Evolution, 55(1), 2001, pp. 176–189

THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE HOUSE FINCH. III. DEVELOPMENTAL BASIS

ALEXANDER V. BADYAEV,[1,2,3] LINDA A. WHITTINGHAM,[4] AND GEOFFREY E. HILL[3]
[1]*Division of Biological Sciences, The University of Montana, Missoula, Montana 59812-1002*
[2]*E-mail: abadyaev@selway.umt.edu*
[3]*Department of Biological Sciences, Auburn University, Auburn, Alabama 36849*
[4]*Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53201*

Abstract.—Sexual size dimorphism of adults proximately results from a combination of sexually dimorphic growth patterns and selection on growing individuals. Yet, most studies of the evolution of dimorphism have focused on correlates of only adult morphologies. Here we examined the ontogeny of sexual size dimorphism in an isolated population of the house finch (*Carpodacus mexicanus*). Sexes differed in growth rates and growth duration; in most traits, females grew faster than males, but males grew for a longer period. Sexual dimorphism in bill traits (bill length, width, depth) and in body traits (wing, tarsus, and tail length; mass) developed during different periods of ontogeny. Growth of bill traits was most different between sexes during the juvenile period (after leaving the nest), whereas growth of body traits was most sexually dimorphic during the first few days after hatching. Postgrowth selection on juveniles strongly influenced sexual dimorphism in all traits; in some traits, this selection canceled or reversed dimorphism patterns produced by growth differences between sexes. The net result was that adult sexual dimorphism, to a large degree, was an outcome of selection for survival during juvenile stages. We suggest that previously documented fast and extensive divergence of house finch populations in sexual size dimorphism may be partially produced by distinct environmental conditions during growth in these populations.

Key words.—Growth; house finch, molecular sex identification, sexual size dimorphism, viability selection.

Sexual size dimorphism is a widespread phenomenon and is commonly regarded as an outcome of sex-specific patterns of current sexual and natural selection (Darwin 1871; Ralls 1976; Lande 1980; Payne 1984; Slatkin 1984; Arak 1988; Shine 1989; Moore 1990; Fairbairn 1997; reviewed in Andersson 1994). Traditionally, studies of the evolution of dimorphism focused on variation in adult sexual dimorphism and examined its ecological, behavioral, and phylogenetic correlates (e.g., Earhart and Johnson 1970; Howard 1981; Leutenegger and Cheverud 1982; Cheverud et al. 1985; Rising 1987; Björklund 1991; Webster 1992; Rogers and Mukherjee 1992; Lindenfors and Tullberg 1998). Indeed, close concordance between current environmental conditions and degree of dimorphism is often documented (e.g., Weatherhead et al. 1987; Webster 1992; Powell and King 1997; Wikelski and Trillmich 1997; Masterson and Hartwig 1998; Ferguson and Fairbairn 1999; reviewed in Badyaev and Hill 1999).

Although this approach provides important information on how sexual dimorphism varies across taxa, it is less satisfactory for revealing the mechanisms underlying the evolution of sexual dimorphism within taxa. This is because the sexual size dimorphism of adults is a result of an often long growth period during which sexually dimorphic growth and maturation patterns are themselves the subject of selection (e.g., Hirnaux 1968; Clutton-Brock et al. 1985; Shea 1986; Leigh 1995; Stamps and Krishnan 1997; Post et al. 1999). Thus, observed adult sexual dimorphism is strongly influenced by the interaction between the ontogeny of sexual dimorphism and selection on juvenile morphology (e.g., Hall 1978; Leigh 1995; Masterson and Leutenegger 1992; Richtsmeier et al. 1993; Leigh and Shea 1996; Merilä et al. 1997). As a result, variation in adult sexual dimorphism can be due to very different evolutionary forces (Wiley 1974; Jarman 1983; Shea 1986; Cheverud et al. 1992; Cooch et al. 1996; Leigh and Shea 1996). This problem is illustrated by examples of the discordance between selection on adult dimorphism and the degree of dimorphism (e.g., strong selection for larger male size in species where males are smaller; Ralls 1976; Arak 1988; Fairbairn and Preziosi 1996; see also Larsson et al. 1998) and by observations that similar levels of sexual dimorphism can be produced by different ontogenetic processes (Wiley 1974; Jarman 1983; Shea 1986; German and Meyers 1989; Cheverud et al. 1992). Therefore, the studies that combine investigations of both the ontogeny of sexual size dimorphism and selection during ontogeny should be especially informative about evolutionary pathways of dimorphism change (e.g., Leigh 1995; de Kogel 1997; Birkhead et al. 1999; Post et al. 1999). Yet, such studies are rare.

Ontogenetic variation in sexual dimorphism can result in adult dimorphism in two general ways. First, sexes can differ in growth patterns, such as size at birth, growth rates, phenotypic and genetic variation in growth patterns (and related differential sensitivity to environmental conditions during growth), and duration of growth (e.g., Gould 1977; Richter 1983; Shea 1985, 1986; Stamps 1990; Teather and Weatherhead 1994; Stamps and Krishnan 1997; Smith and Leigh 1998). In birds, which are the focus of this study, even in some of the most dimorphic species, the sexes do not differ in size at hatching (Teather 1989; Burke 1992; but see Mead et al. 1987). Frequently documented differences between sexes in sensitivity to environmental conditions during growth (Richter 1983; Clutton-Brock et al. 1985; Stinson 1985; Lindström 1999), in birds, seem to be related mostly to size difference between sexes (see below; Teather and Weatherhead 1988, 1994; Sheldon et al. 1998) and not to sex per se. At the same time, sexual dimorphism in growth rates and growth duration is frequently documented in birds (reviewed in Teather and Weatherhead 1994). Second, sexes can be subject to different selection pressures as juveniles (Gebhardt-Henrich and Marks 1993; Leigh 1995; Merilä et al. 1997; re-

viewed in Stamps 1990). Differential selection pressures can be related to differences between sexes in size during growth, such that environmental conditions during growth can have differential effects on the smaller or larger sex (Wegge 1980; Lindén 1981; Fiala and Congdon 1983; Richter 1983; Røskaft and Slagsvold 1985; Weatherhead and Teather 1991; Sheldon et al. 1998; Krijgsveld et al. 1999). In addition, each sex may experience different selective environments during late ontogeny, when males and females engage in different activities, or when young birds compete with other juveniles in population (Shreeve 1977; Wegge 1980; Hochachka and Smith 1991; Lindén et al. 1992; Gowaty 1993; see also Stamps 1990 and references therein). Frequently documented extensive mortality of young individuals (reviewed in Ricklefs et al. 1998) suggests that viability selection before maturity strongly influences adult morphology (e.g., Merilä et al. 1997; see also Stamps and Krishnan 1997). In birds, where competition among siblings and the environment created by parents can strongly influence individual growth patterns (e.g., Bortolotti 1986; Stamps 1990; Ricklefs et al. 1998; Schew and Ricklefs 1998), adaptive adjustment of offspring sex ratio and sex-biased provisioning of nestlings by parents may provide an additional source of sexually dimorphic selection pressures (e.g., Richter 1983; Stamps 1990; Gowaty 1991; Weatherhead and Teather 1991; Cooch et al. 1997; Merilä et al. 1997).

Investigations of the ontogeny of sexual size dimorphism and especially of selection on juvenile dimorphism in natural populations are difficult for several reasons. First, in cross-sectional population studies, it is often difficult to separate sexually dimorphic patterns of growth and sexually dimorphic patterns of selection (e.g., Cooch et al. 1996; Sheldon et al. 1998). Second, selection on juvenile morphology is difficult to evaluate because of extensive and sex-biased natal dispersal. Finally, especially in birds, it is often difficult to phenotypically sex young individuals, which results in underestimation of selection during early ontogeny (Merilä et al. 1997, 1998). As a result, most of our knowledge about selection on juvenile sexual size dimorphism comes from studies of mammalian species (especially primates), where prolonged ontogeny and detailed knowledge of social organization of juveniles has allowed examination of behavioral, social, and ecological correlates of juvenile sexual dimorphism (e.g., Hirnaux 1968; Jarman 1983; Georgiadis 1985; Shea 1986; Leigh 1995; Leigh and Shea 1996; Post et al. 1999), and more generally, from the studies of animals in which growth continues past sexual maturation (reviewed in Stamps 1993).

The recent colonization of ecologically distinct areas in North America by the house finch (*Carpodacus mexicanus*) has been accompanied by strong population divergence in sexual size dimorphism (Badyaev and Hill 2000). In a long-term study of recently established populations in Alabama, Michigan, and Montana, we showed that, in adult finches, current net selection for sexual size dimorphism was highly concordant with observed sexual dimorphism (Badyaev and Martin 2000a, Badyaev et al. 2000). We suggested that this concordance was enabled by moderate heritabilities of sexually dimorphic traits and low phenotypic and genetic covariations among these traits during growth (Badyaev and Martin 2000b). However, to investigate mechanisms of evolutionary change in size dimorphism in this species, it is necessary to establish the developmental basis of dimorphism change. In this paper, we use recent techniques for molecular sex identification to examine the developmental basis of sexual size dimorphism in an isolated population of the house finch. First, we describe sex-specific patterns of growth and evaluate the relative contribution of sexual dimorphism in the growth rates and the age at growth cessation to sexual dimorphism of juveniles. Second, we examine postgrowth selection on male and female juvenile finches, and evaluate the relative contribution of sexually dimorphic patterns of growth and sexually dimorphic selection pressures to the sexual dimorphism of young house finches. Finally, we apply insights from our knowledge of the developmental basis of sexual size dimorphism to the problem of rapid divergence in sexual size dimorphism among recently established house finch populations.

Methods

General Methods and Measurements

The house finch is a small passerine bird, native to western North America. Since 1995, we have studied a large, resident population of this species that occupies an isolated area of suitable nesting habitat in northwestern Montana (USA). The population was established 20–30 years ago by natural expansion of the house finch historical range (Hill 1993; Badyaev and Hill 2000). The study site is located in an open field and contains several hundred 2-m high ornamental bushes used by finches for nesting and several large coniferous trees used by finches for roosting. Within the study site, we maintained three large feeding stations that are used continuously by finches throughout a year. All 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 pairing and nesting affiliations of breeding adults were determined reliably (for detailed description of field techniques, see Badyaev and Martin 2000a). Hatching was monitored continuously and nestlings were individually marked within few hours of hatching.

In 1995–1999 we measured (with Mitutoyo calipers to an accuracy of 0.02 mm): bill length from the angle of the skull to the tip of the upper mandible; bill width at the anterior end of nostrils; bill depth in a vertical plane at the anterior end of the nostrils over both mandibles; tarsus length (left and right); tail length; wing length (left and right, flattened); and body mass (with Pesola balance, to an accuracy of 0.01 g). All morphological measures were repeated twice (i.e., four times for the bilateral traits), and the average of repeated measures was used for further analyses. All birds were measured by the same person. Error variance did not exceed 12% of the total variance and was the largest for bill width and depth (6–12%) and smallest for body mass, wing and tarsus (3–4%; for details, see Badyaev and Martin 2000b).

For the analyses of sexual dimorphism in growth, we only used nestlings that were measured throughout the entire growth period (45 males and 69 females). Sixteen male and 26 female nestlings were measured every second day starting

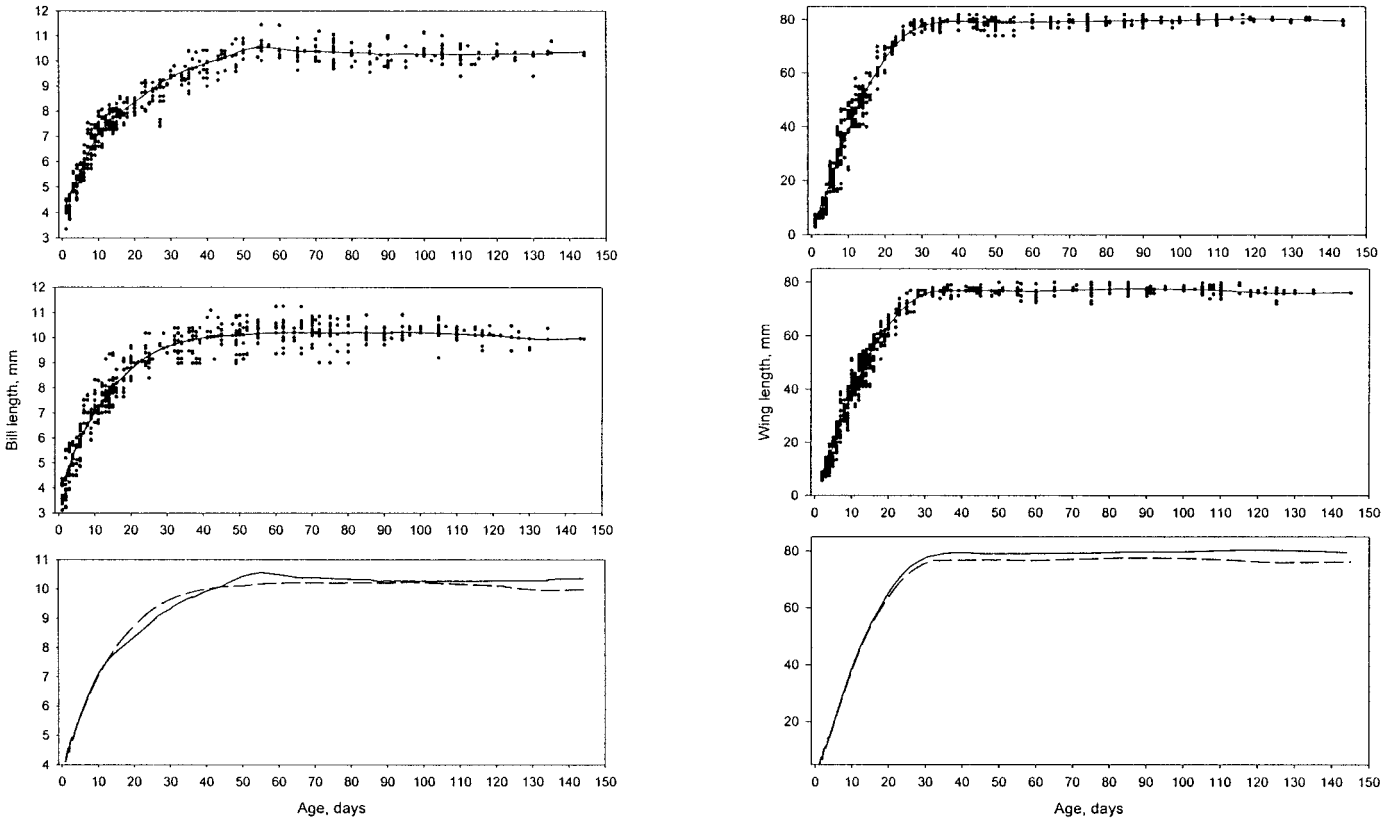

FIG. 1. Growth curves for bill length (left) and wing length (right). Spline curves are shown for males (upper), females (middle), and both sexes (lower; females, dashed line).

from day 1 (the day of hatching), the remaining 29 males and 43 females were measured every second day starting from day 2. After fledging at age 16 days (see below), all birds from this subset were recaptured repeatedly, on average once per 5–6 days until 100–120 days of age (e.g., at least once during every designated growth interval, see below; Fig. 1, for details, see Badyaev and Martin 2000b). The longitudinal data and constant sample size of this dataset allowed us to reliably determine the age of growth cessation for males and females and to examine sexual dimorphism in growth rate. Because sexual dimorphism in growth of a trait is not independent of dimorphism in other traits (Badyaev and Martin 2000b), we adjusted the probabilities of sex differences in dimorphism in growth by the number of traits compared at each age period. Individual male and female nestlings can unequally contribute to sexual dimorphism across several age groups. Thus, we used bootstraping ($n = 300$ runs) to estimate significance of sexual dimorphism at every age (see below e.g., Fig. 4).

For the analysis of viability selection on juvenile birds, we used all available data on known-age birds (i.e., individuals that were measured at longer or fewer intervals). These individuals were included in calculations for age groups older than 65 days (when growth in all traits is completed). Thus, data for ages older than 65 were mixed-longitudinal (i.e., cross-sectionally pooled time-series data of individual growth). This data structure is especially appropriate for comparison of selection between groups (e.g., between males and females). For parametric analyses (linear regression and ANCOVA), all linear data were natural log–transformed, body mass was cube-root transformed, and all data were zero-mean standardized. Hatch date has a strong influence on growth patterns in birds (e.g., Bortolotti 1986; Price 1991), including the development of phenotypic sexual dimorphism (e.g., Cooch et al. 1996). Such effects are often due to differences in timing and duration of compensatory growth between early and late broods (e.g., Larsson and Forslund 1991; Cooch et al. 1997; Larsson et al. 1998). Thus, to control for effects of hatch date, we only used nestlings from the first breeding attempts hatched between mid-April and mid-May (Badyaev and Martin 2000a).

Identification of Sex

No phenotypic indicators of sex exist for house finch nestlings. Thus, sex of nestlings was determined by a molecular sexing technique that amplifies an intron of the CHD1 genes on the sex chromosomes of birds (Griffiths et al. 1996, 1998). In birds, the female is the heterogametic sex having one W and one Z chromosome, whereas males have two Z chromosomes. We used polymerase-chain-reaction (PCR) primers P8 and P2, which anneal to conserved exonic regions and amplify across an intron in both CHD1-W and CHD1-Z genes (Griffiths et al. 1998). The length of the noncoding introns differ between the CHD1-W and CHD1-Z genes with the result that PCR products from males (one band) and females

(two bands) are easily distinguished on an agarose gel (Griffiths et al. 1998).

Each nestling was sampled for blood when 8 days old. Blood samples of 15 L were taken from a puncture of the brachial vein and stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C. DNA was extracted from blood samples using a 5 M salt solution (Miller et al. 1988). PCR was carried out in a total volume of 20 ml with the following final reaction conditions: 50 mM KCl, 10 mM Tris-HCl pH 8.3, 1.5 mM $MgCl_2$, 200 mM of each dNTP, 200 ng of each primer, 0.5 U of Taq polymerase (AmpliTaq DNA polymerase, Perkin-Elmer, Norwalk, CT) and 50–200 ng of genomic DNA. PCR amplifications were performed under the following thermal cycling conditions: an initial denaturing step at 94°C for 2 min followed by 30 cycles of 94°C for 30 sec, 47°C for 45 sec, and 72°C for 45 sec. The program concluded with a final cycle of 48°C for 1 min and 72°C for 5 min. PCR products were electrophoresed for 45–60 min at 10 V/cm in a 2% NuSieve 3:1 agarose (FMC Corp., Rockland, ME) gel stained with ethidium bromide. PCR products were visualized under UV light and scored one band as male and two bands as female. We verified this sexing technique for house finches by amplifying the DNA of 20 different known-sex adults (10 males and 10 females). In all 20 cases, the molecular method correctly identified the sex of these adults.

Growth Analysis

The growth data were analyzed in two steps. First, for each sex we fitted a spline curve to the distribution of trait values for each age (e.g., Cheverud et al. 1992). We calculated the spline curve parameters with the program provided in Schluter (1989). We used spline curves to describe the differences in growth between males and females and to identify periods crucial in the ontogeny of sexual dimorphism. In the second step, we used parametric linear regression and ANOVA to test the effects of age, sex, and their interaction on growth rates during the important ontogenetic periods identified in the first step. Significant effect of interaction between age and sex on a trait during a particular period of growth suggests sexually dimorphic patterns of growth in this trait.

In the spline curve approach (after Schluter 1988, 1989) we selected the growth function that, for n individuals, maximizes the log likelihood, log (f), such that:

$$\log(f) = \sum \log(X_i; A_i, f) - n\lambda J(f), \qquad (1)$$

where f is the growth function from a collection of individual measurements X_i at ages A_i. Term $n\lambda J(f)$ is a penalty for the roughness of regression, because maximizing the log likelihood without this penalty would result in the growth curve passing through each data point. λ, the smoothing parameter, is a nonnegative constant and $J(f)$ is the summed squared curvature of the growth function f (Schluter 1988). Using the algorithm provided in Schluter (1989), for growth in each trait, we selected the value of λ with the maximum predictive power computed using the method of cross-validation. This was done by excluding, with replacement, all individuals in turn for different values of λ (see Schluter 1988, 1989). Confidence intervals for spline curves of sexual dimorphism ontogeny were calculated by bootstrapping (n = 300 runs; Schluter 1989).

Use of nonparametric spline curves to describe growth has several important advantages over existing parametric methods of growth estimation (see also Cheverud et al. 1992). First, in fitting the growth trajectory, the spline curve approach is less sensitive to variation across the entire range of ontogeny than are parametric methods (see also Kirkpatrick and Lofsvold 1989). For example, growth patterns are strongly different between nestling stages and fledgling stages (Badyaev and Martin 2000b) and fitting a single parametric model to the entire growth sequence would bias estimates at some ages, whereas the spline method provides greater accuracy for each growth period. This fidelity to the actual data at each age is especially important given the small magnitude of sexual size dimorphism in the house finch. Second, the spline curve model does not make any assumptions about the shape of growth curves. In addition, spline curves allow discrimination between dimorphism in growth rate and dimorphism in growth cessation, which is not possible with parametric growth models (Cheverud et al. 1992). Finally, with large sample sizes, spline methods are less sensitive to outliers than parametric regressions. However, unlike standard growth models, spline growth curves cannot be readily compared across populations and species. Another disadvantage is the assumption of a normal distribution of trait values for each age and similar variance across ages (Schluter 1988). Both assumptions were satisfied here with transformations of raw data (see above). As with all regressions, spline curves are less reliable at the limits of data distribution, that is, for very early and very late ages.

We used parameters provided by the spline curve analysis to estimate the contribution of sexual dimorphism in growth rates and sexual dimorphism in age of growth cessation to juvenile sexual dimorphism (Cheverud et al. 1992; Leigh 1992). In this approach, differences between predicted male and female trait values were recorded for two ages: at female growth cessation and at male growth cessation. If the male growth period is longer for a particular trait, then the ratio of the difference between the male and female at female growth cessation age to the difference at male growth cessation age will be a proportion of juvenile dimorphism due to dimorphic growth rates (e.g., males grow faster than females). In the absence of selection (see below), the remaining percentage of dimorphism is due to sex differences in the age at growth cessation (i.e., males continue to grow after females stop, sensu Cheverud et al. 1992).

Postgrowth Selection Analysis

Phenology of juvenile house finches in the Montana population.—House finch nestlings leave the nest when 16 days old (A. V. Badyaev, pers. obs.; see also Hill 1993). After leaving the nest, broods stay together in the vicinity of the nest. During the following two weeks (17–30 days of age) most of the food for fledglings is provided by parents, most often by the male. Typically, individual broods of three to five nestlings follow a single parent around the study site begging for food. By age 20–30 days, in addition to regurgitated food provided by parents, young birds forage on small

seeds and on seed particles left by older birds. After age 25–30 days, broods are no longer tended by parents, but typically stay together until 40–50 days of age. By age 50–70 days, most young birds hatched at the study site form small (15–20 birds), single-sex flocks. Sex segregation during this period is probably maintained by male aggression toward females—during this period, juvenile males are dominant to juvenile females and commonly displace them from feeders (A. V. Badyaev, L. A. Whittingham, and G. E. Hill, unpubl. ms.; for similar findings in other cardueline finches, see Shreeve 1977; Benkman 1997). A concurrent experimental study showed that 50–80-day-old females strongly prefer joining feeding groups of juvenile females and avoid feeding groups of juvenile males. Juvenile males show no such discrimination. After 100–110 days of age, single-sex flocks of local finches begin to merge, forming large, late-summer flocks (up to 50–70 individuals). During the following month, these flocks undertake wide movements, eventually leaving the study site (A. V. Badyaev, pers. obs). The isolated location of the study site and limited dispersal of local juveniles before the formation of large, late-summer flocks provides us with an opportunity to evaluate viability selection on young birds.

Estimation of selection.—We assumed that the longitudinal data used in this study accurately reflected change in cross-sectional mean for the entire population, that is, that before growth cessation, growth of morphological traits contributed much more to change in cross-sectional population mean than did selection. This assumption is likely to be valid because during the course of this study we did not document any morphology-dependent mortality of individual nestlings (A. V. Badyaev, unpubl. data), whereas most mortality of young birds takes place during the postgrowth period (see below; see also Richner et al. 1989; Hochachka and Smith 1991; Hill 1993; de Kogel 1997; Sheldon et al. 1998). Several incidents of nestling mortality were due to sharp temperature drops during late snow storms and involved entire broods. There was no nest predation at the study site. In 1999; nestlings in three broods were killed by brown-headed cowbirds (*Molothrus ater*). Mite infestation, that is a common cause of nestling mortality in more southern populations of house finches (G. E. Hill, pers. obs.) was not recorded in the Montana study site. Because data on growth termination used in this study were from repeated measures of individual nestlings, any increase in mean in cross-section of data before the completion of growth was caused by change due to growth and not by differential mortality of smaller sized individuals. However, some selection undoubtedly takes place when growing fledglings start to feed for themselves and compete with conspecifics at feeders. More generally, the environmental effects of early ontogeny are often expressed only after a nestling's independence from its parents (e.g., Richner et al. 1989; de Kogel 1997; reviewed in Stamps 1990; Gebhardt-Henrich and Richner 1998). If selection before growth completion was sexually dimorphic, our analyses are likely to overestimate the contribution of sexual dimorphism in growth to juvenile sexual dimorphism.

If one assumes constant variance and the absence of large fluctuations in sample size across ages in juveniles, then, after termination of growth, any change in the estimated average of the spline curves for a particular age results from changes in individual composition of a population during this age. Changes in individual composition could come from morphology-dependent mortality and/or morphology-related dispersal. Juvenile finches disperse in large late-summer flocks (see above). Before the formation of these flocks, due to the isolated location of the study site and dependency of young birds on large feeding stations within the site, movements of local juvenile finches are limited to the immediate vicinity of the study site. It is possible that some of the cross-sectional changes in postgrowth sexual dimorphism are due to morphology-dependent dispersal. However, most of the changes in postgrowth dimorphism undoubtedly reflect local mortality because the majority of local individuals do not disperse until late summer. We selected age 105–115 days (age 110 hereafter) to estimate juvenile sexual dimorphism. This age is suitable for two main reasons. First, by this age most finches are in large and widely moving flocks and thus, this is the latest time when our assumption of no dispersal is likely to be valid. Second, spline curve estimations of both the morphology of each sex and sexual dimorphism are less reliable at later ages because relatively fewer birds are measured after 115 days of age.

Conventional standardized selection differentials were calculated for each trait as a difference in standardized values between age at growth cessation and age 110, divided by a square root of the before-selection (at age of growth cessation) variance. Standardized selection differentials were calculated to facilitate comparisons between sexes for postgrowth selection and for comparison with survival selection acting on adult finches in this population (Badyaev and Martin 2000a).

Results

Growth Patterns in Males and Females

Spline curves for growth of both sexes are shown in Figures 1 and 2 (for space consideration, original data for each sex are shown for only bill length and wing length growth, Fig. 1). In both sexes, bill traits (bill length, width, and depth) grew slower early in ontogeny than body traits (wing, tail, and tarsus length and body mass). For all traits, except bill depth and body mass, males grew for a longer time than females (Table 1, Figs. 1, 2), and in both sexes, no growth occurred after 65–70 days of age. The percentage of sexual dimorphism at growth cessation (hereafter SD1) due to sex differences in growth rates and sex differences in the age of growth cessation is shown in Table 1. For example, tarsus length predicted from the spline curve at 14 days (the time of female growth cessation) was 20.47 mm for males and 20.48 mm for females. At 17 days (when male growth stops), the predicted values were 20.63 mm and 20.49 mm, respectively. The ratio of the difference between sexes at day 14 to the difference at age 17 is the percentage of SD1 due to differences in growth rates (7% in this case). The remainder of SD1 results from sex differences in duration of growth (i.e., 93% for dimorphism in tarsus length). With the exception of bill length and tarsus length, SD1 was mostly produced by sex differences in growth rates (Table 1, see below).

Parametric tests of growth rate differences between the

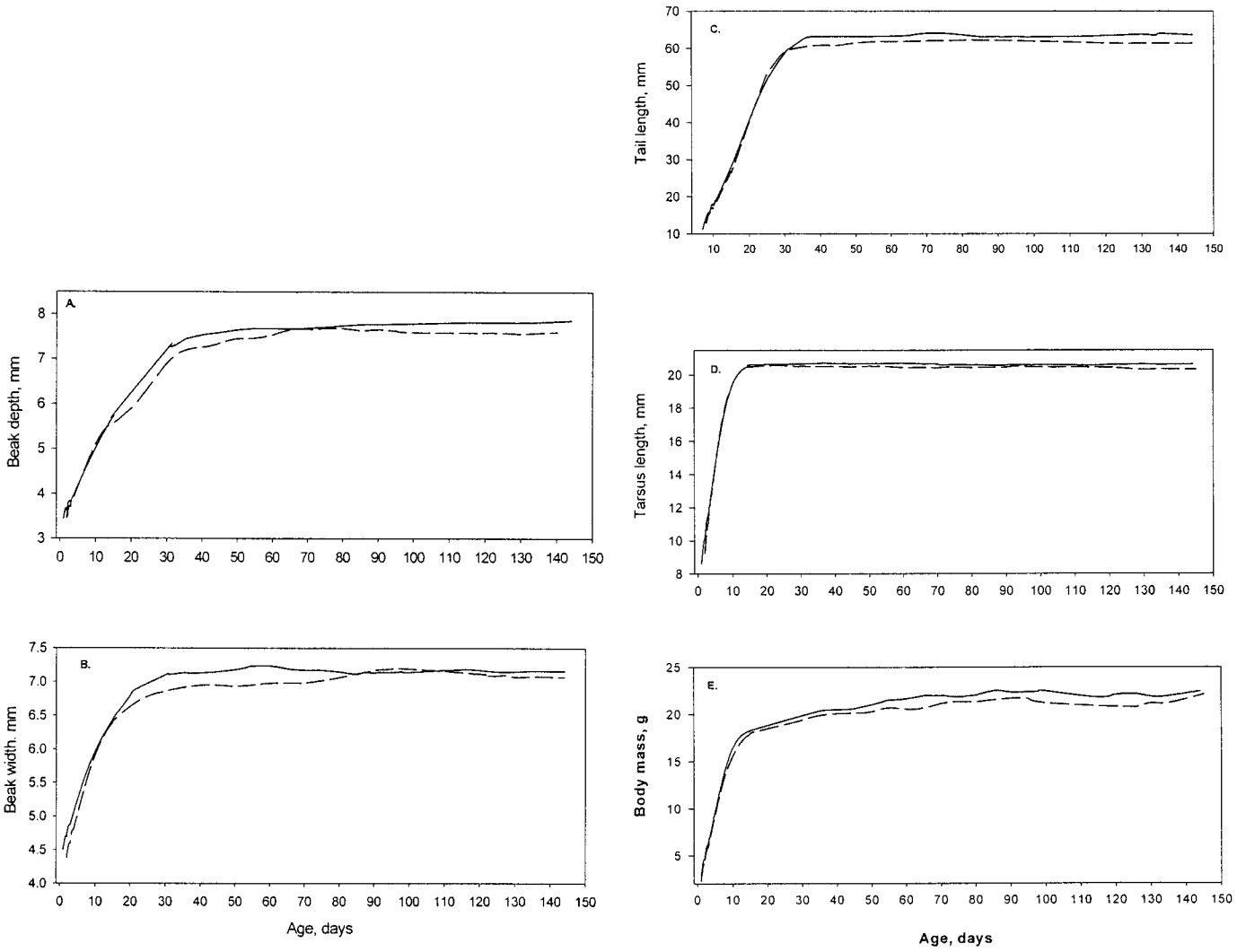

FIG. 2. Growth curves for (A) beak depth; (B) beak width; (C) tail length; (D) tarsus length; and (E) body mass. Spline curves are shown for both sexes (females, dashed line).

TABLE 1. Ontogeny of sexual dimorphism in relation to sex-specific patterns of growth. Shown are dimorphism in age of growth cessation, duration of female growth as a percentage of male growth period, and percent of dimorphism at growth cessation (SD1) due to sex differences in growth rates and in age at growth cessation.

Trait	Age at growth cessation		Male/female growth duration ratio	% SDI due to	
	Male	Female		Growth rate	Age at growth cessation
Bill length	57	44	1.30	5	95
Bill depth	57	64	0.93	100	0
Bill width	55	41	1.34	64	36
Wing length	43	32	1.34	90	10
Tail length	67	43	1.56	72	28
Tarsus length	17	14	1.20	7	93
Body mass[1]	54	61	0.88	100	0

[1] Age of growth cessation for body mass was defined as the age when body mass reaches that of adults for each sex.

sexes (Table 2) were conducted for four or five ontogenetic periods defined by spline curves (Figs. 1, 2). The periods were: early nestling growth (1–6 days), late nestling growth (7–16), fledgling growth (17–27 days), juvenile female growth (e.g., 27 days to age at female growth cessation), and juvenile male growth (after female growth cessation to male growth cessation; Table 2). For early maturing tarsus, we also designated mid-nestling growth period. For bill traits, most differences between the sexes were in juvenile growth rates, whereas for body traits most differences were in nestling growth rates (Table 2). With few exceptions, when sexes differed in growth rates, females grew faster than males, but males grew for a longer time than females (Table 2).

In bill length, females grew significantly faster than males during the juvenile period (27–44 days; Table 2, Fig. 1). During the remainder of ontogeny, the sexes did not differ in growth rates of bill length; dimorphism in this trait resulted mostly from the sex difference in the age of growth cessation (Table 2, Fig. 1). In contrast, in bill depth, females grew faster than males during fledgling (17–27 days), male juvenile

TABLE 2. Sexual dimorphism in growth rate in ontogeny of the house finch. Age categories are from spline curve analysis of the ontogeny of each trait for 45 males and 69 females (growth cessation data are shown in Table 1). Bold *P*-values indicate significant sex differences in growth rate after Bonferroni correction for the number of morphological traits ($n = 7$).

Trait	Age category (days)	Sex	Intercept (SE)	Growth rate (SE)	Probability of growth rate dimorphism
Bill length	1–6	M	1.579 (0.039)	0.057 (0.009)	
		F	1.543 (0.040)	0.065 (0.009)	0.417
	7–16	M	1.907 (0.023)	0.028 (0.002)	
		F	1.924 (0.026)	0.038 (0.002)	0.044
	17–27	M	1.901 (0.061)	0.018 (0.002)	
		F	2.139 (0.044)	0.010 (0.002)	0.124
	28–44	M	2.381 (0.108)	−0.000 (0.004)	
		F	1.880 (0.107)	0.016 (0.004)	**0.031**
	45–57	M	2.330 (0.075)	0.002 (0.002)	
		F	2.246 (0.106)	0.003 (0.002)	0.267
Bill depth	1–6	M	1.377 (0.020)	0.054 (0.005)	
		F	1.412 (0.024)	0.043 (0.005)	0.217
	7–16	M	1.588 (0.027)	0.024 (0.002)	
		F	1.644 (0.029)	0.015 (0.002)	0.203
	17–27	M	1.547 (0.061)	0.013 (0.002)	
		F	1.708 (0.082)	0.028 (0.002)	0.032
	28–57	M	2.080 (0.053)	0.002 (0.001)	
		F	2.028 (0.025)	0.009 (0.001)	**0.023**
	58–64	M	2.178 (0.151)	−0.000 (0.002)	
		F	2.010 (0.072)	0.004 (0.001)	0.050
Bill width	1–6	M	1.634 (0.026)	0.037 (0.006)	
		F	1.578 (0.026)	0.048 (0.006)	0.028
	7–16	M	1.840 (0.019)	0.010 (0.002)	
		F	1.832 (0.020)	0.016 (0.002)	**0.004**
	17–27	M	2.008 (0.038)	0.003 (0.002)	
		F	1.857 (0.056)	0.008 (0.002)	0.068
	28–41	M	2.173 (0.059)	−0.002 (0.002)	
		F	1.687 (0.113)	0.009 (0.003)	0.097
	42–55	M	2.027 (0.051)	0.004 (0.001)	
		F	2.011 (0.052)	0.001 (0.001)	0.042
Wing length	1–6	M	1.743 (0.080)	0.215 (0.019)	
		F	1.662 (0.072)	0.229 (0.016)	**0.001**
	7–16	M	2.983 (0.066)	0.071 (0.006)	
		F	3.014 (0.051)	0.065 (0.005)	**0.012**
	17–32	M	3.909 (0.062)	0.017 (0.003)	
		F	3.911 (0.046)	0.014 (0.002)	0.060
	33–44	M	4.216 (0.045)	0.008 (0.001)	
		F	4.274 (0.066)	0.001 (0.002)	**0.021**
Tail length	7–16	M	2.097 (0.172)	0.080 (0.014)	
		F	2.025 (0.129)	0.092 (0.010)	**0.031**
	17–27	M	3.254 (0.141)	0.028 (0.006)	
		F	3.274 (0.085)	0.027 (0.003)	0.067
	28–43	M	4.067 (0.078)	0.002 (0.002)	
		F	3.874 (0.102)	0.010 (0.003)	0.041
	44–67	M	4.136 (0.035)	0.003 (0.001)	
		F	4.047 (0.047)	0.001 (0.001)	0.062
Tarsus length	1–4	M	2.073 (0.074)	0.136 (0.023)	
		F	2.010 (0.102)	0.161 (0.033)	0.047
	5–9	M	2.547 (0.049)	0.053 (0.006)	
		F	2.568 (0.057)	0.047 (0.008)	**<0.001**
	10–14	M	2.899 (0.051)	0.012 (0.004)	
		F	2.897 (0.031)	0.012 (0.003)	0.917
	15–17	M	2.999 (0.056)	0.004 (0.003)	
		F	3.076 (0.059)	−0.000 (0.004)	0.314
Body mass	1–6	M	1.391 (0.066)	0.170 (0.015)	
		F	1.069 (0.081)	0.279 (0.018)	**0.003**
	7–16	M	2.607 (0.048)	0.023 (0.004)	
		F	2.541 (0.044)	0.051 (0.004)	**<0.001**
	17–32	M	2.916 (0.078)	0.003 (0.003)	
		F	2.818 (0.048)	0.006 (0.002)	0.872
	33–54	M	3.027 (0.043)	0.001 (0.001)	
		F	3.113 (0.052)	−0.001 (0.001)	0.738
	55–61	M	3.139 (0.111)	−0.000 (0.002)	
		F	3.121 (0.194)	−0.001 (0.003)	0.085

period (27–54 days), and female juvenile period (57–64 days), although the difference was statistically significant only during the 27–57-day period (Table 2, Fig. 2). Most of the SD1 in this trait results from sexually dimorphic growth rates (Table 2). In bill width, growth rates were sexually dimorphic during nestling stage; females grew faster than males during early and, especially, late nestling periods (1–16 days; Table 2, Fig. 2). In this trait, females tended to grow faster than males during the rest of the ontogeny until the cessation of their growth at age 41 days. Dimorphism in this trait resulted mostly from growth rate differences before female growth cessation and, to a lesser degree, from a longer male growth period (Tables 1, 2; Fig. 2).

In body traits, the sexes were most different in growth during the nestling period (Table 2). For example, in wing and tarsus length, females grew faster than males during early nestling period (1–6 days for wing and 1–4 days for tarsus), but males grew faster later in the nestling period (7–16 days for wing and 5–9 days for tarsus; Table 2, Fig. 2). In both traits, males continued to grow after female growth ceased (Table 2). In tail length, the sexes tended to differ in growth rates throughout ontogeny (Fig. 2, Table 2). These differences reached statistical significance during the late nestling period (7–16 days), when females grew faster than males. Males continued to grow long after females ceased their growth, thus both growth rate dimorphism and dimorphism in age at growth cessation contributed significantly to dimorphism in tail length (Tables 1, 2; Fig. 2). In body mass, females grew faster during the entire nestling period, but after fledging body mass growth was variable and did not differ between the sexes (Table 2, Fig. 2).

Overall, the sexes differed in both growth rates and duration of growth, with females typically growing faster than males, but males continuing to grow after female growth had ceased. In most bill traits, the sexes were most distinct in growth during the juvenile period, whereas in body traits growth of sexes differed the most during the early nestling period.

Ontogeny of Sexual Dimorphism

Spline curves for ontogenetic changes in sexual dimorphism and their corresponding confidence intervals are shown in Figures 3 and 4. A significant change in sexual dimorphism after growth cessation (shown by arrows in Figs. 3, 4) indicates change due to viability selection or, less likely, due to morphology-specific emigration from the study site (see Methods for discussion).

Sexual dimorphism at age 110-days (SD2 hereafter, see Methods for justification of age) was strongly different from SD1 (Table 3). For example, fledgling females had longer tarsi than males, but 110-day-old juvenile males had longer tarsi than females (Table 3). Using estimations of spline growth curves for sexual dimorphism (Figs. 3, 4), we can roughly measure the change in SD1 between age of growth cessation and age of 110 days, and thus estimate contributions of growth dimorphism (SD1) and postgrowth selection to SD2 (Table 3). For example, in bill length, SD1 was 0.18 mm and SD2 was 0.23 mm. Following growth cessation dimorphism decreased and reached its minimum, 0.05 mm (or 78% reduction of SD1), at age 90 (Fig. 3, Table 3). Thus, the contribution of SD1 to SD2 is 0.05/0.23, or 21%, and the rest is due to a change in dimorphism influenced by postgrowth viability selection (Table 4). Postgrowth selection accounts for all SD2 in bill width and tarsus length and most of SD2 in bill length and body mass. Sexual dimorphism in growth rates contributes strongly to SD2 in bill depth and wing and tail length (Table 3).

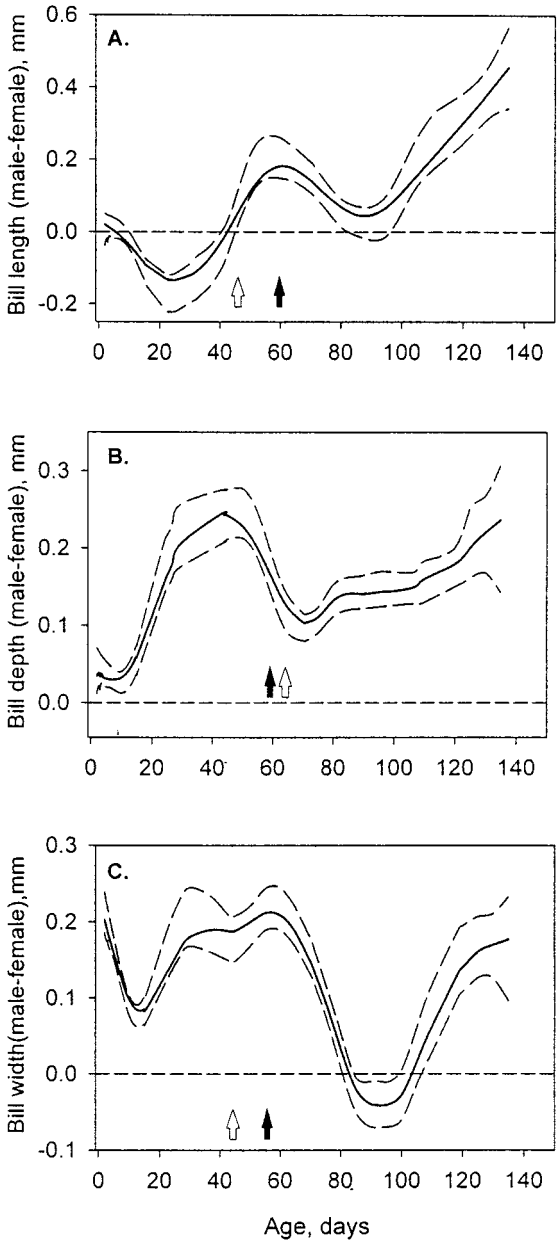

FIG. 3. Sexual dimorphism (male − female) for bill traits in relation to age (days) in the house finch. Arrows indicate age at growth termination for males (black) and females (white). Confidence intervals are calculated by bootstrapping (n = 300).

For example, in bill length, dimorphism decreased following growth cessation (Fig. 4), due to strong selection for shorter bills in males (Fig. 1: 65–70 days; Table 4). An increase in dimorphism after age 90 (Fig. 3) was mostly due

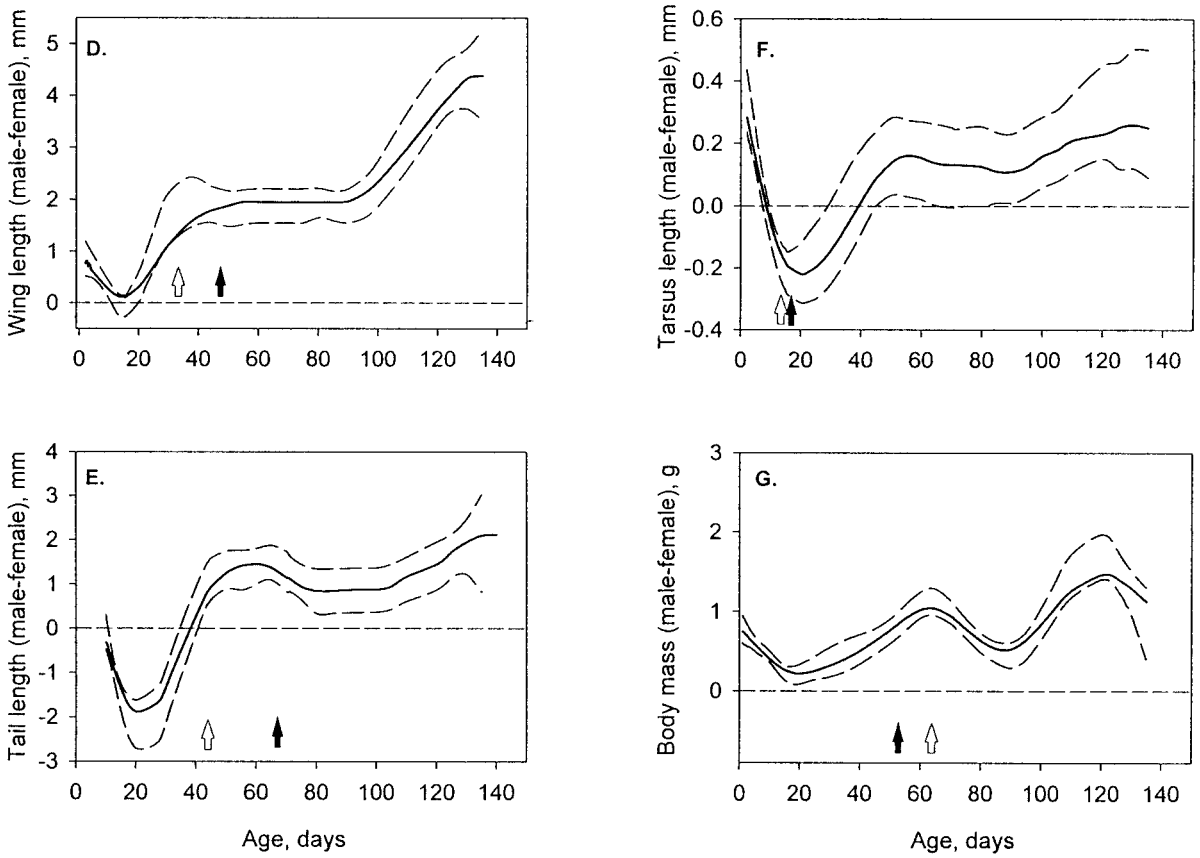

FIG. 4. Sexual dimorphism (male − female) for body traits in relation to age (days) in the house finch. Arrows indicate age at growth termination for males (black) and females (white). Confidence intervals are calculated by bootstrapping, (n = 300).

to selection for shorter bills in females (Fig. 1, Table 4). It is possible that a small portion of the postgrowth decrease in bill length in both sexes was due to wear of the bill sheath; however, it would be unlikely to account for the degree of sexual dimorphism in bill length found here. In bill depth, SD1 and SD2 were similar (Table 3), and increase in dimorphism was due to selection on both sexes after age 85 (Fig. 2, Table 4). In bill width, following growth cessation, there was strong selection for a decrease in males, but an increase in females (Fig. 2, Table 4). Thus, in this trait, the dimorphism produced by growth patterns was largely canceled by strong sexually dimorphic selection on juvenile finches; the dimorphism in bill width was reversed in the population at about 85–95 days (Figs. 2, 3). For this trait, SD2 was due mostly to changes favored by selection operating on both sexes after age 95–100 days (Fig. 2). In wing and tail length, the level of sexual dimorphism produced as a result of growth differences was maintained until age 80–90 days (Figs. 1, 2, 4), after which there was a significant increase in dimorphism favored by strong selection for longer wings in males and less intense selection for shorter wings in females (Table 4, Fig. 4). In tarsus, postgrowth selection favored an increase in males and a decrease in females. Selection was especially intense during 17–50 days of age and

TABLE 3. Ontogeny of sexual dimorphism in relation to sex-specific patterns of selection. SD1, sexual dimorphism at growth cessation (~65 days for most traits; this is dimorphism resulting from sexually dimorphic growth patterns); SD2, sexual dimorphism at 110 days of age (dimorphism resulting from a combination of sexually dimorphic growth patterns and viability selection on juvenile males and females). Shown are mean (min; max) values.

			% of SD2 due to dimorphism in	
Trait	SD1 (65 days)	SD2 (110 days)	Growth (SD1)	Postgrowth selection
Bill length	0.182 (0.148; 0.259)	0.233 (0.185; 0.339)	21	79
Bill depth	0.159 (0.135; 0.188)	0.161 (0.129; 0.183)	63	37
Bill width	0.212 (0.189; 0.244)	0.062 (0.027; 0.117)	0	100
Wing length	1.804 (1.549; 2.236)	3.014 (2.593; 3.699)	65	35
Tail length	1.371 (1.089; 1.871)	1.27 (0.613; 1.613)	68	32
Tarsus length	−0.197 (−0.290; −0.147)	0.212 (0.110; 0.363)	0	100
Body mass	1.036 (0.945; 1.281)	1.259 (1.175; 1.718)	40	60

TABLE 4. Viability selection on juvenile house finches. Shown is morphology (mean [SD]) of males and females at growth cessation (65 days, before) and at 110 days of age (after), and standardized selection differentials (mean, in SD) for survival from age 65 days to age 110 days. Bold indicates selection differentials that are significantly different from zero.

	Males		Females			
Trait	Before (n = 66)	After (n = 27)	Before (n = 76)	After (n = 36)	S_{MALES}	$S_{FEMALES}$
Bill length	10.58 (0.10)	10.34 (0.13)	10.19 (0.15)	10.09 (0.09)	**−0.54**	−0.13
Bill depth	7.74 (0.09)	7.83 (0.06)	7.46 (0.04)	7.56 (0.05)	+0.23	**+0.51**
Bill width	7.28 (0.06)	7.16 (0.04)	6.97 (0.05)	7.06 (0.05)	**−0.47**	**+0.35**
Wing length	78.77 (0.47)	80.11 (0.19)	76.65 (0.33)	76.52 (0.34)	**+0.79**	−0.10
Tail length	61.90 (0.52)	62.81 (0.55)	61.46 (0.48)	60.76 (0.52)	**+0.43**	−0.32
Tarsus length	20.40 (0.04)	20.52 (0.14)	20.63 (0.12)	20.62 (0.15)	+0.25	−0.03
Body mass	21.93 (0.24)	22.05 (0.27)	20.72 (0.38)	20.93 (0.30)	+0.09	+0.16

after 85–90 days (Fig. 4). SD2 in body mass was affected strongly by postgrowth selection on both sexes, however body mass widely fluctuated in both sexes (Figs. 2, 4).

Overall, postgrowth selection strongly influenced juvenile dimorphism in all traits. In some traits, the selection canceled out the dimorphism produced by sex differences in growth patterns. Postgrowth selection operated on both sexes, but, for most traits, selection was the strongest on male morphology.

DISCUSSION

Detailed knowledge of ontogenetic variation is essential for understanding the pathways of evolutionary change in a population (Gould 1977; Alberch et al. 1979; Price and Grant 1985; German and Meyers 1989; Kirkpatrick and Lofsvold 1992; Grant and Grant 1995). However, until recently, studies of evolution of sexual size dimorphism have mostly focused on variation in adult morphologies (e.g., Downhower 1976; Johnstone and Fleisher 1981; Leutenegger and Cheverud 1982; Rising 1987; Björklund and Lindén 1993). At the same time, adult sexual dimorphism results from interaction of sexually dimorphic growth patterns and selection during growth (e.g., Richter 1983; Shea 1986; Slagsvold et al. 1986; Richner et al. 1989; Leigh 1992). Thus, sexual dimorphism of adults can reflect selection pressures during ontogeny, and these selection pressures may not be similar to selection pressures acting on adults (Ralls 1976; Jarman 1983; Price and Grant 1984; Schluter and Smith 1986; Leigh 1992, 1995; Merilä et al. 1997; Larsson et al. 1998; Post et al. 1999; reviewed in Schluter et al. 1991). Moreover, similar levels of adult sexual dimorphism, both within and among species, can be produced by different processes operating during ontogeny (Wiley 1974; Jarman 1983; Georgiadis 1985; Shea 1986; Gebhardt-Henrich 1992; Reeve and Fairbairn 1996) and therefore may reflect different evolutionary history (Zeng 1988; German and Meyers 1989). Thus, studies that address the contribution of sexually dimorphic patterns of growth and sexually dimorphic selection during growth to adult dimorphism are especially informative (Shea 1986; Leigh and Shea 1996; Merilä et al. 1997; Stamps and Krishnan 1997).

Our study of the developmental basis of sexual size dimorphism in the house finch has produced three important results. First, the sexes differed in both growth rates and growth duration; in most traits, females grew faster than males, but males grew for a longer period (Table 1, Figs. 1, 2). Second, development of sexual dimorphism in bill traits (bill length, width, depth) and body traits (wing, tail, and tarsus length and mass) occurred at different times during ontogeny. Growth of bill traits was most different between sexes during the juvenile period (after leaving the nest), whereas growth of body traits was most sexually dimorphic during the first few days after hatching (Table 2). Third, postgrowth selection on juveniles strongly influenced sexual dimorphism in all traits and, in some traits, this selection canceled or reversed dimorphism patterns produced by the growth differences between sexes (Tables 3, 4; Figs. 3, 4). To understand the potential mechanisms behind the variation in sexual size dimorphism in the house finch, we need to address the ecological and evolutionary causes and consequences of growth and selection patterns documented in this study.

Male and female house finches differed in growth rates and growth duration (Table 2, Figs. 1, 2). This dimorphism can represent either adaptive modifications of sex-specific growth patterns for conditions during growth (reviewed in Gebhardt-Henrich and Richner 1998; Schew and Ricklefs 1998) or correlated response to selection acting on adult dimorphism (e.g., Grant 1981; Price and Grant 1985; Reeve and Fairbairn 1996; Smith and Leigh 1998). When sexes differed in growth rates, females (the smaller sex) usually grew faster (Table 2). These results corroborate previous findings that, in altricial birds, the smaller sex often grows faster in both structural size and feather growth (e.g., Richter 1983; but see Richner 1991; reviewed in Teather and Weatherhead 1994). Rapid growth of the smaller sex may be advantageous in competition with larger siblings of the opposite sex (e.g., Werschkul and Jackson 1979; Gebhardt-Henrich and Richner 1998; reviewed in Stamps 1990). Preliminary data from two house finch populations suggest that parents do not discriminate among nestlings in provisioning rates or provisioning volume (A. V. Badyaev and G. E. Hill, pers. obs.), and sibling competition does not seem to mediate access to food. In the house finch, as in other cardueline finches (e.g., Badyaev 1997a), during parents' visitations to the nest all nestlings are fed and all nestlings receive an approximately equal number of food portions. In the absence of strong compensatory growth during the nestling period, this pattern of provisioning is reflected in parallel growth curves for all nestlings within a brood, which are characteristic for cardueline finches (Badyaev 1993, 1994; Björklund 1993, 1994). As a result, size

differences among hatchlings are maintained to fledging. However, in contrast to other studied cardueline finches, house finches show a widespread occurrence of compensatory growth during nestling period, when smaller nestlings accelerate their growth during early ontogeny (Badyaev and Martin 2000b). This compensatory growth of size-related traits (e.g., wing, tarsus) by smaller nestlings (typically females) may enable successful simultaneous fledging of an entire brood. In addition, it is possible that faster structural and body mass growth of female nestlings enables them to achieve greater agility or accumulate larger fat deposits by postfledgling stages, thereby allowing more successful competition with juvenile males (reviewed in Stamps 1990). In house finches, as in many other passerines, juvenile females are subdominant to juvenile males (see below). Slow growth of the larger sex may be adaptive during periods of low food availability (Røskaft and Slagsvold 1985; Slagsvold et al. 1986; Teather and Weatherhead 1988; Schew and Ricklefs 1998). Finally, dimorphism in growth rates may be an allometric consequence of dimorphism in adult sizes (Ricklefs 1968; Teather and Weatherhead 1994). However, despite a small degree of adult dimorphism, male and female finches differ not only in growth rates, but also in the periods of most intense growth (i.e., in growth trajectory shape), thus making the last explanation less likely.

Dimorphism in growth patterns could be a correlated response to divergent selection on adult males and females in this population (Badyaev and Martin 2000a, see also Grant 1981; Price and Grant 1985; Reeve and Fairbairn 1996). The similarity between growth patterns and patterns of selection on adults may be facilitated by significant genetic covariance between parents and offspring throughout the ontogeny of the house finches in the Montana population (Badyaev and Martin 2000b). At the same time, both the strong distinction between adult static and ontogenetic allometries and the relatively low genetic and phenotypic covariation among age-specific trait values indicate that the relationship between selection on adults and growth patterns is not straightforward. Transplant or common-garden experiments with nestlings from populations where adult finches are subject to distinct selection pressures (e.g., Montana and Alabama; Badyaev et al. 2000) are needed to uncover the genetic components of sexual dimorphism in growth.

Bill and body traits differed in the timing of sexual dimorphism development (Figs. 1, 2). This heterochrony may be related to the resources preferentially allocated to the traits with immediate functional importance at a certain age (e.g., O'Connor 1977; Carrier and Leon 1990; Cane 1993; reviewed in Starck 1998). Bill traits are late maturing in cardueline and Emberizidae finches (Grant 1981; Boag 1984; Björklund 1994). The development of sexual dimorphism in these traits may be related to growth and selection patterns accompanying the onset of self-feeding after leaving the nest. In contrast, early development of dimorphism in body traits may reflect the early onset of functional importance of these traits for themoregulation and early fledging in the areas with high nest predation (e.g., Ricklefs 1968; Björklund 1994; Badyaev 1997b; Monk 1998).

We found that postgrowth selection has a strong effect on juvenile sexual dimorphism in the house finch (Tables 3, 4). For example, changes favored by postgrowth selection accounted for all juvenile sexual dimorphism in bill width and tarsus length and most of the dimorphism in bill length and body mass (Table 3). Thus, postgrowth selection on these traits largely cancels out the dimorphism produced by growth patterns (Table 4, Figs. 3, 4). In contrast, in wing and tail, postgrowth selection favored amplification of dimorphism produced during growth (Fig. 4, Table 4). Postgrowth viability selection on juveniles was stronger than overwinter survival selection acting on adults in this study population (Badyaev and Martin 2000a, table 7). For all traits, except wing and tail length, postgrowth viability selection on juveniles and overwinter survival selection on adults favored qualitatively similar changes in morphology (table 4 vs. table 8 in Badyaev and Martin 2000a). Thus, adult sexual dimorphism, to a large degree, is a result of survival selection during juvenile stages (Jarman 1983; Leigh 1992; Merilä et al. 1997; see also Stamps and Krishnan 1997) and, for some traits, viability selection on juveniles may play a more important role in the formation of adult morphologies than does selection on adults (e.g., Georgiadis 1985).

It is noteworthy that periods of most intense selection on juvenile finches corresponded closely to important events of finch phenology. In all traits, especially in bill traits, there was a significant decrease in population-level dimorphism around age 50–70 days (Figs. 3, 4), when juveniles assemble in small (up to 20 birds), single-sex flocks (see Methods). Another period of pronounced change in population-level dimorphism, an increase at the age of 90–110 days (Figs. 3, 4), coincided with merging single-sex flocks and formation of large (up to 70 individuals), both-sex flocks. Thus, postgrowth viability selection, and ultimately adult sexual dimorphism, may be influenced by interactions among conspecifics in juvenile flocks (e.g., Shreeve 1977; Benkman 1997; see also Stamps 1990 and references therein).

With information obtained in this study, we can begin to address the developmental basis of the extensive population divergence in sexual size dimorphism in recently established house finch populations. In a recent study, we showed that this divergence was due to changes in morphology of both sexes, and in all examined populations, the observed sexual dimorphism of adults was highly concordant with dimorphism favored by selection acting on adults (Badyaev and Hill 2000; Badyaev et al. 2000). The results of this study suggest that population differences in sexual dimorphism may be produced partially by distinct environmental conditions during growth. Population variation in adult sexual dimorphism can be a consequence of differential sensitivity of the sexes to environmental conditions during growth (e.g., Hirnaux 1968; Stini 1972; Hall 1978; Clutton-Brock et al. 1995; see also Sheldon et al. 1998). For example, because of different growth patterns of sexes (e.g., more prevalent compensatory growth of females and higher sensitivity of male growth to environmental conditions; reviewed in Stinson 1985), conditions during growth may cause opposing growth responses in the sexes and, in turn, strongly influence adult sexual dimorphism (e.g., Sheldon et al. 1998; Post et al. 1999). In birds, environmental conditions during growth can account for both seasonal (Cooch et al. 1996, 1997) and population variation in sexual dimorphism (Richner 1989;

James 1991; Larsson and Forslund 1991). However, given the sexually dimorphic patterns of growth found in this study and the significant genetic covariation between parents and offspring throughout the ontogeny (Badyaev and Martin 2000b), population differences in adult dimorphism can be also due to genetic differentiation in patterns of growth among populations (e.g., Price and Grant 1985; Alatalo and Gustafsson 1988). Knowledge of growth patterns and selection on juveniles in other populations of the house finch is crucial to inference about mechanisms behind population divergence in adult sexual dimorphism.

Acknowledgments

We thank J. Stamps for stimulating discussion and thorough review of this study. We are grateful to R. Duckworth, A. Dervan, P. Dunn, T. Mousseau, P. Nolan, and two anonymous reviewers for a number of helpful suggestions that we have included here. We thank K. Corll, W. Deschamps, C. Ghalambor, C. Glen, and T. Rapone for help in the field. 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. This research was supported by a Bertha Morton Research Fellowship at The University of Montana, a postdoctoral fellowship from the College of Science and Mathematics at Auburn University, and by the National Science Foundation grant (DEB-0075388) to AVB.

Literature Cited

Alatalo, R. V., and L. Gustafsson. 1988. Genetic component of morphological differentiation in coal tits under competitive release. Evolution 42:200–203.

Alberch, P., S. J. Gould, G. Oster, and D. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

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.

Badyaev, A. V. 1993. Breeding biology of the gold-fronted serin (*Serinus pusillus*) in a subalpine zone of Pamir Mountains. Biol. Sciences (Biol. Nauk.) 348:89–99.

———. 1994. Breeding biology of white-winged grosbeak (*Mycerobas carnipes*) in the Pamir Mountains. Bull. MOIP (Biol. Div.) 99:20–28.

———. 1997a. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. Behav. Ecol. 8:675–690.

———. 1997b. Avian life history variation along altitudinal gradients: an example with cardueline finches. Oecologia 111: 357–364.

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. Proceedings 22nd International ornithology congress, Durban, University of Natal, Durban, South Africa.

———. 2000. The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. Evolution 54:1775–1785.

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., G. E. Hill, A. M. Stoehr, P. M. Nolan, and K. J. McGraw. 2000. The evolution of sexual dimorphism in the house finch. II. Population divergence in relation to local selection. Evolution 54: *in press.*

Benkman, C. W. 1997. Feeding behavior, flock-size dynamics, and variation in sexual selection in crossbills. Auk, 114:163–178.

Birkhead, T. R., F. Fletcher, and E. J. Pellant. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proc. R. Soc. Lond. B 266:385–390.

Björklund, M. 1991. Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). Evolution 45:608–621.

———. 1993. Phenotypic variation of growth trajectories in finches. Evolution 47:1506–1514.

———. 1994. Allometric relations in three species of finches (Aves: Fringillidae). J. Zool. 233:657–668.

Björklund, M., and M. Lindén. 1993. Sexual size dimorphism in the great tit (*Parus major*) in relation to history and current selection. J. Evol. Biol. 6:397–415.

Boag, P. T. 1984. Growth and allometry of external morphology in Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos. J. Zool. 204:413–441.

Bortolotti, G. R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. Am. Nat. 127:495–507.

Burke, W. H. 1992. Sex differences in incubation length and hatching weights of broiler chicks. Poult. Sci. 71:1933–1938.

Cane, W. P. 1993. The ontogeny of postcranial integration in the common tern, *Sterna hirundo.* Evolution 47:1138–1151.

Carrier, D., and L. R. Leon. 1990. Skeletal growth and function in the California gull (*Larus californicus*). J. Zool. 222:375–389.

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.

Cheverud, J. M., P. Wilson, and W. P. J. Dittus. 1992. Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of togue macaques (*Macaca sinica*). J. Hum. Evol. 23:51–77.

Clutton-Brock, T. H., S. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133.

Cooch, E. G., D. B. Lank, and F. Cooke. 1996. Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the lesser show goose. J. Anim. Ecol. 65:439–450.

Cooch, E., D. Lank, R. Robertson, and F. Cooke. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. J. Anim. Ecol. 66:189–202.

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

de Kogel, C. H. 1997. Long-term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. J. Anim. Ecol. 66:167–178.

Downhower, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. Nature 263:558–563.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–264.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: patterns and process in the coevolution of body size in males and females. Annu. Rev. Ecol. Syst. 28:659–687.

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. 1999. Sex-specific selection and sexual size dimorphism in the watersrider *Aquarius remigis.* J. Evol. Biol. 13:160–170.

Fiala, K. L., and J. D. Congdon. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. Ecology 64:642–647.

Gebhardt-Henrich, S. G. 1992. Heritability of growth curve parameters and heritability of final size: a simulation study. GDA 56: 23–34.

Gebhardt-Henrich, S. G., and H. L. Marks. 1993. Heritabilities of growth curve parameters and age-specific expression of genetic

variation under two different feeding regimes in Japanese quail (*Coturnix coturnix*). Gen. Research 62:45–55.
Gebhardt-Henrich, S., and H. Richner. 1998. Causes of growth variation and its consequences for fitness. Pp. 324–339 *in* J. M. Starck and R. E. Ricklefs, eds. Avian growth and development. Oxford Univ. Press, Oxford, U.K.
Georgiadis, N. 1985. Growth patterns, sexual dimorphism and reproduction in African ruminant. Afr. J. Ecol. 23:75–87.
German, R. Z., and L. L. Meyers. 1989. The role of time and size in ontogenetic allometry. II. An empirical study of human growth. GDA 53:107–115.
Gould, S. J., 1977. Ontogeny and phylogeny. Harvard Univ. Press, Cambridge, MA.
Gowaty, P. A. 1991. Facultative manipulation of sex ratio in birds: rare or rarely observed? Curr. Ornithol. 8:141–171.
———. 1993. Differential dispersal, local resource competition, and sex ratio variation in birds. Am. Nat. 141:263–280.
Grant, P. R. 1981. Patterns of growth in Darwin's finches. Proc. R. Soc. Lond. B 212:403–432.
Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241–251.
Griffiths, R., S. Daan, and C. Dijkstra. 1996. Sex identification in birds using two CHD genes. Proc. R. Soc. Lond. B 263: 1251–1256.
Griffiths, R., M. Double, K. Orr, and R. Dawson. 1998. A DNA test to sex most birds. Mol. Ecol. 7:1071–1076.
Hall, R. L. 1978. Sexual dimorphism for size in seven 19th century Northwest Coast populations. Hum. Biol. 50:159–171.
Hill, G. E. 1993. House finch. No. 46 *in* A. Poole, P. Stettenheim, and F. Gill, eds. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA.
Hirnaux, J. 1968. Variabilitie du dimorphisme sexuel de la stature en Afrique subsaharienne at en Europe. Pp. 42–50 *in* Antropologie and Humangenetik. Stuttgart, Germany.
Hochachka, W., and J. N. M. Smith. 1991. Determinants and consequences of nestling condition in song sparrows. J. Anim. Ecol. 60:995–1008.
Howard, R. D. 1981. Sexual dimorphism in bullfrogs. Ecology 62: 303–310.
James, F. C. 1991. Complementary descriptive and experimental studies of clinal variation in birds. Am. Zool. 31:694–706.
Jarman, P. 1983. Mating system and sexual dimorphism in large terrestrial mammalian herbivores. Biol. Rev. 58:485–520.
Johnston, R. F., and R. C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. Auk 98: 504–511.
Kirkpatrick, M., and D. Lofsvold. 1989. The evolution of growth trajectories and other complex quantitative characters. Genome 31:778–783.
———. 1992. Measuring selection and constraints in the evolution of growth. Evolution 46:954–971.
Krijgsveld, K. L., C. Dijkstra, G. H. Visser, and S. Daan. 1999. Energy requirements for growth in relation to sexual size dimorphism in marsh harrier, *Circus aeruginosus* nestlings. Physiol. Zool. 71:693–702.
Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. Evolution 34:292–305.
Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis.* J. Evol. Biol. 4:619–636.
Larsson, K., H. P. van der Jeugd, I. T. van der Veen, and P. Forslund. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52:1169–1184.
Leigh, S. R. 1992. Patterns of variation in the ontogeny of primate body size dimorphism. J. Hum. Evol. 23:27–50.
———. 1995. Socioecology and the ontogeny of sexual size dimorphism in Anthropoid primates. Am. J. Phys. Anthropol. 97: 339–356.
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.
Lindén, H. 1981. Estimations of juvenile mortality in the capercaillie, *Tetrao urogallus,* and the black grouse, *Tetrao tetrix,* from indirect evidence. Finn. Game Resear. 39:52–67.
Lindén, M., L. Gustafsson, and T. Part. 1992. Selection on fledgling mass in collared flycatchers and great tits. Ecology: 73:336–343.
Lindenfors, P., and B. S. Tullberg. 1998. Phylogenetic analyses of primate size evolution: the consequences of sexual selection. Biol. J. Linn. Soc. 64:413–447.
Lindström, J. 1999. Early development and fitness in birds and mammals. Trends Ecol. Evol. 14:343–348.
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.
Mead, P. S., M. L. Morton, and B. E. Fish, 1987. Sexual dimorphism in egg size and implications regarding facultative manipulation of sex in mountain white-crown sparrows. Condor 89:798–803.
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.
Miller, S., D. Dykes, and H. Polesky. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. Nucleic Acids Res. 16:1215.
Monk, D. S. 1998. Parental allocation by birds: analysis of parent and sibling interactions with a new statistical model. Proceedings VII congress of the International Society of Behavioral Ecology, Pacific Grove, CA.
Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual and intersexual selection. Evolution 44:315–331.
O'Connor, R. J. 1977. Differential growth and body composition in altricial passerines. Ibis 119:147–166.
Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual dimorphism in birds. Ornithol. Monogr. 33:1–52.
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.
Post, E., R. Langvatn, M. C. Forchhammer, and N. C. Stenseth. 1999. Environmental variation shapes sexual dimorphism in red deer. Proc. Natl. Acad. Sci. USA. 96:4467–4471.
Price, T. 1991. Environmental and genotype-by-environment influences on chick size in the yellow-browed leaf warbler *Phylloscopus inornatus.* Oecologia 86:535–541.
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.
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.
Richner, H. 1989. Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). J. Anim. Ecol. 58:427–440.
———. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex-specific growth contribute to balanced sex ratio? Funct. Ecol. 5:19–28.
Richner, H., P. Schneiter, and H. Stirnimann. 1989. Life-history consequences of growth rate depression: an experimental study on carrion crows (*Corvis corone corone* L.). Funct. Ecol. 3: 617–624.
Richter, W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. Am. Nat. 121: 158–171.

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.
Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.
Ricklefs, R. E., J. M. Starck, and M. Konarzewski. 1998. Internal constraints on growth in birds. Pp. 266–287 *in* J. M. Starck and R. E. Ricklefs, eds. Avian growth and development. Oxford Univ. Press, Oxford, U.K.
Rising, J. D. 1987. Geographical variation of sexual dimorphism in size of savannah sparrows (*Passerculus sandwichensis*): a test of hypotheses. Evolution 41:514–524.
Rogers, A. R., and A. Mukherjee. 1992. Quantitative genetics of sexual dimorphism in human body size. Evolution 46:226–234.
Røskaft, E., and T. Slagsvold. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. J. Anim. Ecol. 54:261–266.
Schew, W. A., and R. E. Ricklefs. 1998. Developmental plasticity. Pp. 288–304 *in* J. M. Starck and R. E. Ricklefs, eds. Avian growth and development. Oxford Univ. Press, Oxford, U.K.
Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.
———. 1989. Introduction to GLMS. Available via http://www.zoology.ubc.ca/~schluter/splines.html.
Schluter, D., and J. N. M. Smith. 1986. Natural selection on beak and body size in the song sparrow. Evolution 40:221–231.
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.
Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analysis. Can. J. Zool. 69: 82–90.
Shea, B. T. 1985. The ontogeny of sexual dimorphism in the African apes. Am. J. Primat. 8:183–188.
———. 1986. Ontogenetic approaches to sexual dimorphism in anthropoids. Hum. Evol. 1:97–110.
Sheldon, B. C., J. Merilä, G. Lindgren, and H. Ellegren. 1998. Gender and environmental sensitivity in nestling collared flycatchers. Ecology 79:1939–1948.
Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64:419–461.
Shreeve, D. F. 1977. Comparative behavior of Aleutian grey-crowned and brown-capped rosy finches. Ph.D. diss., Cornell University, Ithaca, NY.
Slagsvold, T. E., E. Røskaft, and S. Engen. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. Ornis Scand. 17:117–125.
Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.
Smith, R. J., and S. R. Leigh. 1998. Sexual dimorphism in primate neonatal body mass. J. Hum. Evol. 34:173–201.
Stamps, J. A. 1990. When should avian parents differentially provision sons and daughters? Am. Nat. 135:671–685.
———. 1993. Sexual size dimorphism a in species with asymptotic growth after maturity. Biol. J. Linn. Soc. 50:123–145.
Stamps, J. A., and V. V. Krishnan. 1997. Sexual bimaturation and sexual size dimorphism in animals with asymptotic growth after maturity. Evol. Ecol. 11:21–39.
Starck, J. M. 1998. Structural variants and invariants in avian embyonic and postnatal development. Pp. 59–88 *in* J. M. Starck and R. E. Ricklefs, eds. Avian growth and development. Oxford Univ. Press, Oxford, U.K.
Stini, W. A. 1972. Reduced sexual dimorphism in upper arm muscle circumference associated with protein-deficient diet in a South American population. Am. J. Phys. Anthopol. 36:341–352.
Stinson, S. 1985. Sex differences in environmental sensitivity during growth and development. Yearb. Phys. Anthropol. 28: 123–147.
Teather, K. L. 1989. Sex and egg size in great-tailed grackles. Condor 91:203–205.
Teather, K. L., and P. J. Weatherhead. 1988. Sex-specific energy requirements of great-tailed grackle (*Quiscalus maxicanus*) nestlings. J. Anim Ecol. 57:659–668.
———. 1994. Allometry, adaptation, and the growth and development of sexually dimorphic birds. Oikos 71:515–525.
Weatherhead, P. J., and K. J. Teather. 1991. Are skewed fledgling sex-ratios in sexually dimorphic birds adaptive? Am. Nat. 138: 1159–1172.
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.
Wegge, P. 1980. Distorted sex ratio among small broods of a declining capercaillie population. Ornis Scandin. 11:106–109.
Werschkul, D. F., and J. A. Jackson. 1979. Sibling competition and avian growth rates. Ibis 121:97–102.
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.
Wiley, R. H. 1974. Evolution of social organization and life history patterns among grouse. Q. Rev. Biol. 49:201–227.
Zeng, Z. B. 1988. Long-term correlated response, interpopulation covariation and interspecific allometry. Evolution 42:363–374.

Corresponding Editor: T. Mousseau