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THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE HOUSE FINCH. IV. POPULATION DIVERGENCE IN ONTOGENY

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Abstract.—Differences among taxa in sexual size dimorphism of adults can be produced by changes in distinct developmental processes and thus may reflect different evolutionary histories. Here we examine whether divergence in sexual dimorphism of adults between recently established Montana and Alabama populations of the house finch (*Carpodacus mexicanus*) can be attributed to population differences in growth of males and females. In both populations, males and females were similar at hatching, but as a result of sex-specific growth attained sexual size dimorphism by the time of independence. Timing and extent of growth varied between the sexes: Females maintained maximum rates of growth for a longer time than males, whereas males had higher initial growth rates and achieved maximum growth earlier and at smaller sizes than females. Ontogeny of sexual dimorphism differed between populations, but in each population, sexual dimorphism in growth parameters and sexual dimorphism at the time of nest leaving were similar to sexual dimorphism of adults. Variation in growth of females contributed more to population divergence than did growth of males. In each population, we found close correspondence between patterns of sexual dimorphism in growth and population divergence in morphology of adults: Traits that were the most sexually dimorphic in growth in each population contributed the most to population divergence in both sexes. We suggest that sex-specific expression of phenotypic and genetic variation throughout the ontogeny of house finches can result in different responses to selection between males and females of the same age, and thus produce fast population divergence in the sexual size dimorphism.

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

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The growth of an individual is determined by a combination of phenotypic, genetic, and environmental effects, and the contributions of these effects vary as different genes are expressed and different developmental processes are emphasized through an ontogenetic sequence (Cheverud and Leamy 1985; Cowley and Atchley 1992). The timing and extent of these effects will influence the magnitude and direction of a response to selection and can themselves be a subject of natural selection. Developmental processes and their underlying controls create patterns of variation and covariation both within and among traits during ontogeny and thus strongly influence the potential for microevolutionary change (Gould 1977; Alberch et al. 1979; Atchley 1984, 1987; Leamy and Cheverud 1984; Atchley et al. 1994). Thus, evolutionary change in morphology is determined by the interaction of the timing of selection and the distribution of ontogenetic variation. Detailed assessment of this dynamic interaction is necessary for understanding of morphological evolution (Cheverud 1982; Price and Grant 1985; Creighton and Strauss 1986; Kirkpatrick and Lofsvold 1992; Grant and Grant 1995; Björklund 1996).

Because different underlying mechanisms can give rise to morphologically similar adult phenotypes, studies that focus exclusively on the variation in and selection on adult phenotypes are not generally informative about the mechanisms underlying an evolutionary change (e.g., German and Meyers 1989; Fiorello and German 1997). One particularly illustrative example is the studies of evolution of sexual size dimorphism in animals. Although these studies have frequently documented a close association between sexual dimorphism and various selection pressures acting on adults (e.g., Howard 1981; Leutenegger and Cheverud 1982; Weatherhead et al. 1987; Webster 1992; Wikelski and Trillmich 1997; Ferguson and Fairbairn 2000), the mechanisms behind this correspondence cannot be easily inferred. Similar levels and patterns of adult sexual dimorphism can be produced by highly distinct growth processes, even among closely related species (Jarman 1983; Shea 1986; Brooks 1991; Cheverud et al. 1992; Leigh 1992). Moreover, sexual dimorphism of adults may be a proximate outcome of either sex-specific growth or differential viability selection on juvenile and adult morphologies of males and females (Fiala and Congdon 1983; Georgiadis 1985; Richtsmeier et al. 1993; Leigh 1995; Merilä et al. 1997; Post et al. 1999; Badyaev et al. 2001). The interaction between selection on adults and juveniles of both sexes will shape ontogenetic variation for males and females and ultimately determine the potential for evolutionary change in sexual dimorphism.

The developmental processes of males and females are governed by partially different hormonal and physiological controls (Sørensen 1977; Marks 1985; Stinson 1985; Vasilatos-Younken et al. 1988; Gatford et al. 1998; Nestor et al. 2000). Such sex differences in physiological parameters may translate into sex-specific responses to selection among males and females of the same age and, ultimately, can lead to a rapid change in sexual size dimorphism even under constraints of shared gene pool (e.g., Toelle et al. 1990; Reeve and Fairbairn 1996; Rhen 2000).

Comparisons of the ontogeny of males and females in recently diverged populations that differ in sexual dimorphism of adults may be especially informative for understanding the evolution of sexual dimorphism. The colonization of new regions of North America by the house finch (*Carpodacus mexicanus*) over the last 150 years has produced populations

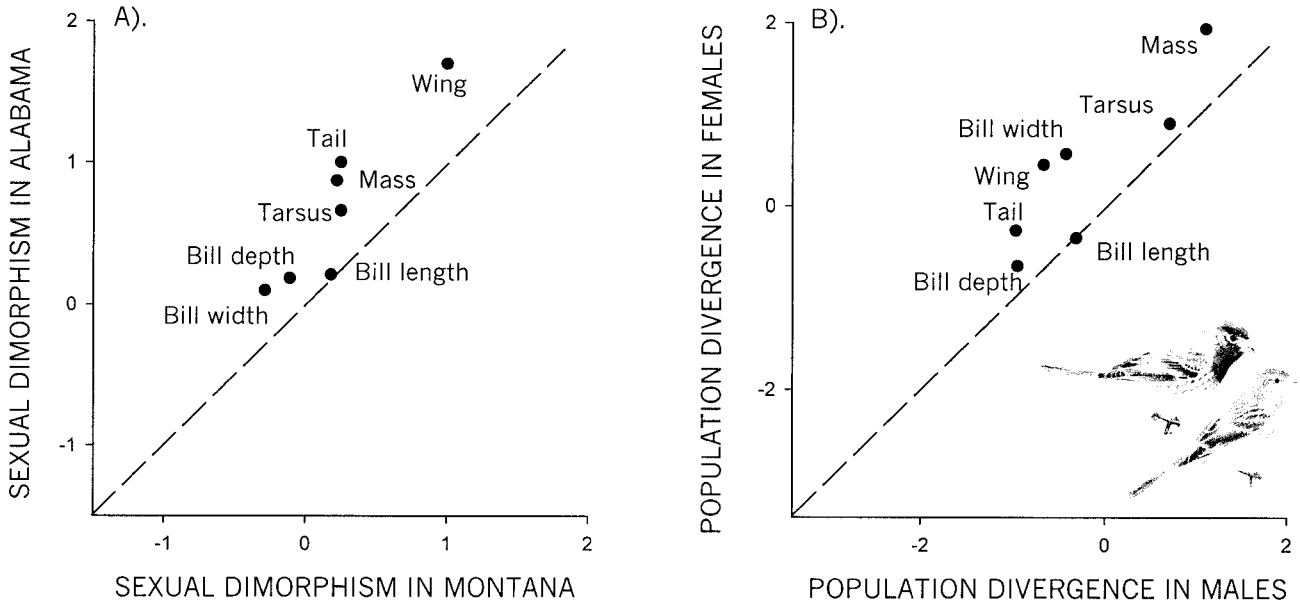

FIG. 1. (A) Population differences in levels of sexual dimorphism (male-female), and (B) population difference (Montana − Alabama) in adult male versus adult female morphology. Units are standard deviations. Dotted line indicates a 1:1 relationship. Points above the line indicate greater dimorphism in Alabama in (A) and greater population divergence in female morphology in (B). Data from Badyaev and Hill (2000).

that differ strongly in the sexual size dimorphism (Badyaev and Hill 2000; Fig. 1A). In previous work, we established that divergence in house finch populations in adult sexual dimorphism arose in response to local selection pressures on adults of both sexes. In each population where selection pressures were examined, sexual dimorphism of adults was highly concordant with net selection for sexual dimorphism (Badyaev et al. 2000). However, the mechanisms behind the population divergence in dimorphism and the evolutionary significance of the observed divergence are not known.

Here we examined whether the divergence in sexual size dimorphism of populations of house finches was enabled by population changes in timing and the extent of the growth of both sexes. We first establish whether ontogeny of sexual dimorphism differs between two populations of house finches (Montana and Alabama) that differ in the patterns and extent of sexual size dimorphism (Fig. 1). We then compare divergence in the ontogeny of sexual dimorphism to population differences in sexual dimorphism of adults. Finally, we discuss the significance of sex-biased variation in growth for the rapid population divergence in sexual dimorphism of adults.

MATERIALS AND METHODS

General Methods and Measurements

We conducted this study in two recently established resident populations of the house finch: in Missoula, Montana, in the northwestern United States, and in Auburn, Alabama, in the southeastern United States. The study site in Montana has been monitored since 1995, when the local population was 25–30 years old. The study site in Alabama has been monitored since 1993, when the local population was 10–15 years old (Badyaev and Hill 2000). For a detailed description of the study sites, see Hill et al. (1999) and Badyaev and Martin (2000a,b). Here we summarize the most essential details of data collection. Every year, all resident birds were individually marked at the Montana study site (Badyaev and Martin 2000b), and about 90% were marked at the Alabama study site (Hill et al. 1999). All resident adult finches were trapped, 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, and all nests were found during nest building (for a detailed description of field techniques, see Badyaev and Martin 2000a,b). Hatching was monitored continuously and nestlings were individually marked within a few hours of hatching (Badyaev et al. 2001). Individual marking was renewed every second day until nestlings could be banded with an aluminum ring at 7–8 days of age.

The data used in this study were collected in 1999–2000 in Montana (hereafter MT) and in 2000 in Alabama (hereafter AL) populations. We measured (with Mitutoyo calipers to an accuracy of 0.02 mm) the following traits of nestlings: bill length from the anterior end of the nostril to the tip of the upper mandible, bill width at the anterior end of the nostrils, bill depth in a vertical plane at the anterior end of the nostrils over both mandibles, tarsus length (left and right), tail length, and wing length (left and right, flattened). Body mass was measured with an electronic 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. To exclude any interobserver bias in measurements, A. V. Badyaev measured all nestlings used in this study in MT in 1999 and in AL in 2000, and a technician measured all nestlings in MT in 2000. A subset of 21 nestlings were measured multiple times by both people in MT in April 2000, and no consistent

TABLE 1. Observed (W_{hatch}, W_{fled}) and estimated (W_{max}) growth curve parameters (mean, standard error) for male (AL: $n = 26$, MT: $n = 27$) and female (AL: $n = 20$, MT: $n = 31$) house finches.

Trait	Population	Sex	W_{hatch}	W_{max}	W_{fled}
Bill length	AL	M	2.17 (0.06)	2.64 (0.09)*†	6.18 (0.09)
		F	2.27 (0.04)	3.02 (0.04)	6.06 (0.08)
	MT	M	2.27 (0.05)	2.75 (0.04)	6.33 (0.25)*
		F	2.34 (0.05)	2.71 (0.04)	6.86 (0.31)
Bill depth	AL	M	2.70 (0.07)	2.19 (0.06)†	5.67 (0.08)
		F	2.74 (0.04)†	2.21 (0.02)†	5.54 (0.09)
	MT	M	2.83 (0.13)	2.34 (0.02)	5.78 (0.15)
		F	2.94 (0.05)	2.30 (0.03)	5.61 (0.11)
Bill width	AL	M	3.31 (0.09)†	2.34 (0.05)†	6.25 (0.07)
		F	3.18 (0.07)†	2.32 (0.02)†	6.31 (0.08)
	MT	M	3.01 (0.10)	2.43 (0.01)	6.24 (0.07)
		F	2.96 (0.06)	2.41 (0.01)	6.30 (0.10)
Wing length	AL	M	5.60 (0.18)†	26.53 (1.45)	57.69 (0.67)*
		F	5.76 (0.13)	27.91 (0.20)	55.73 (0.81)
	MT	M	6.25 (0.19)	26.99 (0.21)*	57.50 (0.97)*
		F	6.06 (0.14)	28.12 (0.09)	55.04 (0.84)
Tarsus length	AL	M	6.42 (0.19)	7.65 (0.03)*†	20.31 (0.15)†
		F	6.67 (0.12)†	7.75 (0.03)†	20.36 (0.24)†
	MT	M	6.10 (0.23)	7.27 (0.04)*	18.87 (0.24)
		F	6.21 (0.13)	7.16 (0.03)	19.40 (0.40)
Tail length	AL	M	0.00 (0.00)	12.53 (0.52)*†	29.97 (0.82)
		F	0.00 (0.00)	15.34 (0.35)	28.47 (0.84)
	MT	M	0.00 (0.00)	14.62 (0.30)*	29.06 (0.83)
		F	0.00 (0.00)	16.09 (0.45)	28.77 (0.87)
Body mass	AL	M	2.00 (0.17)	6.95 (0.25)*†	19.67 (0.41)*†
		F	1.94 (0.10)	7.37 (0.06)	18.91 (0.27)†
	MT	M	2.17 (0.16)	7.34 (0.03)	18.53 (0.21)
		F	2.10 (0.09)	7.31 (0.06)	18.32 (0.21)

* Significant ($P < 0.007$) difference between sexes within a population.
† Significant differences with corresponding sex between populations.

biases in measures were detected (e.g., mean bill length differences = 0.002 mm; $t = 0.16$, $P = 0.85$). Repeatabilities for all traits were high and are presented in Badyaev and Martin (2000a).

Nestlings were measured every second day starting on day 1 (the day of hatching) and continuing until they left the nest (days 16–18). Premature fledgling of nestlings older than 12 days was successfully avoided by covering nests with dark cloth during measurements and by administering water to each nestling to prevent it from giving an alarm call. Hatch date, hatch order, and mite infestation have a strong influence on growth patterns in birds (Price 1991; Potti and Merino 1996; Potti 1999), including the development of phenotypic sexual dimorphism (Cooch et al. 1996; A. V. Badyaev, unpubl. ms.). Neither mite infestation nor nest predation were recorded in the MT population, whereas both were common causes of nestling mortality during late spring and summer in AL (Stoehr et al. 2000; G. E. Hill, pers. obs.). Thus, to control for the effects of hatch date, hatch order, mite infestation, and predation, we only used the subset of the first three hatched nestlings per nest (MT: 27 males, 31 females, $n = 21$ nests; AL: 26 males, 20 females, $n = 16$ nests) from the first breeding attempts (mid-March to late April) that fledged before the appearance of nest mites in AL (13 May) and were measured repeatedly throughout the entire nestling period.

The longitudinal data and constant sample size of this dataset allowed us to reliably determine sexual dimorphism in growth patterns. Because sexual dimorphism in growth of a trait may not be independent of dimorphism in other traits of the same individual, we sequentially adjusted the probabilities of sex differences in dimorphism in growth (Tables 1, 2; Figs. 2, 3) by the number of traits ($n = 7$) compared at each age period.

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). 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 10–15 μl were taken from a puncture of the brachial vein and stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C. For details of DNA extraction, PCR, and electrophoresis, see Badyaev et al. (2001).

Growth Analysis

We fitted the Laird (1966) form of the sigmoid Gompertz curve to our longitudinal growth data:

$$W_t = W_0 e^{(K_1/K_2)(1-e^{-K_2 t})} \quad (1)$$

TABLE 2. Sources of variation in initial growth rate (K) and age at maximum growth (T) in house finches. Bold P-values indicate significance after sequential Bonferonni adjustment.

		Source of variation					
		Sex		Population		Sex × population	
Trait		F	P	F	P	F	P
Bill length	K	3.78	0.04	0.15	0.70	8.95	**0.007**
	T	2.33	0.12	6.60	**0.01**	1.96	0.16
Bill depth	K	16.20	<**0.001**	1.05	0.31	0.00	0.96
	T	4.34	0.07	7.91	**0.005**	0.49	0.48
Bill width	K	5.09	**0.01**	11.09	<**0.001**	1.33	0.24
	T	5.13	**0.02**	8.27	**0.004**	3.97	0.05
Wing length	K	7.95	**0.005**	0.00	0.98	3.60	0.06
	T	0.07	0.78	0.38	0.54	0.24	0.62
Tarsus	K	0.79	0.37	18.29	<**0.001**	0.00	0.98
	T	0.00	0.99	0.73	0.39	0.30	0.58
Tail length	K	0.77	0.38	4.99	**0.02**	1.14	0.28
	T	7.79	**0.005**	3.98	0.04	0.10	0.75
Body mass	K	10.81	**0.001**	5.64	**0.01**	4.31	0.03
	T	1.31	0.25	0.54	0.46	0.25	0.61

where W_t is the measurement at age t, W_0 is the estimated value at hatching, K_1 the initial specific growth rate constant, and K_2 the maturation rate of the exponential rate of decay of the specific growth rate constant (i.e., $1/W_t \times dW_t/dt = Le^{-K_2 t}$). Thus, K_1 describes the first part of growth curve, before the inflection, and K_2 describes the second part in which growth rate decreases until the juvenile size reaches the asymptotic value (A). Traits studied here (with an exception of tarsus length) do not attain their full size by the time of fledging (Badyaev et al. 2001). Thus, for each trait, we supplied A as a value of mean size for each sex and population at the time when growth is completed. Asymptote was allowed to vary within two standard deviations of the mean (by $0.01A$ increments) to estimate the best fit for growth trajectory. The age and measurement value at the point of inflection, where the growth rate is maximum, can be calculated as:

$$T_{\max} = \frac{1}{K_2} \times \ln\left|\frac{K_1}{K_2}\right| \quad \text{and} \tag{2}$$

$$W_{\max} = W_0 \exp\left(\frac{K_1}{K_2} - 1\right). \tag{3}$$

The fitted curve was accepted when absolute difference between sum of squares of the residuals of successive iterations was $<10^{-4}$, and the estimated nonlinear regression function provided the highest R^2 (SAS Institute 1989). In this study we examined sexual dimorphism in estimates of initial growth rate, K_1 (hereafter K), age at maximum growth, $T_{\max}$, and estimated trait size at maximum growth, $W_{\max}$, of fitted growth trajectories as well as observed size of traits at hatching, W_{hatch} (0.5 to 4 h from breaking from the egg shell), and size at fledging, W_{fled} (the last day when nestlings were present in the nest, 16–18 days post-hatching). We estimated these parameters separately for each trait and each individual nestling, using the Marquardt algorithm of PROC NLIN of SAS (SAS Institute 1989), which minimized the sum of squares between predicted and observed values of growth.

To qualitatively illustrate the differences between populations and sexes in growth rate dynamics, we plotted the first derivative of the Gompertz curve (eq. 1), that is growth rate, using average estimates of K_1, K_2, and A for each trait estimated for both sexes within each population (e.g., Richner 1991; Fiorello and German 1997). This is approximately equivalent to dividing the difference in successive predicted size values (W) by the difference in successive age values (t) (i.e., pseudo-velocity curves; Leigh 1992). To further illustrate sex and population divergence in growth patterns, we compared sizes of males and females within each population by plotting predicted sizes (eq. 1) of males versus females at equal ages. In these plots the identity line ($y = x$) represents a completely shared ontogenetic trajectory, whereas deviations from the identity line indicate a size difference at equal ages due to divergence in growth rate and/or growth duration.

The effects of population, sex, and their interactions on the growth curve parameters were estimated with ANOVA. Significant effect of interaction between population and sex on a trait suggests population differences in direction of sexual dimorphism in this trait. For these analyses, all linear data were natural log-transformed, body mass was cube-root transformed, and all data were standardized to a mean zero and unit variance. The standardization enabled comparison between growth parameters and trait means. Use of sex-specific family means instead of individual nestling values did not change the results; thus, we report only the latter analyses. Tests of concordance between patterns of dimorphism in growth and patterns of dimorphism in adult morphology were conducted in two steps. First, we estimated the effects of population, sex, stage (adult or nestling), and their interactions from the mixed linear model for each trait. Significance of population by sex by generation was taken to indicate the lack of concordance in growth versus adult patterns between populations. Within each population, significance of the sex-by-generation term was taken to indicate lack of concordance between growth and adult patterns. Second, we plotted standardized dimorphism values for each trait for growth versus adult traits. Points on the diagonal ($y = x$) indicate complete concordance between stages, and points above the diagonal indicate greater sexual dimorphism in adults. General concordance of dimorphism patterns across all traits for two

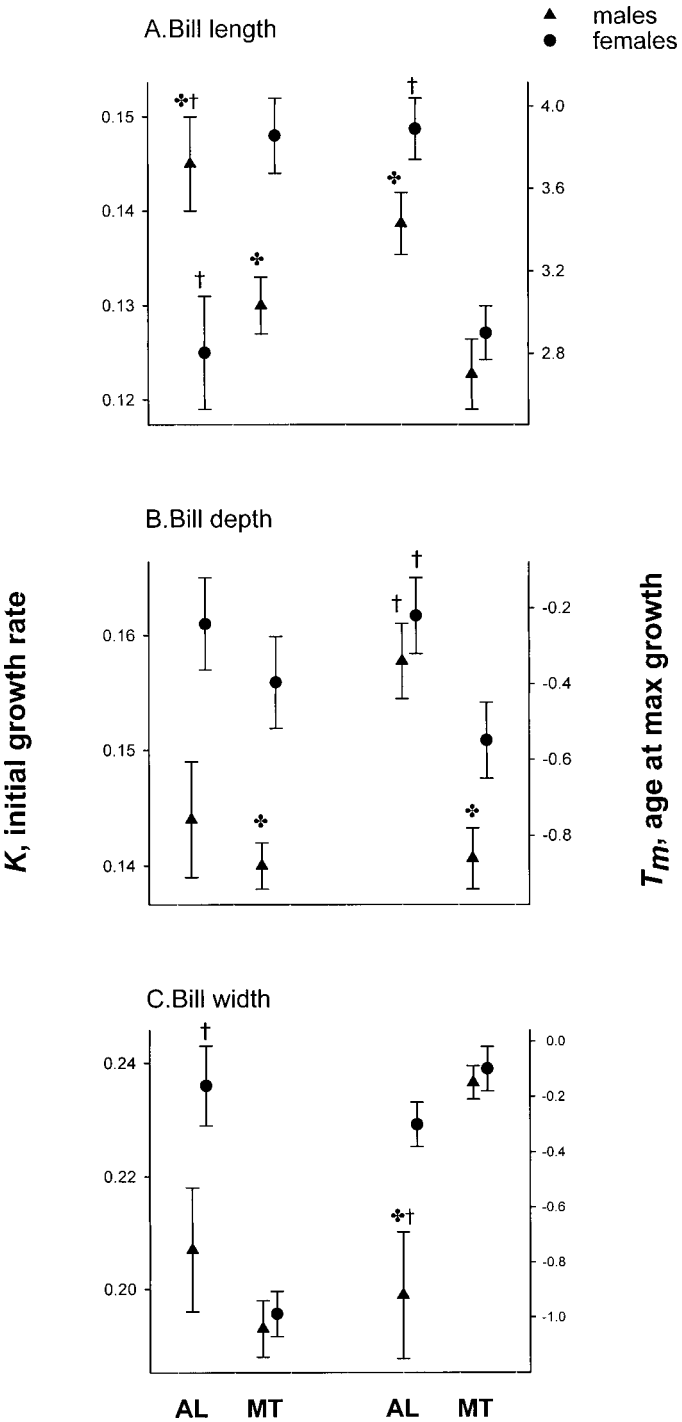

FIG. 2. Sexual dimorphism and population divergence in growth rate (*K*) and age at maximum growth (*T*) for (A) bill length, (B) bill depth, (C) bill width. The symbol ⌘ shows significant differences between sexes within a population; † shows significant differences within corresponding sex between populations. See Table 2 for details.

stages were estimated with Kendall's coefficient of concordance and visualized with a least-square regression line. Of special interest is the hypothesis that traits that are the most dimorphic during growth should be the most dimorphic in adults, thus resulting in positive coefficients of concordance. The latter two methods assume independence of sexual dimorphisms of different traits (and constant allometric relationships during different ontogenetic stages). Thus, these methods are used for only qualitative assessment of concordance.

RESULTS

Sexual Dimorphism in Growth Patterns

In both AL and MT populations, sexes did not differ in size at hatching (Table 1). In the AL population, males had a higher initial growth rates than females for bill length (Figs. 2A, 4A), wing length (Figs. 3A, 5A), and body mass (Figs. 3D, 5D; Table 2). Females tended to grow faster than males in bill depth (Fig. 2B) and bill width (Fig. 2C), and, with the exception of tarsus and tail length, females maintained their maximum growth rate longer than males (Table 2; Figs. 4, 5). Males achieved their maximum growth rate earlier than females for bill length (Fig. 2A), bill width (Fig. 2C), tail length (Fig. 3C), and wing length (Fig. 3A; Table 2). At the time of their maximum growth, males had shorter bill, tarsus, and tail and weighted less than females (Table 1). Throughout the nestling period, females were larger than males of equal ages in bill length (Fig. 4A) and, later in the nestling period, in tail length (Fig. 5C), whereas males had wider bills (Fig. 4C). At the time of nest leaving, males had longer wings and were heavier than females (Table 1).

In the MT population, males had a higher initial growth rate for wing, tail, and body mass (Fig. 3A,C,D), whereas females grew faster in bill length and depth (Fig. 2A,B; Table 2). Males achieved their maximum growth earlier than females in bill width (Fig. 2C) and tail length (Fig. 3C). For all traits, with an exception of tarsus and body mass, females maintained maximum growth rates longer than males (Figs. 4, 5). At the time of their maximum growth, males had shorter wings and tails, but longer tarsi than females (Table 1). Females were larger than males of equal ages in wing and tail length (Fig. 5A,C), but smaller in bill length and bill depth (Fig. 4A,B). At the time of nest leaving, males had shorter bills, but had longer wings and were heavier than females (Table 1). Overall, in both populations, females tended to maintain their maximum growth for a longer time than males, whereas males tended to have high initial growth rates and achieved maximum growth earlier and at smaller sizes than females.

In both populations, patterns of sexual dimorphism in growth rates were qualitatively concordant with the pattern and extent of sexual dimorphism of adults (Table 3; Fig. 6B; AL: Kendal's $\tau = 0.58$, $P = 0.05$, MT: $\tau = 0.43$, $P = 0.08$). In both populations, nestlings had the most sex-specific growth rates in the same traits that were the most different between adult males and females (i.e., lack of significant tests for growth stage in Table 3). Sexual size dimorphism at the time of fledging was qualitatively similar, but smaller in magnitude, to sexual size dimorphism of adults in both populations (Table 3; Fig. 6C). Across all traits, the concordance between dimorphism at fledgling and dimorphism in adults was stronger in AL ($\tau = 0.71$, $P = 0.02$) than in MT ($\tau = 0.54$, $P = 0.05$). Because sexual dimorphism at hatching was not concordant with the pattern of dimorphism present in

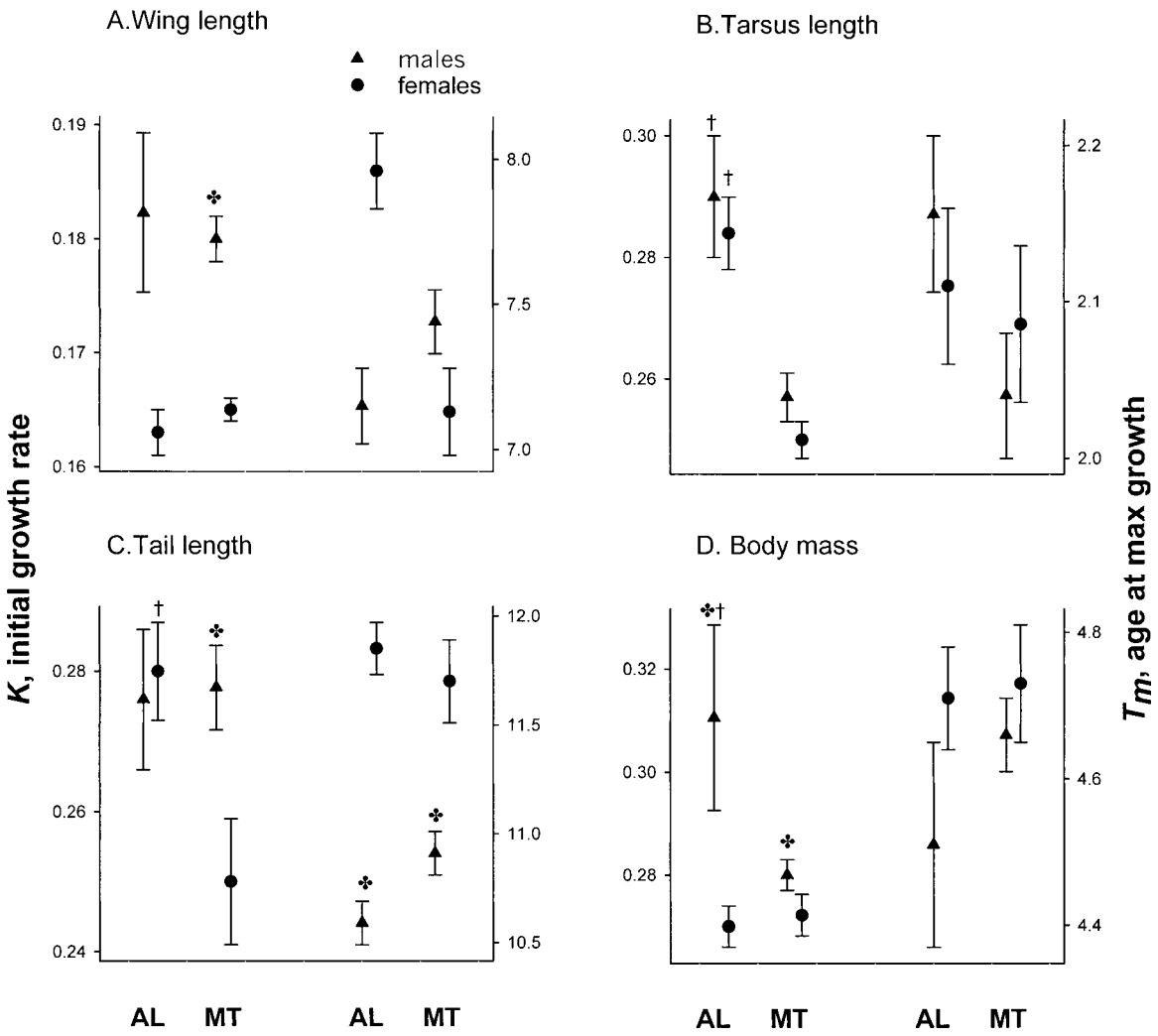

FIG. 3. Sexual dimorphism and population divergence in growth rate (*K*) and age at maximum growth (*T*) for (A) wing length, (B) tarsus length, (C) tail length, and (D) body mass. See Table 2 for details.

adults in both populations (i.e., significant tests in Table 3; Fig. 6A), most of the sexual dimorphism at fledgling can be attributed to sexual dimorphism in growth patterns in both populations (i.e., significant tests of discordance are mostly confined to hatching stage in Table 3; Fig. 6B). The lack of similarity between populations in concordance of patterns of dimorphism in growth and dimorphism in adults (Table 3) is due to population differences in patterns of dimorphism (Fig. 1).

Population Divergence in Growth Patterns and Ontogeny of Sexual Dimorphism

At hatching, AL females had smaller bill depth and longer tarsi compared to MT females, and AL males had shorter wings than MT males (Table 1). In AL, both sexes had wider bills at hatching compared to the MT population (Table 1). In AL, males had faster initial growth rates than males in the MT population in bill length (Fig. 2A), tarsus length, and body mass (Fig. 3B,D; Table 2). AL females grew faster in bill width (Fig. 2C), tail length, and tarsus length (Fig. 3B,C) and slower in bill length (Fig. 2A) compared to MT females (Table 2). Only bill traits differed between populations in the timing of maximum growth (Table 2): Females achieved maximum growth later in bill length and depth in AL compared to MT (Fig. 2A,B). AL males achieved maximum growth later for bill depth, but earlier for bill width compared to MT males (Fig. 2B,C). Populations differed most strongly in ontogeny of sexual dimorphism in bill length and width and wing and tail lengths (Fig. 4, 5; Table 2). In bill length, females were larger than males of equal age in the AL population, but smaller than males in MT (Fig. 4A). In bill width, MT males were much larger than equal aged females for most of the nestling period, whereas in AL the dimorphism was present only at early ages (Fig. 4C; Table 2). In wing length, MT females were larger than faster growing males for most of the nestling period, but there were no differences in the AL population (Fig. 5A; Table 2). In tail length, population divergence in dimorphism was mostly attributed to strong divergence between males in patterns of growth: AL males achieved maximum growth later than MT males but had high-

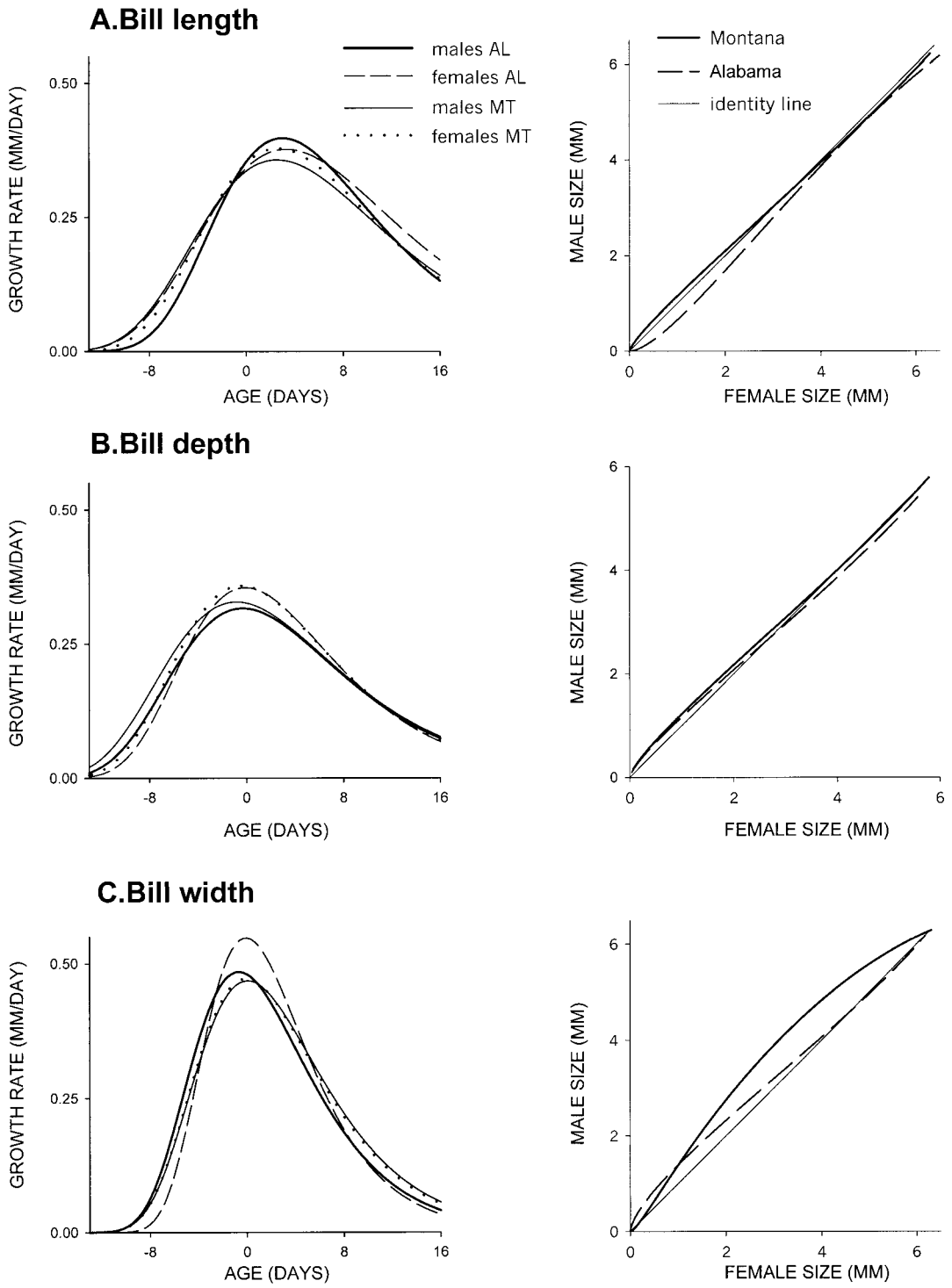

FIG. 4. Growth rates and growth curves for male and female house finches in Montana (MT) and Alabama (AL) populations for (A) bill length, (B) bill depth, and (C) bill width. Shown are growth rate plots (first derivative of growth curve; left column) and size trajectories (plots of predicted size values at equal ages for each sex; right column). The solid line illustrates the $y = x$ relationship. Lines above the solid line indicate the greater size of males.

er growth rates (Fig. 5C; Table 2). MT males had shorter tails compared to equal-aged females for all of the nestling period, whereas in AL, there was no dimorphism in this trait for most of the nestling period (Fig. 5C; Table 2).

Levels of sexual dimorphism in hatching size and in growth rates were similar between MT and AL (i.e., most traits are near the diagonal; Fig. 7A; Table 1). However, AL finches were more dimorphic than MT finches at the time of fledging (i.e., most traits are above the diagonal; Fig. 7C; Tables 1, 3). Sexes contributed similarly to population divergence in

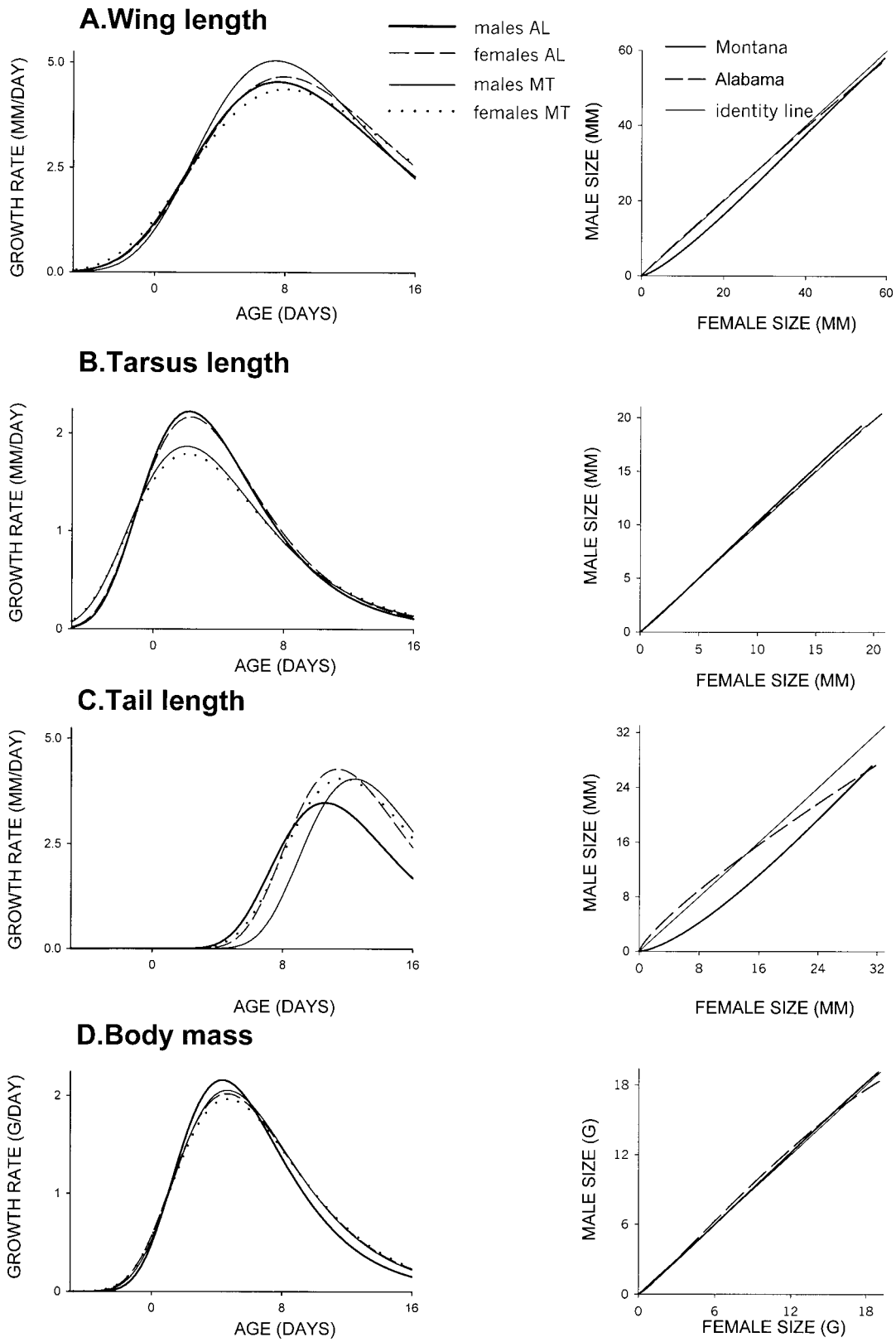

FIG. 5. Growth rates and growth curves for male and female house finches in Montana (MT) and Alabama (AL) populations for (A) wing length, (B) tarsus length, (C) tail length, and (D) body mass.

TABLE 3. Ontogeny of sexual dimorphism patterns in the house finches. Bold *P*-values ($P < 0.05$) indicate significant lack of concordance between patterns of sexual dimorphism at hatching, growth rate (*K*, initial growth rate), and fledgling stage and sexual dimorphism in adults.

	Lack of concordance within populations[1]					
	Alabama		Montana		Lack of concordance between populations[2]	
Trait	*F*	*P*	*F*	*P*	*F*	*P*
Bill length						
Hatching	4.52	**0.04**	1.61	0.20	1.82	0.12
Growth	1.15	0.28	1.99	0.15	2.69	0.04
Fledging	1.26	0.26	3.96	**0.05**	5.91	<**0.01**
Bill depth						
Hatching	3.82	**0.05**	5.70	<**0.01**	3.50	<**0.01**
Growth	0.58	0.34	0.38	0.54	1.09	0.20
Fledging	1.02	0.30	1.32	0.25	2.10	0.09
Bill width						
Hatching	2.72	0.09	1.54	0.20	1.94	0.10
Growth	0.69	0.30	0.05	0.83	3.49	<**0.01**
Fledging	2.98	0.08	0.04	0.91	2.21	0.09
Wing length						
Hatching	4.70	**0.03**	1.9	0.16	3.84	<**0.01**
Growth	7.21	<**0.01**	3.38	0.07	4.49	<**0.01**
Fledging	0.12	0.73	1.03	0.31	2.15	0.07
Tarsus length						
Hatching	4.93	**0.03**	1.08	0.29	11.72	<**0.001**
Growth	0.36	0.54	0.00	0.98	8.57	<**0.001**
Fledging	0.38	0.54	2.73	0.09	29.89	<**0.001**
Tail length						
Growth	2.10	0.12	0.05	0.83	3.84	<**0.01**
Fledging	4.96	**0.02**	1.37	0.24	7.90	<**0.001**
Body mass						
Hatching	4.42	**0.05**	0.14	0.70	2.97	0.078
Growth	1.65	0.20	0.15	0.77	11.9	<**0.001**
Fledging	2.99	0.08	0.02	0.94	9.31	<**0.001**

[1] Lack of concordance within populations is tested with sex × stage (nestlings or adults) term of the general linear model.
[2] Lack of concordance between populations is tested with sex × population × stage term of the general linear model. See Figure 6 for graphical representation.

size at hatching (Fig. 8A), growth rates (Fig. 8B), and size at fledging (Fig. 8C).

Overall, traits that were the most sexually dimorphic in growth rate in each population contributed the most to population divergence, particularly of females (Fig. 9). In females of both populations, traits that were the most different from males in growth also contributed the most to population divergence of females (Fig. 9C,D; AL: Kendall's $\tau = 0.62$, $P = 0.05$, MT: $\tau = 0.71$, $P = 0.02$). Population divergence of males strongly correlated with dimorphism in growth rates in the AL population (Fig. 9B; $\tau = 0.90$, $P = 0.004$), but not in the MT population (Fig. 9A; $\tau = 0.14$, $P = 0.62$). Thus, most of the population divergence could be attributed to variation in growth of females in both populations, the AL population had the most dimorphic growth patterns, and this contributed the most to population divergence in adult morphologies of both sexes.

DISCUSSION

The growth of males and females can be governed by partially independent hormonal and physiological controls (e.g., Sørensen 1977; Vasilatos-Younken et al. 1988), and this can result in sex-specific distribution of phenotypic and genetic variation throughout ontogeny (e.g., Bernon and Chambers 1985; Mignon-Grasteau et al. 1999; Nestor et al. 2000). Such differences between sexes in control of growth and development can lead to differences in the way male and female respond to environmental variation and selection during ontogeny. For example, several studies of birds found that the sexes display different patterns of growth under different conditions (Sørensen 1977; Richner 1989; Toelle et al. 1990; Cooch et al. 1996; Potti and Merino 1996; Potti 1999; Oddie 2000; Teather and Weatherhead 1994; reviewed in Sheldon et al. 1998). The evolutionary significance of these sexually dimorphic growth patterns is twofold. First, differences in the environmental sensitivity of males and females during growth will have strong morphological and life-history consequences for both adults and juveniles (e.g., Hochachka and Smith 1991; Larsson and Forslund 1991; de Kogel 1997; Merilä et al. 1997; Larsson et al. 1998; Birkhead et al. 1999; Bojarinova et al. 1999; reviewed in Clutton-Brock et al. 1985; Lindström 1999). Second, differences in ontogenetic patterns of males and females can enable rapid evolution of sexual dimorphism within a population (Reeve and Fairbairn 1996), as well as rapid divergence among populations in sexual dimorphism under natural selection.

Our study of the population divergence in ontogeny of sexual size dimorphism in the house finch has produced three

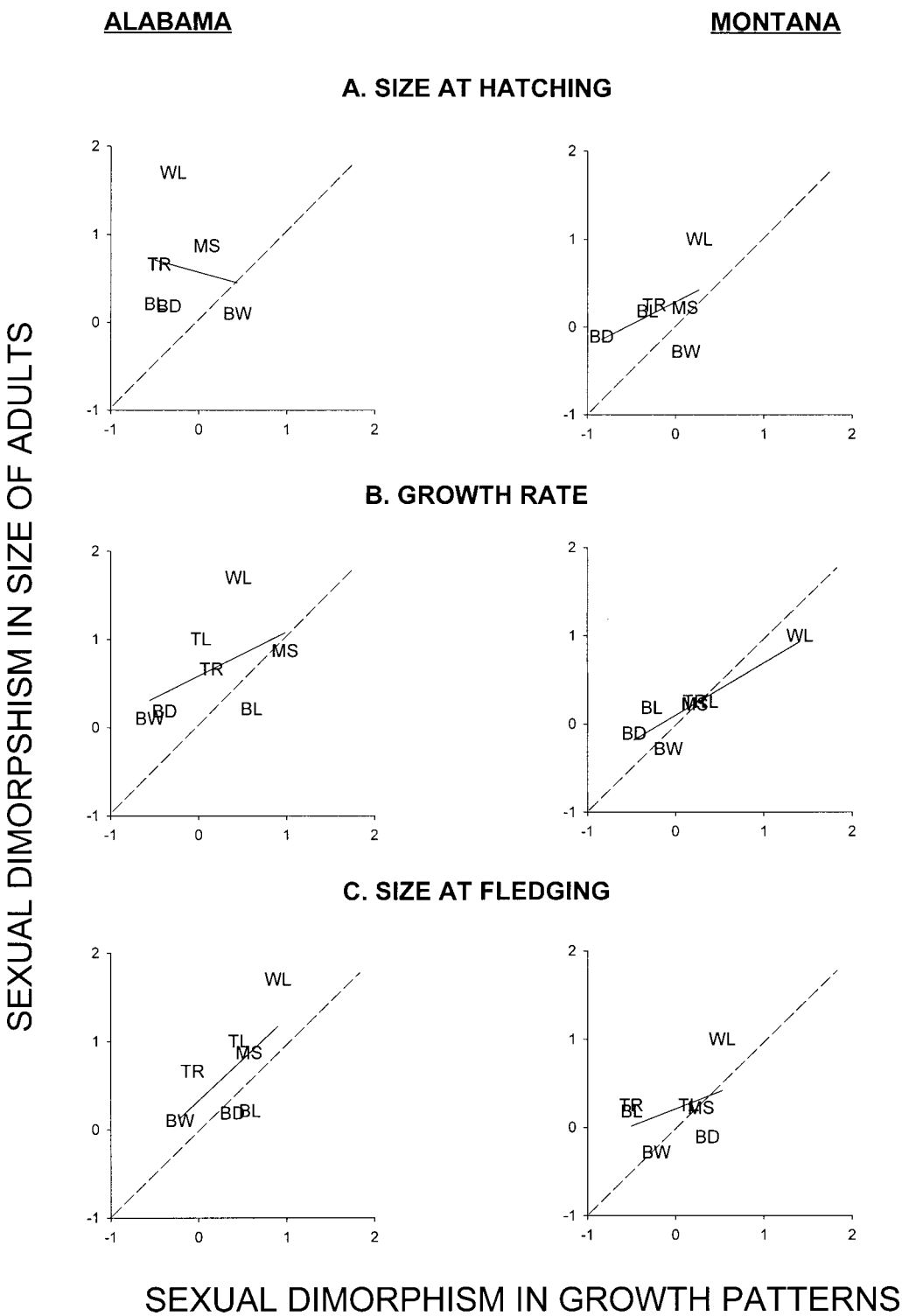

FIG. 6. Correspondence of sexual dimorphism in (A) size at hatching; (B) growth rate, *K*; and (C) size at fledging to the sexual dimorphism in adult morphology in Alabama and Montana populations. Sexual dimorphism is calculated as male minus female values for each trait. Units are standard deviations. Dotted line represents a 1:1 relationship. Points on the line indicate complete concordance between stages, whereas points above the line indicate greater dimorphism at the adult stage. Tests for the concordance of each trait are shown in Table 3. Solid line is the least-squares regression, which is shown for illustration of concordance across traits. BL, bill length; BD, bill depth; BW, bill width; WL, wing length; TR, tarsus length; TL, tail length; MS, body mass. See Results for details.

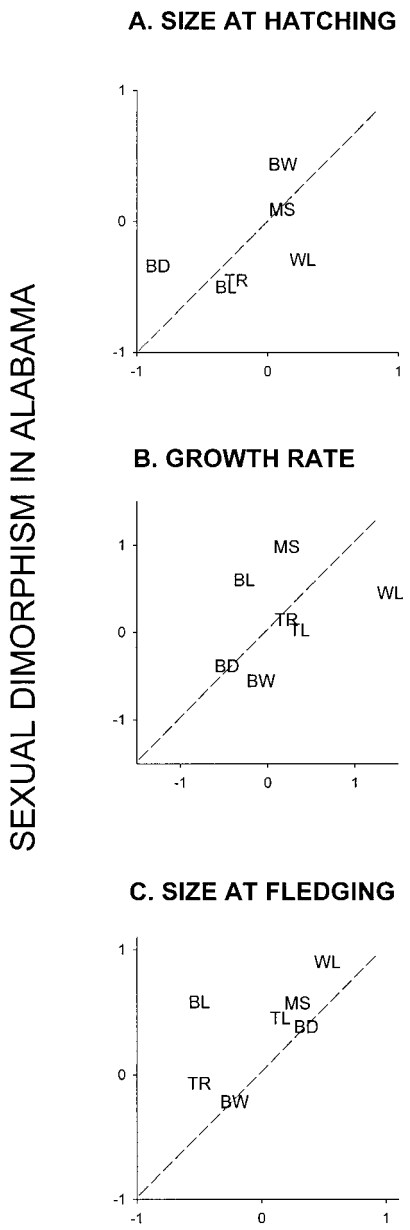

FIG. 7. Population differences in sexual dimorphism in (A) size at hatching, (B) growth rate, and (C) size at fledging. Units are standard deviations. Dotted line represents a 1:1 relationship. See Figure 6 for details.

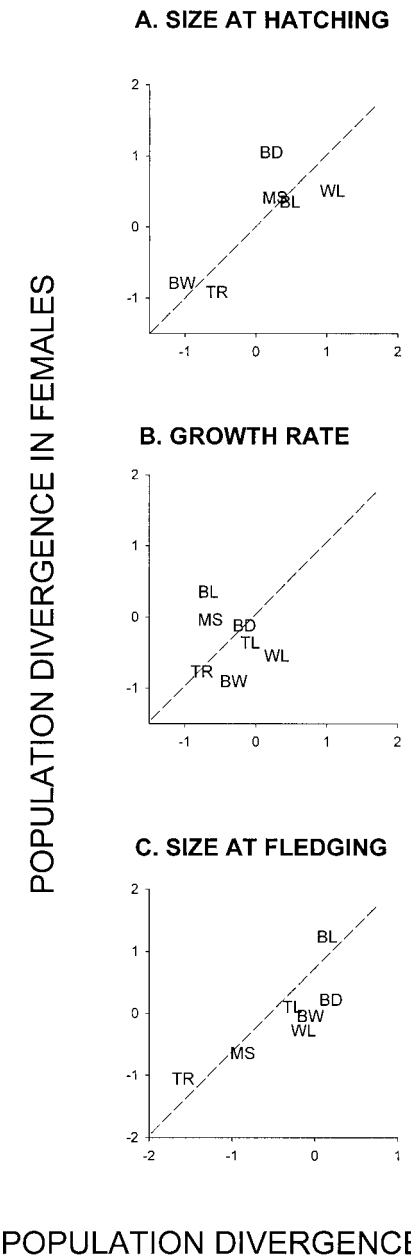

FIG. 8. Population divergence in male versus female morphology in (A) size at hatching, (B) growth rate, and (C) size at fledging. Units are standard deviations. Dotted line represents a 1:1 relationship. Points on the line indicate equal divergence between sexes. Traits are as in Figure 6.

principal results. First, the sexes differed in the timing and extent of growth: Females maintained higher growth rates for longer periods of time than males, whereas males had higher initial growth rates and achieved maximum growth at earlier ages and smaller sizes than females. Second, the ontogeny of sexual dimorphism differed between the study populations, such that population divergence in sexual dimorphism was produced by different processes for different traits. For some traits, the populations were highly divergent in growth patterns, but the pattern was the same for males and females. For example, the tarsi of both males and females grew faster in AL than in MT. For other traits, divergence between the populations in sexual dimorphism was produced when one sex grew differently than the other. For example, in AL males increased their body mass faster than females and this lead to a difference in dimorphism between AL and MT. Third, we found close correspondence between the patterns of ontogeny of sexual dimorphism and the divergence in adult morphology between the populations. These results suggest that the divergence in sexual dimorphism of adult house finches in MT and AL (Badyaev et al. 2000) is prox-

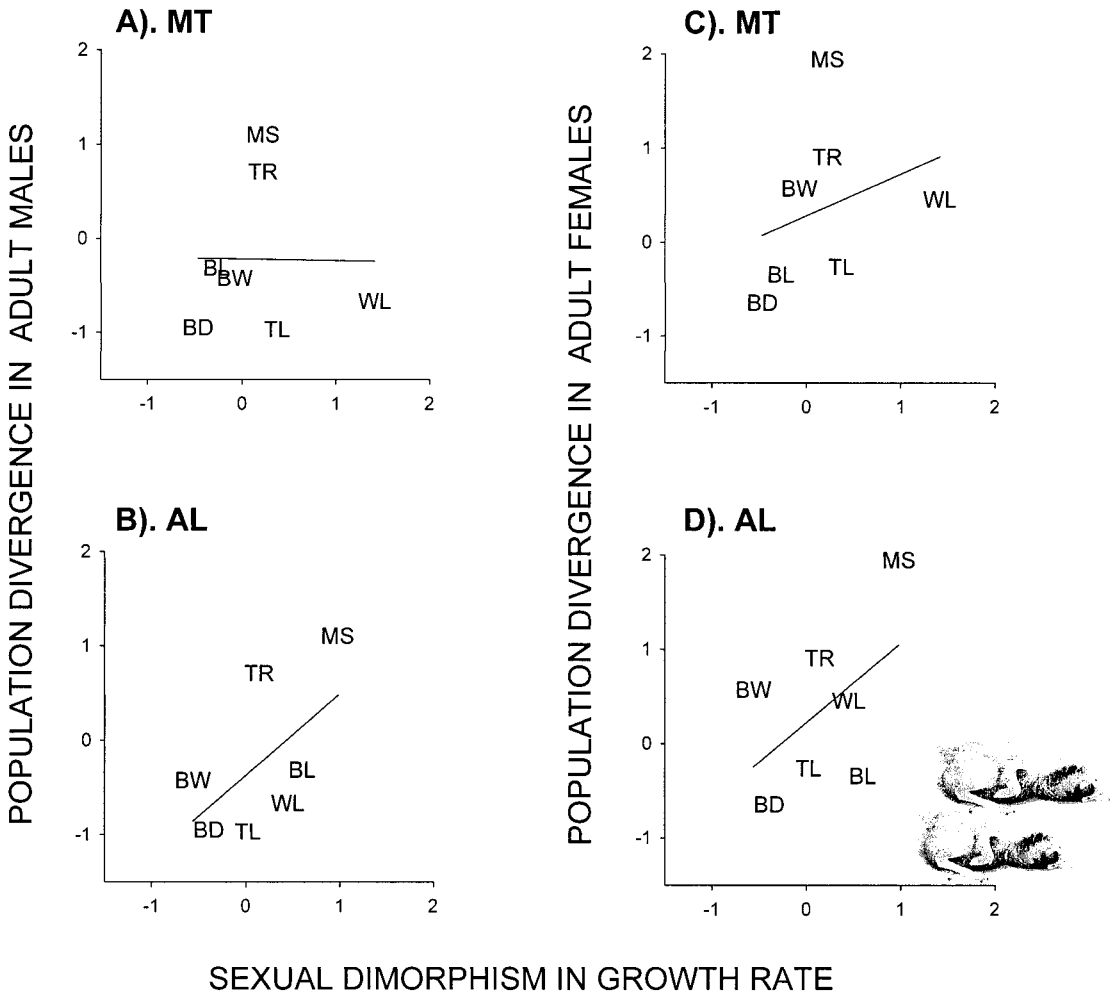

FIG. 9. Relationship between sexual dimorphism in growth rate and population divergence in male and female morphology. (A) MT males, (B) AL males, (C) MT females, and (D) AL females. Units are standard deviations. The solid line is the least-squares regression, which is shown for illustration only. See Results for Kendall's coefficient of concordance and Figure 6 for more details.

imately produced by divergent patterns of growth in both sexes and not by differences in adult mortality at the time of sampling. Moreover, there is close correspondence between the patterns of sexual dimorphism created by growth patterns and the patterns of sexual dimorphism that are favored by selection on adult birds (Badyaev et al. 2000, 2001). These findings raise several questions. First, why do males and females differ in their patterns of growth? Second, what is the mechanism behind the close correspondence of the ontogeny of sexual dimorphism and selection favoring sexual dimorphism in adults? Finally, what are the evolutionary consequences of these sex-specific developmental patterns?

Even in sexually monomorphic bird species, males and females may grow differently under different environmental conditions (e.g., Potti and Merino 1996; Potti 1999). Thus, predictable and consistent patterns of environmental variation during growth, such as seasonal changes in food supply or parasite infestation, may lead to temporal variation in sexual dimorphism (e.g., Bortolotti 1986; Price 1991; Cooch et al. 1996; McCarty 2001). Temporal variation in such sexual dimorphism is influenced by sexual differences in duration and patterns of compensatory growth. For example, when growing under stressful conditions, males may preferentially allocate food resources to mass gain, whereas females may allocate to growth of skeletal structures (Richter 1983; Richner 1991; Merilä et al. 1997; Oddie 2000). In altricial birds, sex-biased environmental effects on nestling growth may be shaped by competition for food within a brood (Werschkul and Jackson 1979; Bortolotti 1986; Nilsson 2001). For example, observations of several passerine species suggest that greater sexual dimorphism (due to faster male growth) under stressful conditions may be due to an enhanced competitive ability of males during nestling and postfledgling periods (e.g., Shreeve 1977; Potti 1999; Oddie 2000). Alternatively, sex-biased environmental effects on growth may reflect physiological properties of males and females (such as a greater sensitivity of male growth to parasites due to greater levels of circulating androgen; e.g., Potti and Merino 1996; Sheldon et al. 1998).

Sexes may differ in their sensitivity to environmental conditions during growth, but the direction of the effects resulting from environmental variation is often inconsistent between sexes and even among traits (reviewed in Teather and Weatherhead 1994; Gebhardt-Henrich and Richner

1998). This suggests that the frequently documented differences in the sensitivity of sexes to environmental effects during growth may be a consequence of a particular mode of growth rather than the male or female phenotype per se (e.g., Sheldon et al. 1998). Regardless, sex-specific expression of environmental variation in growth points to a possibility that different genes can affect the growth of males and females, and that a response to selection (either direct or correlated) acting during growth period can be sex-specific. Indeed, artificial selection studies have shown that the timing of selection during growth can have strong consequences for sexual dimorphism in adults (e.g., Toelle et al. 1990; Anthony et al. 1991b; Mignon-Grasteau et al. 1999; Nestor et al. 2000).

The important implication of sex-specific expression of phenotypic and genetic variation during growth is that it provides a mechanism for rapid evolution of sexual size dimorphism. Because homologous traits are controlled by the same genes in males and females, divergent evolution between the sexes is expected to be constrained (Lande 1980). Indeed, many empirical studies have documented the lack of sex-biased phenotypic and genetic variance in morphological traits of adults (e.g., Toelle et al. 1990; Price and Burley 1993; Merilä et al. 1998; reviewed in Roff 1997, p. 247), and standard quantitative genetics theory suggests that this prevents the short-term evolution of sexual dimorphism (Robertson 1959; Lande 1980). A predicted outcome of this slow evolution of dimorphism is that there should be a poor fit between current ecological conditions and the expression of dimorphism (Rogers and Mukherjee 1992; Price and Burley 1994; Merilä et al. 1998). Yet, numerous empirical examples of rapid evolution of sexual dimorphism in natural populations (see above) emphasize the need for a fuller understanding of mechanisms behind independent morphological changes in males and females. Sexual dimorphism in the action and expression of genes during ontogeny may lead to the evolution of sexual dimorphism even when there is no sex-biased genetic variation in fully grown traits (Reeve and Fairbairn 1996).

In a previous study of sexual dimorphism and selection in house finches in Montana and Alabama, we found that the divergence in sexual dimorphism between the populations was concordant with patterns favored by selection on adult males and females in each population (Badyaev et al. 2000). In the current study, we found that traits that were modified the most as a result of sex-specific growth were the traits that diverged the most between populations, thus implicating sex-specific growth as a mechanism behind population divergence. Two key questions remain to be answered. What is the mechanism that is responsible for close correspondence between ontogeny of sexual size dimorphism and selection favoring sexual size dimorphism in adults? To what degree is the divergence between populations in male and female growth genetically based? The growth patterns of populations may change as a correlated response to selection pressures acting only on adult males and females (e.g., Grant 1981; Price and Grant 1985; Björklund 1996). Alternatively, if changing growth patterns are associated with functional needs or with selection during the nestling period (e.g., O'Connor 1977; Merilä et al. 1997; Potti 1999; Oddie 2000), then divergence in adult morphologies will depend on the timing of selection acting directly on ontogenies (e.g., Hall 1978; Carrier and Leon 1990; Cane 1993; Leigh 1995; Post et al. 1999). Of special interest is the estimation of relative strength and direction of selection acting on juveniles versus adults (Atchley 1987; Price and Grant 1985). If selection for sexual dimorphism is strongest on adults, and there are significant genetic covariations between the traits of adults and juveniles (as found in MT population of house finches; Badyaev and Martin 2000a), then sex-specific distribution of ontogenetic variation may enable genetic divergence in growth patterns. Indeed, population divergence in sexual dimorphism is concordant with selection pressures acting on adults and a likely means by which the size and shape of adults can change in response to selection is by genetically based change in ontogeny of sexual dimorphism (see also Alatalo and Gustafsson 1988). In this study, males and females different populations were more similar to each other at nestling stage compared to the adult stage, suggesting that selection favoring sexual dimorphism of adults may be stronger and/or more consistent than selection favoring sexual dimorphism of juveniles.

One potential source of divergence in sexual size dimorphism between MT and AL populations is population differences in sex-biased parental investment. Within population, if there is sex-bias in maternal effects, postnatal parental care, or egg-laying and incubation patterns, then sex-specific growth will result. In a concurrent study of MT and AL populations, we found no biases in nestling provisioning (A. V. Badyaev, unpubl. data; G. E. Hill, unpubl. ms.). In both populations of house finches, as in many cardueline finches, all nestlings are fed during infrequent nest visits by parents, and approximately equal numbers of food portions are transferred to each nestling. We did find significant differences between populations in seasonal variation in sex-ratio in relation to egg laying sequence (controlled in this study, because pooled data across only the first three hatched nestlings per nest, and only early-season nests were used in this study; see Materials and Methods). Differences between the populations in the seasonal sex-ratio of egg laying order strongly amplified sexual dimorphism in the growth patterns documented in this study (Badyaev et al., in press).

In this study we explicitly focused on population divergence in male and female growth patterns during the nestling period. Thus, we made two important assumptions. First, as growth of some traits continues past fledgling, we assumed that postfledging growth patterns are unlikely to cancel population differences attained during nestling growth. Second, we did not consider selection on juvenile birds. Such selection is often sexually dimorphic and could significantly modify patterns of sexual dimorphism produced by growth (see above). However, the results of this study, as well as our concurrent studies of these two populations, suggest that our assumptions were justified. First, postfledging growth is proportional to nestling growth for a number of traits (Badyaev et al. 2001). Second, there is substantial evidence that body size at fledging correlates with adult body size (e.g., Fig. 6, see above), thus suggesting that postfledging growth is small and/or proportional to growth during nestling period. However, population variation in strength of resemblance of fledg-

ling and adult males and females (Figs. 6, 9) and the strength of postfledgling selection on some traits (Badyaev et al. 2001) point to population differences in postfledgling growth and selection and should be examined further.

In summary, we documented significant divergence in ontogeny of sexual size dimorphism between recently established house finch populations. Patterns of sexual dimorphism in growth varied among traits, revealing significant sex differences in the distribution of ontogenetic variation. These observations established that there is an opportunity for selection during growth to modify sexual size dimorphism. Population divergence in sexual dimorphism was produced by different processes for different traits—for some traits, population divergence was produced by the extension or truncation of the growth period; for other traits, divergence was a result of a change in growth rate. We found that sexual size dimorphism produced as a result of growth was qualitatively similar with sexual size dimorphism of adults in both populations. This suggests that population divergence in house finches that is both rapid and adaptive may be proximately enabled by rapid population changes in ontogeny and not only by differential mortality of adults. For a better understanding of the mechanisms and evolutionary significance of these results, three additional aspects of ontogenetic variation in sexual dimorphism need to be investigated. First, we need a better understanding of effects of sex-biased maternal and post-hatching effects on ontogeny of sexual dimorphism. Second, in each population we need to evaluate the contribution of sex-specific selection acting on adults and juveniles to the evolution of ontogeny of males and females. Finally, we need to establish whether population differences in the ontogeny of sexual dimorphism are genetic or phenotypic. Ultimately, these studies will provide important insights into the paradox of rapid evolution of sexual dimorphism in natural populations (e.g., Reeve and Fairbairn 1996).

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