1972; Lande and Kirkpatrick 1990; Meyer 1992; Quintanilla et al. 1999; Sanna et al. 2002). First, the interaction (negative or positive) between maternal effects and additive genetic variance in either sex can bias a trait response to selection. This can occur when mothers provide different developmental resources, such as food and egg nutrients, to male and female offspring. Second, negative maternal effects resulting from a sex-specific trade-off of resources between maternal and offspring generations can result in interdependencies of maternal and environmental effects and hinder adaptive changes in the offspring generation. For example, when maternal reproductive state is regulated by the same hormones as required for sex-specific growth of offspring, maternal reproductive decisions strongly influence growth of males and females. In Montana house finches, weather-induced early onset of incubation leads to higher circulation of prolactin and lower circulation of testosterone in breeding females during egg production. This, in turn, leads to suboptimal allocation of steroids to male eggs produced during female incubation (Badyaev et al. 2005). Third, when maternal effects vary with maternal (i.e., female) environments, such effects can produce discordance between current selection and offspring response to this selection, especially for male offspring. Finally, maternal effects that are expressed during different periods of offspring ontogeny can strongly bias the offspring response to age-specific selection, leading to variation in sexual size dimorphism because of growth differences between the sexes (Badyaev 2002).

Indeed, empirical studies have documented that the discordance between the observed microevolutionary change and the change predicted from patterns of selection on offspring is often a result of large maternal and environmental effects (Hanrahan 1976; Bandyopadhyay and Ahuja 1990; Grant and Grant 1995, 2002; Thiede 1998; McAdam et al. 2002; Magiafoglou and Hoffman 2003; Garant et al. 2004; Wilson et al. 2005). In a recent study, McAdam and Boutin (2004) found that maternal effects introduced a significant discordance between current selection and response to selection, but the discordance was eliminated when the authors accounted for selection acting on the maternal generation. Whereas it is often assumed that within- and between-generation environmental effects are

independent (Baker 1980; Dodenhoff et al. 1998; Quintanilla et al. 1999), negative and sex-biased trade-offs resulting from resource partitioning or from shared hormonal regulation between generations (Badyaev et al. 2005) are frequently documented and can strongly underestimate maternal effects, as might be the case with maternal effects on daughters in this study. Overall, sex differences in the interaction between maternal effects and selection on offspring have strong implications for microevolutionary change in sexual size dimorphism (Réale et al. 1999; Badyaev 2002).

How and why would greater selection on mothers lead to stronger maternal effects and weaker selection on their male but not their female progeny? I suggest that in this population, maternal effects arise from the maternal adaptations, and their effects on offspring, sometimes adaptive, sometimes maladaptive, are a secondary occurrence. In concurrent studies of endocrinological and physiological aspects of maternal effects, we documented that a sex difference in follicle growth and a corresponding sex bias in egg-laying sequence are favored by selection acting on the maternal generation (Badyaev et al. 2003*b*, 2005; Young and Badyaev 2004). In turn, because sons and daughters differ strongly in their sensitivity to environmental conditions during growth, sex-biased laying order and variable developmental times caused by flexible incubation strategies affect males more than females (Cooch et al. 1996; Badyaev 2002; Badyaev et al. 2003*a*). Similarly, several other studies suggested that greater maternal effects on male offspring are the result of selection acting on the maternal generation as well as the greater sensitivity of sons to environmental condition during growth (Stini 1969; Ono and Boness 1996; Potti and Merino 1996; Dunshea 2001; Laaksonen et al. 2004).

The strength of linear univariate selection is proportional to the variance of the morphological trait on which selection acts. For a number of traits in males, but not females, greater maternal effects correlated with greater phenotypic variance in the preselection populations. This in turn biased selection pressures on juvenile males and females (fig. 4) and in some traits might have influenced microevolutionary change (fig. 1). These results corroborate previous demonstration that the observed divergence in sexual size dimorphism between recently established house finch populations in Montana and Alabama is not predicted from the patterns of growth alone, unless the strong sex-specific maternal effects on phenotypic variance in morphological traits are taken into account (Badyaev et al. 2002*a*). More generally, the ability of organisms to adapt to novel conditions is determined both by their capacity to vary and by the retention (inheritance) of adaptive directionality of this variation between generations. An important implication of the findings reported here is

that in house finches, strong maternal effects accomplish both of these goals because greater maternal effects in this invasive species enable faster local adaptations by enhancing developmental plasticity, apparently without depleting genetic variance (Badyaev and Martin 2000*a*; Badyaev et al. 2000).

How can we reconcile the evidence that maternal effects are closely associated with adaptive population divergence in sexual size dimorphism (Badyaev et al. 2002*b*) with the suggestion that these maternal effects are a by-product of interaction between maternal adaptations and offspring sex-specific sensitivity? In Montana house finches, breeding females that biased the order in which they ovulated male and female oocytes when they had to overlap oogenesis and incubation because of weather conditions had the highest number of surviving offspring (Badyaev et al. 2005). Here, we extend these findings by suggesting that this maternal selection can result in adaptive maternal effects on offspring indirectly, for example, by affecting developmental times of sons and daughters and by increasing phenotypic variation in their growth, thus increasing the likelihood of production of locally adaptive phenotypes. The variation in maternal effects documented here indicates that individual females differ in how they respond to selection and how strongly their response to selection influences their offspring. These results corroborate previous findings that first-breeder (used in this study) and older females differ in their reaction to environmental conditions during breeding and influence offspring morphology by different means (Badyaev et al. 2003*a*). For example, we expect older females to vary less in the amount of hormones, nutrients, and antioxidants they deposit into growing follicles. Because older females are more consistent in the order in which they ovulate male and female eggs (Badyaev et al. 2003*a*), this creates a more predictable environment for the development of offspring—a condition that facilitates the evolution of sex-specific strategies of offspring to maternal behaviors (Morjan 2003).

Thus, what seem to be evolving in populations of this rapidly dispersing species are maternal adaptations to breeding in an ecologically distinct part of its expanding range, and within populations, offspring strategies accommodate these maternal adaptations. Ultimately, the unprecedented success of this species in colonizing new environments and the associated significant change in sexual size dimorphism might be attributed to strong maternal effects on developmental plasticity of offspring; these effects accomplish persistence of population-specific and locally adaptive growth patterns of males and females, while retaining the capacity to change in novel environments.

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