GEOGRAPHIC VARIATION IN ONTOGENY OF THE FOX SPARROW[1]

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Abstract. Ontogeny of two morphologically differentiated populations of Fox Sparrows (*Passerella iliaca*) was compared to reveal the developmental bases of adult morphological differences. Growth of tarsus, wing, bill, and tail length relative to body mass was compared between the two populations to determine if geographic variation in adults results from different relative growth rates or different relative timings of onset and offset of growth. Differences in adult morphologies between populations result from both changes in allometric growth rates and changes in starting points along the same allometric trajectory. Sexual dimorphism in bill length is mostly the result of differences in growth rate occurring late in ontogeny. Differences between populations greatly exceed those between sexes. Factors underlying growth are complex and probably result from many different genetic and environmental factors.

Key words: Ontogeny; geographic variation; allometry; Fox Sparrow; Passerella iliaca; relative growth.

INTRODUCTION

Systematists have studied geographic variation for decades, initially to construct subspecific taxonomies and currently because it offers insights into the evolution of adaptation and the origin of species (Mayr 1963). In traditional microevolutionary models, a gradual, adaptively mediated accumulation of small mutations produces geographic variation in phenotypes (Mayr 1970). However, phenotypic variation also may result from environmental influences (James 1983, Rhymer 1992), stochastic processes (Lynch 1989), or from relatively simple genetic changes in the timing of developmental events that influence suites of morphological characters (Gould 1977). Few studies have addressed the ontogenetic means by which geographic patterns of morphologic variation originate. Comparisons of ontogenetic trajectories (Alberch et al. 1979) can reveal how geographic variation originates as a function of different developmental programs. Examples of developmental shifts include alteration of the timing of onset or offset of growth of a character and alteration of growth rate (Gould 1977, Alberch et al. 1979). Any one or a combination of these developmental shifts may cause adult phenotypic differences, resulting in geographic variation.

Within vertebrates, ontogenies have been described and compared mainly for amphibians (e.g., Alberch and Alberch 1981, Alberch 1983, Wake and Larson 1987) and mammals (e.g., Creighton and Strauss 1986, Hafner and Hafner 1988). Although avian geographic variation has long been studied, few analyses compare ontogenies of morphologically differentiated taxa. Many studies investigate the proximate ecological factors affecting absolute growth rates in birds and compare absolute growth rates between and among species of birds (summarized in Ricklefs 1983); however, these do not focus on the evolutionary origin of morphological differences. Exceptions include an analysis by Starck (1989) that qualitatively compared embryonic growth in six species of altricial and precocial birds, and studies of relative growth in Darwin's finches (summarized in Grant 1986). In this study, I compare differences in relative growth between populations of the Fox Sparrow (*Passerella iliaca*), focusing on the origin of morphological differences between populations.

The Fox Sparrow varies extensively in morphology across its range (Swarth 1920, Linsdale 1928, Zink 1986). This study focuses on two of the most phenotypically divergent populations, one (*P. i. iliaca*) from St. John's, Newfoundland and the other (*P. i. megarhynca/stephensi*) from near Hume, California. I first describe size and

proportion differences in morphological characters of adults and hatchlings between these two populations. I then illustrate and compare ontogenetic patterns of these two populations to determine the developmental bases of morphological differences in adults. Specifically, I compare growth rates and relative timing of onset and offset of growth for tarsus, wing, bill, and tail length in terms of increasing body size.

METHODS

Eighty-two nestlings and fledglings and 10 adults were collected 4.5 miles west of Hume, Fresno Co., California (36°48'N, 118°59'W, altitude 1,950 m). Habitat in the area is roughly 35% mixed coniferous forest and 65% chaparral. For each individual, digital calipers were used to measure the following characters: bill length (exposed culmen), tarsus length, wing length, and tail length (measurements described in Baldwin et al. [1931] and Godfrey [1979]). In addition, birds were weighed using a Pesola scale to the nearest 0.5 g. Young were collected when located; therefore, measurements were taken from each bird only once. Thus, this study does not focus on absolute growth (change in size of a character over time), but instead is concerned with relative growth (change in shape or proportion of a character). Describing character ontogeny in terms of body size instead of time since hatching allows comparison of shape changes among traits. In addition, because many ontogenetic events occur at certain sizes rather than ages, body size may be a better indication of an organism's biological age than chronologic time (McKinney and McNamara 1991). Thus, I use mixed cross-sectional data (Cock 1966) to focus on relative growth of characters as body size increases.

Data for Newfoundland Fox Sparrows are from Blacquiere (1979), who measured birds at Oxen Pond Botanic Park, St. John's, Newfoundland, during the spring and summer of 1977 and 1978. Blacquiere (1979) reported means of external measurements (also taken as in Baldwin et al. [1931] and Godfrey [1979]) for 33 adults and for 3–8 nestlings for each day of growth from hatching to fledging (days 0–9).

To illustrate differences in adult morphologies, means of characters of adult birds from Hume were compared to those of adults from Newfoundland using Student's *t*-tests. Because sample sizes of hatchlings were small (for both populations, $n = 4$), I did not perform *t*-tests or report standard deviations for hatchlings. To compare characters of hatchlings and adults independent of body size, character size was divided by the cube root of body mass. The resulting proportions were compared between adults and between hatchlings of the two populations.

Differences between adults in proportion, i.e., shape, can be described by examining the change in size of one character in relation to another (Huxley 1932). Relative growth of characters can be either isometric or allometric. Allometric relationships are usually expressed in a linear form, $\log y = k \log x + \log b$. The slope of this regression line, k, expresses the degree of allometry and is a measure of relative growth. If $k = 1.0$, growth is isometric and each trait grows at the same rate. When $k < 1.0$, trait x is growing faster than trait y and the relationship between the two traits is described as negative allometry. Conversely, when $k > 1.0$, trait y is growing faster than trait x and the relationship between the two traits is described as positive allometry.

Additionally, the relationship between two traits may reflect a pattern of complex allometry whereby the allometric coefficient (k) changes during ontogeny. In these nonlinear situations, the relative growth rate of the two characters is not constant and growth curves may be approximated by polynomial regression. Although growth rates are changing, the slope (k) at any given point on the curve will indicate the degree to which shape is changing at that point (McKinney 1984).

When allometric coefficients change during ontogeny, the resulting patterns of growth can be illustrated by one of three generalized models (Fig. 1). In Figure 1A, the two populations have different relative growth rates at all stages of growth; thus, they grow along diverging allometric trajectories. As a result, shape changes progressively along both trajectories and the two populations have different proportions during growth and as adults. In Figure 1B, one population has a later onset of growth of character B in relation to character A. But the two populations have the same relative growth rates and duration of growth; thus, adults have different proportions. Although one curve is delayed relative to the other, the two curves would be identical if superimposed on top of each other. A pattern similar to this will also result if a character is already at a proportionately larger size
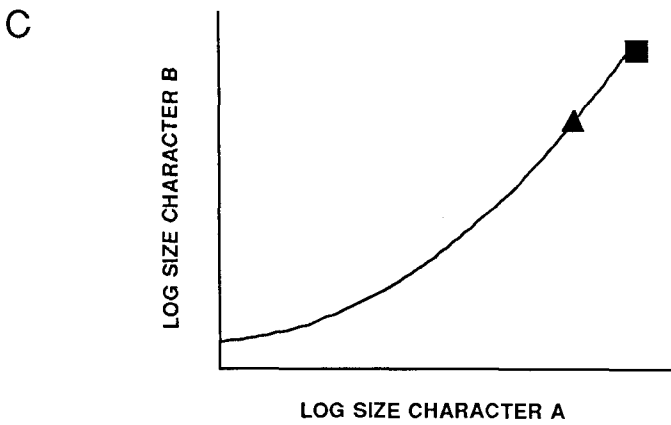
FIGURE 1. Three patterns of relative growth. Each curve on each graph represents relative growth in a different population. The symbol at the end of each curve represents final adult proportions.

TABLE 1.   Sizes ($\bar{x}$) of adult and hatchling Fox Sparrows at Hume, California, and St. John's, Newfoundland.

Group	Character	Newfoundland			Hume			Difference	
		n	$\bar{x}$	SD	n	$\bar{x}$	SD	t	P
Adult	Mass (g)	33	40.0	3.2	10	33.7	2.1	7.42	<0.001
	Tarsus length (mm)	33	25.3	0.8	10	24.5	0.8	2.68	<0.05
	Wing length (mm)	33	86.3	2.8	10	81.0	1.8	6.96	<0.001
	Tail length (mm)	33	72.3	3.1	10	84.6	3.7	−9.55	<0.001
	Bill length (mm)	33	11.8	1.0	10	17.6	0.9	−17.84	<0.001
Hatchlings	Mass (g)	4	3.2	—	4	2.4	—	—	—
	Tarsus length (mm)	4	8.8	—	4	6.6	—	—	—
	Wing length (mm)	4	7.2	—	4	6.1	—	—	—
	Bill length (mm)	4	4.1	—	4	4.7	—	—	—

in one population at hatching. In Figure 1C, lines representing relative growth in the two populations are the same, except in one population character B stops growing earlier in relation to character A, resulting in different adult proportions.

To determine the specific kinds of alterations in relative growth that effect geographic variation in adult proportions, I plotted the growth of tarsus, wing, bill, and tail length relative to body mass for birds at Hume and Newfoundland. Because Fox Sparrows are sexually dimorphic (Linsdale 1928), differences in ontogenetic trajectories between sexes may obscure differences between populations. Therefore, I also plotted the growth of bill length (the most sexually dimorphic character I measured) in relation to body mass separately for males and females of the Hume population. For the Newfoundland population, sex was not determined when the data were collected. All measurements were $\log_{10}$-transformed to make the variance more homogeneous. F-tests were used to determine whether an ontogenetic trajectory was best explained by simple linear regression or a polynomial regression (McKinney 1984, Sokal and Rohlf 1981). Allometric growth curves were first estimated for each character regressed on body mass using simple linear regression. A quadratic term was then added to the equation to see if a significant portion of the residual sums of squares could be removed. F-values were calculated as follows:

$$F = \text{[sum of squares of higher order}$$
$$\text{(quadratic) model}$$
$$- \text{ sum of squares of lower order}$$
$$\text{(linear) model]}$$
$$\div \text{ higher order (quadratic) mean square}$$
$$\text{error}$$

If a quadratic equation provided a significantly improved fit, the F-value comparing quadratic to cubic equations was calculated. This process was repeated until increasing the order of the equation no longer produced a significant F-value at $\alpha = 0.05$. Once the best estimate of the ontogenetic trajectory was determined, k-values were determined at different points on the curve by taking the first derivative and solving for a given x (log body mass) value. The resulting k-values represent the tangential slope at that point on the curve or the allometric growth rate occurring at that body mass.

RESULTS

GEOGRAPHIC VARIATION IN CHARACTER ONTOGENY

Tarsus lengths of adults are similar, although significantly different ($P < 0.05$, Table 1). However, because Newfoundland birds weigh more than Hume birds, tarsus length of Newfoundland adult birds is proportionately smaller than Hume birds (Table 2). Tarsus length is absolutely and proportionately longer in Newfoundland hatchlings (Tables 1, 2). Thus, Newfoundland birds must hatch out with a proportionally larger tarsus, but complete their growth with a proportionately smaller tarsus than Hume birds.

The plot of log tarsus length against log body mass (Fig. 2) reveals that relative growth of tarsus length in relation to body mass changes; thus, tarsus growth reflects a pattern of complex allometry. F-test results indicate that a third order polynomial equation best describes tarsus length relative growth. Early in ontogeny, relative growth rates are different, but they seem to converge as development progresses. Throughout most of ontogeny, relative growth rates are largely sim-

TABLE 2. Proportions of adult and hatchling Fox Sparrows at Hume, California, and St. John's, Newfoundland.

Group	Ratio[a]	New-found-land	Hume
Adults[b]	Tarsus length/mass	7.40	7.59
	Wing length/mass	25.23	25.10
	Tail length/mass	21.14	26.21
	Bill length/mass	3.45	5.43
Hatchlings[c]	Tarsus length/mass	5.99	4.96
	Wing length/mass	4.92	4.54
	Bill length/mass	2.77	3.49

[a] Proportions are presented as the ratio of length measurement (mm) to cube root body mass (g).
[b] Sample size of Newfoundland adults is 33 and sample size of Hume adults is 10.
[c] Sample size of hatchlings in both populations is four.

ilar. Finally, near the end of ontogeny, the Newfoundland population has a much larger allometric coefficient than the Hume population (Fig. 2, Table 3).

As adults and at hatching, Newfoundland birds have longer wings (Table 1). Newfoundland birds also have longer wings in proportion to body mass as hatchlings and as adults (Table 2). Although Newfoundland birds hatch with proportionately longer wings, they grow along an ontogenetic trajectory that is delayed, but strikingly similar to the Hume trajectory (Fig. 3, Table 3). Because Newfoundland hatchlings are proportionately larger and relative rates of growth are similar between the two populations, Newfoundland birds have a proportionately larger wing length as adults.

Newfoundland adults have shorter tails than Hume adults and have shorter tails in proportion to body mass (Tables 1, 2). At hatching, neither population has a measurable tail. Plotting log tail length vs. log body mass for the two populations reveals that Newfoundland birds begin growing tails later than Hume birds relative to body mass (Fig. 4, Table 3). However, relative growth rates of tail length for the two populations are similar, and tail length is proportionately larger in the Hume population from its appearance onward.

Adults differ greatly in bill size and proportions. Newfoundland adults have a shorter bill length and a shorter bill length in proportion to body mass (Tables 1, 2). Bill lengths are more similar between hatchlings than between adults. However, Newfoundland hatchlings do have a shorter bill length and a shorter bill length in proportion to body size. Plotting log bill length versus log body mass for the two populations reveals different allometric growth rates throughout ontogeny (Fig. 5, Table 3).
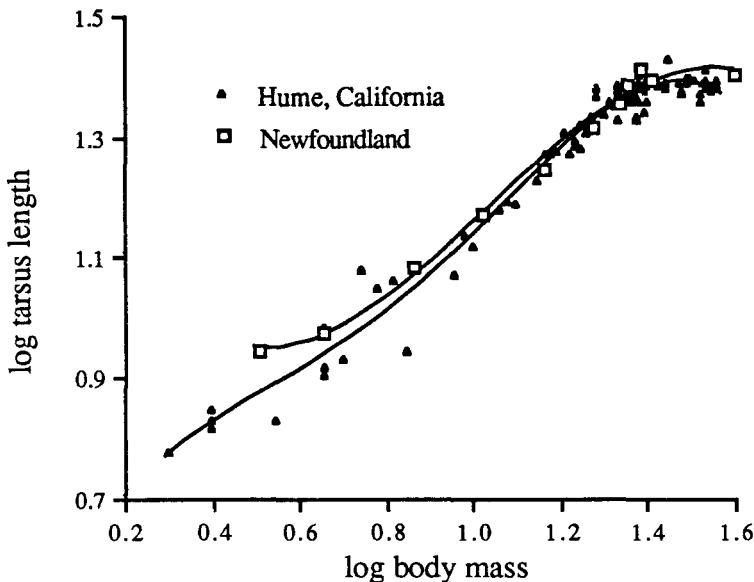

FIGURE 2.   Relative growth of tarsus length in relation to body mass for populations of Fox Sparrows at Hume ($y = 0.45 + 1.77x - 3.09x^2 + 2.93x^3 - 0.91x^4$, $R^2 = 0.98$) and Newfoundland ($y = 1.42 - 2.05x + 2.64x^2 - 0.85x^3$, $R^2 = 0.99$).
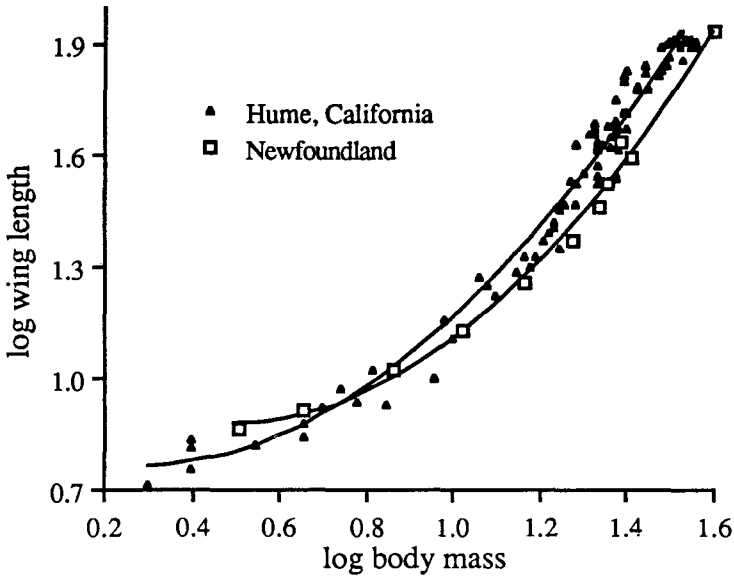
FIGURE 3. Relative growth of wing length in relation to body mass for populations of Fox Sparrows at Hume ($y = 0.81 - 0.38x + 0.73x^2$, $R^2 = 0.97$) and Newfoundland ($y = 1.07 - 0.82x + 0.85x^2$, $R^2 = 0.99$).

SEXUAL DIMORPHISM

Plotting the growth of bill length relative to body mass separately for males and females at Hume reveals that the ontogenetic trajectories are similar (Fig. 6). Differences in bill length between Hume males and females is mostly a result of differences in relative growth rate late in ontogeny. Differences between Hume and Newfoundland populations greatly exceed those between Hume males and females; thus, sexual dimorphism does not obscure the comparison of growth trajectories between populations at Hume and Newfoundland.

DISCUSSION

CHARACTER ONTOGENY

Comparing growth trajectories of the characters (Figs. 2–5) to three different relative growth patterns (Fig. 1) reveals the nature of ontogenetic differences. For tarsus length, the difference in adult proportions mainly results from differences

TABLE 3. Allometric coefficients (k) at given values of log body mass during the character ontogenies of Fox Sparrows from Hume, California, and St. John's, Newfoundland.

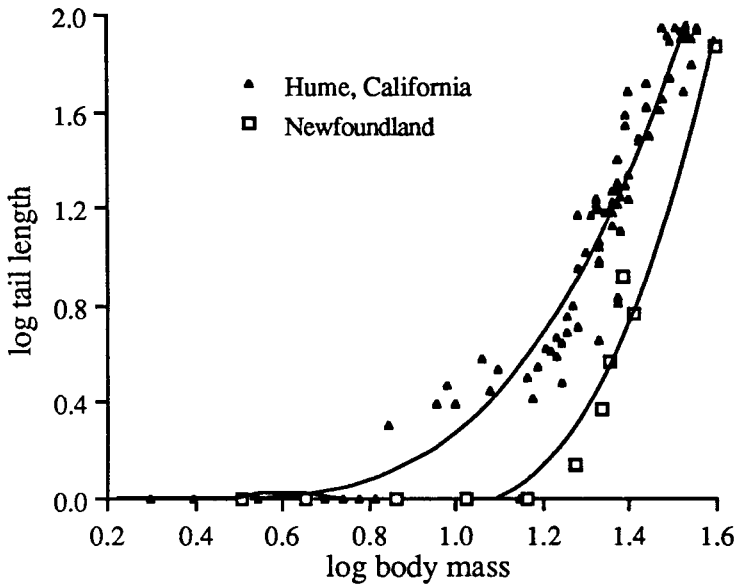|	log body mass						
	0.6	0.8	1.0	1.2	1.4	1.45	1.5
Tarsus length relative growth							
Newfoundland	0.20	0.54	0.68	0.61	0.34	0.24	0.13
Hume	0.44	0.59	0.74	0.72	0.36	0.19	−0.01
Wing length relative growth							
Newfoundland	0.20	0.54	0.88	1.22	1.56	1.65	1.73
Hume	0.50	0.79	1.08	1.37	1.66	1.74	1.81
Tail length relative growth							
Newfoundland	0.00	−0.34	0.25	1.80	4.29	5.06	5.90
Hume	0.11	0.59	1.41	2.56	4.05	4.47	4.90
Bill length relative growth							
Newfoundland	0.46	0.19	0.24	0.45	0.69	0.75	0.79
Hume	0.27	0.39	0.51	0.63	0.75	0.78	0.81

FIGURE 4.   Relative growth of tail length in relation to body mass for populations of Fox Sparrows at Hume
(y = -0.0876 + 0.69x - 1.74x^2 + 1.40x^3, R^2 = 0.94) and Newfoundland (y = -1.58 + 6.77x - 9.20x^2 +
3.96x^3, R^2 = 0.97).

in relative growth rate near the end of ontogeny
(Figs. 1A, 2). Differences in adult wing length
proportions result from a change in relative onset
of growth without changing relative growth rates
(Figs. 1B, 3). For tail length, the two populations
have similar relative growth rates, but the timing
of onset differs between populations (Figs. 1B,
4). Differences in adult bill length relative to body
mass result from different allometric trajectories
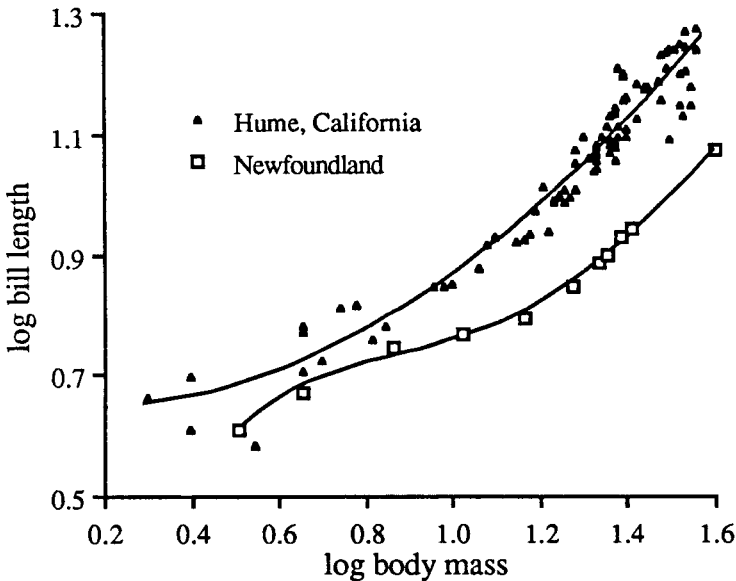in the two populations (Figs. 1A, 5).

FIGURE 5.   Relative growth of bill length in relation to body mass for populations of Fox Sparrows at Hume
(y = 0.65 - 0.0901x + 0.30x^2, R^2 = 0.94) and Newfoundland (y = -0.50 + 4.36x - 5.87x^2 + 3.46x^3 - 0.69x^4,
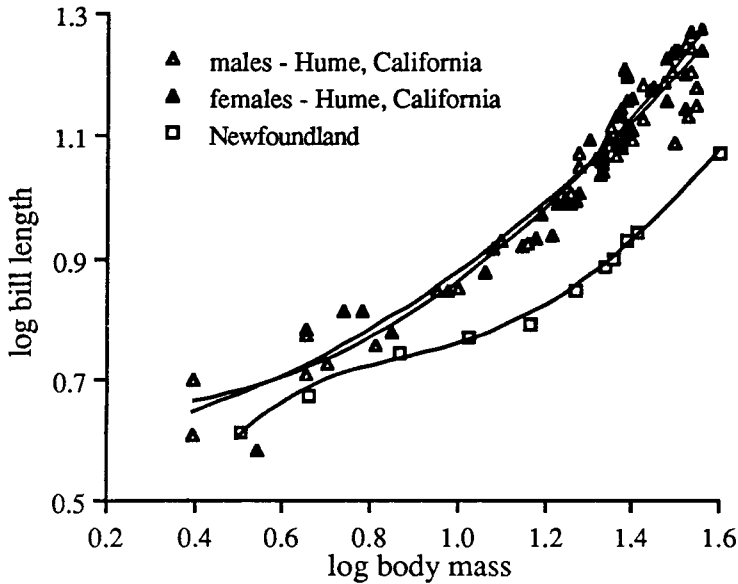R^2 = 0.99).

FIGURE 6. Relative growth of bill length in relation to body mass for Fox Sparrow populations at Hume, California and Newfoundland. For the Hume population, males ($y = 0.59 + 0.046x + 0.24x^2$, $R^2 = 0.94$) and females ($y = 0.67 - 0.16x + 0.35x^2$, $R^2 = 0.94$) are plotted separately.

EVOLUTIONARY SIGNIFICANCE OF ONTOGENETIC COMPARISONS

Although few studies examine interspecific and intraspecific differences in ontogeny, ontogenetic trajectories have been compared between species of Darwin's finches (Grant 1981, Boag 1984, Price and Grant 1985, Grant 1986). Grant (1981) studied five species of Darwin's finches (*Geospiza magnirostris*, *G. conirostris*, *G. difficilis*, *G. fortis*, *Certhidea olivacea*) and a mockingbird (*Nesomimus parvulus*) and found growth rates of wing and tarsus length in relation to body mass varied little among species; however, growth rates of bill dimensions in relation to body mass varied substantially. Boag (1984) compared relative growth trajectories between *Geospiza fortis* and *G. scandens* and found that allometric growth rates for most characters except bill dimensions did not differ between the two species. In addition, Price and Grant (1985) showed that relative growth rates of bill dimensions differ among four species of *Geospiza* (*G. fuliginosa*, *G. fortis*, *G. scandens*, and *G. magnirostris*).

Grant (1981) compared relative growth trajectories for two populations of *Geospiza difficilis* that differ substantially in mass (20.2 vs. 11.6 g) and bill size and shape. For bill length, the two populations grew along the same relative growth trajectory but between different starting and stopping points, resulting in adults in the two populations having different proportions. Bill depth, tarsus length, and wing length (but not bill width) for both populations grew along the same allometric trajectories in relation to body mass between the two populations. In contrast, different bill lengths between populations of Fox Sparrows result from different relative growth rates. Relative growth of characters in the Fox Sparrow resembles the situation between different species of Darwin's finches. Studies comparing other morphologically differentiated populations of birds would clarify the types of growth differences expected between populations and species. Nonetheless, the ontogenetic data presented here are consistent with geographic variation in song and mitochondrial DNA (R. M. Zink, unpubl. data) which suggest that these samples of Fox Sparrows represent different species.

GENETIC AND ENVIRONMENTAL FACTORS

The evolutionary interpretation of geographic variation depends on whether intraspecific differences are genetically or environmentally determined (James 1983, Zink and Remsen 1986, Rhymer 1992). Few studies have investigated the effect of genetic and environmental factors on

relative growth rate and timing of developmental events. Lerner and Gunns (1938) raised chickens at different temperatures, but were unable to alter the growth rates of leg measurements relative to body mass. In addition, Lerner (1943) was unable to select lines of chickens for high and low shank length relative to body mass growth rates. Some mutations affect size or shape at onset of growth, relative growth rates, and absolute growth rates (Cock 1966, Alberch et al. 1979). In addition, several genetic factors contribute to the determination of adult size and shape in chickens (Cock 1969). However, it is not known in general what kinds of changes in growth are more easily influenced by genetic or environmental factors.

Although the present study cannot reveal the role of genetic and environmental factors in shaping adult morphologies, it does provide insight into the nature of the underlying factors. The four characters studied develop differently in the two populations. Geographic variation results from different allometric trajectories (bill length and tarsus length) and different timings of onset along similar allometric trajectories (wing and tail length). If all characters had followed a similar pattern and differed consistently between populations, then a simple genetic or a simple environmental basis would have adequately explained morphological differences among adults. This study, however, shows that one population is not a simple allometric extension of the other population; therefore, a complex of genetic and possibly environmental factors probably influences character ontogenies. Although allozyme studies (Zink 1986, Burns and Zink 1990) failed to detect genetic differences between morphologically differentiated populations of Fox Sparrows, mtDNA analysis (Zink 1991) reveals a historical genetic correlation with morphological differences, including those between Hume and Newfoundland populations (R. M. Zink, in press). Whatever the evolutionary status of these populations, my studies show that different adult morphologies are reached via substantial re-patterning of ontogenetic trajectories.

ACKNOWLEDGMENTS

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